THE DORSAL TRIGEMINAL TRACT IN THE RHESUS MONKEY*

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Although considerable attention and research have been directed to the study of the secondary trigeminothalamic fibre systems because of their great theoretical and practical importance, accurate knowledge of these systems is still incomplete and controversial. The present communication concerning the dorsal trigeminal tract in the rhesus monkey is a report of significant incidental observations made during a study of the brachium conjunctivum.

The following experimental data support the existence of an uncrossed dorsal trigeminal fasciculus originating from the chief sensory nucleus of the trigeminal nerve and probably excludes the possibility of the existence of an uncrossed ascending component of the brachium conjunctivum, as described by Carrea & Mettler (1954).

MATERIAL AND METHODS

Sixteen immature rhesus monkeys weighing from 2800 to 3800 g. were used. In seven of these animals attempts were made to produce localized lesions in various parts of the brachium conjunctivum by stereotaxic methods (Carpenter & Whittier 1952). Electrodes were introduced into the brain in the frontal region and passed ventrocaudally into the dorsolateral portion of the mesencephalon. Successful lesions limited to the brachium conjunctivum were produced in five animals (2118, 2124, 2137, 2190 and 2191). In one (2124) of these animals the lesions destroyed portions of the brachium conjunctivum ventrally and extended caudally into the dorsal part of the chief sensory nucleus of the trigeminal nerve.

In eight monkeys the brachium conjunctivum was sectioned with a small knife caudal to the inferior colliculus. None of these lesions was restricted to the brachium conjunctivum. Adjacent structures commonly involved were the inferior colliculus, the trochlear nerve, the ventral spinocerebellar tract, the lateral lemniscus and dorsal trigeminal tract. In one additional animal (2413) an attempt was made to remove the entire cerebellum by suction. Although small areas of cortex remained about the middle cerebellar peduncle, the removal was virtually complete.

Observations regarding postoperative animal behaviour and neurologic status were recorded at various intervals. Cinematographic records were taken of noteworthy physiologic phenomena. At the conclusion of the observation period (always at least 14 days) animals were examined in a restraining chair, anaesthetized with intravenous Nembutal and perfused with 500 ml. of 10% neutral formalin. The

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brains and portions of the spinal cords were removed and placed in 10% neutral formalin for further fixation. At a later time the brains were cut into slabs approximately 2 mm. thick, perpendicular to the axis of the brain stem. Sections of the brains and portions of the spinal cord were prepared according to the Marchi method. Sections were cut serially at 23 μ and every 10th section was mounted. Sections of the cerebellum were embedded in celloidin (sometimes paraffin), sectioned serially and stained with cresyl violet.

RESULTS

Lesions involving the chief sensory nuclei of the trigeminal nerve. In one animal (2124) bilateral stereotaxic lesions destroyed portions of the chief sensory nucleus, as well as ventral portions of the brachium conjunctivum.

Following surgery the animal was alert but hypokinetic and seemed to have persistent hiccups. On the second postoperative day, it was noted that the animal broke its food into small pieces with its hands and fed directly from the floor. It was obvious that the animal had difficulty chewing food. The jaw hung partially open and could not be closed. Dislocation of the jaw during surgery was suspected, but examination revealed only weakness of the muscles of mastication bilaterally. From the 2nd to the 11th postoperative day the animal tore food into small bits with his teeth, because he was unable to chew. After this time, weakness in the muscles of mastication was no longer apparent. At examination on the 21st postoperative day, prior to sacrifice, only slight pupillary inequality was found. Cranial nerves appeared functionally intact and no sensory deficit could be detected by pin prick or cotton-wool in the trigeminal distribution or elsewhere. Resistance to passive movement seemed diminished in the muscles of the lower extremities. The animal was sacrificed by perfusion with 500 ml. of 10% neutral formalin.

Descriptions of the lesion. On the right side the rostral limit of the lesion began at the level of the trochlear nerve decussation and was located in the ventrolateral third of the brachium conjunctivum which it completely destroyed. At slightly more caudal levels the lesion expanded to destroy some fibres of the lateral lemniscus and the ventral spinocerebellar tract. The dorsal two-thirds of the brachium conjunctivum was preserved and entirely free of Marchi degeneration. Caudally the lesion entered the dorsomedial part of the chief sensory nucleus of the trigeminal nerve where this structure lies ventral to the brachium conjunctivum. Fibres of the mesencephalic root of the trigeminal nerve were interrupted as well as secondary fibres issuing from the chief sensory nucleus. Intense Marchi degeneration was scattered throughout the masticator nucleus and was present in parts of the superior vestibular nucleus.

The lesion on the left side began at the level of the inferior colliculus slightly dorsal to the middle third of the brachium conjunctivum. It expanded caudally to destroy the most ventral and mesial part of the middle thirds of the brachium conjunctivum as well as all structures between the medial concavity of the superior cerebellar peduncle and the lateral border of the periaqueductal gray. The caudal extent of the lesion was situated dorsomedial to the chief sensory nucleus. Fibres of the mesencephalic root of the fifth nerve were interrupted and part of the superior vestibular nucleus was destroyed.

Marchi degeneration. Moderately heavy Marchi degeneration was found in the principal trigeminal root fibres bilaterally; this degeneration was traced peripherally through the lateral portion of the pons on both sides. In the masticator nuclei dense black Marchi granules were seen bilaterally. Clear distinct Marchi degeneration emanating from the chief sensory nuclei and from the area dorsomedial to the chief sensory nuclei was seen. These degenerated fibres formed a triangular-shaped bundle along the medial concavity of the brachium conjunctivum and constituted the first part of the dorsal trigeminal tract. A few degenerated fibres from the area of the lesion passed medially ventral to the genu of the seventh nerve and appeared to enter the medial longitudinal fasciculus; some of these fibres crossed the median raphe to the opposite side. The latter fibres were considered to be vestibulomesencephalic fibres from the superior vestibular nucleus, but a few may have originated in the chief sensory nucleus. No fibres from the chief sensory nucleus were seen to enter the medial lemniscus on either side.

At levels through the inferior colliculus the fibres of the brachium conjunctivum began to move ventromedially preparatory to decussating. The fibres of the brachium conjunctivum passed through the dorsal trigeminal tract from dorsal to ventral and from lateral to medial. Thus, below these levels the dorsal trigeminal tract was medial to the brachium conjunctivum and above them it was dorsal. In this area it was difficult to follow the degeneration in the dorsal trigeminal tract because of co-existing degeneration in the brachium conjunctivum. At the level of the trochlear nuclei the dorsal trigeminal tract was again isolated and distinct, dorsolateral to the medial longitudinal fasciculus. This tract became more clearly separated from the medial longitudinal fasciculus in the region of the third nerve nuclear complex. The tract maintained this position until levels through the posterior commissure were reached. As the tract ascended it moved slightly lateral away from the periaqueductal gray. Above the level of the posterior commissure the tract was a less compact bundle of fibres compared with lower levels. Fibres of the fasciculus retroflexus traversed the dorsal trigeminal tract. Some of the fibres of the dorsal trigeminal tract were medial to the fasciculus retroflexus and some were lateral to it. At this level the dorsal trigeminal tract made an abrupt lateral bend and passed ventrolaterally through the medial part of the centromedian nucleus to enter the arcuate nucleus of the thalamus. It was impossible in this preparation to determine whether some of the fibres terminated in the centromedian nucleus or merely traversed this structure *en route* to the arcuate nucleus. Degeneration was most dense in the arcuate nuclei.

The fibres of the mesencephalic root of the trigeminal nerve were interrupted completely on the left side and in part on the right by the lesions. Degenerated fibres of the mesencephalic root were seen to pass rostrally into the lateral border of the periaqueductal gray. At the level of the trochlear nerve decussation the fibres shifted dorsally and came into apposition to the fibres of the trochlear nerve dorsally and the brachium conjunctivum laterally. Some of the fibres appeared to enter the brachium conjunctivum.

Very slight Marchi degeneration was seen in the descending root of the trigeminal nerve bilaterally. Such degeneration as was present consisted mainly of fine granules with occasional scattered coarse granules. This type of degeneration could be followed only to the level of the inferior olivary nuclear complex and was not impressive. No detectable degeneration was seen emanating from the spinal nucleus of the trigeminal nerve.

Marchi degeneration of the brachium conjunctivum resulting from these lesions could be followed rostrally through the decussation, into the red nuclei, the pre-rubral fields, and into fields H_1 and H_2 of Forel. From these sites degeneration could be followed into the lateroventral nucleus of the thalamus and into the globus pallidus via both the dorsal and ventral divisions of the ansa lenticularis.

Lesions of the dorsal trigeminal tract. Unequivocal Marchi degeneration was found unilaterally in the dorsal trigeminal tract in five animals (2116, 2122, 2123, 2129 and 2179) following surgical lesions of the brachium conjunctivum. In rhesus 2130 bilateral degeneration was found in this tract after bilateral lesions of the brachium conjunctivum. In two additional animals (2119 and 2210) with unilateral surgical section of the brachium conjunctivum 232 and 222 days prior to sacrifice, the dorsal trigeminal tract was fully degenerated and could not be seen in Marchi-stained preparations on the side of the lesions.

Fibres of the dorsal trigeminal tract were interrupted medial to the brachium conjunctivum at levels slightly below the trochlear nerve decussation in these animals. In rhesus 2123 the lesion extended caudally into the dorsal part of the chief sensory nucleus. Degeneration of the dorsal trigeminal tract was clearly seen at the level of the trochlear nuclei and was on the same side as the lesion in every instance. No degeneration was seen in the contralateral dorsal trigeminal tract or in the medial lemniscus in any of these animals. Marchi degeneration in these cases was more impressive and heavier than that seen in rhesus 2124, presumably because the entire tract was destroyed. The ascending course of the degenerated fibres was the same as previously described. Since this was the only thalamic degeneration on the side in question in five of these monkeys (degenerated fibres of the brachium conjunctivum having crossed to the opposite side in the brachial decussation), it was easy to follow the course of the fibres.

In none of these animals was it possible to detect impairment of tactile sense over any part of the face. No special testing procedures were employed, but it is possible that with more careful testing some sensory deficit might have been found.

Total removal of the cerebellum. In rhesus 2413 with virtual total removal of the cerebellum no degeneration was seen in the dorsal trigeminal tracts. The brachium conjunctivum was completely degenerated bilaterally.

Stereotaxic lesions of the brachium conjunctivum. In those animals (2118, 2137, 2190 and 2191) with lesions restricted to various parts of the brachium conjunctivum, no degeneration was found in the dorsal trigeminal tracts.

DISCUSSION

The controversy concerning the existence and nature of the dorsal trigeminal tract has continued over a number of years. This tract, first described by Forel (1877), has been referred to as Forel's Haubenfaszikel (tractus fasciculorum Foreli, not to be confused with Forel's Haubenfeldern H, H_1 and H_2) but many authors prefer to designate it as Wallenberg's fasciculus since he first drew attention to it as a trigeminothalamic pathway. The tract has been considered to be crossed by Hösel (1892), Wallenberg (1896, 1905), Spitzer (1899), van Gehuchten (1901) and Winkler (1921); Hatschek (1902), Lewandowsky (1904), Kohnstamm (1910), von Economo (1911), Papex & Rundles (1937), Hassler (1948), Verhaart (1949), Papez (1951) and Russell (1954) have considered it to be uncrossed. Both crossed and uncrossed fibres of the dorsal trigeminal tract were described by Cajal (1904), Woodburne (1936) and Walker (1939). Most authors have concluded that this tract represents a trigeminothalamic pathway, but this opinion is not unanimous. Fibres of this tract were reported to arise from the spinal nucleus of the fifth nerve by Hösel (1892), Wallenberg (1896), Spitzer (1899) and van Gehuchten (1901). The chief sensory nucleus of the trigeminal nerve was stated to be the origin of these fibres according to Hatschek (1902), Kohnstamm (1910), von Economo (1911), Winkler (1921), Papez & Rundles (1937), Walker (1939) and Papez (1951). Cajal (1904) concluded that the fibres arise from both the spinal and the chief sensory nuclei of the trigeminal nerve. Hassler (1948), on the basis of myelogenetic studies and the examination of varied types of human pathological material, concluded that Forel's fasciculus was a direct secondary vestibulothalamic pathway, but in the investigations of Gray (1926), Rasmussen (1932), Buchanan (1937) and Ferraro, Pacella & Barrera (1904) no degeneration in this tract was observed following lesions in various vestibular nuclei. Verhaart (1949) identified fibres of this tract as contributing to the dorsal and lateral part of the central tegmental fasciculus in man and monkey. Lewandowsky (1904) felt this fibre tract originated in the reticular formation of the medulla and pons. Studies done on cats by Russell (1954) indicated that no dorsal trigeminal tract, either crossed or uncrossed, could be demonstrated following lesions limited to the sensory nuclei of the trigeminal nerve. He expressed the opinion that the fibres usually described as the dorsal trigeminal tract actually represent an uncrossed ascending lateral reticulothalamic pathway. Bürgi (1955) concurred in this view, stating that these fibres probably were part of the ascending reticular activating system. Von Economo (1911) believed that taste was mediated by the dorsal trigeminal tract.

Berry, Anderson & Brooks (1956), in electrophysiologic studies in cats, located a dorsal trigeminal tract lateral to the medial longitudinal fasciculus in the mid-brain which conducted both ipsilateral and contralateral impulses following stimulation of the infraorbital nerve by single shocks. The earlier investigations of Mountcastle & Henneman (1952) indicated that ipsilateral tactile impulses from the face and mouth projecting to the medial part of the arcuate nucleus in the monkey could be demonstrated by electrophysiological methods. These data would seem to support the existence of an uncrossed dorsal trigeminal tract.

The material presented here demonstrates that trigeminothalamic fibres arise from at least the dorsomedial part of the chief sensory nucleus and ascend uncrossed in the dorsal trigeminal tract. The ascending fibres pass medial to the brachium conjunctivum where they appear as a triangular-shaped bundle. At the level of the inferior colliculus the fibres of the brachium conjunctivum pass through those of the dorsal trigeminal tract from dorsal to ventral and from lateral to medial. At the level of the trochlear nucleus and the decussation of the brachium conjunctivum the fibres of the dorsal trigeminal tract lie lateral to the medial longitudinal fasciculus at the border of the periaqueductal gray. Fibres ascend in this position to the level of the fasciculus retroflexus where they make an abrupt ventrolateral bend and sweep into the medial part of the arcuate nucleus of the thalamus. No crossed degeneration was seen in the opposite dorsal trigeminal tract or in the medial lemniscus.

Carrea & Mettler (1954), in their study of the brachium conjunctivum in monkeys, observed uncrossed degenerated fibres ascending to the medial part of the arcuate nucleus of the thalamus in four animals (1120, 1122*a*, 1128 and 1135). Lesions in these animals were inflicted in the same manner as in in the currently reported cases. These authors, however, considered the degeneration in the dorsal trigeminal tract to represent an uncrossed ascending component of the brachium conjunctivum which heretofore had not been described. This 'component of the brachium conjunctivum' was described as originating from the dorsomedial portion of the superior cerebellar peduncle at the level of the inferior colliculus. The tract was stated to form in the following manner: 'When these fibres reach the outer crescent of the medial longitudinal fasciculus, where the uncrossed vestibulomesencephalic and the tectobulbar and the tectospinal tracts are located, this bundle becomes detached from the body of the brachium and remains lateroventral to the medial longitudinal fasciculus' (pages 584–6). The course of the tract was thereafter identical with that described in the current cases for the dorsal trigeminal tract. Since the only portions of the brachium conjunctivum destroyed by the lesions in rhesus 2124 (in addition to parts of the chief sensory nuclei of the trigeminal nerve) were located ventrolaterally, it seems unlikely that these fibres could become 'detached from the body of the brachium' as described above. If the fasciculus in question contained fibres of cerebellar origin passing in the brachium conjunctivum, one would expect that a few degenerated fibres might be seen in those cases with stereotaxic lesions of the brachium conjunctivum and that clear distinct degeneration would certainly be present if the entire cerebellum were removed. No Marchi degeneration in the dorsal trigeminal tract was seen in any of these cases.

Further evidence of another type suggests that the fibres of the dorsal trigeminal tract are in no way related to the brachium conjunctivum. In a series of fifteen rhesus monkeys (Carpenter & Taber, 1956) with lesions of the deep cerebellar nuclei, no degeneration in the dorsal trigeminal tract (uncrossed ascending limb of the brachium conjunctivum of Carrea & Mettler) was found, although degeneration was seen in all parts of the brachium conjunctivum.

SUMMARY AND CONCLUSIONS

This study of the dorsal trigeminal tract in the rhesus monkey was based upon significant incidental observations made during an investigation of the brachium conjunctivum. Sixteen animals were used for this study. Complete lesions of the brachium conjunctivum were produced by surgical section in eight animals and localized partial lesions were produced stereotaxically in five of seven monkeys. In one of the latter animals lesions extended into the chief sensory nucleus of the trigeminal nerve. In another animal the entire cerebellum was removed. Degenerations resulting from these lesions were studied in Marchi serial sections.

The following conclusions were drawn:

1. Secondary trigeminal fibres arising from the dorsal part of the chief sensory nucleus of the trigeminal pass dorsomedially in the upper pontine tegmentum to form the dorsal trigeminal tract which initially lies medial to the brachium conjunctivum. Fibres of the brachium conjunctivum pass through the dorsal trigeminal tract at the level of the inferior colliculus preparatory to decussating.

2. The fibres of the dorsal trigeminal tract ascend lateral to the periaqueductal gray to the level of the fasciculus retroflexus, where they make an abrupt ventrolateral bend and sweep through the medial part of the centromedian nucleus and into the medial part of the arcuate nucleus of the thalamus.

3. The dorsal trigeminal tract is an uncrossed ascending pathway from the chief sensory nucleus of the trigeminal nucleus.

4. No secondary trigeminal fibres originating from the dorsomedial part of the chief sensory nucleus appear to ascend in association with either the medial lemniscus or the spinothalamic tract.

5. The fibres of the dorsal trigeminal tract do not appear to constitute an 'uncrossed ascending limb of the brachium conjunctivum' as has been suggested by certain authors.

6. It is possible that the dorsal trigeminal tract may be a compound fasciculus containing ascending fibres originating from sources other than the chief sensory nucleus of the trigeminal nerve, but the proportion of such fibres, if they exist, is small.

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EXPLANATIONS OF PLATES

PLATE 1

Fig. 1. Rhesus 2124. Section through the pons at the level of the chief sensory nuclei of the trigeminal nerve showing stereotaxic lesions. The lesion on the right destroyed the dorsomedial portion of the chief sensory nucleus and the ventrolateral third of the brachium conjunctivum. The lesion on the left destroyed the ventromedial fibres of the brachium conjunctivum, fibres of the mesencephalic root of the trigeminal, fibres of the dorsal trigeminal tract and a small part of the chief sensory nucleus. Marchi, ×6.

Fig. 2. Rhesus 2124. Photomicrograph demonstrating bilateral degeneration in the dorsal trigeminal tract resulting from lesions shown in Fig. 1. Marchi, ×12.

PLATE 2

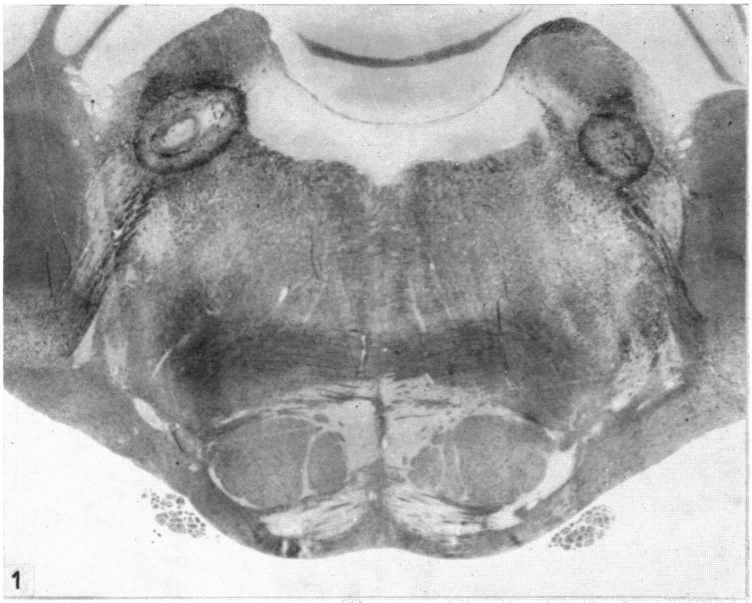
Fig. 3. Rhesus 2123. The brachium conjunctivum and the dorsal trigeminal tract were sectioned on the left side. Degeneration is present in the uncrossed dorsal trigeminal tract (left) and in the brachium conjunctivum above the decussation (right). Marchi, ×7.

Fig. 4. Rhesus 2123. The degenerated dorsal trigeminal tract on the left has become a less compact bundle at the level of the posterior commissure. Degenerated fibres of the brachium conjunctivum can be seen traversing the rostral portion of the red nucleus on the right. Marchi, ×10.

Fig. 5. Rhesus 2123. Degenerated fibres of the left dorsal trigeminal tract can be seen sweeping ventrolaterally through the centromedian nucleus into the medial part of the arcuate nucleus of the thalamus. Marchi, ×14.

PLATE 3

Fig. 6. Semi-schematic drawings showing the course of the dorsal trigeminal tract from its origin in the chief sensory nucleus of the trigeminal nerve to its termination in the medial part of the arcuate nucleus of the thalamus. The uncrossed fibres of the dorsal trigeminal tract are represented by coarse black dots at the following levels: A, chief sensory nucleus of the trigeminal nerve; B, Trochlear nerve decussation; C, inferior colliculus (note that fibres of the brachium conjunctivum pass through the dorsal trigeminal tract); D, trochlear nuclei; E, third nerve nuclear complex; F, Fasciculus retroflexus (note fibres of the dorsal trigeminal tract sweeping into the medial part of the arcuate nucleus).



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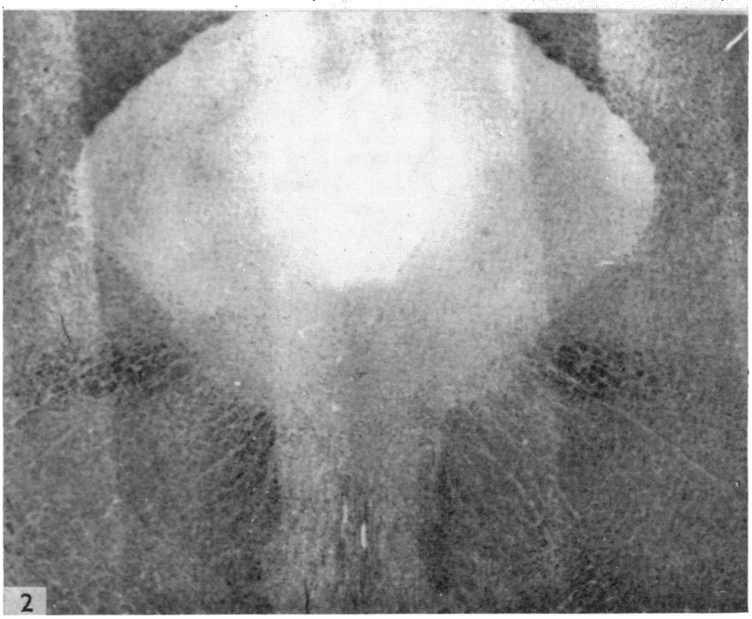

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CARPENTER—DORSAL TRIGEMINAL TRACT IN THE RHESUS MONKEY

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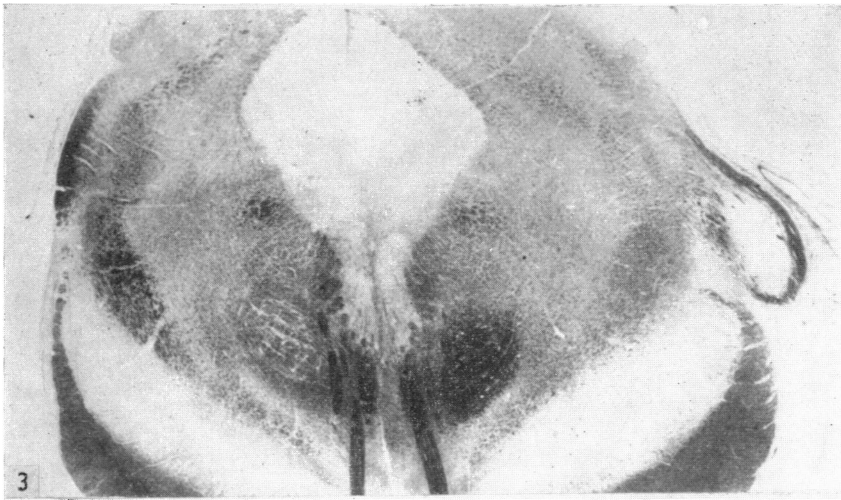

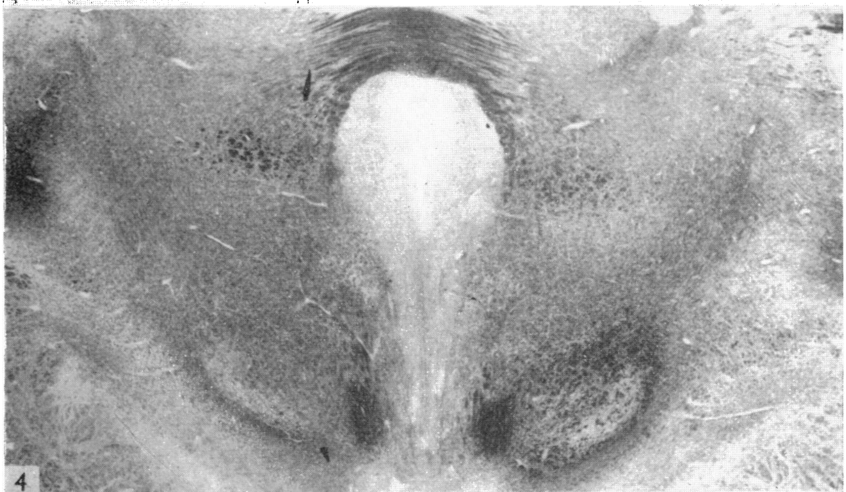

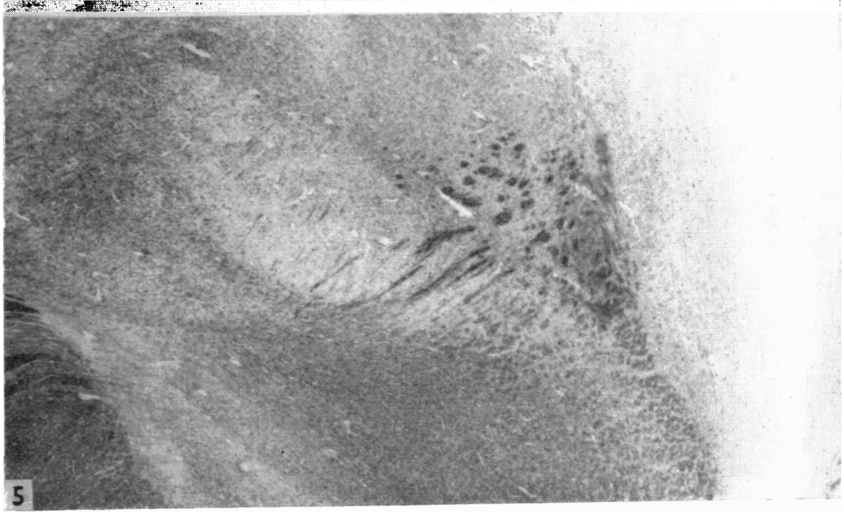

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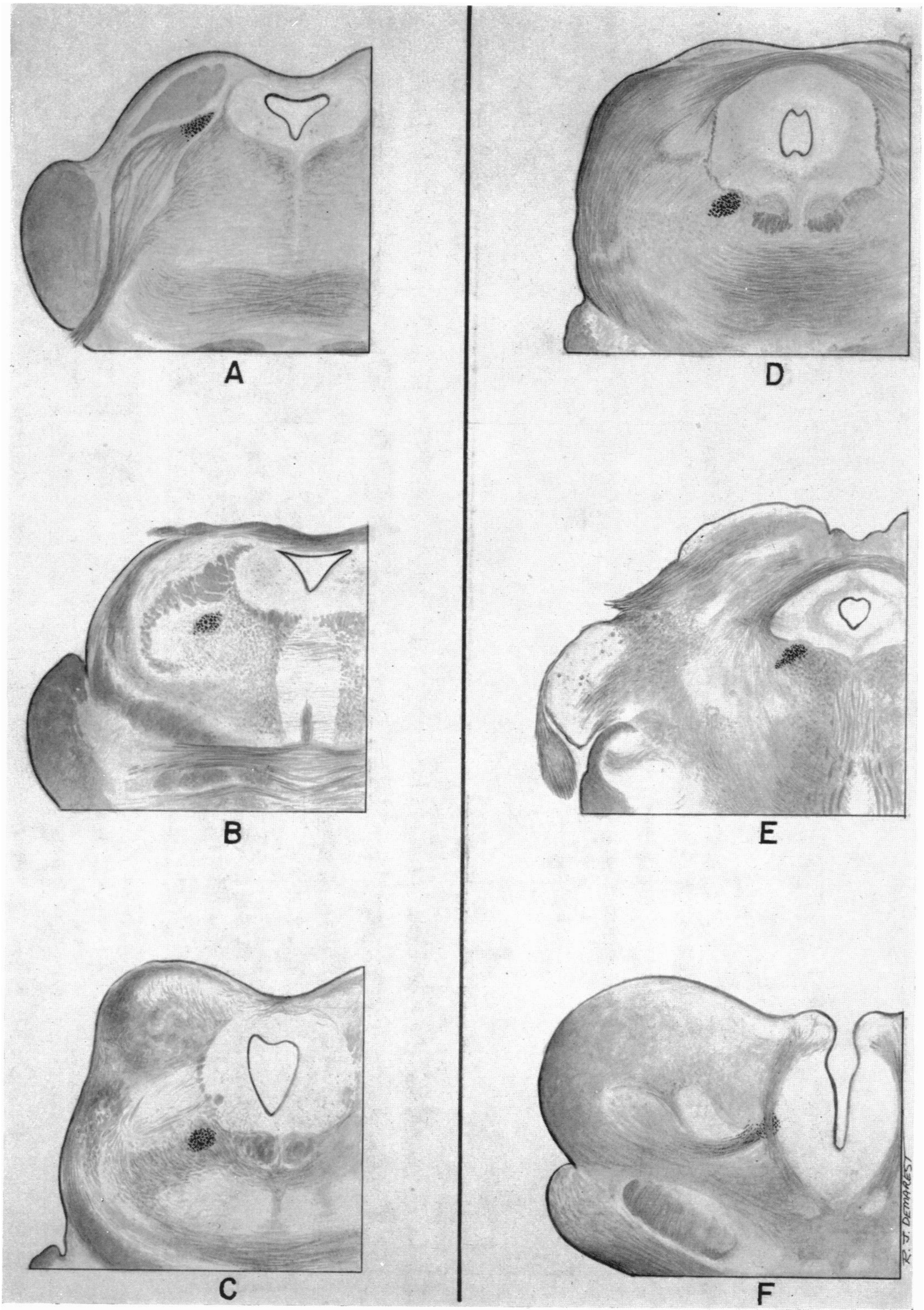

CARPENTER—Dorsal trigeminal tract in the rhesus monkey