

THE SUPERIOR AND INFERIOR COLLICULI OF THE MOLE (*SCALOPUS AQUATICUS MACHRINUS*)

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TEN FIGURES

INTRODUCTION

This investigation is a study of the afferent and efferent connections of the tectum of the midbrain in the mole (*Scalopus aquaticus machrinus*). An attempt is made to correlate these findings with the known habits of the animal.

A subterranean animal of the middle western portion of the United States, *Scalopus aquaticus machrinus* is the largest of the genus *Scalopus* and its habits have been more thoroughly studied than those of others of this genus according to Jackson ('15) and Hamilton ('43). This animal prefers a well-drained, loose soil. It usually frequents open fields and pastures but also is found in thin woods and meadows. Following a rain, new superficial burrows just below the surface of the ground are pushed in all directions to facilitate the capture of worms and other soil life. Ten inches or more below the surface the regular permanent highway is constructed; the mole retreats here during long periods of dry weather or when frost is in the ground. The principal food is earthworms although, under some circumstances, larvae and adult insects are the more usual fare. It has been demonstrated conclusively that, under normal conditions, moles will eat vegetable matter. It seems not improbable that they may take considerable quantities of it at times.

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The single annual litter suggests that moles have few enemies. Their fossorial habits prevent hawks and owls from taking any considerable numbers in spite of the fact that the moles are active at all hours. Nevertheless they do fall prey to predatory birds and mammals.

Reed ('51) described the manner of locomotion. The greatest power is exerted by the mole when the forefeet are thrust out directly laterally; it employs them in this manner when digging the shallow burrows in which the soil is thrust up in a ridge. The mole rotates in its burrow and, thrusting from below with one forefoot, raises the roof of the burrow with the other. Then the animal rotates its whole body 180°, or nearly so, and repeats the process. In excavation of deeper burrows, in which the roof cannot be elevated, only one forefoot is used at a time, while the other is braced against the side of the burrow. The earth is loosened by lateral strokes of first one forelimb and then the other, the earth being thrown back beside and beneath the body. After a period of such activity the mole then turns around in the newly formed burrow, the diameter of which is scarcely more than that of its own body, and proceeds to shove the dirt out, using one outthrust forefoot as a pusher, with the neck and thorax bent to one side and locomotion achieved by use of the other three limbs; this same posture is maintained when pushing dirt out onto the surface. Under such conditions the hind limbs are performing the major part of the locomotor effort. Out of its burrow the mole is a clumsy animal, progressing awkwardly by running with its hind legs while trying to support the heavy front part of the body on its outstretched front legs, which are in contact with the ground only on the edge of the thumb.

The microscopic study shows a poorly developed optic system, a well developed acoustic system and a smaller superior than inferior colliculus. The other afferent and efferent fiber connections of the midbrain generally conform to those of other insectivores, rodents and marsupials.

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MATERIALS AND METHODS^{2,3}

Twelve live specimens were obtained from the vicinity of Lansing, Michigan. The animals were anesthetized with ether and the anterior thoracic walls were opened. Six animals were perfused with ammoniated alcohol and 6 with 10% formalin.

Serial sections of three of the brains that had been fixed in formalin and then sectioned transversely (two) or sagittally (one) were stained with toluidin blue. Two series (one cut transversely, one sagittally) were stained by the Weil technique. Five brains were prepared by the Huber-Guild pyridine silver method. Two of them were sectioned in a transverse, two in a horizontal and one in a sagittal plane.

Photomicrographs were taken of appropriate sections to illustrate the subject matter of this investigation.

LITERATURE

The mammalian midbrain has been a subject of exhaustive study by a large number of investigators. Ganser (1882) provided a classic description of the rostral regions of the mole brain. He was the first to describe the optic pathways of this form in detail. The pioneer work of Ramón y Cajal ('11) presented a detailed account of the histology of the midbrain in various mammals. Castaldi ('23, '24, '26) described the fiber connections of the midbrain of lower mam-

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mals in a series of papers. The work of Ariëns Kappers, Huber and Crosby ('36) includes a thorough account of the structure and fiber connections of the midbrain for a series of mammals.

The more recent work of Huber et al. ('43) contributed much to the knowledge of the nuclear groups of the tegmental portions of the mammalian midbrain from the marsupial to man. Woodburne, Crosby and McCotter ('46) described the connections of the basal ganglia with the midbrain tegmentum in the macaque. Later experimental work by Crosby and Henderson ('48) established certain cortico-tectal connections of the superior colliculi in the macaque and the relation of these centers to automatic eye movements.

Tsai ('25a) traced the optic tracts in the opossum. Brouwer ('27) described the projection of the retina on the superior colliculus of the rabbit and Lashley ('34) demonstrated the distribution of optic tract fibers in the superior colliculus of the rat. Barris, Ingram and Ranson ('35) described the optic connections of the diencephalon and midbrain of the cat. Gillilan ('41) reported the connections of the basal optic root in the shrew and found that this pathway was not so reduced as the optic tract. Many observers have described the optic system in higher mammals.

The gross structure of the brain of various European insectivora has been described by Le Gros Clark ('33). Other references related to the various fiber connections of the midbrain will be incorporated in the description of the material and in the discussion.

NUCLEAR PATTERN OF THE TECTUM

The nuclear pattern of the inferior colliculus

The nucleus of the inferior colliculus is very large in this animal (fig. 9). In it can be recognized a central nucleus with large multipolar cells the axons of which pass through the brachium of the inferior colliculus to enter the medial geniculate nucleus. This central nucleus is surrounded by a

fibrous capsule which is formed by the fibers of the lateral lemniscus and the peduncle of the inferior colliculus together with cells continuous with the outer layers of the superior colliculus as they turn into the nucleus (fig. 9). The chief nucleus is continuous with the periventricular gray of the area in front of it.

The layering of the superior colliculus

Although many of the layers of the optic tectum are reduced, 8 layers (figs. 4 and 5) can be distinguished in the optic tectum of the mole.

1. *Stratum zonale*. This layer is very thin and is composed of a small number of external cortico-tectal fibers. Ganser (1882) did not demonstrate this layer in the mole. It corresponds to w_1 of Frankl-Hochwart ('02) for *Spalax typhlus* (a European mammal corresponding to the American gopher) and to the stratum zonale of Winkler and Potter ('11 and '14) for the rabbit and cat, Tsai ('25b) for the opossum, and Huber and Crosby ('43) for mammals in general.

2. *Stratum griseum superficiale*. This area consists of small and medium-sized cells and some of the endings of the external cortico-tectal fibers. It corresponds to the oberflächliches Grau of Ganser (1882) for the mole, g_1 of Frankl-Hochwart ('02) for *Spalax typhlus* and the stratum griseum superficiale of Winkler and Potter ('11 and '14) for the rabbit and cat, Tsai ('25b) for the opossum and Huber and Crosby ('43) for mammals in general.

3. *Stratum opticum*. This area is extremely minute with small bundles of optic tract fibers which split as they enter the tectum and terminate medially and laterally. This layer is comparable to the oberflächliches Mark of Ganser (1882) for the mole, w_2 of Frankl-Hochwart ('02) for *Spalax typhlus*, to the stratum medullare superficiale of Winkler and Potter ('11 and '14) for the rabbit and cat, and to the stratum opticum of Tsai ('25b) for the opossum and Huber and Crosby ('43) for various mammals.

4. *Stratum griseum intermediale*. This is the layer of termination for the spino-tectal, incerto-tectal, nigro-tectal and habenulo-tectal fibers. It is not clearly delimited from layer 5, the stratum album intermediale, which is the region where the ventral secondary ascending tract of the trigeminal and the internal cortico-tectal fibers end. The stratum griseum intermediale contains medium-sized polygonal cells and fiber fascicles. It corresponds to the mittleres Grau of Ganser (1882) for the mole, to g_2 of Frankl-Hochwart ('02) for *Spalax typhlus*, to stratum griseum intermedium of Winkler and Potter ('11 and '14) for the rabbit and cat, to stratum griseum medius of Tsai ('25b) for the opossum, and to stratum griseum intermediale of Huber and Crosby ('43) for mammals in general.

5. *The stratum album intermediale* is comparable to the mittleres Mark of Ganser (1882) for the mole, w_3 of Frankl-Hochwart ('02) for *Spalax typhlus*, stratum medullare intermedium of Winkler and Potter ('11 and '14) for the rabbit and cat, stratum album medius of Tsai ('25b) for the opossum, and the stratum album intermediale of Huber and Crosby ('43) for mammalian forms.

6. *Stratum griseum profundum*. This layer consists of large and small polygonal cells and fiber fascicles and contains some of the cells of origin of the medial tecto-spinal, tecto-oculomotor, tecto-rubral, tecto-tegmental, lateral tecto-spinal and tecto-nigral tracts. However other cell layers of the superior colliculus also contribute fibers to the efferent paths. It corresponds to the tiefes oder röhrenförmiges Grau of Ganser (1882) for the mole, g_3 of Frankl-Hochwart ('02) for *Spalax typhlus*, stratum griseum profundum of Winkler and Potter ('11 and '14) for the rabbit and cat, Tsai ('25b) for the opossum and Huber and Crosby ('43) for mammals.

7. *Stratum album profundum*. This layer is formed mainly by large parallel bundles of heavily medullated, efferent fibers of the medial tecto-spinal, tecto-oculomotor, tecto-rubral, tecto-tegmental, tecto-pontine, and the lateral tecto-spinal tracts. It is the efferent layer of the superior colliculus and is repre-

sented in the tiefes Mark of Ganser (1882) for the mole, in w_4 of Frankl-Hochwart ('02) for *Spalax typhlus*, in the stratum medullare profundum of Winkler and Potter ('11 and '14) for the rabbit and the cat, and in the stratum album profundum of Tsai ('25b) for the opossum and Huber and Crosby ('43) for mammals.

8. *Stratum griseum periventriculare pars dorsalis*. This layer contains medium- and small-sized cells with the finely medullated and unmedullated acustico-optic fiber fascicles interspersed among the cells. Most students of mammalian brains have not considered the periventricular layers as a part of the optic tectum. Crosby and Woodburne ('43) considered the pars dorsalis of the periventricular gray in the shrew as part of the midbrain tegmentum. Tsai ('25b) referred to the periventricular gray in the midbrain of the opossum as the substantia grisea centralis.

THE FIBER CONNECTIONS OF THE TECTUM

Afferent pathways to the tectum

Optic tract

Le Gros Clark ('33) found that a characteristic feature of a number of insectivores is the very small optic nerve and tract which are associated with a small lateral geniculate body in which the ventral nucleus is larger and the dorsal nucleus is smaller and poorly developed.

The optic chiasma (fig. 2) is microscopic in size as it lies on the ventral surface of the diencephalon. It is not possible to determine whether the optic tract crosses completely in the chiasma in this material. The fibers sweep in a caudo-lateral direction from the chiasma and then dorsolaterad around the ventrolateral border of the diencephalon. As the tract approaches the cerebral peduncle, fibers are given off to the nucleus of the basal optic root. Gillilan ('41) studied the optic tracts and basal optic root in the shrew and concluded that reduction in size of the accessory optic tracts, especially of the tractus opticus basalis or the basal optic

root, is not proportional to the reduction in size of the optic tract. The present material would tend to document this statement for the mole. At the dorsolateral region of the diencephalon part of the fibers enter the lateral geniculate

 ABBREVIATIONS

- AQ., aqueduct.
 BRACH. CONJ., brachium conjunctivum.
 BRACH. I.C., brachium of the inferior colliculus.
 BRACH. PONT., brachium pontis.
 CEREBR. PED., cerebral peduncle.
 COMM. INF. COL., commissure of the inferior colliculus.
 DEC. BRACH. CONJ., decussation of the brachium conjunctivum.
 DEC. TRAP. FIB., decussation of trapezoid fibers.
 D. COCH. NUC., dorsal cochlear nucleus.
 D. NUC. LAT. LEMN., dorsal nucleus of the lateral lemniscus.
 D. NUC. RAPHÉ, dorsal nucleus of raphé.
 D. TEG. DEC., dorsal tegmental decussation.
 EXT. CORT. TECT., external cortico-tectal tract.
 HAB. PED. TR., habenulo-peduncular tract.
 HYPOTHAL., hypothalamus.
 INF. COL., inferior colliculus.
 INF. THAL. RAD., inferior thalamic radiations.
 INT. CORT. TECT., internal cortico-tectal tract.
 INTERPED. NUC., interpeduncular nucleus.
 LAT. GEN. NUC., lateral geniculate nucleus.
 LAT. LEMN., lateral lemniscus.
 LAT. TECT.-SP., lateral tecto-spinal tract.
 MED. GEN. NUC., medial geniculate nucleus.
 MED. LEMN., medial lemniscus.
 MED. TECT.-SP., medial tecto-spinal tract.
 M.L.F., medial longitudinal fasciculus.
 NIG.-TECT., nigro tectal tract.
 NUC., nucleus.
 NUC. DESC. RT. TRIG., nucleus of the descending root of the trigeminal.
 NUC. FAC., nucleus of facial nerve.
 NUC. INF. COL., nucleus of the inferior colliculus.
 NUC. OCUL. N., nucleus of oculomotor nerve.
 NUC. TROCH. N., nucleus of trochlear nerve.
 OP. CH., optic chiasm.
 OP. TR., optic tract.
 PERIV. GR., periventricular gray.
 PONS, pons.
 PONT. GR., pontine gray.
 PRETECT. AREA, pretectal area.
 PYR., pyramid.
 REST. BOD., restiform body.
 R. NUC., red nucleus.
 RT. FAC., root of the facial nerve.
 RT. TRIG. N., root of the trigeminal nerve.
 S. NIGRA, substantia nigra.
 SP.-TECT., spino-tectal tract.
 STR. ALB. PROF., stratum album profundum.
 STR. ALB. INTERMED., stratum album intermediale.
 STR. GRIS. INTERMED., stratum griseum intermediale.
 STR. GRIS. PERIV., stratum griseum periventriculare.
 STR. GRIS. PROF., stratum griseum profundum.
 STR. GRIS. SUPERFIC., stratum griseum superficiale.
 STR. OPT., stratum opticum.
 STR. ZON., stratum zonale.
 SUP. COL., superior colliculus.
 SUP. OL., superior olive.
 SUP. THAL. RAD., superior thalamic radiations.
 TECT.-NIGR., tecto-nigral tract.
 TECT.-PONT., tecto-pontine tract.
 TECT.-RUBR., tecto-rubral tract.
 TECT.-TEG., tecto-tegmental fibers.
 TRAP. FIB., trapezoid fibers.
 VENT. CAUD. NUC. LAT. LEMN., ventral caudal nucleus of lateral lemniscus.
 V. COCH. NUC., ventral cochlear nucleus.
 VENT., ventricle.
 V. SEC. ASC. TR. TRIG., ventral secondary ascending tract of trigeminal.
 V. TEG. DEC., ventral tegmental decussation.
 Z. INC., zona incerta.

nucleus, others continue around the periphery of the diencephalon towards the superior colliculus. Most of the optic tract fibers distributing to the lateral geniculate nucleus terminate in its ventral nucleus, the dorsal nucleus of the lateral geniculate is very poorly developed consisting only of small, scattered cells.

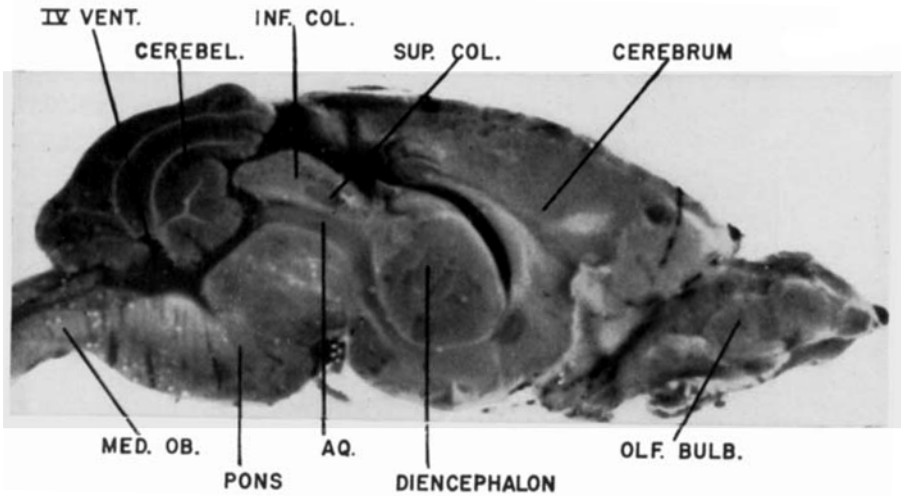


Fig. 1 Photograph of a midsagittal section of the brain of the mole (*Scalopus aquaticus maehrinus*). Note the difference in size of the superior and inferior colliculi. Formalin fixation. $\times 8$.

Tsai ('25a) described the lateral geniculate body in the opossum and pointed out that it formed nearly the entire lateral aspect of the thalamus. He found that the dorsal division of the nucleus is well developed containing both large and small cells; the ventral division contains small cells and fewer optic tract fibers enter it. Woollard ('26) studied the lateral geniculate body of various mammals; he concluded that the pars dorsalis, which is a phylogenetically more recent structure, is better developed in higher than lower mammals and has only slight representation in lower nocturnal mammals. Barris, Ingram and Ranson ('35) offered evidence that few if any fibers of optic tract origin establish synaptic

connections with the ventral nucleus of the lateral geniculate body in the cat, although it is true that many of these fibers pass through this nucleus as they approach the dorsal nucleus.

The optic tract in the mole, very small in size after it has contributed fibers to the nucleus of the basal optic root and to the lateral geniculate nucleus, continues dorsocaudad (figs.

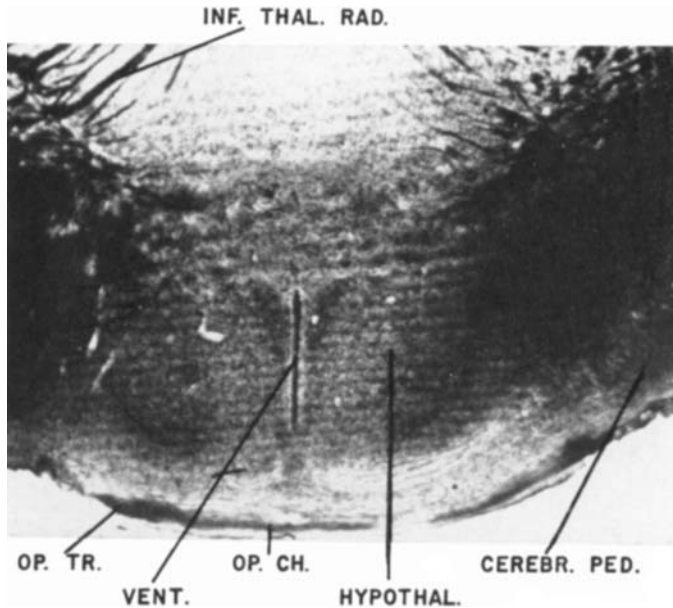


Fig. 2 Photomicrograph of a transverse section passing through the rostral portion of the diencephalon of the mole at the level of the optic chiasm. Silver preparation. $\times 30$.

3 and 4) into the midbrain where the remaining fibers terminate in the superior colliculus. As the optic fibers approach the superior colliculus, they divide so that some of them enter the tectum laterally and the others enter it medially, to repeat the pattern of mammalian optic fiber terminations in the tectum. The number of fibers contributed to the superior colliculus is very slight, nevertheless the superior colliculus in the mole is well developed (figs. 1 and 4). Lashley ('34) described a similar distribution of optic tract fibers

in the superior colliculus of the rat. In the rat the temporal quadrants of the retina are projected to the anterolateral, the nasal quadrants to the posteromedial portions of the superior colliculus; the upper quadrants are projected laterad to the lower quadrants. Brouwer and Zeeman ('26) were unable to establish the pattern of projection of the retina on the superior colliculus of the cat because, according to their own statement, their material was not adequate. However, Brouwer ('27) determined the projection of the retinal quadrants on the superior colliculus of the rabbit and found that the lower quadrants are projected to oral and medial portions and the upper quadrants to caudal and lateral regions. He implied that the superior colliculus is of much higher significance for sight in rabbits than in higher mammals and that it does not serve merely for reflex movements in these rodents.

Auditory system

The dorsal and ventral cochlear nuclei (fig. 10) are very prominent in the mole with large numbers of fibers passing by way of the lateral lemniscus to distribute to the inferior colliculus, where, after relay, they distribute by the peduncle of the inferior colliculus to the medial geniculate nucleus of the thalamus.

Stokes ('12) placed the cochlear nuclei medial to the restiform body in the opossum but this is not their position in the mole where they occupy positions typical for most mammals. The dorsal cochlear nucleus of this insectivore lies dorsolateral to the inferior cerebellar peduncle. The fibers arising from this nucleus are both crossed and uncrossed. Some of the fibers curve around the dorsal border of the inferior cerebellar peduncle, others pass through the peduncle; these fibers then turn ventromedial towards the raphé. Many of them accumulate in the lateral lemniscus of the same side, which lies at this level between the genu of the facial nerve dorsally and the facial nerve and the motor nucleus of that nerve ventrally. The decussating fibers cross the midline dorsal to the genu of

the facial nerve to accumulate in the lateral lemniscus of the opposite side (fig. 10).

The trapezoid fibers arising from the ventral cochlear nucleus pass ventromediad along the border of the pons, then decussate to reach the lateral lemniscus of the opposite side (fig. 10). After decussation many of these fibers enter the superior olivary nucleus, which lies ventrolateral to the motor nucleus of the facial nerve (figs. 9 and 10). The trapezoid fibers cross dorsal to the fiber bundles constituting the basilar part of the pons and through the ventral part of the medial lemniscus (figs. 9 and 10). Fibers from the superior olivary nucleus and the trapezoid body accumulate dorso-lateral to the superior olive and medial to the nucleus of the descending root of the trigeminal (fig. 9 right) and, in this position, join the dorsal cochlear fibers to the lateral lemniscus. The lateral lemniscus as it passes in a dorsal and rostral direction toward the inferior colliculus (figs. 9 to 8) is a very large and prominent bundle of fibers near the lateral surface of the brainstem. Many of the fibers of this bundle are in synaptic relation with the large nuclei of the lateral lemniscus in their course towards the inferior colliculus (fig. 8). These nuclei are very prominent in the lateral portion of the field. In her description of the midbrain of unguates Gillilan ('43) subdivided the gray associated with the lateral lemniscus into a dorsal nucleus, a caudal ventral nucleus, and a rostral ventral nucleus. A dorsal nucleus and a caudal ventral nucleus of the lateral lemniscus are represented in the mole.

Fibers also pass directly from the lateral lemniscus to the medial geniculate body. These fibers of the lateral lemniscus are found at the dorsal tip of the medial lemniscus and they turn laterad into the medial geniculate nucleus with the fibers of the brachium of the inferior colliculus (fig. 7).

From the nucleus of the inferior colliculus, fascicles pass by way of the brachium of the inferior colliculus (figs. 9 to 6) to the massive medial geniculate nucleus (figs. 6 and 5) of the diencephalon, which overlies the lateral surface of the midbrain at the level of the superior colliculi. Many ob-

servers (as Ariëns Kappers, Huber and Crosby, '36) refer to the inferior colliculus as an auditory reflex center which receives auditory impulses and then discharges to the superior colliculus and the medial geniculate nucleus, a meta-thalamic auditory center mediating impulses to the cerebral cortex. Mettler ('32) studied the effects of lesions in the auditory cortex of cats and stated that it is possible that certain of the axis cylinders in the brachium of the inferior colliculus do not stop in the medial geniculate bodies but pass beyond to the cortex. Woollard and Harpman ('40) placed lesions in the inferior colliculus of guinea pigs and cats and suggested that some fibers pass directly from the inferior colliculus to the cerebral cortex. The present material furnished no satisfactory evidence for direct colliculo-cortical fibers.

Spino-tectal tract

The spino-tectal tract occupies a position in the lateral funiculus of the spinal cord adjacent to the spino-thalamic tract in many mammals. It is impossible to ascertain the exact position of this pathway in the spinal cord in normal material. This tract ascends through the spinal cord to enter the ventrolateral region of the medulla oblongata, a position which it maintains at lower medullar levels. At such levels in the mole it lies ventromedial to the spino-thalamic tract and to the nucleus of the descending root of the trigeminal. The spino-tectal tract becomes more distinct as it ascends through the medulla ventromedial to the nucleus of the descending root of the trigeminal and ventrolateral to the internal arcuate fibers as they swing into the sensory decussation. At the level of the inferior olivary nucleus it lies lateral to this olivary nucleus, ventromedial to the nucleus of the descending root of the trigeminal, and in proximity to the ventral secondary ascending tract of the latter. Cerebello-olivary and olivo-cerebellar fibers passing towards the restiform body overlie the tract and the external arcuate fibers are ventral to it along the ventral border of the medulla

oblongata. The spino-tectal tract continues its rostral course with the lateral spino-thalamic and ventral secondary ascending tract of the trigeminal, along the dorsolateral portion of the olive, ventromedial to the secondary ascending tract of the trigeminal. It occupies this position in the ventrolateral region of the medulla throughout the level of the inferior olive. At rostral levels of the medulla it still lies ventrolateral to the descending root of the trigeminal. At the level of the genu of the facial nerve and the decussating dorsal cochlear fibers, the spino-tectal tract lies lateral to the superior olivary nucleus, medial to the descending root of the trigeminal, and lateral to the root of the facial nerve as the latter passes ventrally from the genu (fig. 10). Through the pons, the medial lemniscus is horizontal in position but gradually shifts laterad as it ascends so that above the rostral end of the superior olive it approaches the lateral spino-thalamic and spino-tectal systems (fig. 8). Fibers of the lateral lemniscus en route to the inferior colliculus cross these pathways. At the caudal levels of the superior colliculus the fibers of the spino-tectal tract course dorsad in the lateral region of the midbrain towards the tectum (figs. 7 and 6), entering its stratum album intermediale. These fibers are mingled with fibers from the ventral secondary ascending tract of the trigeminal in their passage towards the tectum. At the level of the dorsal tegmental decussation (fig. 6), the medial lemniscus has turned dorsolateralward with the ventral secondary ascending tract of the trigeminal on its dorsomedial border. Papez ('29) placed the spino-tectal tract at the dorsal tip of the medial lemniscus in the cat. Crosby and Henderson ('48) found that the spino-tectal fascicles form the uppermost part of the macaque medial lemniscus at upper midbrain levels and that these fibers of the spino-tectal system swing in a dorsal direction to enter the superior colliculus external to the stratum album profundum.

Ventral secondary ascending tract of the trigeminal

The trigeminal root in the mole is large, as is to be expected since the animal depends to so great an extent upon

pain, temperature, and tactile sensibility from the nose regions. The descending root fibers occupy a position in the lateral regions of the medulla oblongata and the pons just as they do in other mammals (fig. 10). The nucleus of the descending root of the trigeminal is also very large and lies medial to the descending root in the medulla and pons. The ventral secondary ascending tract crosses in bundles to the opposite side at various levels of the brainstem. At the level of the inferior olivary nucleus and the nucleus and rootlets of the hypoglossal nerve, the fibers of this ventral secondary ascending tract cross to the opposite side through the medial raphé to a position dorsolateral to the inferior olive and lateral to the root of the hypoglossal nerve.

The tract ascends in this position throughout the level of the inferior olivary nucleus as more fiber bundles are added to it in its rostral course. Cerebello-olivary and olivo-cerebellar fibers are mingled with the fibers of the ventral secondary ascending tract as they cross the raphé to reach the inferior cerebellar peduncle. This tract gradually shifts laterad in its forward course through the rostral portion of the medulla and the caudal portion of the pons. At the level of the superior olivary nucleus and the facial root, it lies between the superior olive and the descending root and dorsal to the trapezoid fibers. Some of these trapezoid fibers pass through it in their course towards the opposite side of the brain. At the level of the rostral half of the pons, the tract lies in the ventral portion of the field lateral to the root of the facial nerve, medial to the nucleus of the descending root of the trigeminal nerve, and dorsal to the trapezoid body (fig. 10). It then shifts to a more dorsal position in the tegmental areas (fig. 9). At the level of the rostral third of the inferior colliculus the ventral secondary ascending tract of the trigeminal lies medial to the lateral lemniscus (fig. 8).

After the medial lemniscus has rotated so that its lateral tip has become dorsolateral in position (fig. 7), the fiber bundles of the ventral secondary ascending tract lie medial to the medial lemniscus. Some of the fibers leave the tract

to enter the tectum (fig. 6) by the intermediate white layer of the superior colliculus (fig. 5). The main bundles of fibers then continue forward to the thalamus, medial to the medial lemniscus. Woodburne ('36) described the trigeminal complex in a series of vertebrates and found that in the rabbit and mouse a small number of fibers of the ventral secondary ascending tract of the trigeminal enter the tectum of the superior colliculus. Huber et al. ('43) also maintained that collaterals of the ventral secondary ascending tract of the trigeminal distribute to the mammalian optic tectum, but the spino-thalamic and the main fascicles of the ventral secondary ascending tract of the trigeminal terminate directly in the ventral nucleus of the dorsal thalamus.

Cortico-tectal systems

Two groups of fibers, the internal and the external cortico-tectal tracts, enter the superior colliculus from the cerebral cortex. Beever and Horsley ('02) described occipito-mesencephalic fascicles in the monkey as composed of large fibers which stand out distinctly from the medium-sized, occipito-thalamic fibers and which pass to the entire extent of the stratum griseum profundum of the superior colliculus. They also demonstrated temporo-mesencephalic fibers in the cat passing primarily from the posterior limb of the ecto-Sylvian gyrus to distribute to the superior colliculus. They did not determine the termination of the latter fibers in the superior colliculus. Crosby and Henderson ('48) identified external and internal cortico-tectal pathways in the macaque. These fibers correspond to the temporo-mesencephalic and occipito-mesencephalic tracts, respectively, of Beever and Horsley ('02). Crosby and Henderson traced the external cortico-tectal fibers in their course along the optic pathways; they subdivided the internal system into a dorsal and a ventral division.

In the mole, the internal cortico-tectal fibers from the pre-occipital and occipital areas of the cerebral cortex enter the diencephalon as part of the superior thalamic radiations (fig.

3) through the internal capsule. Immediately on reaching the diencephalon the more dorsomedial fibers of the internal capsule are joined by more lateral bundles which swing across the other internal capsule fibers in a dorsomedial direction. Thus a common internal cortico-tectal system is maintained which proceeds dorsocaudalward. Behind the habenula the fibers pass to the pretectal area (fig. 3), where some may

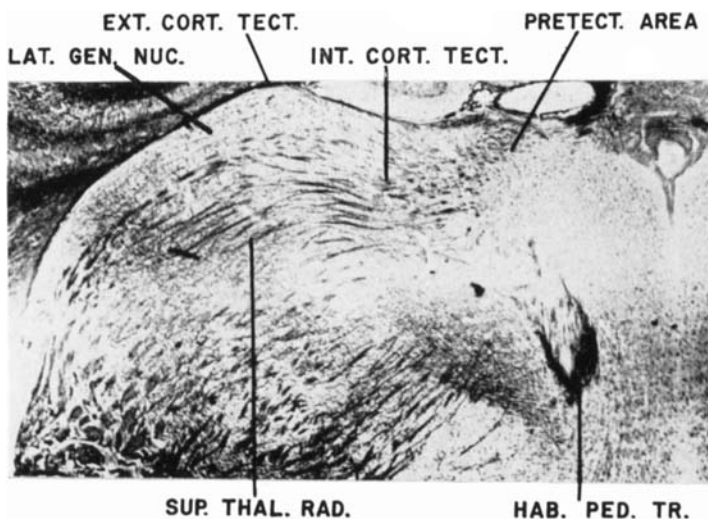


Fig. 3 Photomicrograph of a transverse section through the posterior third of the diencephalon of the mole showing the optic tract fibers to the lateral geniculate nucleus and the lateral geniculate nucleus. Silver preparation. $\times 30$.

synapse, and to the tectum, which they enter by the intermediate white stratum (fig. 4). These fibers cannot be traced from their origin in the cerebrum; they can only be demonstrated from the region where they enter the diencephalon to the tectum.

The external cortico-tectal fibers enter the diencephalon from the temporal lobe by a sublenticular path and join the optic tract as it passes dorsally over the cerebral peduncle. These fibers then pass dorsomedially, external to the optic tract, toward the lateral geniculate nucleus where a large number of the optic tract fibers enter this nucleus. Beyond

the lateral geniculate the cortico-tectal fibers course dorso-medial and caudad along the surface of the diencephalon towards the tectum. They enter the stratum zonale of the superior colliculus (fig. 4); from this stratum zonale some of the fibers turn into the stratum griseum superficiale. The external cortico-tectal fibers were not traced from their origin

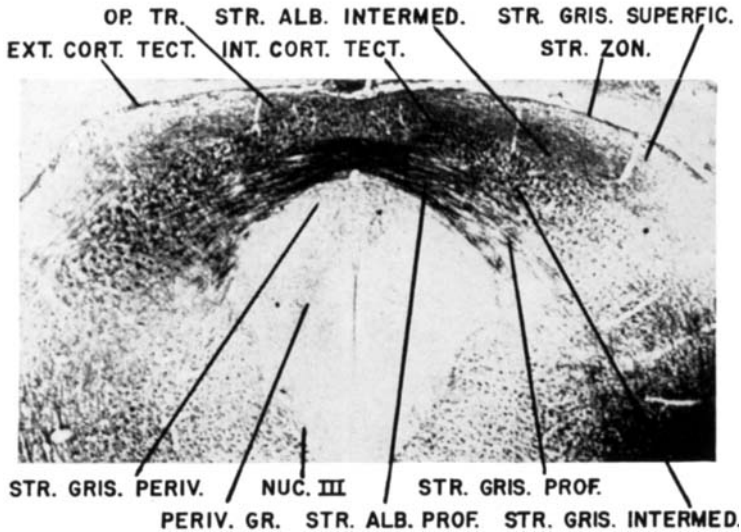


Fig. 4 Photomicrograph of a transverse section passing through the rostral third of the superior colliculus illustrating particularly the layers of the superior colliculus, and the termination of the cortico-tectal systems in the mole. Silver preparation. $\times 30$.

in the cerebral cortex, but only from sublenticular regions of the hemisphere.

Acustico-optic fibers

Ariëns Kappers, Huber and Crosby ('36) described acustico-optic fibers in various mammals and Crosby and Henderson ('48) noted such fascicles passing from the nucleus of the inferior colliculus to the periventricular gray of the superior colliculus in the macaque. There is a like connection in the mole.

The chief nucleus of the inferior colliculus is directly continuous with the periventricular gray of the superior colliculus. The acustico-optic fibers are short, thin, medullated and unmedullated fibers which are found in the nucleus of the inferior colliculus and extend rostralward in the periventricular gray of the superior colliculus to synapse with the dendrites of the periventricular layer. These could not be photographed satisfactorily although they are demonstrable in the material.

Efferent pathways from the tectum

Medial tecto-spinal, tecto-oculomotor and tecto-rubral systems.

The medial tecto-spinal fibers arise from the deep gray layer of the superior colliculus (fig. 5) and, leaving the tectum by the stratum album profundum, pass ventrally around the periventricular gray to cross to the opposite side in the dorsal tegmental decussation and then to attain a position ventral to the medial longitudinal fasciculus (fig. 6). Rasmussen ('36), working with cats, produced lesions in the superior and inferior colliculi which caused degeneration of the medial tecto-spinal tract on the side opposite the lesion but found no degeneration in the tecto-spinal tract on the side of the lesion below the dorsal tegmental decussation, indicating that the tract is entirely crossed. He also placed lesions in the nucleus of the inferior colliculus as far caudally as the plane of the nucleus of the lateral lemniscus and found no degeneration in the medial tecto-spinal tract. Papez and Freeman ('30) reported similar findings in the rat. Tsai ('25b), working with the opossum, reported that the tecto-spinal tract (apparently the medial tecto-spinal of the present account) arises from the entire length of the tectum and that it is both crossed and uncrossed. It is possible that this tract arises from the entire length of the tectum in different animals and that it is both crossed and uncrossed in some animals.

After its decussation, the medial tecto-spinal tract passes caudad through the tegmentum of the midbrain and the pons

in a position ventral to the medial longitudinal fasciculus (figs. 7 to 10). In the caudad portion of the pons, the medial tecto-spinal tract is found near the midline on each side of the raphé (fig. 10) and maintains this position in the medulla oblongata to a level through the caudal end of the inferior olivary nucleus. It assumes a more ventral position when it reaches the level of the motor decussation. At the upper levels of the spinal cord the tract enters the ventral funiculus medial to the ventral horns and ventral to the medial vestibular component of the medial longitudinal fasciculus. Its extent in the cord has not been determined.

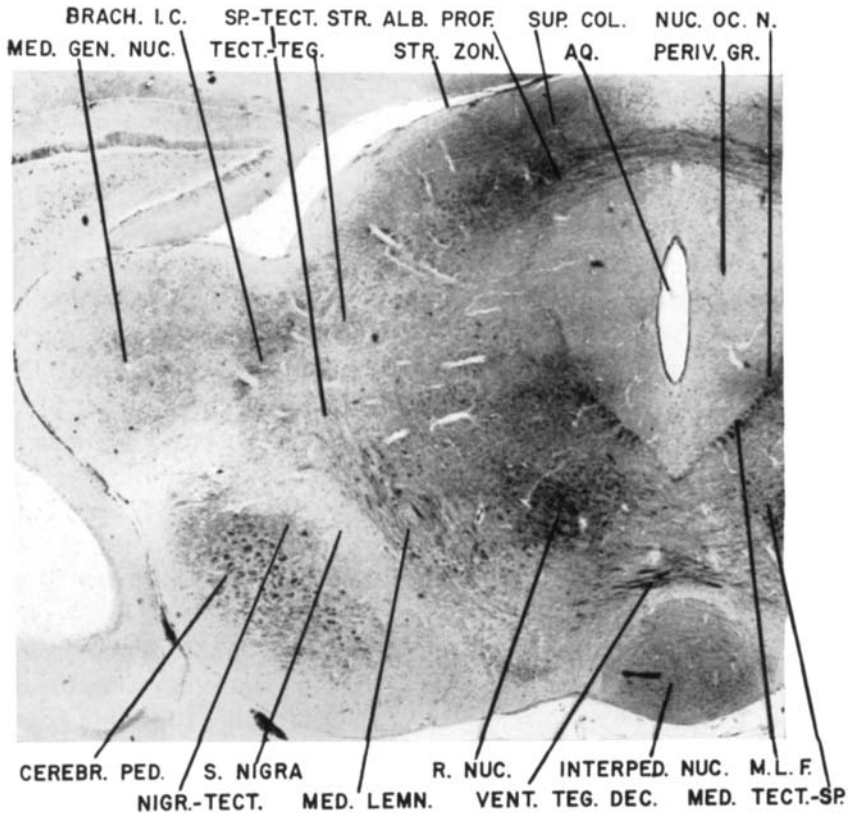


Fig. 5 Photomicrograph of a transverse section through the anterior third of the superior colliculi and the medial geniculate nuclei of the mole. The brachium of the inferior colliculus should be noted. Weil stain. $\times 30$.

As the medial tecto-spinal tracts sweep ventrally from the tectum to enter the dorsal tegmental decussation, tecto-oculomotor fibers accompanying them terminate in part in the homolateral oculomotor nucleus, in part in the contralateral oculomotor gray. Since many of such fibers lose their medullary sheaths at or near their entrance to these nuclei; they are best seen in silver preparations. Ariëns Kappers, Huber and Crosby ('36) have described tecto-oculomotor fibers for numerous mammals and maintain that the tecto-oculomotor tract is an important pathway to the oculomotor nucleus.

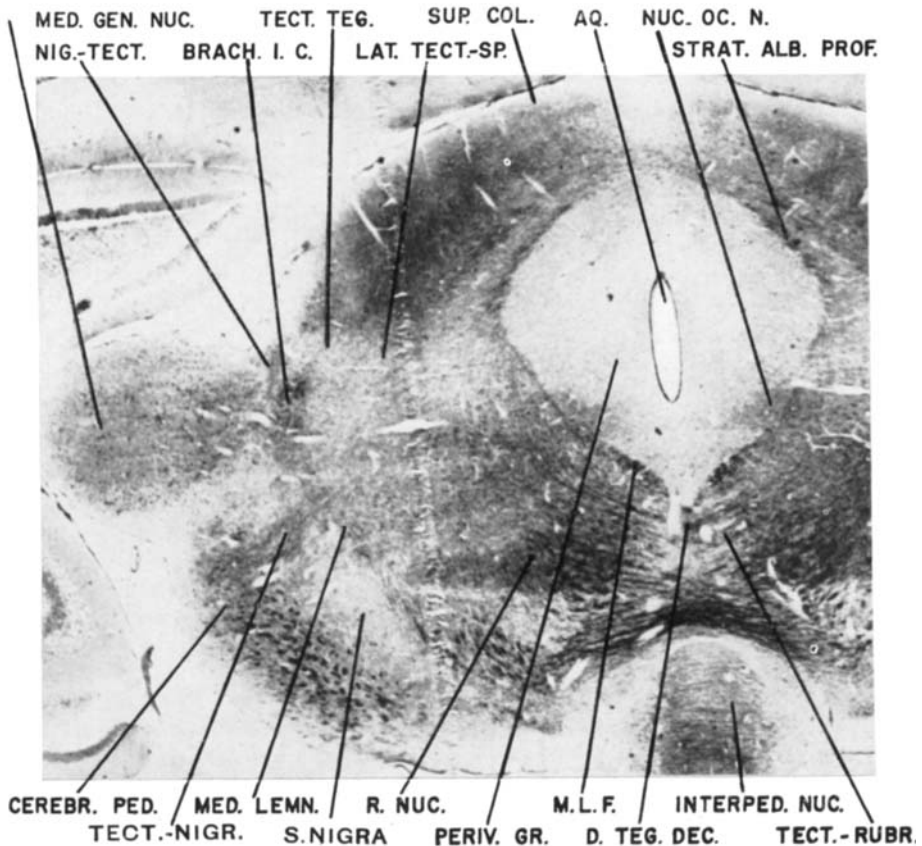


Fig. 6 Photomicrograph of a transverse section passing through the middle third of the superior colliculi, the medial geniculate nuclei, and the interpeduncular nucleus of the mole. The nigro-tectal and tecto-nigral tracts are evident in this figure. Weil stain. $\times 30$.

Fibers from the tectum also pass to the red nuclei of both sides. Some of these tecto-rubral fibers reach the red nucleus after crossing in the dorsal tegmental decussation, other

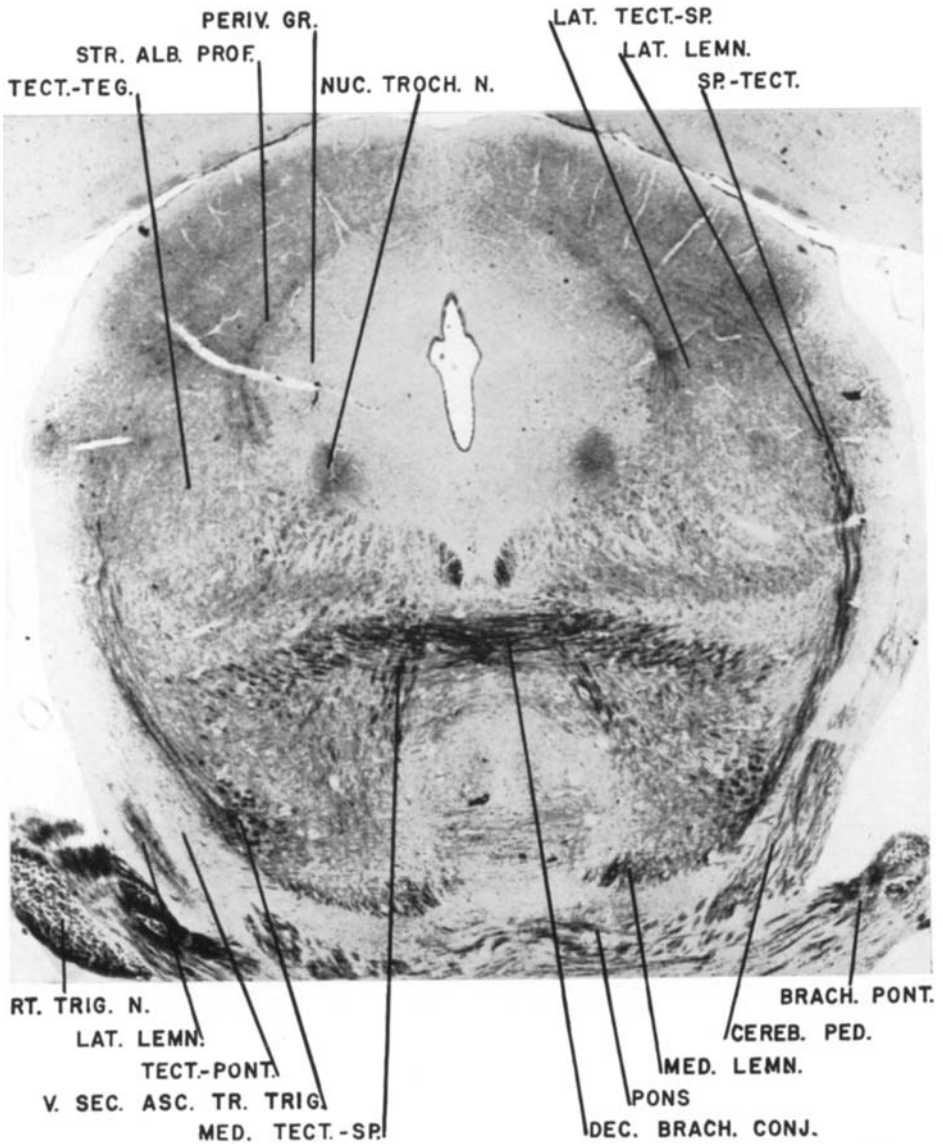


Fig. 7 Photomicrograph of a transverse section passing through the caudal third of the superior colliculi of the mole. Weil stain. $\times 30$.

fibers end directly i.e. without crossing (fig. 5). Rioch ('29) found that in the dog and the cat, the red nucleus is connected with the tectum by three groups of fibers. A medial group accompanies the tecto-oculomotor and medial tecto-spinal tracts but decussates in the dorsal tegmental decussation to enter the red nucleus of the opposite side. A lateral group has both crossed and uncrossed fibers which relate the entire midbrain roof to the red nuclei. A third group of fine fibers connects the superior colliculus with the caudal portion of the red nucleus. Many observers (as Ariëns Kappers, Huber and Crosby, '36) have described tecto-rubral fibers in a wide range of mammals and they are present in man.

Lateral tecto-spinal tract

The lateral tecto-spinal tract arises from the entire length of the tectum. After a partial decussation in the superior colliculus, its fibers leave the tectum in the stratum album profundum just dorsal to those of the medial tecto-spinal tract (figs. 6 and 7). The more rostral fibers of the bundle sweep laterad and ventrad to occupy a position medial to the medial lemniscus (fig. 7 right) and then pass across this lemniscus (fig. 7 left) so that the lateral tecto-spinal tract lies dorsolateral to the brachium conjunctivum and is crossed by the medial lemniscus. Tecto-tegmental fibers are intermingled with the tecto-spinal fibers at this level. Such tecto-tegmental fibers are believed to synapse in the tegmental gray with the cells of origin of the tegmento-spinal fibers to form tecto-tegmento-spinal systems (fig. 6). In its caudal course through the superior collicular level of the midbrain, the lateral tecto-spinal tract shifts ventrad to a position ventral to the fibers of the superior cerebellar peduncle (fig. 8).

Fibers are added to the lateral tecto-spinal tract throughout the inferior collicular levels as the tract courses through the dorsolateral part of the tegmentum ventral to the fibers of the brachium conjunctivum and midway between the medial

longitudinal fasciculus and the lateral lemniscus (figs. 8 and 9). Ariëns Kappers, Huber and Crosby ('36) described a crossed and an uncrossed lateral tecto-spinal system in mammals arising from the entire length of the midbrain.

As the caudal portion of the midbrain is reached the tract gradually moves ventromedially (fig. 9), so that in the pons it occupies a position dorsolateral to the root of the facial nerve and dorsomedial to the descending root of the trigeminal nerve. The ventromedial shift continues and the tract becomes ventral to the rubro-spinal tract (fig. 10) in which position it continues throughout the remainder of its course in the pons.

In the medulla the lateral tecto-spinal tract still lies ventral to the rubro-spinal tract; it is crossed, at the level of the inferior olivary nucleus, by olivo-cerebellar and cerebello-olivary fibers. It proceeds caudalward in the same general relations through inferior olivary and hypoglossal levels.

In the caudal third of the medulla, at the level of transition between medulla oblongata and spinal cord, the tract moves ventrolaterad to enter the lateral funiculus of the spinal cord ventral to the rubro-spinal tract and ventrolateral to the central gray. Its extent in the spinal cord is not known.

Tecto-tegmental tract

The fibers of this tract arise from cells in the stratum griseum profundum of the superior colliculus and sweep ventralward with the medial tecto-spinal, tecto-rubral and tecto-oculomotor fibers. They occupy a dorsolateral position with reference to the latter tracts. At the level of the caudal half of the medial geniculate nucleus (fig. 5) the tecto-tegmental fibers terminate in the tegmental gray of the midbrain medial to the tectal fibers of the medial lemniscus (figs. 6 and 7). Papez and Freeman ('30) produced lesions in the

Fig. 8 Photomicrograph of a transverse section passing through the rostral third of the inferior colliculi. The figure shows especially well the lateral lemnisci with their nuclei and the ventral secondary ascending tracts of the trigeminal in the mole. Weil stain. $\times 30$.

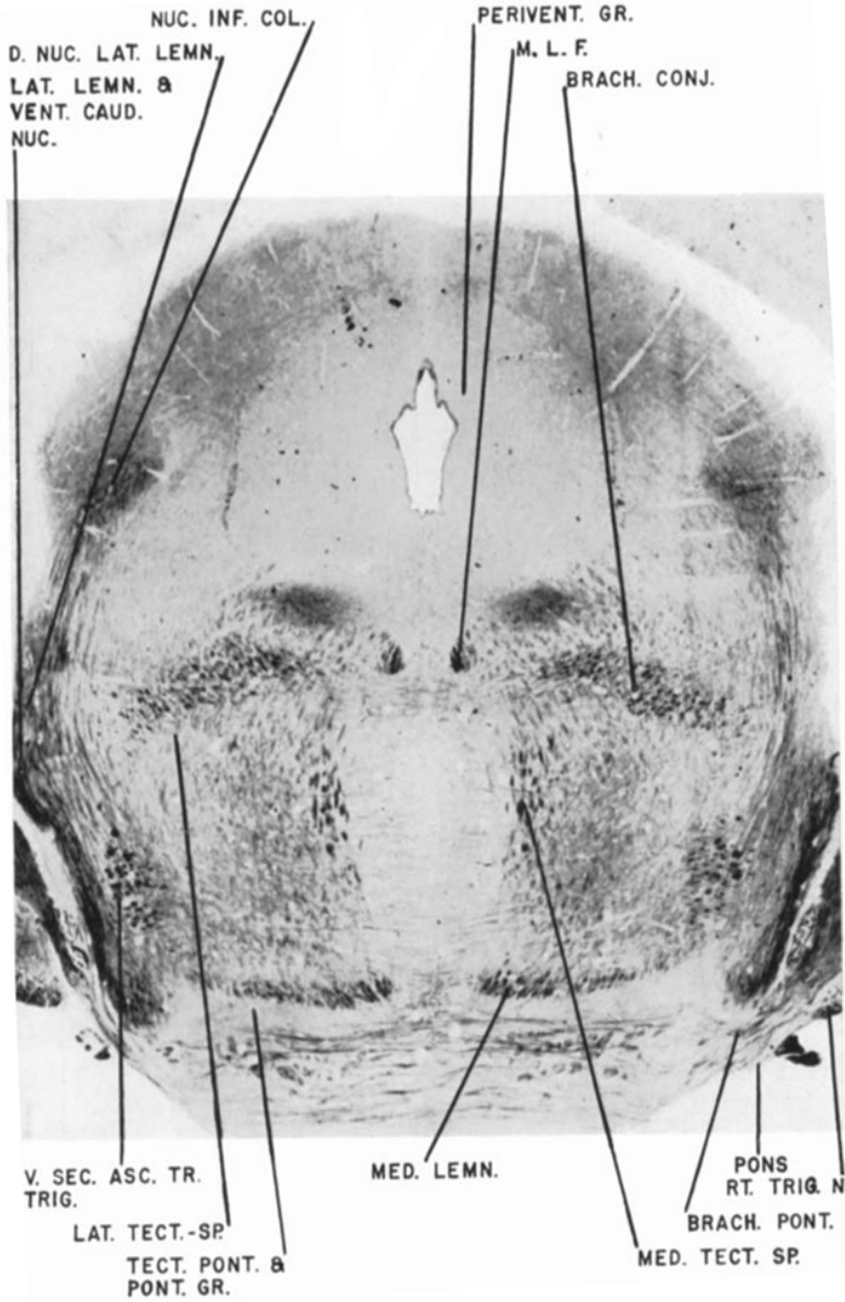


Figure 8

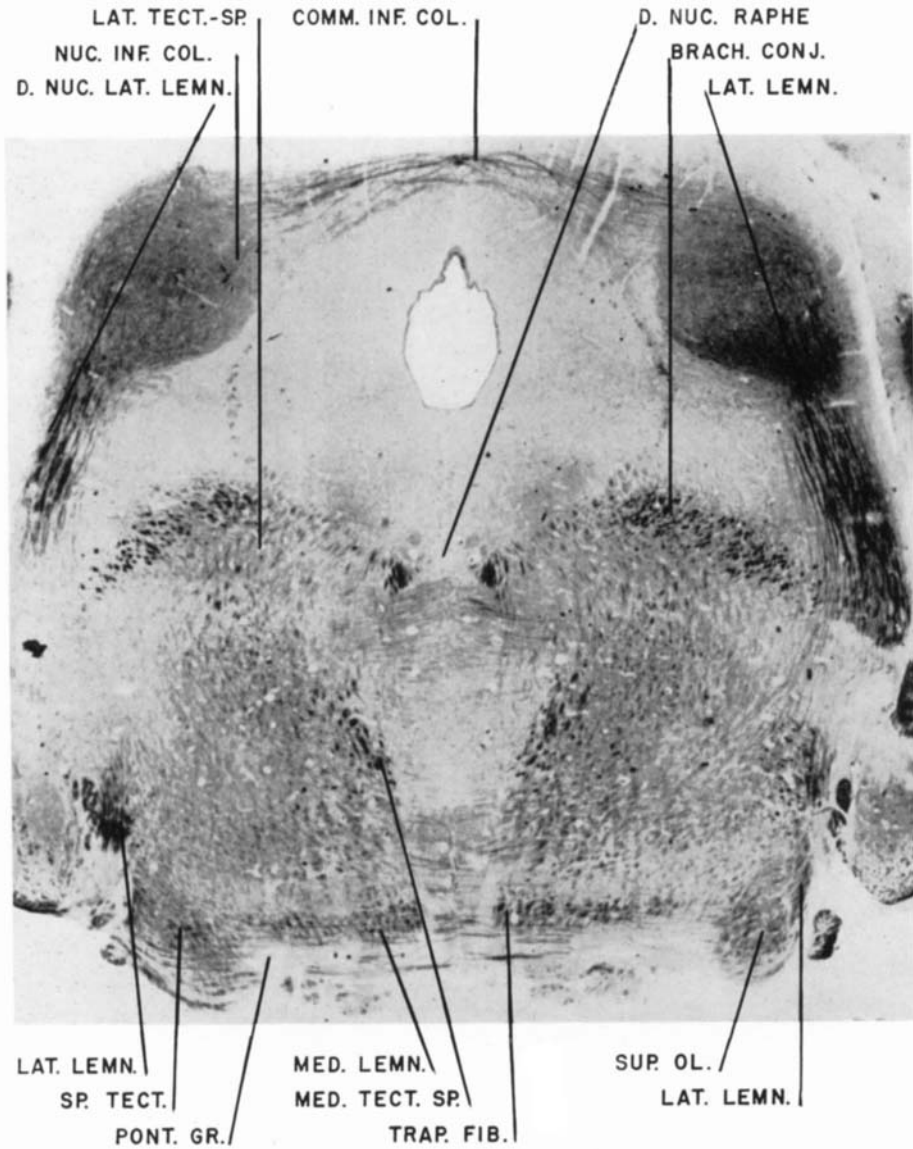


Fig. 9 Photomicrograph of a transverse section through the middle third of the inferior colliculi of the mole. The nucleus of the inferior colliculus and the lateral lemniscus are the outstanding features of this section. Weil stain. $\times 30$.

superior colliculus of rats and noted degeneration of tecto-tegmental fibers which were easily distinguishable from the tecto-spinal tracts.

Tecto-pontine tract

The tecto-pontine tract leaves the stratum album profundum of the superior colliculus and courses laterad and ventrad towards the lateral surface of the midbrain (figs. 6 and 7). The fibers pass dorsal to the dorsal tip of the medial lemniscus as they approach the lateral border of the midbrain

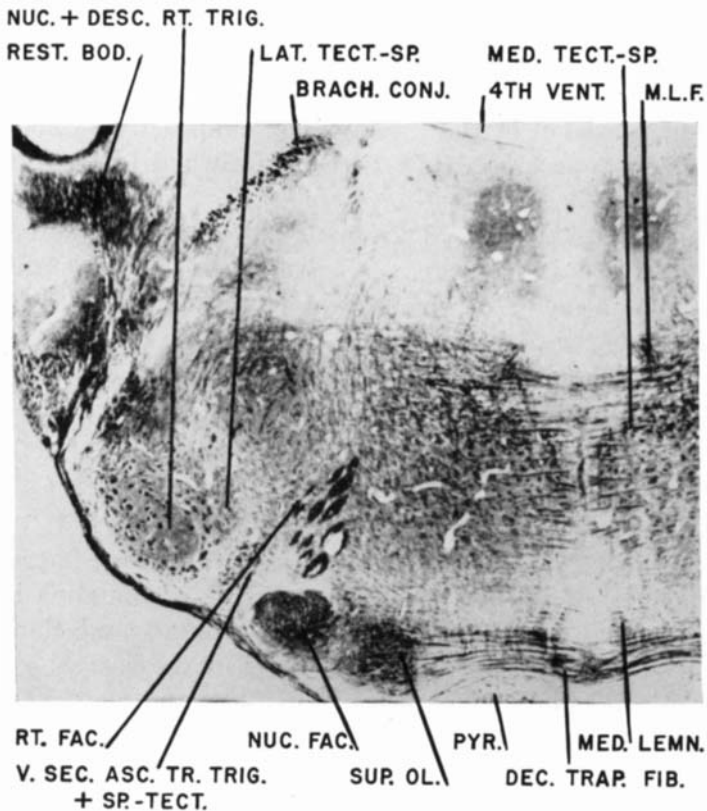


Fig. 10 Photomicrograph of a transverse section through the rostral third of the pons of the mole at the level of the facial roots and the superior olives. This olivary nucleus with its associated fibers and the spino-tectal and ventral secondary ascending tract of the trigeminal deserve especial attention. Weil stain. $\times 30$.

and then they begin to turn in a ventral direction, lateral to the medial lemniscus. They then run in a ventral and caudal direction and, as the lateral lemniscus makes its appearance, they lie lateral to it (fig. 7).

Tsai ('25b) described the tecto-pontine tract in the opossum and found that fibers of this tract arise from nearly the entire length of the tectum, but especially from the inferior colliculus, and that they lie lateral to the lateral lemniscus. He also reported that these fibers are of a smaller caliber and readily distinguishable from the heavier fibers of the lateral lemniscus. The tecto-pontine fibers in the mole are also lighter staining than the fibers of the lateral lemniscus.

The tecto-pontine fibers continue their ventral and caudal course in the lateral portion of the tegmentum of the mid-brain at the level of the inferior colliculus (fig. 8) and when they reach pons levels they turn medialward to terminate in the lateral pontine gray.

After having produced lesions in the superior colliculi of rats, Papez and Freeman ('30) traced fibers descending between the fascicles of the lateral lemniscus and the medial lemniscus to the pontine gray. They found some tecto-pontine fibers lateral to the lateral lemniscus and called these the outlying lateral part of the tecto-pontine bundle.

Interconnections of the tectum with other brain centers
Zona incerta

Gurdjian ('27), working with the rat, described fibers passing primarily from the medial two-thirds of the zona incerta to form small bundles which course caudad and then turn dorsad to reach the tectum at the level of the rostral extreme of the medial geniculate body. Not all of the bundles in this system as it lies in the thalamus are from the zona incerta; the more laterally placed bundles are cortico-tectal in nature.

In the mole fibers from the zona incerta accumulate in separate small bundles. These bundles pass backward through the diencephalon and, in its caudal portion, turn caudodorsad toward the tectum. To reach the superior colliculus they

cross the medial lemniscus, lateral to the habenulo-peduncular tract, and then sweep around the periventricular gray to enter the intermediate gray layer of the tectum.

Rioch ('29) described numerous incerto-tectal and incerto-tegmental fibers in the cat and concluded that the tectum and tegmentum of the midbrain provide the main efferent path for the zona incerta in this form. Bodian ('40) described a similar connection for the opossum.

Substantia nigra

The superior colliculus is connected with the substantia nigra by tecto-nigral and nigro-tectal fibers. The substantia nigra lies in the tegmentum of the midbrain at the level of the rostral third of the superior colliculus. It occupies a position in the lateral portion of the tegmentum dorsal to the cerebral peduncle and ventromedial to the medial geniculate nucleus (figs. 5 and 6).

Rioch ('29) found a rich connection between the pars lateralis of the substantia nigra and the tectum of the dog and the cat. He divided the tectal connections into 4 groups: (1) a diffuse group of fibers spreading out through the tegmentum in their course to the tectum; (2) a group of tecto-nigral fibers entering the pars lateralis; (3 and 4) two groups which are primarily connected with the inferior colliculus.

Fibers from the lateral portion of the substantia nigra course dorsad toward the tectum. As the sections of this portion of the midbrain are followed in a caudal direction, more and more nigro-tectal fibers accumulate from the dorso-lateral portion of this nuclear gray. These fibers then swing around the medial lemniscus in their passage upward towards the tectum (figs. 5 and 6), intermingling with the lateral tecto-spinal, tecto-tegmental, and tecto-pontine fibers in their course. After the nigro-tectal fibers reach the tectum they pass external to emerging fibers of the stratum album profundum to enter the intermediate gray layer of the tectum (fig. 6).

The tecto-nigral fibers leave the tectum in the stratum album profundum with the fibers of the medial tecto-spinal tract. As the fibers of these systems sweep ventrolaterad around the central gray at the level of the rostral half of the medial geniculate body, the medial tecto-spinal fibers continue their course close to the central gray; the tecto-nigral fibers sweep outward and downward to cross the medial lemniscus and to terminate in the pars lateralis of the substantia nigra medial to the origin of the nigro-tectal fibers (fig. 6).

Habenula

Ariëns Kappers, Huber and Crosby ('36) reported connections between the habenula and the superior colliculus in Insectivora. In the mole, the superior colliculus is connected with the lateral habenular nucleus through tecto-habenular and habenulo-tectal fibers. Gurdjian ('25) described the olfactory system in the rat but did not note any connection between the habenula and the superior colliculus. Tsai ('25b), in his paper on the midbrain of the opossum, discussed the habenular complex in detail but did not demonstrate any habenulo-tectal or tecto-habenular fibers. Bodian ('40) illustrated tecto-habenular fibers in his sagittal and horizontal sections of the opossum.

In sagittal sections the habenulo-tectal fibers can be seen in the dorsal region of the diencephalon passing from the lateral habenular nucleus above the periventricular gray to enter the intermediate gray layer of the superior colliculus. The dorsomedial nucleus of the thalamus is rostral to the tectum and the habenulo-peduncular tract can be seen leaving the habenula ventrocaudally to pass along the caudal border of this nucleus. These connections are not illustrated.

Cerebellum

The connections between the tectum of the midbrain and the cerebellum consist of a very small number of fine, lightly

staining fibers passing from the inferior colliculus to the cerebellum. Hines ('29), working with the duckbill platypus (*Ornithorhynchus anatinus*), traced three groups of fibers from the superior colliculus via the anterior medullary velum into the cerebellum. Tsai ('25b) described tecto-cerebellar fibers in the opossum as passing from the nucleus of the inferior colliculus by way of the brachium conjunctivum to the cerebellum.

The fibers from the ventromedial aspect of the nucleus of the inferior colliculus descend ventrocaudad in an arc along the dorsal border of the anterior medullary velum. These fibers cannot be traced to their ultimate termination in normal material for they mingle with other fibers systems upon entering the cerebellum (fig. 9).

DISCUSSION AND SUMMARY

The habits of the animal reflect the poor development of the optic system and the excellent development of the auditory system. As has been noted it is a subterranean animal that burrows into the ground and lives in tunnels below the surface. The marked decrease in the optic system and the excellent development of the auditory system are also reflected in the gross and microscopic material. Even a casual examination of the gross brain will show that the superior colliculus is smaller than the inferior colliculus and yet the former region is a reasonably large quite well differentiated structure even with the great diminution of the optic system. The optic nerves, chiasm, and tracts are demonstrable only in the microscopic material. The basal optic root shows less diminution than the rest of the optic system. As would be expected, the lateral geniculate nucleus, and particularly its dorsal part, is very poorly developed and unlaminate. The optic lamina in the superior colliculus is too small to identify with certainty.

Microscopic study of the superior colliculus shows that it still has rich connections from non-optic centers; from the

spinal cord, by way of the spino-tectal system; from the nucleus of the descending root of the trigeminal by fascicles of the ventral secondary ascending tract of the trigeminal; and from the inferior colliculus by way of acustico-optic fibers. Thus it correlates impulses set up by auditory stimuli and by painful (and perhaps temperature) stimuli on the body and face with the very minimal amount of impulses which reach it over the visual system. As in other mammals, then, the superior colliculus is a sensory correlation area; however, in the mole the visual component is enormously reduced. Impulses from the substantia nigra via nigro-tectal and from the zona incerta via incerto-tectal fibers enrich these correlations.

The descending pathways from the superior colliculus to oculomotor centers, the red nucleus, the substantia nigra, and the tegmentum of the midbrain, to the pontine gray and to the spinal cord are those typical of mammals in general. The tecto-oculomotor fibers, as is to be expected, are very greatly reduced. The tecto-spinal and tecto-tegmental tracts are of average development. Dominating the superior collicular connections are those from the cortical regions of the hemisphere, the external cortico-tectal systems from temporo-occipital association areas and the internal cortico-tectal tracts from occipital and pre-occipital regions of the hemisphere. These pathways are the first neurones in the extra-pyramidal arcs from the cortical areas in which they arise through the superior colliculus to motor centers of the brain stem and spinal cord. They are present in all mammals, increasing as one passes from lower to higher mammalian forms.

The auditory system, including the inferior colliculus, is very highly developed in the mole. It discharges to the brain stem and the spinal cord through a direct lateral tecto-spinal system. In some mammals this discharge is made after a synapse in the superior colliculus.

LITERATURE CITED

- ARIÉNS KAPPERS, C. U., G. C. HUBER AND E. C. CROSBY 1936 The comparative anatomy of the nervous system of vertebrates, including man. The Macmillan Company, New York. 2 vols.
- BARRIS, R. W., W. R. INGRAM AND S. W. RANSON 1935 Optic connections of the diencephalon and midbrain of the cat. *J. Comp. Neur.*, *62*: 117-153.
- BEEVOR, C. E., AND V. HORSLEY 1902 On the pallio-tectal or cortico-mesencephalic system of fibers. *Brain*, *25*: 436-443.
- BODIAN, D. 1940 Studies on the diencephalon of the Virginia opossum. II. The fiber connections in normal and experimental material. *J. Comp. Neur.*, *72*: 207-297.
- BROUWER, B. 1927 Anatomical, phylogenetical, and clinical studies on the central nervous system. Lecture I. The projection of the retina on the brain. The Herter Lectures, Johns Hopkins University School of Medicine. Williams and Wilkins Co., Baltimore. 67 pp.
- BROUWER, B., AND W. P. C. ZEEMAN 1926 The projection of the retina in the primary optic neurone in monkeys. *Brain*, *49*: 1-35.
- CASTALDI, L. 1923 Studi sulla struttura e sullo sviluppo del mesencefalo. I. Ricerche in *Cavia cobaya*. *Arch. Ital. Anat. e Embr.*, *20*: 23-225.
- 1924 Studi, etc. II. *Ibid.*, *21*: 172-263.
- 1926 Studi, etc. III. *Ibid.*, *23*: 481-609.
- CROSBY, E. C., AND R. T. WOODBURN 1943 The nuclear pattern of the non-tectal portions of the midbrain and isthmus in the shrew and the bat. *J. Comp. Neur.*, *78*: 253-288.
- CROSBY, E. C., AND J. W. HENDERSON 1948 The mammalian midbrain and isthmus regions. II. Fiber connections of the superior colliculus. B. Pathways concerned in automatic eye movements. *J. Comp. Neur.*, *88*: 53-92.
- VON FRANKL-HOCHWART, L. 1902 Zur Kenntnis der Anatomie des Gehirns der Blindmaus (*Spalax typhlus*). *Arb. neur. Inst. a.d. Wien. Univ.*, *8*: 190-220.
- GANSER, S. 1882 Vergleichend-anatomische Studien über das Gehirn des Maulwurfs. *Morph. Jahrb.*, *7*: 591-725.
- GILLILAN, L. A. 1941 The connections of the basal optic root (posterior accessory optic tract) and its nucleus in various mammals. *J. Comp. Neur.*, *74*: 367-408.
- 1943 The nuclear pattern of the non-tectal portions of the midbrain and isthmus in ungulates. *J. Comp. Neur.*, *78*: 289-364.
- GURDJIAN, E. S. 1925 Olfactory connections of the albino rat, with special reference to stria medullaris and anterior commissure. *J. Comp. Neur.*, *38*: 127-162.
- 1927 The diencephalon of the albino rat. *J. Comp. Neur.*, *43*: 1-114.
- HAMILTON, W. J., JR. 1943 The mammals of eastern United States. Comstock Publish. Co., Inc., New York. 432 pp.

- HINES, M. 1929 The brain of *Ornithorhynchus anatinus*. *Phil. Trans. Roy. Soc. London*, 3, 217: 155-287.
- HUBER, G. C., E. C. CROSBY, R. T. WOODBURNE, L. A. GILLILAN, J. O. BROWN AND B. TAMTHAI 1943 The mammalian midbrain and isthmus regions. I. Nuclear pattern. *J. Comp. Neur.*, 78: 129-534.
- HUBER, G. C., AND E. C. CROSBY 1943 A comparison of the mammalian and reptilian tecta. *J. Comp. Neur.*, 78: 133-168.
- JACKSON, H. H. T. 1915 A review of the American moles. *North American Fauna. Gov't. Printing Office, Washington, D. C.* 38: 3-100.
- LASHLEY, K. S. 1934 The mechanism of vision. VII. The projection of the retina upon the primary optic centers in the rat. *J. Comp. Neur.*, 59: 341-373.
- LE GROS CLARK, W. E. 1933 The brain of the Insectivora. *Proc. Zool. Soc. London for 1933*, 975-1013.
- METTLER, F. A. 1932 Connections of the auditory cortex in the cat. *J. Comp. Neur.*, 55: 139-183.
- PAPEZ, J. W. 1929 *Comparative neurology*. T. Y. Crowell Co., New York. 518 pp.
- PAPEZ, J. W., AND G. L. FREEMAN 1930 Superior colliculi and their fiber connections in the rat. *J. Comp. Neur.*, 51: 409-439.
- RAMÓN Y CAJAL, S. 1911 *Histologie du système nerveux de l'homme et des vertébrés*. Vol. II. A. Maloine, Paris.
- RASMUSSEN, A. T. 1936 Tractus tecto-spinalis in the cat. *J. Comp. Neur.*, 63: 501-525.
- REED, C. A. 1951 Locomotion and appendicular anatomy in three Soricoid Insectivores. *The American Midland Naturalist. Univ. of Notre Dame Press. Notre Dame, Ind.*, 45: 513-671.
- RIOCH, D. M. 1929 Studies on the diencephalon of Carnivora. II. Certain nuclear configurations and fiber connections of the subthalamus and midbrain of the dog and cat. *J. Comp. Neur.*, 49: 121-153.
- STOKES, J. H. 1912 The acoustic complex and its relations in the brain of the opossum (*Didelphys virginiana*). *Am. J. Anat.*, 12: 401-445.
- TSAI, C. 1925a The optic tracts and centers of the opossum, *Didelphys virginiana*. *J. Comp. Neur.*, 39: 173-216.
- 1925b The descending tracts of the thalamus and midbrain of the opossum, *Didelphys virginiana*. *J. Comp. Neur.*, 39: 217-248.
- WINKLER, C., AND A. POTTER 1911 *An anatomical guide to the experimental researches on the rabbit's brain*. Versluys, Amsterdam. 40 pl.
- 1914 *An anatomical guide to the experimental researches on the cat's brain*. Versluys, Amsterdam. 35 pl.
- WOODBURNE, R. T. 1936 A phylogenetic consideration of the primary and secondary centers and connections of the trigeminal complex in a series of vertebrates. *J. Comp. Neur.*, 65: 403-501.
- WOODBURNE, R. T., E. C. CROSBY AND R. E. McCOTTER 1946 The mammalian midbrain and isthmus regions. Part II. The fiber connections. A. The relations of the tegmentum of the midbrain with the basal ganglia in *Macaca mulatta*. *J. Comp. Neur.*, 85: 67-92.

- WOOLLARD, H. H. 1926 Notes on the retina and lateral geniculate bodies in *Tupaia*, *Tarsius*, *Nycticibus*, and *Hapale*. *Brain*, 49: 77-109.
- WOOLLARD, H. H., AND J. A. HARPMAN 1940 The connections of the inferior colliculus and the dorsal nucleus of the lateral lemniscus. *J. Anat.*, 74: 441-458.