CONNEXIONS OF THE DORSAL TEGMENTAL NUCLEUS IN RAT AND RABBIT

By D. KENT MOREST*

Department of Anatomy, University College, London

INTRODUCTION

The dorsal tegmental nucleus of Gudden (1889) forms a continuation of the central grey of the midbrain in the floor of the fourth ventricle. The relationship of the nucleus to the fibres of the dorsal longitudinal fasciculus is notable, for this fasciculus is thought to convey impulses between the hypothalamus and the bulbar efferent centres (Ariëns Kappers, Huber & Crosby, 1936, p. 593). Although many connexions have been proposed for the dorsal longitudinal fasciculus, few have been confirmed experimentally, nor has the extent of dorsal tegmental participation in this fibre system been precisely determined.

Efferent or afferent connexions of the dorsal tegmental nucleus with the mamillary peduncle were suggested by Koelliker (1896), Déjerine (1901), and Castaldi (1923). Investigations with the Marchi method by Probst (1902) and Bodian (1940) have demonstrated only afferent fibres in the mamillary peduncle to the mamillary body. Akert & Andy (1955) and Guillery (1956) have provided evidence that the dorsal tegmental nucleus may contribute to this projection. The high degree of organization of the connexions of the mamillothalamic system is well documented (Powell, 1958), but it is not known precisely how dorsal tegmental projections may be involved in this system.

The present study establishes that the dorsal tegmental nucleus contributes to the mamillary peduncle and reveals the organization of this projection with respect to the mamillary body and medial forebrain bundle. Evidence is also provided that the dorsal tegmental nucleus is a major synaptic station for the dorsal longitudinal pathways, some of which are elucidated.

MATERIALS AND METHODS

The data were derived from study of eleven rabbits and eight rats. Electrolytic lesions were made in or near the dorsal tegmental nucleus of rabbits under pentobarbitone anaesthesia with the tips of needle electrodes mounted in a stereotaxic device.† Control lesions were placed in the collicular sites traversed by the electrodes in making dorsal tegmental lesions and in the cerebellum and medial vestibular nucleus. Lesions were made in rats under ether anaesthesia by inserting fine curved needles through the foramen magnum and under the cerebellum to the appropriate level of the brain stem. Brains with damage to the brachium con-

* Brown Fellow, Yale University, 1958–59. Present address: Laboratory of Neuroanatomical Sciences, National Institutes of Health, Bethesda 14, Maryland, U.S.A.

† In some rabbits the lesion site was first stimulated, whilst respiration and blood pressure were recorded by Dr B. G. Cragg (1959).

junctivum were not included in the study. The rabbits were kept alive 7–11 and the rats 5–8 days before perfusion with 10% formol saline. The brain stem and cerebellum were fixed in 10% formol saline for 1–6 months before sagittal frozen sections were cut at 20–25 μ. The extent of a lesion was examined in Nissl-stained sections and fibre degeneration in sections impregnated by the Nauta–Gygax method (Nauta & Gygax, 1954) or by a Laidlaw modification of it (Chambers, Liu & Liu, 1956). The unoperated brains of two rats and two rabbits were simultaneously impregnated with the experimental sections for histological controls.

Since the findings involve several regions of the brain in two species, it has been necessary to give considerable attention to control material and to criteria for evaluating degeneration. The appearance of fibres impregnated by the Nauta methods depends on many factors, including the post-operative survival time of the animal, period of fixation, thickness of the sections, exact composition of the solutions, and the times that the sections remain in each solution. Variations among species may be expected to influence the time-course of degeneration. In the present study a longer survival was required to obtain maximum degeneration in the rabbits than in the rats. In general, only fibres that were clearly broken up into irregular droplets and granules, that could be traced from the lesion, and that could not be matched in control materials were finally accepted as degenerating. In appraising the degeneration it was appreciated that fine fibres may disintegrate later than coarse ones (Van Crevel, 1958).

It has been expedient to describe the intensity of degeneration in certain regions, since the intensity often bore a strong correlation with the location of the lesion. Although the apparent intensity may be influenced by any of the factors mentioned above, such factors can be compensated by limiting assessments to optimally impregnated sections at the stage of maximal degeneration. 'Massive', 'dense', 'moderate', and 'sparse' have been used to describe, in that order, decreasing degrees of relative intensity (Pl. 2; Pl. 3, fig. 9). Likewise, 'coarse', 'medium', and 'fine' have been used to describe the relative calibres of degenerating fibres, which in many cases were correlated with their relative sizes in normal material impregnated with the silver method of Holmes (1942).

The terminology of Meessen & Olszewski (1949) is used for the rhombencephalon, of Gillilan (1943) for the mesencephalon, and of Gurdjian (1927) for the diencephalon of both rat and rabbit. For the subdivisions of the dorsal tegmental nucleus a scheme is used which has been suggested by Guillery & Powell. (These workers (unpublished) find, after mamillary lesions in the rat, retrograde degeneration confined to partes centralis and ventromedialis.) The subdivisions are called partes centralis, ventromedialis, anterior, and posterior (Pl. 1, fig. 1). Pars centralis corresponds to nucleus *q* of Meessen & Olszewski and consists of medium-sized cells densely infiltrated with a plexus of fine fibres. Ventromedial to it and more posterior is pars ventromedialis, a small group of medium-sized cells near the median raphé. Pars anterior and pars posterior are the anterior and posterior extensions, respectively, of pars centralis, but they contain smaller, less densely packed cells. Surrounding the dorsal tegmental nucleus are loosely arranged, very small cells, resembling the undifferentiated portions of the central grey.

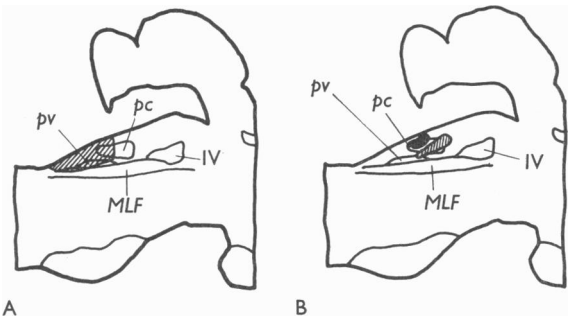
RESULTS

The findings are presented in three parts, anterior connexions, posterior connexions, and control lesions. All the lesions and resulting degeneration are ipsilateral unless otherwise stated.

(1) *Anterior connexions*

(*a*) *Mamillary peduncle*

General observations. Lesions in the dorsal tegmental nucleus produce extensive degeneration in the mamillary peduncle (Pl. 1, fig. 2). There is a correlation between destruction of pars centralis and degeneration in the medial mamillary nucleus and between destruction of pars ventromedialis and degeneration in the lateral mamillary nucleus. Degenerated fibres leaving the mamillary peduncle appear in the medial forebrain bundle and nucleus of the diagonal band of Broca and reach the medial septal nucleus in the diagonal band. In association with the above there is degeneration in the ventral tegmental area of Tsai and the posterior hypothalamic nucleus. Preterminal degeneration also appears in nucleus medialis profundus, centralis superior, and the tegmental reticular nucleus.

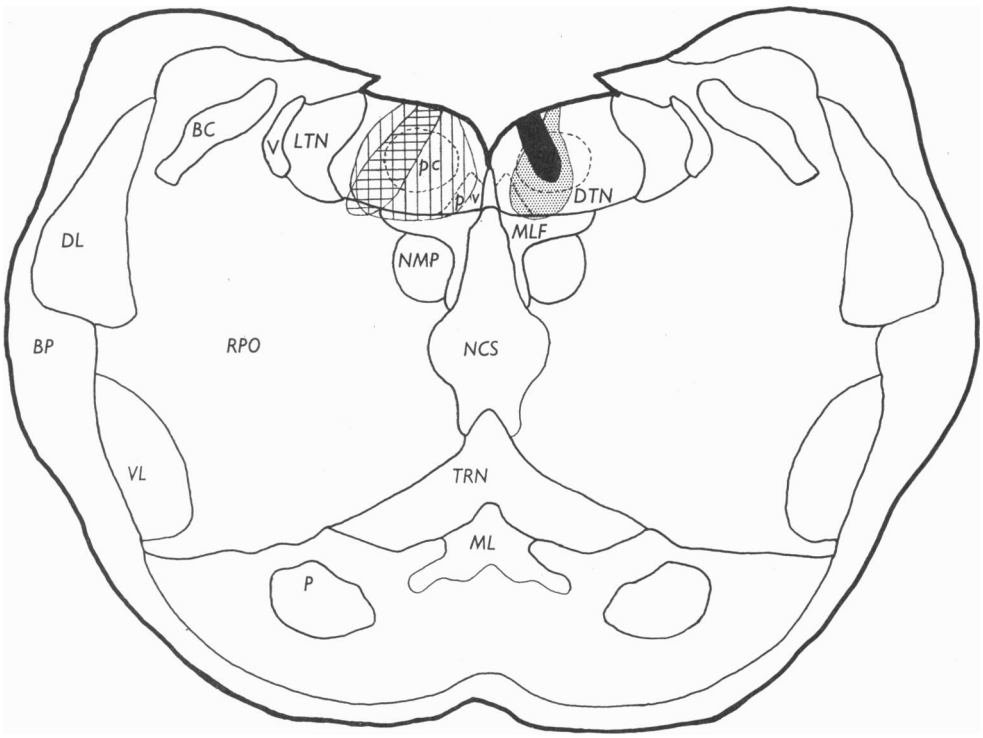


Text-fig. 1. Parasagittal diagram of the maximum extents of the lesions in A, rabbit T2; B, rabbit T7 (black), DT1 (hatched).

Rabbits. In rabbit T2 (Text-figs. 1A, 2) all parts of the dorsal tegmental nucleus are damaged except the anterior half of pars anterior. Massive degeneration of coarse and medium fibres streams anteroventrally through nucleus centralis superior, nucleus medialis profundus (ventral or deep tegmental nucleus of Gudden), and the tegmental reticular nucleus of Bechterew ('Ppl' of Meessen & Olszewski). More laterally there is only sparse degeneration in the reticular formation, whilst in the interpeduncular region the degeneration turns anteriorly into the mamillary peduncle. Degeneration passes through the nuclear groups mentioned in unreduced intensity, although fine degenerated fibres coil about the cells. The coarse degeneration of the mamillary peduncle ends massively in the lateral mamillary nucleus. Medium-sized fibres form a dense nest of degeneration in nucleus premamillaris dorsalis and the medial mamillary nucleus, chiefly in pars medianus* but also anteriorly in pars medialis. Medium-sized degenerated fibres, reduced in

* Although Cowan & Powell (1954) do not delineate in the rabbit the homology of pars medianus of the rat, the term is used to facilitate comparison between these species.

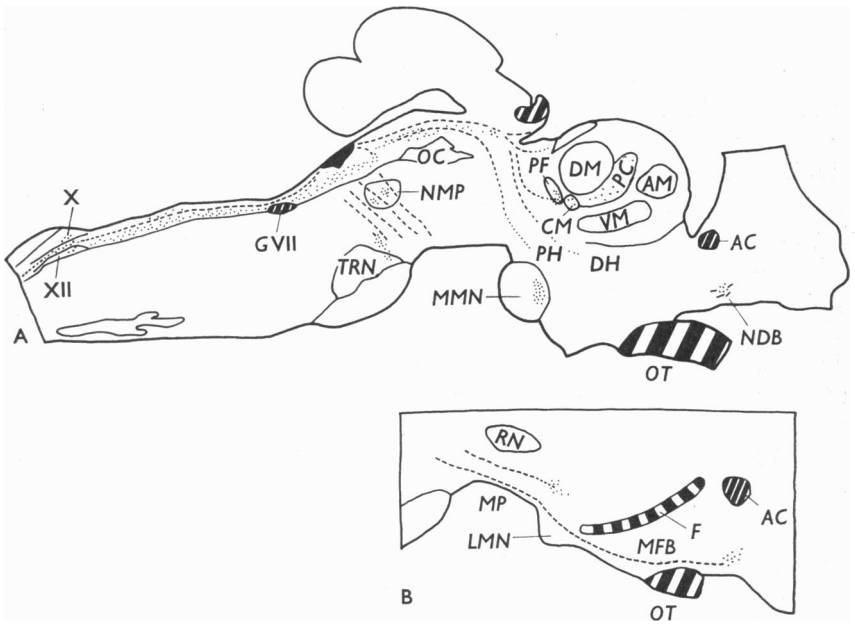
number, can be traced from the mamillary peduncle into the medial forebrain bundle. Decreasing in intensity, they ascend to the lateral preoptic area, and, forming moderate degeneration in the nucleus of the diagonal band, disappear in the region of the medial septal nucleus. At the posterior end of the interpeduncular region a moderate number of degenerated fibres take a course dorsal to, and separate from, the mamillary peduncle and ascend through the ventral tegmental area of Tsai. These medium-sized fibres form a knot of degeneration in the region of the supramamillary decussation. Some of them continue forward into the posterior hypothalamic nucleus and laterally may contribute to the degeneration in the medial forebrain bundle.



Text-fig. 2. Lesions in rabbits T2 (vertical shading), DT3 (horizontal shading), T8 (black), and DT1 (stippling) reconstructed in a transverse plane.

The lesion in rabbit T1 is similar to that in T2 but larger, and the degeneration of the mamillary peduncle follows the same pattern. In rabbit DT1 the lesion (Text-figs. 1B, 2) destroys pars anterior of the dorsal tegmental nucleus and damages partes centralis and ventromedialis; degeneration appears in both the medial and lateral mamillary nuclei. In rabbit DT3 the lesion (Text-fig. 2) lies more anterior than that in DT1 and involves pars centralis, but not pars ventromedialis; the mamillary degeneration is limited to the medial nucleus. The degeneration takes a more anterior course and does not appear in the tegmental reticular nucleus. In DT1 there is a small nest of degeneration in the anterior end of the inter-

peduncular nucleus. Otherwise the pattern of degeneration in both DT1 and DT3 (Pl. 2) resembles that in rabbit T2. In rabbits T7 and T8 the lesions (Text-figs. 1B, 2) involve only the dorsal undifferentiated grey and pars centralis. In both animals the degeneration follows the same pattern as in rabbit T2 but does not appear in the lateral mamillary nucleus (Text-fig. 3). In rabbit DT2 the dorsal tegmental nucleus and the reticular formation posterior to nucleus medialis profundus are destroyed. Transverse sections were made to confirm that the degenerated fibres pass ventrally near the midline until, near the base of the brain, they turn laterally into the mamillary peduncle. There is degeneration in the mamillary body and medial forebrain bundle as in rabbit T2.



Text-fig. 3. Parasagittal drawing of lesion and degeneration in rabbit T8. A, Degeneration in the *dlf* descends dorsal to *G*VII, ascends dorsal to *OC*. B, A more lateral plane. Note degeneration in the ventral tegmental area of Tsai dorsal to that in *MP*. Notes: The isthmus and floor of the fourth ventricle are expanded for clarity. Dots indicate preterminal degeneration; dashes, fibres of passage (not necessarily excluding terminals along their course). All degeneration is ipsilateral to the lesion.

Rats. The lesion in rat 484 involves partes ventromedialis and posterior but spares pars centralis (Text-figs. 4, 5). There is also damage to the posterodorsal portion of nucleus prepositus hypoglossi and to nucleus recessus incertus (Chatfield & Lyman, 1954). The ventral mesencephalic degeneration is the same as in the rabbits. Degeneration in the mamillary body is limited to the lateral mamillary nucleus; no degeneration occurs at more anterior levels. In rat 480 the lesion is limited to partes posterior and centralis, ipsilaterally, and to pars ventromedialis, bilaterally (Text-figs. 4, 5). Degeneration occurs in the medial mamillary nucleus, ipsilaterally, and in the lateral mamillary nucleus, bilaterally. Degeneration enters the ipsi-

lateral medial forebrain bundle, lateral preoptic area, and nucleus of the diagonal band.

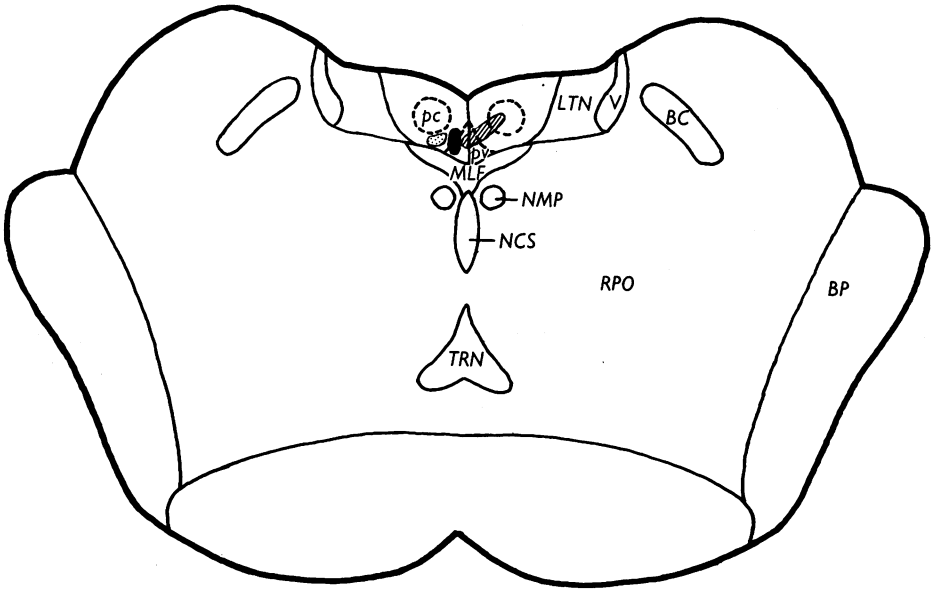
In rat 478 there is damage bilaterally to the posterior floor of the fourth ventricle and unilateral undercutting of pars centralis and damage to pars posterior but not to pars ventromedialis (Text-fig. 4). Transverse sections were made to obtain optimum representation of the medial septal nucleus. Degeneration, ipsilateral to the dorsal tegmental lesion only, passes in the mamillary peduncle to partes medianus and medialis of the medial, but not the lateral, mamillary nucleus. Degenerated fibres ascend in the medial forebrain bundle and through the diagonal band to the medial septal nucleus. A few fine degenerated fibres turn dorsomedially from the mamillary peduncle to ascend beside the habenulo-peduncular tract to the dorsomedial nucleus of the thalamus.

(*b*) *Dorsal longitudinal fasciculus* (*dlf*)

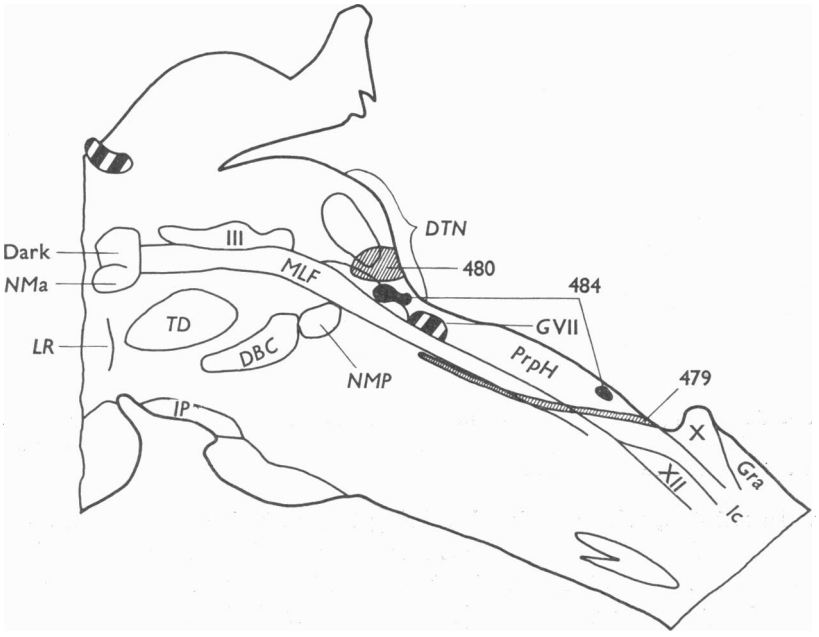
General observations. Lesions in the anterior half of the dorsal tegmental nucleus produce numerous degenerated fibres in the *dlf* supplying the central grey and several midline mesencephalic nuclei. A few such fibres reach the pretectal nucleus, the intralaminar and dorsomedial nuclei of the thalamus, and the posterior and dorsal hypothalamus. Unlike the degeneration in the mamillary peduncle, that in the *dlf* is diffuse, progressively diminishes in intensity, and reflects the presence of multiple synapses. Significant degeneration in the mesencephalic *dlf* does not descend posterior to the dorsal tegmental nucleus. The pattern of degeneration following complete destruction of the mesencephalic *dlf* resembles that following dorsal tegmental lesions but is more extensive and considerably denser.

Ascending fibres. In rabbits T7 and T8 the lesion completely spares the medial longitudinal fasciculus ('*flp*' of Meessen & Olszewski) and nearby tegmental fibres (Text-figs. 1–3). Fine degenerated fibres ascend in the ventral and lateral parts of the central grey (*dlf*). They reach the nucleus of Darkschewitsch and nuclei medialis anterior and linea rostralis anterior to the oculomotor complex and then turn ventrally to merge with the degeneration already described in the ventral tegmental area of Tsai and the posterior hypothalamic nucleus. Other fine fibres enter the pretectal nucleus, whilst some turn ventrally in the periventricular system to the nuclei centrum medianum, parafascicularis, and centralis and, very sparsely, to the posterior paraventricular, ventromedial, and dorsomedial nuclei of the thalamus. The remnant of the periventricular degeneration disappears in the dorsal portion of the posterior hypothalamic nucleus and the posterior region of the dorsal hypothalamic area (Rioch, Wislocki & O'Leary, 1940). In the posterior midbrain the degeneration in the *dlf* is dense, but its intensity progressively diminishes to moderate or sparse in the diencephalon. The degeneration in the other rabbits is similar to the above but more or less intense according to the size of the lesion. In rabbit DT1 with only minor damage to the medial longitudinal fasciculus, degenerated fibres pass from the *dlf* (Pl. 3, fig. 9) to the dorsal nucleus of the raphé and ventrally through the caudal linear grey* to the ventral tegmental area of Tsai. In rabbits T2 and DT3 damaged tegmental fibres near the medial longitudinal

* Nucleus linea caudalis, as so labelled in Gillilan's fig. 5 (1943) but not as in other papers of the same series.



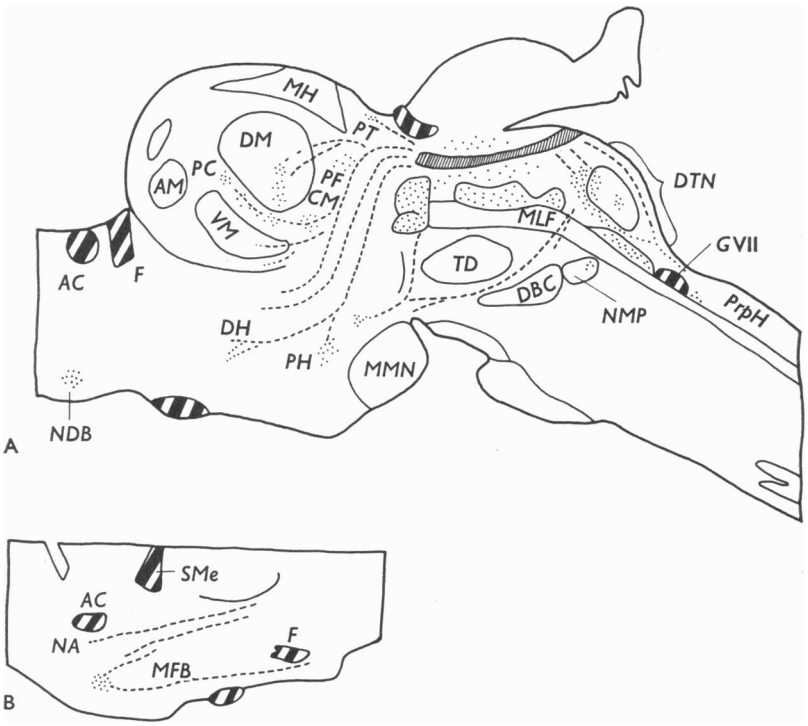
Text-fig. 4. The lesions in rats 480 (diagonal shading), 484 (black), and 478 (stippling) reconstructed in a transverse plane.



Text-fig. 5. Parasagittal drawing of lesions in rats 479, 480, 484. Nucleus prepositus hypoglossi and the dorsal tegmental nucleus are expanded. Nucleus medialis profundus and the facial genu are lateral to the plane of the diagram, but their relative positions are shown.

fasciculus have caused medium and coarse degeneration in several of the thalamic intralaminar nuclei. In DT3 very fine periventricular degeneration of moderate intensity reaches pars dorsalis of the posterior periventricular nucleus of the hypothalamus.

Descending fibres. In rabbit DT1 (Text-fig. 1B) dense degeneration appears throughout the dorsal tegmental nucleus, but only very sparse degeneration passes over the facial genu to the anteroventral portion of nucleus prepositus hypoglossi. The more anterior lesion in rabbit DT3 has caused dense degeneration in all parts of the dorsal tegmental nucleus, especially in its anterior half, but none posterior to the facial genu. There is sparse degeneration in the laterodorsal tegmental nucleus, or locus coeruleus, of both rabbits. The paucity of degeneration posterior to the facial genu in these rabbits contrasts with those in which the lesion involves more posterior portions of the dorsal tegmental nucleus (see rabbit T8 below).



Text-fig. 6. A, Lesion (hatching) and degeneration in rat 474. Note degeneration passing through rostral and caudal linear grey, anterior and posterior, respectively, to *TD*. B, A more lateral plane. For notes see Text-fig. 5.

Rats. In rat 480, with a lesion involving the posterior third of pars centralis, sparse degeneration ascends the *dlf*; a few fibres reach nucleus parafascicularis in the diencephalon. In rat 484, in which the dorsal tegmental lesion is more posterior, and in rats 481 (Text-fig. 7) and 479 (Text-fig. 5), with lesions posterior to the dorsal tegmental nucleus, there is no degeneration in the mesencephalic central grey.

In rat 474 a lesion extends through the entire length of the mesencephalic central grey on one side. It involves neither the tegmental tracts peripherally nor the

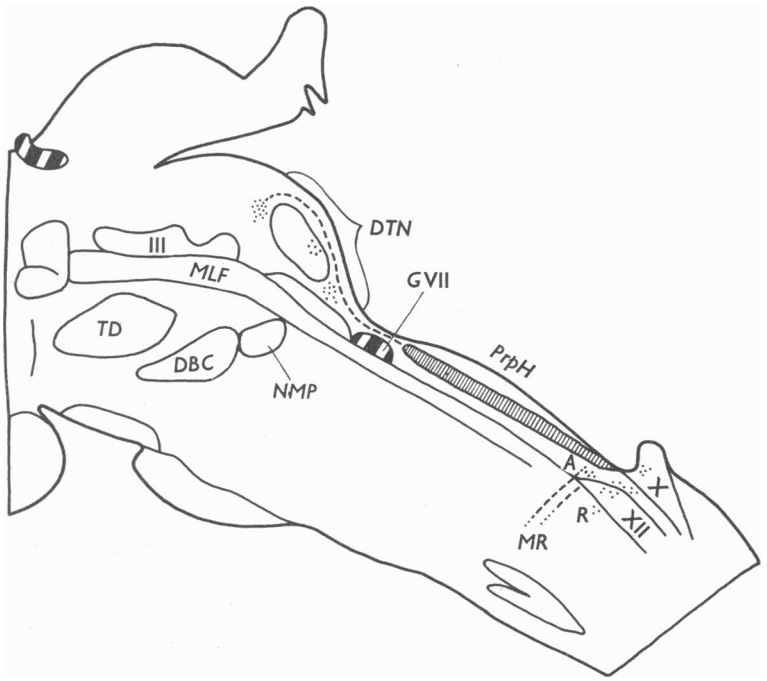
oculomotor complex or dorsal tegmental nucleus but reaches the posteroventral edge of the posterior commissure (Text-fig. 6). The *dlf* is massively degenerated (Pl. 3, fig. 11) and distributes in the midbrain and thalamus essentially as in the rabbits with dorsal tegmental lesions, but considerably more intensely. Degenerated fibres reach all the intralaminar nuclei, including nuclei centralis, paracentralis, and centralis lateralis (lateral part of Gurdjian's paracentralis). Most of the remaining dense periventricular degeneration ends in the posterior hypothalamic nucleus and the dorsal hypothalamic area. A few degenerated fibres reach pars dorsalis of the posterior periventricular nucleus, but none occur further ventrally or in the ventromedial, dorsomedial, filiform, or supraoptic nuclei. Some of the fibres enter the medial forebrain bundle anteriorly, in which degeneration ascends to the nucleus of the diagonal band. More laterally (Text-fig. 6B) degeneration ascends just ventral to the thalamus to the nucleus accumbens and the region ventral to the anterior commissure and anterior to the stria medullaris. Finally, degenerated fibres from the central grey course in moderate intensity through the caudal, intermediate, and rostral linear grey (nuclear groups of Gillilan, 1943) and through the ventral tegmental area of Tsai to the supramamillary region and the medial part of the medial forebrain bundle. Degeneration elsewhere in the reticular formation and in the superior colliculus seems sparse in the sagittal sections used. Descending degeneration reaches all parts of the dorsal tegmental nucleus (dense in pars anterior, moderate in partes posterior and ventromedialis, moderate to sparse in pars centralis) and nucleus recessus incertus. A few degenerated fibres go to the laterodorsal tegmental nucleus and to nuclei medialis profundus and centralis superior. Only sparse degeneration occurs posterior to the facial genu in nucleus prepositus hypoglossi and the medial vestibular nucleus ('Trg' of Meessen & Olszewski).

(2) *Posterior connexions*

Efferent pathways. The lesion in rabbit T8 has produced very fine degenerated fibres passing posteriorly over the facial genu densely into nucleus prepositus hypoglossi (Pl. 3, fig. 12) and sparsely into the anterodorsal region of the medial vestibular nucleus. The intensity of the degeneration diminishes as it descends through nucleus prepositus hypoglossi and, after supplying pars gk 25 (Meessen & Olszewski) just anterior to the hypoglossal nucleus rather densely, enters nucleus intercalatus with less intensity (Text-fig. 3). There is sparse degeneration of very fine fibres in the ventral portion of the dorsal motor vagal nucleus ('Al' of Meessen & Olszewski) and in the dorsal portion of the hypoglossal nucleus and questionable degeneration in pars parvocellularis of nucleus tractus solitarius. Horizontal sections of the upper cervical cord reveal the remnant of the degeneration descending lateral, then ventrolateral, to the central canal. In rabbits T2 and T7 (Text-fig. 1) the pattern is similar, but sparse, medium and coarse degeneration from the medial longitudinal fasciculus of rabbit T2 enters the abducens, vestibular, and hypoglossal nuclei.

In rat 480 (Text-fig. 5) fine degenerated fibres pass over the facial genu into nucleus prepositus hypoglossi. No degenerated fibres seem to reach nucleus intercalatus, but there is sparse degeneration in the posterior nucleus tractus solitarius bilaterally.

Afferent pathways. In rat 481 the lesion is limited entirely to nucleus prepositus hypoglossi (Text-fig. 7). Fine fibres ascend densely over the facial genu to form a nest of degeneration in pars posterior of the dorsal tegmental nucleus (Pl. 3, fig. 13). Other fibres continue anterodorsally to partes anterior and centralis. In rat 479 (Text-fig. 5) fine degenerated fibres occur throughout nucleus prepositus hypoglossi and ascend over the facial genu to pars posterior and the posterior half of pars centralis. In rats 478 and 484 (Text-fig. 5), with damage to the floor of the fourth ventricle, there is dense degeneration throughout the dorsal tegmental nucleus. In none of these animals is there degeneration in the central grey anterior to the dorsal tegmental nucleus.



Text-fig. 7. The lesion and degeneration in rat 481. Degeneration in nucleus prepositus hypoglossi is largely omitted. For notes see Text-fig. 5.

Nucleus prepositus hypoglossi. The lesions in rats 479, 481, and 484 destroyed, besides cells in nucleus prepositus hypoglossi, fibres of passage from the dorsal tegmental nucleus. Consequently degeneration occurs in the same regions directly supplied by the latter nucleus, but additional features are present. In each animal a prominent stream of degenerated fibres passes from pars gk 25 of nucleus prepositus hypoglossi into the medial reticular formation (Text-fig. 7). In the same rats careful examination suggests that the descending fibres enter the hypoglossal nucleus directly at its anterior pole, a few fibres passing to the nucleus of Roller. Degenerating fibres enter the dorsal motor vagal nucleus along its ventral margin from nucleus intercalatus.

(3) *Control lesions*

In rabbits with very small collicular lesions degenerated fibres pass in a ventrolaterally directed arc to the cuneiform area but not to any of the structures previously considered except the colliculi. In one rabbit there is a necrotic area on the cerebellar pyramis but no degeneration in the dorsal tegmental nucleus. In another there is extensive damage to the vermis and roof nuclei of the cerebellum and a small lesion in the medial vestibular nucleus. In this animal medium-sized degenerating fibres pass into nucleus prepositus hypoglossi and sparsely into nucleus intercalatus. Degeneration is also present in the laterodorsal tegmental nucleus, the medial longitudinal fasciculus and abducens nucleus, the brachium conjunctivum and the pontine reticular formation. There is no degeneration in the dorsal tegmental nucleus or supragenual grey nor in the vagal or hypoglossal nuclei. This material shows that degeneration arising from the electrode tracks did not contribute to the degeneration previously described and that the dorsal tegmental lesions themselves probably did not interrupt fibres of passage from the cerebellum or medial vestibular nucleus.

DISCUSSION

First, the origin and distribution of the mamillary peduncle will be discussed; second, the dorsal tegmental connexions with certain paramedian nuclei of the pons and midbrain; and third, the relation of the dorsal tegmental nucleus to the *dlf* and its connexions.

(1) *Mamillary peduncle*

Origin. The Marchi studies of Probst (1902), Bodian (1940), and Morin (1950) have failed to support the contention that the dorsal tegmental nucleus is a terminal site of mamillary peduncle fibres (Koelliker, 1896). Instead the present study demonstrates that the dorsal tegmental nucleus is a major source of the mamillary peduncle, as suggested by Guillery (1956) in the rat and Akert & Andy (1955) in the cat. Evidence that nucleus medialis profundus contributes to the mamillary peduncle has been provided by retrograde degeneration studies in the cat (Fox, 1941; Akert & Andy, 1955). There is no conclusive evidence that the nucleus of the mamillary peduncle (Papez, 1932) contributes to this tract, although retrograde degeneration has been observed in this nucleus following posterior hypothalamic lesions (Fox, 1941). Ramón y Cajal (1955, p. 461) and Wallenberg (1899) have sought a contribution from the medial lemniscus, but numerous investigations do not support such a proposal (e.g. Ranson & Ingram, 1932). The possibility that the tegmental reticular nucleus and nucleus centralis superior may contribute should be considered, for these nuclei are associated with the tegmental fibres to the mamillary peduncle and from the mamillary (Guillery, 1957) and limbic (Nauta, 1958) projection sites of the peduncle.

Distribution. Gudden (1880) observed the connexion between the mamillary peduncle and the lateral mamillary nucleus, and Wallenberg (1899), using the Marchi method, demonstrated ascending fibres in the mamillary peduncle of the rabbit, chiefly to the lateral mamillary nucleus. Subsequent Marchi investigations by

Probst (1902), Bodian (1940), and Fox (1941) in several species have established endings of the mamillary peduncle in both the lateral and medial mamillary nuclei, especially the anteromedial part of the latter (see also Ramón y Cajal, 1955; Tello, 1936–37; Morin, 1950). Using the Nauta method in the rat, Guillery (1956) observed degeneration from the mamillary peduncle in the medial forebrain bundle and the diagonal band of Broca. Nauta & Kuypers (1958) in the cat have produced degeneration in the mamillary peduncle, medial forebrain bundle, and medial septal nucleus with lesions in the anteromedial pontine reticular formation. From the present study it is clear that the distribution of dorsal tegmental fibres in the mamillary peduncle coincides with the overall distribution of this tract. Degeneration in the medial, but not the lateral, mamillary nucleus was always accompanied by degeneration in the medial forebrain bundle. It is probable that some medial forebrain fibres are collaterals of axons supplying the medial mamillary nucleus, as observed by Tello (1936–37).

The mamillary nuclei receive hippocampal and pre-mamillary hypothalamic fibres via the fornix and medial forebrain bundle (Guillery, 1957) and send a prominent projection to the anterior thalamic nuclei, which in turn relay to the cingulate cortex (Cowan & Powell, 1954; Powell, 1958). Studies of the hippocampus and cingulate cortex by Kaada (1951) and MacLean (1957) suggest that these pathways may be concerned with autonomic and behavioural functions. Moreover, the mamillary bodies, in view of their important pre-mamillary and mesencephalic connexions, probably play a part in regulating descending impulses from the hypothalamus. Hence it is likely that the dorsal tegmental fibres in the mamillary peduncle are involved in central autonomic regulation by their projections to the mamillary, lateral hypothalamic, and medial septal nuclei, the last of which projects to the hippocampus (Daitz & Powell, 1954). Analysis of the role of the dorsal tegmental nucleus in this system should include the localized connexions between the dorsal tegmental and mamillary nuclear subdivisions and the fact that the latter can return impulses to the former by the mamillo-tegmental tract. The lateral mamillary nucleus may be the major source of such fibres (Guillery, 1956), which seem to have a localized ending in pars centralis of the dorsal tegmental nucleus (R. W. Guillery, unpublished).

(2) *Pons and midbrain*

In supplying fibres to the ventral tegmental area of Tsai and the posterior hypothalamic nucleus, the dorsal tegmental nucleus does not differ from more anterior regions of the central grey, but its connexions with nucleus medialis profundus, centralis superior, and the tegmental reticular nucleus may be established by collaterals of axons entering the mamillary peduncle. These nuclei are significant because of their hypothalamic (Sanz Ibañez, 1935; Guillery, 1957), limbic (Nauta, 1956, 1958), and cerebellar (Mettler & Zimmerman, 1943; Brodal, 1954) connexions. Furthermore, it is known that nucleus prepositus hypoglossi, with intense dorsal tegmental connexions, receives from (Thomas, Kaufman, Sprague & Chambers, 1956), and projects to (Brodal, 1952), the cerebellum. By these pathways the cerebellum may be involved in the central regulation of autonomic and behavioural functions (Chambers, 1947; Zanchetti & Zoccolini, 1954; Anand, Malhotra, Singh

& Dua, 1959). The significance of the dorsal tegmental connexions with these nuclei remains to be elucidated, but the present study reveals no direct dorsal tegmental connexions with the cerebellum nor is the author aware of any evidence for one.

(3) *Dorsal longitudinal fasciculus*

Schütz (1891) described in man the fasciculus which bears his name as a more or less diffuse collection of fine fibres situated in the central grey beside the central canal. In the upper cervical cord it surrounds the central canal as a corona. It passes between the dorsal motor vagal and hypoglossal nuclei and at pontine levels lies in the floor of the fourth ventricle near the midline (nucleus prepositus hypoglossi). In the posterior midbrain the fibres (corresponding to the ventral part of Ramón y Cajal's 'voie longitudinale périependymaire'; 1955, p. 193) collect ventral and lateral to the aqueduct but are dispersed laterally and dorsally at more anterior levels. Schütz did not describe the *dlf* proper beyond the mesencephalodiencephalic junction, but he observed that tracts in the thalamic and hypothalamic periventricular regions are continuous with the *dlf*. As Ariëns Kappers, Huker & Crosby (1936, p. 1182) have remarked, the diencephalic periventricular system is part of the *dlf*; hence use of the term 'tractus periventricularis of Gurdjian' for this portion seems unnecessary. Schütz suggested that the *dlf* contains both ascending and descending fibres with connexions at all levels of the brain stem. Marburg (1931) and Ariëns Kappers *et al.* (1936) have reviewed the literature concerning the *dlf* in several species, whilst Thompson (1942) in the opossum and Crosby & Woodburne (1951) in the monkey have proposed many nuclear connexions besides those of Schütz. Of special interest is the great density of the fibre plexus observed in the dorsal tegmental nucleus, which is said to have reciprocal connexions with the *dlf*. Accordingly it has been proposed that the dorsal tegmental nucleus is 'a relay station for impulses passing between the diencephalic olfactory correlation centres and efferent centres of the brain stem' (Ariëns Kappers *et al.* 1936, p. 661).

Distribution. Few of the many proposed connexions of the *dlf* have been experimentally verified. Fibres have been shown to enter the central grey from the habenular nuclei (Bürgi & Bucher, 1955), the anterolateral spinal cord (Nauta & Kuypers, 1958), the bulbar reticular formation (Russell, 1954), and the cerebellum (Thomas *et al.* 1956). Fibres have been traced from the central grey to the inferior olive (Walberg, 1956), ventral tegmental area of Tsai, posterior hypothalamic nucleus and 'ventromediocaudal parts of massa intermedia' (Bucher & Bürgi, 1953), and widely to the mesencephalic tegmentum and tectum and hypothalamus (Nauta, 1958). In the present study degeneration in a rat with destruction of the mesencephalic *dlf* is recorded in detail. The intense hypothalamic projections indicate the importance in central autonomic activity of the *dlf*, which is already known to carry hypothalamic efferents (Guillery, 1957). Other axons from the central grey reach the hypothalamus after passing to the ventral tegmental area of Tsai and ascending to the posterior hypothalamic nucleus and medial forebrain bundle. The medial pre-mamillary hypothalamus, except the posterior periventricular nucleus and dorsal hypothalamic area, was notable for its lack of degeneration, although the impregnation revealed the very finest degenerated fibres in adjacent parts of the hypothalamus. Nevertheless, Nauta (1958) has briefly noted degeneration in

'medial hypothalamic cell groups' following destruction of the central grey of a cat. The bulbar *dlf* is distributed to nuclei prepositus hypoglossi and intercalatus and the upper cervical cord. A few fibres supply the dorsal motor vagal and hypoglossal nuclei. There are possibly connexions with the medial vestibular, motor glossopharyngeal, and superior salivatory nuclei, nucleus tractus solitarius, and the cervical ventral horn. No evidence was found for contributions to the motor trigeminal, abducens, or facial nuclei or to nucleus ambiguus. The descending system may be supplemented by secondary projections from nucleus prepositus hypoglossi to the nucleus of Roller and the medial reticular formation.

Dorsal tegmental nucleus. Since the *dlf* is a multisynaptic system, it is difficult to determine the ultimate destination of pathways in it from the dorsal tegmental nucleus alone with degeneration methods. However, it is clear that this nucleus must be a major, if not essential, synaptic station for fibres of the *dlf* both to and from the hypothalamus. Ascending fibres in the bulbar portion of the *dlf* synapse primarily in the posterior half of the nucleus, although many fibres or their collaterals also reach pars anterior. The anterior half of the dorsal tegmental nucleus gives rise to most of the ascending dorsal longitudinal axons from this nucleus. The bulk of the descending fibres in the mesencephalic *dlf* synapse throughout the dorsal tegmental nucleus, especially in pars anterior, whilst the *dlf* is continued by an intense bulbar projection of dorsal tegmental fibres.

Several investigations have pointed to close vagal-hypothalamic relationships (Ingram, 1940). It seems probable that the dorsal tegmental nucleus participates in such relationships. It is worth noting that, when stimulating the vagus nerve, Dell & Olson (1951*a*, *b*) recorded evoked potentials with the shortest latencies in regions to which the dorsal tegmental nucleus projects. Although there are reports that lesions in the ala cinerea produce 'retrograde changes' in the hypothalamic paraventricular nucleus of a dog (Urechia & Nitescu, 1925) and Marchi degeneration in the mamillary peduncle of opossums (Papez, 1932), sufficient details to permit evaluation of these claims are not available. The present evidence indicates that direct vago-hypothalamic fibres, if they exist, are not conveyed by the *dlf* or the mamillary peduncle in the rat. The dorsal longitudinal terminals in the dorsal motor vagal nucleus seem scarce, but this nucleus has an extremely poor fibre plexus (Ramón y Cajal, 1955, p. 247). It may be that nucleus intercalatus plays a key role in the mediation of impulses between the *dlf* and the dorsal vagal nuclei.

Although the functional characteristics of the dorsal tegmental nucleus are undetermined, several studies have implicated the dorsal isthmus region in bladder (Barrington, 1925; Tang, 1955) and respiratory (Johnson & Russell, 1952; Baxter & Olszewski, 1955) functions. Cragg (1959) produced a characteristic increase in the frequency and amplitude of respiration by stimulation at sites limited to the preoptic area, stria medullaris, habenular nuclei, interpeduncular nucleus, and dorsal tegmental nucleus, all of which are connected by a pathway involving the habenulo-peduncular tract and the pedunculo-tegmental tract of Ganser. Impulses conveyed in this pathway to the dorsal tegmental nucleus may reach bulbar respiratory neurons (Pitts, Magoun & Ranson, 1939) via nucleus prepositus hypoglossi and its projection to the medial medullary reticular formation. Other impulses may possibly descend through the *dlf* to motor cells of the phrenic nerve.

SUMMARY

1. Degeneration in the homolateral connexions of the dorsal tegmental nucleus was studied with the Nauta methods in rabbits and rats.

2. The nucleus is a major source of the fibres in the mamillary peduncle, which supply the mamillary nuclei, medial forebrain bundle, nucleus of the diagonal band of Broca, and medial septal nucleus.

3. Pars centralis projects to the anterior portion of the medial, and pars ventromedialis to the lateral mamillary nucleus.

4. Dorsal tegmental fibres also reach nuclei medialis profundus and centralis superior, the tegmental reticular nucleus, the ventral tegmental area of Tsai, and the posterior hypothalamic nucleus.

5. The nucleus is a major synaptic station for the pathways of the dorsal longitudinal fasciculus between the diencephalon and lower brain stem.

6. The dorsal tegmental nucleus and its connexions are probably involved in central autonomic regulation.

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REFERENCES

AKERT, K. & ANDY, O. J. (1955). Experimental studies on corpus mammillare and tegmento-mammillary system in the cat. *Amer. J. Physiol.* **183**, 591.

ANAND, B. K., MALHOTRA, C.L., SINGH, B. & DUA, S. (1959). Cerebellar projections to limbic system. *J. Neurophysiol.* **22**, 451–457.

ARIËNS KAPPERS, C. U., HUBER, G. C. & CROSBY, E. C. (1936). *The Comparative Anatomy of the Nervous System of Vertebrates, Including Man.* New York: Macmillan.

BARRINGTON, F. J. F. (1925). The effect of lesions of the hind- and mid-brain on micturition in the cat. *Quart. J. exp. Physiol.* **15**, 81–102.

BAXTER, D. W. & OLSZEWSKI, J. (1955). Respiratory responses evoked by electrical stimulation of pons and mesencephalon. *J. Neurophysiol.* **18**, 276–287.

BODIAN, D. (1940). Studies on the diencephalon of the Virginia opossum. Part II. The fiber connections in normal and experimental material. *J. comp. Neurol.* **72**, 207–297.

BRODAL, A. (1954). Afferent cerebellar connections. In *Aspects of Cerebellar Anatomy* (ed. Jansen & Brodal), p. 124. Oslo: J. G. Tanum.

BRODAL, A. (1952). Experimental demonstration of cerebellar connexions from the peri-hypoglossal nuclei (nucleus intercalatus, nucleus praepositus hypoglossi and nucleus of Roller) in the cat. *J. Anat., Lond.*, **86**, 110–129.

BUCHER, V. M. & BÜRGI, S. M. (1953). Some observations on the fiber connections of the di- and mesencephalon in the cat. IV. The ansa lenticularis, pars ascendens mesencephalica, with observations on other systems ascending from and descending to the mesencephalon. *J. comp. Neurol.* **99**, 415–435.

BÜRGI, S. M. & BUCHER, V. M. (1955). Über einige rhinencephale Verbindungen des Zwischen- und Mittelhirns. *Dtsch. Z. Nervenheilk.* **174**, 89–106.

CASTALDI, L. (1923). Studi sulla struttura e sullo sviluppo del mesencefalo. Ricerche in Cavia cobaya. Parte primo. *Arch. ital. Anat. embriol.* **20**, 23–225.

CHAMBERS, W. W. (1947). Electrical stimulation of the interior of the cerebellum in the cat. *Amer. J. Anat.* **80**, 55–93.

CHAMBERS, W. W., LIU, C. & LIU, C. (1956). A modification of the Nauta technique for staining of degenerating axons in the central nervous system. *Anat. Rec.* **124**, 391–392.

CHATFIELD, P. O. & LYMAN, C. P. (1954). An unusual structure in the floor of the fourth ventricle of the golden hamster (*Mesocricetus auratus*). *J. comp. Neurol.* **101**, 225–231.

COWAN, W. M. & POWELL, T. P. S. (1954). An experimental study of the relation between the medial mamillary nucleus and the cingulate cortex. *Proc. roy. Soc.* B, **143**, 114–125.

CRAGG, B. G. (1959). A heat-loss mechanism involving the habenular, interpeduncular and dorsal tegmental nuclei. *Nature, Lond.*, **184**, 1724.

CROSBY, E. C. & WOODBURNE, R. T. (1951). The mammalian mid-brain and isthmus regions. Part. II. The fiber connections. C. The hypothalamo-tegmental pathways. *J. comp. Neurol.* **94**, 1–32.

DAITZ, H. M. & POWELL, T. P. S. (1954). Studies of the connexions of the fornix system. *J. Neurol. Psychiat.* **17**, 75–82.

DÉJERINE, J. (1901). *Anatomie des Centres Nerveux*, t. II, p. 302. Paris: Rueff.

DELL, P. & OLSON, R. (1951*a*). Projections thalamiques, corticales et cérébelleuses des afférences viscérales vagales. *C.R. Soc. Biol., Paris*, **145**, 1084–1088.

DELL, P. & OLSON, R. (1951*b*). Projections 'secondaires' mésencéphaliques, diencéphaliques et amygdaliennes des afférences viscérales vagales. *C.R. Soc. Biol., Paris*, **145**, 1088–1091.

FOX, C. A. (1941). The mamillary peduncle and ventral tegmental nucleus in the cat. *J. comp. Neurol.* **75**, 411–425.

GILLILAN, L. A. (1943). The nuclear pattern of the non-tectal portions of the midbrain and isthmus in rodents. *J. comp. Neurol.* **78**, 213–251.

GUDDEN, B. (1880). Beitrag zur Kenntniss des Corpus mammillare und der sogenannten Schenkel des Fornix. *Arch. Psychiat. Nervenkr.* **11**, 428–452.

GUDDEN, B. (1889). *Gesammelte und hinterlassene Abhandlungen*, pp. 190–192. Wiesbaden: Bergmann.

GUILLERY, R. W. (1956). Degeneration in the postcommissural fornix and the mamillary peduncle of the rat. *J. Anat., Lond.*, **90**, 350–370.

GUILLERY, R. W. (1957). Degeneration in the hypothalamic connexions of the albino rat. *J. Anat., Lond.*, **91**, 91–115.

GURDJIAN, E. S. (1927). The diencephalon of the albino rat. *J. comp. Neurol.* **43**, 1–114.

HOLMES, W. (1942). A new method for the impregnation of nerve axons in mounted paraffin sections. *J. Path. Bact.* **54**, 132–136.

INGRAM, W. R. (1940). Nuclear organization and chief connections of the primate hypothalamus. *Res. Publ. Ass. nerv. ment. Dis.* **20**, 195–244.

JOHNSON, F. H. & RUSSELL, G. V. (1952). The locus coeruleus as a pneumotaxic center. *Anat. Rec.* **112**, 348.

KAADA, B. R. (1951). Somatomotor, autonomic and electrocorticographic responses to electrical stimulation of 'rhinencephalic' and other structures in primates, cat and dog. *Acta physiol. scand.* **24**, (Suppl. 83), 1–285.

KOELLIKER, A. (1896). *Handbuch der Gewebelehre des Menschen*, 6th aufl., bd. 2, p. 492. Leipzig: Engelmann.

MACLEAN, P. D. (1957). Chemical and electrical stimulation of hippocampus in unrestrained animals. II. Behavioral findings. *Arch. Neurol. Psychiat., Chicago*, **78**, 128–142.

MARBURG, O. (1931). Das dorsale Längsbündel von Schütz—Fasciculus periependymalis—und seine Beziehungen zu den Kernen des zentralen Höhlengrau. *Arb. neurol. Inst. Univ. Wien*, **33**, 135–164.

MEESSEN, H. & OLSZEWSKI, J. (1949). *A Cytoarchitectonic Atlas of the Rhombencephalon of the Rabbit.* New York: Karger.

METTLER, F. A. & ZIMMERMAN, F. T. (1943). Homolateral reflex exaggeration after brain-stem lesion. *J. comp. Neurol.* **78**, 113–128.

MORIN, F. (1950). An experimental study of hypothalamic connections in the guinea pig. *J. comp. Neurol.* **92**, 193–213.

NAUTA, W. J. H. (1956). An experimental study of the fornix system in the rat. *J. comp. Neurol.* **104**, 247–271.

NAUTA, W. J. H. (1958). Hippocampal projections and related neural pathways to the midbrain in the cat. *Brain*, **81**, 319–340.

NAUTA, W. J. H. & GYGAX, P. A. (1954). Silver impregnation of degenerating axons in the central nervous system: a modified technique. *Stain Tech.* **29**, 91–93.

NAUTA, W. J. H. & KUYPERS, H. G. J. M. (1958). Some ascending pathways in the brain stem reticular formation. In *Reticular Formation of the Brain*, p. 8. Boston: Little, Brown.

PAPEZ, J. W. (1932). The nucleus of the mammillary peduncle. *Anat. Rec.* **52**, 72–73.

PITTS, R. F., MAGOUN, H. W. & RANSON, S. W. (1939). Localization of the medullary respiratory centers in the cat. *Amer. J. Physiol.* **126**, 673–688.

POWELL, T. P. S. (1958). The organization and connexions of the hippocampal and intralaminar systems. *Recent Progr. in Psychiatry*, **3**, 54–74.

PROBST, M. (1902). Experimentelle Untersuchungen über die Anatomie und Physiologie der Leitungsbahnen des Gehirnstammes. *Arch. Anat. Physiol., Anat. Abt., Lpz.*, pp. 147–254.

RAMÓN Y CAJAL, S. (1955). *Histologie du Système Nerveux de l'Homme et des Vertébrés*, t. II. Madrid: Instituto Ramón y Cajal.

RANSON, S. W. & INGRAM, W. R. (1932). The diencephalic course and termination of the medial lemniscus and the brachium conjunctivum. *J. comp. Neurol.* **56**, 257–275.

RIOCH, D. MCK., WISLOCKI, G. B. & O'LEARY, J. L. (1940). A précis of preoptic, hypothalamic and hypophysial terminology with atlas. *Res. Publ. Ass. nerv. ment. Dis.* **20**, 3–30.

RUSSELL, G. V. (1954). The dorsal trigemino-thalamic tract in the cat reconsidered as a lateral reticulo-thalamic system of connections. *J. comp. Neurol.* **101**, 237–263.

SANZ IBAÑEZ, J. (1935). Étude de la dégénération du fascicule tegmental de Gudden consécutif à la lésion expérimentale du noyau mamillaire externe. *Trab. Lab. Invest. biol. Univ. Madr.* **30**, 211–219.

SCHÜTZ, H. (1891). Anatomische Untersuchungen über den Faserverlauf im centralen Höhlengrau und den Nervenfaserschwund in demselben bei der progressiven Paralyse der Irren. *Arch. Psychiat. Nervenkr.* **22**, 527–587.

TANG, P. C. (1955). Levels of brain stem and diencephalon controlling micturition reflex. *J. Neurophysiol.* **18**, 583–595.

TELLO, J. F. (1936–37). Évolution, structure et connexions du corps mamillaire chez la souris blanche, avec des indications chez d'autres mammifères. *Trab. Lab. Invest. biol. Univ. Madr.* **31**, 77–142.

THOMAS, D. M., KAUFMAN, R. P., SPRAGUE, J. M. & CHAMBERS, W. W. (1956). Experimental studies of the vermal cerebellar projections in the brain stem of the cat (Fastigio-bulbar tract). *J. Anat., Lond.*, **90**, 371–385.

THOMPSON, E. L. (1942). The dorsal longitudinal fasciculus in Didelphis Virginiana. *J. comp. Neurol.* **76**, 239–281.

URECHIA, C. I. & NITESCU, I. (1925). Le rôle des noyaux du 'tuber cinereum' dans le diabète expérimental. *Bull. Acad. Méd., Paris*, **93**, 188–194.

VAN CREVEL, H. (1958). *The Rate of Secondary Degeneration in the Central Nervous System. An Experimental Study in the Pyramid and Optic Nerve of the Cat.* Doctoral Thesis, University of Leiden. Leiden: Eduard Ijdo N.V.

WALBERG, F. (1956). Descending connections to the inferior olive. An experimental study in the cat. *J. comp. Neurol.* **104**, 77–173.

WALLENBERG, A. (1899). Notiz über einen Schleifenursprung des Pedunculus corporis mamillaris beim Kaninchen. *Anat. Anz.* **16**, 156–158.

ZANCHETTI, A. & ZOCCOLINI, A. (1954). Autonomic hypothalamic outbursts elicited by cerebellar stimulation. *J. Neurophysiol.* **17**, 475–483.

LIST OF ABBREVIATIONS

A	Nucleus prepositus hypoglossi, pars gk 25	*Ic*	Nucleus intercalatus
AC	Anterior commissure	*IP*	Interpeduncular nucleus
AM	Anteromedial nucleus of the thalamus	*LMN*	Lateral mamillary nucleus
BC	Brachium conjunctivum	*LR*	Nucleus linea rostralis
BP	Brachium pontis	*LTN*	Laterodorsal tegmental nucleus
CM	Nucleus centrum medianum	*MFB*	Medial forebrain bundle
Dark	Nucleus of Darkschewitsch	*MH*	Medial habenular nucleus
DBC	Decussation of brachium conjunctivum	*ML*	Medial lemniscus
DH	Dorsal hypothalamic area	*NCS*	Nucleus centralis superior
DL	Dorsal nucleus of lateral lemniscus	*NDB*	Nucleus of the diagonal band
DM	Dorsomedial nucleus of the thalamus	*NMa*	Nucleus medialis anterior
DTN	Dorsal tegmental nucleus	*NMP*	Nucleus medialis profundus
F	Fornix	*OC*	Oculomotor complex
Gra	Nucleus gracilis	*OT*	Optic tract
I	Nucleus recessus incertus	*P*	Pyramidal tract
		PC	Nucleus paracentralis of the thalamus

pc	Pars centralis of *DTN*
PF	Nucleus parafascicularis
PH	Posterior hypothalamic nucleus
pv	Pars ventromedialis of *DTN*
PrpH	Nucleus prepositus hypoglossi
PT	Pretectal nucleus
R	Nucleus of Roller
RN	Red nucleus
RPO	Pontine reticular nucleus, pars oralis
SMe	Stria medullaris
TD	Tegmental decussations
TRN	Tegmental reticular nucleus
VL	Ventral nucleus of lateral lemniscus
VM	Ventromedial nucleus of the thalamus
III	Oculomotor nucleus
MLF	Medial longitudinal fasciculus
MMN	Medial mamillary nucleus
MP	Mamillary peduncle
MR	Medial medullary reticular formation
NA	Nucleus accumbens
IV	Trochlear nucleus
V	Mesencephalic trigeminal nucleus
*G*VII	Genu of the facial nerve
X	Dorsal motor vagal nucleus
XII	Hypoglossal nucleus

EXPLANATION OF PLATES

All sections are in the parasagittal plane and, except in Fig. 1, have been prepared by the Nauta–Gygax method. All degeneration shown is ipsilateral to the lesions.

Plate 1

Fig. 1. Dorsal tegmental nucleus of a rat. Frozen section, cresyl violet. ×45.

Fig. 2. Massive degeneration in the mamillary peduncle of rabbit DT1 following a dorsal tegmental lesion. Contrast the normal oculomotor (vertical) fibres, some of which are incompletely suppressed but none of which meet any of the author's criteria for degeneration (see Materials and Methods). ×150.

Fig. 3. From the contralateral mamillary peduncle of rabbit DT1. The vertical oculomotor fibres and large horizontal fibres of the mamillary peduncle are unquestionably normal. This particular section was chosen to show the finer fibres of the mamillary peduncle which, due to a low degree of suppression, are stained intermittently at regular intervals but are not broken up and are seen in specimens without lesions. ×160.

Plate 2

Fig. 4. Massive degeneration in the lateral mamillary nucleus of rabbit DT1 following a dorsal tegmental lesion. ×100.

Fig. 5. From previous field. ×400.

Fig. 6. Dense degeneration in the medial mamillary nucleus of rabbit DT3 following a dorsal tegmental lesion. Note the normal efferent (vertical) fibres, to the right (posterior) of which there is no degeneration. ×130.

Fig. 7. Degeneration from previous field. ×400.

Fig. 8. Typical normal fibres from the contralateral lateral mamillary nucleus of rabbit DT1 (field corresponding to Fig. 5). ×400.

Plate 3

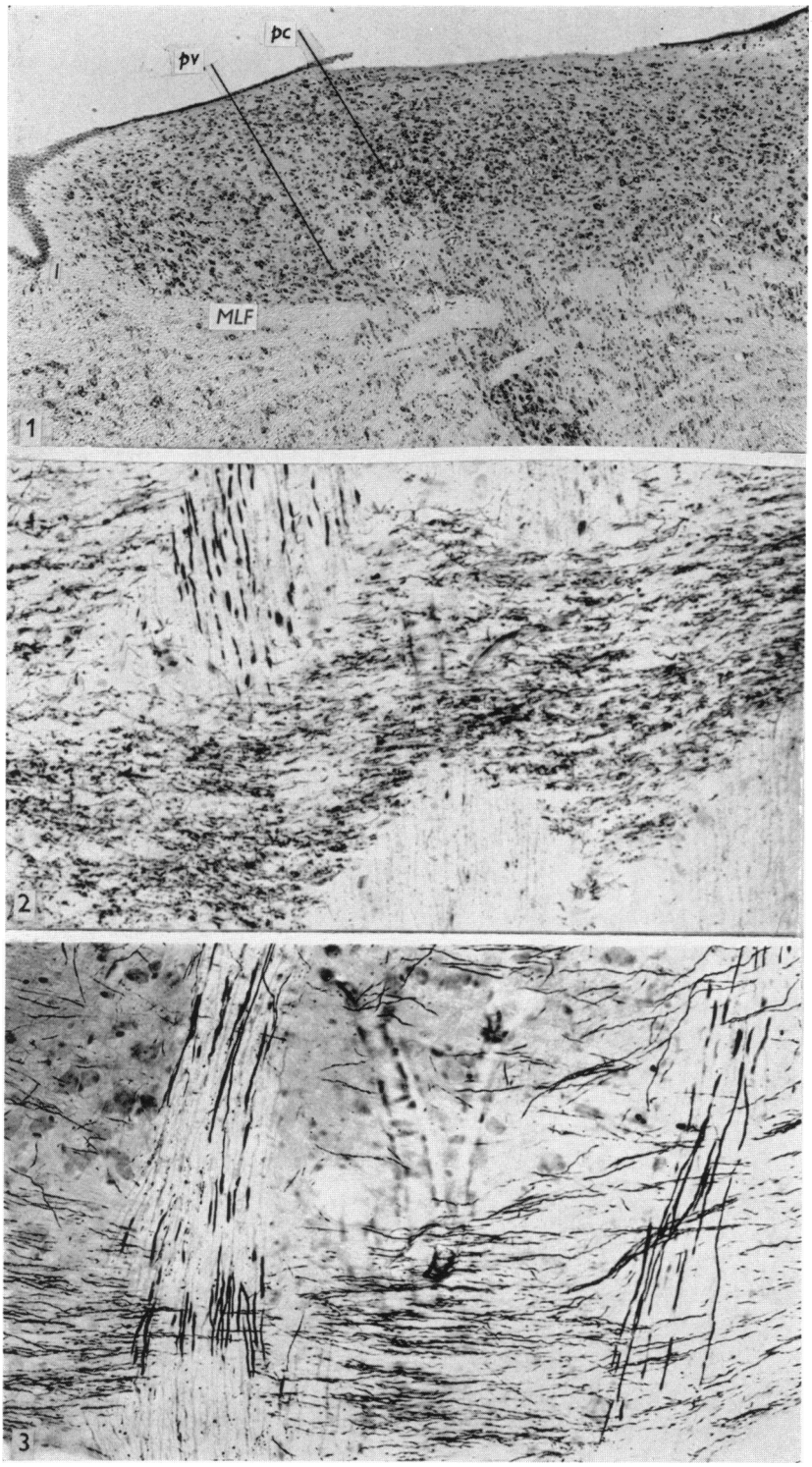
Fig. 9. Moderate degeneration in the dorsal longitudinal fasciculus of rabbit DT1 following a dorsal tegmental lesion. ×480.

Fig. 10. Normal fibres and nuclei of cells from the dorsal longitudinal fasciculus of an unoperated rabbit in a section simultaneously impregnated with that of Fig. 9. ×480.

Fig. 11. Massive degeneration of the dorsal longitudinal fasciculus at the mesencephalo-diencephalic junction following destruction of the central grey of rat 474. ×120.

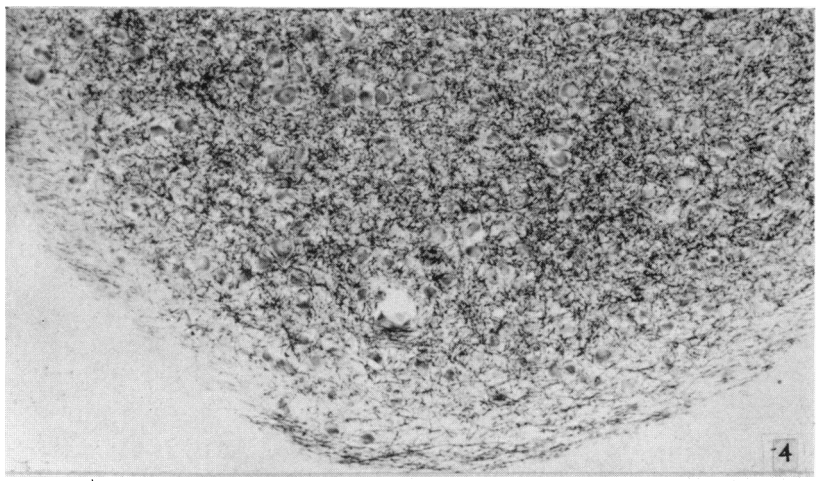
Fig. 12. Degeneration in nucleus prepositus hypoglossi of rabbit T8 following a dorsal tegmental lesion. Fibres of passage concentrate dorsally (upper part of field) whilst ventrally fibres are dispersed among the cell bodies. ×320.

Fig. 13. Degeneration in pars posterior of the dorsal tegmental nucleus of rat 481 following a lesion in nucleus prepositus hypoglossi. Note the pericellular coiling that characterizes preterminal degeneration. ×320.



MOREST—DORSAL TEGMENTAL CONNEXIONS

(*Facing p.* 246)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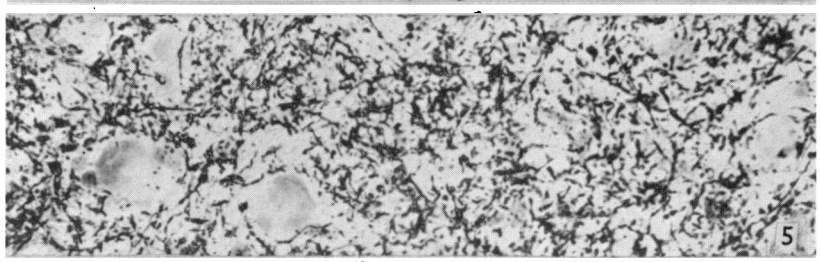
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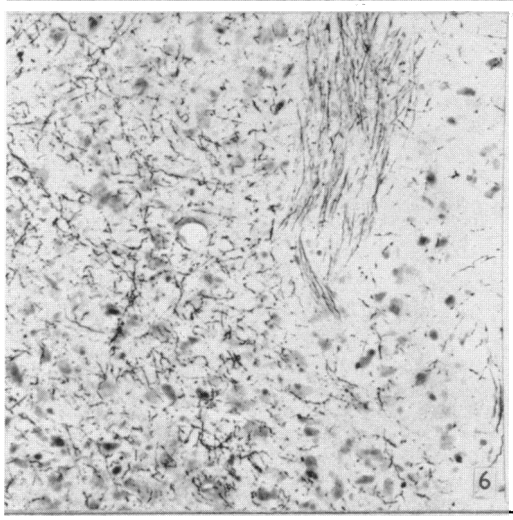
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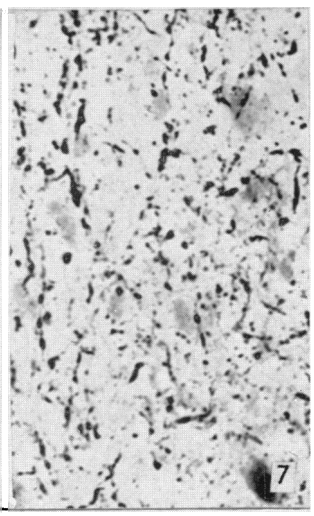
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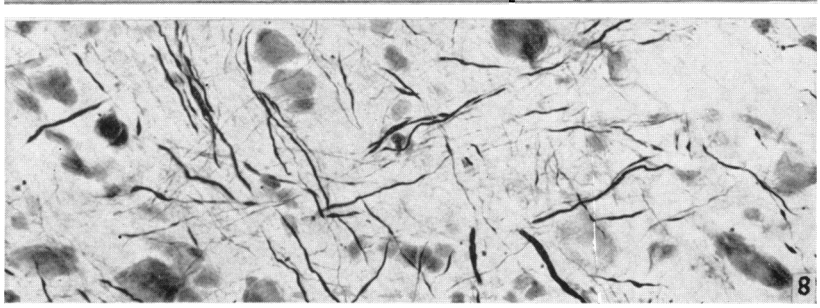
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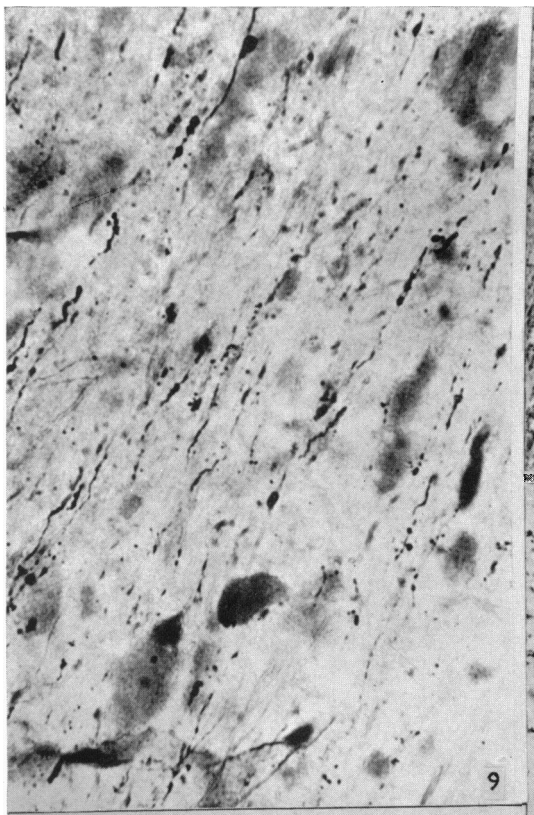
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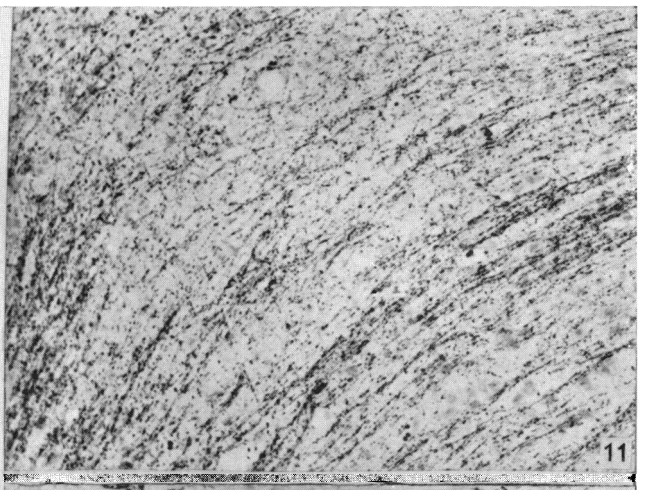
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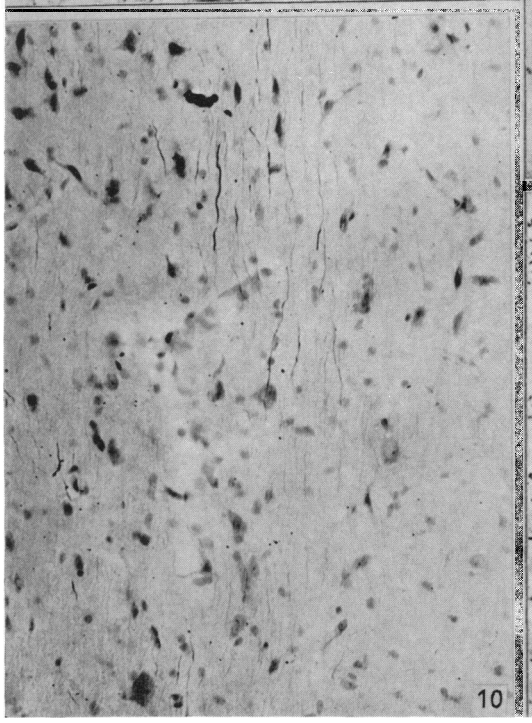
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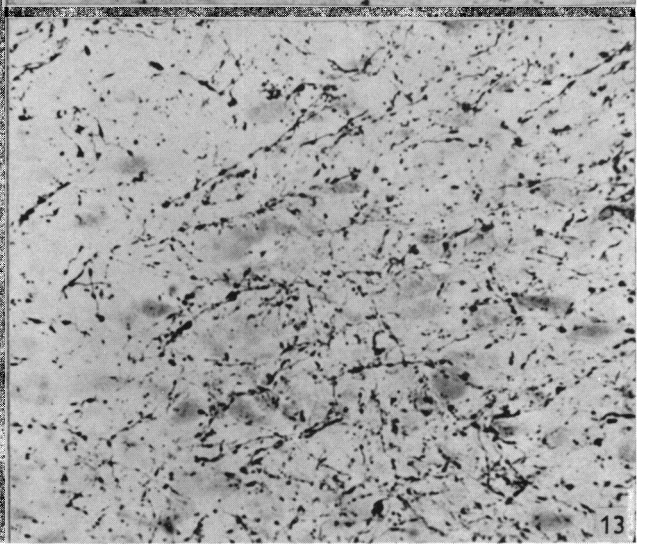
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