INFORMATION TO USERS

This material was produced from a microfilm copy of the original document. While the most advanced technological means to photograph and reproduce this document have been used, the quality is heavily dependent upon the quality of the original submitted.

The following explanation of techniques is provided to help you understand markings or patterns which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting thru an image and duplicating adjacent pages to insure you complete continuity.

2. When an image on the film is obliterated with a large round black mark, it is an indication that the photographer suspected that the copy may have moved during exposure and thus cause a blurred image. You will find a good image of the page in the adjacent frame.

3. When a map, drawing or chart, etc., was part of the material being photographed the photographer followed a definite method in "sectioning" the material. It is customary to begin photoing at the upper left hand corner of a large sheet and to continue photoing from left to right in equal sections with a small overlap. If necessary, sectioning is continued again — beginning below the first row and continuing on until complete.

4. The majority of users indicate that the textual content is of greatest value, however, a somewhat higher quality reproduction could be made from "photographs" if essential to the understanding of the dissertation. Silver prints of "photographs" may be ordered at additional charge by writing the Order Department, giving the catalog number, title, author and specific pages you wish reproduced.

5. PLEASE NOTE: Some pages may have indistinct print. Filmed as received.

Xerox University Microfilms
300 North Zeeb Road
Ann Arbor, Michigan 48106

75-10,153

COTTER, John Robert, III, 1944-
UNIT RESPONSES IN THE OPTIC TECTUM AND TORAL REGION OF GALLUS DOMESTICUS TO VISUAL, AUDITORY, AND SOMESTHETIC STIMULI.

The University of Michigan, Ph.D., 1974
Anatomy

Xerox University Microfilms, Ann Arbor, Michigan 48106

THIS DISSERTATION HAS BEEN MICROFILMED EXACTLY AS RECEIVED.

UNIT RESPONSES IN THE OPTIC TECTUM AND TORAL REGION OF *GALLUS DOMESTICUS* TO VISUAL, AUDITORY, AND SOMESTHETIC STIMULI

by
John Robert Cotter III

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Anatomy)
in The University of Michigan
1974

Doctoral Committee:

Assistant Professor Peter Coyle, Chairman
Professor Charles M. Butter
Assistant Professor Leslie J. Fisher
Professor Charles L. Votaw
Assistant Professor Sarah S. Winans

TABLE OF CONTENTS

LIST OF TABLES..... iv

LIST OF ILLUSTRATIONS..... v

INTRODUCTION..... 1

MATERIALS AND METHODS..... 6

Presurgical Procedures..... 6
Surgical Procedure..... 7
Anesthesia During Recording Sessions..... 9
Stimuli..... 10
Stimulus Protocol..... 11
Histologic Techniques..... 14

RESULTS..... 16

Cytoarchitecture Of The Toral Region..... 16
Physiologic Results..... 19
General Features Of Units Recorded From Avian Tectal Regions..... 19
Units Recorded From The Superficial Laminae Of The Optic Tectum..... 22
Units Recorded From The Deep Laminae Of The Optic Tectum..... 28
Units Recorded From The Toral Region..... 30
Somesthetic Units..... 31
Auditory and Bimodal Auditory-Somesthetic Units..... 35
Localization Of Unit Data In The Toral Region..... 37

DISCUSSION..... 39

Evolution Of The Tectum..... 39
The Optic Tectum..... 40
The Multisensory Hypothesis..... 41
Intrinsic Organization Of The Optic Tectum..... 43

Afferent Fiber Connections..... 45
Correlative Considerations Of
The Optic Tectum..... 48
The Toral Region..... 50
Cytoarchitectonic Organization
Of The Toral Region..... 50
Afferent Fiber Connections..... 53
Correlative Considerations Of The
Toral Region..... 55
The Physiologic Basis For Multisensory
Information Processing In Tectal Regions..... 57
The Deep Layers Of The Optic Tectum..... 57
The Superficial Layers Of The
Optic Tectum..... 59
The Toral Region..... 60
Correlative Considerations..... 62
Comparison Of Avian Physiologic Data
With That Of Mammalian Forms..... 64
The Deep Layers Of The Superior
Colliculus..... 64
The Superficial Layers Of The
Superior Colliculus..... 66
The Inferior Colliculus..... 67
Functional Considerations..... 68
The Deep Layers Of The Optic Tectum..... 69
The Superficial Layers Of The
Optic Tectum..... 73
The Toral Region..... 74
Homologies..... 75
General..... 75
The Deep Layers Of The Optic Tectum..... 76
The Stratum Griseum Periventriculare
Of The Toral Region..... 77
The Nucleus Intercollicularis Of The
Toral Region..... 82

SUMMARY AND CONCLUSIONS..... 85

BIBLIOGRAPHY..... 89

ILLUSTRATIONS.....103

LIST OF TABLES

Page

TABLE 1 Summary of unit data recorded from the optic lobe..... 19

TABLE 2 Percentage of 124 units driven with different sensory modalities..... 20

TABLE 3 Types of movement sensitive units recorded from 40 electrode penetrations of the optic tectum (29 animals)..... 24

TABLE 4 Contralateral visual and nonvisual stimuli activating units in 7 electrode penetrations of the stratum griseum centrale (7 animals)... 29

TABLE 5 Nonvisual units sampled from 25 electrode penetrations of the torus (20 animals)..... 31

TABLE 6 Terminology for nuclei of the toral region.... 51

LIST OF ILLUSTRATIONS

Figure		Page
1.	Visual stimuli utilized in isolating non-spontaneous units	105
2.	Line drawing of avian tectal regions in cross section	107
3.	Sagittal section through the torus semicircularis of the chicken	109
4.	Sagittal section through the torus semicircularis of the chicken at a level medial to that pictured in figure 3	111
5.	Sagittal section through the torus semicircularis of the chicken at a level medial to that pictured in figure 4	113
6.	Sagittal section through the torus semicircularis of the chicken at a level medial to that pictured in figure 5	115
7.	Sagittal section through the torus semicircularis of the chicken at a level medial to that pictured in figure 6	117
8.	Sagittal section through the torus semicircularis of the chicken at a level medial to that pictured in figure 7	119
9.	Sagittal section through the torus semicircularis of the chicken at a level medial to that pictured in figure 8	121
10.	Composite figure of the optic lobe illustrating the locations of 72 electrode tracts	123
11.	Response characteristics of a unidirectional unit recorded from lamina a of the optic tectum	125

Figure Page

12. Pandirectional unit recorded from lamina i of the optic tectum..... 127

13. Multidirectional unit recorded from lamina b of the optic tectum..... 129

14. Excitatory and inhibitory receptive fields..... 131

15. Visual unit recorded from the stratum opticum habituated to prolonged stimulation..... 133

16. Bimodal unit recorded from the stratum griseum centrale of the optic tectum..... 135

17. Light pressure unit recorded from the stratum griseum periventriculare..... 137

18. Feather movement unit recorded from the nucleus intercollicularis..... 137

19. Bimodal unit recorded from the nucleus intercollicularis..... 139

INTRODUCTION

The investigations of Huber and Crosby ('33a, '33b, '34, '43) Ariëns Kappers, Huber, and Crosby ('36), Ariëns Kappers ('47), and Herrick ('48) stress the concept of visual and nonvisual integrative functions by tectal structures. Tectal regions in all vertebrates are located on the dorsal aspect of the midbrain. Nonmammalian tectal structures include the optic tectum and the torus semicircularis or its homologues (Johnston, '06). The optic tectum forms the roof of the midbrain. In the tailed amphibians, forms exhibiting the simplest organization of the optic tectum, there are two distinct layers; the stratum album and stratum griseum (Herrick, '17, '42). In other amphibians, fishes, reptiles, and birds, the optic tectum is composed of more complex laminations consisting of alternating cell layers and plexiform fibers (Ariëns Kappers, Huber and Crosby '36). The most elaborate structural patterns are found in the optic tectum of birds (Huber and Crosby, '33b, '34).

Other midbrain structures caudal or ventral to the optic tectum but located dorsal to the midbrain tegmental gray will be referred to as being in the toral region. The toral region is nonlaminated and contains a number of neuronal masses. Included in the avian toral region are the nucleus mesencephalicus lateralis, pars dorsalis (LMD), often referred to as the homologue of the mammalian inferior colliculus, the nucleus intercollicularis (ICO), and the stratum griseum (SGP) et fibrosum (SFP) periventriculare (Karten, '67; Karten and Hodos, '67).

In nonmammals above the teleosts, a small medial division of the optic tract projects fibers to diencephalic structures while the larger lateral division further subdivides before terminating in tectal structures (Herrick, '41). A vast amount of literature documents optic tract fiber terminations in the optic tectum and the reader is referred to the discussion section for such documentation. Spinotectal, lateral lemniscal, and trigeminal lemniscal fibers were, on the basis of normal fiber studies, considered to terminate in the superficial layers of the reptilian optic tectum (Huber and Crosby, '26, '33a, '33b, '43). Contributions of the spinotectal component appear to be minor (Ariëns Kappers, '47) and distribute only to the

caudal portion of the optic tectum along the outer edge of the stratum griseum centrale (Ariëns Kappers, Huber, and Crosby, '36). Documented support, based upon fiber degeneration studies, for possible somesthetic integrations with visual information in the deep layers of the optic tectum of nonmammals is available (Goldby and Robinson, '62; Karten, '63; Ebbesson, '67, '69; Hayle, '73). Auditory related information was thought to be relayed to the optic tectum by internuclear fiber connections with the toral region (Huber and Crosby, '26, '33a, '33b) and the nucleus isthmi (Huber and Crosby, '33b).

The projection of afferent fiber systems from sensory areas of the spinal cord and the brain stem to the toral region were also identified. The acousticolateral fiber system (Herrick, '17; Ariëns Kappers, Huber, and Crosby, '36) or lateral lemniscus (Huber and Crosby, '26, '33a, '29; Craigie, '28, '30) was considered to transfer vibratory and auditory information and distribute fibers chiefly to caudal and lateral parts of the torus (Herrick, '17; Ariëns Kappers, '47). The trigeminal lemniscus and spinomesencephalic tracts (Edinger, '08; Ariëns Kappers, Huber, and Crosby, '36) were considered to propagate somesthetic impulses. Rostral and medial toral structures

receive fibers of the spinomesencephalic tract (Ariëns Kappers, '47). Recent degeneration studies confirmed fiber contributions of the spinomesencephalic tract and lateral lemniscus to the toral region (Karten, '63; Ebbesson, '67, '69; Brood, '68, '69).

On the basis of such anatomic studies, Huber and Crosby ('33a, '33b, '34, '43), Ariëns Kappers, Huber, and Crosby ('36), Ariëns Kappers ('47), and Herrick ('48) believed visual, somesthetic, auditory, and vibratory information was received and correlated in nonmammalian tectal regions. The optic tectum was thought to process visual, auditory and somesthetic information. Toral structures were thought to process vibratory, tactile, and auditory impulses. Recent electrophysiologic studies in nonmammals support the notion of multisensory information processing by cells of the periventricular gray of the optic tectum of the salamander (Grüsser-Cornehls and Himstadt, '73), the frog (Fite, '69), and the turtle (Robbins, '72), and portions of the torus of the toad (Ewert and Borchers, '71; Ewert, '74).

In this study I have tested the classical concept for sensory representations in chicken tectal regions - the optic tectum and toral structures in order to deter-

mine if multimodal responses to visual, auditory, and/or somesthetic stimuli occur in individual cells or whether sensory representations are segregated according to lamination and nuclear mass patterns. Electrophysiologic studies have heretofore not dealt with the multisensory concept in avian forms. To investigate this hypothesis a recording technique with microelectrodes was selected as previous morphologic studies provided untested inferences. The chicken was selected for this investigation because numerous laminae are found in the optic tectum and nuclei of the torus are well segregated. Such highly developed structural features, not present in other nonmammalian forms, might have functional sensory differences not anatomically separable in more simply organized tectal regions. A functional study of this animal could also provide evidence for clarification of homologies between tectal structures in a comparative series of animals.

MATERIALS AND METHODS

Presurgical Procedures

Sixty-eight adult White Leghorn chickens (Gallus domesticus) weighing 1.0 to 2.5 kilograms were fasted from solids 16 hours prior to surgery. Lights in the animal room were generally scheduled 10 hours off and 14 hours on. Chickens, easily excited birds, were transported from the animal quarters to the laboratory in large covered cardboard boxes. Birds transported in this manner remained quiet thereby reducing the possiblity of cardiovascular and respiratory failure sometimes observed in excited animals following administration of the anesthetic agent.

The animals were initially anesthetized with 2.5 ml/kg Equithesin (Jansen-Salsbury), a solution containing 21.25 g chloral hydrate, 4.86 g pentobarbital, 10.63 g magnesium sulfate, 42.8% propylene glycol, and 11.5% alcohol per 500 ml sterile aqueous solution. Injections were made into the right pectoral muscle and the animals were permitted to stand and walk about within a confined space while the drugs took effect. When the anesthetic

became effective, the animal's head was fixed in a Kopf stereotaxic instrument between hollow 1½ inch long earbars.

Surgical Procedure

To permit entry of the earbars, the openings to the external acoustic meatuses were enlarged by a single incision made in the skin surrounding each of these structures. The beak was cemented to a stable aluminum rod to reduce movement of the head in the horizontal and vertical planes.

The upper eyelids were removed and the stereotaxic frame adapted so as not to obstruct the anterior visual field and portions of the lateral field of either eye. For the same reason, the lower eyelids were intermittently retracted by a piece of surgical silk sutured near the edge of the eyelids. Eye movements were limited in unparalyzed preparations by cementing an immovable ring to the bulbar conjunctiva.

The dorsal surface of the frontal and parietal bones were set parallel to the surface of the operating table. A midsagittal incision was made and skin flaps were retracted. The periosteum was scraped from the skull surface. A small burr hole was made with a dental drill in the bone overlying the tectum. After reflecting the

dura, a microelectrode was advanced through the cerebral hemisphere to the optic tectum. Positioning of the electrode was accomplished in some cases with stereotaxic coordinates established by Van Tienhoven and Juhasz ('63). In 25 animals the bony tentorium found between the hemisphere and the tectum limited the area sampled by the microelectrode to medial and anterior aspects of the tectum. Therefore, in 43 of 68 animals the microelectrode was positioned in the tectum by gross inspection of the tectal surface following a more extensive exposure of the optic tectum. This procedure involved removal of a larger portion of the parietal bone and the tentorium as well as a hemispherectomy. During the surgery, care was taken not to damage the transverse sinus or branches of the posterior cerebral artery which supply the dorsal surface of the tectum. Hemorrhaging of the hemisphere's vessels was controlled with gelfoam and a 0.01% saline solution. No differences in unit activity were noted between the two surgical groups. A 4% agar-gel solution was applied to the tectal surface to prevent surface drying and exposure to room temperature. The trachea was cannulated with an endotracheal tube to facilitate respiration. During the entire experimental procedure the rectal temperature was monitored with a thermistor

probe (Yellow Springs Inst. Co.) and body temperature was maintained between 37° and 41° C with the aid of a water bottle or infrared heating lamp.

Anesthesia During Recording Sessions

Forty-eight of the 68 animals were maintained on either ketamine hydrochloride (6 animals) or ether (42 animals) following surgical procedures. Ketamine was injected into the left pectoral muscle in a dose of 32 mg/kg/2 hr (Bree and Gross, '69). Ether was administered intermittently from a receptacle position so that ether vapors were inhaled by the animal. Following surgical procedures, the remaining 20 animals received flaxedil (gallamine triethiodide) intravenously at a rate of 1 mg/ml/hr through a catheter placed in a superficial wing vein. Paralyzed animals were artificially respirated by undirectional airflow (Burger and Lorenz, '60) and all pressure points and surgical incisions were infiltrated with a 2% lidocaine anesthetic solution. Lidocaine was reinfiltrated at 1½ to 2 hr intervals. Care was taken to avoid any nociceptive procedures in this type preparation.

Stimuli

Visual stimuli consisted of dark lines, irregular geometric patterns, and bars and blocks of varying visual angles moved across a white screen. Some of the patterns were affixed to small magnets. Movement of a pattern was accomplished in some cases by coupling to an additional magnet held behind the screen. In other cases, patterns attached to a hand held wand were moved across the screen. The screen was positioned approximately 450 mm from the eye of the animal and illuminated with diffuse white light. The velocity of object movement was not regulated.

Somesthetic stimuli consisted of touching and pressing the animal's body surface with a small camel hair brush or blunt instruments having tip diameters of 1mm and 1 cm. Individual feather movements were accomplished by touching the vane, rachis or calamus of the feather with a blunt probe. Other somesthetic stimuli consisted of gentle puffs of air or rotation of limbs, mandible or other body structures across a joint.

Binaural and monaural auditory stimuli were presented free field. Auditory stimuli consisted of complex noises produced by hand claps or shaking a set of keys; and pure tones. Tones ranging from 150 to 14 kilohertz were produced with a Hewlett-Packard wave function generator,

audioamplifier and speaker system. The speaker was positioned 5.0 ft directly above the animal's head.

Tones with rise-fall times of 80 msec were presented as bursts of 500 msec duration by means of an electronic switch. Room noise level was 60 dB and stimulus intensities ranged from 60 to 90 dB as measured by a sound intensity meter (General Radio Co.) which was placed in a position comparable to the animal's head.

Stimulus Protocol

A standard regimen was routinely used to test the responsiveness of units to each stimulus type and certain parameters of the stimulus. However, the regimen was made as flexible as possible so as not to exclude novel stimuli or receptive field organization not anticipated in the protocol format.

Spontaneously active units were tested for responses to either somesthetic or auditory stimuli before being tested for responses to visual stimuli. Receptive fields of units responsive to somesthetic stimuli were tested for field size, shape, and somatotopy. The receptive fields of somesthetic units were plotted on an outline body sketch of the animal. Units were tested with binaural and monaural stimuli for responses to complex noises

(hand claps, jangling keys, hissing sounds) and specific pure tone frequencies. Complex noises were also employed to test the responsiveness of the units to different stimulus positions and movements. Spontaneously active units were tested for visual responses in a fashion described below for non-spontaneous units.

Non-spontaneous units were sampled following presentation of visual stimuli. This was done by moving one of three visual stimuli (Fig. 1) in the animal's visual field and simultaneously advancing the micro-electrode until a unit responsive to the stimulus was encountered. One stimulus consisted of a complex series of parallel black lines 0.1^{o} of visual angle on a white background, another was a black silhouette approximately 2.5^{o} x 3.5^{o} of visual angle which had many edges, and the third consisted of a large dark square that occupied at least one quadrant of the animal's visual field. In most experiments in order to expedite the testing procedure, units were immediately tested for nonvisual responses after isolation with such stimuli. In other experiments the receptive fields of units isolated with one of these stimuli were tested with a second group of bars and blocks as small as 0.5^{o} x 3.0^{o} of visual angle for field size, shape, and general visual

field locus. Once the boundaries of the unit's receptive field were determined, a bar smaller than the field was moved in different directions through the unit's receptive field to determine the responsiveness of the unit to movement of the bar in different directions. Units held for sufficiently long periods (approximately three hours) of time were also tested for responses to specific somesthetic and auditory stimuli as described above.

In evaluating the effectiveness of each stimulus type, due caution was exercised to avoid confusing concurrent, uncontrolled, and undetermined stimuli possibly associated with the test stimulus. Therefore, the eyes were closed and nonvisual stimuli were sometimes delivered in the dark to prevent shadows from falling across the eye; the investigator was careful not to touch the animal or create air currents; or the hollow ear bars were sealed off, during appropriate portions of the testing procedure which did not involve stimulation of the retina, body surface, or cochlea.

Records of the type and order of stimulus presentations and manipulations were made by verbal dictation and stored simultaneously with all unit activity on magnetic tape.

Histologic Techniques

Electrode tracts and recording sites within each tract for reported data were marked by small lesions. A lesion was normally made at each point in the track from which a response was obtained. When three or four responses were recorded along a single tract, the deepest and most superficial recording sites were marked. The lesions were produced by passing nearly 1 microampere anodal current through the recording electrode for 15-60 seconds. After sacrifice of the animal with an overdose of Equithesin, transcardiac perfusion was made with a solution containing potassium ferri- and ferro-cyanide, trichloroacetic acid and formalin. The deposited iron from the tip of the microelectrode was selectively stained blue in situ. Following removal of the brain from the skull, the tissue was stored in the perfusion solution for two to three days prior to being processed by routine paraffin histologic methods.

Serial sections of brain tissue were cut at 25-50 micra, mounted, and stained for Nissl substance with basic fuchsin (Szabó, '65). Anatomical sites from which recordings were made were determined from lesions found in each track. Physiologic data accrued from electrode tracts and recording sites not localized in the prepared tissue

were discarded.

The cytoarchitectonic organization of avian tectal regions was studied with Nissl stained chicken (Gallus domesticus) and pigeon (Columbia livia) brain material. Two chickens were anesthetized and perfused intracardially with saline followed by 10% buffered formalin. Brain material was processed by standard paraffin techniques, cut serially in the sagittal or horizontal plane at 30 micra and stained with thionin. Additional avian material was provided by the Laboratory of Comparative Neuroanatomy, Department of Anatomy, The University of Michigan. Chicken material included serial transverse and sagittally sectioned brain tissue stained with toluidine blue. Pigeon material utilized included sagittal (haemotoxylin), transverse (toluidine blue), and horizontal (azure I) serial tissue sections.

Tissue sections were studied with the light microscope to determine the arrangement of nuclear groups in the avian torus semicircularis. Observations were recorded as freehand line drawings. Thionin stained sagittal sections of chicken material representative of the nuclear patterns found in the torus were photographed.

RESULTS

Cytoarchitecture of the Toral Region

The toral region is located beneath the tectal cortex. Dorsally the torus is bound by the optic ventricle; ventrally it is bound by the midbrain tegmentum. Figures 3 - 9 illustrate the lateral to medial organization of the torus. A description of the boundaries and relations of areas in the avian toral region identified by Karten ('67) and Karten and Hodos ('67) was essential. The necessity for the description is twofold: first, to clarify anatomical relationships of the toral region to the avian optic tectum; and second, to provide a basis for localizing physiologic recordings. The relationship of surrounding areas to the toral region depicted in figures 3 - 9 is illustrated in figure 2 and the approximate distribution of sagittal sections illustrated in figures 3 - 9 is given in figure 10. These should be read in conjunction with the following description of the cellular organization of the torus.

The stratum griseum et fibrosum periventriculare of the torus semicircularis is continuous with the similarly

designated stratum of the optic tectum (e.g. fig. 3, 7, 8, 9). In contrast to the sparsely scattered, small, pale staining cells found in these layers of the optic tectum, cells of the periventricular toral region are larger and more darkly stained in thionin preparations.

The toral periventricular gray forms a large nucleus; the appearance changes with the level of section. The nucleus is laminated by fibers. The nuclear lamination is prominent at places where the periventricular gray of the optic tectum turns from the optic tectum to acquire a position in the torus. Rostral to the LMD, fiber laminae segregate small multipolar cells into several subnuclei (e.g. fig. 6) which merge indistinctly with the remainder of the periventricular complex. In the region lateral to the LMD, cells of the toral SGP are tightly packed and form a band many cells thick that separate the ICO and the LMD from the ventricular surface (e.g. fig. 4). The cells forming a sort of cap over the LMD are medium sized and multipolar in shape. The band is gradually diminished in size from lateral to medial as the LMD increases in size (e.g. fig. 5). At levels where the LMD bulges towards the ventricle (e.g. fig. 6), the toral SGP above the LMD is reduced to a

thin layer of cells. Medially (e.g. fig. 7, 8) the toral SGP gradually resumes a position between the periventricular fibers and the ICO. Further medial (e.f. fig. 9) where the toral region merges with the optic tectum, the SGP cells acquire the staining characteristics of periventricular cells in the optic tectum. Some SGP cells appear to merge and cross the tectal commissure as do periventricular cells of the optic tectum.

The nucleus mesencephalicus lateralis, pars dorsalis (LMD) is embedded ventrally in cells of the intercollicular nucleus (e.g. fig. 4 - 8). The LMD is distinguished from other nuclei of the torus by its oval appearance in saggittal sections and high concentration of large darkly staining neurons dispersed within its borders.

The nucleus intercollicularis (ICO) consists of densely packed round cells which extend the length and breadth of the torus (e.g. fig. 3 - 9). Occasionally patches of large and medium sized cells are also identified. At levels at which the LMD is large, the ICO, while remaining confluent on the ventral surface of the LMD, lies rostral and caudal to the LMD (e.g. fig. 6). Medially, the rostral portions of the ICO are replaced by the periventricular gray; caudal cells of the ICO

can be followed to the central gray below the aqueduct (e.g. fig. 7 - 9). Although there is no obvious boundary between the nucleus intercollicularis and the nucleus mesencephalicus lateralis, pars dorsalis, the small poorly staining character and size of cells in the nucleus serve to differentiate the ICO from the LMD. At levels where the ICO is juxtaposed to the toral SGP, contrasting cell type and fiber laminae delineate one from the other (e.g. fig. 3, 9).

Physiologic Results

General Features of Units Recorded from Avian Tectal Regions

A total number of 375 electrode penetrations was made in 68 animals (refer to Table 1).

TABLE 1.--Summary of unit data recorded from the optic lobe

Animals	Electrode Penetrations	Units	Percentage Units Driven
68	375	273	45.4

Of 273 units, 45.4% were driven with at least one modality tested. The percentage of unimodal and bimodal units encountered is given in Table 2.

TABLE 2.--Percentage of 124 units driven with different sensory modalities

Visual	Auditory	Somesthetic	Bimodal
63.7	3.2	19.4	13.7

Eighty five units were located in the tectal cortex, 39 in the toral region (refer to tables 3 - 5). Figure 10 shows the locations of 72 electrode tracks from which these data were obtained.

Spontaneous and non-spontaneous firing units were encountered. Units sampled in the toral region and occasionally those of the stratum opticum and deep layers of the optic tectum exhibited spontaneous discharges in nonburst modes. In contrast, units recorded from intermediate strata of the optic tectum did not spontaneously fire and so could not be isolated without the aid of moving visual stimuli. Such units returned to quiescence following stimulation periods. Spontaneous cells were found in animals receiving ether, and ketamine anesthesia. Clearly, more spontaneous firings were encountered in the gallamine preparations.

The level of spontaneous discharge was always low enough to enable an analysis of the unit's responsiveness to each stimulus employed. By listening and observing

transient changes in spike train patterns during experimental procedures, the frequency of discharge before, during, and following stimulus presentations could be compared. By these means a simple but appropriate analysis of the data could be undertaken. Spike trains were documented on photographic papers.

The form of unit action potentials, while nearly consistent in amplitude, shape, and polarity for a given unit varied among the units studied. Spike amplitude, shape, direction, and polarity of wave form were noted to differ in various trains. Negative monophasic potentials and triphasic waveforms, first positive, then negative, then positive were less than 0.5 milliseconds in duration and 100 microvolts to 1 millivolt peak to peak in amplitude. Biphasic positive - negative or negative - positive potentials were approximately 1 millisecond in duration and 500 microvolts to 3 millivolts in amplitude.

Monophasic and triphasic action potentials were considered to represent activity recorded from axons. Biphasic potentials were probably recorded from cell bodies in accordance with criteria established by Freygang ('58), Bishop, Burke, and Davis ('62), Holden ('68), and Cooper, Robinson and Waldron ('69).

Units Recorded from the Superficial Laminae of the Optic Tectum

Units recorded from the superficial laminae of the optic tectum responded to moving visual stimuli. In view of the non-spontaneous nature of these units, this feature provided an excellent means of isolating units before tests for auditory or somesthetic responses were begun. Areas of the visual field from which stimuli were effective in eliciting increased discharge rates were identified as the unit's excitatory receptive field. Field sizes ranged from 1/2 degree to 12 degrees of visual angle, the smaller being recorded from the stratum opticum, the larger from the deepest laminae of the superficial gray and white layers. Objects shifted into the excitatory receptive field and permitted to remain stationary did not usually elicit responses after coming to rest in the field unless moved again. Units with these characteristics were referred to as being movement sensitive.

Characteristically most movement sensitive units responded in a biphasic fashion to object movement. The response was triggered by movement of the object's leading or trailing edge as each moved across the field. Figure 11 illustrates the characteristic on-off receptive field property apparently common to many movement sensitive

cells in the avian tectum. In 11A, as the bar's leading edge was moved continually across the cell's receptive field, the cell briskly fired. This corresponds to an off response because the unit fired when the bar interrupted illumination of the unit's receptive field. In 11B, the bar completely covered the cell's receptive field, no edge was present, and the activity previously initiated was not sustained. In 11C, as the trailing edge of the bar was moved across the cell's receptive field, the cell fired again. This corresponds to an on response because the unit fired when the receptive field was reilluminated. Objects smaller than the excitatory field gave monophasic responses when both edges were present in the field simultaneously.

The edge of an object always elicited good responses and the frequency of discharge seemed dependent upon object velocity and edge size. No attempt was made to quantitate this relationship.

Movement sensitive units discharge differentially to bar movements in different directions through the cell's receptive field. On the basis of their responsiveness to the directionality of the moving stimulus, three movement sensitive types were detected: (a) pan-

directional units - those that responded to movements of a bar in all directions through the receptive field of the cell; (b) unidirectional units - those that responded best to movements made in only one direction; and (c) multidirectional units - those that respond to movements made in more than one but less than all directions through the units' receptive field.

Table 3 summarizes the data obtained from 32 units in the stratum opticum and stratum griseum et fibrosum superficiale of the optic tectum which were studied for movement sensitivity.

TABLE 3.--Types of movement sensitive units recorded from 40 electrode penetrations of the optic tectum (29 animals).

	Locale and Number of Units	
	Stratum Opticum	Stratum Griseum et Fibrosum Superficiale
1. Type determined		
a. pandirectional	5	17
b. unidirectional	2	2
c. multidirectional	0	6
	7	25
2. Type undetermined	10	36

Pandirectional units predominate, especially in the SGFS. An additional 46 units responded to movement in at least one direction but were not studied in detail either because the unit was not held for a long enough duration or because tests for responses to other stimulus modalities received priority. Electrode tracks from which data presented in table 3 was obtained is illustrated in figure 10.

Pandirectional units appeared to have uniform excitatory fields: responses could be obtained by moving an object in any direction through the receptive field. Figure 12 is an example of such a unit responsive to horizontal and vertical bar movements. As was typical of this unit class, movements of the bar in rostral, ventral, dorsal or caudal directions with respect to the animal were effective in eliciting discharges. Though not illustrated, movements of the bar in oblique directions were equally effective in eliciting discharges from the pandirectional units. Unidirectional and multidirectional units were less often encountered. Figure 11 is an example of a unidirectional unit which fired to bar movement in a dorsal direction. Of 4 unidirectional units, 2 discharged to dorsal movements,

2 discharged to ventral movements. Multidirectional units fired over a range of bar movements intermediate to those effective for driving unidirectional or pan-directional units. Four of 6 multidirectional units discharged to movements in rostral directions. Figure 13 is an example of a multidirectional unit. In this case, the cell fired to a wide range of movements directed rostrally. A response was obtained when the bar in the vertical position was moved along the horizontal meridian. Movements in the caudal, dorsal, or ventral directions elicited no discharges or, in general, yielded fewer discharges.

The receptive fields of most units encountered appeared to consist of excitatory areas. Probing the receptive fields of some units however, revealed the existence of adjacent areas within which stimulation diminished or extinguished responses from the excitatory area. Suppressive or inhibitory areas appeared to flank excitatory areas. A bar, for example, moved from above or below into the excitatory field (figure 14A) caused the unit to discharge. In contrast, a bar moved such that the bar overlapped both excitatory and inhibitory areas (figure 14B) did not elicit a spike train.

Providing the overlap occurred, the direction of movement could vary and still yield the same response. On the other hand, when the entire length of a long edge of a bar extended across the excitatory field (figure 14C), very strong responses were obtained.

Most units fired to repeated stimulation of their excitatory receptive field. Others fired briskly only to the first or second stimulus movements. Upon further stimulation, the response frequency decreased to zero. The difference in discharge frequency was considered to represent habituation. The manifestation of this phenomena was not always immediately obvious. At times, one had the impression the unit was lost. The responsiveness usually returned after 30-60 seconds whereupon units could be driven only to rapidly habituate again. Figure 15 is an example of a unit habituated to prolonged stimulation of its excitatory receptive field. In 15A, the unit's response was habituated by continually moving the bar back and forth through its receptive field. In one case the habituation was immediately erased by turning the room lights off and on. Then, movements of the bar through the receptive field once again gave responses. (Figure 15B).

The recognition of such receptive field features as movement sensitivity and habituation, were used to secure the isolation of non-spontaneous tectal units before somesthetic and auditory tests were performed. Of 78 units, 64 were tested; however no visual unit in the superficial laminae was found to be responsive to the nonvisual stimulus employed. Repeated attempts to drive such units with routine and novel stimuli invariably resulted in no detected change in unit activity.

Units Recorded from the Deep Laminae of the Optic Tectum

Seven units were recorded from the stratum griseum centrale of the optic tectum (refer to table 4). Five units responded intermittently to objects moved through almost an entire visual field quadrant. Movement of the edge of objects illustrated in Figures 1B and 1C drove the units. Long or short edges evoked a response. The units located in the dorsocaudal optic tectum were always driven from the superior and posterior visual field. The receptive field of one unit had a well-defined activating region 15 degrees by 30 degrees of visual angle and less sensitive patchy surrounding excitatory areas. Such wide field units fired to objects moved in any direction through

the field. However, rapid oscillating stimulation at any one spot within the field caused habituation. Dishabituation was effected by moving the stimulus to a new spot in the field or withdrawing the stimulus from the field for 30-60 seconds before reentry. Table 4 summarizes nonvisual and visual stimulus types effective for driving units found in the stratum.

TABLE 4.--Contralateral visual and nonvisual stimuli activating units in 7 electrode penetrations of the stratum griseum centrale (7 animals).

Unit	Visual	Auditory	Somesthetic
1.	edge movement	hand claps	----
2.	----	----	feather movement
3.	----	hand claps	feather movement
4.	edge movement	----	feather movement
5.	edge movement	----	feather movement
6.	edge movement	----	feather movement
7.	edge movement	----	----

Some units were driven by movement of the animal's feathers. Four units discharged to movement of the feathers on the following regions contralateral to the recording electrode: the caudal head, neck, wing, leg,

and body wall. A fifth unit responded only to movement of the feathers on the back of the head contralateral to the recording electrode. Two units responded in a fast adapting manner to hand claps, presented from areas behind the animal and contralateral to the recording site. Only a few spikes were elicited by each stimulus.

Of the seven units recorded from the stratum griseum centrale, five units responded to more than one modality: one responded in a bimodal fashion to visual-auditory stimuli; three to visual-somesthetic stimuli; and one to auditory-somesthetic stimuli. Figure 10 shows the position of 7 electrode tracks from which these data were obtained.

Figure 16 is an example of a unit responsive to somesthetic and visual stimuli. In 16A, the unit responded with a burst of spikes nearly every time feathers of the neck were moved. Similar responses were elicited by lightly touching other feathered body surfaces. In 16B, the same unit responded when tested with visual stimuli. Stimulation of a small area in a wide visual field elicited responses by movement of the bar in rostral, caudal, dorsal or ventral directions.

Units Recorded from the Toral Region

Thirty-nine units recorded from the torus semicircu-

laris were responsive to nonvisual stimuli. Table 5 summarizes the locale and number of units responsive to somesthetic, auditory, and auditory-somesthetic stimuli. Electrode tracks from which these units were recorded are illustrated in figure 10. No toral units sampled responded to visual stimuli.

TABLE 5.--Nonvisual units sampled from 25 electrode penetrations of the torus (20 animals).

	Somesthetic	Auditory	Auditory-Somesthetic
Stratum griseum periventriculare of the torus semicircularis	18	0	6
Nucleus intercollicularis	5	1	6
Nucleus mesencephalicus lateralis, pars dorsalis	0	3	0

Somesthetic Units

Rather than attempt to classify units according to various body sensations i.e. pain, or according to stimuli which might be interpreted as giving rise to these sensations, i.e. nociceptive, units were referred to as somesthetic units and described according to the kinds of physical stimuli capable of driving them, as a matter of convenience.

Deep pressure stimuli were accomplished in anesthetized animals by forceful indentation of the skin surface with a blunt probe. Such stimuli applied to superficial cutaneous areas were transmitted to underlying deep tissues. Five units responsive to such stimulations were fast adapting and fired only upon applications of the stimulus. Four units had receptive fields in the lower limb region particularly in areas of heavily keratinized skin. Some receptive fields included the entire lower extremity. One unit responded to deep pressure in the tail region.

Pressure units also responded to stimuli applied to joint capsules or during extreme flexion or extension of limbs across joints found in the same receptive field. One unit responded to pressure stimulations of the metatarsophalangeal joint capsule alone.

Although one unit responded when the mandible was maximally depressed, three units responded during gentle downward movements of the mandible or to pressure applied to muscle masses of the face ipsilateral to the recording site. Three other mandibular units responded to pressure stimuli moved along the superior border of the mandible.

The discharge of 9 units was altered with light pressure stimuli. Such stimuli were produced by lightly

touching cutaneous areas with a blunt probe. Units had receptive fields in the head region and were either fast or slow adapting to the stimuli. Figure 17 is an example of such a unit inhibited by light pressure stimuli applied to a somesthetic field on the face.

The most extraordinary somesthetic units (twelve units) fired during rapid feather movements. Exquisitely sensitive slow adapting units discharged for the duration of the stimulus obtained by gentle puffs of air that produced rapid vibrating movement of the feathers. The units adapted rapidly to movement of the feathers by a probe. Light pressure stimuli applied to the skin were also effective in driving feather movement units though it was not clear if these units responded to pressure on the skin or concomitant feather movement.

The receptive fields of feather movement units and light pressure units were small, moderate or large. Moderate and large fields appeared to include pterylae and apteria. Small receptive fields (10 units) ranged in size from about one square centimeter to fields that included one side of the neck. The small fields were always localized to a portion of the posterior head or neck region.

Figure 18 is an example of a unit's firings to feather

movements on the side of the neck. A stimulus probe was moved from the lower to upper regions of the neck. Feather movement was accomplished by touching the vane and rachis of the feather. Movement of the stimulus through the receptive field in the lower neck inhibited the unit; as the stimulus moved out of the inhibitory area, the spontaneous firing rate of the unit was reestablished. As the stimulus entered the upper region of the neck, the discharge rate was greatly increased. Of all the somesthetic units studied, this was the only case of a somesthetic unit with excitatory and inhibitory receptive fields.

Fields including two body regions, as for example, a wing and the ventral body surface, were referred to as moderate size fields (8 units). Some fields confined to one side of the body surface were contralateral to the recording electrode; others had bilateral representation. Usually the representation of body regions on the side contralateral to the recording site was greater than that of the ipsilateral side whenever fields included both sides of the body surface. Fields appeared to be continuous, though responses from various parts of the entire field differed with respect to probability of response or

number of spikes elicited.

Large fields (3 units) comprised nearly the whole body surface. Units with large fields responded in a similar fashion to stimuli applied to various parts of the field. Although considered to be total body units, definitive and repeatable responses were not always obtained after stimulation of the face or leg regions. Receptive fields always included the feathered areas of the animal's body. A few moderate and large sized field units had spots in the field from which more vigorous responses were obtained.

Moderate and large sized fields were not identified in ketamine and ether preparations. Deep pressure units were never sought in gallamine preparations.

Auditory and Bimodal Auditory-Somesthetic Units

Somesthetic and auditory, but not visual, stimuli drove twelve toral units. The somesthetic receptive field properties of bimodal auditory-somesthetic units did not differ from those of somesthetic units described above. Discharge patterns of four units tested for auditory, visual, and somesthetic responses were only altered by auditory stimuli as described below.

Responses to auditory stimuli were obtained following complex sounds or pure tones. The discharge pattern

elicited by hand claps, keys, and hissing noises was affected by the side of stimulus presentation. Usually, but not always, bilateral or ipsilateral presentations inhibited unit activity while stimuli presented contralateral to the recording electrode increased the rate of unit firing.

Similar localization effects were obtained with pure tone stimuli. Furthermore, not only did the side of presentation affect the kind of unit response but the frequency and intensity of each pure tone was observed to affect the magnitude and type of response (fig. 19).

Figure 19 is an example of a unit that discharged to somesthetic and to auditory stimuli. The first trace illustrates a somesthetic response; the latter three, the response of the unit to pure tones. The somesthetic response was elicited following movement of a small group of feathers on the head of the animal. Figure 19A illustrates the response of the unit to gentle puffs of air. In B, C, and D the unit was subjected bilaterally to a series of pure tones. In B and D pure tones of 300 and 400 Hz inhibited spontaneous activity for the duration of the stimulus. Spontaneous activity returned however, as soon as the stimuli were turned off. In contrast, a

frequency of 350 Hz excited this unit.

Localization of Unit Data in the Toral Region

The locations of units recorded from the torus semicircularis were examined to determine whether units were segregated in toral nuclei according to sensory modality or in the case of somesthetic units according to a somatotopic pattern.

Table 5 summarizes the regional distribution of units responsive to different sensory modalities. Of four units responsive to auditory stimuli alone, three were recorded from the LMD. Somesthetic units were recorded from both the SGP of the torus semicircularis and the nucleus intercollicularis.

Seventy-five percent or eighteen of twenty-three somesthetic units occupied sites in the periventricular gray. Bimodal auditory-somesthetic units were also found in the periventricular gray but represented a smaller population. On the other hand, auditory and bimodal units comprised slightly more than 50 percent or seven of twelve units recorded from the intercollicular nucleus.

The distribution of somesthetic and bimodal units recorded from the periventricular layer was studied with respect to small, moderate and large somesthetic field

types. Small field units (9 units) were found in the medial parts of the periventricular gray. Firings were driven from receptive fields localized principally from the head and neck. Nearly all sites were contralateral to the recording electrode. An apparent area representing caudal body parts was located lateral to the area representing the head. In contrast, most units recorded from lateral areas (14 units) responded from fields that included large areas of the body. No discernable somatotopic pattern was found for units recorded from the ICO.

DISCUSSION

Evolution of the Tectum

Tectal structures are thought to evolve from a midbrain similar in composition to the midbrain of the tailed amphibians (Johnston, '06). The midbrain of these forms is reticular-like in organization (Herrick, '17, '42) and cells of the tectal region were considered to be multisensory and to correlate information from different sensory systems. Johnston ('06) and Herrick ('26) considered that this reticular area was progressively segregated into two distinct nuclear zones, each with its own unique afferent fiber connections. According to this scheme, a lateral zone in nonmammals evolved to form the torus semicircularis; cells in the lateral zone came to occupy a position below the ventricle. The primary afferent connections of this region were with the acousticolateral area of the brain stem. A medial zone, on the other hand, became the optic tectum and the primary afferent fibers to cells in this region were from the optic tract. In mammalian forms, the medial zone evolved into the

superior colliculus; the lateral zone became the inferior colliculus which in contrast to the nonmammals remained near the surface of the brain stem. The main afferent to the superior colliculus continued to be the optic tract while the lateral lemniscus became the primary afferent input to the inferior colliculus.

The Optic Tectum

Cytoarchitectonic Organization of the Optic Tectum

The optic tectum of the tailed amphibians is composed of an external plexiform layer and an internal layer of cells. In fishes, reptiles and birds, the cytoarchitectonic patterns of the optic tectum are more complex. In avian forms 3-15 layers were identified (Bellonci, 1883; Ramón y Cajal, 1891, '11; van Gehuchten, 1892; von Köliker, 1896; Ramón, 1898; Ris, 1899).

As an attempt to find a common basis for comparing the various laminar patterns found in the optic tectum of different vertebrate forms, Huber and Crosby ('33a, '33b, '34, '43) divided the optic tectum of mammals and nonmammals into six homologous strata. Each strata was named according to its appearance and fiber connections. Although the appearance of the strata did change according to the vertebrate class studied,

the basic functional relationships of each strata were considered to remain constant (Huber and Crosby, '33b, '34). Beginning at the tectal surface and proceeding toward the optic ventricle, the strata in order of appearance include: the stratum opticum (SO), the stratum griseum et fibrosum superficiale (SGFS), the stratum griseum centrale (SGC), the stratum album centrale (SAC), the stratum griseum periventriculare (SGP), and the stratum fibrosum periventriculare (SFP).

Of the 14 alternating neuron and plexiform laminae identified in the optic tectum of birds by Ramón y Cajal (1891, '11) and Ramón (1898), Huber and Crosby ('33b) grouped ten laminae in the SGFS. Cowan, Adamson, and Powell ('61) assigned alphabetic characters a - j to these unnamed laminae. The remaining 4 laminae correspond to the SO, SGC, SAC, and periventricular layers. A primitive stratum zonale overlays the stratum opticum in some nonmammalian forms. The development of the stratum zonale in mammalian forms is correlated with the development of the neocortex.

The Multisensory Hypothesis

Although the number of cells contained within any one stratum of the optic tectum varies among the

vertebrate classes, each stratum described by Huber and Crosby was thought to comprise a specialized functional-morphological unit (Huber and Crosby, '33a, '33b, '34, '43). The SGFS formed the main receptive area. Within the confines of the SGFS, dendrites and cell bodies of this stratum and deeper strata were conceived to be in synaptic contact mainly with visual and somesthetic but also auditory information. Visual information was derived directly from the retina and conveyed to the superficial layers by the optic tract via the overlying SO. In forms having a cortex, visual information from the cortex entered via the internal corticotectal tracts (Huber and Crosby, '43). Somesthetic information was considered to be relayed to the tectum from the spinal cord over the spinobulbo-tectal tract and from the medulla by way of trigeminotectal tracts. Auditory information was received from the lateral lemniscus indirectly through internuclear connections of the optic tectum and other midbrain nuclei. Other types of information more complex in nature were transferred from the dorsal thalamus, pretectal and subtectal areas via the thalamotectal and associated tracts. The SGC constituted the major efferent zone of the optic tectum. From the SGC, visual, auditory, and somesthetic information

integrated in the superficial laminae discharged through the SAC and ultimately, by way of tectospinal and tectothalamic tracts, distributed to more caudal and rostral regions, respectively, for further processing. The deepest layers of the optic tectum, the periventricular layers, were considered to be receptive as well as efferent in character. The SGP received fibers from preoptic, hypothalamic, midline tegmental gray and acoustic areas and discharged to other areas of the periventricular gray. Tectal efferent and afferent fibers were located in the SFP.

Intrinsic Organization of the Optic Tectum

Cragg, Evans, and Hamlyn ('54) and Stone and Freeman ('71) divided the avian optic tectum into superficial, intermediate, and deep plexiform layers. Cell dendritic orientations in these layers may be correlated with increasing visual receptive field sizes encountered in the chicken optic tectum with increasing recording depth. Hamdi and Whitteridge ('54), Revzin ('70), and Jassik-Gerschenfeld ('71, '72) observed similar changes in receptive field size in their studies of the pigeon.

In general, dendrites of optic tectal cells are oriented in either a horizontal or radial direction

(Cragg, Evans, and Hamlyn, '54; Lavail and Cowan, '71; O'Flaherty, '71; Stone and Freeman, '71). In the superficial layers, horizontal dendrites are found in lamina a (Stone and Freeman, '71) and laminae a to d of the SGFS (Lavail and Cowan, '71). These dendrites spread circumferentially within the tectal laminae and receive some terminations of fibers from different retinal loci. Internuclear connections with other tectal cells may involve excitatory or inhibitory processes. The majority of dendrites of the superficial laminae cells are elongated in the vertical plane (Cragg, Evans, and Hamlyn, '54; Lavail and Cowan, '71; Stone and Freeman, '71). Cells with such dendritic orientations are probably activated by direct retinal terminations and indirectly by synapses with horizontal cell dendrites. Such synaptic configuration may regulate the area of the retina effective in driving units in the superficial laminae.

Large multipolar cells are found in the SGC (Lavail and Cowan, '71). The dendrites of these deep lamina cells either arborize in the SGC (Stone and Freeman, '71) or reach into the superficial tectal layers (Lavail and Cowan, '71; O'Flaherty, '71). The horizontal spread of the dendrites of these cells is huge. Lavail and Cowan

('71) and O'Flaherty ('71) traced dendrites as far as one and one and a half millimeters from the cell body. The large dendritic tree receives intratectal connections of neurons found in the more superficial laminae of the tectum (Lavail and Cowan, '71; Stone and Freeman, '71). The dendritic spread of these cells may be correlated with the fact that units of the SGC are driven by stimuli in any part of one visual field quadrant.

Afferent Fiber Connections

The optic tectum receives a substantial number of fibers from the lateral division of the optic tract. Ariëns Kappers, Huber, and Crosby ('36) reviewed the contributions of early workers. Recent experimental investigations studied projections of retinotectal fibers to the tectum of various nonmammalian forms. In all vertebrates studied including the shark (Ebbesson and Ramsey, '68; Graeber and Ebbesson, '72), the bony fish (Campbell and Ebbesson, '69; Ebbesson, '68; Vanegas and Ebbesson, '73), the salamander (Jakway and Riss, '72), the frog (Scalia, Knapp, Halpern and Riss, '68; Lázár and Szekely, '69), the alligator (Riss, Knapp, Scalia, '63), the crocodile (Burns and Goodman, '67), the turtle (Kosareva, '67; Knapp and Kang, '68a, '68b), the snake

(Armstrong, '50, '51) and the lizard (Bulter and Northcutt, '71), retinotectal fibers project to the contralateral optic tectum. Burns and Goodman ('63) and Kosareva ('67) also demonstrated an ipsilateral projection in the crocodile and the turtle. In the pigeon, the projection of retinotectal fibers to the optic tectum is completely crossed (Cowan, Adamson, and Powell, '61; McGill, '64; McGill, Powell and Cowan, '66; Repérant, '73).

Edinger ('08) refered to a system of fibers that extend from the spinal cord to the midbrain as the spinomesencephalic tract. The components of the system reaching the optic tectum were referred to as the spinal lemniscus (Herrick, '17, '30, '42), the spinal tectal or spinal mesencephalic tract (Ariëns Kappers, Huber and Crosby, '36) and the spinobulbar mesencephalic tract (Ariëns Kappers, '47). Huber and Crosby ('33b, '34) considered somesthetic impulses to reach the superficial layers of the optic tectum of fishes, amphibians, and birds via the spinobulbotectal or spinotectal paths.

Herrick ('17, '30, '42) followed the spinal lemniscus in Necturus and Ambystoma through the rostral-caudal extent of the optic tectum. In 1926 and 1933, Huber and Crosby ('26, '33a) reported that spinal tectal fibers in the alligator, turtle, and lizard could be followed into the

outer part of the stratum griseum centrale. Some evidence of terminations within the SFGS was obtained in these studies. Following lesions of the spinal cord, other workers observed degenerating fibers in deep layers of the optic tectum of the dogfish (Hayle, '73), lizard, snake and turtle (Goldby and Robinson, '62; Ebbesson, '67, '69), and the pigeon (Karten, '63). In the frog (Szekely, '73; Hayle, '73; Ebbesson, '69) and the carp (Hayle, '73), degenerating fibers were traced from the spinal cord to the mesencephalic reticular formation. Tegmentotectal degeneration was identified following destruction of the mesencephalic tegmental gray substance (Szekely, '73; Szekely, Sétálo, Lázár, '73) of the frog.

According to Huber and Crosby ('33b, '43), trigeminotectal fibers entered the optic tectum. Woodburne ('36) believed certain secondary connections of the sensory trigeminal nucleus were present in all nonmammalian forms. He considered fibers of this system to reach the midbrain region, largely the optic tectum.

The optic tectum also has internuclear fiber connections with the toral region (Huber and Crosby, '26, '33a, '33b) and the nucleus isthmi. According to these workers, auditory impulses were carried from the torus to the stratum griseum periventriculare through fibers of the stratum

fibrosum periventriculare (Huber and Crosby, '26, '33a, '33b). Similar impulses from nucleus isthmi were considered to enter the stratum album centrale and stratum griseum centrale (Huber and Crosby, '33b).

Correlative Considerations of the Optic Tectum

Huber and Crosby ('34) correlated the progressive development of different cellular arrangements within the ascending phylogenetic series of vertebrates with the relative development of nonvisual fibers terminating in the periventricular and superficial receptive zones of the optic tectum. Recent anatomic studies (Goldby and Robinson, '62; Karten, '63; Ebbesson, '67, '69; Hayle, '73) indicate that the projection of the spinal tectal tract is more limited in its termination within the optic tectum than was previously observed by Huber and Crosby. The significance of the highly ordered organization of cells in the optic tectum, particularly the superficial layers of birds and reptiles, remains to be fully elucidated.

Electrophysiologic and anatomic studies in the optic tectum of the frog indicate a segregation of terminals from various functionally defined retinal ganglion cell types. Lettvin, Maturana, McCulloch, and Pitts,

('59) and Maturana and coworkers ('60) recorded five operational types of fibers from four different levels of the anuran optic tectum. Anatomic investigations of the optic tract projection to the optic tectum (Scalia, Knapp, Halpern, and Riss, '68; Lázár and Szekely, '69) demonstrated the organization of four separate sheets of retinofugal fibers in the optic tectum of the frog. Similar anatomic results were reported for the teleost (Campbell and Ebbesson, '69) and the turtle (Karareva, '67). A spatial correspondence therefore exists in the optic tectum of the frog between stratified optic fibers and different retinal ganglion units identified electrophysiologically.

In the bird, a creature with an elaborate visual apparatus, the lamination of the optic tectum is most highly developed. Each of the laminae in the superficial layers of the avian optic tectum may contain specific classes of tectal cells or represent the level of termination of different functional classes of retinal ganglion cells. The complexity of interneuronal connections makes the former idea unlikely. Furthermore, the predominance of pandirectional units recorded from the superficial layers of the chicken optic tectum might provide evidence

against the segregation of tectal cell types to specific laminae.

The Toral Region

Cytoarchitectonic Organization of the Toral Region

Early anatomists referred to the semicircular ridge immediately below the optic ventricle of fishes, amphibians, and reptiles as the the torus semicircularis (Ariëns Kappers, '06). This region is the colliculus of Johnston ('06) and the corpus posticum of Herrick ('17, '30, '42). In birds, a portion of the torus semicircularis was designated the ganglion laterale by Wallenberg (1898) and the nucleus mesencephalicus lateralis, pars dorsalis by Ariëns Kappers ('21). Craigie ('28, '30) identified the nucleus mesencephalicus lateralis, pars dorsalis and a surrounding area. As suggested by Craigie ('28), the term semicircularis should be applied to the entire subtectal area between the optic ventricle and the deep tegmental gray of the chicken to emphasize the ancestral relationship of this region to possible homologous neuronal masses found in fishes, amphibians, and reptiles.

Within the boundaries of the avian torus semicircularis, Craigie ('28, '30), Huber and Crosby ('29), and

TABLE 6.--Terminology for nuclei of the toral region

Potter ('65)	Ebbesson ('67, '69)	Pritz ('74)	Karten ('67)
frog	lizard, snake, turtle	alligator	pigeon
laminar nucleus	nucleus laminaris	external nucleus	stratum griseum et fibrosum periventriculare
magnocellular nucleus	nucleus intercollicularis		nucleus intercollicularis
principle nucleus	nucleus centralis	central nucleus	nucleus mesencephalicus lateralis pars dorsalis

Jungherr ('45) observed a central area of medium sized cells, the central nucleus of the nucleus mesencephalicus lateralis pars dorsalis, and a surrounding parvocellular capsule. In Karten's ('67) and Karten and Hodos' ('67) description of the pigeon torus, the central nucleus was identified as the LMD and the parvocellular region was partitioned into the nucleus intercollicularis, the stratum griseum et fibrosum periventriculare, and the central gray region. On the basis of light microscopic observations, the nuclear configurations of Columbiformes and Galliformes are similar in position and cell sizes.

Nuclear masses comparable to those found in avian forms (refer to Table 6) were identified in amphibians and reptiles (Potter, '65; Ebbesson, '67, '69; Pritz, '74). The principle nucleus of the torus of the frog (Potter, '65) and the central nucleus of the frog, snake, lizard, alligator, and turtle (Ebbesson, '67, '69; Pritz, '74) correspond on the basis of cell locations to the LMD of the pigeon (Karten, '67) and the chicken. In birds, the stratum griseum et fibrosum periventriculare of Karten ('67) and the current study correspond to the laminar nucleus of the torus semicircularis in the frog, snake, lizard, and turtle (Potter, '65; Ebbesson, '67) and the

external nucleus of the alligator (Pritz, '74). The intercollicular nucleus of reptilian forms, which was also identified in the pigeon (Karten, '67; Karten and Hodos, '67) and the chicken, was equated by Ebbesson ('67) with the magnocellular nucleus of the torus in the frog (Potter, '65). In teleosts, the torus simply consists of four layers of cells (Ito, '74).

Afferent Fiber Connections

Early workers investigated the central afferent connections of the torus semicircularis from spinal and medullary sensory areas. Edinger ('08) followed a spino-mesencephalic tract from the spinal cord to the midbrain. The majority of such fibers identified by Ariëns Kappers ('47) as components of the spinobulbar mesencephalic tract were followed into the toral region (anterior tegmental nucleus) in fishes, amphibians, reptiles, and birds. The general bulbar lemniscus including secondary fibers from the sensory trigeminal nucleus (Ariëns Kappers, Huber, and Crosby, '36; Woodburne, '36) and fibers from the acousticolateral area were considered to terminate in the torus (lateral tegmental nucleus) of fishes and amphibians (Ariëns Kappers, '06, '47; Pearson, '36) and the caudolateral part of the torus in amphibians (Herrick, '17, '30,

'42). Fibers arising from the trigeminal nucleus were referred to as the trigeminal lemniscus; fibers from the acousticolateral area were referred to as acousticolateral lemniscus (Pearson, '36), fasiculus longitudinalis lateralis (Ariëns Kappers, '06), the bulbar lemniscus (Johnson, '01) in fishes and the tractus bulbotectalis lateralis (Herrick, '17, '30, '42) in tailed amphibians. In reptiles (Huber and Crosby, '26, '33a; Ariëns Kappers, Huber, and Crosby, '36) and birds (Craigie, '28, '30; Huber and Crosby, '29; Ariëns Kappers, Huber and Crosby, '36), a fiber system comparable in origin to that of the acousticolateral lemniscus is referred to as the lateral lemniscus. Termination of the lateral lemniscus was in the LMD. Other input fiber systems arise from the nucleus isthmi (Ariëns Kappers, Huber, and Crosby, '36) and the contralateral torus (Ariëns Kappers, Huber, and Crosby, '36; Karten, '67).

On the basis of afferent connections with cutaneous, lateral line, auditory, and vestibular receptive areas of the medulla and spinal cord, Ariëns Kappers ('29, '47), Herrick ('48), and Ariëns Kappers, Huber, and Crosby ('36) considered the torus semicircularis to be a region involved in the correlation of vibratory, tactile, and vestibular impulses in nonmammalian aquatic forms and auditory

and tactile impulses in terrestrial nonmammals. As defined by Herrick ('48), the term correlation is employed here to refer to the interaction of different sensory inputs at the level of individual neurons.

More recently, degeneration studies confirmed fiber contributions of the spinomesencephalic tract to the torus semicircularis of tailless amphibians, reptiles, and avian forms (Karten, '63; Ebbesson, '67, '69). In the frog, snake, lizard, turtle, and pigeon, terminal degenerating fibers of the spinomesencephalic tract were localized to the stratum griseum periventriculare and the intercollicular nucleus. In addition, Karten ('67) identified terminal degeneration in the intercollicular nucleus after destruction of the dorsal column nuclei of the pigeon. Brood ('68, '69) followed fibers in the pigeon from the nucleus of the lateral lemniscus to the LMD. Though this re-evaluation of afferent toral fiber systems substantiates several fiber systems described by earlier workers, the experimental anatomic evidence suggests that different sensory systems remain segregated from one another.

Correlative Considerations of the Toral Region

Anatomic differentiation of the toral region into

several nuclear groups may be related to information processing which is different from that suggested by classical anatomical studies. Recently, experimental evidence suggests various fiber systems and related sensory modalities are segregated to specific areas of the avian midbrain (Cowan, Adamson, and Powell, '61; Karten, '63, '67; Brood, '68, '69). Differences in nuclear organization that do exist in different species, as indicated above, may be correlated with the progressive segregation of fiber systems into nuclear zones as suggested by Johnston ('06). Evidence in support of either segregation or nonsegregation of sensory information at the level of the avian midbrain remained untested or unreported prior to this current study. This study shows that there is segregation: visual information to the superficial optic tectum layers; auditory to the LMD, and somesthetic to the toral SGP. On the other hand, the deep layers of the optic tectum and the ICO are regions from which multisensory units were recorded. These data therefore support both viewpoints; the multisensory hypothesis of Ariëns Kappers, Herrick, Huber and Crosby and the segregation hypothesis of Johnston.

The Physiologic Basis for Multisensory Information Processing in Tectal Regions

The Deep Layers of the Optic Tectum

Recent electrophysiologic studies discussed below support the notion of multisensory correlations by individual cells in the deep layers of the nonmammalian optic tectum. In species with only periventricular cell layers or poorly developed SGC and SGFS laminae, multimodal units were recorded in the periventricular layers. In the salamander, units were found to be responsive to visual, whole body vibratory, and tactile stimuli (Grüsser-Cornehls and Himstadt, '73). In the frog, units were responsive to visual, vibratory, tactile, and auditory stimuli (Fite, '69). In the turtle, a creature with well developed periventricular, SGC, and SGFS laminar patterns, firings following visual, tactile, and auditory stimuli were only obtained in the periventricular layers (Robbins, '72). Although the studies of Fite ('69), Robbins ('72), and Grüsser-Cornehls and Himstadt ('73) support the multisensory character of cells in the periventricular layers, the existence of similar neurons in the two major strata of the optic tectum, the SGC and SGFS are not supported by these studies.

My investigations do however indicate multimodal

units are located in the stratum griseum centrale of the chicken optic tectum. Here were found bimodal units which responded to visual, auditory, and somesthetic stimuli. This result therefore evidences multisensory functions of the deep lamina of the optic tectum. Furthermore, the low number of units encountered may be indicative of the sparsity of nonvisual afferents from which spontaneous cells encountered in the deeper layers derive tonic discharges. This result is in agreement with the observation that the spinomesencephalic tract contributes only a small number of fibers to the optic tectum (Ariëns Kappers, '47).

The experimental methodology employed included biasing factors possibly favoring the recording from the optic tectum visual units to the exclusion of those driven by nonvisual stimuli. Electrode configuration, nonspontaneity of cells in the lamina, the use of inappropriate isolating stimuli, or a failure to test cell responsiveness with proper stimuli could contribute to the inability to detect such units, if present.

For the following reasons factors which may have biased these results were believed to be taken into account. Visual units were recorded from the superficial

laminae which contain very small cells. Stimulus features necessary to isolate and drive nonspontaneous visual units were also determined. Furthermore, units from other tectal regions were driven by auditory and somesthetic stimuli indicating proper stimuli were employed, the ascending fiber systems were functioning, and the responsiveness included excitation. Given these guidelines, the possibility still exists that very small cells were not isolated or inhibitory effects were undetected in nonspontaneous units.

The Superficial Layers of the Optic Tectum

In the present study, units responsive to visual stimuli were recorded from all laminae of the optic tectum except the stratum album centrale and the stratum griseum et fibrosum periventriculare. Although maximum efforts were made to drive units in the superficial laminae with auditory and somesthetic stimuli, in no instance were units located there responsive to the stimuli. Therefore, cells of the superficial laminae were not found to integrate visual and nonvisual sensory information as implied by the anatomic and functional descriptions of Huber and Crosby.

These results are in accordance with Karten ('63) who

could not substantiate the existence of direct spino-tectal fibers to the superficial layers of the optic tectum. The findings of this study would suggest the elaborate development of the optic tectum is dependent on visual afferents rather than nonvisual afferent fiber systems.

The Toral Region

Ewert and Borchers ('71) and Ewert ('74) recorded multimodal responses from units in areas surrounding the principal nucleus of the toad. Units reported by these workers responded to visual, auditory, vibratory, and tactile stimuli. Many of Ewert and Borchers' recordings were obtained from a region designated by Potter ('65) as the laminar nucleus of the torus semicircularis. In the goldfish, frog, and crocodile, auditory units were recorded from widespread areas of the torus (Potter, '65; Page, '70; Manley, '71) but unfortunately, responsiveness to other sensory modalities were not reported. Multisensory neurons in toral structures in forms other than the toad were not identified previous to the current study.

Somesthetic, auditory, and bimodal auditory-somesthetic responses were obtained in the present study

from the SGP and ICO structures of the torus known to receive input from the avian somesthetic system by way of fibers in the lateral funiculus of the spinal cord and the medial lemniscus of the brain stem (Karten, '63, '67). Evidence for auditory inputs to structures surrounding the LMD, were heretofore undetermined. In this study no toral units were responsive to visual stimuli.

In the torus, units responsive to auditory stimuli were reported in goldfish, frog, reptile and bird. As discussed above, auditory units in nonmammals other than birds were recorded from widespread areas of the torus. The multisensory functional organization within the aquatic forms remains unknown. In birds studied, responses to auditory stimuli were recorded from the LMD of the pigeon (Hamdi and Witteridge, '54; Harmon and Phillips, '67), the barbary dove (Biedermann-Thorson, '68), and the Japanese quail (Potask, '70). In this study of the chicken, units recorded from the LMD responded to auditory but not visual or somesthetic stimuli. This indicates auditory information relayed to some LMD cells remains segregated from other sensory modalities.

Correlative Considerations

The results, taken together with those of other workers, indicate that in the bird visual, auditory, and somesthetic fiber systems are segregated in midbrain structures, as originally predicted by Johnston ('06). The bird optic tectum might best be considered to have superficial and deep functional divisions. The superficial layers receive optic tract fibers and are involved with integration of visual information; whereas the deep layers process visual and nonvisual information. The superficial layers could act as an interface for conveying a certain kind of information to the deep layers of the optic tectum, as discussed below, and also for projecting visual information forward to thalamic and pretectal regions.

Harting, Hall, Diamond, and Martin ('73) found a similar dichotomy of collicular projection in the superior colliculus of the tree shrew. Harting, Hall, Diamond, and Martin ('73) and Casagrande and coworkers ('72) suggest the organizational features of the tectum described by them may correspond to a functional differentiation of the superior colliculus. Behavioral studies by these workers indicate the superficial layers of the superior colliculus (stratum zonale, stratum

griseum superficiale, stratum opticum) are involved in pattern discriminations. In contrast, the deep laminae are thought to be involved in visual localization and tracking behavior.

Whether two separate tectal efferent projection systems exists in birds needs verification. Anatomic and electrophysiologic studies have demonstrated a projection from the deep layers to the nucleus rotundus (Karten and Revzin, '66; Revzin and Karten, '66). If a superficial system does exist in birds the functional relationship of such a system is unclear, for birds do not appear to possess an external corticotectal system and superficial tectal layers comparable to those found in mammals (Huber and Crosby, '43).

Tectothalamic tracts from the toral region may carry very specific types of information to the diencephalon. Karten ('67), on an anatomic basis, identified an auditory projection system from the LMD to nucleus ovoidalis. Projection systems from the ICO may also exist. If present in avian forms, this system would carry multisensory information to the diencephalon. A comparable system may exist in mammals (Jane, Yashon, and Diamond, '68).

Comparison of Avian Physiologic Data with that of Mammalian Forms

The Deep Layers of the Superior Colliculus

Electrophysiologic studies of the mammalian optic tectum (superior colliculus) reported numerous examples of multimodal tectal cells. Such tectal cells were reported in the cat (Bell et al, '64; Jassik-Gerschenfeld, '65; Straschill and Hoffmann, '69; Wickelgren, '71; Stein and Arigbede, '72, and Gordon, '73), the rabbit (Hill, '66; and Masland, et al '71), and the monkey (Cynader and Berman, '72). These studies indicated multimodal units in mammals, as in the chicken, were located in the deep layers of the superior colliculus.

Multimodal units of the mammalian superior colliculus were reported to be wide field types, with a low probability for responding to visual stimuli in the cat (Stein and Arigbede, '72) or with a characteristic habituating manner in the rabbit (Horn and Hill, '66). The convergence of nonvisual sensory modalities upon units which respond to novel stimuli were described by Straschill and Hoffmann ('69) for the cat and Cynader and Berman ('72) for the monkey. In the stratum griseum centrale of the chicken, visual units also responsive to

nonvisual stimuli exhibited similar wide fields and habituation response features.

The stimulus requirements for driving tectal units and response properties of chicken tectal cells are comparable to those reported for units of the mammalian superior colliculus. In cat (Bell, Sierra, Buendia, and Segundo, '64; Stein and Arigbede, '72; and Gordon, '73) hair movements, as feather movements in the chicken, provide effective stimuli. A variety of auditory stimuli were found to be effective in activating tectal units. Contralateral pure tones gave excitatory responses (Stein and Arigbede, '72). Gordon ('73) found complex sounds (hissing sounds, jangling keys, and rattling aluminum foil) were more effective than pure tones. In this study complex sounds (hand claps) were effective.

Tectal units in the chicken also exhibited field sizes comparable to those reported for cells of the superior colliculus in other species. In the rabbit (Horn and Hill, '66) and the cat (Bell et al, '64; Stein and Arigbede, '72) large visual and somesthetic receptive fields were described. Some visual units could be driven from one-half of the animal's visual field. Somesthetic fields were also large. In some instances they were

contained to a few square centimeters but more often included the entire body surface contralateral to the recording site. Bell and his coworkers ('64) reported entire body units but were less certain of the recording position in the brainstem.

Wickelgren ('71) and Gordon ('73) documented spatially restricted auditory receptive fields. Auditory fields occasionally overlapped visual receptive fields of bimodal visual-auditory units. Most bimodal units also required movement across the receptive field and many were directionally selective to both stimuli. Somesthetic fields of bimodal visual-somesthetic units were commonly localized on the cat's head and visual were near the center of vision. In the chicken, receptive fields of visual, auditory, and somesthetic bimodal units of the stratum griseum centrale were spatially organized with respect to the animal's head. Bimodal SGC units shared common if not congruent receptive fields behind the head of the animal but did not require auditory stimulus movement.

The Superficial Layers of the Superior Colliculus

The superficial layers of the mammalian superior colliculus, in general, contain three kinds of visual

units (Sprague, Berlucchi, and Rizzolatti, '73). These include directionally selective units, meridian selective units, and units which exhibit no directional selectivity. In each case these units are particularly sensitive to moving stimuli. Directionally selective units discharge to stimulus movement but respond best to stimulus movements in one direction. Meridian selective units discharge to stimuli moved along either the horizontal or vertical meridian. Although the terminology applied to visual units observed in the current study differs from that used by Sprague and coworkers ('73), directionally selective units found in mammals correspond to unidirectional and multidirectional units recorded from the superficial laminae of the Gallus optic tectum. Pandirectional units correspond to those units which exhibit no directional selectivity. Meridian selective tectal units were not encountered.

The Inferior Colliculus

Beneath the surface of the gross structure referred to as the inferior colliculus in the cat, Berman ('68) identified three nuclei. These divisions include the central nucleus of the inferior colliculus, the pericentral nucleus of the inferior colliculus, and the

external nucleus of the inferior colliculus. Units responsive to auditory stimuli were recorded from each nucleus. The central nucleus was tonotopically organized; the external and pericentral nuclei were not (Rose, Gross, Geisler and Hind, '66; Aitkin, Fryman, Blake and Webster, '72). Units recorded from the toral region of the chicken in the present study responded to specific pure tone frequencies but the sample studied did not allow for conclusions to be drawn concerning the tonotopic organization of the region.

Functional Considerations

In the development of the optic tectum and the toral region described by Johnston ('06), for the vertebrate series, the optic tectum was considered to become involved in functions usually attributed to the mammalian neocortex (Elliot, '69). The elaborate tectal cortex of non-mammals prompted Elliot ('69) to believe visual perceptual processes occurred in this structure. The dimunition in the size of the optic tectum and the complexity of laminar patterns, on the one hand, and the development of neocortex, on the other, in mammals led workers to consider that perceptual functions were transferred in the evolution of mammals from nonmammals

from the midbrain to the telencephalon. Accordingly, the mammalian superior colliculus was considered to be involved in visual reflex functions only. Present evidence suggests that this structure has remained functionally stable in both mammals and nonmammals (Riss and Jakway, '70). At all levels of vertebrate phylogeny the optic tectum is now considered to be a sensory-motor correlation center important in eliciting a group of reflexes broadly referred to as visual orienting responses.

The Deep Layers of the Optic Tectum

Gross body orientations were elicited in fish (Meyer, Schorr, Schaefer, '70), amphibians (Ewert, '70), and reptiles (Goodman and Simpson, '60; Shapiro and Goodman, '69) following stimulation of the optic tectum. Presumably in natural situations such responses are initiated at least in part by visual stimuli. A visual stimulus activates neurons in the superficial layers via retinotectal projections. Activity enters the deep layers and from there the tectobulbospinal tract conveys impulses to neurons involved in orienting responses.

Deep laminae unit receptive fields, in the current study, were large and responded to stimulus movements

in all directions. These units also habituated to repeated stimuli. Similar units were recorded from the deep layers of the optic tectum in the frog (Lettvin, Maturana, Pitts, and McCullough, '61; Fite, '69), bird (Jassik-Gerschenfeld and Guichard, '72), rabbit (Horn and Hill, '66), cat (Straschill and Hoffmann, '69), and the monkey (Cynader and Berman, '72).

An obvious difference in field sizes between units of the superficial and deep laminae suggests that visual information is conveyed to the deep laminae for purposes of enlarging spatial information from the superficial layers. Such deep lamina cells may be summators. Deep lamina cells would appear to amplify the area of the visual field effective in initiating motor outflow. It could appear that this information would enable an animal to only roughly localize visual stimuli which initiated the orienting response. More subtle aspects of orientation than those which are found in tectal stimulation experiments may involve different parts of the animal's visual system. Finally, the habituating property of deep lamina tectal cells may be useful in preventing the animal from orienting indiscriminantly to any visual stimulus appearing in its visual field.

Nonvisual stimuli were observed to cause initiations (Tinbergen, '53; Ingle, '73) or alterations (Ewert and Borchers, '71; Ewert, '74) in orienting responses ordinarily elicited by visual stimuli. Multimodal tectal neurons may provide physiologic correlates of such behavioral observations. According to Wickelgren ('71) and Gordon ('73) the activation of feline tectal cells by somesthetic and auditory stimuli appear to provide a mechanism enabling the cat to orient toward and visually track the source of nonvisual stimuli. Similarities in field position and movement sensitivity were presumably the key features of different stimulus modalities responsible for this function. In the frog and the toad, nonvisual stimuli were considered by Ewert ('74) to arouse the animal or to focus attention toward stimuli in the visual field. In awake behaving primates, neurons displaying "attentional" properties to visual stimuli were described by Goldberg and Wurtz ('72).

In the present study, bimodal units recorded from the deep layers of the optic tectum responded to visual, auditory, and somesthetic stimuli presented from similar spatial areas. This appears to be of potential behavioral value for two reasons. First, somesthetic and auditory

stimuli may provide spatial and temporal information not available visually. Such information could be used to orient to a new area of visual interest if this was behaviorally appropriate. Secondly, somesthetic and auditory stimuli could, as Ewert and Borchers ('71) suggest, lower the threshold of tectal units to a level where subsequent activation by a visual stimulus might increase the possibility or lower the threshold of a behavioral action. In the chicken, such information processing would affect the level of preparedness for an object about to appear in the animal's visual field. The subsequent reaction of the animal to a visual stimulus would be determined not by one, but at least two bits of different information. Such a mechanism would be highly desirable since, based on such associations, an animal as stereotyped in visual behavior as the chicken would be able to more selectively react to different environmental situations.

Finally, Schiller and Koerner ('71) and Wurtz and Goldberg ('72) discovered units in the deep layers of the primate superior colliculus that discharged in association with eye movements. In the present experiments the head and eyes of the chicken were fixed.

A close relationship of deep laminae cells to motor behaviors may account for the low number of units encountered in the deep layers of the avian optic tectum.

The Superficial Layers of the Optic Tectum

In this study, visual units were sensitive to moving visual stimuli. Pandirectional, unidirectional, and multidirectional units were identified. The stimulus requirements of these units were essentially the same as those reported previously in pigeon and duck by Holden ('69), Jassik-Gerschenfeld, Minois, and Condé-Courtine ('70a, '70b), Revzin ('70), Jassik-Gerschenfeld and Guichard ('71, '72), and O'Flaherty ('72).

The stimulus parameters needed to drive these units appeared to be less exacting than at the level of the retina (Maturana, '62; Maturana and Frenk, '63). The superficial layers are therefore involved in the correlation of visual information derived from the retina.

Tectal units may be important in detecting moving objects. Pandirectional units are clearly event detectors which signal the presence of moving objects. Multidirectional units may be involved in increasing the sensitivity of detecting object movement beyond that encountered at the level of the retina.

A relationship between tectal function and the predominance of directionally selective units in the optic tectum was formed by some workers. It is suggested that certain unit types are important in specific orienting behaviors. In this study, directionally selective units, which respond preferentially to movements in just one direction were found. The number of units sampled does not permit conclusions concerning the relative abundance of such units in the chicken tectum. However, a number of multidirectional units encountered were selective to rostrally directed stimulus movements. Ingle ('73) suggests these units are merely biased for receptive field events encountered by a chicken. Such conclusions can only be tested in physiologic experiments which employ freely moving animals.

The Toral Region

It is more difficult to ascribe significance to units recorded from the torus semicircularis because a conceptual framework with which to interpret physiologic data is not available. By means of the lateral line system of organs which detect low frequency water vibrations, fishes become aware of nearby moving objects (Romer, '62). Peripheral receptor organs are localized

primarily along the side of the head; centrally, secondary connections of the acousticolateral line nuclei terminate in the torus semicircularis. Parallel functions between the acousticolateral line system and the type of unit data recorded from the SGP of the avian torus are evident. Somesthetic receptive fields were localized to the neck and head and optimal stimuli consisted of feather vibrations. By analogy, one might speculate that neurons of the avian torus receiving feather movement information may perform similar functions to neurons found in the torus of the fish. Furthermore, the inferior colliculus has been implicated in auditory localization functions (Rose et al, '66). Likewise the LMD may be involved in similar functions. Available evidence suggests the avian ICO is involved in vocalizations (Potash, '70; Newman, '70, '72). In the cat, Kanai and Wang ('62) elicited screaming, growling, and wail-like crys following electrical stimulation of the stratum profundum of the superior colliculus. The predominance of somesthetic and auditory units may provide inputs relating to such behaviors.

Homologies

General

Differences in gross positional relationships of

tectal structures, changes in peripherial nerve end organs, and changes in central connections which occur in the evolutionary history of the vertebrate midbrain have made it difficult to determine homologies for the various tectal structures found in mammals and non-mammals. Traditionally, the six basic laminae in the mammalian superior colliculus were considered to be homologous to the six laminae found in nonmammalian optic tectum (Huber and Crosby, '33b). The inferior colliculus is reputed to be the homologue of a portion of the torus referred to in avian forms as the LMD (Huber and Crosby, '29). The homology of the LMD with the inferior colliculus is still accepted. Current workers (Karten, '63; Ebbesson, '67, '69; Ingle, '73) attempted to homologize the deep layers of the superior colliculus with other structures of the toral region. The differences may be one of interpretation, for in spite of the opinions expressed, corresponding tectal structures in mammals and nonmammals are possibly more alike than was recognized by workers past and present.

The Deep Layers of the Optic Tectum

In mammals auditory impulses reach the superior colliculus by way of interneuronal connections with the

inferior colliculus (Crosby, Humphrey, Lauer, '62). Somesthetic information is conveyed to the stratum profundum of the superior colliculus via the spinal lemniscus (Nauta and Kuypers, '58; Anderson and Berry, '59; Mehler, '69). Comparable systems have been reported in the dogfish (Hayle, '73), lizard, snake, and turtle (Ebbesson, '67, '69) and the pigeon (Karten, '63). Though terminations of spinotectal fibers in the nonmammalian optic tectum and mammalian superior colliculus are apparently small in number, an anatomic basis for somesthetic activation of multisensory units exists in the deep layers of mammals and nonmammals. Therefore, in conjunction with comparative studies, the present work suggests, on the basis of unit recordings and known fiber connections, the stratum griseum centrale of the avian optic tectum is homologous to the stratum griseum profundum of the superior colliculus. A similar homology probably exists for the dogfish, lizard, snake, and turtle but must await the identification of multisensory visual and nonvisual units in these forms.

The Stratum Griseum Periventriculare of the Toral Region

The relationship of mammalian tectal regions to the

stratum griseum periventriculare of the avian torus semicircularis remain to be clarified. Some workers suggest that the anuran torus semicircularis (Ingle, '73) or certain structures of the avian (Karten, '63) and reptilian (Ebbesson, '67) torus are homologous to the stratum profundum of the mammlain superior colliculus.

Ingle's ('73) conclusion is based on his unpublished study and that of Ewert and Borchers ('71), both of which report the presence of visual and nonvisual bimodal and trimodal units in the torus of the frog and the toad. Tactile and auditory responses described by Ewert and Borchers ('71) and later by Ewert ('74) were similar in type to those reported in this study of the chicken torus. However, visual responses similar to those reported by Ewert and Borchers ('71) were only obtained in the optic tectum.

Taken in the context of Johnston's description of midbrain evolution, discrepancies between unit types found in toral regions of the frog, toad, and chicken result from incomplete separation of somesthetic and visual systems in the anuran subtectum. This was particularly evident for recordings near the lateral border of the laminated nucleus. The majority of bimodal

and trimodal units responsive to visual stimuli were apparently recorded from this region of the nucleus (Ewert and Borchers, '71). Assuming their localization was correct, dendrites of subtectal cells may reach into the optic tectum of the toad as suggested by Herrick ('26). Electrophysiologic evidence for such an organization in chicken was not obtained. In development of toral structures in the chicken, synaptic connections with the optic system were evidently lost while those of the somesthetic systems were retained. Considering visual and nonvisual multimodal cells were identified in the tectal region usually assigned this function, the stratum griseum periventriculare of the optic tectum of the frog (Fite, '69), certain areas of the torus may be homologous to mammalian tectal regions other than the deep layers of the superior colliculus.

Karten's ('63) suggestion of a homology between the stratum profundum of the mammalian superior colliculus and toral structures exclusive of the LMD in the pigeon was reiterated by Ebbesson ('67) for the stratum profundum and the laminar nucleus of the torus in the reptile. These homologies were based upon similarities of projection patterns of the spinotectal tract fibers to the stratum profundum of mammals, the torus of the pigeon,

and the laminar nucleus of the reptile.

While workers (Crosby, Humphrey, and Lauer, '62) recognize the termination of spinotectal projections in the deep gray layers of the mammalian superior colliculus, Nauta and Kuypers ('58) and Anderson and Berry ('59) identified the densest terminal degeneration of the spinotectal tract lateral to the rostral pole of the inferior colliculus. These workers and Mehler ('69) also point out that only a small proportion of the spinotectal tract fibers actually reach the deep laminae of the superior colliculus. According to Mehler ('69), in the opossum, rat, rhesus monkey, and chimpanzee most fibers of the spinotectal tract terminate in the portion of the stratum griseum profundum of the superior colliculus that corresponds to the intercollicular nucleus.

In a preliminary report, Robards, Watkins, and Masterton ('74) described units with large bilateral somesthetic receptive fields located in the intercollicular nucleus of the opssum. Claims of wide field somesthetic units were made by workers studying somesthetic receptive field properties of deep laminae in the cat, and the rabbit superior colliculus (Bell et al, '64; Horn and Hill, '66; Stein and Arigbede, '72). Whether

studies of the deep laminae of the superior colliculus also involved the intercollicular nucleus can not be determined from material presented by Bell and his coworkers ('64), Horn and Hill ('66) or Stein and Arigbede, ('72).

While Robards and her coworkers ('74) suggested the intercollicular nucleus was involved in the integration of only somesthetic information, Gordon ('73) recorded large field somesthetic units and auditory units from lateral and caudal collicular regions. Her diagrams of unit recording sites appear to border or may even include the intercollicular nucleus of the cat. In this recording region she noted the absence of units responsive to visual stimuli.

The results of the present investigation, interpreted with data currently available on the mammalian intercollicular nucleus, suggests a similarity of the toral SGP, not with the deep laminae of the superior colliculus proper as proposed by Karten ('63), Ebbesson ('67), and Ingle ('73), but with the mammalian nucleus intercollicularis. Three different findings make this correlation credible. First, the cytoarchitectonic features found for the chicken torus reveal the continuity of the toral SGP with the stratum griseum periventriculare of the optic tectum. Cells of the

mammalian nucleus intercollicularis are continuous with and similar in shape to those of the stratum griseum profundum of the superior colliculus (Olszewski and Baxter, '54). Second, cells of the chicken toral SGP and mammalian nucleus intercollicularis were shown to have similar structural relations to the intertectal commissure. Finally, single unit data obtained from the SGP of the torus is remarkably similar in sensory types to that recorded from the mammalian nucleus intercollicularis. Units sampled in both locations are predominantly somesthetic; generally have large somesthetic receptive fields; can be driven by auditory stimuli; but never respond to visual stimuli.

The Nucleus Intercollicularis of the Toral Region

Schroeder and Jane ('71) and Jane and Schroeder ('71) followed fiber projections from the dorsal column nuclei and spinal afferents to the midbrain in the tree shrew and hedgehog. Terminations of the dorsal column nuclei were in the nucleus externus; the majority of such spinal afferents terminate further medial and rostral in the area corresponding to the intercollicular nucleus. Rose, Gross, Geisler, and Hind ('66) recorded auditory units in the external nucleus and Jane, Yashon, and Diamond

('68) demonstrated an efferent connection of the central nucleus of the inferior colliculus to the external nucleus.

In the pigeon Karten identified projections from the nucleus gracilis, nucleus cuneatus, and the spinal cord to the ICO. Interconnections from auditory related systems to the ICO remain to be reported.

In the current study, an intimate structural relationship of the ICO with the LMD, the homologue of the inferior colliculus, was demonstrated. Single unit response properties of units recorded from the ICO indicate that the majority encountered were driven by auditory and somesthetic stimuli. This result suggests that the ICO is involved in auditory and somesthetic integration functions. For this reason the ICO is considered to be the possible homologue of the mammalian external nucleus.

Implicit in this present discussion is the concept of an homologous relationship between the SGP and the mammalian nucleus intercollicularis, on the one hand, and the avian ICO and mammalian external nucleus, on the other. The validity of these homologies is classically dependent upon similarities in embryologic orgin, gross relationships, and neural circuitry of each neuronal field considered. Palmgren ('21) indicated toral and inferior

collicular fields do not develop from the same embryologic field. Gross relationships do not appear to be strikingly the same, but there are subtle similarities. Neural connections and neuronal response properties suggest at least an analogy between these structures. In light of scanty experimental evidence on the structure and function of the intercollicular nucleus, and external nucleus, one can only predict this homology. A more definitive determination awaits further studies in a variety of vertebrate forms.

SUMMARY AND CONCLUSIONS

1. Tectal regions in the chicken include the optic tectum and the toral region. Structurally, the optic tectum is divided into superficial and deep layers. The superficial layers consist of the stratum opticum and stratum griseum et fibrosum superficiale; the deep layers, the stratum griseum centrale, the stratum album centrale, and the stratum griseum et fibrosum periventriculare. Nuclei of the chicken toral region correspond to toral nuclei in the pigeon designated by Karten ('67) and Karten and Hodos ('67) as the nucleus mesencephalicus lateralis, pars dorsalis (LMD), the nucleus intercollicularis (ICO), and the stratum griseum periventriculare (SGP). The results support the conclusion that several neuronal fields process particular sorts of exteroceptive information.

2. Units of the superficial layers were responsive to moving visual stimuli. On the basis of responsiveness to the directionality of a moving stimulus, pandirectional, multidirectional, and unidirectional unit types were

identified. These units were not responsive to either somesthetic or auditory stimuli. Visual receptive fields were larger and stimulus parameters less precise than those demonstrated by others at the level of the retina. The superficial laminae are therefore involved in the integration of visual information. The classical concept of visual and nonvisual correlations by neurons of the superficial laminae of the avian optic tectum is fallacious.

3. Bimodal units were recorded from the deep layer (the stratum griseum centrale) of the optic tectum. This stratum processes visual and nonvisual information. Visual receptive fields of such units are larger than those recorded from the superficial layers. These findings are indicative of visual information processing between the superficial and deep laminae. Feather movements and hand claps were also effective in driving deep layer units. Nonvisual information may be used by chickens in orienting responses. On the basis of comparable neuronal types and fiber connections found in mammals, the stratum griseum centrale of the chicken is considered to be homologous to the stratum griseum profundum of the mammalian superior colliculus.

4. The majority of units recorded from the stratum

griseum periventriculare of the torus semicircularis and nucleus intercollicularis were responsive to somesthetic stimuli. Unit discharges increased or decreased in response to feather movements, deep and light-touch pressure and rotation of body structures across joints. The most effective stimuli were rapid feather movements. Somesthetic units had small, medium, or large receptive fields. Small fields were found on the head and neck and ranged from one square centimeter to fields that included one side of the neck. Large fields included nearly the entire body surface. Moderate fields were intermediate in size to small and large fields. The predominance of somesthetic units recorded from the stratum griseum periventriculare, the similarity of receptive field properties to those reported for mammalian tectal regions, and comparable fiber connections found in avian and mammalian forms suggest that the stratum griseum periventriculare of the chicken is homologous to the mammalian nucleus intercollicularis. Functionally, this region may be involved in orienting responses to somesthetic stimuli.

5. The majority of units recorded from the intercollicular nucleus responded in a bimodal fashion to auditory and somesthetic stimuli. Increased or decreased

discharge rates were elicited with complex noises and pure tones. Auditory responses elicited from the stratum griseum periventriculare were obtained with similar stimuli. The intercollicular nucleus may be homologous to the external nucleus of the mammalian inferior colliculus.

BIBLIOGRAPHY

Anderson, F.D. and Berry, C.M. Degenerating studies of long ascending fiber systems in the cat brain stem. J. Comp. Neurol. 111:195-229 (1959).

Aitkin, L.M., Fryman, S., Blake, D.W., and Webster, W.R. Responses of neurons in the rabbit inferior colliculus. I. Frequency-specificity and topographic arrangement. Brain Res. 47:77-90 (1972).

Ariëns Kappers, C.U. The structure of the teleostean and selachian brain. J. Comp. Neurol. 26:1-101 (1906).

Ariëns Kappers, C.U. Vergleichende Anatomie des Nervensystems. E.F. Bohn, Haarlem (1921).

Ariëns Kappers, C.U. The Evolution of the Nervous System. E.F. Bohn, Haarlem (1929).

Ariëns Kappers, C.U. Anatomie Comparée du Système Nerveux. Masson, Paris (1947).

Ariëns Kappers, C.U., Huber, G.C., and Crosby, E.C. The Comparative Anatomy of the Nervous System of Vertebrates Including Man. The Macmillian Co., N.Y., 1-2: (1936).

Armstrong, J.A. An experimental study of the visual pathways in a reptile (Lacerta vivipara). J. Anat., Lond. 84:146-167 (1950).

Armstrong, J.A. An experimental study of visual pathways in a snake (Natrix natrix). J. Anat., Lond. 85:275-288 (1951).

Bell, C., Sierra, G., Buendia, N., and Segundo, J.D. Sensory properties of neurons in the mesencephalic reticular formation. J. Neurophysiol. 27:961-987 (1964).

Bellonci, M.J. Les lobes optiques des oiseau. Arch. Ital. Biol. 4:21-26 (1883).

Berman, A.L. The brain stem of the cat. The University of Wisconsin Press, Madison (1968).

Biedermann-Thorson, M. Auditory responses of neurones in the lateral mesencephalic nucleus (inferior colliculus) of the barbary dove. J. Physiol., Lond. 193:695-705 (1968).

Bishop, P.O., Burke, W., and Davis, R. The identification of single units in central visual pathways. J. Physiol., Lond. 162:409-431 (1962).

Boord, R.L. Ascending projections of the primary cochlear nuclei and nucleus laminaris in the pigeon. J. Comp. Neurol. 133:523-541 (1968).

Boord, R.L. The anatomy of the avian auditory system; in Petros and Nobach Comparative and evolutionary aspects of the vertebrate central nervous system, Ann. N.Y. Acad. Sci. 167:186-198 (1969).

Bree, M.M. and Gross, N.B. Anesthesia of pigeons with CI 581 (Ketamine) and pentobarbital. Lab. Anim. Care 19:500-502 (1969).

Bulter, A.B. and Northcutt, R.G. Retinal projections in Iguana iguana and Anolis curolinensi. Brain Res. 26:1-13 (1971).

Burger, R.E. and Lorenz, F.W. Artificial respiration in birds by unidirectional air flow. Poultry Sci. 39: 236-237 (1960).

Burns, A.N. and Goodman, D.C. Retinofugal projections of Caiman sklerops. Exp. Neurol. 18:105-115 (1967).

Campbell, C.B.G. and Ebbesson, S.O.E. The optic system of a teleost: Holocentrus re-examined. Brain Behav. Evol. 2:415-430 (1969).

Casagrande, V.A., Harting, J.K., Hall, W.C., Diamond, I.T., Martin, G.F. Superior colliculus of the tree shrew: a structural and functional subdivision into superficial and deep layers, Science 177:444-447 (1972).

Cooper, G.F., Robinson, J.G., and Waldron, I. The action potentials recorded from undamaged nerve fibers with micro-electrodes. J. Physiol., Lond. 200:9p-11p (1969).

Cowan, W.M., Adamson, L., and Powell, T.P.S. An experimental study of the avian visual system. J. Anat., Lond. 95:545-563 (1961).

Cragg, B.G., Evans, D.H.L., and Hamlyn, L.H. The optic tectum of Gallus domesticus: a correlation of the electrical responses with the histological structure. J. Anat. 88:292-307 (1954).

Craigie, E.H. Observations on the brain of the humming bird (Chrysolampis mosquitus Linn. and Chlorostilbon caribaeus Lawr.) J. Comp. Neurol. 45:377-481 (1928).

Craigie, E.H. Studies on the brain of the kiwi (Apteryx australis). J. Comp. Neurol. 49:223-357 (1930).

Crosby, E.C., Humphrey, T., and Lauer, E.W. Correlative Anatomy of the Nervous System. Macmillan Co., New York (1962).

Cynader, M. and Berman, N. Receptive-field organization of monkey superior colliculus. J. Neurophysiol. 35: 187-201 (1972).

Ebbesson, S.O.E. Ascending axon degeneration following hemisection of the spinal cord in the tegu lizard (Tupinambis nigropunctatus). Brain Res. 5:178-206 (1967).

Ebbesson, S.O.E. Retinal projections in two teleost fishes (Opsanus tau and Gymnothorax funebris). An experimental study with silver impregnation methods. Brain Behav. Evol. 1:134-154 (1968).

Ebbesson, S.O.E. Brain stem afferents from the spinal cord in a sample of reptilian and amphibian species; in Petros and Nobach Comparative and Evolutionary Aspects of the Vertebrate Central Nervous System. Ann. N.Y. Acad. Sci. 167:80-101 (1969).

Ebbesson, S.O.E. and Ramsey, J.S. The optic tracts of two species of sharks (Galeocerdo cuvieri and Gingly-mostoma cirratum). Brain Res. 8:36-53 (1968).

Edinger, L. Vorlesungen über den Bau der nervösen Centralorgane des Menschen und der Thiere. Vogel, Leipzig (1908); in Ariens Kappers, Huber, and Crosby The Comparative Anatomy of the Nervous System of Vertebrates Including Man. The Macmillian Co., N.Y., 1-2: (1936).

Elliot, H.C. Textbook of Neuroanatomy. J.B. Lippincott Co., Phila. (1969).

Ewert, J.-P. Neural mechanisms of prey-catching and avoidance behavior in the toad (Bufo bufo L.) Brain, Behav. Evol. 3:36-56 (1970).

Ewert, J.-P. The neural basis of visually guided behavior. Sc. Amer. 230:34-42 (1974).

Ewert, J.-P. und Borchers, H.-W. Reaktionscharakteristik von neuronen aus dem tectum opticum und subtectum der erdkrote(Bufo bufo L.). Z. vergl. Physiol. 71: 165-189 (1971).

Fite, K.V. Single-unit analysis of binocular neurons in the frog optic tectum. Exp. Neurol. 24:475-486 (1969).

Freygang, W.H., Jr. An analysis of extracellular potentials from single neurons in the lateral geneculate nucleus of the cat. J. Gen. Physiol. 41:543-564 (1958).

Golby, F. and Robinson, L.A. The central connexions of dorsal spinal nerve roots and the ascending tracts in the spinal cord of Lacerta viridis. J. Anat., Lond. 96:153-170 (1962).

Goldberg, M.E. and Wurtz, R.H. Activity of superior colliculus in behaving monkey. II effect of attention on neuronal responses. J. Neurophysiol. 35:560-574 (1972).

Goodman, D.C. and Simpson, J.T., Jr. Cerebellar stimulation in unrestrained and ananesthetized alligator. J. Comp. Neurol. 114:727-735 (1960).

Gordon, B. Receptive fields in deep layers of cat superior colliculus. J. Neurophysiol. 36:157-178 (1973).

Graeber, R.C. and Ebbesson, S.O.E. Tectal projections in the lemon shark (Negaprion brevirostris) Brain Behav. Evol. 5:461-477 (1972).

Green, J.D. A simple microelectrode for recording from the central nervous system. Nature, Lond. 182: 962 (1958).

Grüsser-Cornehls, U. and Himstedt, W. Responses of retinal and tectal neurons of the salamander (Salamandra salamandra L.) to moving visual stimuli. Brain Behav. Evol. 7:145-168 (1973).

Hamdi, F.A. and Whitteridge, D. The representation of the retina on the optic tectum of the pigeon. Quat. J. Exp. Physiol. 39:111-118 (1954).

Harman, A.L. and Phillips, R.E. Responses in the avian midbrain, thalamus and forebrain evoked by click stimuli. Exp. Neurol. 18:276-286 (1967).

Harting, J.K., Hall, W.C., Diamond, I.T., and Martin, G.F. Anterograde degeneration study of the superior colliculus in Tupaia glis: evidence for a subdivision between superficial and deep layers. J. Comp. Neurol. 148:361-385 (1973).

Hayle, T.H. Comparative study of spinal projections to the brain (except cerebellum) in three classes of porkilothermic vertebrate. J. Comp. Neurol. 149: 463-476 (1973).

Herrick, C.J. The internal structure of the midbrain and thalamus of Necturus. J. Comp. Neurol. 28:215-348 (1917).

Herrick, C.J. Brains of Rats and Man. The University of Chicago Press, Chicago (1926).

Herrick, C.J. The medulla oblongata of Necturus. J. Comp. Neurol. 50:1-96 (1930).

Herrick, C.J. Development of the optic nerves of Amblystoma. J. Comp. Neurol. 74:473-534 (1941).

Herrick, C.J. Optic postoptic systems in the brain of Amblystoma tigrinum. J. Comp. Neurol. 77:191-353 (1942).

Herrick, C.J. The Brain of the Tiger Salamander. The University of Chicago Press, Chicago (1948).

Hill, R.M. Receptive field properties of the superior colliculus of the rabbit. Nature, Lond. 211:1407-1409 (1966).

Holden, A.L. Types of unitary response and correlation with the field potential profile during activation of the avian optic tectum. J. Physiol., Lond. 194: 91-104 (1968).

Holden, A.L. Receptive properties of retinal cells and tectal cells in the pigeon. J. Physiol., Lond. 201: 56P-57P (1969).

Horn, G. and Hill, R.M. Responsiveness to sensory stimulation of units in the superior colliculus and subjacent tectotegmental regions of the rabbit. Exp. Neurol. 14:199-223 (1966).

Huber, G.C. and Crosby, E.C. On thalamic and tectal nuclei and fiber paths in the brain of the American alligator. J. Comp. Neurol. 40:97-227 (1926).

Huber, G.C. and Crosby, E.C. The nuclei and fiber paths of the avian diencephalon, with consideration of telencephalic and certain mesencephalic centers and connections. J. Comp. Neurol. 48:1-225 (1929).

Huber, G.C. and Crosby, E.C. The reptilian optic tectum. J. Comp. Neurol. 57: 57-163 (1933a).

Huber, G.C. and Crosby, E.C. A phylogenetic consideration of the optic tectum. Proc. Nat. Acad. Sci. (USA) 19: 15-22 (1933b).

Huber, G.C. and Crosby, E.C. The influences of afferent paths on the cytoarchitectonic structure of the submammalian optic tectum. Psychiat. Neurol. Bl. (Amst.) 3-4: 1-16 (1934).

Huber, G.C. and Crosby, E.C. A comparison of the mammalian and reptilian tecta. J. Comp. Neurol. 78: 133-168 (1943).

Ingle, D. Evolutionary perspectives on the function of the optic tectum. Brain, Behav. Evol. 8:211-237 (1973).

Ito, H. Fine structure of the torus semicircularis of some teleosts. J. Morph. 142:137-152 (1974).

Jakway, J.S. and Riss, W. The retinal projections of the tiger salamander (Ambystoma tigrinum). Brain, Behav. Evol. 5:501-442 (1972).

Jane, J.A. and Schroeder, D.M. A comparison of dorsal columnum nuclei and spinal afferents in the European Hedgehog (Erinaceus europeaus). Exp. Neurol. 30: 1-

Jane, J.A., Yashon, D., and Diamond, I.T. An anatomic basis for multimodal thalamic units. Exp. Neurol. 22:464-471 (1968).

Jassik-Gerschenfeld, D. Somesthetic and visual responses of superior colliculus neurons. Nature, Lond. 208:898-900 (1965).

Jassik-Gerschenfeld, D., et Guichard, J. Propriétés fonctionnelles et locaisation des cellules visullés du troit optiques du pigeon. J. Physiol., Paris 63: 239A (1971).

Jassik-Gerschenfeld, D., and Guichard, J. Visual receptive fields of single cells in the pigeon's optic tectum. Brain Res. 40:303-317 (1972).

Jassik-Gerschenfeld, D., Minois, F., and Condé-Courtine, F. Receptive field properties of directionally selective units in the pigeon's optic tectum. Brain Res. 24: 407-421 (1970a).

Jassik-Gerschenfeld, D., Minois, F., and Condé-Courtine, F. Caractéristiques fontionnelles des champs recepteurs du troit optique du pigeon. J. Physiol., Paris 62: 169 (1970b).

Johnston, J.B. The brain of acipenser; a contribution to the morphology of the vertebrate brain. Zool. Jahrb. Abth. f. Anat. n Ontog. 15:59-263 (1901).

Johnston, J.B. The Nervous System of Vertebrates. P. Blakiston's Son and Co., Phila. (1906).

Jungherr, E. Certain nuclear groups of the avian mesencephalon. J. Comp. Neurol. 82:55-75 (1945).

Kanai, T. and Wang, S.C. Localization of the central vocalization mechanism in the brain stem of the cat. Exp. Neurol. 6:426-434 (1962).

Karten, H.J. Ascending pathways from the spinal cord in the pigeon (Columbia livia). Proc. 16th Int. Cong. Zool. 2:23 (1963).

Karten, H.J. The organization of the ascending auditory pathway in the pigeon (Columbia livia) 1. Diencephalic projections of the inferior colliculus (nucleus mesencephali lateralis, pars dorsalis). Brain Res. 6: 409-427 (1967).

Karten, H.J. and Revzin, A.M. The afferent connections of the nucleus rotundus in the pigeon. Brain Res. 2:368-377 (1966).

Karten, H.J. and Hodos, W. A stereotaxic atlas of the brain of the pigeon (Columbia livia). The Johns Hopkins Press, Baltimore (1967).

Knapp, H. and Kang, D.S. The visual pathways of the snapping turtle (Chelydra serpentina). Brain, Behav. Evol. 1:19-42 (1968a).

Knapp, H. and Kang, D.S. The retinal projections of the side-necked turtle (Podocnemis unifilis) with some notes on the possible origin of the pars doralis of the lateral geniculate body. Brain, Behav. Evol. 1: 369-404 (1968b).

Kosareva, A.A. Projection of optic fibers to visual centers in a turtle (Emys orbicularis) J. Comp. Neurol. 130:263-275 (1967).

Lavail, J.H. and Cowan, W.M. The development of the chicken optic tectum. I. Normal morphology and cyto-architectonic development. Brain Res. 28:391-419 (1971).

Lázár, G. and Szekely, G. Distribution of optic terminals and the different optic centers of the frog. Brain Res. 16: 1-14 (1969).

Lettvin, H.Y., Maturana, H.R., McCulloch, W.S., and Pitts, W.H. What the frog's eyes tells the frog's brain. Proc. Inst. Rodio. Engl. 47:1940-1951 (1959).

Lettvin, J.Y., Maturana, H.R., Pitts, W.H., and McCulloch, W.H. Two remarks on the visual system of the frog; in Rosenblith Sensory Communications. Wiley, N.Y. (1961).

Manley, J.A. Single unit studies in the midbrain auditory area of Caiman. Z. vergl. Physiol. 71:255-261 (1971).

Masland, R.H., Chow, L.L., and Stewart, D.L. Receptive field characteristics of superior collicular neurons in the rabbit. J. Neurophysiol. 34:148-156 (1971).

Maturana, H.R., Lettvin, J.Y., McCulloch, W.S., and Pitts, W.H. Anatomy and physiology of vision in the frog (Rana pipens). J. Gen. Physiol. 43:129-175 (1960).

Maturana, H.R. Functional organization of the pigeon retina; in Pro. Int. Union Physiol. Scil, 22 Int. Congr., Leyden, 170-178 (1962).

Maturana, H.R. and Frenk, S. Directional movement and horizontal edge detectors in the pigeon retina. Science. 142:977-979 (1963).

McGill, J.I. Organization within the central and centrifugal fibre pathways in the avian visual system. Nature, Lond. 204:295-396 (1964).

McGill, J.I., Powell, T.P.S., and Cowan, W.M. The organization of the projection of the centrifugal fibers to the retina in the pigeon. J. Anat., Lond. 100:35-49 (1966).

Mehler, W.R. Some neurological species differences - a posteriori; in Petros and Nobach Comparative and Evolutionary Aspects of the Vertebrate Central Nervous System. Ann. N.Y. Acad. Sci. 167:424-465 (1969).

Meyer, D.L., Schoor, D., Schaefer, K.-P. Reizversuche im Tectum opticum freischwimmender Kabeljue bzw. Dorsche (Gadus morrhera L). Pflug. Achv. 314:240-252 (1970).

Newman, J.D. Midbrain regions relevant to auditory communication in songbirds. Brain Res. 22:259-261 (1970).

Newman, J.D. Midbrain control of vocalizations in redwinged blackbirds (Agelaius Phoeniceus). Brain Res. 48: 227-242 (1972).

Nauta, W.J.H. and Kuypers, H.G.J.M. Some ascending pathways in the brain stem reticular formation; in Jasper, Proctor, Knighton, Noshay, and Cosletto. Reticular Formation of the Brain. Little, Brown, and Co., Boston (1958).

O'Flaherty, J.J. A Golgi analysis of the optic tectum of the mallard duck. J. Hirnforsch 12:389-404 (1971).

O'Flaherty, J.J. Analisi delle proprieta' funzionali di unita' sensibili al movimento nel tetto ottico degli uccelli. Boll. Soc. Bio. Sper. 48:135-137 (1972).

Olszewski, J. and Baxter, D. Cytoarchetecture of the human brain stem. J.B. Lippencott Co., Phila. (1954).

Page, C.H. Electrophysiologic study of the auditory responses in the goldfish brain. J. Neurophysiol. 33:116-129 (1970).

Palmgren, A. Embryological and morphological studies on the midbrain and cerebellum of vertebrates. Acta. Zool. 2:1-94 (1921).

Pearson, A.A. The acoustico-lateral centers and the cerebellum with fiber connections, of fish. J. Comp. Neurol. 65:201-294 (1936).

Potash, L.M. Neuroanatomical regions relevant to production and analysis of vocalization within the avian torus semicircularis. Experimentia (Basel) 26: 1104-1105 (1970).

Potter, H.D. Mesencephalic auditory region of the bullfrog. J. Neurophysiol. 28:1132-1154 (1965).

Pritz, M. Ascending connections of a midbrain auditory area in a crocodile, Caiman crocodilus. J. Comp. Neurol. 153:179-198 (1974).

Ramón, P. Centros opticos de las aves. Rev. trimestr. micrograf. 3:141-197 (1898).

Ramón y Cajal, S. Sur la fini structure des lobe optique des oiseau et sur l'origeni réelle des nerfs optiques. Intern. Monatsschritt Anat. und Physiol. 8:337-366 (1891).

Ramón y Cajal, S. Le lobe optique des vertébrés inférieurs in Histologie du Systeme Nerveux de L'Homme et des Vertebres. Inst. R. Cajal, Madrid. Chapt. X, 2:196-276 (1911).

Repérant, J. Nouvelles donnees sur les projections visuelles chez le Pigeon (Columbia livia) J. Hirnforsch 14:151-187 (1973).

Revzin, A.M. Some characteristics of wide-field units in the brain of the pigeon. Brain, Behav. Evol. 3: 195-204 (1970).

Revzin, A.M. and Karten, H. Rostral projections of the optic tectum and the nucleus rotundus in the pigeon. Brain Res. 3:264-276 (1966).

Ris, F. Ueber den Bau des Lobus opticus der Vögel. Arch. mekros Anat. 53:106 (1899); in Ariens Kappers, Huber, and Crosby The Comparative Anatomy of the Nervous System of Vertebrates Including Man. The Macmillian Co., N.Y., 1-2: (1936).

Riss, W., Knapp, H., and Scalia, F. Optic pathways in Cryptobranchus allegheniensis as revealed by the Nauta technique. J. Comp. Neurol. 121:31-43 (1963).

Riss, W. and Jakway, J.S. A perspective in the fundamental retinal projections of vertebrates. Brain, Behav. Evol. 3:30-35 (1970).

Robards, M.J., Watkins, D.W., and Masterton, R.B. Nucleus intercollicularis: the somesthetic tectum. Anat. Rec. 178:448 (1974).

Robbins, D.O. Coding of intensity and wavelength in optic tectal cells of the turtle. Brain, Behav. Evol. 5:124-142 (1972).

Romer, A.S. The Vertebrate Body. W.B. Saunders Co., Phila. (1962).

Rose, J.E., Gross, N.B., Geisler, C.D., and Hind, J.E. Some neural mechanisms in the inferior colliculus of the cat which may be relevant to localization of a sound source. J. Neurophysiol. 29:288-314 (1966).

Scalia, F., Kna;;, H., Halpern, M., and Riss, W. New observations on the retinal projection in the frog. Brain, Behav. Evol. 1:324-353 (1968).

Schapiro, H. and Goodman, D.C. Motor functions and their anatomical basis in the forebrain and tectum of the alligator. Exp. Neurol. 24:187-195 (1969).

Schiller, P.H. and Koerner, F. Discharge characteristics of single units in superior colliculus of the alert rhesus monkey. J. Neurophysiol. 34:920-936 (1971).

Schroeder, D.M. and Jane, J.A. Projection of dorsal column nuclei and spinal cord to brainstem and thalamus in the tree shrew, Tupaia glis. J. Comp. Neurol. 142: 309-350 (1971).

Sprague, J.M., Berlucchi, G., and Rizzolatti, G. The role of the superior colliculus and pretectum in vision and visually guided behavior; in Visual Centers in the Brain. Chapt. 14, p. 27-101, Springer-Verlag, N.Y. (1973).

Stein, B.E. and Arigbede, M.O. Unimodal and multimodal response properties of nuerons in the cat's superior colliculus. Exp. Neurol. 36:179-196 (1972).

Stone, J. Sampling properties of microelectrodes assessed in the cat's retina. J. Neurophysiol. 36: 1071-1079 (1973).

Stone, J. and Freeman, J.A. Synaptic organization of the pigeon's optic tectum: A Golgi and current source density analysis. Brain Res. 27: 203-221 (1971).

Straschill, M. and Hoffmann, K.P. Functional aspects of localization in the cat's tectum opticum. Brain Res. 13:274-283 (1969).

Szabó, I. Combined staining of central nervous system tissue with luxol fast blue and basic fuchsin. Acta Morph. Acad. Sci. (Huag) 13:251-254 (1965).

Szekely, G. Anatomy and synaptology of the optic tectum; in Visual Centers in the Brain. Chapt. 13, p. 1-26, Springer-Verlag, N.Y. (1972).

Szekely, G., Setalo, G., and Lazar, Gy. Fine structure of the frog's optic tectum; optic fibre termination layers. J. Hirnforsch 14:189-225 (1973).

Tinbergen, N. The Herring Gull's World. Collins, London (1953).

Vanegas, H. and Ebbesson, S.O.E. Retinal projections in the perch-like teleost Eugerres plumieri. J. Comp. Neurol. 151: 331-358 (1973).

Van Tienhoven, A. and Juhász, L.P. The chicken telencephalon diencephalon, and mesencephalon in stereotaxic coordinates. J. Comp. Neurol. 118:185-197 (1962).

Van Gehuchten, A. La structure des lobes optiques chez l'embryon de poulet. La Cellule 8:7-43 (1892).

Von Kölliker, A. Handbuck der Gewebelehre der Menschen Aufl 6, Bd. 2. Engelmann, Leipzig (1896); in Ariens Kappers, Huber, and Crosby The Comparative Anatomy of the Nervous System of Vertebrates Including Man. The Macmillian Co., N.Y., 1-2: (1936).

Wallenberg, A. Die secundäre acousticusbahn der taube. Anat. Anz. 14:353-369 (1898); in Hubers and Crosby The nuclei and fiber paths of the avian diencephalon, with consideration of telencephalic and certain mesencephalic centers and connections. J. Comp. Neurol. 48:1-225 (1929).

Wickelgren, B.G. Superior colliculus: Some receptive field properties of bimodally responsive cells. Science. 173:69-71 (1971).

Woodburne, R.T. A phylogenetic consideration of the primary and secondary centers and connections of the trigeminal complex in a series of vertebrates. J. Comp. Neurol. 65:405-501 (1936).

Wurtz, R.H. and Goldberg, M.E. Activity of superior colliculus in behaving monkey. III. cells discharging before eye movements. J. Neurophysiol. 35:575-586 (1972).

ILLUSTRATIONS

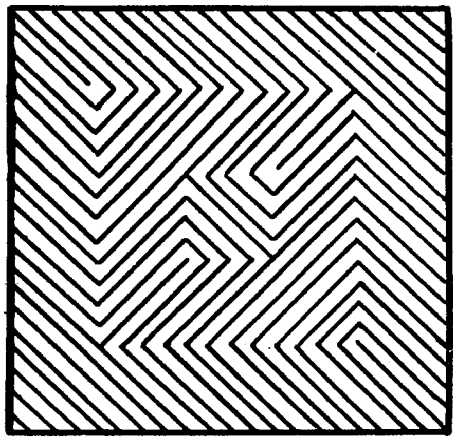
Figure 1. Visual stimuli utilized in isolating nonspontaneous units.

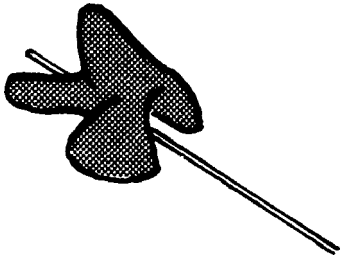
A. A complex series of lines drawn on a 440 cm^2 white sheet of cardboard.

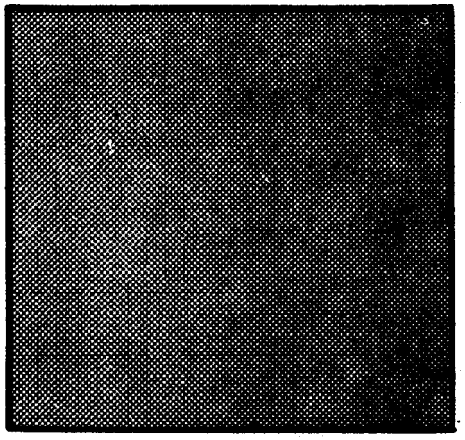
B. Many edged object approximately 5 cm^2 attached to a wand.

C. A 500 cm^2 black cardboard square.

(Illustrations are not scaled to actual size.)







① A B C

Figure 2. Line drawing of avian tectal regions in cross section. A rectangle outlines tectal areas illustrated in figures 3 through 9.

CB - Cerebellum

CG - Central gray

FRL - Lateral reticular formation

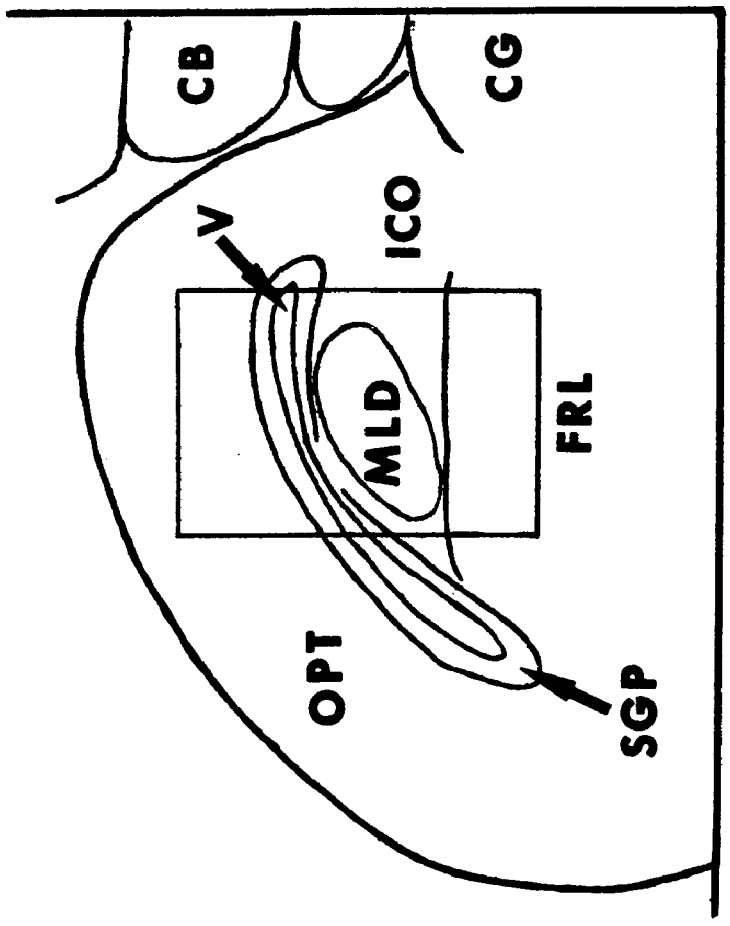
ICO - Nucleus intercollicularis

MLD - Nucleus mesencephalicus lateralis, pars dorsalis

OPT - Optic tectum

SGP - Stratum griseum periventriculare

V - Optic Ventricle



(2)

Figure 3. Sagittal section through the torus semicircularis of the chicken. Nucleus intercollicularis located between the stratum griseum periventriculare of the torus and the midbrain tegmentum. In this figure and all subsequent figures of the toral region tissue sections are stained with thionin and the bar scale represents 300 micra.

ICO - Nucleus intercollicularis

SGP - Stratum griseum periventriculare

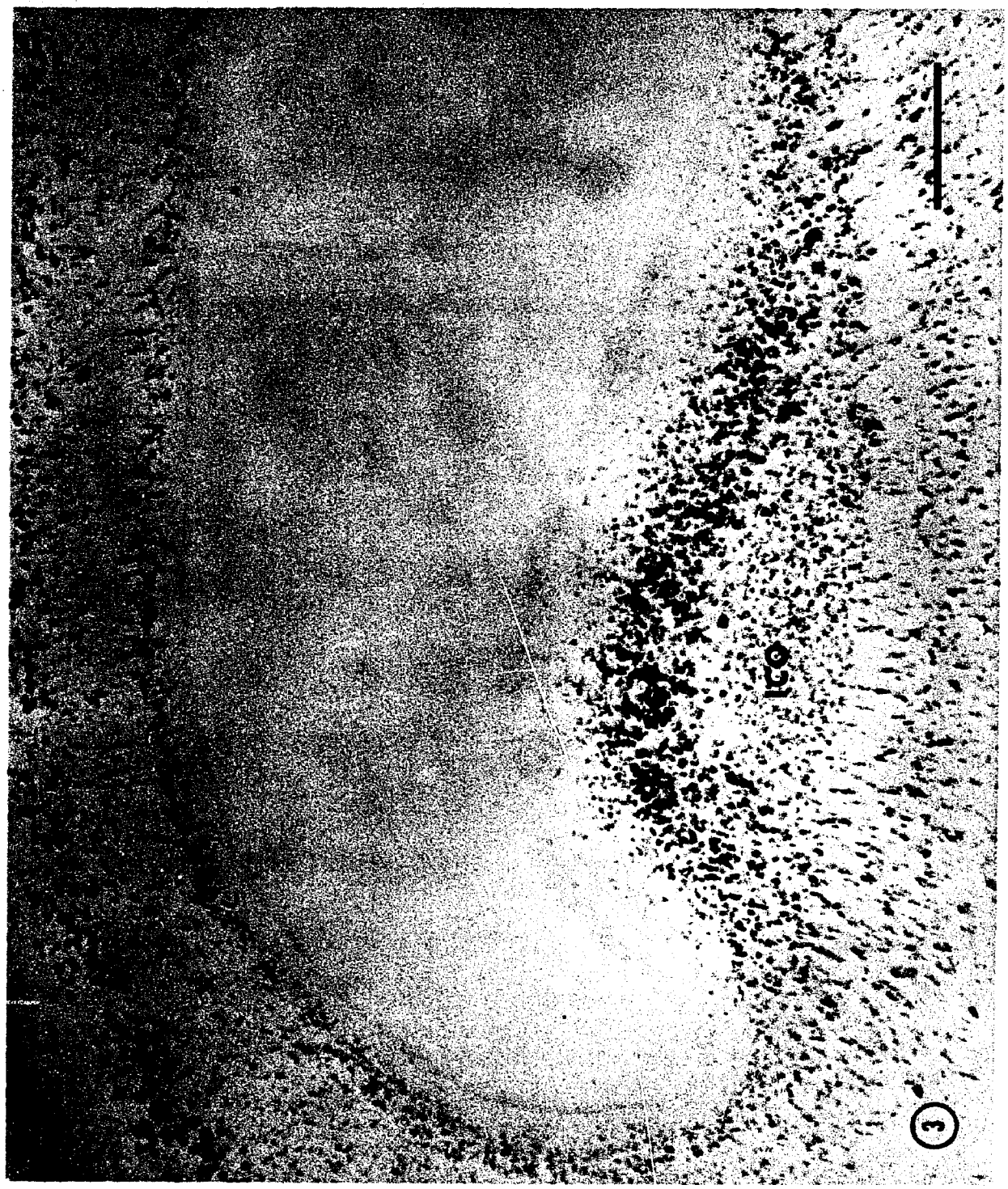

(3)

Figure 4. Sagittal section through the torus semicircularis of the chicken at a level medial to that pictured in figure 3. Note small number of cells of the nucleus mesencephalicus lateralis, pars dorsalis in the nucleus intercollicularis.

ICO - Nucleus intercollicularis

LMD - Nucleus mesencephalicus lateralis pars dorsalis

SGP - Stratum griseum periventriculare

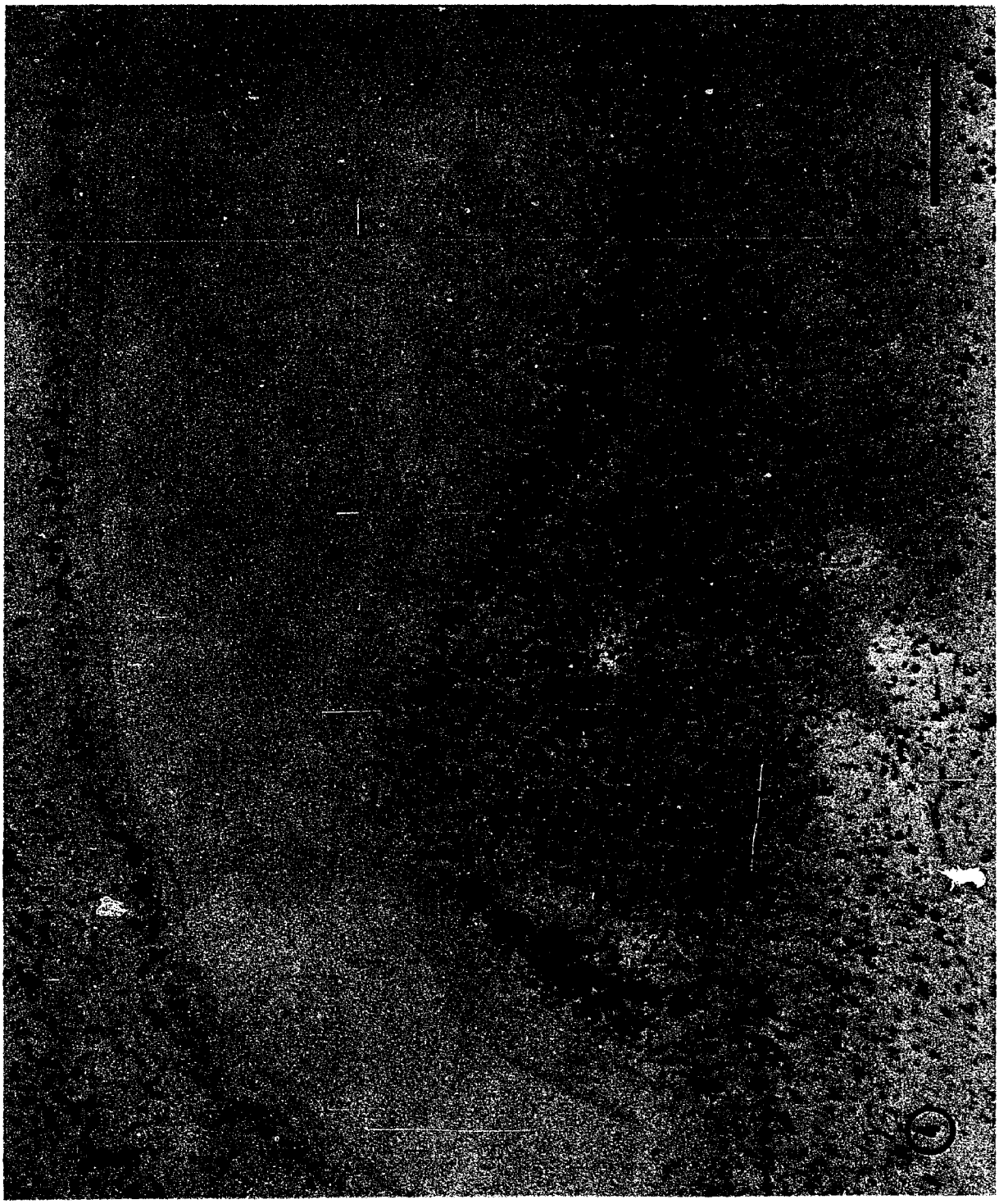


Figure 5. Sagittal section through the torus semicircularis of the chicken at a level medial to that pictured in figure 4. Note enlargement of the nucleus mesencephalicus lateralis, pars dorsalis and reduction in cell number of the overlying stratum griseum periventriculare.

LMD - Nucleus mesencephalicus lateralis, pars dorsalis.

ICO - Nucleus intercollicularis

SGP - Stratum griseum periventriculare

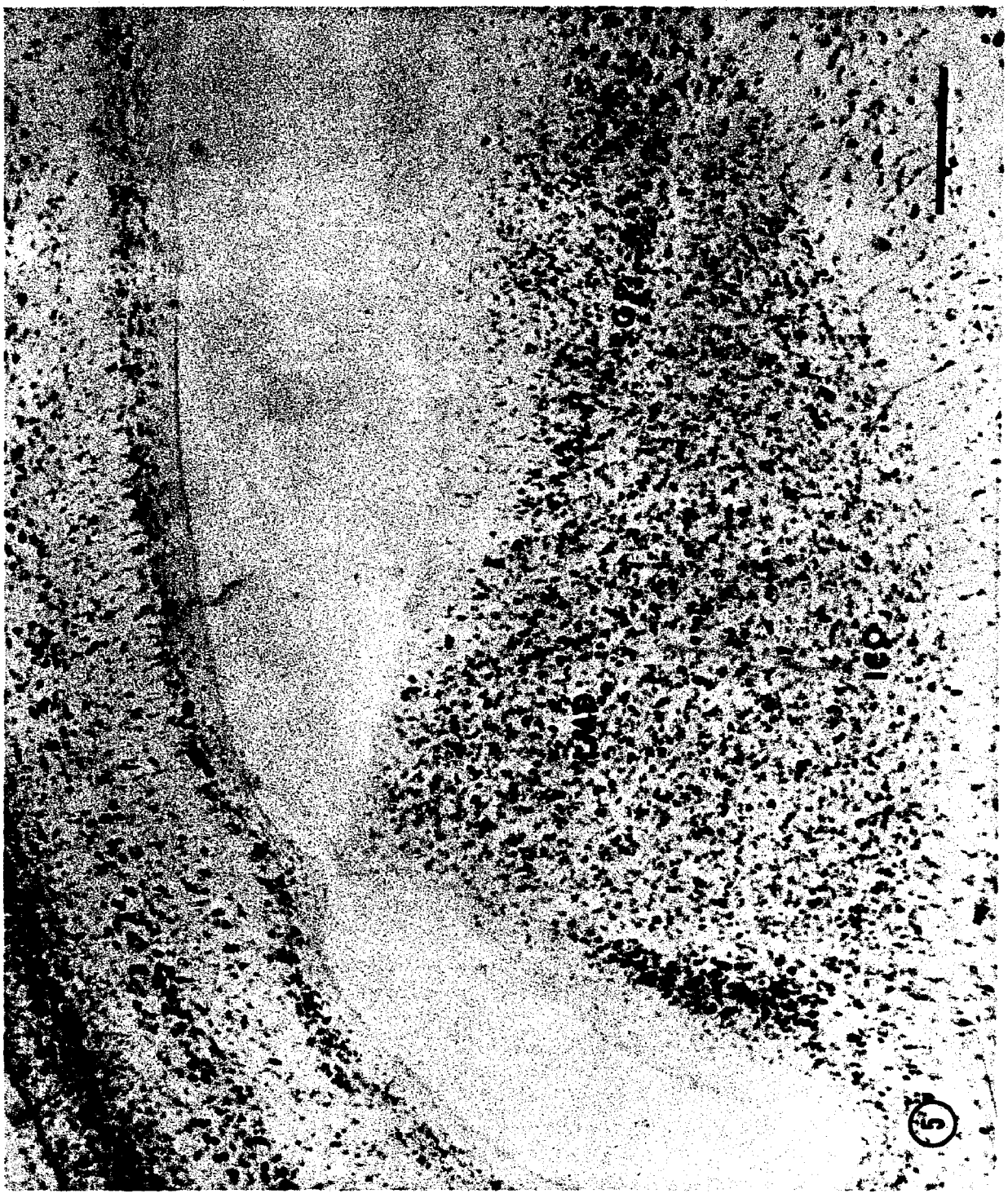

5

Figure 6. Sagittal section through the torus semicircularis of the chicken at a level medial to that pictured in figure 5. The nucleus mescencephalicus lateralis, pars dorsalis bulges into the optic ventricle, Nucleus intercollicularis separated into rostral and caudal parts. Arrows indicate subnuclei of the stratum griseum periventriculare.

LMD - Nucleus mesencephalicus lateralis, pars dorsalis.

ICO - Nucleus intercollicularis

SGP - Stratum griseum periventriculare

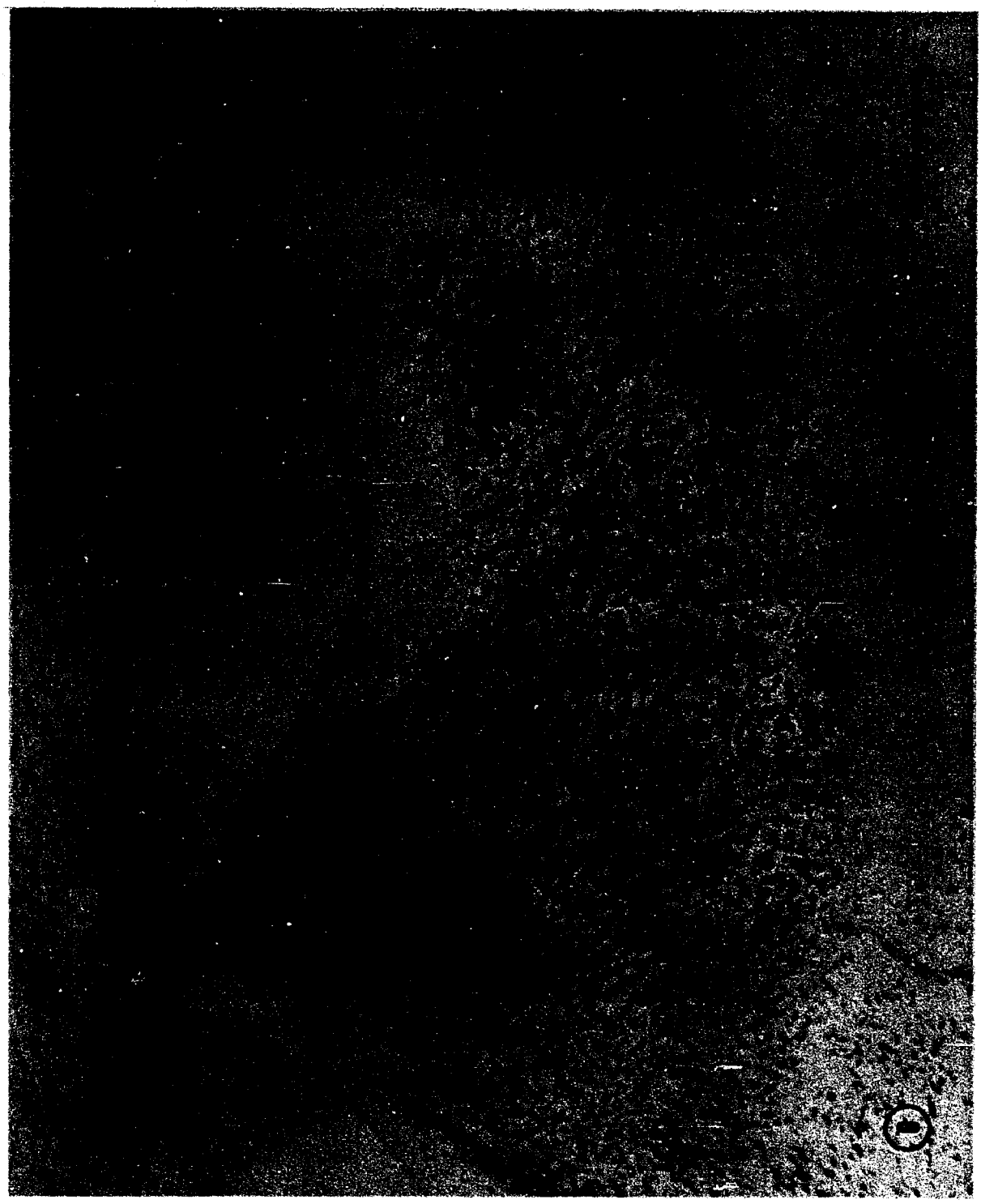


Figure 7. Sagittal section through the torus semicircularis of the chicken at a level medial to that pictured in figure 6. Nucleus mesencephalicus lateralis, pars dorsalis located between the stratum griseum periventriculare and caudal portion of the nucleus intercollicularis.

LMD - Nucleus mesencephalicus lateralis, pars dorsalis.

ICO - Nucleus intercollicularis

SGP - Stratum griseum periventriculare

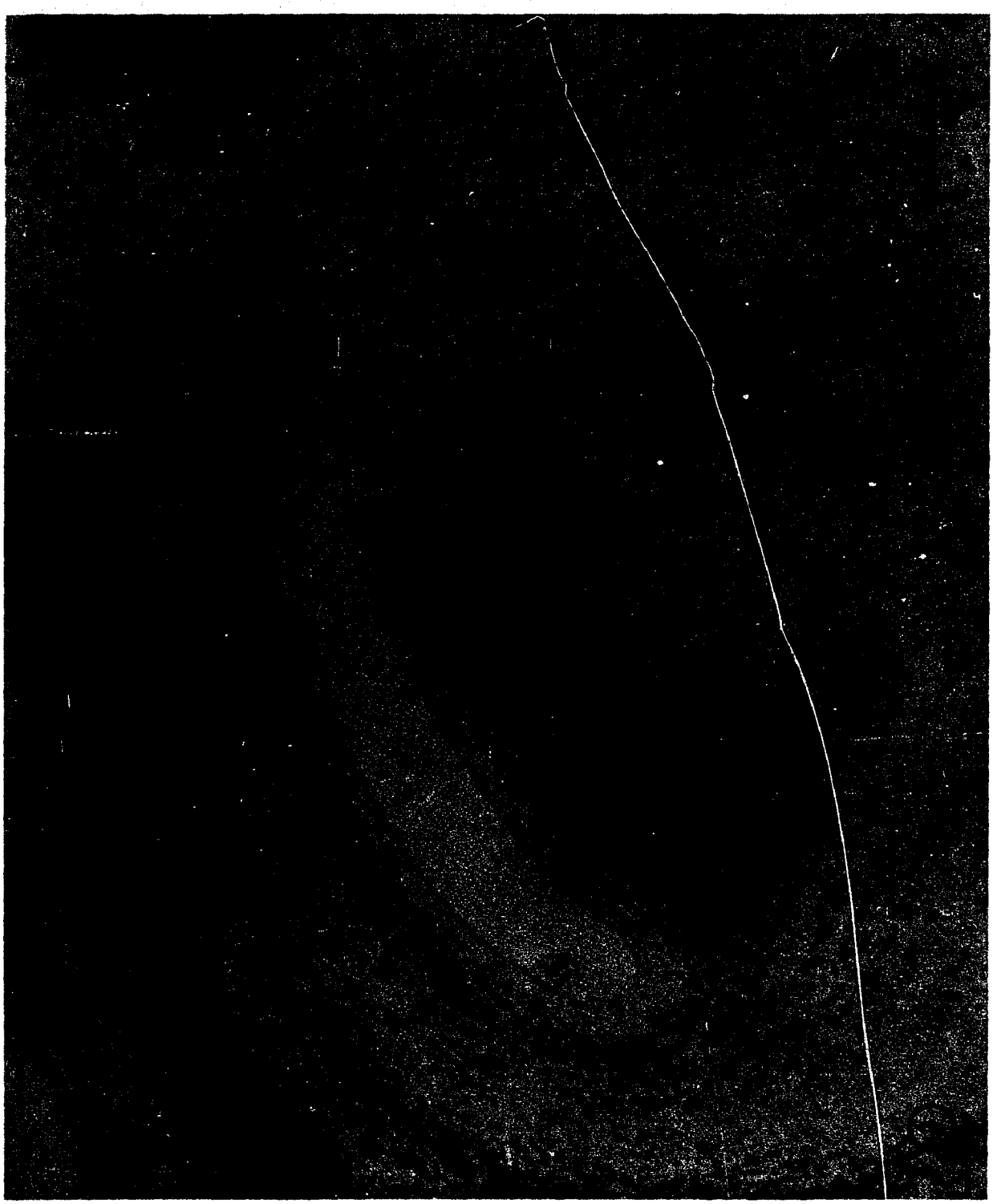


Figure 8. Sagittal section through the torus semicircularis of the chicken at a level medial to that pictured in figure 7. Nucleus mesencephalicus lateralis, pars dorsalis greatly reduced in size.

LMD - Nucleus mesencephalicus lateralis, pars dorsalis

ICO - Nucleus intercollicularis

SGP - Stratum griseum periventriculare

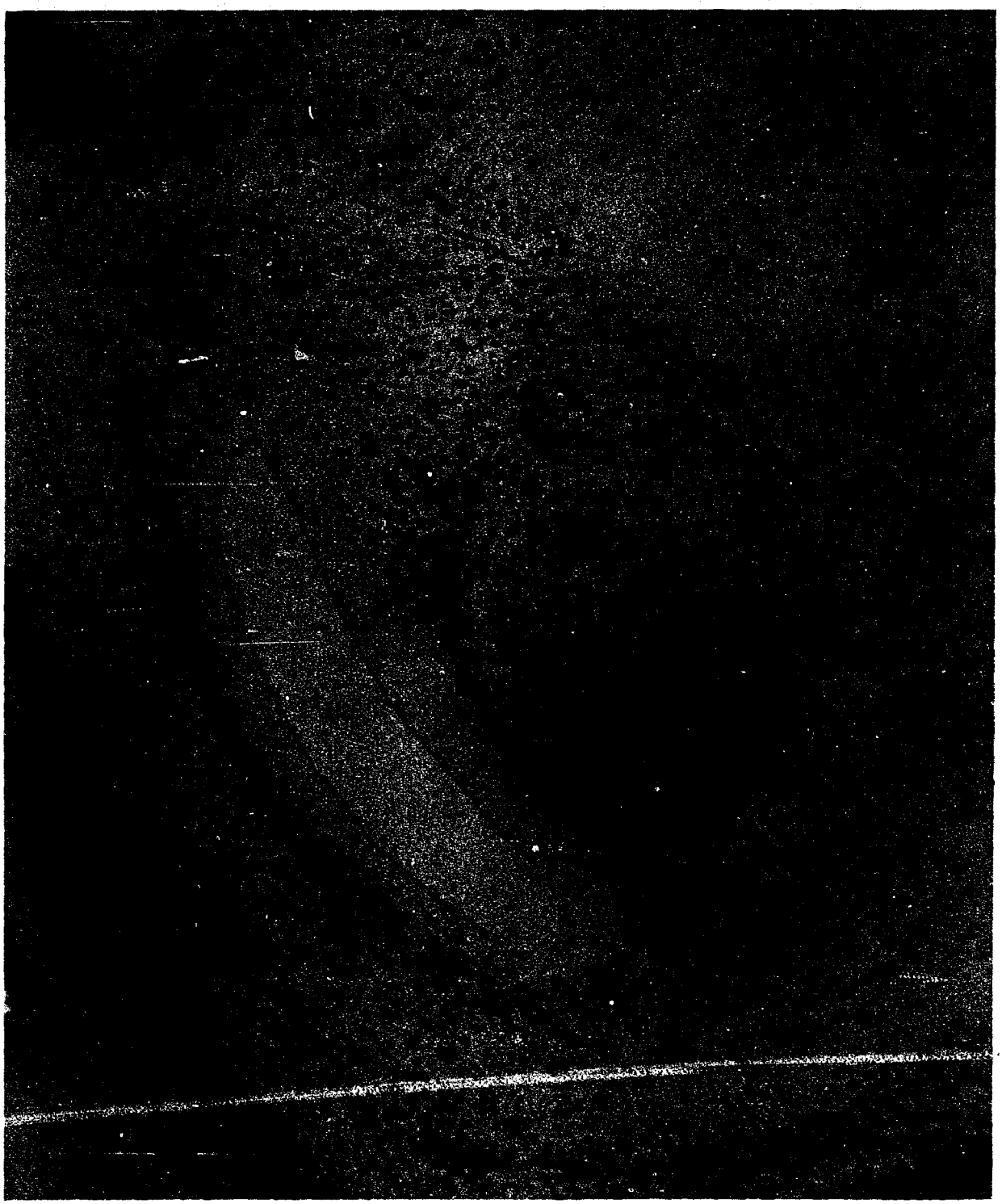


Figure 9. Sagittal section through the torus semicircularis of the chicken at a level medial to that pictured in figure 8. Nucleus intercollicularis nearly replaced by cells of the stratum griseum periventriculare.

ICO - Nucleus intercollicularis

SGP - Stratum griseum periventriculare

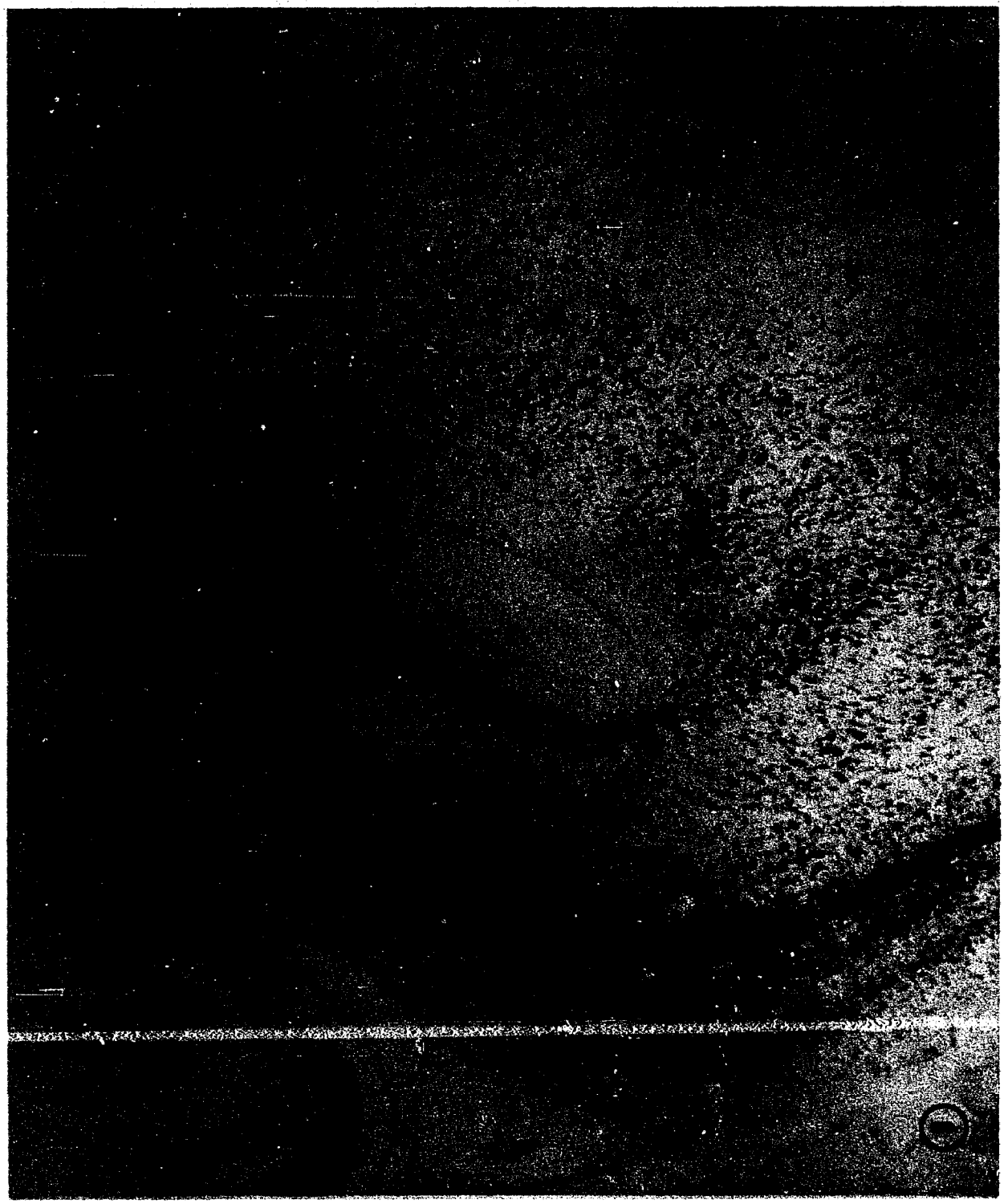


Figure 10. Composite figure of the optic lobe illustrating the locations of 72 electrode tracts.

The area of the optic lobe is indicated by the solid black line. The dashed line indicates the area of the torus. Numbers 3-9, indicate levels which correspond to sagittal sections of Fig. 3-9.

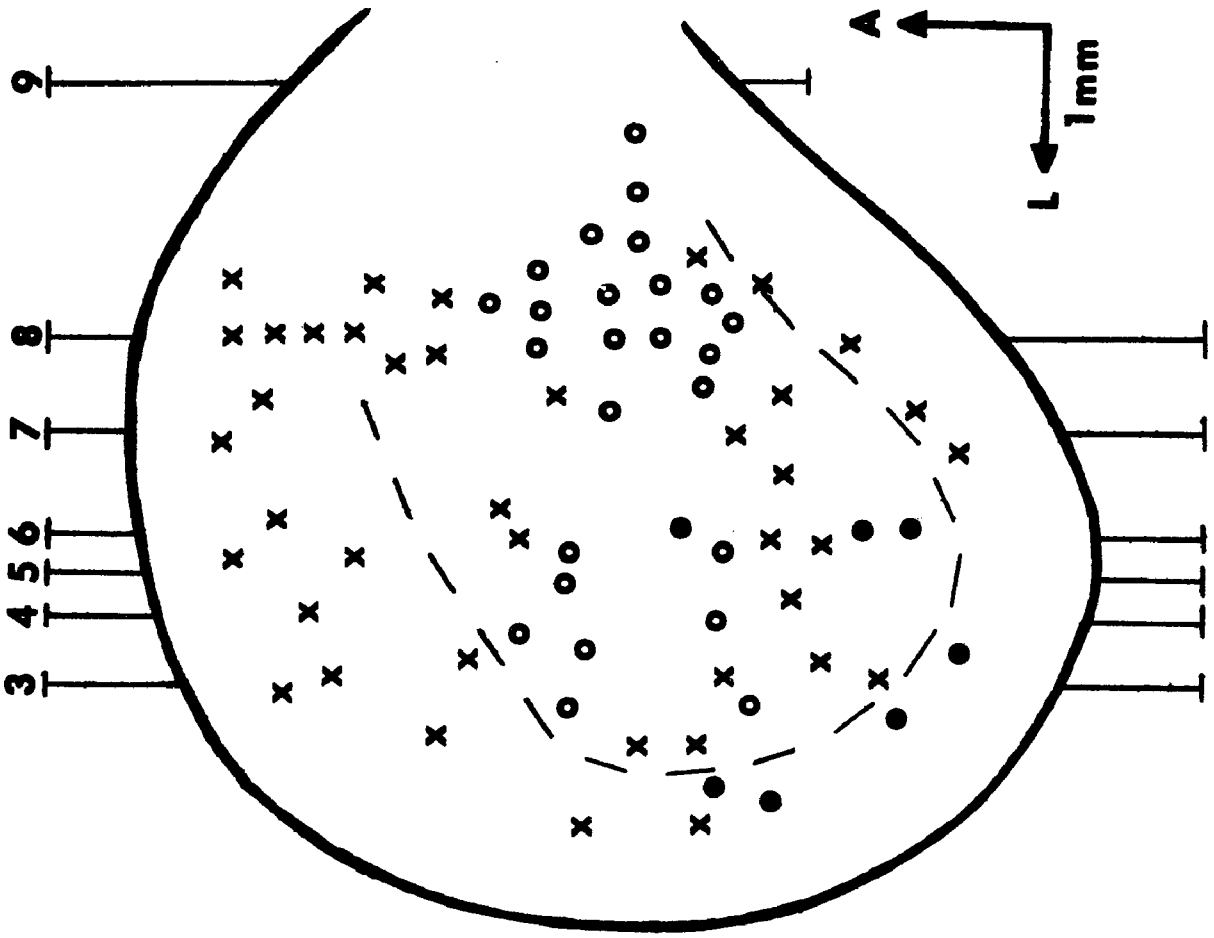
x - penetrations in which units were recorded from the stratum griseum et fibrosum superficiale of the optic tectum.

o - penetrations in which units were recorded from the toral region.

● - penetrations in which units were recorded from the stratum griseum centrale of the optic tectum.

A - anterior

L - lateral



⑩

Figure 11. Response characteristics of a unidirectional unit recorded from lamina a of the optic tectum.

An excitatory receptive field region is indicated by the outlined box. A solid black bar stimulus is represented by stippled bars. Arrows indicate direction of movement through the field.

A. Numerous spikes occurred when the leading edge of the bar was moved across receptive field.

B. No firings occurred when the receptive field region was covered by the bar.

C. A single action potential occurred when the trailing edge of the bar was moved across the receptive field.

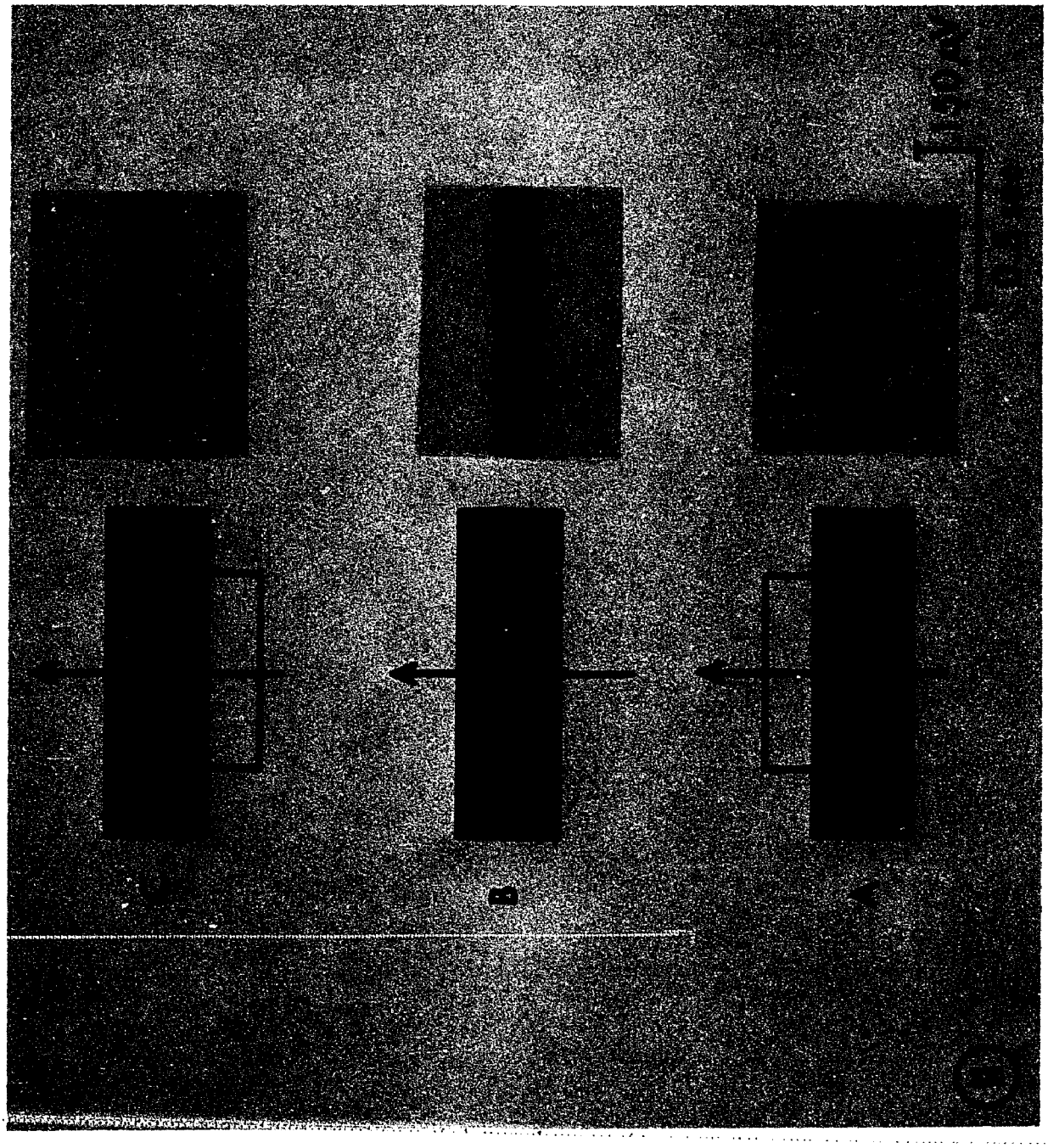


Figure 12. Pandirectional unit recorded from lamina i of the optic tectum.

The area of the unit's receptive field is indicated by the outlined box. Solid black bar stimuli are represented by stippled bars. Arrows indicate directions of stimulus movements through the unit's receptive field.

Firing pattern types during movement in rostral (A), ventral (B), caudal (C), and dorsal (D) directions are similar.

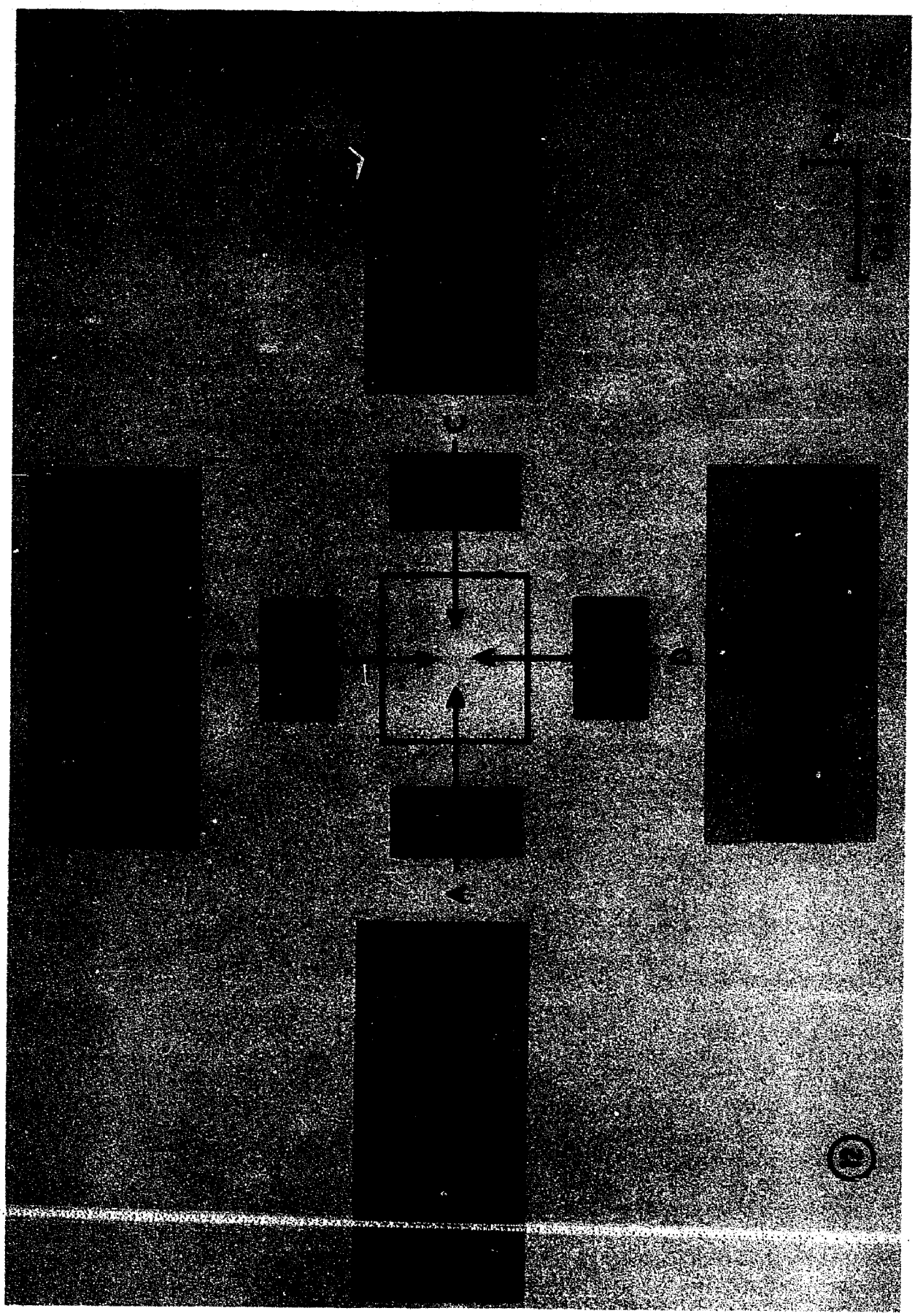


Figure 13. Multidirectional unit recorded from lamina b of the optic tectum.

The unit's receptive field is indicated by the outlined box. Solid black bar stimuli are represented by stippled bars. Arrows indicate horizontal (A), vertical (B) and oblique (C, D) directions of stimulus movements through the unit's receptive field. Arrows pointed to the right indicate rostral movements; arrows pointed to the left, caudal movements. Those pointed down indicate ventral movements; and those pointed up indicate dorsal movements. Spike trains have been retouched for clarity.

Numerous large amplitude spikes occur during movements of bar in rostral directions. Bar movements in caudal directions evoke few or no large amplitude spikes. Note small amplitude spikes occur during movements in ventral and dorsal directions.

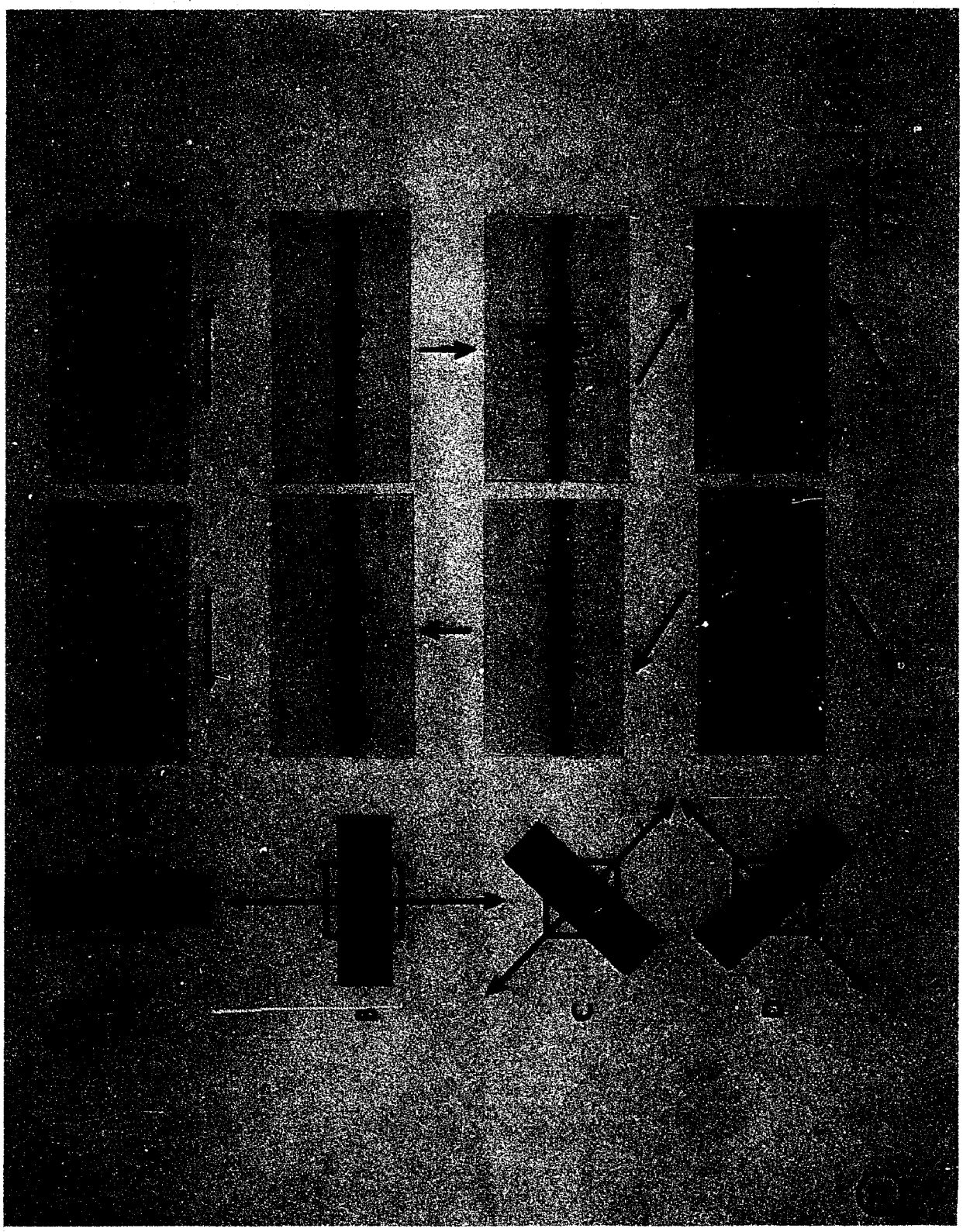


Figure 14. Excitatory and inhibitory receptive fields. Unit recorded from stratum opticum of the optic tectum.

Inhibitory regions indicated by striped areas flank a central excitatory receptive field. Arrows indicate movement of a solid black bar stimulus. Stimuli are represented by stippled bars.

In A note bar movements confined to excitatory regions elicited large spike discharges. In B simultaneous movement through excitatory and inhibitory regions resulted in a dominant inhibition. In C bar movements from the excitatory to the inhibitory area elicited large spike discharges.

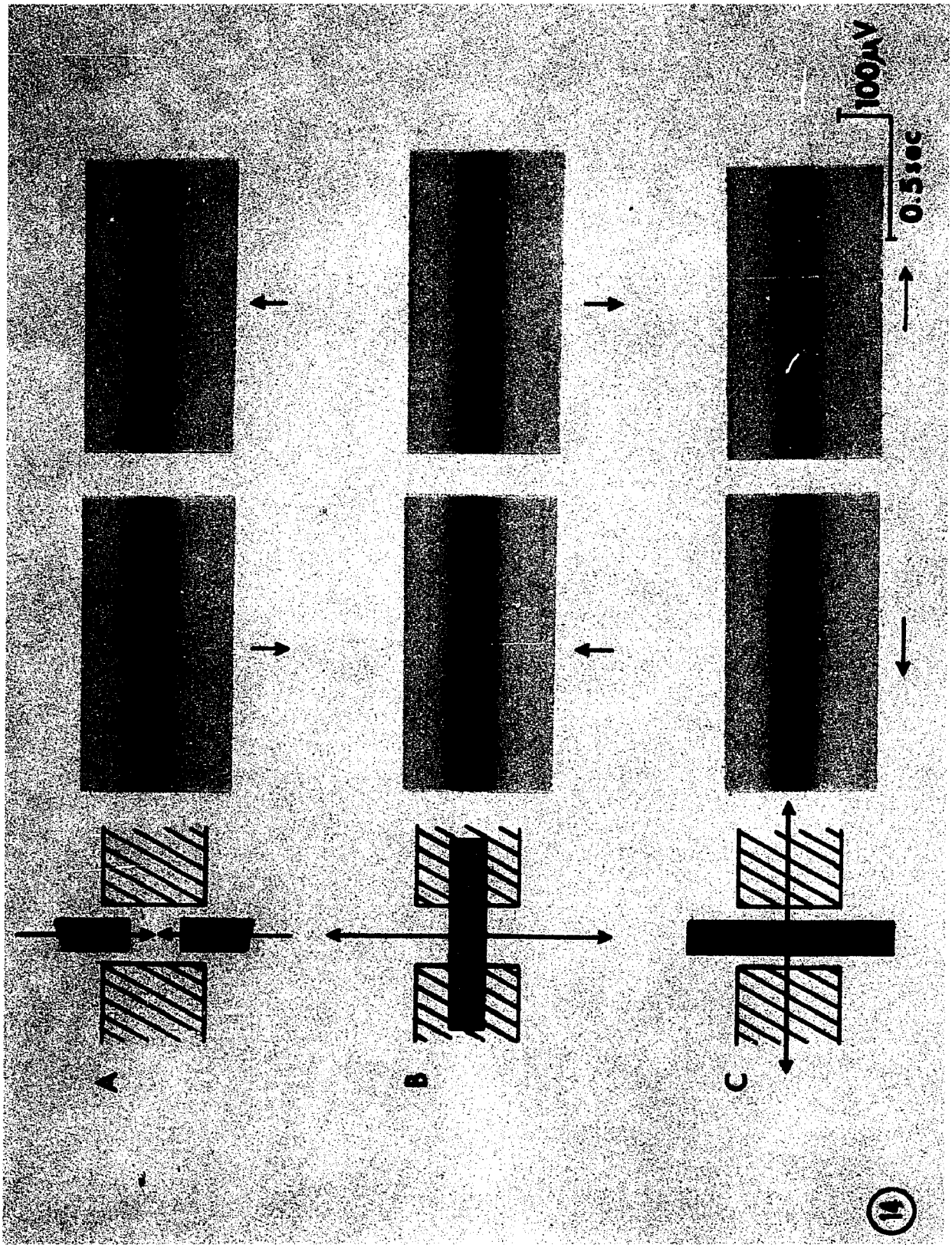

100μV
0.5sec
A
B
C

Figure 15. Visual unit recorded from the stratum opticum habituated to prolonged stimulation.

Striped areas represent inhibitory receptive field regions, with interposed excitatory receptive field region. Stippled bars represent solid black bar stimuli. Arrows indicate stimulus movements.

A. Unit habituated to prolonged stimulation of receptive field regions.

B. Unit discharge patterns following dishabituation induced by turning overhead lights off/on between sample times A and B.

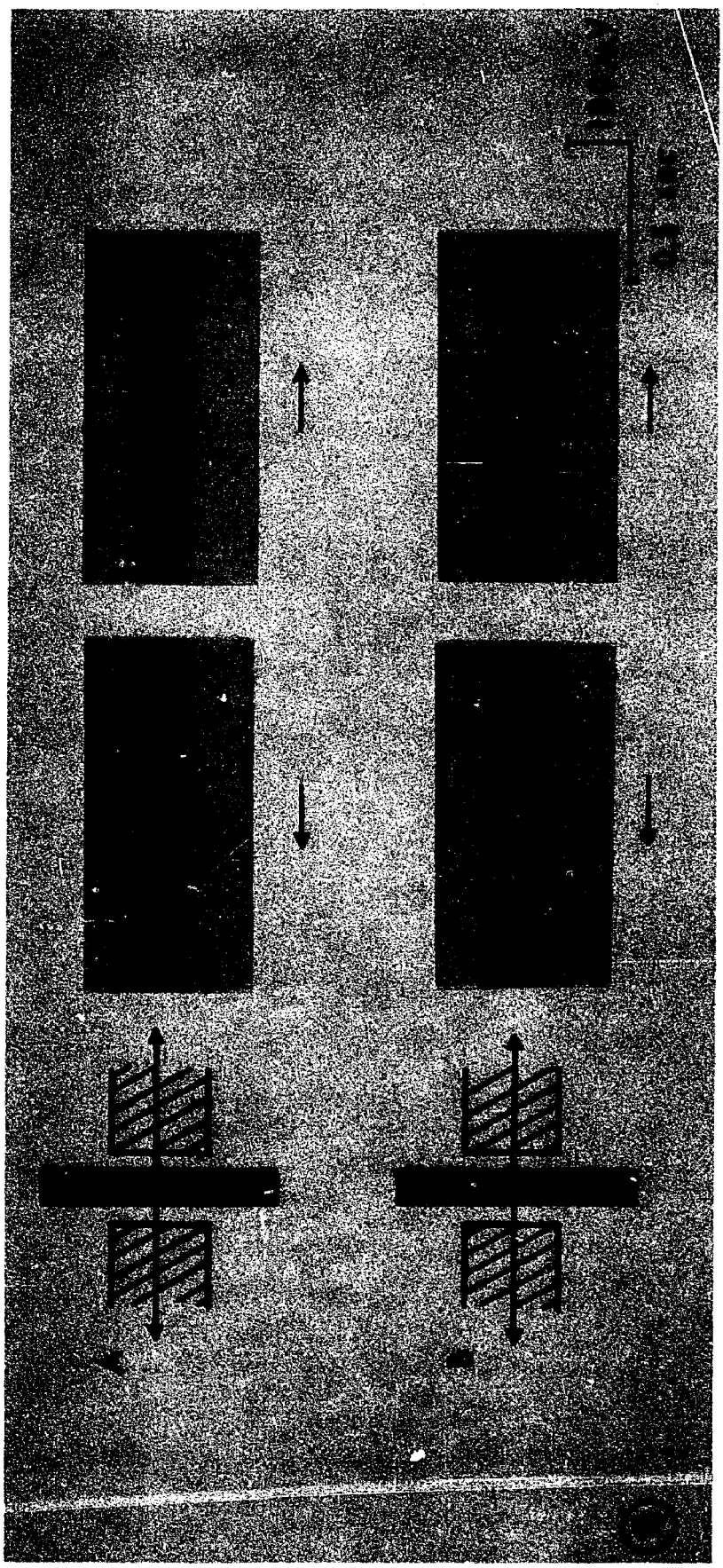


Figure 16. Bimodal unit recorded from the stratum griseum centrale of the optic tectum. Responses to somesthetic and visual stimuli.

A. Somesthetic response. Somesthetic receptive fields included the feathered body surface. Arrows indicate times the neck feathers were gently moved.

B. Visual response. The visual receptive field included almost one visual field quadrant. Tracings illustrate responses to movement of a solid black bar in rostral, ventral, dorsal, and caudal directions through the unit's receptive field. Solid black line below tracings indicate times the bar was moved.

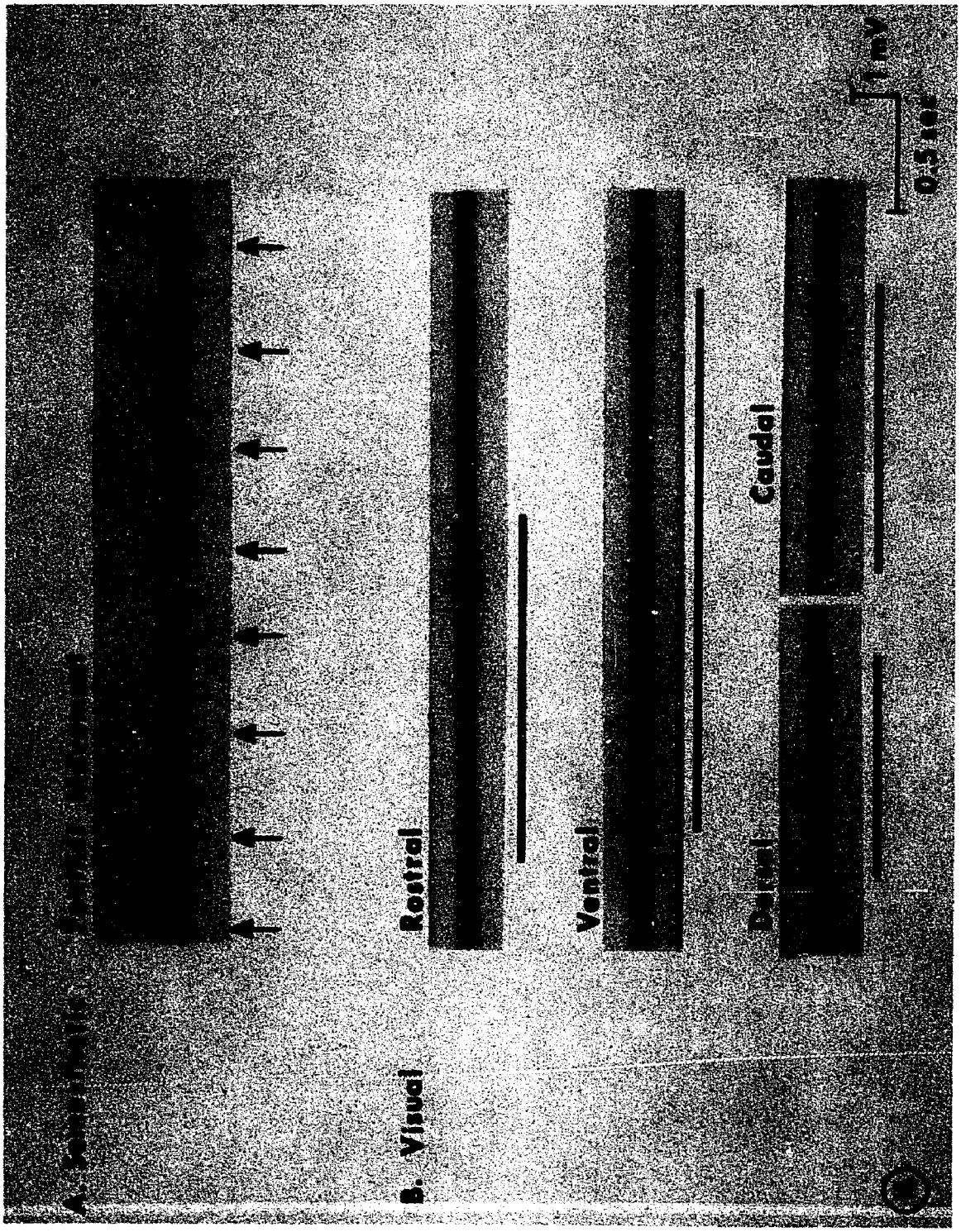

A. Auditory
B. Visual
Rostral
Ventral
Caudal
Dorsal
1 mV
0.5 sec

Figure 17. Light pressure unit recorded from the stratum griseum periventriculare.

Responses were elicited from a small receptive field located on the face. Arrows indicate times at which stimuli were applied. Note firing frequency was reduced immediately following stimulus presentations.

Figure 18. Feather movement unit recorded from the nucleus intercollicularis.

The long arrow indicates movement of a stimulus probe from lower to upper regions of the animal's neck. Note absence of firings immediately following onset of stimulus presentation. Later, discharge frequency increased to a level higher than the spontaneous rate immediately preceding the onset of stimuli.

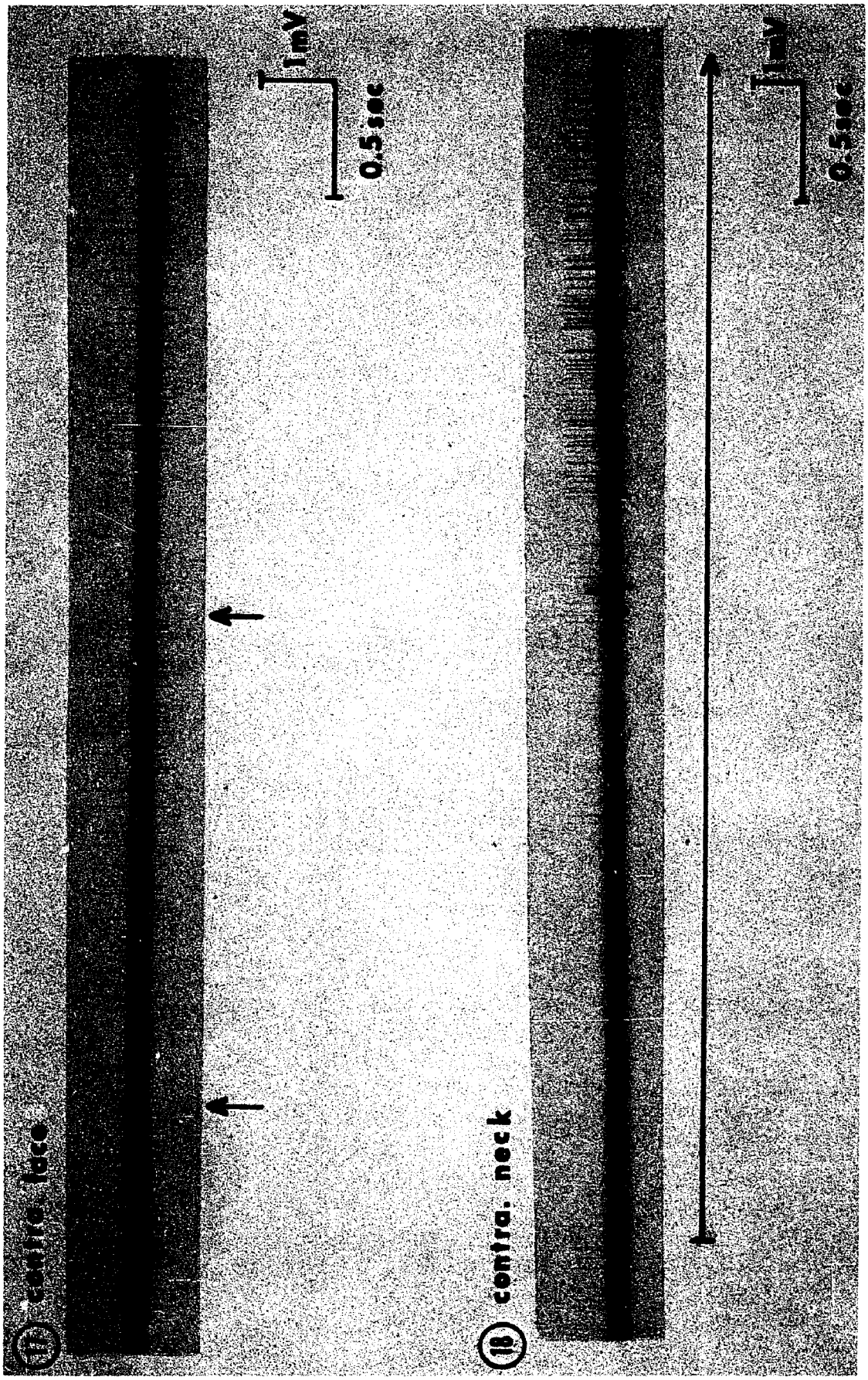

1mV
0.5sec
(17) contra. face
(18) contra. neck
1mV
0.5sec

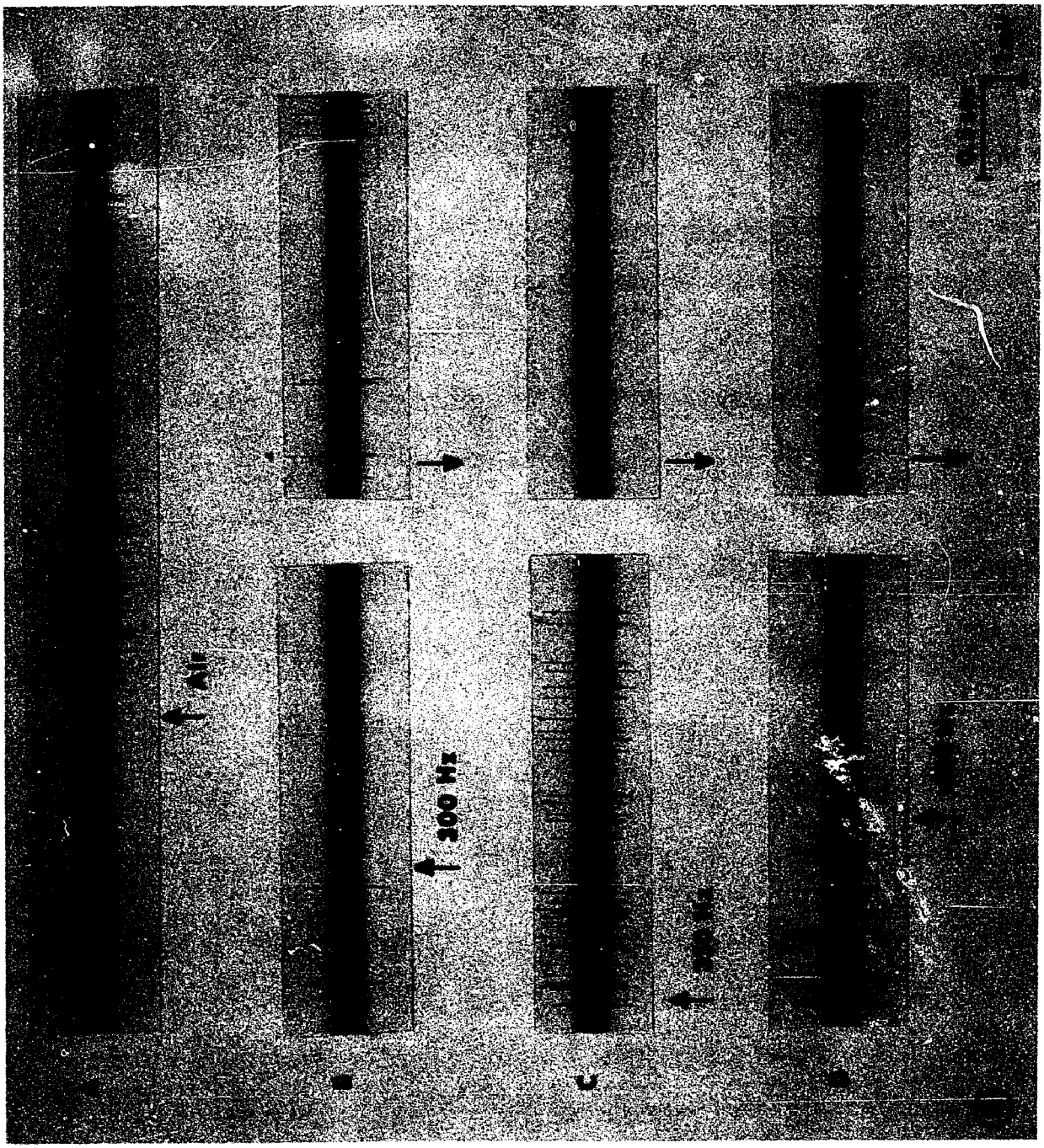
Figure 19. Bimodal unit recorded from the nucleus intercollicularis. Responses to auditory and somesthetic stimuli.

In A the arrow indicates the time when an air stimulus was applied to the feathers of the head contralateral to the recording site. In B, C, and D the break in background activity indicates records were not continuous. Arrows pointed up represent onsets of pure tone stimuli presented bilaterally; arrows pointed down represent times pure tone stimuli were terminated.

A. Firing pattern following a gentle puff of air to small group feathers on the head.

B & D. Large spikes did not occur during a continuous pure tone of 300 Hz (B), 400 Hz (D).

C. Firing pattern during a continuous pure tone of 350 Hz.


AIR
300 Hz