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ELECTRIC RESPONSE TO PHOTIC STIMULATION IN BULLFROG'S BRAIN, CHIEFLY OPTIC LOBE

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The cerebral cortex in lower vertebrates is immature compared with that in mammals and the optic nerve fibers from the retina of the frog pass chiefly to the optic lobe (tectum). Although the main visual center in the frog is the optic lobe, numerous fibers also arrive at the diencephalon and the telencephalon.

In the present experiment responses to photic stimulation were studied in the bullfrog's brain, chiefly in the optic lobe. The evoked potential from the contralateral tectum to a single light flash consisted of a positive wave followed by two negative components which were denominated as N_1 and N_2. These two negative deflections showed different behaviors to light intensity, strychnine, ethyl ether, anoxia and repetitive stimulation. On the other hand, the first positive wave was resistant to strychnine, ethyl ether, anoxia and superficial damage and apt to follow repetitive stimulation. The photically evoked potential was recorded also in the ipsilateral tectum and the responses resembling that from the optic lobe were obtained from the diencephalon and the telencephalon.

The discussion was especially focussed on the nature of each component of the contralateral tectal response on the basis of the physiological and the anatomical findings.

INTRODUCTION

It is a well-known fact that in lower vertebrates such as the fish and the frog the main visual center is the optic lobe (optic tectum, tectal lobe) of the midbrain, which is homologous with the superior colliculus in mammals. Evoked potentials to visual stimulation were studied in mammals by many investigators such as Bartley and Bishop (1933), Bishop and O'Leary (1936), Marshall *et al.* (1943) and Chang and Kaada (1950). On the other hand, there have been published a number of papers dealing with the evoked potential in lower vertebrates (Buser, 1955: Motokawa *et al.*, 1958: Schadé and Weiler, 1959: Konishi, 1960 a, b). Nevertheless, as to the evoked potential in lower vertebrates, not to mention that of the mammalian, there still remain many problems to be elucidated. This study was undertaken to investigate the evoked potential to photic stimulation in the bullfrog's brain, chiefly in the optic lobe.

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METHODS

Experiments were carried out on about 50 adult bullfrogs, *Rana Catesbiana*, weighing 200–300 g. In the present experiments animals were immobilized on the board without any anesthesia. The top of the skull was removed to expose the brain, on which a little liquid paraffin was dropped to prevent from drying. A part of the nictitating membrane of one eye was cut off in order to be lightened enough and the other eye was entirely excised.

For photic stimulation a photostimulator, with which white flashes from a xenon lamp were illuminated on the eye diffusely, was employed. The stimulus frequency could be varied from 1 to 40 flashes per sec without change in duration of a single light flash which was 10 μsec, and when a series of flicker stimulation was given, the flashes were repeated every 10–15 sec. The peak light intensity of the flashes was measured on the corneal surface using an illuminometer. It was difficult, however, to measure the luminous intensity of a single light flash because of shortness of its duration. To pick up the electrical activity from the brain, monopolar leading was used. A silver ball electrode with a tip diameter of about 0.3 mm and insulated except at the tip was placed on various regions of the exposed brain, while an indifferent electrode was put on the tissue near the outer nostril. Action potentials from the brain were amplified by a RC coupled amplifier having a time constant of 10 msec and displayed on a dual-beam cathode-ray oscilloscope. An inkwriting oscillograph, which was connected parallel with the oscilloscope, was also employed to record the brain activity. Some of recordings were made simultaneously from both halves of the brain. In all the records negativity of the exploring electrodes was recorded as an upward deflection. The recordings were usually made in the quiet and dim room, while photic stimulation was performed after dark-adaptation of 15–30 min. The experiments were carried out through all seasons, but chiefly during autumn and winter. The room temperature was kept at 21–26°C.

RESULTS

1. Response to a single light flash

(1) Pattern of response in optic lobe

In response to a single light flash applied to an eye the characteristic potential change was observed in the tectum. In Fig. 2 are illustrated the responses to the sufficient light intensity, which were taken from the mid-nasal part of the tectum contralateral to the illuminated eye (E in Fig. 1). The first sequense of the contralateral response consisted of a positive component with a latency of 40–50 msec, having in some preparations small positive spikes superimposed on it, and this positive wave was usually followed by two negative components showing different amplitudes. The second negative deflection

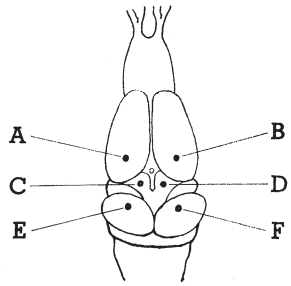

FIG. 1. Dorsal view of the brain of the bullfrog.
A, B: Caudal region of the telencephalon.
C, D: The diencephalon.
E, F: Mid-nasal region of the optic lobe.

TABLE 1. Latency of N_1 and N_2 taken from ten bullfrogs.

Case	N_1 (msec)	N_2 (msec)
1	48	64
2	54	70
3	52	68
4	62	80
5	53	68
6	59	66
7	56	72
8	50	68
9	58	78
10	52	69
Average	53	70

was larger in height than the first negative when the stimulus intensity was sufficient. For convenience' sake these two negative waves are designated as N_1 and N_2 respectively in this paper. After the second negative wave a larger positive slow phase followed, having a small negative deflection on it in some preparations. There were more or less variations in waveform of the response from frog to frog as A, B and C in Fig. 2, and even from the same frog at different times during

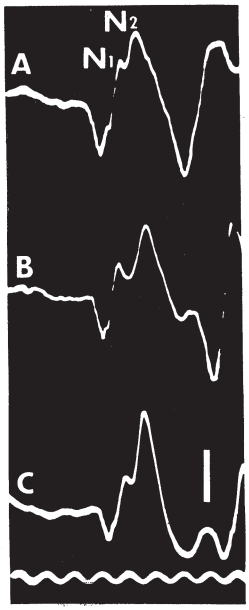

FIG. 2. Evoked potentials to a single light flash in contralateral tectum obtained from three different bullfrogs. Time mark: 60 cps. Voltage calibration: 50 μV.

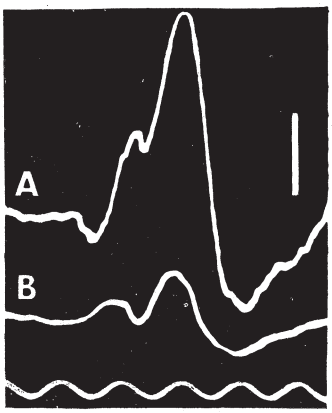

FIG. 3. Responses recorded simultaneously from both tectums. Record A shows contralateral response and record B illustrates ipsilateral one. Time mark: 60 cps. Voltage calibration: 50 μV.

the experimental session. The latency of N_1 and N_2 obtained from ten bullfrogs is illustrated in Table 1. Fig. 3 shows the simultaneous records taken from both tectums (E and F in Fig. 1). As was seen in the lower record in Fig. 3, response from the ipsilateral tectum exhibited a waveform which was different from that of the contralateral one, that is, usually beginning with a very small negative deflection. This first negative wave was so small that it was often not distinguishable from the spontaneous tectal activity. It had a slightly delayed latency in comparison with the contralateral response. Next a rather larger negative wave followed and finally a positive slow phase ensuied. As was seen in Fig. 3, the response in the contralateral tectum (upper record) was considerably large in height compared with that in the ipsilateral one (lower record).

(*2*) *Response from diencephalon and telencephalon*

In the present experiments the evoked potential to photic stimulation was also recorded from the diencephalon and the telencephalon to compare with the tectal response. The left column in Fig. 4 represents the simultaneous records taken from both diencephalon (C and D in Fig. 1). As was seen in the figure, the response from the diencephalon showed a waveform similar to the tectal response, though the difference of size between the contralateral response (upper record) and the ipsilateral one (lower record) was not so distinguished as the response in the tectum. In the right column in Fig. 4 are shown the simultaneous records obtained from both telencephalon (A and B in Fig. 1). In the telencephalon the spontaneous activity was considerably large in height, whereas the response to photic stimulation was so small that it was difficult to record a typical waveform. As was illustrated in the figure, the waveform in the telencephalon resembled the tectal response as well as the response in the diencephalon.

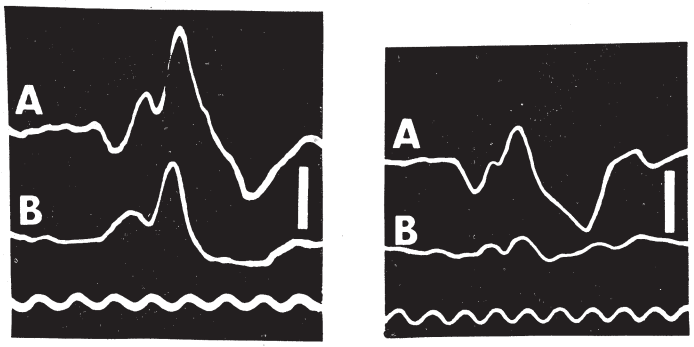

FIG. 4. Evoked potentials taken from the diencephalon (left column) and the telencephalon (right column). Upper records in each column show contralateral responses and lower records represent ipsilateral ones. Time mark: 60 cps. Voltage calibration: 50 μV.

(3) *Effect of light intensity*

A series of records in Fig. 5 shows the development of each component of the contralateral tectal responses to various light intensities. The light strength was regulated by changing the distance from the light sourse in the present experiments. When the light intensity was weak, only the first positive deflection with a delayed latency appeared (A). As the stimulus strength was increased gradually, the negative wave representing N_2 occured (B). Then a small preceding negative deflection showing N_1 was recognized, whereas N_2 grew considerably in size (C). With stronger stimulation the first negative deflection was augmented to its maximum (D). When the light intensity reached a certain level, the two negative components were fused (E) and finally a typical waveform appeared (F). As was seen in the figure, N_2 seemed to be more sensitive than N_1 to photic stimulation.

(4) *Effect of strychnine*

In order to observe the effect of strychnine on the tectal response, a small

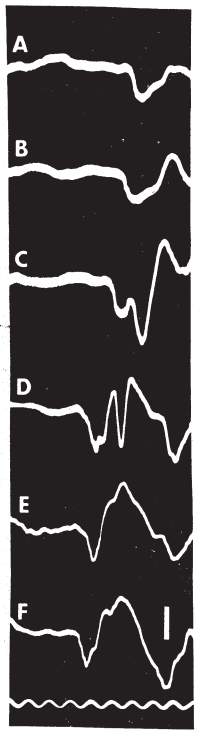

FIG. 5. Series of records illustrating effect of light intensity on each component of contralateral tectal responses. Time mark: 60 cps. Voltage calibration: 50 μV.

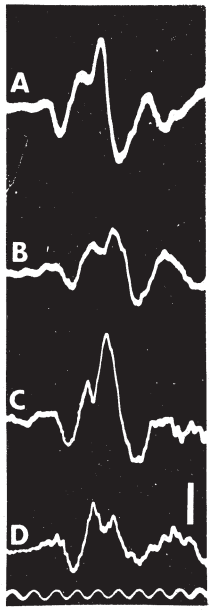

FIG. 6. Effect of strychnine on contralateral tectal responses. Record A is taken before application of strychnine. Record B, C and D were taken 2', 5' and 10' after application of strychnine. Time mark: 60 cps. Voltage calibration: 50 μV.

piece of filter paper soaked with 0.1% aqueous solution of strychnine was applied topically on the surface of the tectum. As was seen in Fig. 6, N_1 was affected remarkably during strychnization, whereas both the first positive wave and N_1 were changed slightly. It is striking that in B and D the wave of N_2 was depressed enormously, while in C it was enhanced in size. It has been generally believed that strychnine possesses a depressant action as well as a stimulant effect on the brain activity. In the present experiments it was found that N_2 was affected almost selectively by strychnine.

(5) *Effect of ethyl ether*

The effect of ethyl ether on the evoked potential in the contralateral tectum was observed in some experiments. A piece of absorbent cotton soaked with ethyl ether was placed on the bullfrog's outer nostrils for inhalation of the volatile anesthetic. As was seen in Fig. 7, N_2 was depressed remarkably by this anesthetic and N_1 was also diminished in size, but to a lesser degree. On the contrary, the first positive wave was little influenced by this drug and maintained almost constant amplitude in the process of ether anesthesia. From this result it was supposed that N_2 was more susceptible than N_1 to ethyl ether.

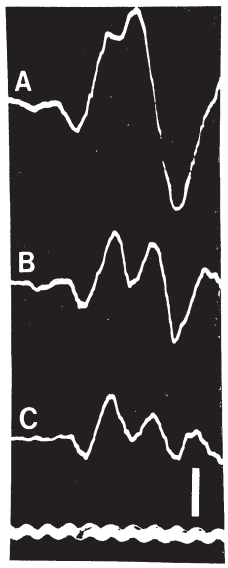

FIG. 7. Effect of ethyl ether on responses in contralateral tectum. Records from A down to C were taken before inhalation of ethyl ether, 2′ and 5′ thereafter. Time mark: 60 cps. Voltage calibration: 50 μV.

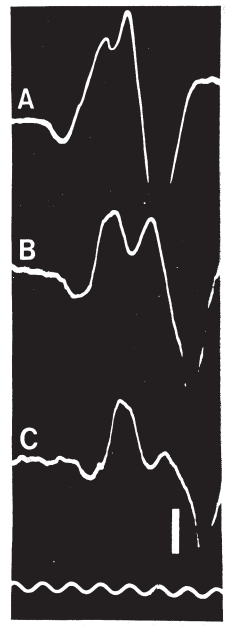

FIG. 8. Effect of anoxia on contralateral tectal responses. Record A shows response taken before inhalation of nitrogen. Record B and C were obtained 1′ and 3′ after the inhalation. Time mark: 60 cps. Voltage calibration: 50 μV.

(6) *Effect of anoxia*

The effect of anoxia on the tectal response was examined by using pure nitrogen. Nitrogen was administered endotracheally to the animal through the nostrils by means of a common anesthesia apparatus. It was, however, not certain whether the effect of oxygen lack was perfect or not under this condition, because the frog has a different respiratory system from that of the mammal.

As was illustrated in Fig. 8, the most vulnerable component during anoxia was N_2 and it underwent marked decrease in a few minites after nitrogen administration. The first positive wave and N_1 was far more resistant to the effect of oxygen lack; they persisted throughout the duration of anoxia in this experiment. It is clear from this evidence that N_2 is uniquely susceptible to anoxia.

(7) *Effect of superficial damage*

The tectal surface was scratched with a needle to observe the effect of superficial damage on the tectal response. The effect of mechanical damage on the

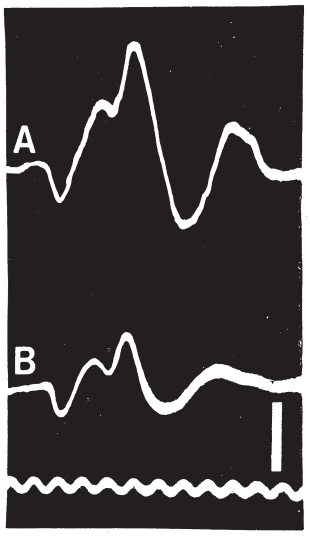

FIG. 9. Effect of superficial damage on evoked potentials in contralateral optic lobe. Record A was taken before exertion of mechanical damage and record B was taken after the damage. Time mark: 60 cps. Voltage calibration: 50 μV.

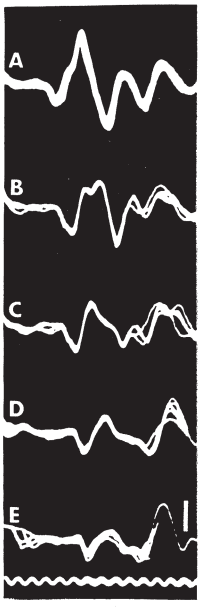

FIG. 10. Effect of repetitive stimulation on contralateral tectal responses. Repetition frequencies from the top downwards are 1, 2, 3, 4 and 5 cps respectively. Each tracing has five superimposed sweeps excluding responses to the first flash of repeated stimulation. Time mark: 60 cps. Voltage calibration: 50 μV.

tectal potential is illustrated in Fig. 9, in which A is a control record obtained before the damage and B is a record taken after the application of the injury. Compared B with A it is clearly demonstrated that both N_1 and N_2 except the first positive component were reduced greatly by this method. This finding leads to an assumption that both N_1 and N_2 are originated in the intratectal structure.

2. Response to repetitive light flash

(1) Effect of repetitive stimulation

An example of the response to repetitive stimulation observed in the contralateral tectum is illustrated in Fig. 10. In the records, however, the responses to the first flash of repeated stimulation were excluded. As was shown in the figure, N_2 was not able to follow repeated stimulation at the frequency of about 3 cps, whereas N_1 could follow the flicker until approximately 5 cps. On the other hand, the first positive wave was little affected by repetitive stimulation. From this finding it is suggested that both N_1 and N_2, especially N_2, are labile to repetitive stimulation, while the first positive wave is apt to follow repetitive flashes.

(2) General characteristics of flicker response

Observations of the main features of responses to flicker stimulation were performed, especially dealing with patterns at various frequencies. A series of flicker responses (1–40 cps) recorded simultaneously from both tectums is

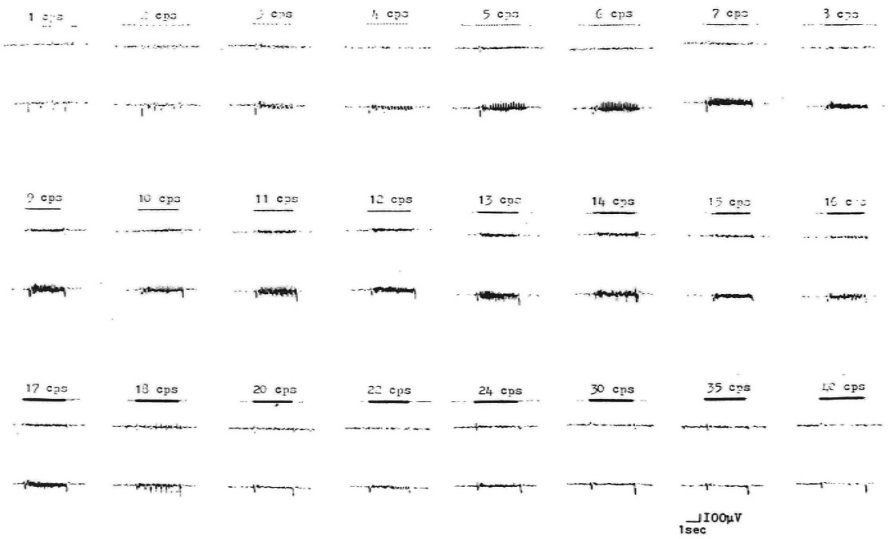

FIG. 11. Series of flicker responses of 1 to 40 cps recorded simultaneously from ipsilateral (upper records in each frequency) and contralateral (lower records) tectums.

illustrated in Fig. 11. As the figure shows, there were differences in flicker-following types according to the stimulus rates. Usually, flicker responses followed the flash rate up to approximately 10 cps, being accompanied by waxing and waning above 5-6 cps. Then, as the frequency of the flash was raised, a one-to-one correspondence could not be maintained. As a rule, the first flash provoked the maximum response. With the flicker in the neighborhood of 20 cps or higher rates flicker responses tended to be suppressed during the stimulation except on-response which occurred at the first flash and off-response which appeared at cessation of the illumination. Speaking of off-response, it came out at cessation of the last flash when the stimulus frequency reached the certain rate. As was observed in the figure, flicker responses from the contralateral half of the optic lobe were several times as large as those from the ipsilateral one.

3. Off-response

Off-response which was evoked at cessation of the illumination at 20, 30 and 40 cps were observed. Fig. 12 shows the typical responses obtained simultaneously from both tectums. Off-response from the contralateral tectum (upper record) had at first a large positive wave followed by a negative one, and then positive-negative wavelets occurred. On the other hand, the response from the ipsilateral tectum (lower record) exhibited initially a small negative wave with a delayed latency and usually this was followed by a slow positive deflection. Although some differences in waveform between the responses to a single light flash and off-response were observed in both contra- and ipsilateral responses, it should be emphasized that the first positive wave which was seen in the contralateral response was absent in the ipsilateral one.

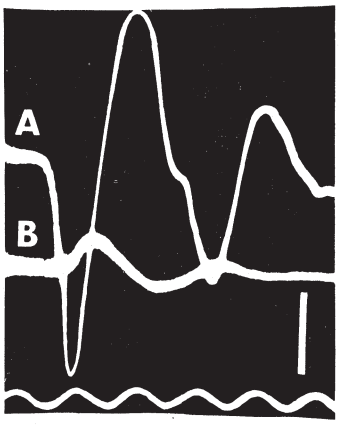

FIG. 12. Typical off-responses obtained simultaneously from both tectums following cessation of illumination. Record A is contralateral off-response and record B is ipsilateral one. Time mark: 60 cps. Voltage calibration: 100 μV.

DISCUSSION

The evoked potential in the visual center of mammals as well as lower vertebrates has been studied by many investigators.

Chang and Kaada (1950) analyzed the primary cortical response to optic nerve stimulation in cats and differentiated it into 6 deflections. The first

deflection, consisting of a diphasic or triphasic small wave, was interpreted as being caused by the potential difference in the transient electrical field created by a synchronous volley traveling along the optic nerve in a volume conductor. Deflections 2, 3 and 4, all of which were surface-positive spike-like potentials, were assignable to the activities of three systems of geniculo-cortical neurons. Deflection 5, the most prominant and broad positive wave, was assigned to intracortical neurons. The long-lasting negative potential following the wave 5 might be an indication of the passage of impulses in the apical dendrites of the pyramids and the activity of other cortical internuncial neurons.

Bishop and Clare (1952) reported the cortical response of the cat to a single volley from the optic tract. A few spikes superimposed on a surface-positive phase was followed by a surface-negative wave somewhat longer. In their experiments the first spike was assigned to the arrival of impulses over the optic radiation. The second spike was found at about the level of layer IV of the cortex, and the following two or three spikes arose from successively higher levels of the cortex. The positive wave was inferred to represent the activity of basal dendrites of the neurons of which the spikes represented the activity of the cell bodies. The negative wave was ascribed to conducted activities from the cell bodies along apical dendrites toward the cortical surface.

As mentioned previously, the main visual center in lower vertebrates is the optic lobe, and there has been much discussion concerning the nature of each component in the evoked potential following electric and photic stimulation.

Mitarai (1955) observed the response of the optic lobe to photic stimulation using the isolated brain-eyeball-preparation of the toad. The response observed in the experiments consisted of two or three main waves; first negative monophasic or first diphasic with initial positive abrupt and a series of successive monophasic waves. He inferred that the former showed the activities of the afferent terminals, while the latter represented the activities of the synaptic process and motor cells.

Motokawa *et al.* (1958) reported that the evoked potential of the optic tectum in the carp to electrical stimulation of the optic nerve was composed of two positive spikes, a positive deflection and a negative wave followed by a second negative deflection when the stimulus was sufficiently strong. It was suggested by them that the two preceding positive spikes and probably the positive deflection were of presynaptic origin. On the other hand, the first negative deflection was attributed to the synaptic potential at receiving cells and the second negative one was ascribed to polysynaptic excitation.

Schadé and Weiler (1959) studied the response of the optic tectum in the goldfish to single light flashes and divided it into the "A complex" of the first diphasic components and the "B complex" of the successive large negative

wave. They assumed that the "A complex" was due to the synaptic potential occurring between entering optic nerve fibers and the tectal neurons and the "B complex" was a sign of subsequent activity in the deeper cell layers.

Recently, Konishi (1960 b) investigated the electric response of visual center to optic nerve stimulation in fishes. He concluded from the results that the two surface negative waves following a surface positive deflection were assignable to the postsynaptic potential and that the latter component of the negative waves had higher threshold than the early one of the negative.

In the frog the optic nerve fibers from the retina arrive chiefly at the optic tectum and they cross almost all in the chiasma on their way to the tectum. On the other hand, numerous fibers pass to the dorsal thalamus of the diencephalon, particularly to the lateral geniculate nucleus and the nucleus of Bellonci, where are synaptic fields. The tectum in the amphibian has several rather indistinct layers. At the surface of the tectum is a relatively wide band termed the stratum album where the fibers of the optic nerve make synapses, and this layer consists of medulated fibers to a considerable extent. Internal to the stratum album are the cellular layers of the tectum, collectively termed the stratum griseum. One of the typical neurons of the tectum has its cell body in the stratum griseum and sends its dendrites into the stratum album. Such neuraxes or apical dendrites from certain granular cells situated more deeply ascend to the optic fiber layer and appear to join it. In the frog between the tectum and the optic thalamic center are fibers which interconnect the two areas and also the fibers from the dorsal thalamus passes to the telencephalon. It seems probable that the first connection from the thalamus to the telencephalon occurs in the amphibian (Gaupp, 1896: Herrick, 1925: Kappers *et al.*, 1960: Muntz, 1962).

In the present experiments the evoked potential to photic stimulation was observed chiefly in the optic tectum and also a similar response was obtained from the diencephalon and the telencephalon. As stated above, in the case of a single flash stimulation the response of a positive wave followed by two negative components with different amplitudes was recorded in the contralateral tectum. This waveform obtained from the bullfrog coincides approximately with the response from the carp reported by Motokawa *et al.* (1958) and Konishi (1960 b). The early negative deflection (N_1) was usually smaller than the second negative one (N_2) in amplitude and they showed different behaviors to light intensity, strychnine, ethyl ether, anoxia and repetitive light flash.

First of all, in the process of increasing light strength N_2 appeared at earlier stage than N_1 and the former reached its maximum height sooner than the latter as light intensity became stronger. This findings leads to a consideration that N_2 is more photo-sensitive component than N_1.

After local application of strychnine on the tectal surface N_2 was en hanced in amplitude following an initial depression, while N_1 revealed no manifest

changes. Chang (1953) reported the similarity in action between curare and strychnine on the cortical neurons and suggested that both curare and strychnine possessed two competitive actions on the central nervous system: (i) the action of depressing the synaptic function, and (ii) the action of increasing the cortical activity. Although the exact mechanism of the strychnine effect is not clear, it seems justifiable to state that N_2 represents the tectal element which is susceptible to strychnine.

After inhalation of ethyl ether and nitrogen, N_2 diminished remarkably but N_1 decreased to a lesser degree. From this observation it is clear that N_2 is more susceptible to anesthetics or anoxia in comparison with N_1.

As to the effect of repetitive stimulation, the critical frequencies up to which N_1 and N_2 could follow were not identical; N_1 was able to follow higher rates than N_2. The difference in the critical frequencies seems in part to depend upon the refractory periods.

After the application of superficial damage both N_1 and N_2 diminished in size. This fact indicates that they belong to the activity in the intratectal tissue.

From the foregoing findings there can be no doubt that N_2 may represent more unstable component in the tectal process than N_1 differing in origin.

Speaking of the first positive wave, it was resistant to strychnine, ethyl ether, anoxia and superficial damage and apt to follow repetitive stimulation. Furthermore, it was absent in the ipsilateral response. These observations, including the anatomical findings, imply that it may be attributable to the action potential of the optic nerve fibers.

As concerns the large positive deflection following N_2 there is no evidence for interpretation at present.

It should be emphasized here that the tectum or the optic nerve are not necessarily the major structure capable of provoking the response; there is abundant possibility of the influence of the retina, the thalamus and the brain-stem upon the tectal response. The structure of the frog's optic lobe, with only one-fifteenth of the total number of nerve cells of the retina, appeares more adapted to handle an already simplified pattern than to handle the complete raw data initially registered by the receptors. Thus, the retina should be expected to perform the first step in the analysis of the visual events and to transmit the abstructed information to the visual center as reported by Maturana *et al.* (1960).

It remains to be determined whether the evoked potential in the bullfrog is able to be divided into the primary response and the secondary response as the response in the mammal.

SUMMARY

Responses to photic stimulation were studied in the bullfrog's brain, chiefly

in the optic lobe (tectum).

1. The response from the contralateral tectum to a single light flash was usually composed of a positive wave followed by two negative deflections with different amplitudes. On the other hand, the response from the ipsilateral tectum consisted of a small negative wave followed by a larger negative one. The evoked potential in the ipsilateral tectum had a considerably smaller size and a slightly delayed latency compared with that in the contralateral one.

2. The response similar to that from the tectum was obtained also from the diencephalon and the telencephalon.

3. The second negative component (N_2) in the contralateral tectum was affected more easily than the early negative component (N_1) in various conditions, that is, variation in light intensity, repetition of illumination and application of drugs (strychnine, ethyl ether) or of nitrogen. After superficial damage both N_1 and N_2 diminished in size.

4. The first positive wave in the contralateral tectum was resistant to strychnine, ethyl ether, anoxia and superficial damage and apt to follow repetitive stimulation.

5. Off-response from the contralateral tectum consisted of a large positive wave followed by a negative one, while that from the ipsilateral one exhibited initially a small negative wave with a delayed latency. The amplitude of the contralateral response was several times as large as that of the ipsilateral one.

6. Based on the above mentioned observations and the anatomical findings, it is suggested that N_1 and N_2 may be from different origin in the intratectal process; the latter may represent more unstable component than the former. On the other hand, the first positive wave in the contralateral tectum may be attributable to the activity of the optic nerve fibers.

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