

THE MAMMALIAN MIDBRAIN AND ISTHMUS REGIONS

PART II. THE FIBER CONNECTIONS

C. The hypothalamo-tegmental pathways

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SEVENTEEN FIGURES

INTRODUCTION

The tegmentum of the midbrain consists chiefly of a complex of interlacing fiber tracts. Lesions placed in this region involve portions of two or more systems and the tracts affected are difficult to analyze. One method of attack upon such a problem is to trace paths from their origins (or terminations) outside of the midbrain into or through its tegmentum. In this way many fiber systems can be identified (Woodburne, Crosby and McCotter, '46; Crosby and Henderson, '48) and the unknown connections stand out more clearly and are more easily analyzed. Such has been the method employed in the series of studies (Huber et al., '43) of which this paper is a part. The present account deals with various descending paths from the hypothalamus which have been traced to their periventricular and tegmental terminations in the brainstem.

Certain texts have been especially useful in providing a background for this report. The nuclear configuration of the hypothalamus of the monkey is described in the work of Grünthal ('31), Crouch ('34), Papez and Aronson ('34), Le

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Gros Clark ('38), and Ingram ('40). The atlas by Rioch, Wislocki and O'Leary ('40), which establishes the terminology here employed, has been used in various studies on the hypothalamus, notably those in the collection of papers on this region published by the Association for Research in Nervous and Mental Diseases in 1940. A discussion of the comparative anatomy of the hypothalamic regions is to be found in the contributions by Ariëns Kappers, Huber and Crosby ('36), Boon ('38), and Crosby and Woodburne ('40). The fiber connections have been considered by many observers (Gurdjian, '27; Krieg, '32; Ariëns Kappers, Huber and Crosby, '36; Crosby and Woodburne, '40; Ingram, '40; and many others). A general review of the functional significance of the hypothalamus as a whole is presented in the papers by Ranson ('34, '37, and elsewhere).

The present account deals particularly with paths descending from the hypothalamus through the midbrain and makes no attempt to analyze many hypothalamic connections which have been recognized by others. An example of such a well-known tract is the supraoptico-hypophyseal system. This tract or its nucleus (the supraoptic nucleus), or both, have been described in normal and experimental preparations (and often related to water balance) by Lewy ('24), Croll ('28), Gaupp and Scharrer ('35), Fisher, Ingram and Ranson ('35), Fisher, Ingram, Hare and Ranson ('35), Ingram, Fisher and Ranson ('36), Ingram and Fisher ('36), Rasmussen ('37, '38, and '40), and Magoun and Ranson ('39). In our macaque series the tract is fairly well developed, as Ranson ('37 and elsewhere) and his associates believed, and not small, as the material studied by Mahoney and Sheehan ('36) and Foerster, Gagel and Mahoney ('37) seemed to indicate.

The material on which the present paper is based is 4 series of transverse serial sections of the brain of the macaque (*Macaca mulatta*). These sections were prepared for the tracing of fiber tracts by the Weil or the pyridine silver methods and for study of nuclear configuration by staining with toluidin blue. The photomicrographs were made by Mr.

George Smith, research technician in the Department of Anatomy. For his assistance the writers wish to express their sincere thanks.

DESCRIPTION AND DISCUSSION OF MATERIAL

Medial forebrain bundle

The medial forebrain bundle (figs. 1 to 6), an ascending and descending system connecting the ventromedial base of the hemisphere and the preoptic and hypothalamic regions, has been described in so many forms and by so many observers (as for example, Ariens Kappers, Huber and Crosby, '36; Ingram, '40) that it does not need further description here. It is generally agreed that the hypothalamus contains centers which are regulatory over the sympathetic system (Karplus and Kreidl, '12; Bard, '28 and '34; Cannon, '29; Ranson, '34 and '37; Kabat, Anson, Magoun and Ranson, '35; Foerster, '36; Bronk, Lewy and Larrabee, '36; Magoun, Ranson and Hetherington, '38; Magoun, '40; and many others). It has been suggested that the medial forebrain bundle carries fibers which play important roles in this discharge to sympathetic preganglionic centers (Ranson, '37; Ranson and Magoun, '39; Magoun, '40; and others). However, there is still some difference of opinion as to the number of components which should be included in this bundle and consequently as to its caudal extent; certain observers (Krieg, '32, in the rat) carry it back into the midbrain. The present writers have preferred to consider certain more caudally extending tracts as separate fiber systems (the anterior and the posterior hypothalamo-tegmental tracts) accompanying the medial forebrain bundle rather than constituting a part of it. These tracts are believed to have a special functional significance, being links in neuron chains connecting the hypothalamus, through the midbrain, with sympathetic preganglionic centers and consequently important pathways in the discharge from the hypothalamus to lower centers.

Anterior hypothalamo-tegmental tract

The anterior hypothalamo-tegmental tract is made up of fascicles which accumulate from the preoptic area and the anterior hypothalamic nucleus. They form a rather compact bundle (fig. 1) of thinly medullated fibers which proceeds along the ventromedial angle (figs. 2 to 5) of the medial forebrain bundle. As the ventromedial hypothalamic nucleus (fig. 5) is reached, the fibers turning out from it to form a portion of the posterior hypothalamo-tegmental system join the anterior hypothalamo-tegmental tract at its dorsomedial border. After the more dorsal portion of the posterior hypothalamo-tegmental tract is formed by fibers from the posterior hypothalamic area, the composite hypothalamo-tegmental system (fig. 6) constitutes a mass of fibers which passes through the lateral hypothalamic area with the anterior tract ventrolateral to the posterior bundle. This fiber complex proceeds into the ventromedial portion of the midbrain tegmentum. In its caudal course it is crossed by various components of the commissure of Forel (fig. 7) and some of its fibers decussate in this commissure. Behind the commissure (fig. 8) the anterior hypothalamo-tegmental tract bends dorsolaterad to come into relation with the nucleus mesencephalicus profundus pars ventralis (fig. 9) which appears to be its chief center of termination. Possibly some fibers of the bundle continue into the tegmentum but, if so, their final destination has not been determined. These anatomical relations have been checked not only in normal material but also in Marchi preparations made after destruction of the anterior hypothalamic and medial preoptic areas.

The hypothalamus is generally recognized to be a center concerned with the regulation of body temperature. This has been verified by the work of many observers (among others, Isenschmidt and Schnitzler, '14; Davison and Selby, '35; Ranson and Ingram, '35; Ranson, '37 and '40; Ranson, Fisher and Ingram, '37; Magoun, Harrison, Brobeck and Ranson, '38; Clark, Magoun and Ranson, '39a; and '39b). Due particularly to the work of Ranson and his colleagues, the anterior

hypothalamic area (Teague and Ranson, '36) is regarded as regulating against heat and the posterior hypothalamic regions against cold. Their experimental results have indicated that these regulations are carried on over neuron paths which run in the lateral hypothalamic area, so that a lesion in the posterolateral portion of the hypothalamus (Ranson, '37) will produce a poikilothermic animal.

The exact location of the pathways by which these impulses are relayed from hypothalamic levels through the brainstem to preganglionic centers of the cord is not known, although their general positions at various levels have been indicated by the work of such observers as Beattie, Brow and Long ('30), Langworthy and Richter ('30), Keller ('33), Ranson, Kabat and Magoun ('35), Foerster ('36), Kabat, Magoun and Ranson ('36), Spiegel and Hunsicker ('36), Magoun, Ranson and Hetherington ('38), Wang and Ranson ('39) and Magoun ('40).

In order to understand the significance of the anterior hypothalamo-tegmental tract, the present writers placed bilateral lesions in the lateral part of the preoptic and anterior hypothalamic regions in two monkeys. When such an operated monkey and a normal monkey were placed in a very warm box and allowed to remain there about half an hour, the temperature of the operated monkey rose to 107° to 108° (rectal temperature), 2° to 3° higher than the highest temperature of the normal monkey, which ordinarily shows a swing from 100° to 105°. It would appear that such operated animals have lost to some extent their ability to regulate against heat, a result in accord with previous findings. The loss of regulating power proved to be due to injury of the anterior hypothalamo-tegmental tracts, which in postmortem material were seen to have been partially severed.

In another series of monkeys the more ventral part of the lateral preoptico-hypothalamic area was stimulated by use of the McCulloch modification of the Horsley-Clarke stereotaxic apparatus. There was a resultant increase in amplitude and rate of respiration see also Ranson and Magoun, '33). This

respiratory change is a part of the mechanism of temperature regulation. In the writers' opinion, the pathway concerned in conducting these impulses from preoptico-hypothalamic regions to the tegmentum of the midbrain is the anterior (preoptico-) hypothalamo-tegmental tract, since fibers can be traced into it from the region stimulated and since stimulation of the area which it occupies at the base of the midbrain just lateral to the oculomotor roots (fig. 8) produces increased respiration.

In this connection it should be emphasized that stimulation more dorsally in the preoptic area (Kabat, '36), in the region ventral to the anterior commissure, leads to a decrease in respiratory rate. This part of the preoptic area is in the course of the discharge path from the posterior orbital region of the hemisphere (Delgrado and Livingston, '48) through the tegmentum of the midbrain to brainstem respiratory centers where stimulation of the proper area produced, in the monkeys studied, a slowing or complete inhibition of respiration. The impulses relayed by this discharge path probably act as inhibitors. The anterior hypothalamo-tegmental tract is not a part of the neuron chain functionally associated with this decreased respiratory activity. Various observers (recently, Le Gros Clark, '48, and von Bonin and Green, '49) have affirmed the existence of cortico-hypothalamic fibers.

Posterior hypothalamo-tegmental tract

This fiber bundle can be traced from the ventromedial hypothalamic nucleus and the posterior hypothalamic area to the tegmental region of the midbrain. The more rostral fascicles swing ventrolaterad from the ventromedial nucleus, interdigitate with those of the mammillo-thalamic tract (fig. 5), and course to a position in the lateral hypothalamic area. Here they lie dorsomedial to the anterior hypothalamo-tegmental tract (fig. 6). Whether there are other components in this composite bundle has not as yet been ascertained. The tract proceeds into the tegmentum of the midbrain, lying in a position lateral to and crossed by the emerging oculomotor roots

(fig. 8). The medial part of the bundle appears to synapse, after some decussation in the commissure of Forel, in pars ventralis of nucleus mesencephalicus profundus at red nuclear levels. Probably some of the fibers of the composite hypothalamo-tegmental bundle proceed caudad but their final termination has not been determined.

Stimulation of the posterior hypothalamic area in cats (Bard, '28; Cannon, '29) produces a series of somatic and visceral responses which result in the condition called sham rage. It is believed that the posterior hypothalamo-tegmental system in the cat is a part of the major discharge path from the hypothalamus to the sympathetic and the motor centers of the brainstem and the spinal cord and that it is the stimulation of these centers which produces the signs of sham rage. There are indications of emotional discharges of somatic type from the hypothalamus in the cat and in the monkey, as expressed in facial movements, vocalization, and respiratory changes according to Magoun, Atlas, Ingersoll and Ranson ('37), and from midbrain tegmentum as reported by Keller ('32) and Ingram, Ranson, Hannett, Zeiss and Terwilliger ('32). It has not been possible to obtain sham rage in monkeys through hypothalamic stimulation; nevertheless, the monkey too expresses dislike or anger by biting, by sweating on the pads of the feet, and by cries. It is probable that the posterior hypothalamo-tegmental paths serving as descending systems to motor and sympathetic centers act in the monkey as they do in the cat. Various observers have shown that in the cat and the monkey, lesions in the region between the mammillary bodies and the oculomotor nerve and lateral or dorsolateral to the mammillary bodies produce a somnolent state (Ranson, '34, '37, and '39; Ingram, Barris, Fisher and Ranson, '36; and Harrison, '40). Often this is accompanied by a plastic tone which gives it the character of catalepsy (Ranson and Ingram, '32).

Dorsal hypothalamo-tegmental tract

The dorsal hypothalamo-tegmental tract (figs. 7 and 8) is related to the ventromedial hypothalamic nucleus and the posterior hypothalamic area. The fibers arch upward and then accompany the posterior hypothalamo-tegmental fibers on their upper border, so that the two appear, at caudal hypothalamic levels, to be a single band of fibers, part of which decussate in the commissure of Forel (supramammillary decussation). Rostral to the red nucleus, the dorsal hypothalamo-tegmental tract turns dorsad and then swings above the nucleus. It terminates, in part, in nucleus mesencephalicus profundus pars dorsalis and probably in the interstitial nucleus of the medial longitudinal fasciculus.

Fornix

The fornix (figs. 1 to 6) arises as a continuation of the fimbria and extends forward from the rostral tip of the hippocampus to the region of the anterior commissure. At anterior commissure levels, it breaks up into a precommissural and a postcommissural division. The precommissural fibers (Loo, '31) pass in front of the anterior commissure to turn ventrad and supply the preoptic and anterior hypothalamic areas, including the paraventricular nucleus. This system is often called the fornix longus. The fibers of the postcommissural component of the fornix may in turn be divided into two portions. The more medial bundles of the postcommissural division, as they swing into the septal area, cross above the anterior commissure, forming a ventral hippocampal commissure. After decussation, some of them end in the bed nucleus of the ventral hippocampal commissure and others turn dorsally to enter the hippocampus. The main bundles of the postcommissural fornix turn caudoventrad to reach the hypothalamic region (figs. 1 to 6). They distribute to the paraventricular, the anterior, the dorsomedial, the dorsal, and the ventromedial hypothalamic nuclear groups, but they terminate chiefly in the medial and intermediate nuclei of the

mammillary body. A few of the fascicles accompanying this fornix system do not pass to the mammillary body but cross in a supramammillary decussation, the commissure of Forel (fig. 7), to enter the midbrain, where they turn toward the oculomotor nucleus. Their final termination is not known. In some ways these fibers to the tegmentum resemble the fibers of Jelgersma (Huber and Crosby, '29) in the bird. Such fascicles of the fornix system to the mammalian tegmentum were described for the rabbit by Edinger and Wallenberg ('01).

Mammillo-thalamic and mammillo-tegmental tracts

Arising from the medial, intermediate, and lateral portions of the mammillary body is a strong bundle of fibers which proceeds dorsorostrad. Within the hypothalamic area it divides into a rostradorsally running bundle, the mammillo-thalamic tract (figs. 6 to 2), and a caudodorsally coursing bundle, the mammillo-tegmental system (figs. 6 to 8). The mammillo-thalamic tract ends in the anterior nuclear group of the dorsal thalamus, projecting upon it olfacto-visceral impulses from the hypothalamus. It has been described so frequently that it needs no further description here. The mammillo-tegmental tract (Ramón y Cajal, '11; and many others) continues caudodorsally to end in the dorsal tegmental nucleus. This latter tract is of interest here because it provides a hypothalamic discharge to the dorsal tegmental nucleus, which in turn has relations with the dorsal longitudinal fasciculus.

Mammillo-peduncular tract

The mammillo-peduncular fascicles in the monkey are composed of very thinly medullated fibers passing between the medial mammillary nucleus (fig. 7) and the interpeduncular nucleus (fig. 9) of the midbrain (Ramón y Cajal, '11). Throughout their course they lie close to the ventral surface of the brain, either medial to or crossed by the rootlets of the third nerve. They break up in the rostral end of the inter-

peduncular nucleus. They do not show in the photomicrographs although they are fairly clear in the material itself.

Mammillary peduncle

In the following account, the mammillary peduncle is described without reference to its direction of conduction. Fibers (fig. 6) accumulate from the lateral and the medial mammillary nuclei to form a small, clear-cut bundle. In the region just dorsocaudal to the mammillary body (fig. 7), this bundle passes through nuclear gray to part of which the name of interstitial nucleus of the mammillary peduncle has been given by Papez ('23) and Fox ('41). This region is a somewhat differentiated portion of the ventral tegmental area of Tsai (Tsai, '25; see also Huber et al., '43). Here the bundle spreads out, probably giving and receiving contributions, and then continues in a dorsolateral direction (figs. 7 and 8) to join the ventromedial border of the medial lemniscus, of which it ultimately becomes an indistinguishable component in normal preparations. In its course toward the medial lemniscus, it interdigitates with the roots of the oculomotor nerve. The more medial fascicles of the mammillary peduncle do not combine with the medial lemniscus; instead they proceed dorso-caudad (figs. 8 to 19) near the midline to end ultimately in the ventral tegmental nucleus.

The mammillary peduncle has received consideration from many observers (for example, Ramón y Cajal, '11; Papez, '23; and Fox, '41). Some workers (as Wallenberg, '04) believe that it arises from the gray of fasciculus solitarius and, after decussation, accompanies the medial lemniscus forward until the rostral end of the midbrain is reached, where it turns off to the hypothalamus. The studies of Ramón y Cajal, Papez and Fox show that this peduncle consists of more than a single component. Fox stated that it may provide a connection from the ventral tegmental nucleus to the hypothalamus—the medial component described in the present account. He suggested that it may be the second neuron in a pathway forward

from the gray of fasciculus solitarius, the first neuron running in the dorsal longitudinal fasciculus. So far as our observations go, they tend to confirm this interpretation.

Dorsal longitudinal fasciculus

Throughout practically the whole extent of the preoptic and hypothalamic regions, the ventricle is bordered by thinly medullated and unmedullated fibers which have a dorsal or a dorsocaudal course through the field. The system, which at these levels is often designated the diencephalic periventricular system, is in reality a part of the dorsal longitudinal fasciculus. The term dorsal longitudinal fasciculus, as originally applied by Schütz, included a diencephalic component (Ramón y Cajal, '11; Krieg, '32; Ariëns Kappers, Huber and Crosby, '36; Crosby and Woodburne, '40; Thompson, '42; Furstenberg and Crosby, '45, and elsewhere; and others). Sometimes the name dorsal longitudinal fasciculus has been applied only to that portion of the system which arises from or lies in relationship with the dorsal tegmental nucleus and extends caudal to it (Gurdjian, '27, and others). In the present account, the term dorsal longitudinal fasciculus is used in its widest sense, as a series of periventricular, ascending and descending fascicles from the preoptic and hypothalamic levels to the caudal end of the brainstem. Such fascicles are admittedly difficult to trace anatomically and much of our information about them has been obtained through experimental work or from the study of clinical cases. No one as yet has given a complete account of this system, and no two authors have discussed exactly the same components. Rather, certain components have been described that fitted into the particular problem which the authors were attempting to solve. Especial interest has been aroused in this bundle by those (as Beattie, Brow and Long, '30) who regard the preoptic and anterior hypothalamic areas as concerned with regulation of the parasympathetic system. This is in opposition to the view of Ranson ('39), and others of the Ranson school, who believed that the

hypothalamus regulates only or chiefly the sympathetic discharge.

In 1947 Hess published a review and documentation of the results obtained by him and his associates during about 20 years of study of the relations of the diencephalic centers to autonomic functions. This series of studies is largely physiological in character. The anatomical data presented by this group of observers as documentation of their findings, while adequate for their purposes, is difficult to relate to any of the more detailed anatomical and experimental studies of the nuclear groups and fiber connections of the region. It would appear that their results were obtained in some cases by stimulation of the nuclear groups and in other cases by stimulation of the fiber systems. They stated that in the diencephalon "the function of various autonomic organs pertaining to the ergotrope sector (mediated by the Sympathetic)" are synthesized so that they may cooperate in carrying on appropriate activities. According to these experiments "the trophotrope-endophylactic sector (activated by the Parasympathetic) is represented in fields with diffuse boundaries." Such fields are regarded as definitely coordinative in function.

In the following account, beginning with the preoptic area and proceeding caudad, the components of the dorsal longitudinal fasciculus recognizable in the available material are described. The rostral part of the dorsal longitudinal fasciculus consists primarily, although not exclusively, of fascicles which interconnect the hypothalamus and the dorsal thalamus. To differentiate this rostral portion from the main mass of the dorsal longitudinal fasciculus, it has been designated as the thalamic portion of that system. Bundles A, B, C, and D of the following account belong to such a thalamic portion. The main, or brainstem, portion of the dorsal longitudinal fasciculus, which extends to cord levels, consists of ascending and descending fibers, part of which are related to the hypothalamus and the preoptic area.

Bundle A (figs. 1 and 2) consists of fascicles which connect, perhaps interconnect, the nucleus reuniens, the anterior peri-

ventricular nucleus, and the ventromedial portion of the anteroventral thalamic nucleus with the medial preoptic area and the paraventricular nucleus of the hypothalamus. The bundle is reasonably well circumscribed from the rest of the system but its constituent fibers are small and only thinly medullated or unmedullated.

The fascicles of bundle B (F.L.D.TH.B, fig. 3) pass from the dorsomedial nucleus of the dorsal thalamus in a ventro-rostral direction to the dorsal hypothalamic area, the paraventricular nucleus, and the anterior hypothalamic nucleus. This bundle is not sharply delimited along its caudal border from the fibers of bundle C.

The constituent fibers of bundle C (F.L.D.TH.C, fig. 4) swing ventromedial from the midportion of the dorsomedial nucleus of the dorsal thalamus. Then they take a more directly ventral course to come into relationship with the dorsal hypothalamic area and the dorsomedial hypothalamic nucleus.

The fascicles forming bundle D (F.L.D.TH.D, figs. 5 and 6) can be traced between the ventromedial hypothalamic nucleus and the posterior hypothalamic area on the one hand and the more caudal portions of the dorsomedial thalamic nucleus on the other hand. During their course in the hypothalamus, they are joined by fibers from the mammillary body.

The brainstem portion, or main mass, of the dorsal longitudinal fasciculus begins rostrally with fascicles (F.L.D., fig. 6) which proceed along the edge of the ventricle toward the midbrain area but are not clearly separated from bundle D. They are supplemented by marked additions from the most caudal end of the hypothalamus and, as a sizeable fiber mass, pass into the mesencephalon (fig. 7). The bundle is also enriched by periventricular fibers from all levels of the preoptic area and the hypothalamus, which have continued caudad close to the ventricle. This midbrain portion of the system is thought to arise from all of the hypothalamic areas except the supraoptic and the ventromedial hypothalamic nuclei.

Just within the mesencephalon, the dorsal longitudinal fasciculus contributes fibers to the rostral Edinger-Westphal nu-

cleus (fig. 8). The tectal component (figs. 9 to 13) swings dorsally and caudally to distribute to the dendrites of the periventricular cells of the superior colliculus, thus projecting upon this midbrain area olfacto-visceral impulses from the hypothalamus. The tegmental bundle turns into a position medial to the nucleus of Darkschewitch and dorsal to the oculomotor nucleus. In this position, fascicles are contributed to the caudal end of the Eninger-Westphal nucleus. Throughout its course at superior collicular levels, the bundle gradually falls into a dorsal part, which is called here the lateral or dorsolateral portion of the system and which is associated with the lateral tegmental gray, and a medial part, which has a more caudal termination (figs. 9 to 12). The lateral portion ends in the lateral nucleus of the central gray (GR.CENT.P. LAT.), but also sends fibers laterad into the tegmental areas of the midbrain where they come into relation with the nuclear masses ventral to the superior colliculus. A small fascicle of this lateral part swings over the dorsal surface of the medial bundle (fig. 12) to reach the lateral part of the periventricular gray where it rides over the dorsolateral angle of the laterodorsal tegmental nucleus. Behind the level of this nucleus, these fibers are supplemented by other fascicles of the lateral bundle (figs. 13 and 14) and approach the main mass of the dorsal longitudinal fasciculus but pass, it is believed, independently to the superior salivatory nucleus (fig. 15). It may be stressed in this relation that the lateral part of the dorsal longitudinal fasciculus comes from more rostral levels of the hypothalamus than does the medial part.

The medial portion of the dorsal longitudinal fasciculus, at inferior collicular levels, contributes to the dorsal nucleus of the raphé (fig. 12) and then continues into intimate relation with the laterodorsal nucleus of the tegmentum. It gives fibers to the laterodorsal tegmental nucleus (fig. 13), in part encapsulating it, and distributes to adjacent tegmental gray. After giving fibers to and receiving fibers from the dorsal tegmental nucleus, it proceeds caudad in the periventricular region. It distributes to the tegmental gray of the pons, to the

abducens nucleus (fig. 15), and to the motor facial nucleus (fig. 15). In the medulla it lies in close relationship to the dorsal efferent nucleus of the vagus and the hypoglossal nucleus, to both of which it contributes fibers (fig. 17). There is no question that the medial reticular gray of the medulla oblongata receives fascicles from this bundle and there is indication that the inferior salivatory nucleus (fig. 16), and nucleus ambiguus are also supplied from it. Fascicles from the gray of fasciculus solitarius (fig. 17) enter this bundle, therefore it is both an ascending and a descending system. The bundle continues beyond the level of the hypoglossal nucleus to about the plane of transition between brainstem and spinal cord.

The dorsal longitudinal fasciculus has somewhat the same relationship to the parasympathetic centers that the hypothalamo-tegmental systems have to the sympathetic. It has seemed to the writers quite certain that this bundle does terminate in part in preganglionic centers of the brainstem. It is made up of finely medullated and unmedullated fibers and it is not surprising that it should appear much less striking than do the more heavily medullated paths related to the hypothalamus. In addition to carrying impulses from preoptic and hypothalamic regions to parasympathetic centers, the dorsal longitudinal fasciculus has been shown to have ascending paths and connections with the tectum. The relative importance of descending paths from the hypothalamus in the periventricular region was questioned by Magoun, Ranson and Hetherington ('38) and Magoun ('40).

SUMMARY

Among the pathways of the macaque's brain here described there are certain connections which the authors wish to emphasize.

1. The anterior hypothalamo-tegmental system consists of bundles of fibers traceable from the preoptic and anterior hypothalamic areas through the lateral hypothalamus to the tectum of the midbrain. There, after partial decussation

through the commissure of Forel, they terminate in the nucleus mesencephalicus profundus pars ventralis which lies ventral to the magnocellular part of the red nucleus.

2. The posterior hypothalamo-tegmental tract from the ventromedial hypothalamic nucleus and perhaps the posterior hypothalamic area joins the dorsomedial border of the anterior hypothalamo-tegmental tract at caudal levels of the lateral hypothalamic area. After partial crossing in the commissure of Forel, it enters the nucleus mesencephalicus profundus pars ventralis.

3. The dorsal hypothalamo-tegmental tract can be traced from the ventromedial hypothalamic nucleus caudally to a position dorsal to the red nucleus where it comes into relation with nucleus mesencephalicus profundus pars dorsalis.

4. In addition to the customarily recognized distribution of the fornix a few fibers of this system can be traced caudalward into the tegmentum of the midbrain where they turn toward the oculomotor nucleus. Such fascicles are comparable to those described by Edinger and Wallenberg ('05) in the rabbit.

5. The dorsal longitudinal fasciculus can be followed throughout its extent in the brain and the following components can be recognized: (a) internuclear connections between thalamus and hypothalamus; (b) fascicles terminating in all the preganglionic parasympathetic centers of the brainstem; (c) fibers to the motor nuclei of the brainstem except the eye muscle nuclei; (d) fascicles arising and (or) terminating in periventricular and tegmental gray at midbrain and pons levels such as the dorsal nucleus of the raphé, the laterodorsal tegmental nucleus, and the dorsal tegmental nucleus; (e) fibers contributed from the dorsal visceral gray of the fasciculus solitarius.

6. In the discussion of each system, morphological findings, experimental results, and data from the literature have been correlated in an endeavor to interpret its functional significance.

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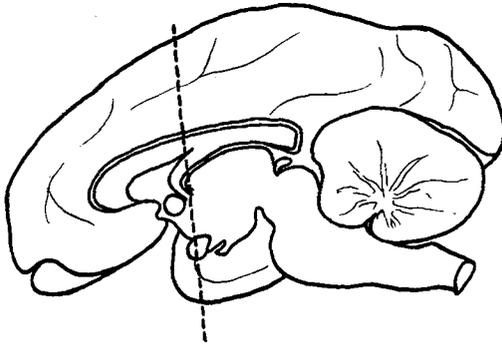
ABBREVIATIONS

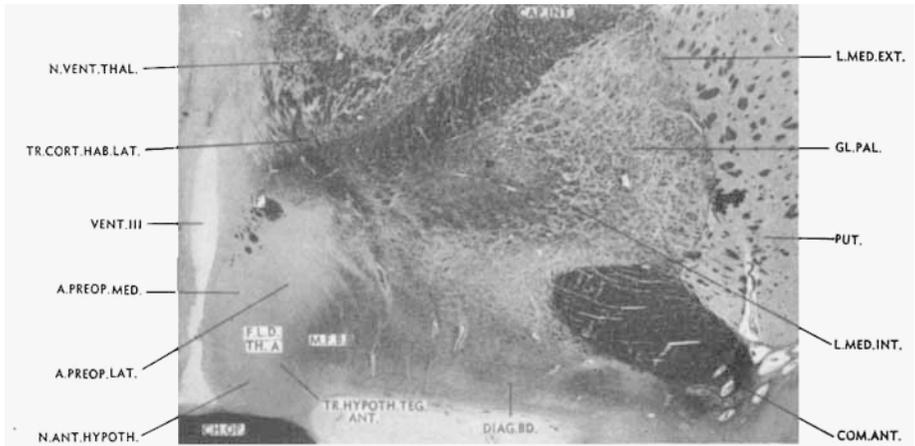
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|---|--|
| A.HYPOTH.LAT., lateral hypothalamic area | F.L.D.T., dorsal longitudinal fasciculus, tectal portion |
| A.PREOP.LAT., lateral preoptic area | F.L.D.TH.A, dorsal longitudinal fasciculus, thalamic portion, bundle A |
| A.PREOP.MED., medial preoptic area | F.L.D.TH.B, dorsal longitudinal fasciculus, thalamic portion, bundle B |
| ANSA LENT., ansa lenticularis | F.L.D.TH.C, dorsal longitudinal fasciculus, thalamic portion, bundle C |
| AQ., aqueduct | F.L.D.TH.D, dorsal longitudinal fasciculus, thalamic portion, bundle D |
| BR.CONJ., brachium conjunctivum | F.LENT., lenticular fasciculus |
| BR.PON., brachium pontis | F.L.M., medial longitudinal fasciculus |
| CAP.INT., internal capsule | F.SOL., solitary fasciculus |
| CEREBELL., cerebellum | F.SUBTHAL., subthalamic fasciculus |
| CH.OP., optic chiasm | G.VII, genu of VII |
| COL.INF., inferior colliculus | GL.PAL., globus pallidus |
| COL.SUP., superior colliculus | GR.CENT.P.DORS., central gray, dorsal part |
| COM.ANT., anterior commissure | GR.CENT.P.LAT., central gray, lateral part |
| COM.COL.SUP., commissure of superior colliculus | GR.CENT.P.VENT., central gray, ventral part |
| COM.FOREL, commissure of Forel (supramammillary commissure) | L.CER., locus coeruleus |
| COMB SYSTEM, comb system | L.MED.EXT., external medullary lamina |
| CORP.MAM., mammillary body | L.MED.INT., internal medullary lamina |
| D.E.N.X., dorsal efferent nucleus of vagus | LEM.LAT., lateral lemniscus |
| D.R.V., descending root of trigeminal | LEM.MED., medial lemniscus |
| DEC.BR.CONJ., decussation of brachium conjunctivum | M.F.B., medial forebrain bundle |
| DEC.TEG.DORS., dorsal tegmental decussation | N.III, oculomotor nucleus |
| DEC.TEG.VENT., ventral tegmental decussation | N.IV, trochlear nucleus |
| DIAG.BD., diagonal band of Broca | N.VI, abducens nucleus |
| F., fornix | N.VII, facial nucleus |
| F.F., field of Forel | N.XII, hypoglossal nucleus |
| F.L.D., dorsal longitudinal fasciculus | N.AM., nucleus ambiguus |
| F.L.D.L., dorsal longitudinal fasciculus, lateral portion | |
| F.L.D.M., dorsal longitudinal fasciculus, medial portion | |

- N.ANT.HYPOTH., anterior hypothalamic nucleus
 N.CENT.THAL., central nucleus of dorsal thalamus
 N.D.R.V, nucleus of descending root of trigeminal
 N.DORS.HYPOTH., dorsal hypothalamic nucleus
 N.DORS.RAPHE, dorsal nucleus of raphé
 N.DORS.TEG., dorsal tegmental nucleus
 N.DORSOMED.HYPOTH., dorsomedial hypothalamic nucleus
 N.DORSOMED.THAL., dorsomedial thalamic nucleus
 N.GEN.LAT., lateral geniculate nucleus
 N.INTERPED., interpeduncular nucleus
 N.LAT.DORS.TEG., laterodorsal tegmental nucleus
 N.MES.PROF.P.LAT.CAUD., caudal portion of the lateral part of nucleus mesencephalicus profundus
 N.MES.PROF.P.VENT., ventral part of nucleus mesencephalicus profundus
 N.POST.HYPOTHAL., posterior hypothalamic nucleus
 N.RUB., red nucleus
 N.S.V., sensory trigeminal nucleus
 N.SALV.INF., inferior salivatory nucleus
 N.SALV.SUP., superior salivatory nucleus
 N.SUBTHAL., subthalamic nucleus
 N.VENT.MED.HYPOTH., ventromedial hypothalamic nucleus
 N.VENT.THAL., ventral nucleus of dorsal thalamus
 N.VENT.TEG., ventral tegmental nucleus
 NN.III, oculomotor nerve
 NN.IV, trochlear nerve
 NN.V, trigeminal nerve
 NN.VII, facial nerve
 OL.INF., inferior olivary nucleus
 OL.SUP., superior olivary nucleus
 PED.CER., cerebral peduncle
 PED.MAM., mammillary peduncle
 PED.MAM.A, mammillary peduncle, bundle A
 PED.MAM.B, mammillary peduncle, bundle B
 PED.THAL.INF., inferior thalamic peduncle
 PONS, pons
 PUL., pulvinar
 PUT., putamen
 PYR., pyramid
 R.MES.V, mesencephalic root of the trigeminal
 SUB.NIGRA, substantia nigra
 THAL.DORS., dorsal thalamus
 TR.CORT.HAB.LAT., lateral cortico-habenular tract
 TR.CORT.TECT.EXT., external cortico-tectal tract
 TR.CORT.TECT.INT., internal cortico-tectal tract
 TR.HAB.PED., habenulo-peduncular tract
 TR.HYPOTH.TEG.ANT., anterior hypothalamo-tegmental tract
 TR.HYPOTH.TEG.DORS., dorsal hypothalamo-tegmental tract
 TR.HYPOTH.TEG.POST., posterior hypothalamo-tegmental tract
 TR.MAM.PED., mammi-lo-peduncular tract
 TR.MAM.THAL., mammi-lo-thalamic tract
 TR.MAM.TEG., mammi-lo-tegmental tract
 TR.OP., optic tract
 TR.PALL.HYPOTH., pallido-hypothalamic tract
 TR.PALL.INC.OL., pallido-incerto-olivary tract
 TR.RUB.SP., rubro-spinal tract
 TR.RUB.SP.CAUD., caudal rubro-spinal tract
 TR.SUBTHAL.TEG., subthalamo-tegmental tract
 VENT.III, third ventricle
 Z.INC., zona incerta

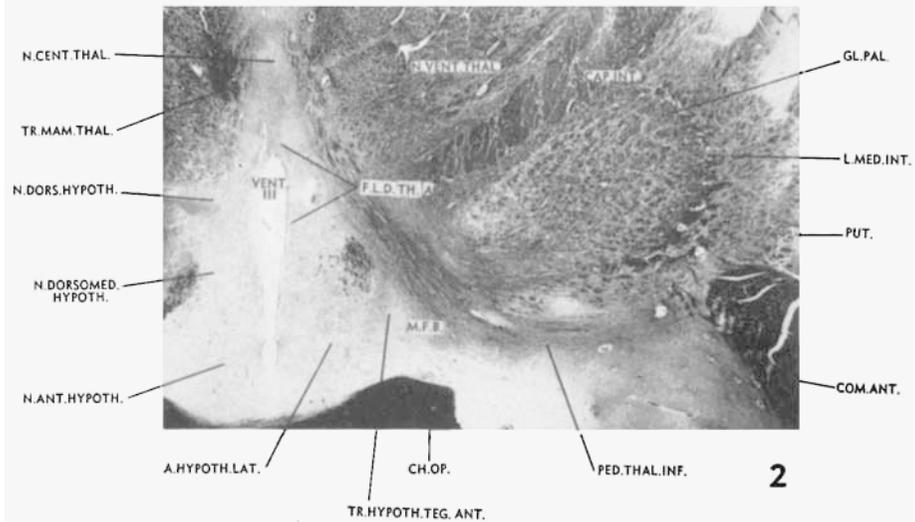
FIGURE DESCRIPTION

The figures, reproductions of photomicrographs of selected transverse sections through various levels of the macaque brain, are from the same Weil series. Figure 1 passes through the preoptic area and the anterior commissure and those following are in rostrocaudal order. In the diagram below, the plane of section of figure 1, and so of the series, is indicated. The last figure represents a level through the hypoglossal nucleus. The structures necessary for recognition of the levels, as well as the fiber tracts described and the nuclear groups related to them, are labeled on the figures. $\times 6.5$.

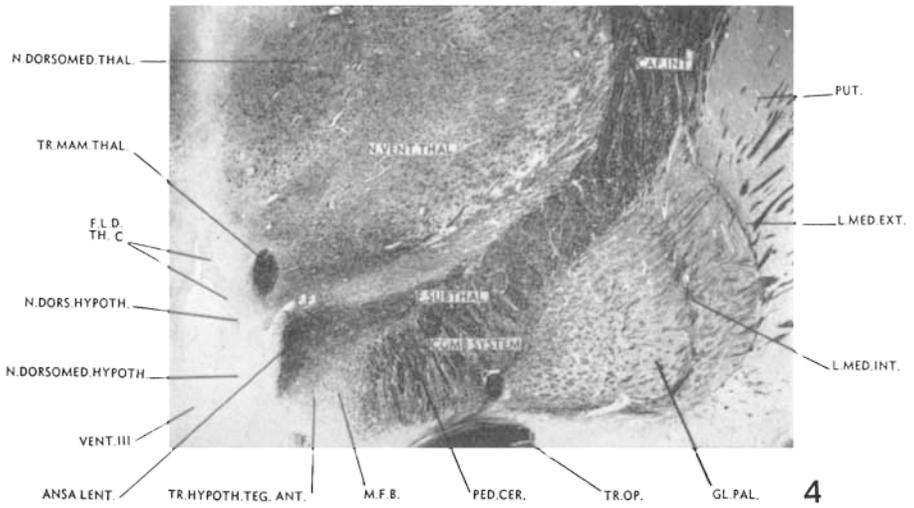
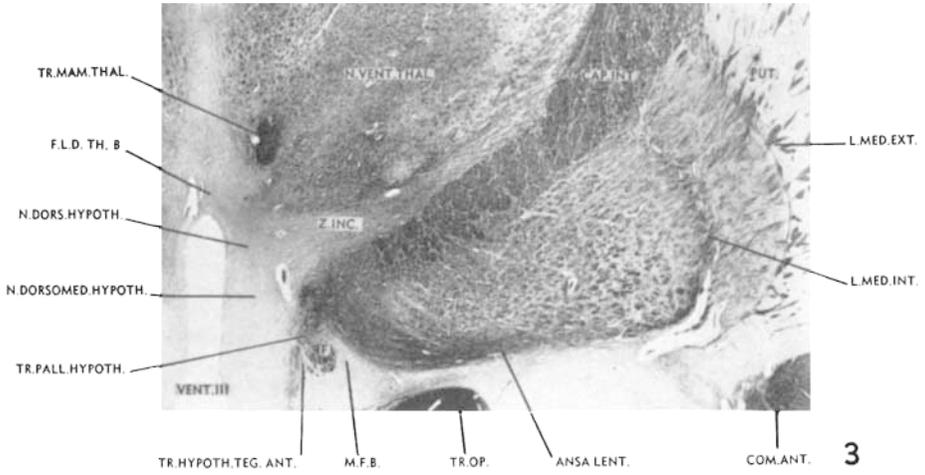


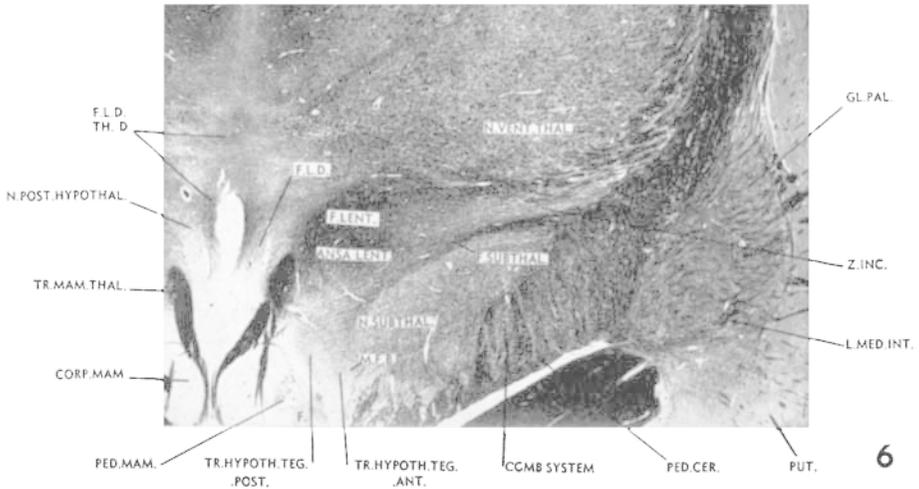
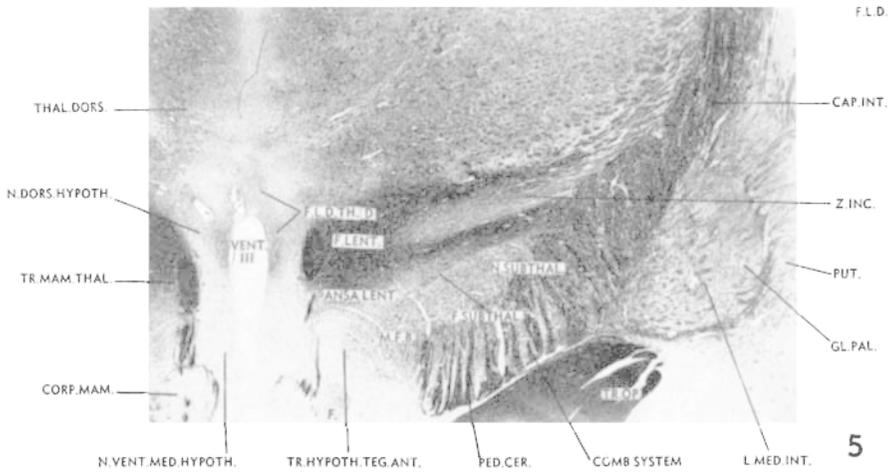


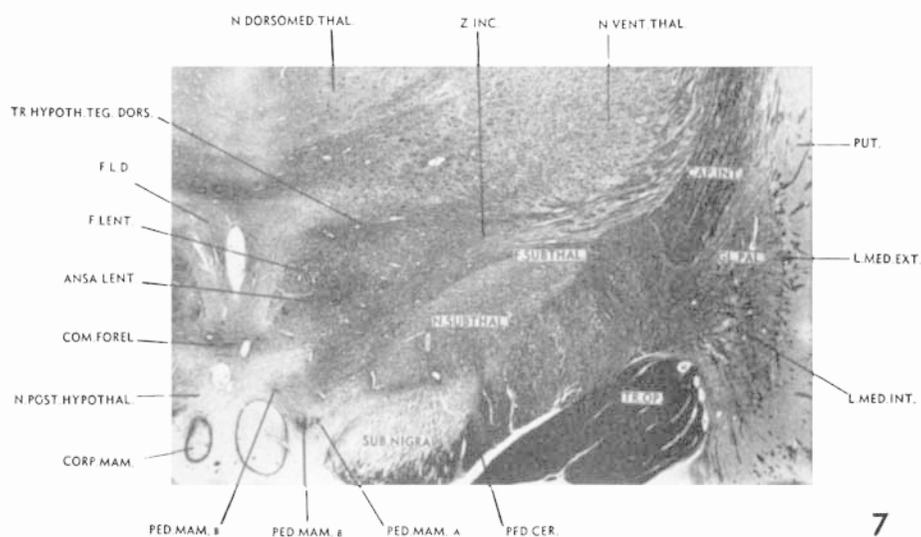
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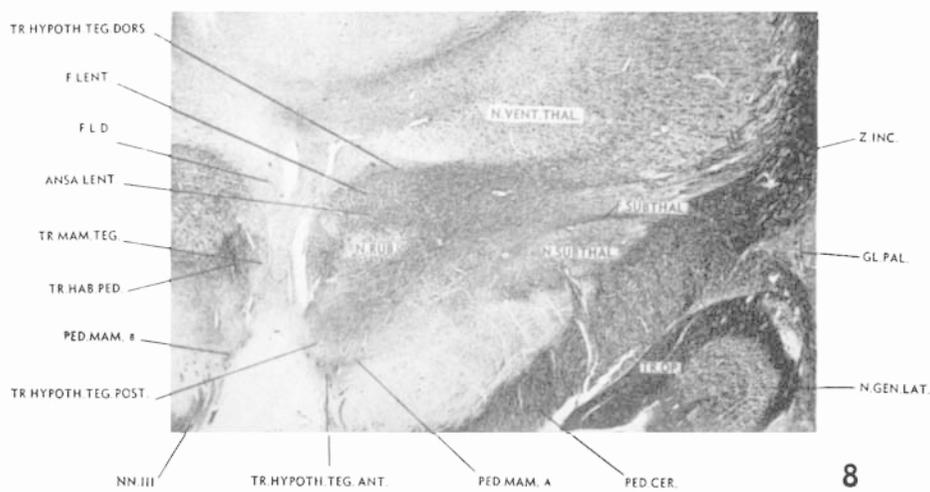
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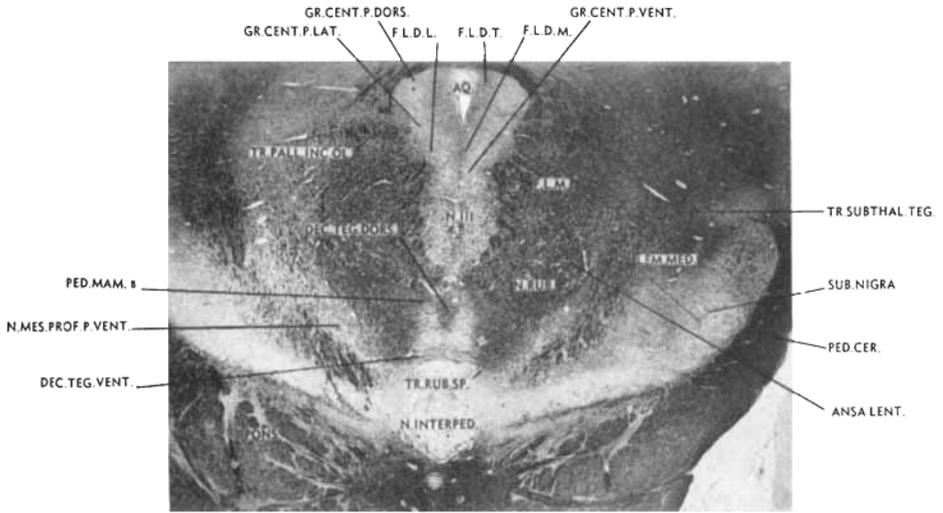




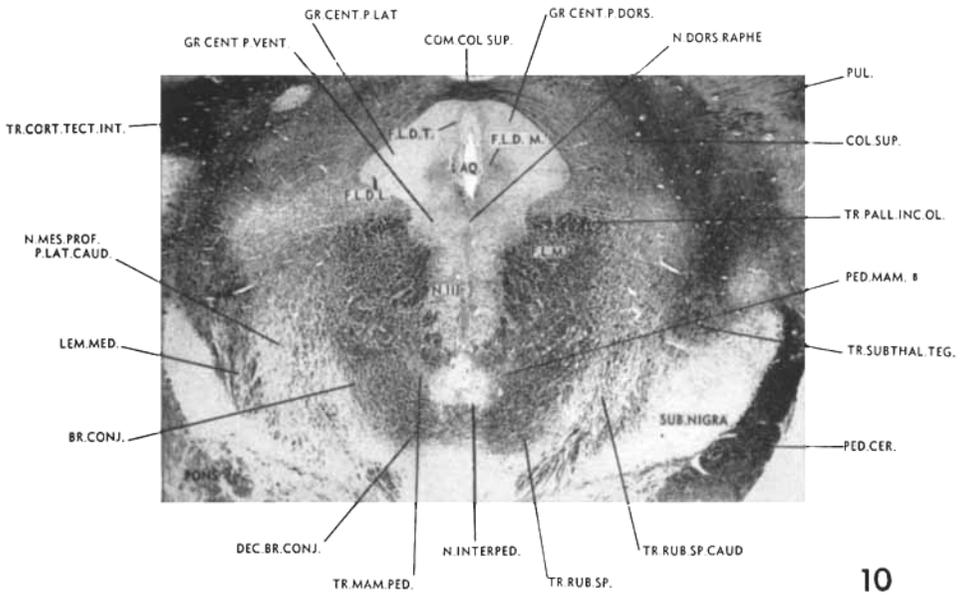
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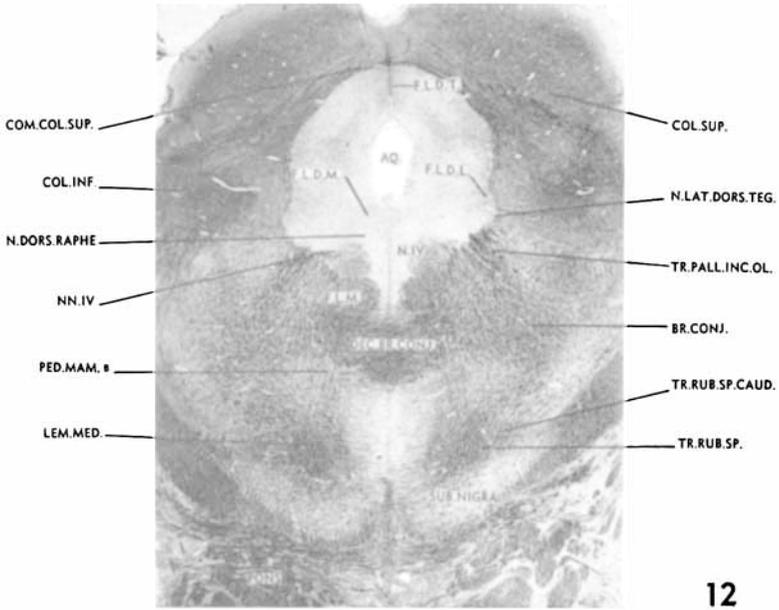
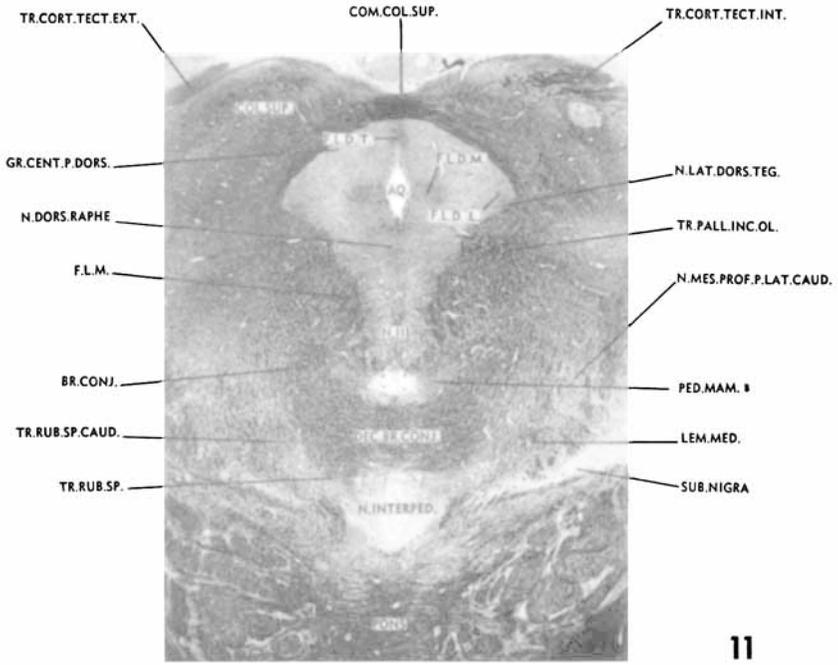
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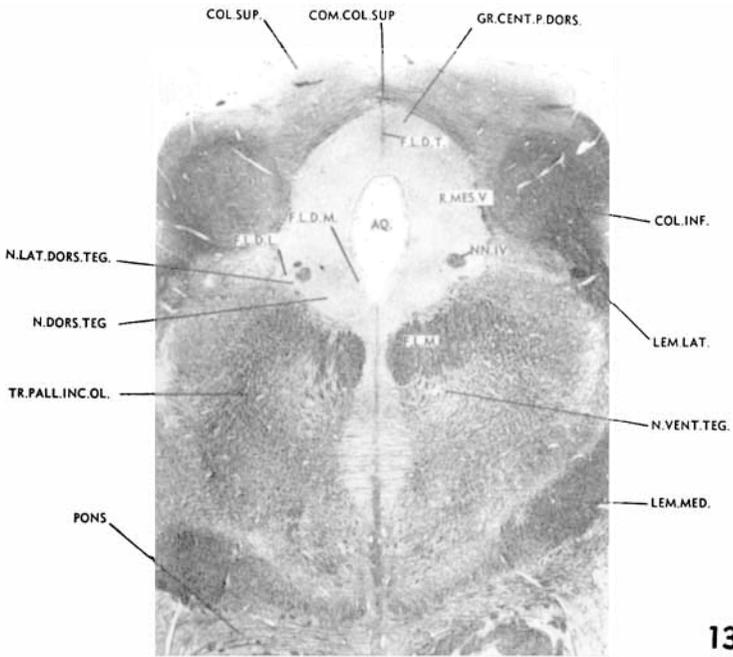


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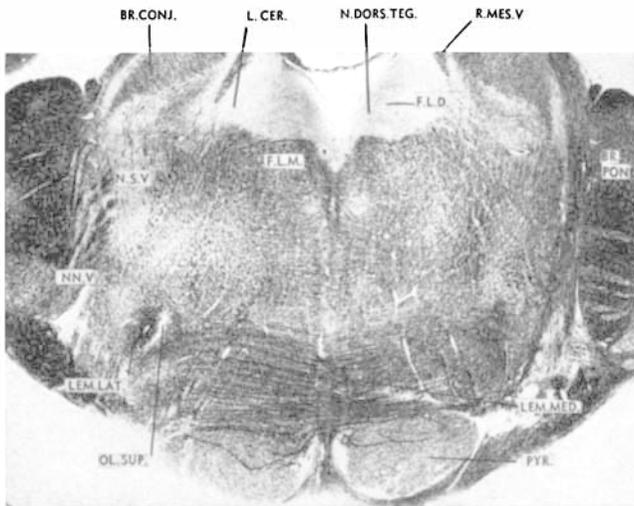


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