THE MAMMALIAN MIDBRAIN AND ISTHMUS REGIONS

PART II. FIBER CONNECTIONS OF THE SUPERIOR COLLICULUS

B. Pathways concerned in automatic eye movements

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THIRTEEN FIGURES

INTRODUCTION

Eye movements in primates are of interest both from experimental and clinical standpoints. The pathways which are concerned in producing these movements in response to various stimuli are of considerable importance. Ocular motion may be discussed as a subcortical reflex mechanism, as a cortical automatism, or as a voluntary act which of necessity involves cortical function. The present paper is concerned primarily with the pathways underlying certain automatic eye movements. In such pathways the tectal and the tegmental regions of the midbrain are important centers.

This paper represents a portion (Part II, section B) of the series of studies on the midbrain being carried on in the Department of Anatomy at the University of Michigan. The series as a whole aims to study intensively the nuclear pattern, the fiber connections, and the functional significance of the various portions of this brain region.

MATERIAL AND METHODS

The animal used for this report was Macaca mulatta. The normal and the experimental series of the brain of this primate were prepared by the Weil technique. The experimental work was performed, after exposure of area 19 and, in some instances, of area 17, by stimulating a selected region with a minimal faradic current and noting the eye movements produced. The anesthetics used are discussed under the account of the experimental work.

The determination of the exact cortical areas involved at various levels was aided by the use of a model which had been constructed by Dr. Isabel Lockard as part of her doctorate program. The paper is illustrated by photomicrographs which were made by Mr. George Smith, Research Technical Assistant in the Department of Anatomy.

CONSIDERATION OF ANATOMICAL MATERIAL

Optic Tract

The optic tract consists of large, interlacing fascicles, which, after partial decussation, course lateralward from the region of the chiasma along the surface of the diencephalon (fig. 2). According to LeGros Clark ('42) about 40% of these fibers remain uncrossed. As the lateral geniculate nucleus is reached, fascicles pass over its rostral pole and its medial, lateral, and dorsal surfaces, the main distribution of the tract being to this nucleus (fig. 3). Nevertheless, throughout the extent of the nucleus, optic fibers can be traced caudalward at its ventro-medial and ventro-lateral angles and along the inner border of its hilus. Some of these distribute to the caudal pole of the lateral geniculate nucleus, but other bundles swing dorsalward behind this nucleus to reach the pretectal nucleus and the optic stratum of the superior colliculus (figs. 4 to 11). The fibers ending in the pretectal nucleus are of pupillo-constrictor character (Hare, Magoun and Ranson, '35). The optic fibers are joined by the external cortico-tectal tract, which lies in a position immediately lateral to the optic tract;

both systems pass together toward the superior colliculus (fig. 9). As this region is reached, the optic fibers enter stratum opticum (see fig. 5) and the external cortico-tectal tract passes to the superficial zone of the superior colliculus. Part of the optic fibers continue caudalward along the under side of the superior colliculus toward its caudal pole to reach a medial position (as in fig. 10) and distribute through the optic stratum to its caudal half.

Brouwer and Zeeman ('26) and Brouwer ('27) presented the pattern of localization of the optic tract on the superior colliculi in the rabbit and, less clearly, in the monkey. Their results indicate that impulses from the inferior temporal and inferior nasal quadrants of the retina (or the superior visual fields) are projected on the anteromedial portions of the superior colliculi and those from the superior temporal and superior nasal quadrants (or inferior visual fields) on the caudolateral part of this area. They did not trace macular fibers to the superior colliculi. A comparable pattern of projection on this midbrain region was obtained in the rat by Lashley ('34).

The material available for study is inadequate for determining whether there are any connections from the lateral geniculate nucleus to the superior colliculus. Opinions differ as to the existence of such connections but it seems probable to the writers that such fibers do exist but not in any great amount.

Visual Radiations

The visual radiations constitute the main discharge path, possibly the only efferent tract, of the lateral geniculate nucleus. They end in the visual cortex (area 17). In the monkey (Poliak, '32 and '33) and in the chimpanzee (Poliak and Hayashi, '36) a complete, rapid retrograde degeneration of the lateral geniculate nucleus following the destruction of this cortical area has been found.

The course of the visual radiations (figs. 4 to 7, 13) from the lateral geniculate nucleus to area 17 (fig. 13) has been

described in various primates and need not be repeated here, although the system has been traced in the preparations. Poliak showed its pattern of distribution as to retinal quadrants on the cortex. He used the calcarine fissure as the horizontal meridian, demarcating upper from lower retinal quadrants. He stated (Poliak, '32, p. 172); "The upper quadrants of both homonymous hemiretinae, excluding the macula, are projected upon the upper lip of the fissura calcarina; the lower quadrants upon the lower lip." He found the macular projection to be mainly upon the occipital pole and occipital operculum in the monkey. The fibers are thought to end primarily in lamina IVc.

Even in Weigert preparations, the visual area (area 17) is easily recognized through the presence of the stripe of Gennari (fig. 13, G), which differentiates it from the bordering area 18. In Macaca mulatta, as Poliak ('32) and others have shown, area 17 lies not only on the medial surface of the hemisphere, but also occupies the greater portion of the lateral hemisphere wall (fig. 1) in the occipital region. There is, however, a narrow strip of cortex (area 18) bordering area 17 on all sides and cut off in part from the more rostral cortical area 19 by a fissure.

Intracortical Associations of Visual Cortex

From the inferior half of area 17, on both medial and lateral surfaces of the hemisphere, bundles can be traced to the adjoining portions of area 18, thus connecting area 17 with area 18. From such more ventral portions of 18 fascicles pass to the upper region of area 19. There is no evidence that fibers pass directly between area 17 and area 19, although there is a possibility that they may be present but unrecognized in the material. However, a connection of area 17 with area 18 and area 18 with areas 19 and 17 would appear to be indicated by the results of von Bonin, Garol and McCulloch ('41) and McCulloch ('44), who, by use of the oscillograph, obtained such a sequence. Moreover, LeGros Clark ('42), after devascularization of portions of area striata (area 17), obtained evidence

in Marchi material of degenerating fibers from adjoining parastriate cortex (area 18). It should be stressed again that it is the inferior half of area 17 which appears to project, by way of the inferior portions of area 18, upon the upper part of area 19.

From the superior half of area 17, on both the medial and lateral surfaces of the hemisphere, fibers can be traced to the adjoining area 18, and from here (Lockard, see reference list) to the more inferior region of area 19 (C, fig. 1). Between the upper and the lower zones of area 19 (A and C, fig. 1) is an intermediate field (B, fig. 1). This is connected by way of area 18 with intermediate parts of area 17, that is, with portions bordering the calcarine fissure.

By means of the connections just discussed the lower portions of area 17, which are stimulated by impulses set up in the inferior retinal quadrants, project through a two-neuron path (from area 17 to area 18 and from area 18 to area 19) on the uppermost region of area 19. That part of area 17 stimulated by impulses from the superior retinal quadrants projects through area 18 to lower portions of area 19. Finally, the portions of area 17 receiving impulses from both dorsal and ventral retinal quadrants project by way of area 18 on the intermediate region of area 19. Area 19 has been shown (Foerster, '31, and others) to be the center for certain automatic eye movements in primates. These connections indicate that such movements are set off by impulses initiated in the various retinal quadrants. The pattern of such movements is considered in the discussion.

McCulloch's work ('44) indicates that, in the monkey, the region of the frontal lobe (primarily area 8) functionally related to voluntary eye movements sends out brain waves to area 18 but that no impulses pass in the opposite direction. Since area 18 is connected with area 19, it appears that the center mediating voluntary eye movements is dominant over those fields (areas 18 and 19) concerned with automatic eye movements.

Auditory Radiations

Recently, Lockard (see reference list) has studied the auditory radiations (fig. 3) in the macaque in their course from the medial geniculate nucleus to the auditory cortex. This cortex lies on the opercular portion and, to some extent, on the upper, lateral surface of the superior temporal gyrus (fig. 1), in approximately the position indicated by Poliak ('32) and Walker ('38). Lockard's description of this fiber system will be published within the year. Since it is based on material used for this article, the auditory radiations will not be described here.

Intracortical Connections of the Auditory Cortex

From the auditory area Lockard (see reference list) traced association fibers to that part of the superior temporal gyrus lying ventral to the auditory projection cortex and to more caudal portions of the temporal lobe situated ventral to the superior temporal fissure (areas 20 and 21 of Walker, '38). These connections have been verified in the present study. Some of these association fibers pass from the auditory projection cortex to the region of origin of the external cortico-tectal tract (see p. 60). Impulses are relayed over this bundle to the superior colliculus. Thus an anatomical basis is provided for certain automatic responses to auditory stimuli.

Certain Discharge Paths from Cortical Areas to Brainstem

Cortico-tectal and cortico-tegmental systems have been described only in part in earlier contributions. To facilitate an understanding of these systems some additions to the current terminology have been devised. The cortico-tectal tract, auditory division, corresponds to the efferent component of the auditory radiations identified by various authors (for example, Riley, '43). The external cortico-tectal tract was described in relation to the optic tectum by Huber and Crosby (Huber et al.,

'43) and may be comparable, in part at least, to the temporo-thalamic fasciculus of Riley ('43). In the material studied, a considerable portion of the bundle, if not all of it, appears to pass beyond the pulvinar to the superior colliculus.

The internal cortico-tectal system has been considered as an efferent cortical system of cortico-collicular character by many observers (for example, Probst, '02 and Barris, Ingram and Ranson, '35). It has been described under various names such as the pallio-tectal (Beevor and Horsley, '02) or cortico-mesencephalic (Beevor and Horsley, '02, and Mettler, '35) tract, or as the internal cortico-tectal system (Huber and Crosby, in Huber et al., '43). This system is broken up, in the following account, into components from the occipital lobe (the occipital division) and bundles from the preoccipital areas (the preoccipital division). Each division has been sub-divided into a dorsal and a ventral part on the basis of origin from upper or lower portions of the occipital or preoccipital area respectively. These further subdivisions have been made to facilitate the description of pathways involved in automatic eye movements in various planes. The cortico-tegmental fas-cicles are so named because of their relations to various non-tectal brainstem areas.

Cortico-tectal tract, auditory division

The auditory radiations contain fascicles which pass caudal-ward (figs. 7 to 12) along the inner border of the medial geniculate nucleus to enter the rostral part of the capsule of the inferior colliculus (fig. 12). Following section of the temporal lobe in the monkey, Mettler ('35a) described degen-erated fibers in the region of the rostral pole of this tectal area, and the bundle here traced quite probably corresponds to such fibers. According to Riley ('43), the auditory radia-tions in man carry not only geniculo-cortical bundles but also descending fibers from cortical auditory areas to the inferior colliculus and the medial geniculate nucleus.

External cortico-tectal tract

In the material available, the external cortico-tectal tract is indistinguishable at its origin from the more ventral fibers of the temporal division of the temporo-parieto-cortico-pontine system. The temporal division arises from the region of the temporal lobe ventral to the superior temporal sulcus, chiefly from area 21 near its junction with area 19b (fig. 1; see also Walker, '38, fig. 28, p. 116) and from area 20. The fascicles accumulate in the deep white layer of the cortex and then break up into bundles which are in part sublenticular and in part pass through the ventral portion of the lenticular nucleus. In this course they proceed almost directly medialward until the rostrolateral surface of the lateral geniculate nucleus is approached. Here the external cortico-tectal tract and the temporo-cortico-pontine system separate from each other. The temporo-cortico-pontine fibers swing over the dorsal surface of the lateral geniculate nucleus and, joined by the parieto-cortico-pontine bundle, enter the cerebral peduncle (fig. 2), where they proceed caudalward as the most lateral part of the peduncle (fig. 3), until pons levels are reached. Then they break up among the fascicles of the ponto-cerebellar system, to end in the customary way in relation to the pontine gray.

The external cortico-tectal tract maintains a position immediately adjacent to the ventrolateral border of the lateral geniculate nucleus. Here it lies as a triangularly-shaped bundle dorsal to stria terminalis and, for a time, ventral to the temporo-cortico-pontine tract. Then the external cortico-tectal tract shifts ventralward as the visual radiations (from the lateral geniculate nucleus to the visual cortex) increase, and lies, as a band-shaped bundle (figs. 3 and 4), along the surface of the cerebral hemisphere, dorsomedial, then medial and then ventro-medial to stria terminalis. It gradually slips ventralward and, behind the caudal pole of the lateral geniculate nucleus is situated along the ventro-lateral surface of the pulvinar (fig. 5), a position which it retains (figs. 7 to 10) to the level where the pulvinar becomes separated from the hemisphere. During the last part of its course, some of the

bundles of the external cortico-tectal tract shift medialward through the pulvinar and gradually join the optic tract at the caudal pole of this nucleus. The fibers then swing almost immediately dorsalward and forward to reach the lateral border of the superior colliculus (figs. 6 to 9), being the most caudal fascicles to enter the midbrain from the pulvinar. At the upper border of the superior colliculus, the bundle breaks up into 3 portions. (1) One part continues rostralward (figs. 7 to 4) to distribute to the front end of the superior colliculus forming its most superficial fiber layer. The fascicles of this portion which approach the midline, having reached the sulcus separating the median portion of the tectal eminence from the superior colliculus proper, proceed caudalward in this position to distribute to the caudal end of the superior colliculus (figs. 8 to 10). (2) A second portion of the external cortico-tectal tract turns immediately into the superficial layer of the superior colliculus (fig. 7) and distributes through the remainder of the rostral end of this area. (3) A third portion continues caudalward (figs. 8 and 9) along the lateral border of the superior collicular eminence to enter its caudal third and caudal pole.

The study of Weil preparations suggests that the largest portion of the external cortico-tectal fibers distributes to the rostral two-fifths of the superior colliculus. The next distribution, which is small compared with the first, is to the caudal pole and to the caudal one-fifth of the superior colliculus. The intermediate regions of the colliculus receive only a very small number of fibers.

Another point in the anatomical relations should be stressed. These external cortico-tectal fibers lie in very close apposition to the optic tract throughout its course. Both systems send fibers into the superficial gray layer and it is not possible, in every instance, to distinguish between the optic and the external cortico-tectal fibers, although the latter are the more numerous and, on the whole, the more highly medullated. Tsang ('37) showed that the superficial gray layer degenerated after section of the optic nerve in the young rat.

Internal cortico-tectal tract, occipital division

In the macaque the occipital division of the internal cortico-tectal tract arises from the occipital cortex (area 18 and possibly area 17, fig. 1). The fibers run forward along the border of the visual radiations into the internal capsule. Within the internal capsule it is not possible to delimit this occipital division sharply from other components but its general position and the fact that its fibers do not cross each other in course can be determined easily. Throughout its course in the hemisphere those fascicles from the upper half of the occipital area are most dorsal and those from the lower half most ventral, a relationship which is maintained forward to pulvinar levels.

Ventral part. At the most caudo-medial border of the pulvinar the more ventral portion of the bundle (*int.cort.tect. tr., oc.div., vent.p.*, fig. 10), supplemented by fibers which cut through this thalamic nucleus, swings dorsally. Slightly farther forward (fig. 9) where the pulvinar joins the midbrain, this ventral portion of the occipital division of the internal cortico-tectal tract adjoins medially the external cortico-tectal bundle. Still farther rostralward (fig. 8) it lies just ventro-lateral to the external cortico-tectal system and retains this position (figs. 7 and 6) until its entrance into the superior colliculus, deep to stratum opticum. It distributes to the rostro-medial part of this region (figs. 5 and 4, *x*). Whether any fibers cross to the contralateral superior colliculus before terminating has not been determined.

Dorsal part. As the ventral part of the occipital division of the internal cortico-tectal tract swings dorsally, its ventral boundary (fig. 8) is formed by a fan of slightly less compact fibers which have emerged from the internal capsule and crossed the pulvinar to reach this position. This fan of fibers constitutes the dorsal part of the occipital division of the tract (*int.cort.tect.tr., oc.div., dors.p., fig. 8*). The bundles have proceeded with the optic radiations from the upper half of the occipital area and have occupied a position in the internal

capsule overlying the ventral portion of this occipital division and radiate across the pulvinar dorsal to it (fig. 9). They enter the superior colliculus deep to stratum opticum, reaching the same layer (x) as does the ventral part of this division. They distribute caudalward rather than rostralward from their point of entrance and terminate in the caudolateral part of the superior colliculus.

Internal cortico-tectal tract, preoccipital division

From area 19, which contributes the preoccipital division of the internal cortico-tectal tract, fibers, somewhat finer than those just described, join the white matter of the hemisphere in company with the occipital division of this system and the visual radiations and proceed forward with them into the internal capsule. This preoccipital division can be broken up also into dorsal and ventral portions.

Dorsal part. At levels at which the ventral portion of the occipital division of the internal cortico-tectal tract is distributing to the superior colliculus, other fascicles are crossing the pulvinar transversely to accumulate toward its medial border, preparatory to entrance into the midbrain (figs. 5 and 6). Whether or not such fibers receive any contributions from the pulvinar is uncertain. Traced forward they enter the midbrain at the lower, lateral border of the superior colliculus (fig. 5). Then, as this bundle proceeds caudalward, its more dorsal fibers enter the superior colliculus, deep to the heavily medullated fascicles of the occipital division of the internal cortico-tectal tract, to end in the rostromedial half of the superior colliculus (figs. 5 and 4, y). There is some indication that part of these fibers cross in the superior collicular commissure. The remainder of the bundle constitutes the tegmental part of the preoccipital division of the internal cortico-tectal system and forms a component of the cortico-tegmental tract.

Ventral part. The fibers from lower portions of 19 (see C, fig. 1) can be followed, in both normal and experimental ma-

terial, diagonally dorsomedialward from the internal capsule across the pulvinar (figs. 5 and 4), intersecting in course the dorsal part of the preoccipital bundle. They approach the pretectal area and cross it on their way to the superior colliculus. Probably some of them synapse in this area. The bundle enters the superior colliculus at its most rostral levels, reaching a position (y, fig. 4) in the colliculus ventral to that of the fibers of the occipital part (x) of the internal cortico-tectal system. It proceeds caudalward in this position (y, figs. 5 and 12) to distribute to the caudolateral half of the superior colliculus. Degeneration preparations have made it possible to trace these fascicles from C of area 19 (fig. 1) forward through the internal capsule, across the pulvinar, into the superior colliculus and then caudalward.

Cortico-tegmental tract

Between the dorsal and ventral portions of the occipital division of the internal cortico-tectal tract are fascicles which do not enter the superior colliculus but which accumulate in a bundle running caudally along its base (figs. 7 and 8). These fascicles are derived from the occipital division. They are joined beneath the lateral border of the superior colliculus (figs. 5 and 6) by fibers from the preoccipital division of the internal cortico-tectal tract, and the 2 components are indistinguishable from each other from this point on in the material available for study. Some of the fascicles of the composite tegmental bundle swing medially into the region at least of the oculomotor nucleus, the nucleus of Darkschewitch, and the interstitial nucleus of the medial longitudinal fasciculus. Such connections were predicted by Spiegel and Sommer ('44). Mettler ('35), on severance of the occipital lobe of the monkey, obtained degeneration granules in the nucleus of Darkschewitch, the interstitial nucleus of the medial longitudinal fasciculus and the oculomotor nucleus but did not give a description of the fiber connections involved. Certain cortico-tegmental fibers synapse in tegmental gray which lies dorsal

to the medial geniculate nucleus and ventral to the tectum. They can be traced into this position in the tegmentum in degenerated material prepared for this study. From this tegmental area, descending fascicles (figs. 7 to 12) can be followed caudalward through the tegmentum of the midbrain, but their final terminus has not been ascertained with certainty. They are believed to go to the para-abducens and the abducens nuclei.

Pertinent Non-cortical Connections of Superior Colliculus

It is not within the scope of the present paper to discuss all the non-cortical afferent connections of the superior colliculus. Certain pathways, however, are so pertinent to an understanding of the problems in mind that some reference to them must be made. These are the optic tract, the spino-tectal system, the collaterals of the ventral secondary ascending tract of V, and the acustico-optic pathway which connects the inferior with the superior colliculus.

Ascending connections from lower centers

As upper midbrain is reached, the dorsal component of the medial lemniscus is the spino-tectal tract. Its extent in the cord is not known with certainty for any primate, although some clinical data suggest that it may have a considerable course. It is part of the pathway over which nervous impulses initiated in pain and temperature endings at the surface of the body are carried to higher centers. At midbrain levels, where there is a change in tilt of the medial lemniscus, the spino-tectal bundles form the uppermost part of this fiber complex, and can be seen, even in normal material, to swing dorsally (fig. 5) to enter the superior colliculus external to stratum album. Together with probable fascicles of the ventral secondary ascending tract of V, they constitute a lemniscal component to this midbrain area and are the justification for calling the layer which they occupy in the superior colliculus,

stratum lemnisci. Actually in many mammals, and particularly in primates, they are completely overshadowed by the bundles of heavily medullated fibers of the internal cortico-tectal system.

Acustico-optic fascicles

The chief nucleus of the inferior colliculus (Huber and Crosby in Huber et al., '43) is directly continuous with the periventricular gray at superior collicular levels. Accompanying these periventricular cells are thinly medullated and unmedullated fiber bundles which constitute an acustico-optic system, connecting the inferior with the superior colliculus. It seems probable that there are other connections between these regions, but they have not been demonstrated in the available material.

Discharge paths

Obliquely running tecto-oculomotor fibers (figs. 4–10) swing down from various levels of superior colliculus along the border of the periventricular gray. Some of them are intermingled with fascicles of the medial tecto-spinal tract. They pass ventral to the medial longitudinal fasciculus, thus approaching the oculomotor nucleus on its ventral border. Some of them end in this nucleus, others decussate to enter the contralateral oculomotor gray, approaching it either on its ventral or its medial border. It is to be emphasized that these tecto-oculomotor fascicles cannot be traced for their full extent in any single transverse section, since they tend to swing obliquely caudalward to reach their regions of termination. No fibers were followed into the trochlear nucleus.

From the superior colliculus discharge paths pass to the underlying tegmental gray (figs. 6, 8, and 10) including the homolateral and contralateral red nuclei. A medial tecto-spinal tract (figs. 6, 8, and 10), after decussation beneath the ventricle, extends to upper cord levels (Rasmussen, '36), and tecto-pontine fibers (figs. 8 to 11) terminate in relation to pontine gray. These and other efferent midbrain connections

will be discussed in a succeeding paper in this series (Crosby, to be published).

CONSIDERATION OF EXPERIMENTAL RESULTS

The series of experiments carried on for this report was designed to investigate the functions of area 19 (fig. 1) in relation to eye movements. The work of Foerster ('31 and elsewhere) and others on primates, including man, indicates that portions of area 19 are concerned with conjugate deviation of the eyes in a horizontal plane, the movement being toward the side opposite the stimulation.

Under ether anesthesia area 19 was exposed and its various portions (indicated in fig. 1) were stimulated. For descriptive purposes these portions have been termed upper area 19 (A, fig. 1), upper-intermediate area 19 (A', fig. 1), middle area 19 (B, fig. 1), lower-intermediate area 19 (C', fig. 1), and lower area 19 (C, fig. 1). It will be noted that lower area 19 is a relative term, since the region so designated does not reach the most ventral portions of the area. Under a relatively light ether anesthesia, from the middle portion (B) of area 19 it was possible to elicit conjugate deviation of the eyes in a horizontal plane toward the side opposite the stimulation, thus obtaining the results reported in the literature. From other regions of 19 movements in other planes were produced if the experiments were carried out at that stage in the ether anesthesia in which the animal had just lost voluntary control of eye movements, but where the blink reflex to stimulation of cilia still persisted. Under such conditions, stimulation (1) of the dorsal part (A) of area 19 resulted in conjugate deviation of the eyes upward, (2) of the upper-intermediate part (A') of area 19 in conjugate deviation obliquely upward toward the opposite side, (3) of the lower-intermediate portion (C') of area 19 in conjugate deviation obliquely downward toward the opposite side and (4) of the ventral part (C) of area 19 in conjugate deviation downward. Slightly deeper anesthesia abolished the upward movements first, then the downward, but conjugate deviation in a horizontal plane persisted. In-

creased ether anesthesia ultimately abolished even the horizontal movements. They were succeeded by irregular ocular deviations, then by nystagmoid jerkings and finally by no response at all to the stimulation applied. In all cases there was a tendency for the eyes to return to center, and continued stimulation at times produced nystagmus, with the slow component corresponding to the direction of the conjugate deviation.

If the anesthetic were changed and sodium pentobarbital, following premedication of ¼ grain of morphine sulphate, were used, the same results did not follow. Only horizontal deviation to the opposite side was obtained from stimulation of area 19, with very rare slight indications of vertical responses from the appropriate regions. As the effects of the anesthetic became deeper, no response at all followed stimulation. If the animal were then given picrotoxin in suitable doses, thus eliminating in part the influence of the pentobarbital, vertical movements as well as horizontal movements could be obtained on stimulation of the appropriate portions of area 19. These followed the same pattern as those obtained under ether anesthesia. It is of some interest to note that the movement most difficult to obtain and the last to return was conjugate deviation upward.

The results obtained in the various experiments in which ether anesthesia was used are summarized in table 1. An inspection of this table shows that the results were not entirely consistent, particularly in differentiating between stimulation of lower (or upper) areas and of intermediate areas. Some of this inconsistency was due to a varying depth of anesthesia. The depth of the anesthesia is of the greatest importance, and only under optimal conditions can pure vertical movements, and particularly the upward movements, be obtained. As was stated before, this degree of ether anesthesia is just beyond the level at which voluntary eye movements can be elicited, but at such a depth that the blink reflex can still be obtained. Moreover, the kind of anesthetic employed is also important. Sodium pentobarbital, as used in this series of experiments,

TABLE 1

MONKEY	DATE OF EXPERIMENT	ANESTHETIC	SIDE	STIMULATION	RESULTS IN TERMS OF EYE MOVEMENTS (See figure 1, with description).
M201	2/13/46	ether	left	faradic current	Upper 19 — on stimulation — deviation to right.
M201	2/16/46	ether	right	faradic current	Upper 19 — deviation upward to right, chiefly upward. Middle 19 — slow movement to left. Lower 19 — slow downward deviation slightly to left.
M202	2/20/46	ether	left	faradic current	Upper 19 — slow upward deviation. Upper intermediate 19 — slow upward movement to left. Middle 19 — horizontal, slow to right. Lower intermediate 19 — downward movement and downward to right.
M202	2/27/46	ether	right	faradic current	Middle 19 — deviation to left — repeated on successive stimulation.
M202	2/27/46	ether	left	faradic current	Upper 19 — upward movement. Upper intermediate 19 — upward and to right. Middle 19 — horizontal deviation to right. Lower intermediate 19 — downward and slightly to left.
M203	3/13/46	ether	right	faradic current	Middle 19 — deviation to left. Lower intermediate 19 — down to left. Lower 19 — downward deviation.
M203	3/20/46	ether	left	faradic current	Upper 19 — upward deviation — slightly to right. Middle 19 — deviation to right. Lower intermediate 19 — downward and to right.
M204	3/27/46	ether	left	faradic current	Upper 19 — faint upward deviation. Middle 19 — deviation to right. Lower intermediate 19 — downward and to right, Lower 19 — chiefly downward deviation slightly to right.
M204	4/ 9/46	ether	right	faradic current	Middle 19 — downward and to left. Lower intermediate 19 — downward and to left. Lower 19 — downward deviation.
M205	4/17/46	ether	left	faradic current	Upper 19 — upward deviation. Upper intermediate 19 — upward and to right. Middle 19 — horizontal deviation to right. Lower intermediate 19 — downward and to right. Lower 19 — downward deviation.

brought the animal too quickly to a depth of anesthesia where only the horizontal movements could be elicited, and even these tended to disappear.

Movements of more than one type were elicited under the conditions of the experiments. As the animal was just reaching the stage of ether anesthesia, where movements in vertical planes could be obtained, these movements tended to be of a to and fro or nystagmoid character, with the slow component in the direction of the movements here cited. As the anesthesia became slightly deeper, the eyes tended to be held in the appropriate conjugate position, with slower return to "eyes front" and frequently, but not invariably, after the cessation of stimulation the eyes moved into the opposite position. Nystagmoid and irregular movements of various sorts appeared as the anesthesia passed beyond the optimal depth. So far as these experiments go, there appeared to be no marked dominance of either hemisphere.

In connection with the experiments involving area 19, upper and lower portions of area 17 were explored. Stimulation of the upper half of area 17 (fig. 1, F) resulted in a conjugate deviation of the eyes downward and toward the opposite side. Stimulation in the region indicated in E of figure 1, in the lower portion of area 17, produced conjugate deviation of the eyes upward and toward the opposite side. This latter result agrees with that obtained by Walker and Weaver ('40), who stimulated this area in monkeys under light anesthesia.

DISCUSSION

Having presented the results of anatomical, experimental and degeneration studies, it is now necessary to synthesize this material, to compare it with previous findings, and to show to what extent the results illustrate the relations between structure and function. Studies on subprimates and primates have indicated that the rostral or, sometimes, the rostro-medial portions of the superior colliculi are concerned with impulses from the superior visual fields, and the caudal or caudo-lateral portions with impulses from the inferior visual fields. The

projection pattern has been worked out carefully in rabbits by Brouwer and Zeeman ('26) and in rats by Lashley ('34). Because of the relatively small number of optic fibers which reach the superior colliculi Brouwer ('27) was unable to establish so definite a pattern in the monkey, although he believed it to be comparable to that in the rabbit. There is certainly no reason to expect that the pattern would be different in monkeys than in other mammals. Clinical evidence (based on involvement of the superior colliculi by pineal tumors in man) indicates that the frontal portions of the human superior colliculi are concerned with upward conjugate movements of the eyes, the response to stimuli in the superior visual fields. In the monkey, and probably in other primates, the rostral portions of the superior colliculi are connected with the rostral parts of the oculomotor nuclei by tecto-oculomotor fibers, and more caudal portions of these colliculi with the more caudal parts of the oculomotor complex. Most observers (see Ariëns Kappers, Huber and Crosby, '36) have believed that the frontal portions of the oculomotor nuclei in mammals, including primates, function in lifting the lids and turning the eyes upward, and that the caudal areas of the nuclei (together with the trochlear nuclei) are related to downward movements of the eyes. The midportions of the oculomotor nuclei with neurons distributing to the medial recti muscles are activated during convergence. The outstanding opponents of this localization in the oculomotor nuclei are Bender and Weinstein ('43), who, by electrical stimulation, produced a pattern in the oculomotor nuclei of the monkey which is on the whole a reversal of that obtained by other workers. It is hard to see how the pattern which these latter authors suggest fits in with the anatomical localization in other parts of the visual reflex arcs.

As an example of the way in which the visual reflex arc works, the pathways by which impulses from the superior visual fields result in turning the eyes upward may be traced. Light impulses from the superior visual fields fall on the inferior quadrants of each retina. The nervous impulses thus

initiated pass over the optic nerves and (after partial decussation) the optic tracts to terminate in the rostral or rostromedial portions of the superior colliculi. Tecto-oculomotor fibers from each superior colliculus end on the rostral portion of the homolateral oculomotor nucleus. Stimulation of rostral parts of the oculomotor nuclei produces elevation of the lids and conjugate deviation of the eyes upward, the normal response to stimuli in the superior visual fields.

The number of fibers of the optic tracts which pass directly from the retinae to the superior colliculi is exceedingly small in monkeys, as in all primates, although these animals have numerous optic fibers terminating in the optic thalamic centers, the lateral geniculate nuclei. These facts must be kept in mind in evaluating the types of visual reflexes seen in primates as compared with those exhibited by subprimates, in which the superior colliculi are main terminal stations for direct optic fascicles. In many mammals, at least, there are connections from the occipital regions of the cerebral hemispheres, and, in a lesser degree, from the temporal regions, to the superior colliculi. Such connections, which have not been demonstrated in submammals, increase proportionately from lower to higher mammals and are particularly outstanding in primates and man. Thus, as the direct optic connections to the superior colliculi decrease, the cortico-tectal fibers increase. There is a great augmentation in the pathways making possible automatic eye movements — that is, movements resembling those of reflex type but influenced from the cortex — and a decrease in the purely subcortical reflex (see also Tsang, '37) apparatus in primates as compared with subprimates.

The visual impulses which have terminated in each lateral geniculate nucleus are relayed to the visual cortex (area 17). In the monkey (Poliak, '33) this cortex lies not only on the medial surface of each occipital lobe but over the lateral surface of the caudal pole of each cerebral hemisphere as well. The calcarine fissure incompletely separates each visual area into a superior and an inferior portion. Poliak has shown that the superior portion of area 17 receives impulses from the

inferior visual field, and the inferior portion from the superior visual field. The present report indicates that there are numerous connections from area 17 to the adjoining regions of area 18, this latter area separating area 17 from other cortical regions. From that part of area 18 bordering the lower half of area 17, fibers have been traced in the material studied to the upper portion of area 19. The connections from area 17 to area 18, and area 18 to area 19 document the work done by McCulloch ('44) and his colleagues in which they were able to trace brain waves in this sequence. By this series of connections, impulses set up in the superior visual field are relayed to the upper part of area 19. From the upper part of area 19, cortico-tectal fibers have been traced to the rostromedial half of the superior colliculus, where, after synapse, they are relayed (as were the visual reflexes) to the more rostral part of the oculomotor nucleus. By this somewhat roundabout path conjugate deviation in the upward plane, in response to impulses from the superior visual field, occurs as a cortical automatism. Due to the presence of connections from the upper half of area 17, via area 18, to the lower part of area 19 and from there, by way of the caudolateral end of the superior colliculus, to the oculomotor nucleus, automatic responses to impulses from the inferior visual field are possible. Thus the pathway for cortical automatisms has been superimposed upon the primitive reflex paths producing like movements.

Turning now from the arcs for automatic eye movements involving area 19, consideration may be given to those circuits which pass only through areas 17 and 18. As was stated earlier in the description of the connections, the available material has not permitted differentiation of the boundary between areas 17 and 18, and the exact origin of the pathways now to be considered is in some doubt, although it is certain that they arise from the cortex caudal to area 19. Pathways arising from the upper part of this occipital region have been traced to the caudolateral end of the superior colliculus, and those from the lower portion of this occipital area to the fronto-

medial portion of the tectal region. Thus impulses reaching the upper portion of this occipital area must pass, via the caudal end of the superior colliculus, to the caudal part of the oculomotor nucleus and to the trochlear nucleus. They result in turning the eyes obliquely downward toward the other side. Eye movements obliquely upward and toward the other side are obtained by pathways which pass from the inferior portion of the occipital region (areas 17 and 18) to the rostral part of the superior colliculus, and from there to the front half of the oculomotor nucleus.

Evidently the upper part of this occipital region has relations to the superior colliculus comparable to those of the lower portion of area 19, and the lower part of the occipital area discharges to collicular regions which receive impulses from upper portions of area 19. Thus the patterns on the occipital cortex and on area 19 are reversed.

These cortical patterns for eye movements in various directions which have just been cited are of course dependent for their function upon the complete arc from the cortex through the superior colliculus and oculomotor nucleus to the extraocular muscles. The basic direction of eye movement is vested in the interrelationship between the retinal pattern on the superior colliculus and the oculomotor nuclear arrangement, an interrelationship common to all vertebrates. The cortical connections which appear in mammals as cortico-tectal systems can modify the intensity but cannot change the direction of such movements. The localization pattern on area 19 for eye movements in various directions is merely a reflection of the early established representation on the superior colliculus. This is a character common to many patterns of cortical localization, which are frequently reflections of an earlier established pattern laid down at lower levels.

From midportions of area 19 and from unidentified regions of the occipital cortex, fibers pass to the tegmentum of the midbrain, turning off from the main cortico-tectal systems beneath the superior colliculus. Part of the bundle from the occipital cortex and area 19 enters the superior colliculus in

its midportions, but the rest of the composite bundle proceeds caudalward through the tegmentum, undergoing in its course considerable synapse. There is evidence, not entirely conclusive, that the bundle proceeds caudalward to the nucleus of the sixth nerve, terminating in this nucleus and in the para-abducens nucleus. It is generally recognized (Spiegel and Sommer, '44) that the para-abducens nucleus is a coordinator of the activities of the lateral and the medial recti muscles giving rise to correlating fibers necessary for conjugate movement of the eyes in a horizontal plane. The results obtained would indicate that the pathways for automatic eye movements in a horizontal plane do not pass directly to either the superior colliculus or to the oculomotor nucleus.

Another interesting fact concerning the connections of the superior colliculi is easily demonstrable in the material studied. It is the existence of cortico-tectal pathways from areas which are auditory or auditory-visual association regions. Such connections are furnished by the descending fibers in the auditory radiations (Mettler, '35a) and by the external cortico-tectal tract. Since the inferior colliculi are known to connect with the superior colliculi by the so-called acustico-optic fibers, since hypothalamic impulses reach the superior colliculi by the dorsal longitudinal fasciculi (Huber and Crosby in Huber et al., '43) and moreover, since spino-tectal fascicles and collaterals of the ventral secondary ascending tract of V can be traced to this same midbrain region, obviously the superior colliculi have other and more complex functions than those of visual reflex centers. They are regions of correlation of auditory and visual impulses on both basal and cortical planes. They interrelate impulses set up by painful and tactile stimuli of the body and head with those aroused by auditory and visual sensations. The final common paths which arise in the superior colliculi carry responses to a wide range of stimuli. The largest connections are those from the visual association areas of the cortex, and it seems likely that visual impulses will be dominant in determining the responses.

However, such visual responses will be greatly modified by other elements in the field.

SUMMARY

1. In Macaca.mulatta stimulation of the most dorsal portions of area 19 results in upward conjugate deviation of the eyes, of middle portions of this area in conjugate horizontal deviation to the side opposite the stimulation, and of lower portions of area 19 (see fig. 1) in conjugate downward movements. Stimulation of the intermediate areas elicits combined movements.

2. Stimulation of the occipital regions of the hemisphere confirms the work of Walker and Weaver ('40).

3. Normal and degeneration material were used in establishing the cortico-tectal connections and their patterns of distribution on the superior colliculus. It was found that upper area 19 and the lower occipital region are connected with the rostromedial part of the superior colliculus, and that the lower part of area 19 and the upper occipital region are similarly related, by cortico-tectal systems, with the caudolateral part of this midbrain area. From the part of area 19 stimulation of which produces horizontal deviation of the eyes, fibers can be traced to the tegmentum of the midbrain.

4. In the discussion, the anatomical patterns and the experimental results are interrelated and the basic character of the collicular localization is stressed.

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ABBREVIATIONS

aq., aqueduct.

aud. a., auditory area.

aud.rad., auditory radiations.

calc.f., calcarine fissure.

caud.n., caudate nucleus.

cer.ped., cerebral peduncle.

cerebel., cerebellum.

corp.cal., corpus callosum.

corp.m., mammillary body.

cort.teg.tr., cortico-tegmental tract.

cort.tect.tr., aud.div., cortico-tectal tract, auditory division.

dorsomed.thal.n., dorsomedial thalamic nucleus.

ext.cort.tect.tr., external cortico-tectal tract.

F, fornix.

fim., fimbria.

G, stripe of Gennari.

hip., hippocampus.

hip.g., hippocampal gyrus.

inf.col., inferior colliculus.

int.cap.post.lb., posterior limb of internal capsule.

int.cort.tect.tr., oc.div.dors.p., internal cortico-tectal tract, occipital division, dorsal part.

int.cort.tect.tr., oc.div.vent.p., internal cortico-tectal tract, occipital division, ventral part.

int.cort.tect.tr., preoc.div.dors.p., internal cortico-tectal tract, preoccipital division, dorsal part.

int.cort.tect.tr., preoc.div.vent.p., internal cortico-tectal tract, preoccipital division, ventral part.

lat.gen.n., lateral geniculate nucleus.

lat.lem., lateral lemniscus.

lat.thal.n., lateral thalamic nucleus.

lent.n., lenticular nucleus.

m.l.f., medial longitudinal fasciculus.

med.gen.n., medial geniculate nucleus.

med.lem., medial lemniscus.

med.tect.sp.tr., medial tecto-spinal tract.

n.III, oculomotor nucleus.

n.IV, trochlear nucleus.

op.str., optic stratum.

op.tr., optic tract.

parieto.cort.pont.tr., parieto-cortico-pontine tract.

ped.inf.col., peduncle of inferior colliculus.

pul., pulvinar.

red n., red nucleus.

sp.tect.tr., spino-tectal tract.

str.med., stria medullaris.

str.med.prof., deep medullary stratum.

str.term., stria terminalis.

sub.nig., substantia nigra.

sub.thal.n., subthalamic nucleus.

sup.cerebel.dec., decussation of superior cerebellar peduncle.

sup.col., superior colliculus.

sup.col.com., superior collicular commissure.

tect.oc.tr., tecto-oculomotor tract.

tect. pont.tr., tecto-pontine tract.

tect. teg.tr., tecto-tegmental tract.

temp.cort.pont.tr., temporo-cortico-pontine tract.

temp.parieto.cort.pont.tr., temporo-parieto-cortico-pontine tract.

thal.cort.f., thalamo-cortical fascicles.

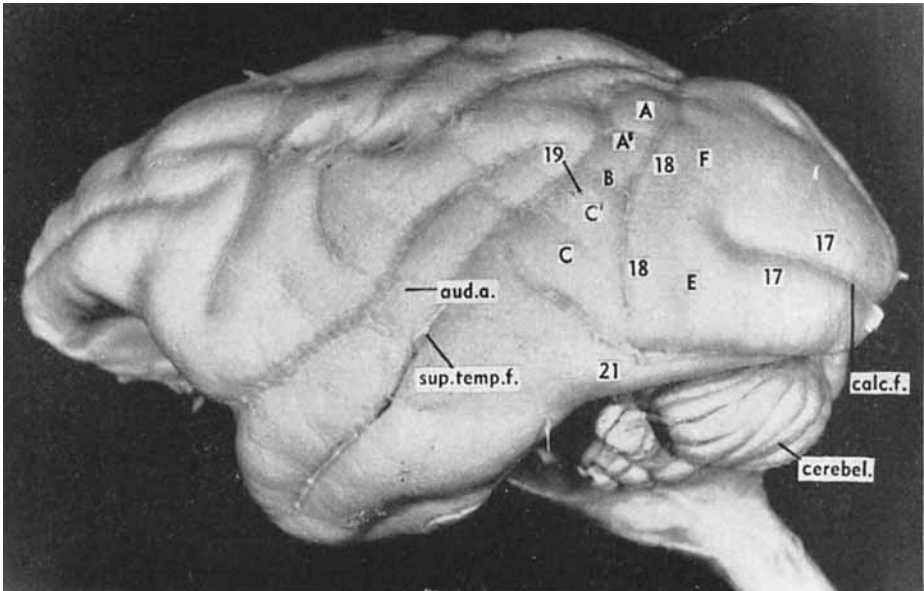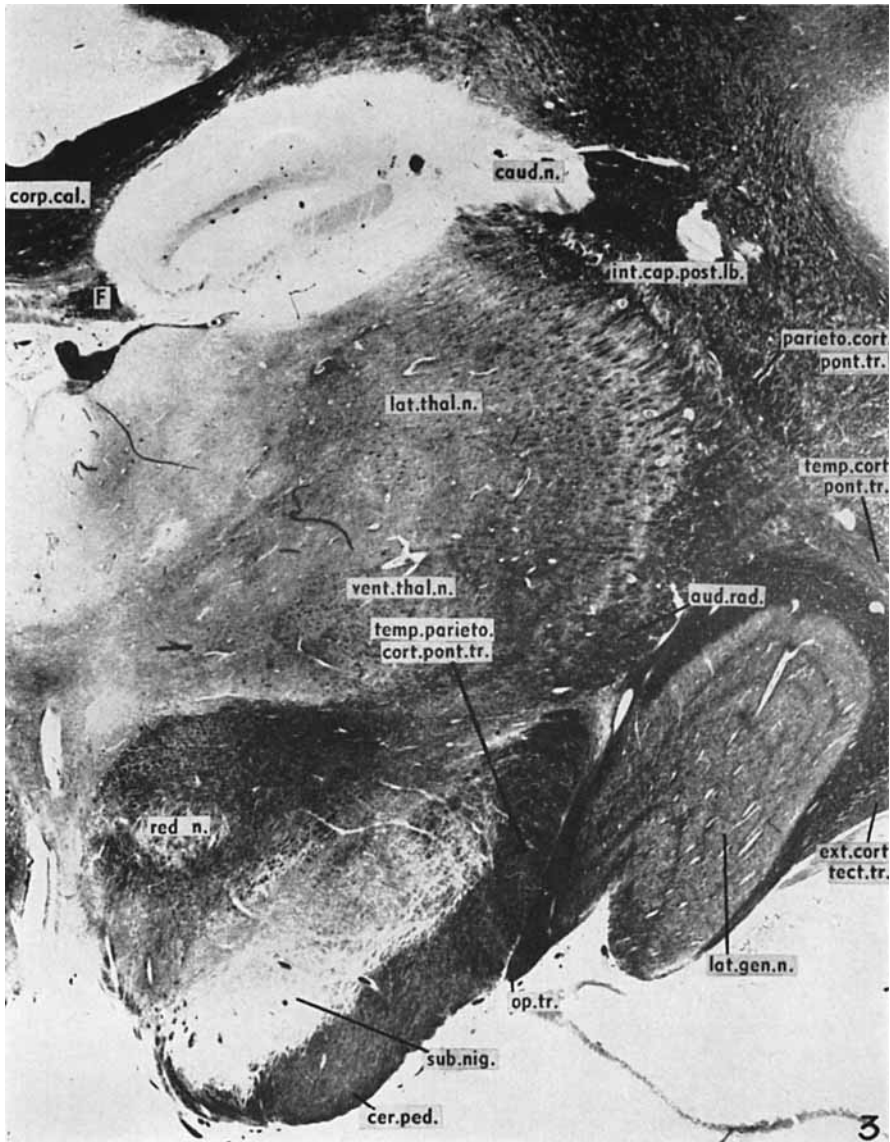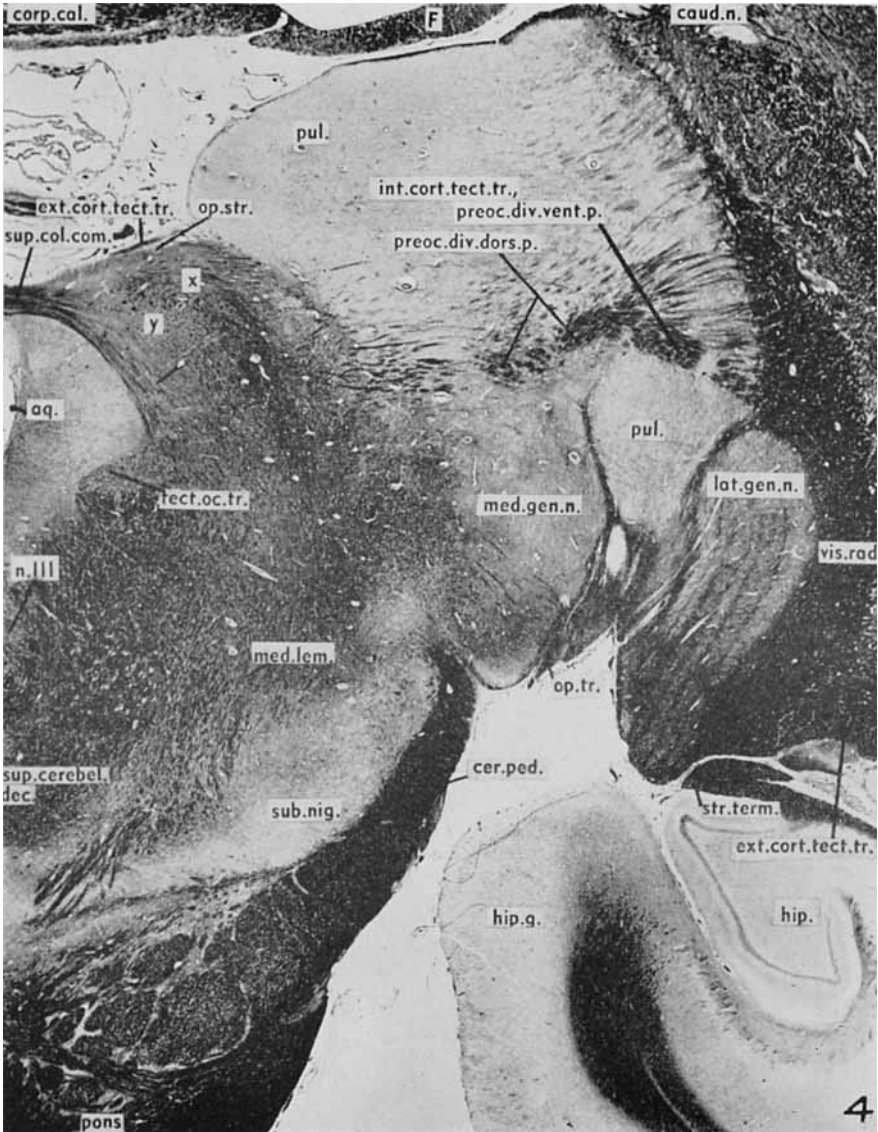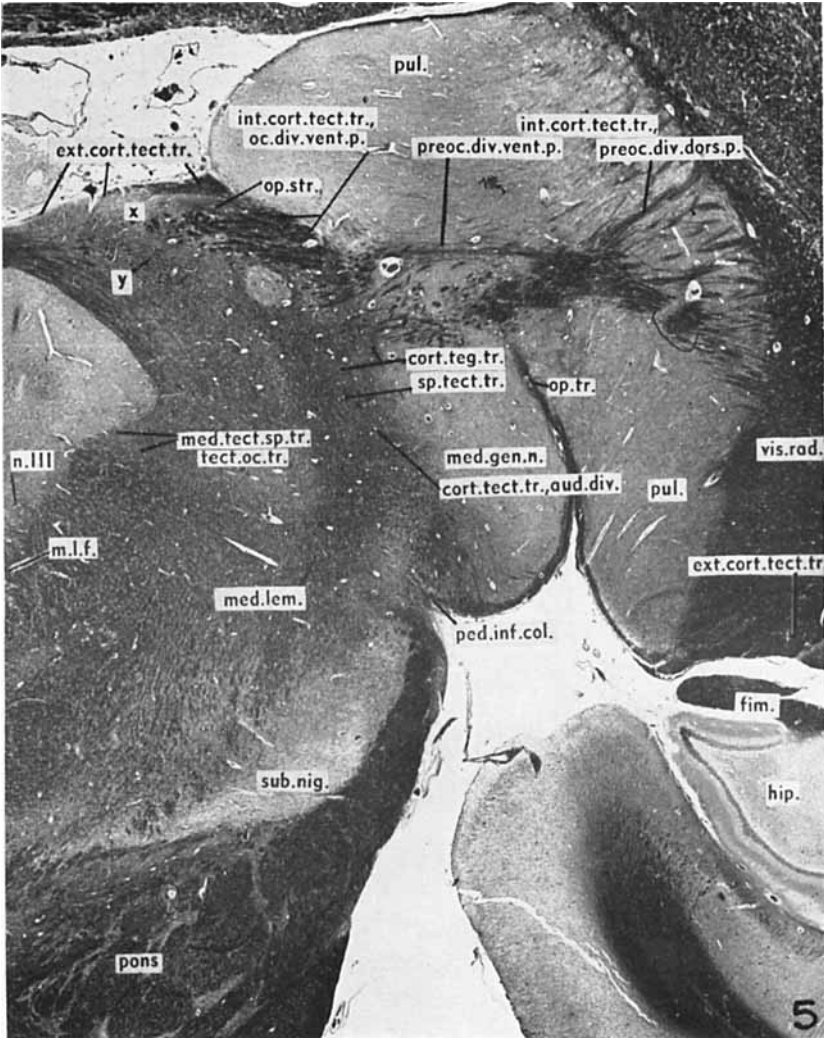vent.thal.n., ventral thalamic nucleus.

vis.rad., visual radiations.

x, termination of occipital division of internal cortico-tectal tract in superior colliculus.

y, termination of preoccipital division of internal cortico-tectal tract in superior colliculus.

17, area 17.

18, area 18.

19, area 19.

21, area 21.

Fig. 1   A photograph of the left side of the brain of Macaca mulatta ($\times$ 1.8). Areas 17, 18, 19, and 21 are designated. On area 19 the various points from which eye movements were elicited are indicated by letters. Stimulation of A produced conjugate upward deviation of the eyes, of A' conjugate deviation obliquely upward toward the right, of B conjugate horizontal deviation toward the right, of C' conjugate deviation obliquely downward to the right, and of C, conjugate downward deviation. Stimulation in the region of E (area 17) resulted in oblique conjugate deviation of the eyes upward and toward the right and in the region of F in conjugate deviation obliquely downward to the right.
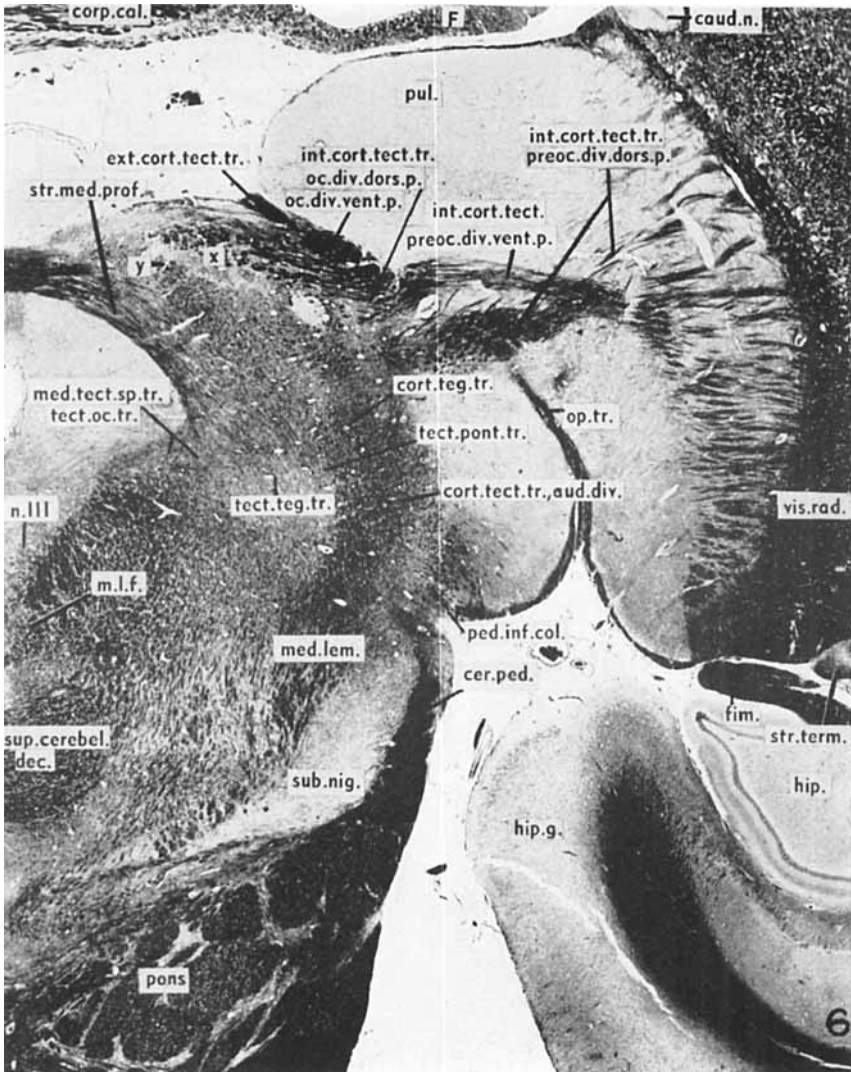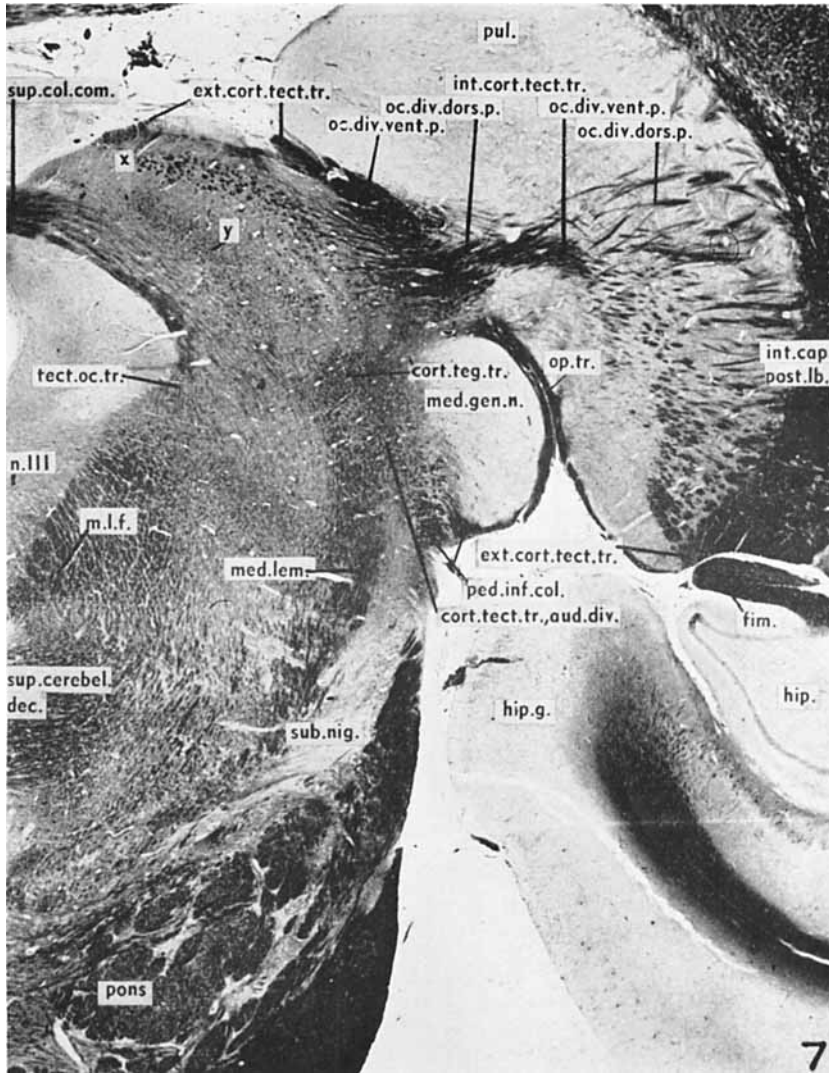
Figs. 2 to 12 inclusive   Photomicrographs of sections selected at various levels from a transverse series of a Macaca mulatta brain stained by the Weil technique, ($\times$ 4). The illustrations are arranged serially, beginning at a level through the rostral pole of the lateral geniculate nucleus and continuing to a plane through the beginning of the inferior colliculus. The levels were chosen to illustrate the connections of the superior colliculi, particularly their external and internal cortico-tectal systems. For the series, x indicates the termination of the occipital division and y of the preoccipital division of the internal cortico-tectal systems within the superior colliculus. On figure 4, *str. term.* should be *fim.*
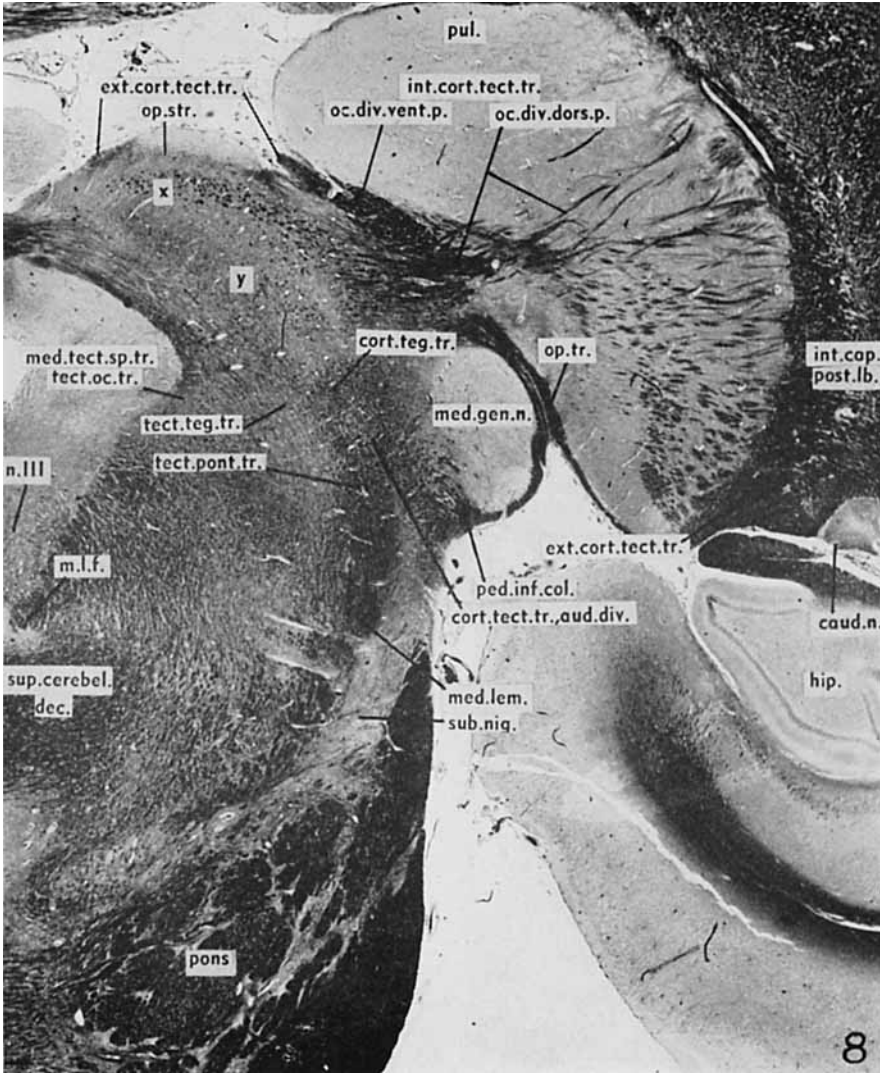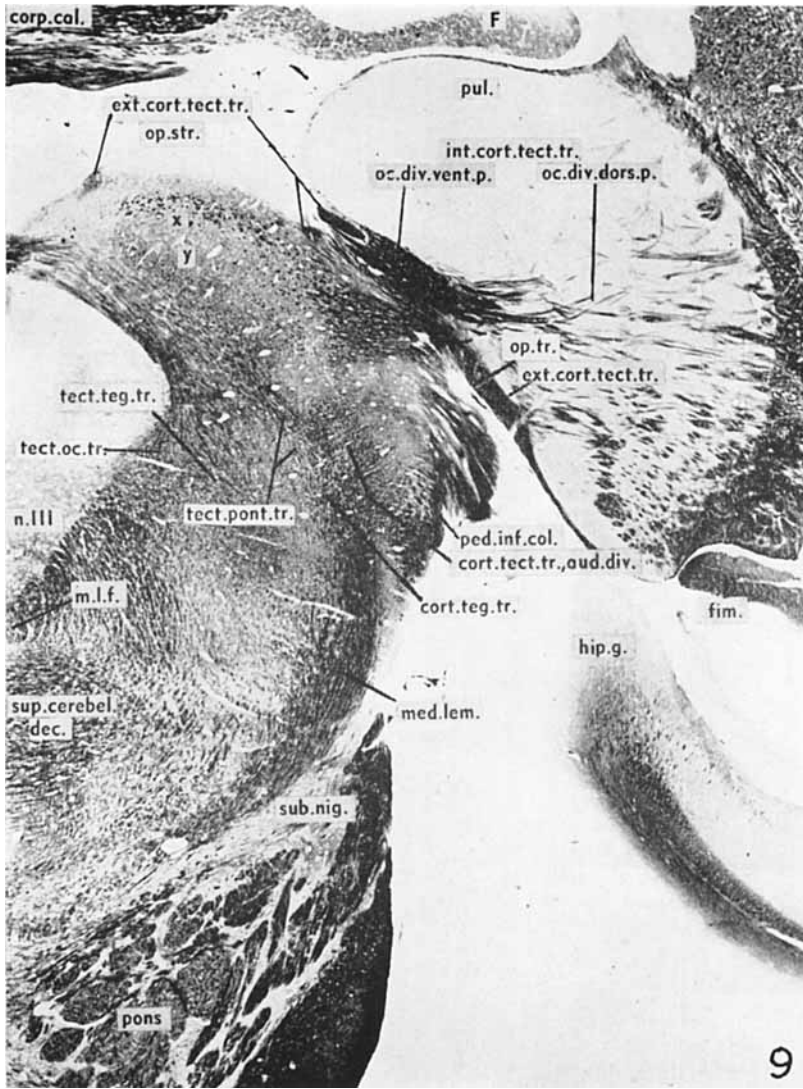
corp.cal.
F
caud.n.
pul.
ext.cort.tect.tr.
int.cort.tect.tr.
oc.div.dors.p.
oc.div.vent.p.
int.cort.tect.tr.
preoc.div.dors.p.
str.med.prof.
int.cort.tect.
preoc.div.vent.p.
y
x
med.tect.sp.tr.
tect.oc.tr.
cort.teg.tr.
op.tr.
tect.pont.tr.
n.III
tect.teg.tr.
cort.tect.tr.,aud.div.
vis.rad.
m.l.f.
med.lem.
ped.inf.col.
cer.ped.
fim.
sup.cerebel.
dec.
str.term.
sub.nig.
hip.
hip.g.
pons
6

corp.cal.

ext.cort.tect.tr.

F

x

y

sup.col.

str.med.prof.

ped.inf.col.

n.IV

lat.lem.

m.l.f.

inf.col.
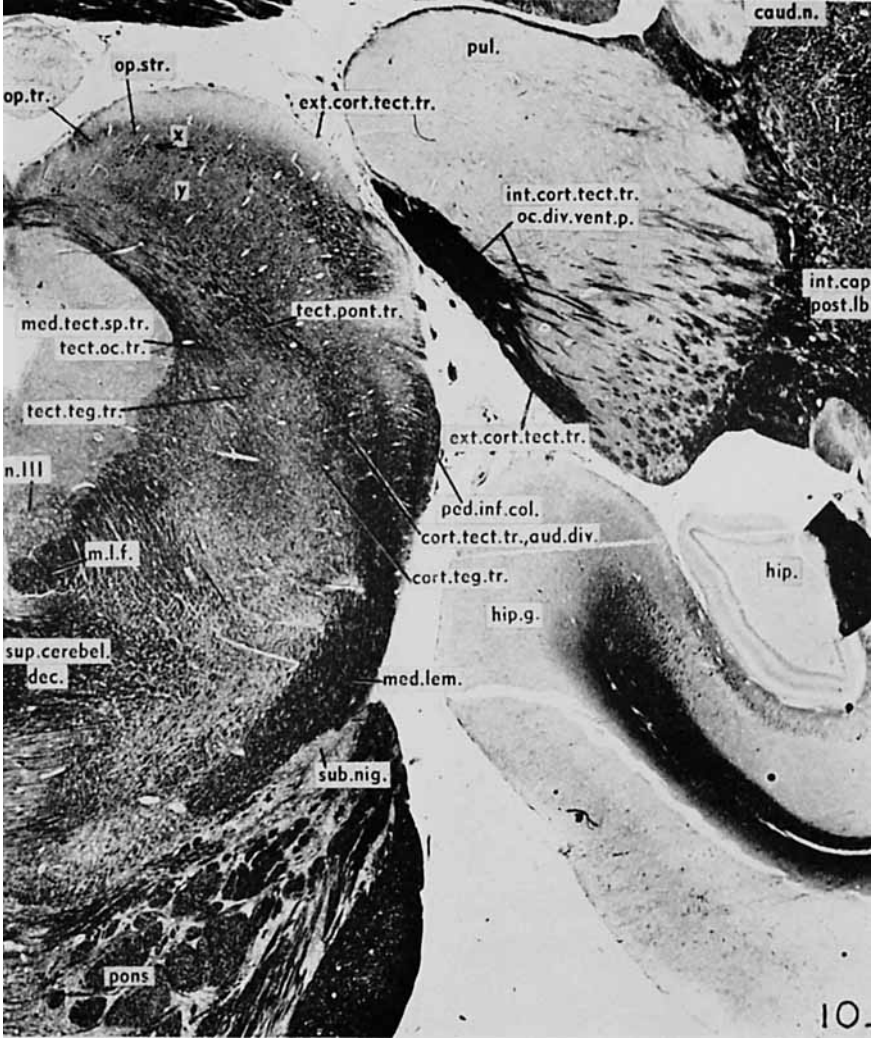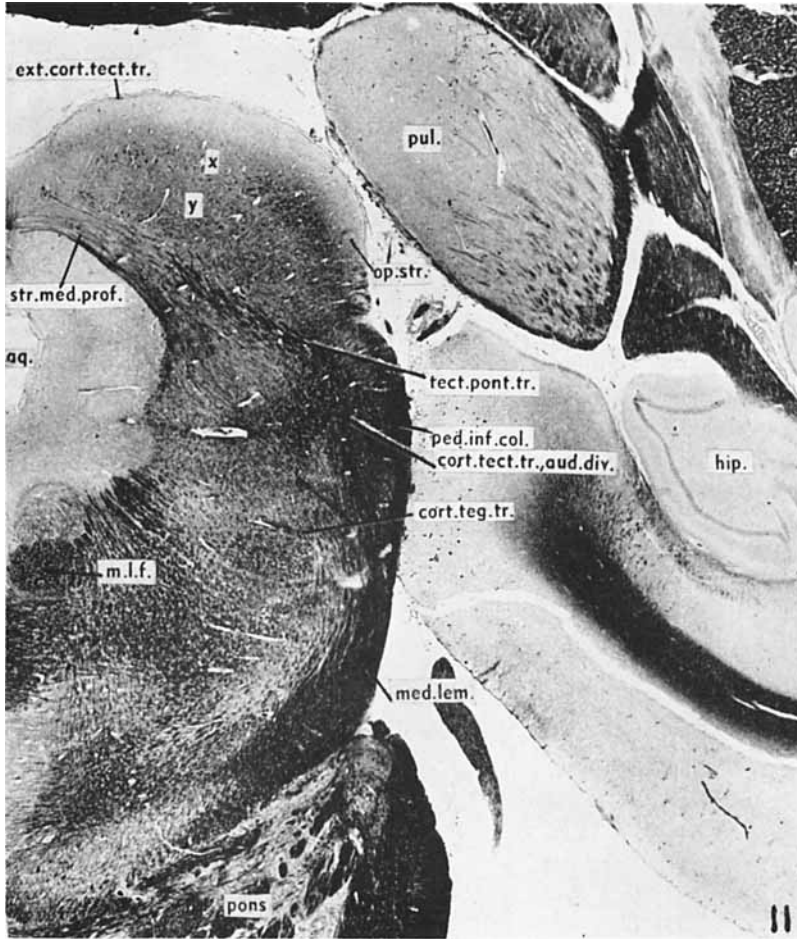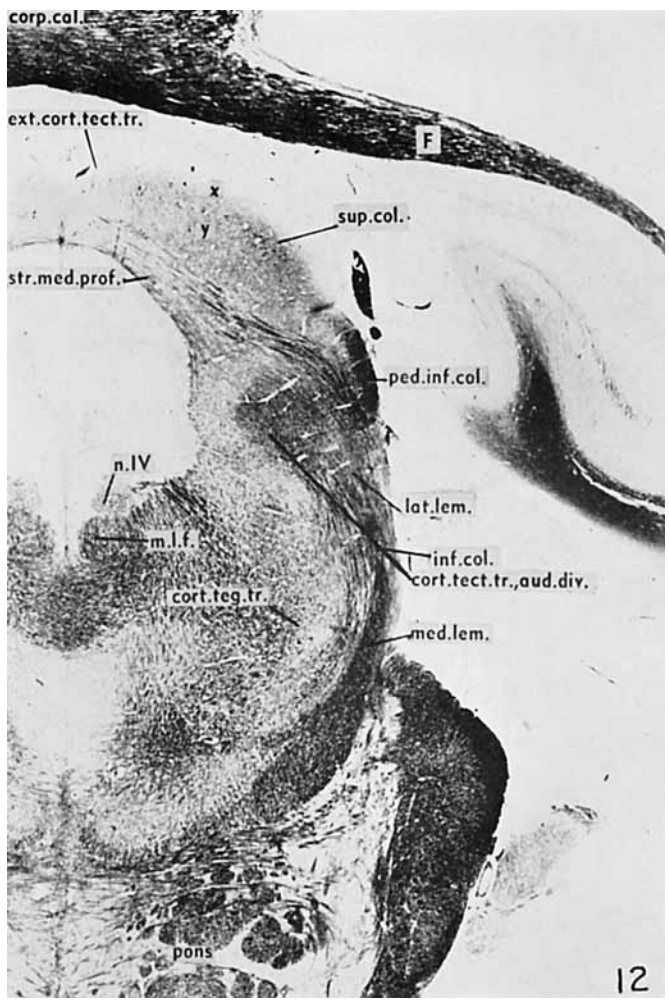
cort.teg.tr.

cort.tect.tr.,aud.div.

med.lem.

pons

12

Fig. 13 A photomicrograph of a cross section through the right occipital lobe of the brain of Macaca mulatta. This is from the same series illustrated in the previous figures. (× 8).