RESPONSE AREAS OF THE MESENCEPHALON, THE THALAMUS, AND THE FOREBRAIN OF CHICKENS TO CLICK STIMULATION

by

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The author also wishes to acknowledge her husband for his assistance, patience, support, and encouragement throughout this study.

INTRODUCTION

The earliest investigators of avian neuroanatomy studied gross structure and connections. In the early years of the twentieth century researchers paid more attention to the microscopic anatomy of the brain including descriptions of nuclei and the connecting fiber tracts. Anatomical studies of Edinger, Wallenberg, and Holmes (1903, quoted from Sanders, 1929) on the forebrain and those of Huber and Crosby (1929) on the diencephalon are very valuable today to avian neuroanatomists and neurophysiologists.

As to the physiology of the avian brain, some workers described the behavior of birds after extirpating parts of the brain. Kalischer (1900, quoted from Huber and Crosby, 1929) gives accounts of experiments involving extirpation and electrical stimulation which enabled him to deduce the functions of various parts of the forebrain. Other investigators directed most of their attention to optic fibers or structures of the sense of sight.

A few publications are available on audition in birds with most of this material describing the end organ and the secondary and tertiary nuclei in the medulla. The end organ of birds is much simpler than that of mammals. The cochlea of birds is uncoiled and lacks such specialized mammalian features as internal and external hair cells, tunnels, and complex spiral fiber arrangements (Boord, 1961). The middle ear of birds is composed of parts morphologically different

from those of mammals: instead of the chain of auditory ossicles, birds possess only the columella. However, the function of the middle ear is rather similar with similar continuous-sound stimuli treated with equal efficiency in both. In the internal ear the structures are homologous although the mechanisms involved seem to be different. In some birds the lack of a scala vestibuli and the very short basilar membrane appear to account for this difference. The auditory pathway to the brain of birds contains about the same number of first order neurons as in mammals; the number is linearly related to the length of the basilar membrane. The secondary and tertiary centers in the medulla show a very conservative development in most birds, being almost uninfluenced by the birds' size. (Schwartzkopff, 1963).

Auditory tracts beyond the midbrain are unknown anatomically. However, Erulkar (1955) found evoked potentials in the neostriatum caudale in his investigations in a pigeon, and confirmed anatomical studies which identified the nucleus isthmi complex, including the nucleus semilunaris, as having auditory connections by finding these areas responsive to click stimulation. Thalamic nuclei that he explored did not respond to clicks.

The purpose of the present investigation was to find areas in the midbrain, thalamus and forebrain of chickens responsive to click stimulation. This study will increase

the knowledge of hearing in birds by supplying physiological information of this function in the aforementioned areas of the brain. This work will perhaps provide further enlightenment concerning possible homologies of the avian and mammalian brains.

LITERATURE REVIEW

The microscopic anatomy of the auditory pathway in birds has been described by Wallenberg (1898, quoted from Sanders, 1929); by Ramón y Cajal (1909, quoted from Sanders, 1929), who contributed the most detailed and complete description of the nuclei of termination of the acoustic root fibers and the fiber relations of these nuclei to higher centers; by Craigie (1928), who worked with the brain of hummingbirds; by Sanders (1929); by Schroeder (1911); by Papez (1929); and reviewed by Ariëns Kappers, Huber, and Crosby (1936).

The posterior branch of the auditory nerve innervates the ampullae posterior, the sacculus, the macula neglecta, and the papilla basilaris cochleae (Ariëns Kappers, Huber, and Crosby, 1936). The central ends of the fibers of the auditory division of the eighth nerve terminate upon the cells of the nucleus angularis and nucleus magnocellularis of the same side. Although many of these fibers penetrate the nucleus laminaris to reach the nucleus magnocellularis, morphological studies indicate that they do not establish direct connection with cells of the laminaris (Boord and Rasmussen, 1963). This nucleus appears to form part of the auditory system, but on anatomical grounds is thought to receive its input secondarily from the nucleus magnocellularis (Brandis, 1894, quoted from Stopp and Whitfield, 1961). However, evoked potential studies would indicate that there

is a direct connection with the cochlear nerve (Erulkar, 1955; Stopp and Whitfield, 1961).

Crossed and uncrossed connections of the auditory centers of the medulla to the midbrain is by the lateral lemniscus which runs forward to the midbrain in company with other ascending systems and terminates in the nucleus semilunaris, nucleus isthmi, and nucleus mesencephalicus lateralis pars dorsalis named as the probable homologue of the inferior colliculus of mammals by Ariëns Kappers (1921, quoted from Huber and Crosby, 1929). Craigie (1928) could not trace acoustic fibers with certainty to the nucleus mesencephalicus lateralis pars dorsalis; however, Wallenberg (1898, quoted from Craigie, 1928) showed that this nucleus receives endings of the lateral lemniscus. Erulkar (1955) in his experiments on pigeons using the evoked potential technique raised the same question as to whether fibers of the lateral lemniscus terminate in the mesencephalicus lateralis pars dorsalis. He found that the complex of the nucleus isthmi was easily and regularly activated by clicks but that the nucleus mesencephalicus lateralis pars dorsalis remained essentially unresponsive to acoustic stimuli. He suggested that some or all components of the complex of nucleus isthmi rather than the nucleus mesencephalicus lateralis pars dorsalis are homologous to the mammalian inferior colliculus.

Papez proposed without experimental verification a central auditory tract in the American robin which passes from the mesencephalic nucleus or torus semilunaris forward between the tectothalamic tract and the striocerebellar tract and appears to send fibers into the largest part of the medial geniculate body. Here, medial to the nucleus rotundus, the tract turns dorsally to end in the spiriform nucleus (nucleus ovoidalis of the atlas used in this paper). From this nucleus fibers are contributed to the thalamofrontal bundle and pass to the striatum.

The only evidence of an auditory function in centers beyond the midbrain centers appears in the work of Erulkar (1955). He verified the auditory function of the nuclei angularis, magnocellularis, and laminaris, which responded to ipsilateral but not to contralateral click stimuli, and the isthmi complex in the midbrain; but could find no responsive areas in the thalamus. He did find the neostriatum caudale in the forebrain was activated by click stimulation. This summarizes the available information on the afferent auditory pathway in birds.

TECHNIQUES

Preparation

In these experiments 27 adult female white leghorn chickens were used. Urethane anesthetic was administered in doses of 3.0-3.5 g to begin with and 0.5-1.0 g when deemed necessary during the experiment in order to keep the chicken from moving. The animal's head was immobilized in a Baltimore stereotaxic apparatus with hollow earbars. The head was leveled as suggested by van Tienhoven and Juhasz (1962) in their atlas of the chicken brain. This atlas was used to determine the locations of structures to be explored, and their nomenclature is followed throughout. The coordinates to be used during the experiment were marked on the skull. This portion of the skull was removed with a small trephine (3.4 mm in diameter) and the dura mater cut just enough to allow the electrode to enter the brain. Cotton soaked with a 0.75% saline solution and kept warm was placed over the exposed areas of the brain to prevent drying out. Rectal temperature was found throughout the experiments to remain at 41.5°C. A total of 80 tracks were made and 1156 sites were explored during the investigation.

Recording Electrodes

Bipolar, concentric electrodes were made of stainless steel tubes in which a 0.005 in. diameter enamel-insulated

Nilstain wire was placed with 1 mm of the wire projecting beyond the end of the tube. The outer electrode was insulated with Insulex and about 0.5 mm of the core electrode was scraped bare. The dimensions of the electrode were approximately 400 μ for the shell diameter and approximately 100 μ for the core electrode.

Recording and Stimulation Apparatus

Click stimuli were produced by 0.05 msec rectangular pulses from a Grass S4 stimulator to a crystal earphone. Except when the effects of increased intensity on the response were being observed, constant stimulus intensity was used. Rubber tubing, used to eliminate bone conduction of the stimuli, connected the microphone on both sides to the hollow earbars which were inserted into the external canals of the head. Evoked potentials were displayed on a Tektronix 565 oscilloscope driven by a 2A61 plug-in-preamplifier. Permanent records were made by photographing the trace with a Tektronix C-12 oscilloscope camera. The shell of the recording electrode was negative with reference to the core and recordings were so arranged that positive potentials are up and negative ones down. Intervals between stimuli were no less than 1 sec and were usually longer except when the object was to examine the effect of stimulus frequency on response. Pairs of clicks were used to determine the interval taken for recovery of the response. The usual procedure was to record in 0.5 mm steps along each electrode track.

Anatomical Verification

To facilitate sectioning of the brain, steel insect pins were implanted parallel and rostral to the electrode tracks before removing the bird from the stereotaxic instrument. Brains were perfused through the carotid arteries with 0.75% saline and subsequently with 10% buffered formalin containing 1% potassium ferrocyanide. The head stayed in the formalin at least a day before the skull and dura mater were removed. The brain was then washed in water for an hour, embedded in gelatin at 40°C for 5 hr. After cooling, the block of gelatin containing the brain was placed in formalin for another day or two then washed for 1 hr. in water, trimmed, and aligned on the freezing microtome. Sections 50 μ thick were cut and only those sections needed for determining the position of the exploring electrode track were retained. Half of these sections were mounted in glycerol and the other half were stained with cresyl violet and mounted in Permount. The brain sections were traced using a Bausch and Lomb microprojector Model 42-63-59-01 which magnified five times the original size. To determine the exact location of the electrode tip, ferric ions were deposited by passing a direct current at 10 v for 3 sec through the electrode at the end of the track and at another known site usually 5 mm up from the bottom of the track. Reaction with the potassium ferrocyanide produced Prussian blue spots where the tips had been.

New Technique

A new, quick way to locate electrode tracks was used for this investigation. Sections cut at 50 μ and placed in distilled water showed surprising contrast between the white and gray matter. With either microscope or microprojector, both fiber tracts and nuclei can be seen in the same section. The sections can be taken from water, placed on slides, and either traced, using a microprojector or microphotographed for permanent records. The elimination of staining reduces the amount of time spent on histology. Figure 1 shows one of the photographs obtained this way.

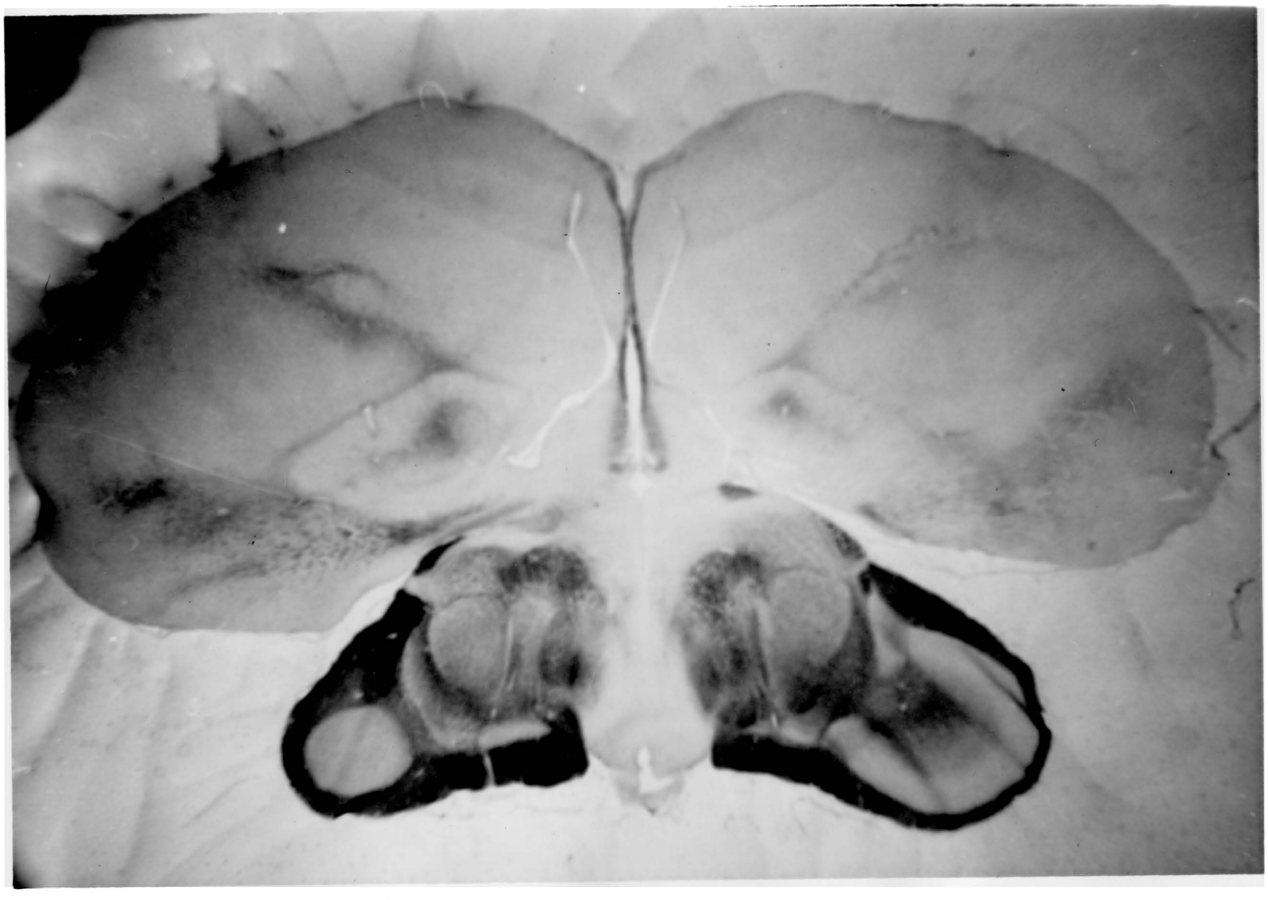


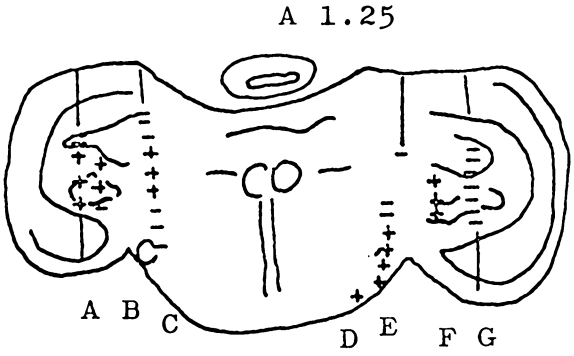
Fig. 1. Illustration of a new, quicker technique for track location. Frozen section of the chicken brain showing the atlas coordinate of rostral 6.0 on the right side and rostral 7.0 on the left side of the picture. This is an example of the contrast that can be obtained between the white and gray matter of the brain by photographing the wet slide. The picture was taken on Kodak Panatomic-X. Wrinkles along the margins of the brain were caused by gelatin embedding. Thickness of the section is 50 u. Mag. 6.2X.

RESULTS

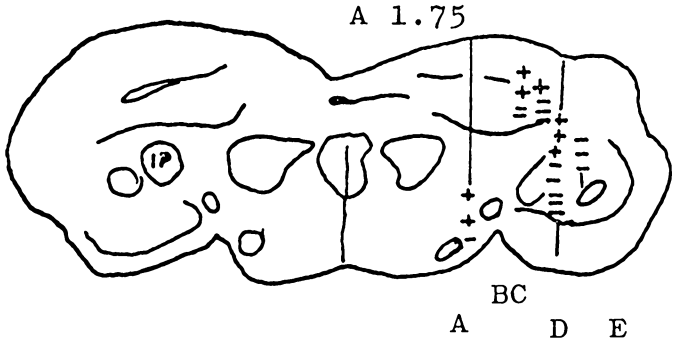
Regions Explored for Responses to Auditory Stimulation

Midbrain. The nucleus isthmi pars principalis parvocellularis was entered 9 times. In all experiments this nucleus was readily activated by clicks delivered to either ear. Figures 2 and 3 show the locations of the electrode tracks made in the mesencephalon and the dorsoventral dimensions of the regions activated by click stimuli along each track. Latencies of the responses varied in different regions of the nucleus. In the most medial part the latent period was 1.5 to 5.0 msec; in the lateral portion of the nucleus it was 3.0 to 10.0 msec. The nucleus isthmi pars principalis magnocellularis had a latency of 5 to 6 msec, but activity was not regularly evoked by clicks. Near the nucleus semilunaris the latency to contralateral stimuli was 3 to 4 msec. The ready activation of this nucleus and nucleus isthmi pars principalis parvocellularis confirms the conclusions of several investigators (Papez, Ariens Kappers, Huber and Crosby) that this nucleus, as well as the nuclei isthmi and mesencephalicus lateralis pars dorsalis, receive acoustic fibers.

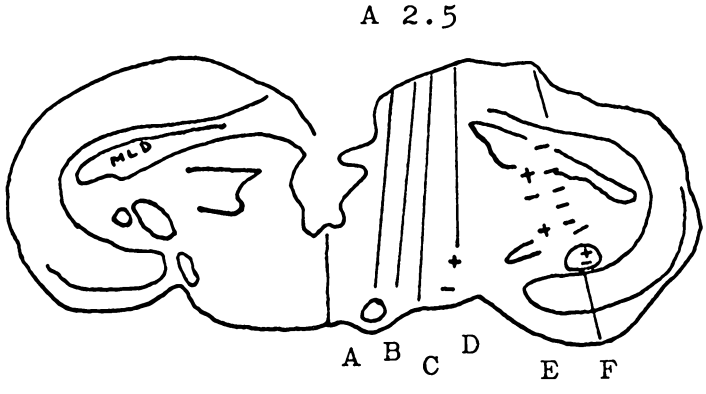
The nucleus mesencephalicus lateralis pars dorsalis, entered 14 times, was as responsive to auditory stimuli as were the nuclei of isthmi. Erulkar (1955), working with a pigeon, found that activity was never regularly evoked by clicks and that the amplitudes of these responses were hardly above the baseline activity. In chickens



Exper.	Tr.
A-64-4-H	2
B-64-19-H	2
C-64-4-H	1
D-63-22	2
E-64-4-H	3
F-64-19-H	2
G-64-4-H	4

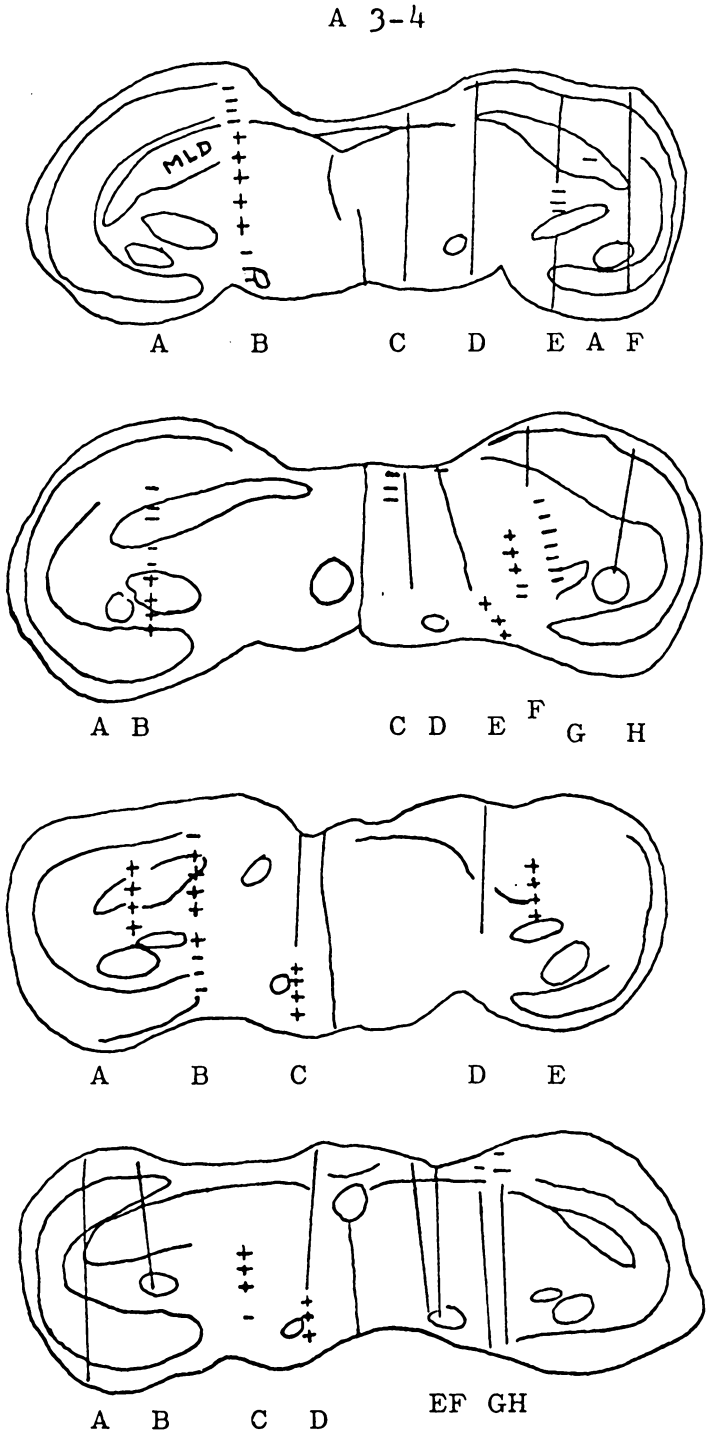


A-63-38	1
B-64-25-H	2
C-64-23-H	2
D-64-5-H	4
E-64-24-H	5



A-63-29	3
B-63-34	3
C-64-5-H	3
D-63-29	4
E-64-20-H	2
F-64-2-H	2

Fig. 2 Location of caudal regions in the mesencephalon activated by click stimuli. This shows the complex of the nucleus isthmi and the nucleus mesencephalicus lateralis pars dorsalis as seen from above downwards. Solid lines indicate unresponsive areas. Here and in subsequent figures (+) designates a positive potential and (-), a negative potential. The right side indicates ipsilateral stimulation; the left, contralateral stimulation. Letters identify the experiment and track numbers. Thickness 50 μ. Mag. 5X.



Exper.	Tr.
A-64-21-H	3
B-64-7-H	1
C-63-34	4
D-64-5-H	3
E-63-22	3
F-63-22	4

A-63-31	1
B-64-2-H	3
C-63-21	5
D-63-29	1
E-63-33	3
F-63-34	1
G-63-33	2
H-63-33	1

A-64-17-H	1
B-64-6-H	1
C-64-10-H	4
D-63-29	2
E-64-17-H	1

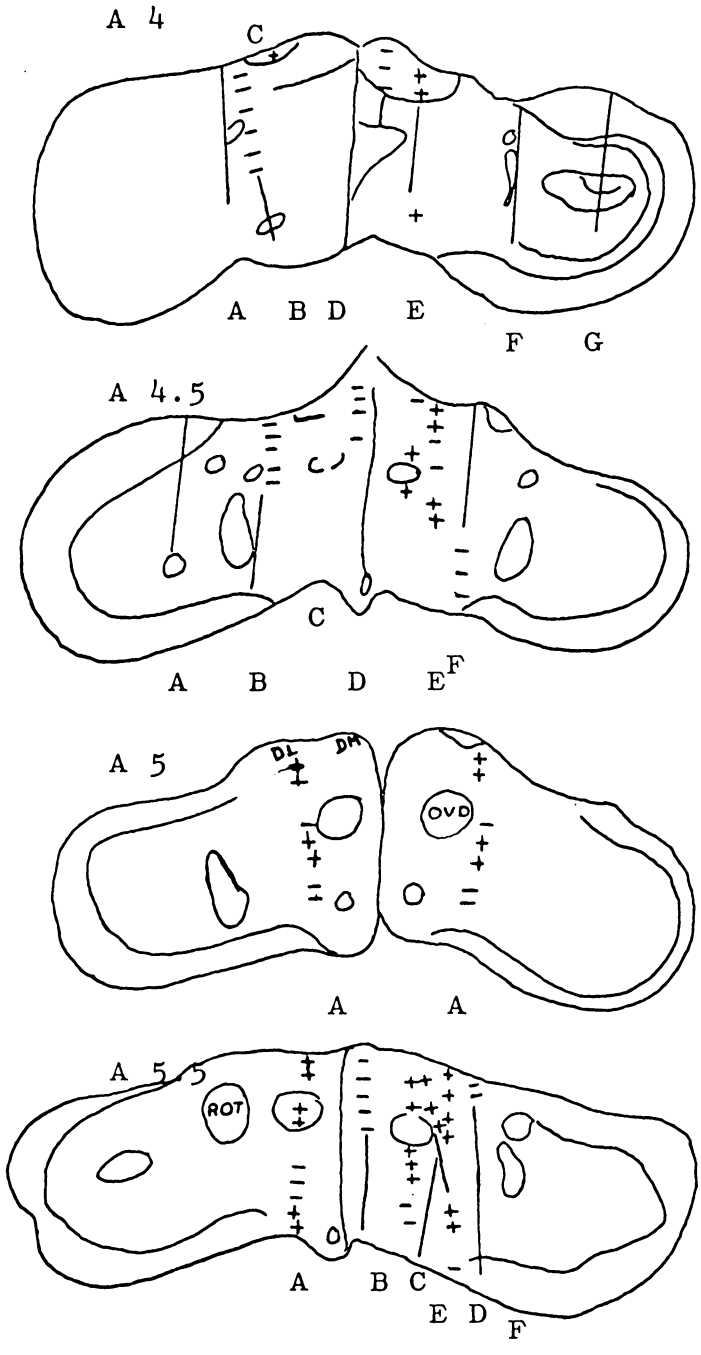
A-63-31	1
B-63-31	2
C-64-5-H	2
D-64-10-H	1
E-63-14	4
F-63-33	4
G-63-38	3
H-63-38	4

Fig. 3 Location of rostral regions in the mesencephalon activated by click stimuli. Solid lines indicate unresponsive areas. The right side indicates ipsilateral stimulation; the left, contralateral stimulation. Letters identify the experiment and track numbers. Thickness 50 μ. Mag. 5X.

amplitudes in this nucleus ranged from 10 to 300 μv with most of them in the order of 50 μv. In the isthmi they ranged from 15 to 400 μv but were usually about 50 to 75 μv. Latent periods in the nucleus mesencephalicus lateralis pars dorsalis ranged from 3 to 6 msec in the central, lateral and medial parts of the nucleus, except that in the medial part contralateral stimulation produced responses at 2 to 4 msec.

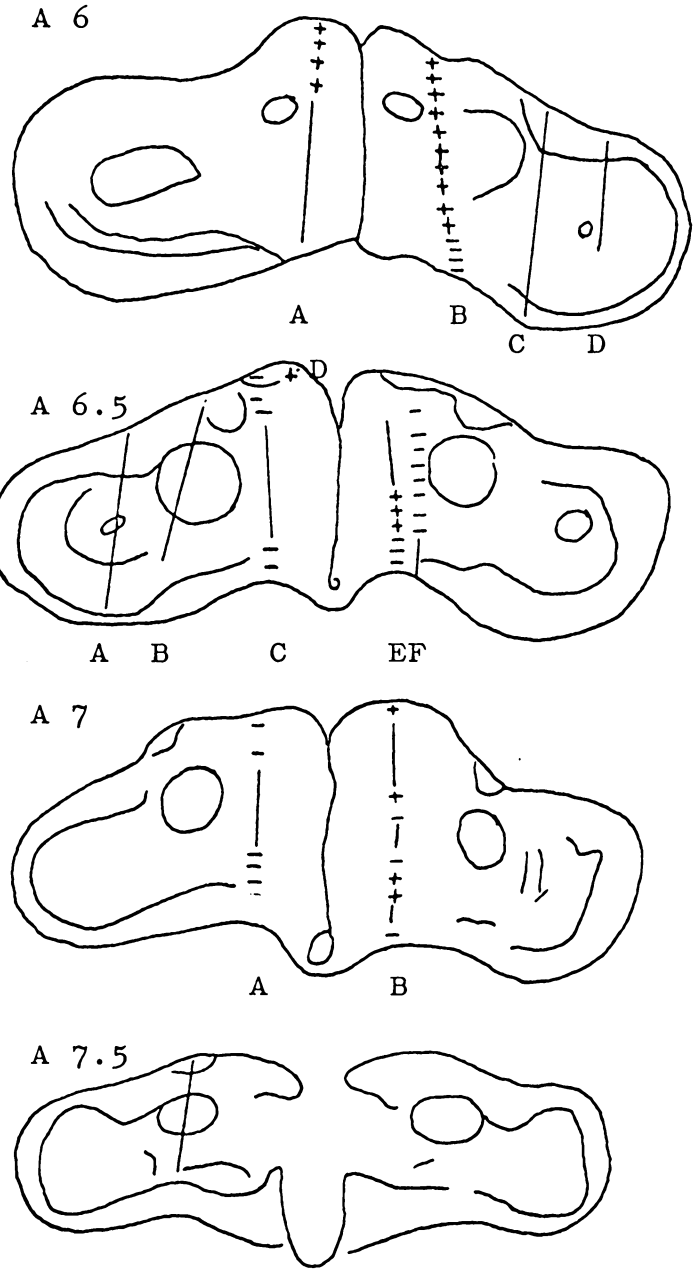
Other regions of the mesencephalon were activated by clicks but contained no identifyable nuclei, nor could the responses be definitely ascribed to any of the fiber tracts. At the atlas coordinates of A 1.25-1.75, L 3.5-4.0, V 2.5-3.0, the response had a latent period ranging from 4 to 6 msec with an average amplitude of 160 μ. At atlas coordinate A 3.5-4.0, L 2-2.5, V 4 contralateral clicks elicited responses having a latency of 3 to 4 msec.

Thalamus. The thalamus was responsive to clicks as shown in Figures 4 and 5. The nucleus dorsolateralis was entered by the recording electrode 20 times. It responded to clicks in either ear every time the electrode entered this area. The latency of the response was from 10 to 16 msec, usually, but sometimes was as much as 20 msec. The nucleus dorsomedialis also responded to either contralateral or ipsilateral stimuli. Latencies to both were 13 to 16 msec. The nucleus ovoidalis responded to clicks with relatively small amplitude responses with latent periods of 10 to 12



Exper.	Tr.
A-63-31	3
B-64-6-H	2
C-64-17-H	1
D-64-23-H	1
E-63-33	6
F-63-33	5
G-63-33	4
A-63-35	1
B-64-7-H	2
C-64-28-H	2
D-63-35	4
E-63-21	4
F-63-14	
A-64-13-H	
A-64-10-H	2
B-63-34	5
C-64-24-H	7
D-64-25-H	1
E-63-34	6
F-64-7-H	3

Fig. 4 Location of caudal regions in the thalamus activated by click stimuli. Solid lines indicate unresponsive areas. The right side indicates ipsilateral stimulation; the left, contralateral stimulation. Letters identify the experiment and track numbers. Thickness 50 u. Mag. 5X.



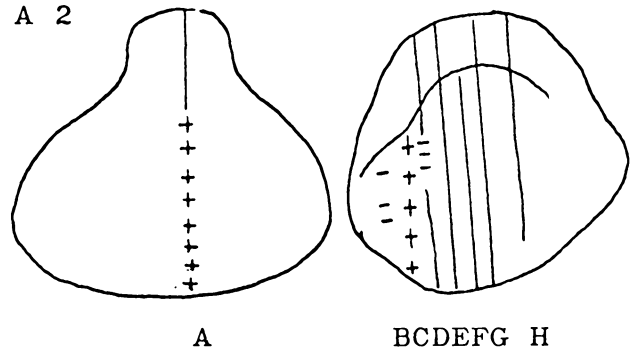
Exper.	Tr.
A-63-35	2
B-64-26-H	5
C-64-26-H	3
D-64-26-H	4
A-64-26-H	1
B-64-26-H	2
C-64-9-H	1
D-64-24-H	6
E-64-25-H	3
F-64-24-H	4
A-64-10-H	3
B-64-24-H	6
64-9-H	2

Fig. 5 Location of rostral regions in the thalamus activated by click stimuli. Solid lines indicate unresponsive areas. The right side indicates ipsilateral stimulation; the left, contralateral stimulation. Letters identify the experiment and track numbers. Thickness 50 μ. Mag. 5X.

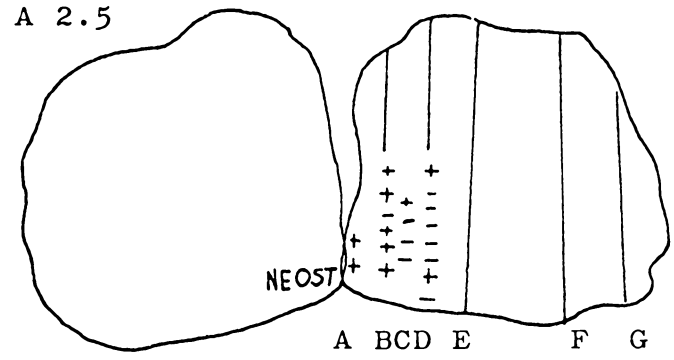
msec. The nucleus subrotundus appeared to respond to auditory stimuli, but this is evidence from only one track through this area. The response latency was 10 to 12 msec. Several sites located 2 mm ventral and 1 mm lateral to the nucleus ovoidalis were responsive to click stimuli (fig. 4) with latencies of 6 to 11 msec. In a position approximately 1.5 mm from the medial wall of the diencephalon and 1 mm from the bottom of this region at atlas coordinates A5.5-7.0 (figs. 4 and 5) latencies were very short (4.5 to 8 msec) compared to others found in the thalamus. These short latencies seemed to follow the same regions through which the quinto-frontalis tract passes. In more rostral sections and in an area containing the decussatio supraoptica dorsalis and ventralis short latency responses also occurred.

Striatal complex. The striatal complex was explored on 72 tracks. The neostriatum caudale ventrale, the region in which Erulkar (1955) found responses to auditory stimuli in pigeons, also responded to both ipsilateral and to contralateral stimuli in chickens. Latent periods were from 11 to 16 msec in most cases but 6, 10, and 16 to 18 msec latencies also were recorded. In the response with 6 msec latency the larger component came at 14 msec. This was an area readily activated by clicks (figs. 6 and 7).

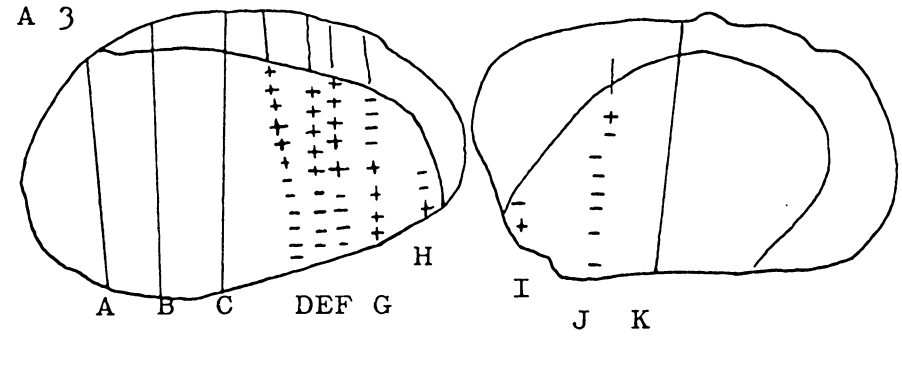
The posterior division of the neostriatum caudale central to the neostriatum caudale ventrale responded to both ipsilateral and contralateral clicks. Fig. 5 shows



Exper.	Tr.
A-64-7-H	1
B-63-33	3
C-63-29	5
D-63-29	1
E-64-4-H	3
F-63-28	3
G-63-38	2
H-64-4-H	4

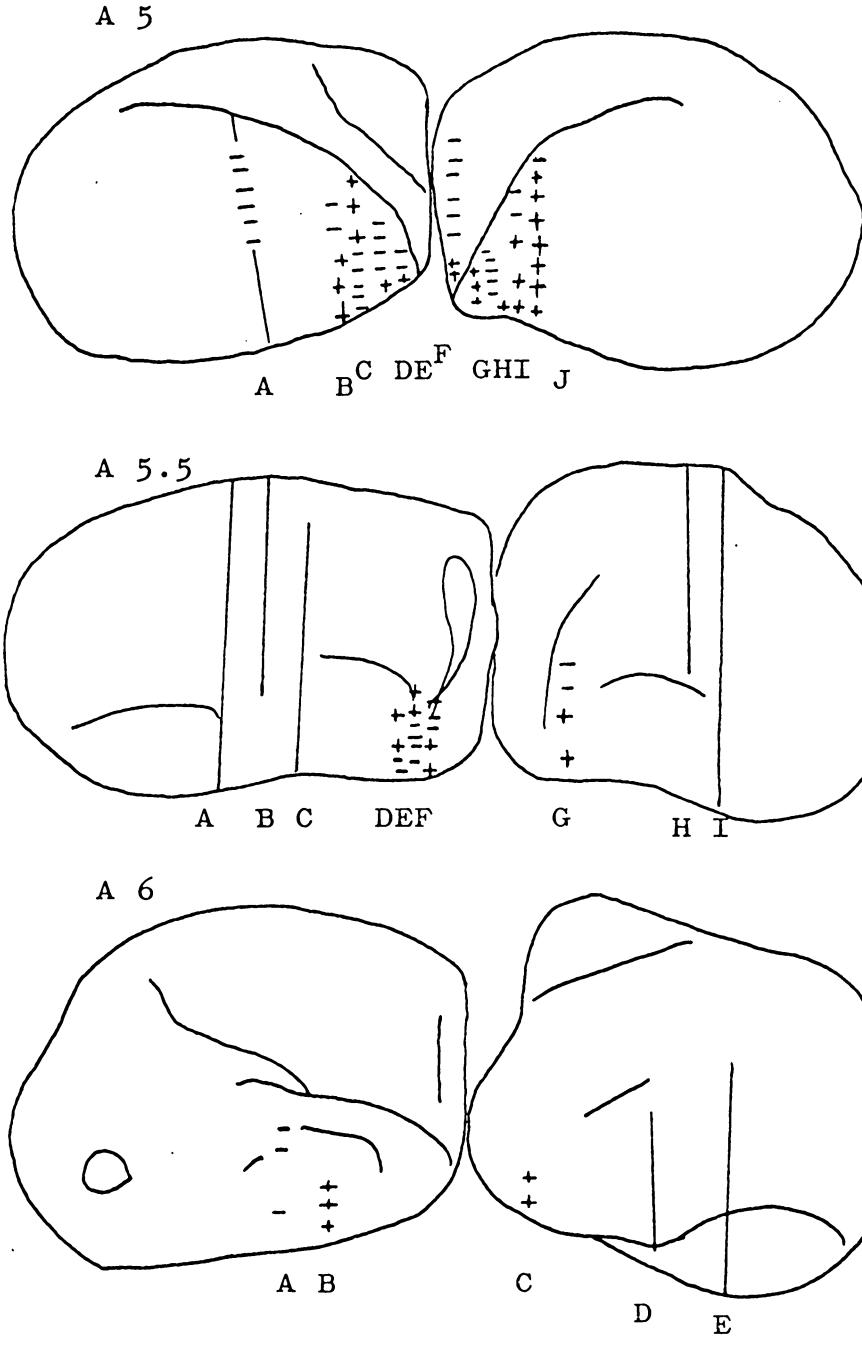


A-63-34	3
B-63-33	6
C-64-17-H	2
D-64-5-H	3
E-63-33	5
F-63-33	4
G-64-5-H	4



A-63-31	1
B-63-31	2
C-63-47	1
D-64-6-H	1
E-64-6-H	2
F-64-5-H	2
G-63-31	3
H-64-10-H	4
I-64-25-H	1
J-64-7-H	3
K-63-47	2

Fig. 6 Location of caudal regions in the neostriatum activated by clicks. Solid lines indicate unresponsive areas. The right side indicates ipsilateral stimulation; the left contralateral stimulation. Letters identify the experiment and track numbers. Thickness 50 μ. Mag. 5X.



Exper.	Tr.
A-63-35	2
B-64-16-H	1
C-64-16-H	2
D-64-13-H	3
E-64-21-H	2
F-64-10-H	1
G-63-34	5
H-64-23-H	1
I-64-16-H	1
J-63-34	6

A-63-44	3
B-63-35	1
C-64-9-H	2
D-64-10-H	2
E-64-9-H	1
F-64-10-H	2
G-64-24-H	4
H-63-45	1
I-63-44	2

A-64-26-H	1
B-64-26-H	2
C-64-26-H	5
D-64-26-H	3
E-64-26-H	4

Fig. 7 Location of rostral regions in the neostriatum activated by clicks. Solid lines indicate ipsilateral stimulation; the left, contralateral stimulation. Letters identify the experiment and track numbers. Designations of (+) and (-) mark areas of positive and negative potentials. Thickness 50 μ. Mag. 5X.

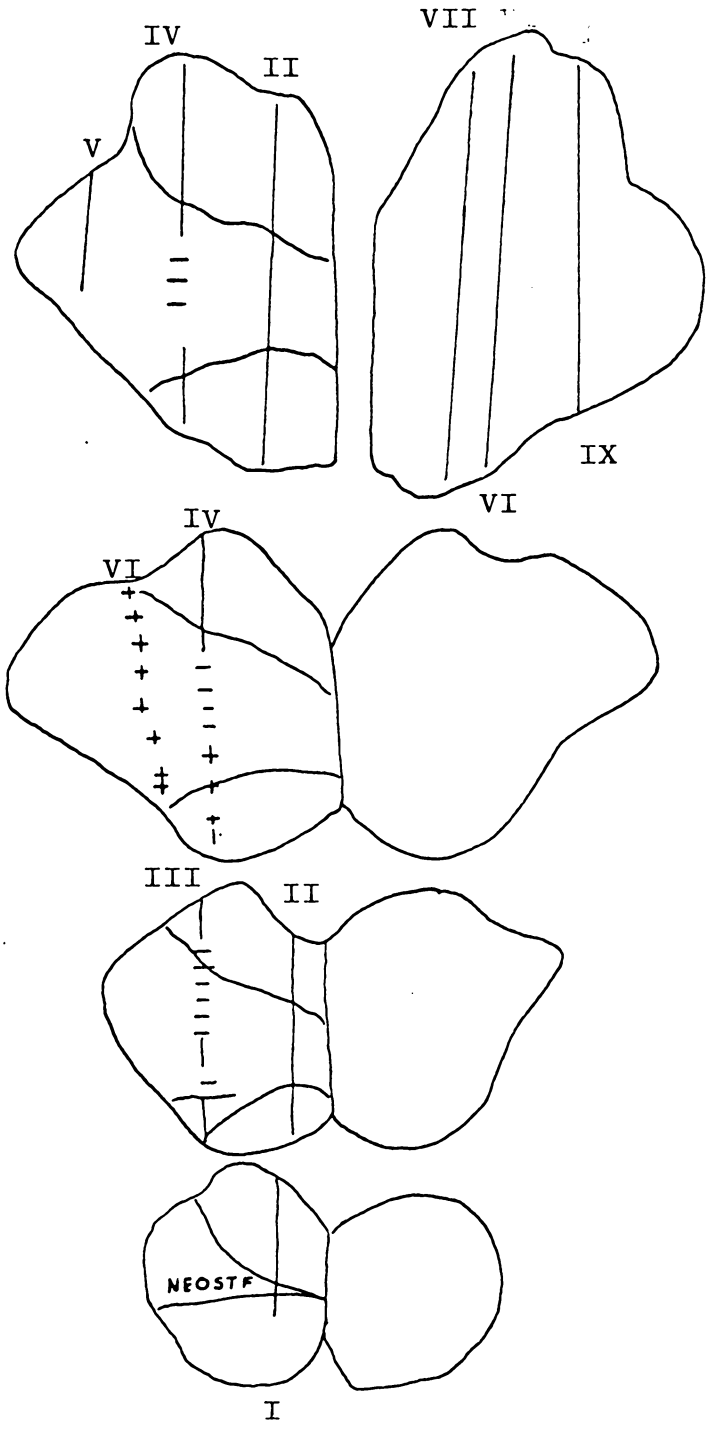
this area. This area had latencies of 9 to 16 msec, although in one response the latent period was as short as 5.5 msec. The main component of this response was one of 12 to 14 msec. In another response the latent period was as long as 24 msec and the response was 50 msec broad.

Another area activated by auditory stimuli was the neostriatum located beyond the ektostriatum. Here the neostriatum touches the medial wall of the hemisphere (fig. 8). The responses occurred in a somewhat central region of the neostriatum; the medial part was not responsive nor was the lateral region found to be responsive. No responses to auditory stimuli were found in the neostriatum intermediale.

Responses were evoked in the paleostriatum especially in the paleostriatum primitivum (figs. 9 and 10). Of the 5 electrodes penetrating this area 4 picked up evoked potentials. Latent periods were from 11 to 17 msec. The augmentatum was less frequently activated by click stimuli than was the paleostriatum primitivum. The latent periods here were from 10 to 14 msec.

The shortest latencies found in striatal areas were in the neostriatum frontale. These latencies ranged from 5.5 to 12 msec.

A 11.5-12.5



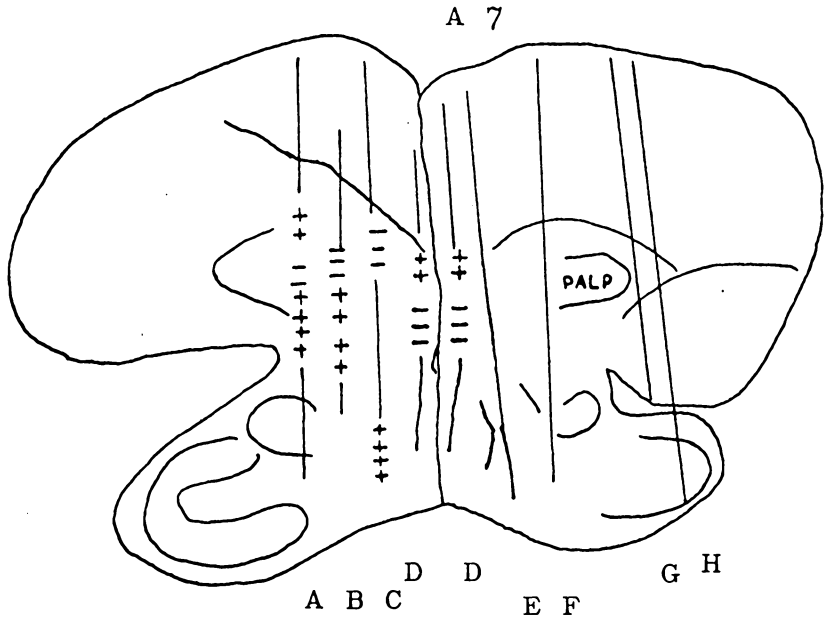
V, IV, II, VII, VI, IX indicate tracks from bird 63-28.

VI, IV indicate tracks from bird 63-27.

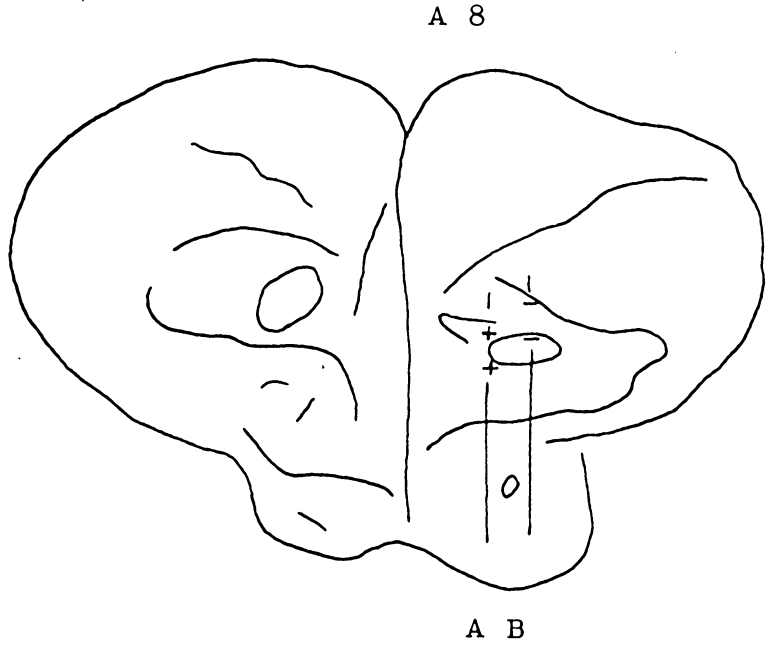
III, II indicate tracks from bird 63-27.

I indicates track from bird 63-27.

Fig. 8 Location of responsive areas in the neostriatum frontale. Solid lines indicate unresponsive areas. Areas of positive and negative responses are designated by (+) and (-), respectively. Thickness 50 µ. Mag. 5X.



Exper.	Tr.
A-64-8-H	1
B-64-16-H	3
C-64-8-H	2
D-64-16-H	2
E-64-8-H	4
F-64-8-H	3
G-63-44	1
H-63-44	2



A-63-37	1
B-63-37	2

Fig. 9 Location of responsive areas in rostral regions of the forebrain. Solid lines indicate unresponsive areas. Letters identify the experiment and track numbers. Thickness 50 μ. Mag. 5X.

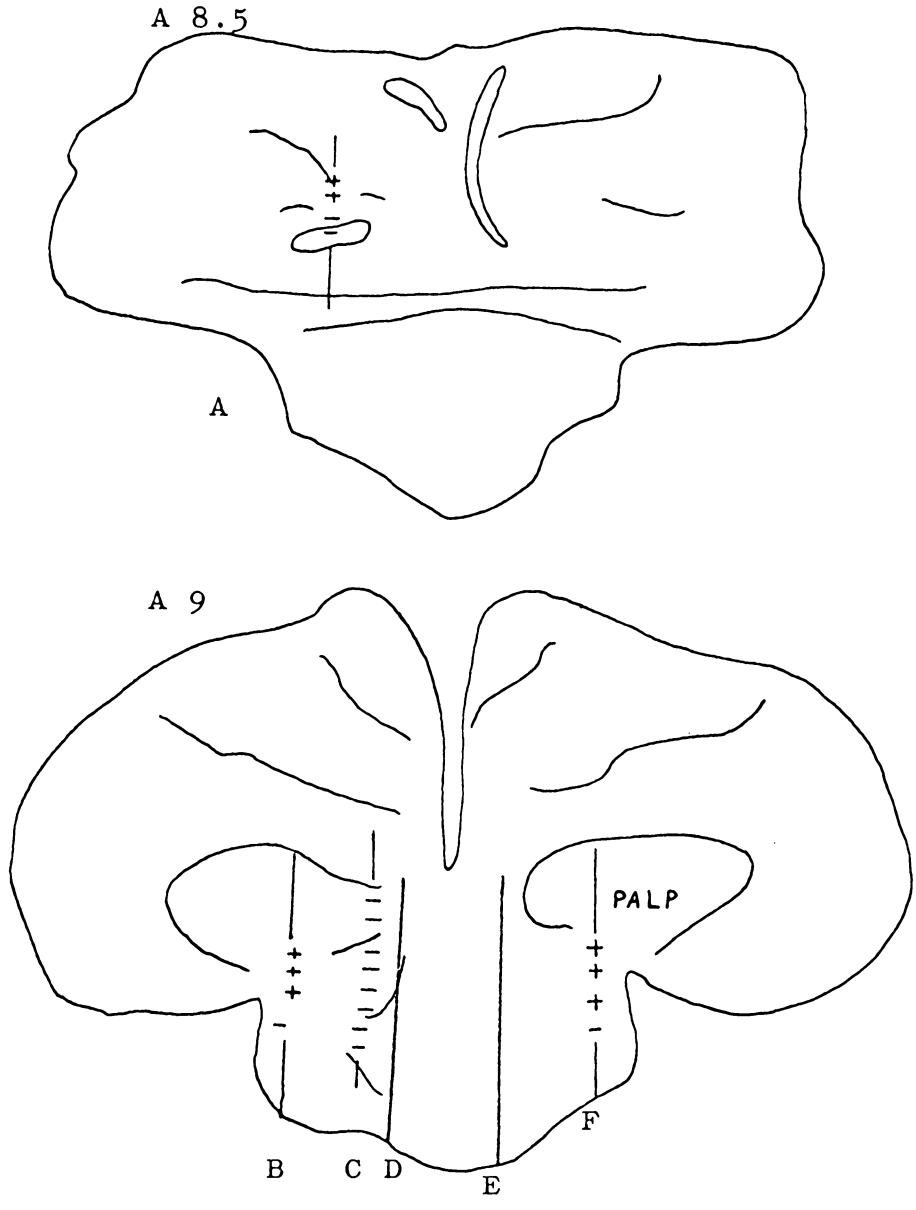


Fig. 10 The location of responsive areas in the paleostriatum. Solid lines indicate unresponsive regions. Areas of positive and negative responses are designated by (+) and (-), respectively. The letter A represents experiment 63-46, track 1; letters B,D,E,F represent experiment 64-13-H, tracks 1 and 2; and the letter C represents experiment 64-28-H, track 1. Thickness 50 μ. Mag. 5X.

Physiology of Evoked Potentials

Responses of mesencephalic nuclei. Ipsilateral clicks produced evoked potentials in the lateral parts of the nucleus mesencephalicus lateralis pars dorsalis consisting, in most cases, of an initial negative wave of about 8 to 10 msec duration and 10 to 25 μv amplitude, with a latency of 4 to 6 msec, followed by a slower positive wave lasting about 5 to 6 msec with 50 μv amplitude at a latency of about 6 to 8 msec (Table 1).

In a central part of the nucleus ipsilateral clicks produced evoked potentials most of which consisted of a positive wave with 2.5 msec duration, 40 to 100 μv amplitude and 5 msec latency. A negative wave followed with a duration of 6 to 7 msec, an amplitude of 85 to 250 μv and latent period of 6 to 10 msec. In most cases a slower positive wave with a much longer duration than the earlier parts of the response was seen. This wave had a duration of 12 to 16 msec with an amplitude of 10 to 25 μv and latency of 10 to 16 msec.

The lateral part of this nucleus responded to clicks introduced in the contralateral ear with negative waves having a latency of 6 msec and small amplitudes of 10 to 25 μv. In the central region of the nucleus, click stimuli to the contralateral ear produced responses consisting of a biphasic wave. The first part of the wave was negative, having a latency of 5 msec and an amplitude of 5 to 25 μv

Table I. Physiological characteristics of potentials evoked by click stimuli in the nucleus mesencephalicus lateralis pars dorsalis.

Lateral						Medial						Central					
No.	Tr.	S	P	L	A	No.	Tr.	S	P	L	A	No.	Tr.	S	L	A	
64-4-H	4	17	-	5	10**	64-4-H	1	17	-	2	15 *	64-23-H	2	1	+ 5	20	**
		18	-	5	20			18	+	2	10-50				- 7	25	
64-4-H	2	15	-	6	10 *			19	+	2	20-60				-12	50	
		16	-	6	25	64-7-H	1	17	+	4	10 *	64-2-H		16	- 5	5	
		17	+	6	80			18	+	4	40-50				+10	25	
64-5-H	5	17	-	5	30**	64-6-H	1	17	+3	.2	50 *			17	- 5	25	
		18	+	6	40-50				+	4	35				+ 8	25-50	
		19	+	5	50				+5	.4	25	64-17-H	1	6	+ 5	10	**
			+	8	30				+	6	45				- 9	10	
		20	-	2	20			18	+3	.2	60				+14-16	10	
			+	4	30	63-33	2	10	+	4	20-25**			7	+ 5		
			+5	.5	40				-	5	20				- 9		
			+	6	40				+	7	50			8	- 3		
64-24-H	5	1	-3	.5	20**			11	-	5	25				- 5		
			-4	.5	25				+	6	25				-6-10		
			+	8	50				-	8	40				+12		
						64-4-H	3	6	-	5	40 **			9	+ 5	150	
															- 8	100	
												64-21-H	3	3	- 3	40	** *
															+ 5	10	
															+ 8	90	

** Ipsilateral stimuli
* Contralateral stimuli
No. = Number of experiment
Tr. = Track
S = Site
P = Polarity of component
L = Latency in msec.
A = Amplitude in microvolts

with a duration of 5 msec. The second part consisted of a positive wave, having a latency of 8 to 10 msec with an amplitude of 25 to 50 μv and lasting 12 msec in some cases.

Stimulation presented to both ears at the same time evoked potentials in the central part of the nucleus which consisted of a triphasic response; a 40 μv negative wave at 3 msec latency, a 10 μv position wave with latent period of 5 msec, and a 90 μv negative wave lasting 8 to 10 msec and peaking at 8 msec. A positive slow wave followed (Table 1).

Evoked potentials in the lateral part of the nucleus isthmi pars principalis parvocellularis to ipsilateral clicks consisted of a negative wave having a latency of 6 to 9 msec and an amplitude of 25 to 40 μv (Table 2). Earlier waves at 3 and 4 msec were sometimes seen.

Evoked potentials in the lateral part of this nucleus to contralateral clicks consisted of a positive wave of small amplitude and latency of 10 msec. From a medial part of this nucleus the evoked potential was much more complicated. The most stable part of the response was a positive wave at 5.5 to 7 msec latency and had a 50-400 μv amplitude followed by a 60 μv negative wave at 10 msec. When the stimulus was to both ears, simultaneously, the response was a positive wave having a 4 msec duration and an amplitude of 30 to 100 μv, with a latent period of 4 to 7 msec, followed by a slow negative wave (Table 2).

Table 2. Physiological characteristics of potentials evoked in the nucleus isthmi pars principalis parvocellularis by click stimuli

Part of nucleus	Stimulus	No.	Tr.	P	Latency in msec	Amplitude in microvolts
Medial	Contralateral	64-2-H	3	-	1.5	100
				-	3.0	100
				+	5.5	400
		64-6-H	1	+	2.4	30-50
				+	2.8	45
				-	7.0	50
				-	2.4	10
				-	3.2	25
		63-33	2	+	5.0	65
				-	5.5	25
				-	7.0	75
Lateral	Ipsilateral	64-2-H	2	-	8.9	25
				-	8.0	30
		64-5-H	4	-	3.0	25
				+	4.0	50
				-	6.0	25
				-	6.0	40
	Contralateral	64-4-H	2	+	10.0	15
	Both ears	64-20-H	2	+	7.0	50*

Tr. = Track
P = Polarity
* = Peak followed by a slow wave lasting 33 msec with an amplitude of 100 microvolts

Responses in the nucleus semilunaris contralateral to the stimulated ear were all negative in polarity and had very short latent periods of 2 to 4 msec with amplitudes of 20 to 40 microvolts. To ipsilateral clicks, the evoked potentials in this nucleus were positive, had latent periods of 5 to 6 msec, and had much greater amplitudes than those responses evoked by stimulating the contralateral ear (80 to 350 vs. 20 to 40 microvolts). See table 3.

Multiple stimuli. In the mesencephalon the time required for restoration of the amplitude of the response after the action of the stimulus was investigated with paired clicks. Figure 11 shows that when the interval between clicks was 1.6 msec there was no response to the second click stimulus; but when the interval was 3.6 msec, response to the second click could be seen. At the interval of 2.6 msec the shape of the first stimulus response was affected although a second spike could not be seen. The response reached its initial amplitude when the interval was 3.6 msec. Although the figure used to demonstrate the action of twin pulses on the amplitude of the evoked potential came from data on the mesencephalicus lateralis pars dorsalis, the time required for restoration of the amplitude was generally the same in all areas of the mesencephalon.

Repetitive stimulation at different frequencies as well as the effects of an increased sound intensity were

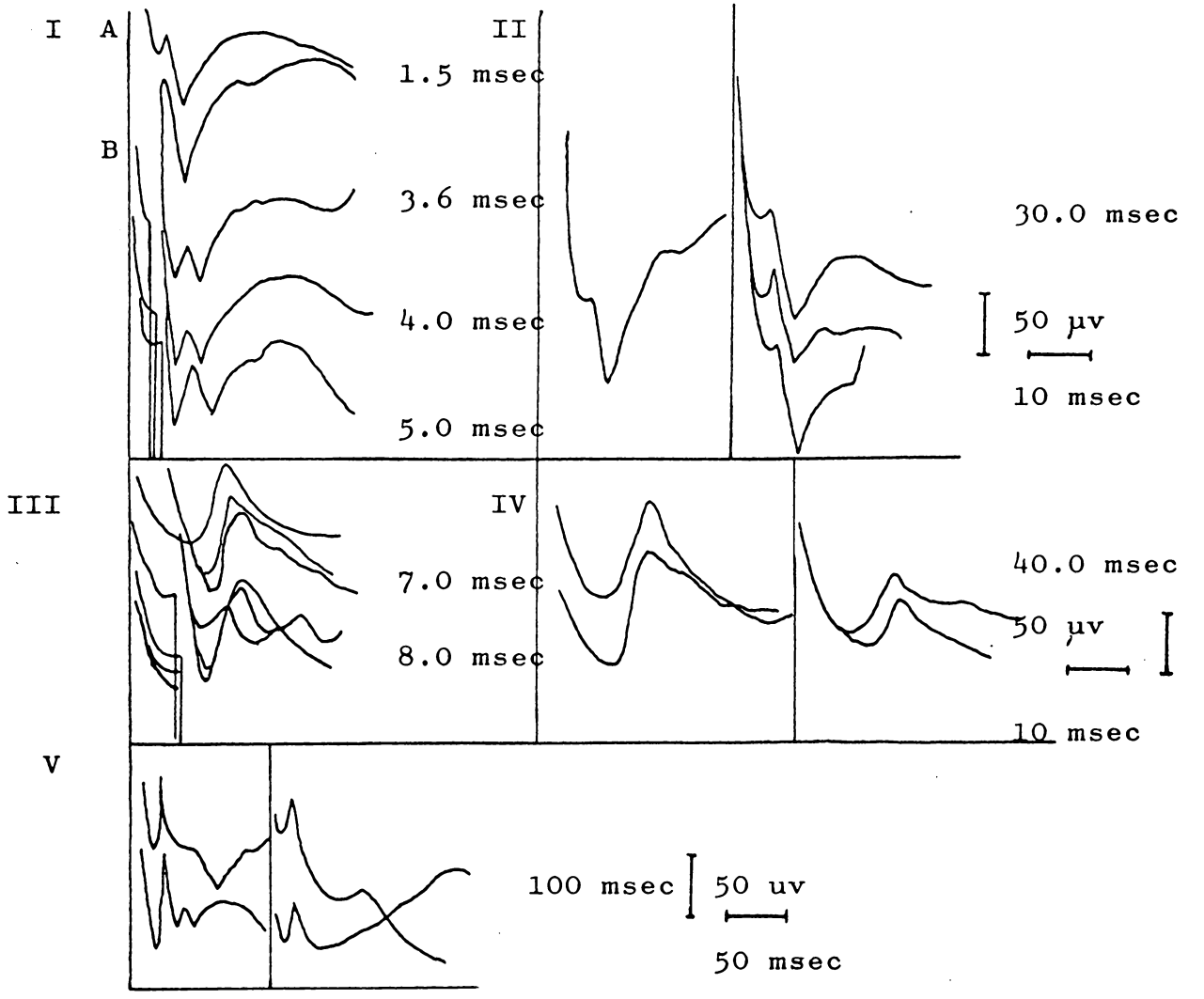


Fig. 11 Differences in responses of the mesencephalon and neostriatum caudale when tested for absolute refractory period. Groups I and II are negative potentials taken from experiment 64-21-H, track 3, site 3 in the nucleus mesencephalicus lateralis pars dorsalis. A-single pulse; B-the second negative potential is the test response. Groups III, IV, and V are potentials taken from experiment 64-21-H, track 2, site 1 in the neostriatum caudale ventrale. The potential at the top of group II was produced by a single pulse. The second response shown in II, IV, and V is the result of the test stimulus. Parameters are given to the right of each set of responses. Vertical lines indicate the stimulus artifacts.

Table 3. Physiological characteristics of potentials evoked by click stimuli in areas of the mesencephalon

Location	Bird	Tr.	S	P	Latency in msec	Amplitude in microvolts	
Nucleus							
Semilunaris	64-4-H	1	26	-	2.0	25	*
	64-4-H	3	23	+	6.0	350	**
	64-7-H	1	24	-	4.0	25	*
	63-34	1		-	3.0	25	*
				+	3.5	35	
				-	4.0	40	
	63-29	4		+	5.0	75	**
		5		+	5.0	100	
Atlas Coordinates A 1.25-1.75 L 3.5-4.0 V 2.5-3.0	64-4-H	3	20	-	5.5-6	120	**
			21	-	5.5-6	450	
	63-33	3		-	4.0	60	
				+	6.0	75	
	64-4-H	3	24	-	6.0	75-100	**

Tr. = Track number
S = Site number
P = Polarity
* = Contralateral
** = Ipsilateral

investigated. Amplitude of responses generally decreased with increased stimulus frequency. The decrease seemed to be a linear one. The large evoked potentials in the mesencephalicus lateralis pars dorsalis and semilunaris were still seen even at stimulus frequencies above 100/sec. Stimulus frequencies below 10/sec caused a waxing and waning of response amplitudes. Increasing the intensity of the stimulus increased the response amplitude up to a point at which further loudness of the stimulus had no additional effect. Another observation was that by increasing the loudness to a high value then returning to a much lower one, a response could then be seen which could not otherwise be elicited.

Secondary responses. Secondary responses, so called because they were inconsistent in latency and duration and of small amplitude, were found at the atlas coordinates of A 3.5-4.0, L 1.5-2.5 and V 1.5-2.5 (Fig. 3).

Responses of the thalamus. In the thalamus evoked potentials to either contralateral or ipsilateral stimulation usually were simple, monophasic responses (Tables 4 and 5). When other components were observed, they were very inconsistent and faded rapidly when evoked repetitively. The amplitudes of these slower components were usually not as high as the main part of the response.

Table 4. Physiological characteristics of evoked potentials in two thalamic nuclei.

Nucleus	Bird	Tr.	S	P	Latency in msec	Amplitude in microvolts
Dorsolateralis	64-6-H	2		-	10-16	50 *
	64-7-H	2	14	-	12	50-75
			15	-	12	50-80
			16	-	12	10-75
	64-26-H	5		+	13	120 **
				+	13-14	50
				+	13-14	40
	64-25-H	1	3	+	16	125-150**
				+	32-45***	
	63-34	6	14	+	14-15	75 **
			15	+	12-13	20-40
			16	+	14-16	50
	64-24-H	7	1	+	14-15	65 **
					60 ****	30
			2	+	14	30
Dorsomedialis	64-13-H	3	9	+	14-16	50-100
				+	26	20
			10	+	16	70
				+	22	25
				+	32-36	40
	64-28-H	2		-	14	75-100
				-	34-35	60
	64-23-H	1	5	-	16-18	20-40 **
			6	-	16-18	25
	63-34	5		-	13	40 **
				-	20	10-20
				-	28	35
	64-10-H	2	5	+	14	40-60 *
			6	+	14	35
	64-9-H	1	8	-	14	50-80 *
			9	-	14	50
	63-35	2	15	+	14	150 *
			16	+	14	40
	64-24-H	6	10	+	14	35 *
				-	15-16	220

Tr. = Track number
S = Site number
P = Polarity

* Contralateral stimulus
** Ipsilateral stimulus
*** Response lasts 100-170 msec
**** Component inconsistent

Table 5. Physiological characteristics of evoked potentials in areas of the thalamus

Location		Tr.	S	P	Latency in msec	Amplitude in microvolts	
Nucleus Ovoidalis	64-10-H	2	8	+	11	50	*
			9	+	12	80	
	64-28-H	2	2	+	10	50	*
			3	+	10	50	
			2	+	10	50	**
			3	+	10	50	
Laterally to nu. OVD	64-25-H	1	4	+	10	60-100	**
			5	+	11-12	10	
	64-26-H	5	7	+	10-12	50	
			8	+	9-11	40-45	
Ventrally to nu. OVD for 1.5-2 mm	64-13-H	3	13	-	8	30	*
			14	+	8	50-75	
			15	+	8	50-75	
	64-13-H	3	13	-	8	30	**
			14	+	8	50-75	
			15	+	8	50-75	
	64-10-H	2	11	+	9.5	80	*
			12	-	9	30-50	
	64-24-H	7	4	+	10	50-75	**
			5	+	10	100-110	
			6	-	10	75-90	
A 5-5.5 V 2-3 L 1.5-3	64-13-H	3	17	-	8	100-150	*
			18	-	8	75	
				-	16	15-20	
			19	-	8	75	
				-	16	15-20	
			17	-	8	100-110	**
			18	-	8	75	
				-	16	15-20	
			19	-	8	75	
				-	16	15-20	
	64-24-H	7	7	-	6	65-90	**
				-	8	25-50	
	64-25-H	1	9	+	12	90	**
			10	+	10-12	30-40	

Table 5. (continued)

Location	Bird	Tr.	S	P	Latency in msec	Amplitude in microvolts	
A 6.0-7.0	64-26-H	5	11	+	6-7	100	**
V 1.5-4.0			12	+	7	110	
L 1.5-3.0			13	+	5	45	
			14	-	5-7	150	
			15	-	5-6	125	
			16	-	5	175	
			17	-	5	45	
	64-25-H	3	6	+	6	20	**
			7	+	8	25	
			8	+	10	25	
			9	+	9	25-40	
			10	-	5.5	40	
			11	-	5.5	10	
	64-24-H	6	8	+	5	30	**
			9	+	5	40	
			11	-	4.5	45	
			12	-	4.5	10	
	64-9-H	1	16	-	5-6	50	*
			17	-	7-8	25-30	
	64-8-H	2	21	-	8	40	*
			22	-	8	40	
			23	+	6-7	45	
			24	+	4	50	
A 7.5-9	64-13-H	2	7	+	8	45	*
V 5.5-6			8	+	8	45	
L 2-3.0			9	+	8	30	
			11	-	8	50	
			7	+	8	45	**
			8	+	8	45	
			9	+	8	30	
			11	-	8	50	
	64-16-H	3	7	-	12	40	*
					15		
			8	-	12	35-40	
			9	+	11-12	40-60	
			9	+	12	10-50	**
			10	+	12	50-60	*
			11	+	10	100	*

OVD = Nucleus ovoidalis
* = Contralateral stimulus
** = Ipsilateral stimulus

Tr. = Track number
S = Site number
P = Polarity
AVL = Atlas coordinates

Thalamic areas with the highest amplitudes and the longest latencies to the initial response were the nuclei dorsolateralis and dorsomedialis. In the dorsolateralis clicks presented to the contralateral ear produced a negative wave with duration of 9 to 22 msec, amplitude of 50 to 120 μv and latent periods ranging from 10 to 16 msec. The most frequent latent period was 12 to 14 msec. Click stimulation of the contralateral ear produced an evoked potential in the dorsomedial nucleus which was more complex than the one produced in the dorsolateralis. The initial response was a positive wave having a 9 to 11 msec duration and 50 to 100 μv amplitude, with a latency of 14 to 16 msec. The other components were of smaller amplitude (10 to 60 μv) and had latent periods of 20 to 36 msec with a duration of about 14 msec and longer.

Evoked potentials to clicks presented ipsilaterally were opposite in polarity to those following contralateral stimulation. In the nucleus dorsolateralis, clicks presented to the ipsilateral ear evoked a positive wave at 12 to 20 msec with amplitudes ranging from 20 to 170 μv. The most common latency and amplitude were 13 to 14 msec and 50 to 120 μv, respectively. Sometimes an inconsistent slower wave was observed having a 32 to 60 msec latency and duration of about 80 to 100 msec. In the nucleus dorsomedialis stimulation the response had an initial negative wave of about 9 msec duration and 20 to 40 μv amplitude with a

latent period of 13 to 18 msec. A slower negative wave of 20 to 28 msec latency (10 to 35 μv amplitude) sometimes appeared. (Table 4).

The responses recorded in the nucleus ovoidalis to contralateral stimulation were of shorter latency and were less complex than those in the nucleus dorsomedialis and nucleus dorsolateralis. All responses in the nucleus ovoidalis were positive potentials, ranging in latent periods from 10 to 12 msec. The amplitudes of these evoked potentials were 50 to 80 μv and the duration was 6 msec (Table 5).

Just ventral to the nucleus ovoidalis most responses evoked by ipsilateral stimulation were positive, had durations of 14 to 15 msec, amplitudes of 50 μv, and latent periods of 10 msec. To contralateral stimulation, responses recorded from the same sites were practically the same (a positive potential having an 8 msec duration, a 50 μv amplitude and a latent period of 10 msec). No response could be seen at 100 clicks/sec, although one could still be observed at 10/sec. On the lateral side of the nucleus ovoidalis potentials were of both negative and positive polarity but most were positive. Ipsilateral stimulation produced responses here that were not very sharp, consisting of positive waves with 9 to 12 msec latent periods and amplitudes 10 to 100 μv. (Table 5).

In an area located ventral to and down 1.5 to 2.0 mm from the nucleus ovoidalis (fig. 4; Table 5) latencies were from 6 to 11 msec when evoked by either ipsilateral or contralateral stimuli. The amplitudes of these responses were 30 to 150 μv. The polarity was not consistent for either stimulation but generally the spikes were negative. In a position ventral to the region just described (A 5.0-5.5; V 2-3; L 1.5-3.0), evoked potentials had short latencies (4.5 to 7.0 msec), relatively high amplitudes (65 to 175 μv) and about 4 to 6 msec duration with mostly negative polarities. The responses faded rapidly at stimulation frequencies from 10 to 20/sec; at over 20/sec no response could be seen. This area is in the region of the tractus quintofrontalis in its thalamic course and is located at A 5.5-6.0, L 1.5, V 2.5-5 (figs. 4 and 5), and in more rostral sections this site becomes the area of the decussatio supraoptica dorsalis and ventralis (see Juhasz and van Tienhoven, 1962). Similar responses were observed medial and ventral to the nucleus rotundus, which was not responsive to click stimuli (figs. 4 and 5). These short latency responses were not over 40 to 50 μv and most of them were smaller. Other responses with much longer latencies were observed in this area although they were not often seen. Their amplitudes were low (10 to 30 μv) with latencies of 14 to 17 msec.

At atlas coordinates of A 7.5-9, V 5.5-6, and L 2-3.0 responses had latent periods of 8 to 12 msec and amplitudes of 30 to 100 μv, but the responses were not sharp. These responses were much more consistent to contralateral than to ipsilateral stimulation. To repetitive stimulation, clicks up to 8/sec elicited responses. Above 8/sec, however, no responses could be seen. Most of the responses were positive in polarity. The second of a pair of clicks elicited no response at intervals less than 10 msec. (Table 5).

Responses from nuclear regions of the forebrain. Responses were evoked in the paleostriatum more frequently from the paleostriatum primitivum than from the paleostriatum augumentatum. The responses in the paleostriatum primitivum to contralateral stimuli were mostly negative waves of 8 to 15 msec duration, 35 to 110 μv amplitude, and 11 to 17 msec latency with 12 to 13 msec being the most frequent latent period. Responses to ipsilateral stimulation were the same (Table 6).

In the neostriatum caudale laterale most of the responses evoked by click stimulation of the contralateral ear were positive in the dorsal parts of the area and negative in the ventral part to either contralateral or ipsilateral stimulation. (Table 6). The responses were complex ones in comparison with those of the thalamic area. In the neostriatum the evoked potentials consisted

Table 6. Physiological characteristics of potentials evoked by click stimuli as recorded in the paleostriatum pars primitivum and augmentatum

Location	Bird	Tr.	S	P	Latency in msec	Amplitude in microvolts	
Primitivum	64-26-H	2	1	+	13	75-90	*
			2	+	13	65-75	
	64-8-H	1	4	-	12	65-100	*
			5	-	12	75-100	
	63-37	2	1	-	13	100	**
			2	-	13	100	
			3	-	11	40	
				-	13	50	
	63-46	1	3	-	15-16	100	*
			4	-	15-16	100	
Augmentatum	64-26-H	1	1	-	10	10-15	*
			2	-	9-10	25	
	63-37	1	3	+	13	50	**
			4	+	13	50	
			5	-	11	40	
				-	13	50	
	64-8-H	2	1	+	12	15	*
			2	+	12	15	
	64-16-H	3	1	-	12	40	*

Tr = Track number
S = Site number
P = Polarity

of an initial positive wave having a duration of 5 to 10 msec and an amplitude ranging from 50 to 1,000 μv with latent periods ranging from 9 to 16 msec, with 12 to 16 msec being the most frequent. A slower wave component was seen in most cases having an inconsistent duration but not more than 20 msec and amplitudes of 50 to 175 μv. Latent periods were from 18 to 26 msec in these slower components. In most cases neither latency, duration, nor amplitude were consistent, and these responses faded away more quickly at lower frequencies than the initial wave. In some cases, preceding the initial response was a shorter latency (7 to 9 msec), usually negative wave of small amplitude (10 to 25 μv). Responses faded at frequencies of 10/sec and came very infrequently at higher frequency stimulation. Responses to stimulation of the ipsilateral ear were smaller in amplitude (10 to 130 μv), but the latency range seemed to be the same for the initial response (12 to 16 msec). The initial response was negative and consistent. The later components were inconsistent in latency, amplitude, and polarity (Table 7).

To stimulation of the contralateral ear evoked potentials in the neostriatum caudale ventrale usually consisted of an initial negative spike with a duration of about 6 msec and amplitude of 25 to 250 μv with the latent periods of 13 to 17 msec but 14 to 16 msec being the most frequent. Most responses were negative waves with 18 to

Table 7. Physiological characteristics of evoked potentials located in the neostriatum caudale laterale

Bird	Tr.	S	P	L	A	
64-5-H	3	4	-	17	50	**
		5	-	16	20-60	
			-	19	40	
			-	22	10-70	
		6	-	16	20-60	
			-	22-24	75-130	
64-5-H	2	1	-	12	10-75*	
			+	16	75-90	
			-	21	25-40	
		2	-	12	10-75	
			+	16	150	
			-	21	25-40	
		3	+	16	200-400	
			+	24	50-175	
		4	+	16	50-100	
			+	24	40	
		5	-	16	20-25	
		6	-	16	20	
64-6-H	1	1	+	10	20	*
		2	+	10	40-60	
		3	+	10	30-70	
		5	-	11-12	10-20	
		6	-	9-12	20	
64-6-H	2	5	+	10	390	*
			+	15	150	
		6	+	10	600	
		7	+	9	1100	
		8	+	9	800	
		9	+	9	100	
		10	+	9	50	
63-29	2	1	+	14	20	**
		2	+	14	25	

Bird	Tr.	S	P	L	A	
64-7-H	1	6	-	11	20	*
			+	13-14	200	
			-	16	75	
		7	+	19-20	50	
			-	11	20	
			+	13-14	100-300	
			-	16	70	
			+	19-20	20	
		8	-	5-7	30	
			+	12-14	135	
			+	18-19	40	
		9	+	11	50	
		10	-	11	25-50	
		11	-	11	20-25	
64-7-H	2	1	+	11	25	*
		2	+	11	30-100	
		3	+	12	200	
		4	+	12	150-200	
		5	-	9	20	
			+	12	100-170	
			+	22	50	
		6	+	9	25	
			-	12	160	
			+	15	30	
			-	22	100	
			-	30	30	
		7	-	12	100-200	
			-	24-26	50	
64-7-H	3	4	+	12	50-90	**
		5	-	12	10-40	
		6	-	13	100	
		7	-	12-13	50-70	
		8	-	13	50	
		9	-	12-13	20-40	

* Contralateral stimulus
** Ipsilateral stimulus
Tr =Track number

S = Site Number
L = Latency in msec
A = Amplitude in microvolts

40 msec latencies amplitudes of 30 to 300 μv and durations of 11 to 96 msec (Table 8). In most cases a smaller wave with 8 to 13 msec latency and 20 to 35 μv amplitude preceded the initial response. The duration of this response varied from 3 to 6 msec. Usually all of the initial negative spikes were recorded in the dorsal part of the neostriatum caudale ventrale with the positive potentials occurring in the ventral part of this region. The positive potentials were smaller (30 to 50 μv) than the negative potentials and were not as complicated.

When stimulation was applied to the ipsilateral ear, most of the potentials in the neostriatum caudale ventrale were negative, with latencies of 10 to 19 msec, with the most frequent ones being 14 to 16 msec with amplitudes of 50 to 200 μv and duration of 12 to 16 msec. Slower components had latencies of 12 msec and 10 to 15 μv amplitudes.

When both ears were stimulated potentials lasted 20 to 30 msec, had 65 to 110 μv amplitudes, and 13 to 15 msec latencies. Duration was longer than when either ear was stimulated alone and smaller components at 20 msec were seen. Contralateral stimuli produced shorter latencies, larger amplitudes, and much more consistent responses than did ipsilateral stimuli.

Evoked potentials faded more rapidly with increased frequency in the neostriatum caudale than did those in the mesencephalon. (fig. 12). When stimulation was either to both ears simultaneously or separately, the responses could not be evoked when the interval between the twin

Table 8. Physiological characteristics of evoked potentials found in the neostriatum caudale ventrale

Bird	Tr	S	P	L	A	
63-33	3	1	-	15	20	**
		2	-	13	30	
		3	-	14-16	25	
63-29	3	1	-	12	30	
		2	-	13	10	
		3	-	14	10-15	
63-31	3	1	-	15-16	75	
		2	+	17-18	60	
		3	-	15	125	
			+	18	100	
		4	+	16	30-50	
			-	18-19	40	
64-23-H1	1		+	12	10-15	**
			+	15-19	110	
		2	+	16-17	150	
		3	+	16-17	70	
64-10-H1	1		-	14	135	*
		2	+	14	25-35	
		3	+	14	25-35	*
64-10-H4	1		-	14-16	50	
		2	-	15	40	
		4	+	15	35	
63-35-	6	1	+	12	60	*
			-	16	160	
		2	-	14	60	
		3	-	11-12	75	
			+	16	50	
			-	22-24	50	
			+	44-50	75	
		4	-	10	40	
63-33	6	1	+	6	10	
			+	14	20	
			-	20	40	
		2	-	16-22	70	
		3	-	16-22	50-150	
		4	-	16	20	

Bird	Tr	S	P	L	A	
63-34	5	1	-	24	25	**
		2	-	14	25	
		3	-	14	25	
		4	-	16	45	
		5	-	15	20	
			-	23	20-40	
			-	30	10-20	
		6	-	11	25-40	
			+	15	60-75	
			-	23	15	
			+	32	10	
		7	+	16	75-90	
			+	22	40	
			+	34	25	
			+	42	40	
64-10-H2	1		-	14	160	*
		2	-	14	160	
		3	-	14	100	
			+	24	50	
		4	+	13-14	75	
			+	24	30	
64-10-H1	1		+	14	25	*
		2	+	14	40	
		4	-	14	10-15	
		5	-	14	15	
64-26-H	5	1	+	11	10-15	**
			+	14-16	35-40	
			+	22	50	
		2	+	11	10-15	
			+	14-16	35-40	
			+	22	50	
		3	+	13-14	80-150	
		4	+	13-14	80-150	
63-35	4	1	-	15-16	35	
		2	-	15-16	35	

Tr = Track number
S = Site number
P = Polarity
L = Latency in msec
A = Amplitude in microvolts
* Contralateral stimulus
** Ipsilateral stimulus

Table 8. (continued)

Bird	Tr	S	P	L	A	
64-9-H	1	1	-	11-12	20-50	*
			+	16	100	
			-	22	25-75	
		2	-	11-12	20-50	
			+	16	100	
			-	22	25-70	
		3	-	12-13	130	
			+	18	60	
			+	21	25	
		4	-	14	110-150	
			+	18	40-60	
			-	28	35	
63-35	2	1	+	12	40	*
			-	15	80	
			+	20	110	
			+	32	20-80	
63-35	2	2	-	16-18	30	
		3	-	14	100-200	
		4	-	13	200-250	
64-13-H	3	3	-	15-16	25	***
		4	-	14-16	75	
		5	-	15-16	120	
			-	34-36	180	
			-	64	100	
		7	-	17	100	
			-	22	30	
			-	32-40	25	
		8	+	8	25-30	
			-	16	25-50	
			-	18	35	

Tr = Track number
S = Site number
P = Polarity
L = Latency in msec
A = Amplitude in microvolts
*Contralateral stimulus
**Ipsilateral stimulus
***Same for both ipsilateral and contralateral stimuli except contralateral more consistent and clearer

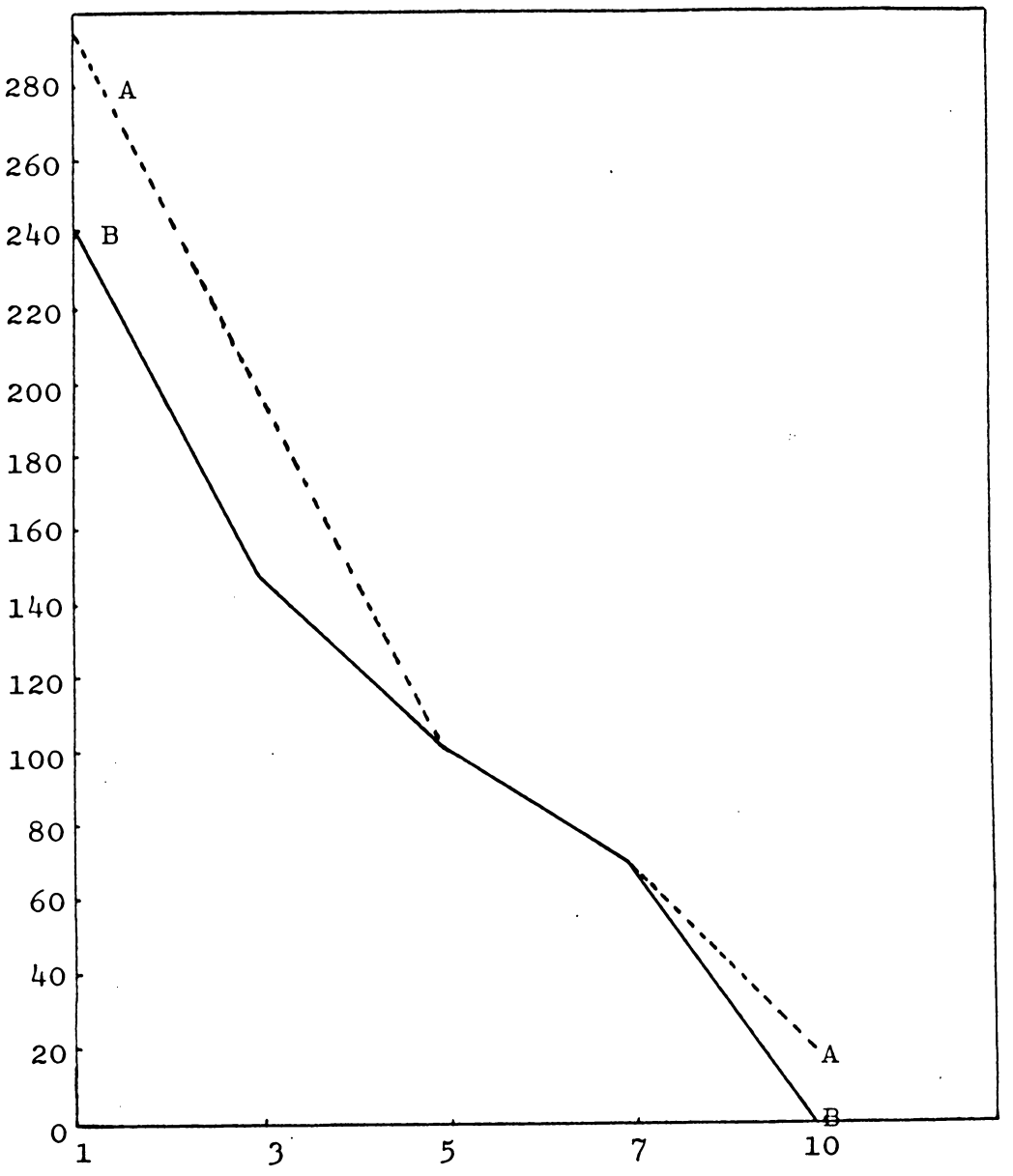


Fig. 12. Graph showing the relationship of stimulus intensity and frequency on the response amplitude. Dotted line - 50 volt stimulus intensity Solid line - 15 volt intensity. Abscissa-click frequency per sec; ordinate-amplitude of response in microvolts. Data from the neostriatum, bird 64-7-H, track 1.

pulses was less than 7 msec. Increased intensity seemed to either inhibit or obscure some of the components of the response (fig. 13).

In the neostriatum, which is located just rostrally to the neostriatum intermediale (Table 9), some responses to contralateral stimulation were negative waves of 8 to 11 msec latency and 10 to 250 μv amplitude. Positive waves had latent periods of 8 to 12 msec with amplitudes of 100 to 110 μv. These waves had slower components at 14 to 25 msec latency with amplitudes of 40 to 110 μv. Sometimes shorter latency (5.5 to 8 msec, 50 to 70 μv) negative potentials preceded these positive waves.

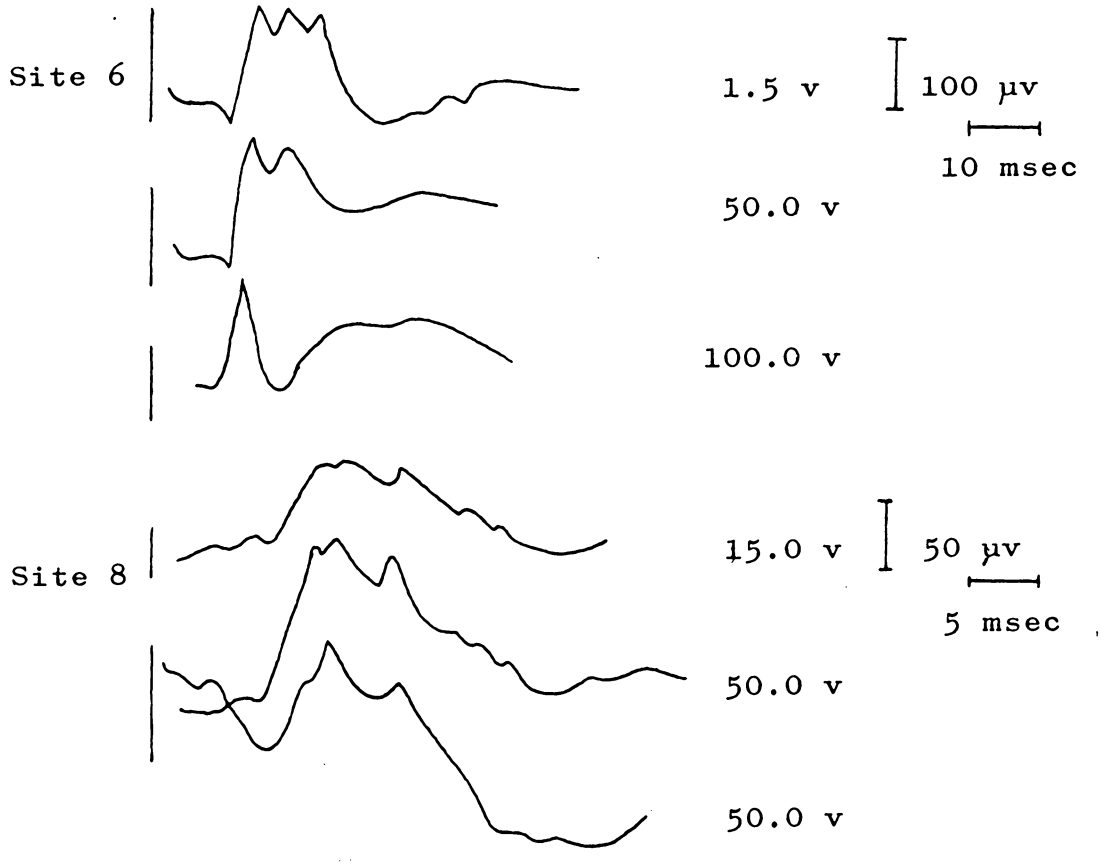


Fig. 13. Effects which increasing the intensity of the stimulus has on the shape of the response. The stimulation was to the contralateral ear.

Table 9. Physiological characteristics of evoked potentials found in the neostriatum frontale

Bird	Tr.	S	P	L	A
63-27	6	1	+	10	40
		2	+	8.0-12	100
			-	14	40
		3	+	10.0-12	150
			+	16.0-18	40
		4	+	5.5-6	75
			-	10	100
			+	11.0-12	50
		5	+	6	50
			-	9.0-10	250
			+	12	70
			-	25	110
		6	-	7.0-8	50
			+	11	110
			+	15	40
		7	-	7.0-8	50
			+	11	110
			+	15	40
63-27	6	8	-	5.5-6	50
			+	11	110
			+	15	40
		9	-	5.5-6	50
			+	11	110
			+	15	40
63-27-	4	1	-	10	25-40
		2	-	10	25-40
		3	-	10	25-40
		4	-	10	10
63-27	3	1	-	8.0-9	10-40
		2	-	8	10-40
		3	-	11	25
		4	-	10	10-25

Tr = Track number
S = Site number
P = Polarity
L = Latency in msec
A = Amplitude in microvolts

DISCUSSION

Interpretation of Response Components of Evoked Potentials

Interpretation of action potentials recorded in the central nervous system is difficult. One difficulty is in identifying the sign of the recorded potential (Grundfest, 1940). In a volume conductor, such as the brain, the sign signifies nothing more than that a current is flowing past electrodes in a certain direction. The sign may vary with simple movement of the electrode or may change as the electrode passes through a generator of potential from one pole to the other (Gusel'nikov and Supin, 1964). In relatively simple situations, it is possible to show this reversal and to utilize it for important deductions. In more complex situations, which are the rule, certain identification of the sign is impossible.

In the central nervous system the lack of homogeneity in volume conductor properties is an added complexity. Neuronal tissues have about four times the resistivity of normal saline and the resistivity of white matter is 1.5 times that of grey. In the central nervous system the connections are complex since fibers from many different trunks synapse to several final paths. It follows that impulses in one fiber, since it connects with so many cells, may facilitate the effect of impulses in other neurones and the conditions for a response in any given cell group are a complex of these effects. Thus multiple

pathways and networks of the central nervous system introduce many complexities in the records of its electrical potentials (Brazier, 1958).

Bishop and O'Leary (1942), using bipolar electrodes found changes of record form with the position of the electrode in relation to cells of the geniculate body in mammals: reversals are never simple inversions but go through a diphasic or triphasic stage and in this the pre- and post-synaptic spikes differ characteristically.

For the pre-synaptic waves, the first deflection of the diphasic form remains positive (as the needle goes deeper, negative ones developing progressively at the expense of the positive ones). The initial positive wave, however, is not entirely abolished. A second terminal positive deflection may develop in turn from the tail of the negative spike, as the needle passes beyond the optic tract, to form the typical triphasic record of a tract adjacent to an electrode in a conducting medium. However, the post-synaptic positive spike develops an initial deflection to form a diphasic wave at the cell boundary, and becomes wholly negative as the electrode passes through cell layers, remaining negative well into the medial geniculate body beyond the region of active elements.

Changes of form in the pre-synaptic response record can be rather simply interpreted as derived from a linear pathway ending at the geniculate, a positive phase being recorded from activity on either side of the electrode and

at a distance from it, and a negative phase when an impulse arrives at or passes close to electrode position. The form of any record is thus a function of conduction. The time of negative phase in the total record then depends on the position of the electrode along fibers recorded from and the final phase can be interpreted as that of the synaptic terminal.

Conduction is not the chief factor in determining the form of the post-synaptic response. Rather there is indicated an overall polarity of sheets of cells such that each unit throughout its activity is strongly negative toward its dendrite and relatively positive toward its axon. This sets up a bipolar field of sufficient intensity and duration to mask or reverse the expected negativity assignable to the activity of radiation axons.

According to the discussion above, it seems reasonable to interpret responses of this study as coming from activated regions with the polarity of the potentials being determined by the position of the recording electrode with respect to the location of the active regions.

Analysis of Potentials in the Midbrain.

When an electrode is located within or near the superior olivary nucleus of mammals, the slow waves generally have an early sharp peak and a later slow element. Such parts of the potential have been interpreted as an arriving impulse, followed by a postsynaptic discharge within the nearest collection of cells. (Galambos et al., 1959). The early wave found in the lateral division of the

mesencephalicus lateralis pars dorsalis, having a latency of 4 to 6 msec and an amplitude of 10 to 25 μv when stimulated by clicks presented to the ipsilateral ear, could therefore be described as a presynaptic potential. The later or slower part of this response, which had a latency of 6 to 8 msec, could then be considered a post-synaptic potential.

Other responses found in different parts of the nucleus mesencephalicus could be interpreted in the same manner. Thus, in the central division of this nucleus, the earliest element of response at 5 msec would fit a pre-synaptic definition with the slower component resulting from activity of the cell bodies of this nucleus. This same evoked potential had a very slow constituent with latency of 11 to 16 msec which cannot be interpreted by the above. Gusel'nikov and Supin (1964) explained such a wave in the forebrain of lizards as a polysynaptic potential. This potential causes a temporal dispersion which in many cases would obscure the pre-synaptic component. In many of the responses found in the mesencephalon this seems to have happened.

Using the foregoing explanation of pre-synaptic and post-synaptic potentials, the components of the responses to contralateral stimulation can be explained. In the central division of the nucleus, the wave having latency of 8 to 10 msec would appear to be the pre-synaptic potential; the wave having the latency of 10 to 25 msec

becomes the post-synaptic one. In the lateral division, the potential having a latency of 5 msec and an amplitude of 5 to 25 μv could be described as the pre-synaptic wave. The response of the medial division had waves with latent periods of 2, 3.2, and 4 msec. The very fast components at 2 and 3.2 could be due to either distant pickup or to afferent potentials having fewer synapses in their pathway than the slower components. The slower wave (having a longer latency period of 5.4 to 6 msec) is then interpreted as the post-synaptic potential being caused by the activity of the cells and dendrites of this nucleus itself. The very early components to contralateral stimulation could not be seen with ipsilateral stimulation, suggesting that impulses coming from the opposite ear have a more direct route to this nucleus than do impulses arriving from the ipsilateral ear. Throughout the responsive areas of the brain the response to contralateral stimuli seemed to be much more consistent and in most instances larger in amplitude than the potentials evoked by ipsilateral clicks.

When both sides were stimulated simultaneously, the response was triphasic, consisting of an initial wave at 3 msec with a slower component at 8 msec latency. The first part of the response is probably the pre-synaptic response with the later wave possibly a post-synaptic one. The third component was noticed at 5 msec (10 μv). The

complexity of this response is probably due to binaural interaction (Wever, 1949). When clicks were delivered separately to the ears, differences were noted in the responses to the two stimulations.

The lateral side of the nucleus isthmi pars principalis parvocellularis responded to stimulation of either ear with a latency of 6 to 10 msec. Clicks presented to the opposite ear produced a more complex response in the medial part of this nucleus. It had a stable wave at 5.5 to 7 msec latency. Earlier components (1.5 to 3 msec) could be attributed to impulses arriving at the nucleus by way of axons, with the later wave the result of the firing of cells within the nucleus. Simultaneous clicks to the two ears caused an ealier response within the nucleus, suggesting interaction by facilitation.

The nucleus semilunaris responded to contralateral stimulation of the ear with potentials having latent periods of 2 to 4 msec and negative polarities. Ipsilateral stimulation resulted in positive potentials at a latency of 5 to 6 msec, with amplitudes of at least 35 μv above those evoked by contralateral clicks. The opposition in polarity could have been caused by differences in the position of the recording electrodes with respect to this nucleus but it seems more probable that the afferent fibers of the two were in opposite positions. In such a dipole field the polarity of the potential is determined by the stimulation (Biedenbach and Freeman, 1964).

Analysis of Potentials in the Thalamus

The responses of the nucleus ovoidalis were not as complicated as those obtained in the forebrain or as some of the ones found in the nuclei of the mesencephalon. (fig. 14). The response indicates that this nucleus could be a relay station in the thalamus. The response had a long duration (9 to 15 msec), suggesting that the potential recorded was from the cell bodies of the nucleus.

Another response location in the thalamus included an area ventral and lateral to the nucleus ovoidalis and medial and ventral to the nucleus rotundus, which was not responsive to auditory stimuli. This area could contribute to the central acoustic tract that Papez has postulated and will be discussed further in the next section.

The area ventral to the nucleus ovoidalis responded to frequencies as high as 500/sec, suggesting responses from a fiber tract. The test stimulus elicited no response when the interval between the conditioning and test stimulus was 7 msec or less. In and near the nucleus ovoidalis, stimulus frequencies up to 10/sec evoked responses with no change in the amplitude, while frequencies of 100/sec did not elicit a response.

The responsive area of A 5-5.5, V 2-3, L 1.5-3 responded to stimulus frequencies up to 400/sec suggesting

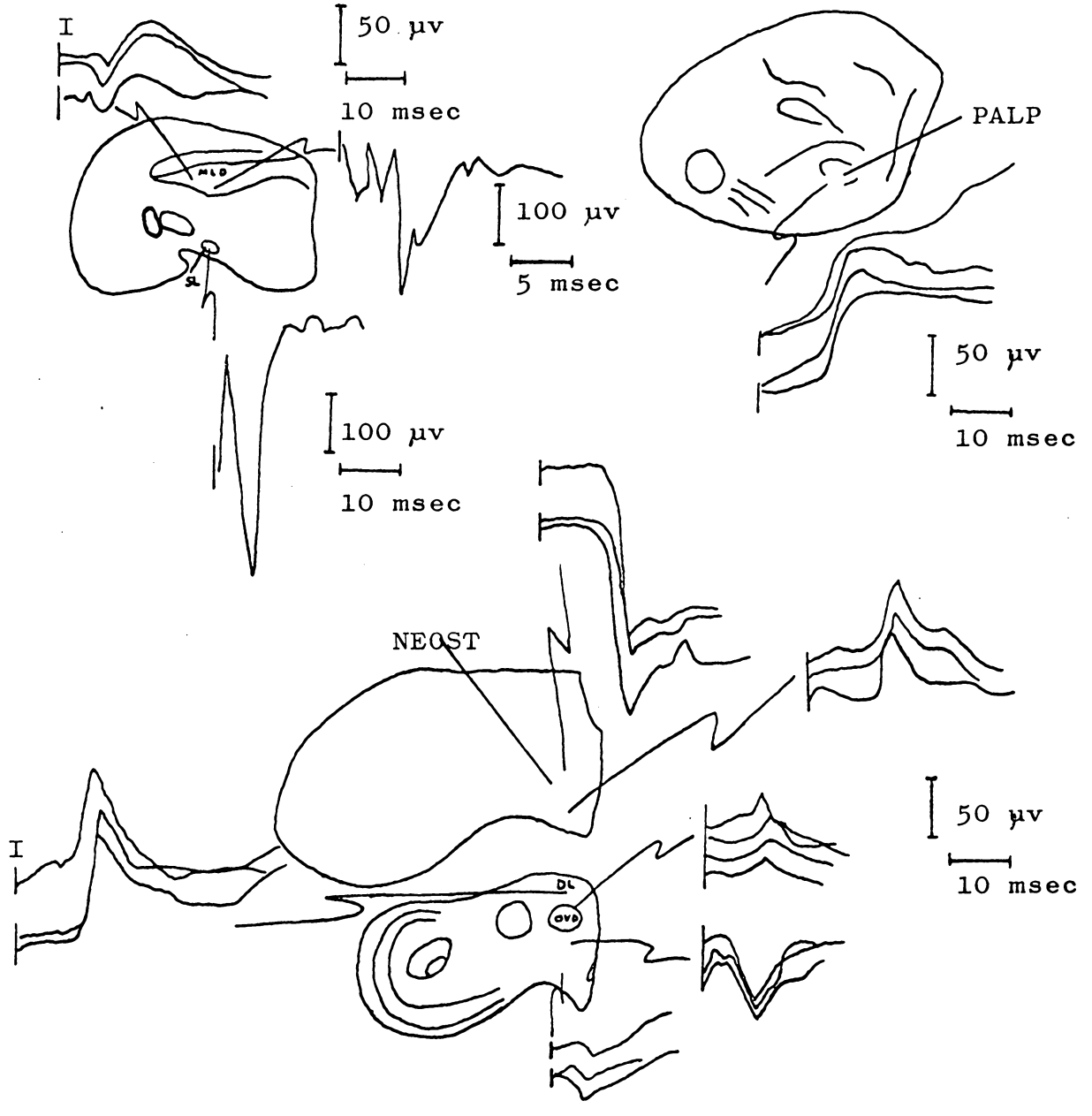


Fig. 14. Configuration of responses found in certain areas of the brain. This shows the differences in the responses found in the mesencephalon, the thalamus, and the forebrain. I-potential evoked by clicks presented to the ipsilateral ear: all other potentials evoked by stimulation of the opposite ear. Calibration given to the right of each response. All responses of the bottom figure are 50 v, 10 msec.

responses from a fiber tract. With an interval of 6 to 7 msec the test stimulus gave a response but at smaller intervals there was no response.

It seems reasonable to believe that both the nucleus dorsolateralis and the nucleus dorsomedialis are intercalated in or closely related to the direct ascending auditory pathway. The responses in these two nuclei were generally more complicated than those found in the nucleus ovoidalis and usually had more than one component. This suggests that these two nuclei function to a greater extent in audition than the nucleus ovoidalis. When clicks were presented contralaterally or ipsilaterally, responses in these two nuclei ranged from 12 to 16 msec. When waves of longer latencies occurred, they were usually inconsistent. The inconsistency, as well as the length of the latency, suggests that these later waves may be the result of efferent impulses or of afferent impulses arriving from an unknown pathway. Speculations are all that can be made at the present time. The latencies of most of the elements in the cerebellum are 10 to 14 msec with exceptional latencies as long as 35 to 40 msec and as short as 2.5 msec (Schwartzkopff, 1963). It is possible that impulses have been delayed by coming through the cerebellum before being processed in the nucleus dorsolateral and dorsomedialis. Ades (1954) has discussed the need to think of multiple neuronal pathways and temporal delay, and inhibitory as well as excitatory activity at synapses when varying latencies occur.

Analysis of Forebrain Responses

The responses of the neostriatal areas and the paleostriatal areas seem to be real responses. They seem not to be the spread of an electric field from either the thalamus or mesencephalon. The evidence for this is that in the striatal areas the responses disappeared much more rapidly than those of the thalamic or mesencephalic areas. This indicates that more synapses are involved in the pathway to the striatal areas than to either the mesencephalon or thalamus, which is expected. Also, differences in responses to the test of intervals between stimuli using twin pulses were noted in the three regions. In the mesencephalon the responses could be seen when intervals were as small as 3.6 msec; in the thalamus the interval at which the effects of the second stimulus could be seen had to be at least 6 to 7 msec. In the striatal areas the interval was 7 to 8 and sometimes 10 msec before the second response could be seen. The shapes of the responses of the striatum were also different from those of the mesencephalon as can be seen in figure 14.

Some of the first waves are of extremely short duration and low amplitude, thus suggesting that these are presynaptic potentials. These responses spreading physically from other parts of the brain seem to be responsible for producing potentials in striatal areas (Gusel'nikov and Supin, 1964). The polarity of these responses could be due

to the position of the electrode relative to the activated regions. These early waves are not always observed.

A stable latency, an amplitude over 50 μv, and duration over 10 msec suggest that the component following the earliest waves is caused by activated cells of the striatum. Both polarities were found in all areas and one polarity was not confined to one area without the other. It seems that in order to determine the significance of the polarity of these responses a more detailed study of the cells in relation to their dendrites will have to be made.

Components of the response from 14 to 36 msec and later are probable due to temporal dispersion of afferent impulses from lower auditory centers. In mammals the presynaptic components of evoked potentials have latencies contingent upon the fiber diameter and the conduction distance of a given system. Temporal dispersion of presynaptic impulses passing along a bundle of fibers of different sizes may make the time of arrival at that point of recording vary over a wide range (Hsiang-Tung Chang, 1959).

Possible Auditory Pathways in Chickens

Basing assumptions on experimental evidence, as well as on a postulation made by Papez (1929) of a central acoustic pathway running from the nucleus mesencephalicus lateralis pars dorsalis to the nucleus ovoidalis, two hypotheses regarding an ascending auditory pathway involving the thalamus have been proposed. A direct mesencephalo-striatal pathway with a secondary projection to the thalamus is one possibility. The other possibility is that the thalamic nuclei responding to clicks form a relay from the midbrain to the forebrain. The sequence of latencies observed successively in the nucleus semilunaris (2 to 4 msec); the nucleus isthmi pars principalis parvocellularis (6 to 10 msec); the thalamic nuclei, ovoidalis (10 to 12 msec), dorsolateralis (12 to 15 msec), and dorsomedialis (13 to 16 msec); and the striatal areas, the neostriatum frontale (5.5 to 12 msec), the paleostriatum (12 to 13 msec), and the neostriatum caudale (12 to 16 msec) show the nuclei most likely involved in these pathways.

Several of these nuclei have been identified anatomically as having auditory functions; the nucleus semilunaris, the nucleus isthmi pars principalis parvo-cellularis and the nucleus mesencephalicus lateralis pars dorsalis have been identified as such. The nucleus ovoidalis has only been proposed as having an auditory function. The responses found in this nucleus make

reasonable its inclusion in this pathway. Uncertainty exists as to whether this nucleus and the dorsolateralis and the dorsomecialis form a relay in the thalamus or whether they are possibly only secondary projections.

If these nuclei form part of a relay system, the long latencies recorded in them indicate that fibers from the mesencephalic nuclei must synapse before reaching these nuclei. The most likely area for this synapse seems to be in the area ventral to the nucleus rotundus where latent periods of 5 to 11 msec were recorded.

Fibers contributed by the nucleus ovoidalis to the thalamofrontal bundle of Papez (1929) or the forebrain bundle of Huber and Crosby (1929) are connected to striatal areas of the forebrain. Huber and Crosby (1929) described in a sparrow a connection between the nuclei dorsolateralis anterior and posterior and the nucleus ovoidalis and the hemisphere wall by the tractus thalamo-frontalis medialis. The pars frontalis of this tract connects with the neostriatum intermediale and frontal, and with the medial portion of the hyperstriatum ventrale. Moreover, the bundle courses through the paleostriatum augmentatum, where it appears to either give or receive fibers.

The pars caudalis is a large bundle which lies in the more caudal portion of the medial part of the hemisphere. Its fibers connect particularly with the neostriatum caudale, including its more posterior portion and to some

extent with the periventricular gray in the region underlying the neostriatum. Fibers join the bundle from the paleostriatum augmentatum and paleostriatum primitivum. The opinion of Huber and Crosby was that these may distribute in part at least with the strio-tegmental system, but the evidence for this was inconclusive. These authors also suggested connection of the dorsolateralis and dorsomedialis and the nucleus ovoidalis with the paleostriatum. The existence of this tract connecting the nuclei ovoidalis, dorsolateralis, and dorsomedialis to striatal areas responding to clicks supports the possibility of a relay between midbrain and forebrain auditory centers.

Fibers of the tractus thalamo-frontalis intermedialis swing from the tectum directly medialward somewhat ventral to the main tecto-thalamic paths and dorsal to the lateral geniculate and among the cells in part of the nucleus tract-thalamici cruciati. They are joined ventromedially by a few delicate fibers from that latter nucleus and then turn dorsalward occupying a position among the cells of the nucleus intercalatus which lies as a broad cell band between the nucleus rotundus and the ventral penduncle of the forebrain bundle. After entrance in the forebrain, it has not been delimited. The direction of conduction is unknown of this tract (Huber and Crosby, 1929). The existence of this tract plus the fact that responses seemed to occur in some of its pathway (waves observed

medial and ventral to the nucleus rotundus) give some indication of a possible direct route from the midbrain to the forebrain.

The shorter latencies recorded in the neostriatum frontale than in the paleostriatum and the neostriatum caudale indicate that the neostriatum frontale might receive acoustical fibers involving fewer synapses than the other striatal areas. The responses of 4.5 to 7 msec recorded in the ventral, caudal part of the thalamus in the region of the quinto-frontal tract and in the region of the supraoptic decussation in the frontal part of the thalamus indicate that these fiber tracts could play a part in the pathway of these impulses to the neostriatum frontale. The quinto-frontal tract is, according to Huber and Crosby, connected with the neostriatum frontale but it has not been recorded as having connections in the mesencephalon. The tractus striotegmentalis et striocerebellaris seems to be a more likely path. It runs through the diencephalon and connects to the decussatio supraoptica dorsalis and ventralis. It joins the quinto-frontalis and their fibers intermingle as they both course with the lateral forebrain bundle up to the paleostriatum with some of its fibers going to the neostriatum. This tract has been named a strio-cerebellar conduction pathway which would indicate, however, that it carries impulses away from striatal areas instead of to these areas.

Powell and Cowan (1961) found in a pigeon by retrograde cell degeneration technique that the nucleus ovoidalis has connections with the paleostriatum augmentatum (medial part of this nuclear region), and by this same technique indicated that the neostriatum does not receive a projection from the thalamus. The experimental results of this paper might offer some support to their findings that the nucleus ovoidalis is connected to the paleostriatum; however, the responses in the nucleus ovoidalis were not as pronounced as those in the paleostriatum primitivum. They also observed that the dorsal group of nuclei which includes the nuclei dorsolateralis and dorsomedialis projects through the septomesencephalic tract to either the accessory hyperstriatum or adjacent entorhinal cortical area. These two nuclei, however, appear to have other forebrain connections which have been discussed to some extent earlier in this presentation.

Comparison of These Results with Those from a Pigeon and Mammals

The presence of responses in the nucleus mesencephalicus lateralis pars dorsalis of chickens differs from the results obtained by Erulkar (1955) in pigeons. He found that this nucleus was unresponsive to cochlear stimulation and thus questioned its connection with the lateral lemniscus. The present physiological evidence that the n. mesencephalicus pars dorsalis in the midbrain receives acoustical impulses is, however, in agreement with anatomical

investigations (such as Wallenberg's and Ariens Kappers'). The latencies found in the mesencephalicus lateralis pars dorsalis of chickens are similar to the 6 to 9 msec latencies Tasaki (1957) reported in the inferior colliculus of mammals. Both the mesencephalicus lateralis pars dorsalis and the inferior colliculus are midbrain nuclei.

The presence of responses in the thalamus also differs from the results of Erulkar (1955), for he found that neither the nucleus ovoidalis nor the rest of the thalamus was activated by clicks. He explained this could have been caused by the deep anesthetization of the pigeons. When strong click stimuli were used with mammals, the latency of the response found in the medial geniculate body (auditory relay station in the thalamus) ranged from 7 to 10 msec as compared to the 10 to 12 msec latencies found in the nucleus ovoidalis of birds. The longer latency found in this thalamic nucleus of birds could be attributed to the synaptic delay of impulses in other, as yet undetected, nuclei located in the thalamus. Some of the nuclei in this region of the brain are small and could have been missed during the exploration.

Although Erulkar (1955) did not mention getting responses in the paleostriatum or neostriatum frontale, he recorded latencies in the neostriatum caudale ranging from 12 to 15 msec. This is approximately the same range of latencies (12 to 16 msec) as recorded in the neostriatum caudale of chickens. For comparison, the

response of the mammalian cortex to strong click stimuli was 8 to 12 msec (Tasaki, 1957). Although the response latencies of the neostriatum caudale are longer than those recorded in the mammalian cortex, the latencies recorded from the neostriatum frontale are the same.

SUMMARY

1. The evoked potential technique has been used to provide functional and anatomical data concerning the afferent auditory system in the chicken brain.
2. Mesencephalon, diencephalon, and telencephalon were explored with bipolar electrodes to determine those areas responsive to click stimuli.
3. Potentials were recorded from the nucleus mesencephalicus lateralis pars dorsalis (2 to 6 msec latency), the nucleus isthmi pars principalis parvocellularis (4 to 6 msec latency), and the nucleus semilunaris (2 to 4 msec latency).
4. Potentials were recorded from thalamic areas, including the nucleus ovoidalis (10 to 12 msec latency), the nuclei dorsolateralis (12 to 15 msec), and dorsomedialis (13 to 16 msec latency), and areas ventral and lateral to the nucleus ovoidalis.
5. Potentials were recorded from the neostriatum frontale (5.5 to 12 msec latency), the paleostriatum (12 to 13 msec latency), and the neostriatum caudale (14 to 16 msec latency) in the forebrain.
6. The data suggest that the nucleus mesencephalicus lateralis pars dorsalis in birds may be equivalent to the inferior colliculus in mammals.
7. The results also suggest that the impulses of the afferent auditory pathway travel through the thalamus

in a relay system in order to reach the forebrain or that a direct pathway may be involved.

8. The results suggest that there may be a direct auditory system from the midbrain nuclei, through the ventral part of the thalamus to the neostriatum frontale in birds.

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APPENDIX

ABBREVIATIONS

(Nomenclature used by van Tienhoven and Juhasz, 1962)

DL, nucleus dorsolateralis

DM, nucleus dorsomedialis

IP, nucleus isthmi pars principalis parvocellularis

MLD, nucleus mesencephalicus lateralis pars dorsalis

NEOST, Neostriatum

NEOSTF, Neostriatum frontale

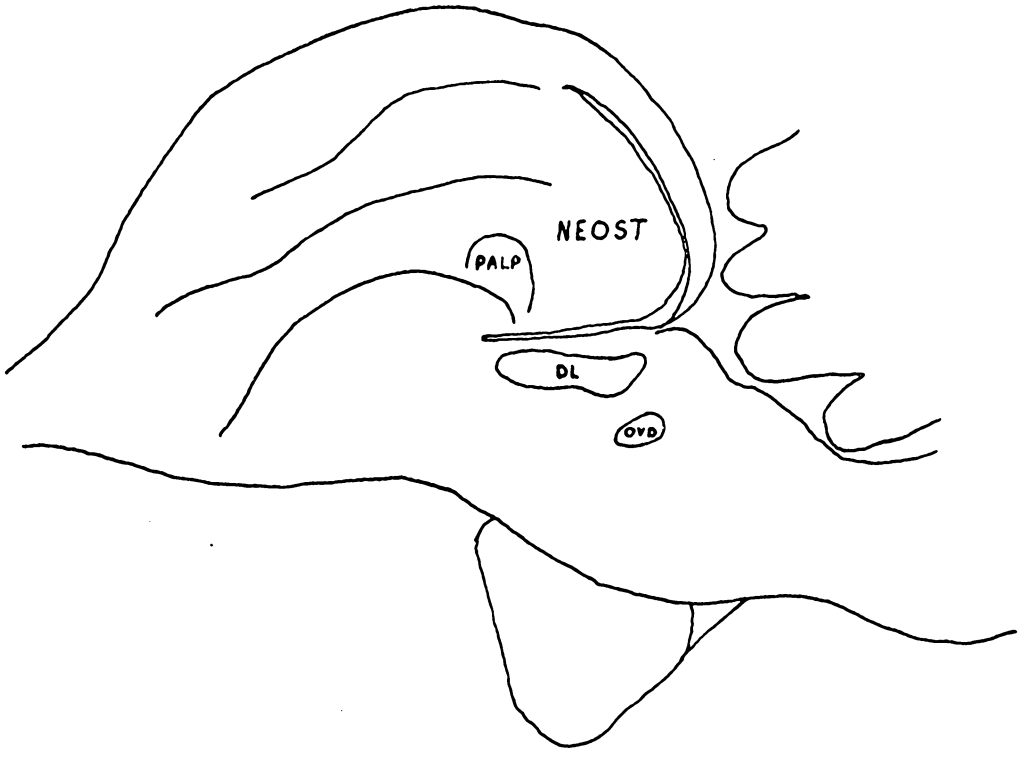
OVD, nucleus ovoidalis

PALP, Paleostriatum pars primativum

ROT, nucleus rotundus

SL, nucleus semilunaris

APPENDIX B



Sagittal section through the thalamus and forebrain showing the relative positions of several activated nuclei.

ABSTRACT

Electrophysiological studies of chickens revealed areas in the mesencephalon, the thalamus, and the forebrain responding to click stimulation. Mesencephalic nuclei responding to clicks were the semilunaris, the isthmi pars principalis parvocellularis, and the mesencephalicus lateralis pars dorsalis with latencies of 2 to 4 msec, 4 to 6 msec, and 2 to 6 msec, respecitvely, regardless of whether the stimulation was to the ipsilateral or contralateral ear. Thalamic nuclei responding with latencies ranging from 10 to 16 msec were the dorsolateralis, dorsomedialis, and ovoidalis. Areas located ventral and lateral to the ovoidalis responded with latencies ranging from 4 to 12 msec. The nucleus rotundus was not responsive to click stimulation. Responding striatal areas were the paleostriatum with latencies of 9 to 16 msec, the neostriatum caudale with potentials ranging in latency from 11 to 32 msec, and the neostriatum frontale with component latencies ranging from 5.5 to 25 msec with the most frequent latencies at 5.5 to 12 msec. These results suggest a probable afferent auditory pathway in birds involving thalamic areas as well as mesencephalic and striatal areas.