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Certain Experimentally Demonstrated Connections Of The Chief Sensory Trigeminal Nucleus In The Squirrel Monkey, Saimiri Sciureus.

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The University of Alabama in Birmingham Medical Center, Ph.D., 1973
Anatomy

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CERTAIN EXPERIMENTALLY DEMONSTRATED CONNECTIONS OF THE CHIEF SENSORY TRIGEMINAL NUCLEUS IN THE SQUIRREL MONKEY, *SAIMIRI SCIUREUS*

by

JAMES ROBERT AUGUSTINE

A DISSERTATION

Submitted in partial fulfillment of the requirements for
the degree of Doctor of Philosophy in the Department
of Anatomy in The Graduate School of the
University of Alabama in Birmingham

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1973

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INTRODUCTION

Impulses from the cutaneous regions of the head are carried to the central nervous system over the peripheral branches of the trigeminal or fifth cranial nerve (V). Such impulses of an exteroceptive nature enter the brain stem at the level of the pons and then pass to appropriate nuclear groups depending upon the specific modality of sensation involved. Either the chief sensory nucleus of V or the nucleus of the spinal tract of V may serve as the center of reception for these exteroceptive impulses. From either or both of these nuclear groups, secondary ascending systems arise which pass to the thalamus. At thalamic levels vibratory sense, gross tactile, pain and gross temperature are thought to come into consciousness. Discrimination of small variations in degree of temperature, finer tactile and proprioceptive impulses require cortical participation. These more discriminatory impulses are relayed from the thalamus to the cerebral cortex where they may come into consciousness.

Two entirely separate projection systems have been described from these brain stem trigeminal nuclear groups. The first detailed report of the existence of a secondary trigeminal pathway originating in the sensory trigeminal nuclei and coursing to higher centers was presented by Hösel (1892). A number of workers has subsequently studied, in normal and experimental material, these secondary pathways from the sensory trigeminal nuclei. Electrophysiological data have also been reported regarding these paths.

The first of these projection systems, the ventral secondary ascending tract of V, has been studied extensively and its origin, course and termination well documented in the literature both clinically and experimentally. The dorsal secondary ascending tract of V has also been studied extensively. In spite of this, much disagreement still exists in the literature regarding this pathway.

More than thirty papers have been published concerning the dorsal secondary ascending tract of V using various animals and a considerable range of techniques. The pathway most often referred to as this dorsal tract of V follows closely that described by Wallenberg (1905) and is sometimes referred to as Wallenberg's fascicle. Hassler (1956) has suggested that this dorsal path is not a trigeminal path but arises from the vestibular nuclear region of the same side. It was earlier reported by Russell (1954) that there was no dorsal secondary ascending tract of V arising from the chief sensory nucleus of V but that a lateral reticulothalamic path occupied the position previously ascribed to the dorsal trigeminothalamic tract.

In light of the controversy which still exists in the literature regarding the dorsal secondary ascending tract of V, the present project was initiated. Using stereotaxic methods and silver impregnation techniques, an attempt was made to determine the central projections from the chief sensory trigeminal nucleus in the squirrel monkey in hopes of shedding new light on the origin, course and termination of this dorsal tract of V. No paper dealing with this path in the squirrel monkey has been found in the available literature.

REVIEW OF LITERATURE

A. Anatomical Studies

There are innumerable anatomical accounts in the literature of the nuclei and fiber connections of the trigeminal nerve. The papers to be discussed in this review were chosen because they provide an example of some of the studies which have been carried out on the dorsal secondary ascending tract of V using normal material of representative mammalian and primate forms prepared for anatomical study.

Hatschek (1902) was one of the first authors to study the dorsal secondary ascending tract of V in a large series of animals. He noted a dorsal tract in the brain of the horse, the calf, the cat, the ass, the ox, the dog, the macaque, the gibbon, and man. However, he could not distinguish this path in the brain of the seal, the dolphin, the guinea pig, the mouse, the armadillo, or the marten. In his Weigert stained material Hatschek (1902) observed an uncrossed dorsal secondary ascending tract of V originating from the chief sensory nucleus of V and terminating in the medial portion of the ventral posterior nucleus of the thalamus.

The Golgi method was used by Ramón y Cajal (1909-1911) to study the nervous system of various small mammals. He described a group of short central paths and also a group of long central paths as the central pathways of the trigeminal nuclei. He considered these long central paths as a long distance system which chiefly ascended perhaps as high as the optic bed or perhaps even higher. The dorsal long central path was thought to be a crossed path, the fibers of which approach the hypoglossal nucleus and cross the midline to take up a position in the reticular substance on the opposite side. At higher levels this path was described as situated at the dorsal limit of the reticular substance medial to the superior cerebellar peduncle. It finally terminated in the semilunar nucleus of the thalamus.

The anatomy of the trigeminal nerve was studied in the normal rabbit brain by Winkler (1921). In addition to a ventral tract he recognized a dorsal trigeminothalamic path which was entirely crossed.

Papez and Rundles (1937) traced the connections of the dorsal trigeminal tract using a complete series of transverse sections of the rabbit, the cat, the sheep and three human brain stems. They also studied a _Macaca_ brain and the brain stem of a horse. From their studies of these forms it was noted that the dorsal trigeminal tract ended in the centré median nucleus of Luys. The course and ending of this path was found to be practically the same in all forms although there was some individual variation. Its caudal end could be traced by Papez and Rundles (1937) into the reticular formation medial to the trigeminal nuclei in the pons. In their monkey material the caudal end of this path could not be clearly identified in the pons and isthmus region. In the available human material the brachium conjunctivum and the central tegmental fasciculus obscured the dorsal tract of V as a separate entity below the level of the decussation of the superior cerebellar peduncle. In the lower mammals Papez and Rundles (1937) found this path to enter the centré median nucleus of Luys through the posterior part of the internal medullary lamina where it ended abruptly. These authors did point out that it seemed probable that not all of the dorsal tract of V terminated in the centré median nucleus but that perhaps a third of the fibers passed into the external medullary lamina toward the pars externa of the ventral nucleus of the thalamus.

In a Weigert stained series of a sheep brain stem the origin of the dorsal trigeminothalamic tract from the main sensory nucleus of V in the pons was noted by Papez (1951). From the rostral end of this nucleus the path was described as inclining dorsomedially toward the nucleus of the locus caeruleus and passing rostrally through the dorsal tegmentum of the midbrain as a well-defined tract. Papez (1951) observed that this path terminated in the dorsomedial surface of the arcuate nucleus, the nucleus centromedianus and in "laminar nuclei".

The course and fiber structure of the dorsal tract of V was studied by Verhaart (1954) in the brain stem of normal *Macaca ira*, normal gibbons and goats. The results of his experimental studies will be mentioned later in the second segment of this review. In *Macaca ira*, Verhaart (1954) described a dorsal capsule in the rostral end of the chief sensory nucleus of V which consisted of fibers from two to four microns in diameter. This triangular bundle was located ventral to the medial part of the brachium conjunctivum and ventrolateral to the mesencephalic root of V. At the isthmus region this tract was found close to the medial longitudinal fasciculus. Remaining in this position the tract was followed rostrally by Verhaart (1954) through the mesencephalon lying dorsal to the red nucleus and was seen entering the ventral part of the centromedian nucleus. The same path was observed by this author also in the gibbon although the bundle was somewhat smaller in size and its fibers slightly thicker. The tract, however, could not be followed in the gibbon further than its entrance into the internal medullary lamina. The dorsal trigeminal tract of V in the goat was very conspicuous according to Verhaart (1954) and occupied a position along the lateral margin of the central gray laterodorsal to the nucleus of IV. Within the thalamus the bundle could be traced into the medial medullary lamina to the centromedian nucleus. In all forms studied by Verhaart (1954) this path was found to be uncrossed. Because of its termination in the centromedian nucleus he suggested that some functional connection with the thalamic intralaminar nuclei was possible.

In addition to the previously mentioned experimental studies by Verhaart (1954), further studies on the dorsal trigeminal path were presented by Verhaart and Busch (1960). They reported their findings in preparations of the brain stem of the goat, the cow, the sheep, the pig, the horse, the dog, the primate, the cat, the rat and man. In that of the cat and the rat, a secondary ipsilateral dorsal tract of V from the chief sensory nucleus of V was either too small to be detected or non-existent according to Verhaart and Busch (1960). These writers pointed out that an uncrossed trigeminothalamic pathway could be found in the goat and monkey which runs in the mesencephalic fasciculus tegmenti and proceeds to the thalamus. They also pointed out that in the horse it is much smaller and much less marked than in the goat. In the goat, cow, sheep and pig a fascicle was observed in the mesencephalic tegmentum which could be traced to the internal medullary lamina of the thalamus and caudally into the pontine tegmentum and then proved to be continuous with the rostral tip of the chief sensory nucleus of V. In the dog as in the cat and rat a distinct pathway could not be observed in the normal material leaving the chief sensory nucleus of V. In primates and man a tract could be followed into the chief sensory nucleus of V from the mesencephalic tegmentum where it was intermingled with the central tegmental bundle. At lower mesencephalic levels it was obscured by the superior cerebellar peduncle.

The secondary connections of the sensory trigeminal nuclear complex were observed in the hedgehog by Brown (1965). Using standard Weigert and Nissl techniques, this author was able to trace the formation of the ventral and dorsal secondary ascending tracts of V. The dorsal tract of V was found to be formed by both crossed and uncrossed fibers from the chief sensory nucleus of V and from the oral levels of the nucleus of the spinal tract of V. Brown (1965) observed that this path lies ventrolateral to the mesencephalic root. The contralateral fibers to it decussate immediately below the central gray somewhat ventral to the brachium conjunctivum. A dorsal trigeminal decussation at the level of the chief sensory nucleus was said to be conspicuously developed in the opossum by Brown (1965). No other descriptive information on the dorsal secondary ascending tract of V was given by this author.

In conclusion, attention is drawn to the fact that fascicles believed to be the equivalent of the dorsal secondary ascending tract of V have been described in reptiles by Woodburne (1936), and in birds by Wallenberg (1905), Huber and Crosby (1929), Ariëns Kappers et al. (1936), and Crosby and Yoss (1954). The phylogenetic significance and relations of this path have been considered in a series of submammalian and mammalian brains by Crosby and Yoss (1954). Since this path in reptiles and birds is part of the quinto-frontal path with significant relations to striatal areas it will not be discussed further in this paper.

B. Experimental Studies

Attention was first drawn to the experimental study of the dorsal secondary ascending tract of V by Wallenberg (1896). He made lesions by hand at various levels of the brain stem in rabbits, using the Marchi technique to study the resulting degeneration. As a result of these methods, Wallenberg (1896) described a crossed pathway which ascended to the thalamus to terminate in the medial part of the ventral thalamic nucleus. He designated this pathway as the dorsal trigeminothalamic tract. Van Gehuchten (1901) obtained similar results employing the same methods and the same animal as had Wallenberg (1896), thereby lending further support to the existence of a crossed dorsal secondary ascending tract of V as described previously.

In a later paper, Wallenberg (1905) observed the degeneration which resulted from lesions of the chief sensory nucleus of V in the rabbit. This work yielded a description of two distinct pathways, fibers of which are both crossed and uncrossed. One group of rather large fibers originating from the dorsal part of the chief sensory nucleus of V ascended ipsilaterally as high as the midbrain. Other fibers from this same dorsal part of the chief sensory nucleus of V crossed the midline to follow the dorsal secondary pathway and terminate in the nucleus centromedianus. A second group of somewhat thinner fibers was noted by Wallenberg (1905) to cross the midline and ascend either through the medial lemniscus or somewhat dorsal to it. Again these fibers terminated in the region of the nucleus centromedianus.

In a study of the retrograde cellular changes in the chief sensory nucleus of V in the rabbit resulting from unilateral brain stem lesions, Kohnstamm (1910) made note of significant changes in cells of the contralateral side. Only a few cells appeared to be altered in the dorsal portion of the ipsilateral nucleus.

Experimental lesions of the chief sensory nucleus of V were reported for the first time in a primate by von Economo (1911). Using a macaque, this author noted a dorsal tract arising from the most medial part of the chief sensory nucleus of V which passed forward through the lateral tegmental region just ventral to the brachium conjunctivum and remained ipsilateral to its cells of origin. The thalamic termination of this path was found to be in the more medial and inferior portion of the arcuate nucleus. Von Economo (1911) pointed out that this dorsal path dealt with taste rather than somesthetic sensibilities from the face. In addition to this ipsilateral pathway some fibers passing from the main sensory nucleus of V were also described. These continued forward to the contralateral arcuate nucleus of the thalamus, accompanying the medial lemniscus to reach their point of termination.

Further studies on certain ascending paths to the thalamus were carried out in a macaque by Le Gros Clark (1936). He made lesions with a small curved knife at various levels of the cord, the medulla and the midbrain. Although he attempted to place a lesion in the chief sensory nucleus of V, he was not successful. Le Gros Clark (1936) clearly pointed out that no positive evidence was obtained as to the thalamic termination of paths from the chief sensory nucleus of V. It was known at this time that the pars arcuata of the ventral thalamic nucleus projects, at least in part, onto the face area of the precentral or postcentral gyrus. When Le Gros Clark (1936) found definite evidence of termination of degenerating fibers in the arcuate nucleus in one experiment, he surmised that this must be due to involvement in the lesion of secondary ascending fibers from the chief sensory nucleus of V. However, Le Gros Clark (1936), again cautious, pointed out that many fiber systems at the caudal boundary of the thalamus must have been cut in this experiment so that no certain conclusion can be drawn from this observation.

Walker (1939) also carried out experimental studies of secondary pathways of the trigeminal nuclei in primates. Using a sharp scalpel and a posterior suboccipital craniotomy he made lesions in the chief sensory nucleus of V in three immature Macaca mulatta monkeys. Because his lesions involved a number of pontine and even cerebellar structures, Walker (1939) suggested that his results required rather critical analysis. He pointed out that it was almost impossible, using the sharp scalpel method, to destroy a deep lying structure such as the chief sensory nucleus of V without involving neighboring gray masses or fiber tracts in the lesion. In spite of this, Walker (1939) concluded that a poorly defined system of fibers could be seen originating from the rostral portion of the reticular substance lying between the posterior longitudinal bundle and the brachium conjunctivum with some of the fibers crossing the midline and passing forward in the dorsolateral reticular substance of the opposite side. The uncrossed fibers seemed to be much more numerous. A few of the fibers reached the contralateral motor nucleus of V. From the depths of the superior colliculus, fibers passed into the mesencephalon through the accessory oculomotor nuclei and then turned laterally to cross the habenulopeduncular tract to enter the arcuate nucleus of the thalamus via the internal medullary lamina. Walker (1939) described the majority of the fibers as terminating in the medial part of the ventral posteromedial nucleus of the thalamus although some seemed to terminate in the nucleus centromedianus. Although the origin of this system from the chief sensory nucleus of V had not been proven by this study, Walker (1939) concluded that the system he described represented the dorsal secondary ascending tract of V.

Experimental studies of the central tegmental tract in _Macaca ira_ by Verhaart (1949) revealed a rather distinct, thick-fibered tract in the area of the mesencephalon designated as the central tegmental tract by Tilney and Riley (1928). According to Verhaart (1949), however, the area designated central tegmental tract probably does not belong to that bundle. The distinct thick-fibered tract seen in that area in _Macaca ira_, when severed, degenerates rostrally and terminates in the medial part of the ventral posteromedial nucleus of the thalamus. This path appeared to take origin from the chief sensory nucleus of V and was considered by Verhaart (1949) to be the "tractus secundarius dorsalis nervus trigemini". Verhaart (1949) noted this tract in man but pointed out that it is less conspicuous, as the surrounding central tegmental tract contains more fibers. No mention was made as to the crossed or uncrossed course of its fibers.

Stereotaxic lesions were made in the lateral tegmental reticular formation at the level of the midbrain in cats by Johnson (1951). Among the fibers interrupted were those forming the dorsal trigeminothalamic tract which this author stated arose from the chief sensory nucleus of V in the pons to ascend and terminate in the nucleus parafascicularis, nucleus centromedianus and nucleus arcuatus. No information was given in Johnson's (1951) abstract as to whether the path he mentioned was crossed or uncrossed or both.

Another abstract, published by Papez (1951), suggested that an uncrossed tract was found in the cat following lesions in the chief sensory nucleus of V. Papez (1951) seemed to imply that this path, the dorsal trigeminothalamic tract, had an origin and termination in the cat similar to those he had observed in the brains of the horse and the sheep. However, he did not specifically mention the course this tract takes in the cat but only pointed out its uncrossed degenerated fascicles following lesions of the chief sensory nucleus of V.

Further experimental studies on the dorsal trigeminothalamic path were carried out by Russell (1954). Using stereotaxic methods he placed unilateral electrolytic lesions in the brains of three cats. These lesions were limited to the sensory trigeminal nuclei without encroaching upon the more medial reticular formation. Based upon the results obtained in these three animals and in three other animals with lesions of the dorsolateral reticular formation of the upper medulla and pons, Russell (1954) concluded that there was an absence of a demonstrable dorsal trigeminothalamic path arising from the chief sensory nucleus of V. Occupying the position previously ascribed to the dorsal tract of V, Russell (1954) described a lateral reticulothalamic pathway. In reaching this conclusion Russell (1954) contended that previous reports of a dorsal trigeminothalamic tract had been based upon more extensive lesions than those in his work.

Verhaart (1954) turned his attention to a more detailed discussion of the dorsal tract of V than he had previously reported (1949). Experimental lesions were placed in four monkeys but the methods for doing so were not reported. In cases of destruction of the macaque chief sensory nucleus of V the tractus trigeminalis of Wallenberg, emerging from the chief sensory nucleus of V and proceeding through the mesencephalic tegmentum to the centromedian nucleus of the thalamus was reported by Verhaart (1954). In an animal where this tract was severed at its entrance into the thalamus, retrograde degeneration could be followed into the chief sensory nucleus of V. As destruction of this nucleus caused degeneration only in the ipsilateral tract, Verhaart (1954) considered this tract to consist of uncrossed fibers. The technique used by Verhaart (1954) to study this path was Haggqvist's staining method which had not been employed by other authors who studied this pathway.

A physiological approach to an understanding of the secondary pathways of the trigeminal nerve was reported by Berry, Anderson and Brooks (1955). While stimulating the infraorbital branch of V, these authors explored the brain stem in the cat with small, unipolar electrodes. A crossed and an uncrossed dorsal secondary ascending tract of V were found just lateral to the medial longitudinal fasciculus. The impulses conducted by this tract were observed in the midbrain within two milliseconds.

The Marchi stained material from the Hess (1932) collection of one hundred cats with lesions at various levels of the nervous system was used in the study of the dorsal secondary ascending tract of V by Bürgi (1955). In fifteen of these cats, Bürgi (1955) found that the dorsal secondary tract of V had been interrupted by the lesion. Based on the anatomical findings this author felt that Wallenberg's tract or the dorsal secondary ascending tract of V is the anatomical substrate of the reticular activating system which had been described by Morruzzi and Magoun (1949).

Anatomical and physiological studies in the cat by Stotler and Kerr (1955) were thought, by these authors, to indicate the presence of four ascending somesthetic paths within the brain stem tegmentum. One of these paths was referred to in their abstract as an ascending component of the central tegmental fasciculus. It was thought to be a multisynaptic path with bilateral representation although consisting predominantly of fibers of contralateral origin. These fibers terminated in what Stotler and Kerr (1955) refer to as the phylogenetically older portions of the medial thalamus. The dorsal secondary ascending tract of V was thought to be contained within this ascending somesthetic component.

One of the authors of this last mentioned paper, Kerr, and his co-workers, Haugen and Melzack (1955), subsequently reported further experimental studies in the cat. On the basis of anatomically determined locations, the wave forms, the behavior during repetitive stimulation with various frequencies and its modification by anesthesia, the potential changes during stimulation were recorded from the brain stem by these investigators and differentiated into functional groups. One of these groups was the dorsal secondary ascending tract of V which these authors also felt to be the ascending portion of the central tegmental fasciculus. It was thought to be a bilateral projection of medium latency from six to eight milliseconds and was traced to the medial nuclei of the thalamus. Medium latency potentials were demonstrated in the nucleus parafascicularis and subparafascicularis which were thought to represent caudal extensions of the nucleus centralis forming relay nuclei into the nucleus centromedianus and other more rostral medial nuclei. This dorsal secondary ascending tract of V of the central tegmental fasciculi was suggested by Kerr, Haugen and Melzack (1955) as representing the phylogenetically old reticulothalamic afferent system.

Berry, Anderson and Brooks (1956) also applied the techniques of stimulation and recording to study the ascending pathways of the sensory trigeminal nuclei in the cat. These authors explored the medulla, the midbrain and the posterior thalamus with unipolar electrodes while stimulating a branch of the maxillary nerve peripherally. Ipsilateral and contralateral activity in dorsal regions of the midbrain was demonstrated. It occurred in the dorsal ascending tract just lateral to the medial longitudinal fasciculus as well as in the dorsally located single units of the midbrain. These single units fired repetitively in response to both ipsilateral and contralateral trigeminal nerve stimulation.

By this time the experimental studies on the dorsal secondary ascending tract of V yielded a rather confusing picture as to its existence, its course, if present, and its thalamic termination. Adding further to the uncertainty about this path were the results reported by Hassler (1956). Upon stimulation of the dorsal secondary tract of V in the cat, Hassler (1956) observed horizontal turning toward the side. Based upon this observation he suggested that this dorsal path was not a trigeminal pathway but arose from the vestibular nuclear region of the same side.

During a study of the brachium conjunctivum, Carpenter (1957) reported a number of incidental observations. In his opinion, these experimental data supported the existence of an uncrossed dorsal trigeminal fasciculus originating from the chief sensory nucleus of V. In one immature _Macaca mulatta_ a stereotaxic lesion was produced in the brachium conjunctivum ventrally and extended caudally into the dorsal part of the chief sensory nucleus of V. In eight other rhesus monkeys the brachium conjunctivum was sectioned with a small knife caudal to the inferior colliculus. None of these lesions was limited to the brachium conjunctivum, rather they involved such structures as the inferior colliculus, the fourth nerve and such paths as the dorsal secondary ascending tract of V, the lateral lemniscus and the ventral spinocerebellar path. The Marchi method was used to study the resulting degeneration. In animal 2124 there was bilateral destruction of the chief sensory nucleus of V and the ventral portion of the brachium conjunctivum. From the chief sensory nucleus of V and the area dorsomedial to it, Carpenter (1957) described a triangular shaped bundle along the medial concavity of the brachium conjunctivum which he considered constituted the dorsal tract of V. Above the level of the inferior colliculus this path was dorsal to the brachium conjunctivum although it was difficult in this area to follow the degeneration in the dorsal tract because of co-existing degeneration in the brachium conjunctivum. At the level of the fourth nucleus the dorsal secondary ascending tract of V was again isolated and distinct occupying a position dorsolateral to the medial longitudinal fasciculus. The separation of this path from the medial longitudinal fasciculus was more evident in the region of the oculomotor nucleus. Above the posterior commissure, Carpenter (1957) observed this path to bend laterally and pass ventrolaterally through the medial part of the centromedian nucleus to enter the medial part of the arcuate nucleus of the thalamus. Although degeneration was most dense in the arcuate nucleus, it was not possible to determine whether some fibers terminated in the centromedian nucleus or merely passed through it.

In cases where surgical lesions were made in the dorsal path with a small knife, Carpenter (1957) observed a similar ascending course of the degenerated fibers as previously described. The degenerated path was always on the same side as the lesion in very instance. No crossed degeneration was seen in the opposite dorsal trigeminal tract or in the medial lemniscus. In none of these animals was Carpenter (1957) able to detect impairment of tactile sense over any part of the face; however, no special testing procedures were employed.

Torvik (1957) studied the course of ascending fibers from the chief sensory nucleus of V in young kittens. He employed the technique of retrograde degeneration after partial or complete transections of the rostral brain stem. These lesions were made with a blunt spatula inserted through the occipital pole after which cell losses were observed in the chief sensory nucleus of V. Following such one-sided lesions, Torvik (1957) observed changes in cell accumulation in the dorsomedial portion of the chief sensory nucleus of V on the side of the lesion. No cells were altered in the ventral portion of the nucleus on the side of the lesion or in the dorsomedial portion contralaterally. Torvik (1957) concluded, from the nine animals studied, that most of the trigeminothalamic fibers from the chief sensory nucleus of V, mainly those from the ventral part, were crossed. However, all fibers from the smaller dorsal part of the nucleus reached the thalamus via an uncrossed pathway. This study confirmed the existence of a bilateral trigeminothalamic path from the chief sensory nucleus of V but Torvik (1957) pointed out that his results did not support the assumption that there was a crossed dorsal secondary ascending tract of V from this nucleus. The dorsal pathway demonstrated by him was essentially uncrossed.

Nauta and Kuypers (1958) performed experiments in the cat to study some ascending pathways in the brain stem reticular formation. Small electrolytic lesions were placed in the brain stem reticular formation with the aid of a stereotaxic apparatus and the axon degeneration resulting from these lesions was demonstrated histologically with the aid of the silver impregnation method of Nauta and Gygax (1954). In several cases a lesion was placed in the chief sensory nucleus of V with involvement of cells which lie between the chief sensory nucleus of V and the motor nucleus of V. Nauta and Kuypers (1958) referred to these cells as a reticular zone which they considered as constituting a zone of passage of a lateral reticular ascending system. From lesions in the chief sensory nucleus of V, these authors were able to trace a large number of degenerating fibers which they felt corresponded to those originally demonstrated by Wallenberg (1905). Nauta and Kuypers (1958) emphasized that degeneration of such fibers occurred only in those cases in which the lesion involved the narrow reticular zone described above. It was concluded from this that it was highly probable that Wallenberg's uncrossed dorsal trigeminal tract from the chief sensory nucleus of V represented an ascending pathway from the lateral reticular formation in the medulla.

The studies reported by Verhaart (1954) on *Macaca ira* were expanded by Verhaart and Busch (1960). The systems under consideration by these authors included: 1. a pontine path known as the fasciculus tegmentalis dorso-lateralis (F.t.d.) as depicted in Riley's (1943) atlas lying medio-ventral to the superior cerebellar peduncle; 2. a mesencephalic tract known as the fasciculus tegmenti (F.t.) of Forel located in the dorsal path of the mesencephalic tegmentum, near the lateral margin of the central gray matter; and 3. the secondary dorsal trigeminal tract as described in the rabbit by Wallenberg (1905). According to Verhaart and Busch (1960) the site of the dorsal secondary ascending tract of V in the rostral mesencephalon is identical with that of Forel's fascicles. In addition to the two monkeys previously described by Verhaart (1954) another monkey was studied in which the fasciculus tegmenti of Forel was severed at the transition of the thalamus and the mesencephalon twenty-one months before death. In this animal both the fasciculus tegmenti of Forel and the fasciculus tegmentalis dorso-lateralis proved to be absent, whereas the rostral part of the chief sensory nucleus of V was much reduced in size. Some demyelination was found in the dorsolateral corner of the upper pontine reticular formation. In a fourth animal destruction of the motor nucleus of V along with most of the entering sensory fibers of V was carried out with no appreciable reduction in the size of the fasciculus tegmentalis dorso-lateralis or the fasciculus tegmenti of Forel. However, because of the type of staining methods used slight changes in fiber pattern or content could not be observed. In a young goat a lesion was made by these authors which involved the rostro-dorsal half of the chief sensory nucleus of V, the brachium pontis and part of the restiform body. There was a second lesion at the base of the inferior colliculus. Ipsilateral to the lesion the area of the fasciculus tegmentalis dorso-lateralis was almost entirely degenerated; however, this same bundle was entirely normal in its appearance on the contralateral side. Rostrally degenerated fibers were found in Forel's fascicle on the side of the lesion intermingled with a group of normal fibers. The amount of degeneration was about the same as that seen previously. No degeneration was demonstrated in the mesencephalon contralateral to the lesion.

In several other goats, Verhaart and Busch (1960) made unilateral lesions in the nucleus of the spinal tract of V and the posterior horn at the transition of the medulla to the cord. In none of these could the crossed component of the secondary ascending tract of V be found. Cats which had been experimented upon for other purposes were also reported upon by these authors. Electrolytic lesions had been made in the brain stem but only the mesencephalic fasciculus tegmenti was considered. Substantial degeneration in this path could be brought about only by a large lesion of the rostral pole of the chief sensory nucleus of V and the adjacent reticular formation: fibers seemed to be derived chiefly from the latter formation at a high pontine level. The crossed system within the medulla and pons could not be found. Experiments in the cat indicated that the fasciculus tegmenti took its origin almost entirely from the dorsolateral part of the ipsilateral rostral pontine reticular formation. In the cat apparently an ipsilateral dorsal secondary ascending tract of V derived from the chief sensory nucleus of V was either too small to be detected with the techniques employed or nonexistent according to these authors. Vestibular lesions mostly of large size and in different nuclei in the cat as well as in the dog both failed to cause any fiber degeneration in the fasciculi of Forel. Therefore Verhaart and Busch (1960) concluded that the fasciculus tegmenti did not consist chiefly of vestibulothalamic projection fibers as suggested by Hassler (1956).

In a small number of rats these same authors made lesions in the rostral part of the sensory trigeminal nuclear complex. Fibers arising in the chief sensory nucleus of V and the rostral part of the nucleus of the spinal tract of V were found to form an important part of the contralateral mesencephalic medial lemniscus but did not travel in the ipsilateral pontine and mesencephalic tegmentum. Fibers from the nucleus of the spinal tract of V in its lower portions were present only in the contralateral lemniscus. In the rat, as in the cat, the ipsilateral dorsal secondary ascending tract of V was not detected or was nonexistent.

Verhaart and Busch (1960) suggested that the component from the chief sensory nucleus of V be called the "Fasciculus tegmentalis dorsolateralis" and the whole tract in the mesencephalon be referred to as the "Fasciculus tegmentalis of Forel". Both fascicles are occasionally called "Wallenberg's dorsal secondary trigeminal tract". These authors contended that their results made it advisable to restrict Wallenberg's name to the pontine chief sensory nucleus of V component since this was the only part of which the trigeminal origin had been established. To apply Wallenberg's name to the mesencephalic fasciculus tegmenti was not justified in their view, since in many animals it probably did not contain trigeminal fibers, although an uncrossed trigeminothalamic pathway could be considered as established in the goat and monkey running in the mesencephalic fasciculus tegmenti and forward to the thalamus.

Eisenman, Fromm, Landgren and Novin (1964) studied the ascending projections of trigeminal neurons in the cat using antidromic stimulation. Electrodes were placed in the contralateral trigeminal lemniscus and the ipsilateral dorsal secondary ascending tract of V stereotaxically and these areas were then stimulated. Antidromic responses were then evoked in single trigeminal neurons and these cells were then localized to the chief sensory nucleus of V or the rostral subdivision of the nucleus of the spinal tract of V and classified into groups. Based upon such methods these authors observed that cells located in the dorsomedial part of the chief sensory nucleus of V were secondary "touch" cells with small oral receptive fields the axons of which entered the ipsilateral dorsal secondary ascending tract of V. Cells located in the lateral and ventrolateral parts of the chief sensory or the rostral subdivision of the nucleus of the spinal tract of V were found to project into the contralateral trigeminal lemniscus. These cells were thought to be secondary "touch" cells with small perioral or periorbital receptive fields. Eisenman, Fromm, Landgren and Novin (1964) located the ipsilateral dorsal secondary ascending tract of V in a region ventrolateral to the central gray and dorsal to the red nucleus. They also recorded from single cells in the ventral posteromedial nucleus of the thalamus of the cat and found that several of these cells responded to tactile stimulation of the tongue as well as to electrical stimulation in the region of the dorsal secondary ascending tract of V on the ipsilateral side at the mesencephalic level. On the basis of these observations, along with those previously mentioned, these authors concluded that an ipsilateral dorsal secondary ascending tract of V originating in the dorsomedial part of the chief sensory nucleus of V and ending in the nucleus ventralis posteromedialis of the thalamus exists and conducts tactile impulses from the oral cavity.

Retrograde cell degeneration experiments were performed by Karamanlidis and Voogd (1970) to study the trigeminothalamic connections in the goat. In five adult goats stereotaxic lesions were placed in the dorsal or ventral part of the chief sensory nucleus of V together with part of the oral subdivision of the nucleus of the spinal tract of V. The degenerated fibers were then studied by means of the Nauta-Gygax (1954) method. In one of the experiments the lesion comprised the whole chief sensory nucleus of V. Although the lesions were different in each case, the degenerated fibers were always found in the area of the dorsal trigeminothalamic tract and the preterminal degeneration in the ventral posteromedial nucleus of the thalamus. The dorsal tract of V was considered by these authors to occupy a circumscribed area lying lateral to the central gray at levels just rostral to the lesion. At the level of the inferior colliculus the dorsal secondary ascending tract of V was obscured by the degenerating fibers of the brachium conjunctivum passing medially towards their decussation. On the side of the lesion the dorsal trigeminothalamic tract occupied, at the level of emergence of the third nerve, the lateral part of the central gray somewhat dorsolateral to the dorsal tip of the medial longitudinal fasciculus (Karamanlidis and Voogd, 1970, Fig. 2, p. 602). The retrograde cell degeneration experiments performed by Karamanlidis and Voogd (1970) were carried out in very young goats of 6 to 12 days of age. In fourteen animals the caudal part of the thalamus was destroyed. From these experiments the authors felt that the origin of the dorsal trigeminothalamic tract in the goat could be more precisely determined. Their findings showed that in the goat the chief sensory nucleus of V sends fibers only to the ipsilateral thalamus and that these fibers arise from the whole nucleus except its very small ventral part. This ventral part did not seem to project to the thalamus. It seemed probable to Karamanlidis and Voogd (1970) that the nucleus of the spinal tract of V, especially its rostral part, does send fibers to the thalamus via the dorsal secondary ascending tract of V but that these fibers are not numerous. Consequently when the tract was sectioned at thalamic levels, no retrograde cell degeneration was evident in the nucleus of the spinal tract of V.

The results obtained for the goat by the previous authors were quite different from those reported in the dog and the pig by Michail and Karamanlidis (1970). Their study suggested that the chief sensory nucleus of V in these two animals sent fibers bilaterally to the thalamus. For these experiments a thalamic lesion was carried out destroying the ventral posterior nuclei and causing retrograde cell changes and cell losses in the trigeminal sensory nuclear complex in seven dogs and seven pigs. These cell changes were studied with the aid of the Klüver-Barrera method or with the thionin technique. In both groups of animals the dorsal part of the ipsilateral and the ventral part of the contralateral chief sensory nucleus of V exhibited neuronal degeneration and cell losses to a greater or lesser degree. In the nucleus of the spinal tract of V there were also cell losses confined to the most rostral part of the rostral subdivision of the contralateral nucleus. It was carefully pointed out, however, by Michail and Karamanlidis (1970), that the absence of signs of cell degeneration in the interpolar and the caudal subdivisions of the nucleus of the spinal tract of V did not exclude the possibility that these parts also send fibers to the thalamus, since they believed that in retrograde degeneration experiments only positive results are of significant value. The authors also suggested that in the midbrain the ipsilateral fibers run more medially than the contralateral ones and that they terminate in the ventral posteromedial nucleus of the thalamus but that the contralateral fibers project to the ventral posterolateral nucleus of the thalamus.

The uncrossed fibers were considered to correspond to the dorsal trigeminothalamic tract described by previous authors.

Mizuno (1970) made electrolytic lesions stereotaxically in the chief sensory nucleus of V and the supratrigeminal region of the cat and studied the resulting degeneration with the aid of the Nauta (1957) or the Fink-Heimer (1967) method. The results in the cat were compared with those obtained from Marchi preparations of Japanese monkeys (_Macaca fuscata_). In these monkeys lesions were produced in the lower brain stem by free-hand insertion of a small knife or a slender drill through an opening in the basilar portion of the occipital bone. The results reported by Mizuno (1970) were based upon findings obtained in five cats and two monkeys. An uncrossed dorsal trigeminothalamic tract was traced rostrally to the ventral posteromedial nucleus of the thalamus which ascended through Forel's tegmental fasciculus. It was pointed out by the author, however, that Forel's tegmental fasciculus was composed mainly of the ascending reticular fibers terminating in the intralaminar nuclei of the thalamus and in the subthalamus. When the experimental lesion was confined to the chief sensory nucleus of V and/or the supratrigeminal region degeneration in Forel's tegmental fasciculus and the thalamus was not heavy and if the experimental lesion was confined to the interpolar and rostralis subdivisions of the nucleus of the spinal tract of V, no degeneration was found in Forel's fascicle. No evidence of the existence of a crossed dorsal secondary ascending tract of V arising from the chief sensory nucleus of V was found in this study.

Mogami, Kuroda, Hayakawa and Akagi (1971) reported their findings regarding the ascending paths from the spinal trigeminal nucleus and its adjacent structures in the cat. Lesions were placed longitudinally in the nucleus of the spinal tract of V with a small piece of safety razor under direct vision. Three ascending paths from the nucleus of the spinal tract of V were demonstrated with the Marchi and Nauta degeneration methods. The second group of ascending paths was thought to comprise the dorsal tract of V described by Wallenberg (1896). This last path was reported to ascend predominantly in the contralateral reticular formation and terminated in the intralaminar nuclei and the ventral posteromedial nucleus of the thalamus. The degenerating fibers of the dorsal secondary tract of V appeared to be more widespread in the Nauta material than in the Marchi material.

In their study, using the Marchi method, Mogami et al. (1971) noted that the dorsal tract of V originated from the nucleus of the spinal tract of V cephalad to the pyramidal decussation. Although many fibers of this dorsal path ascend contralaterally, a few fibers were found ipsilaterally with the Nauta technique. These authors concluded that since the cells of origin of the dorsal tract of V were thought to be analogous to the cells of the nucleus posterioris cornu proprius this tract was assumed to be functionally similar to the ventral spinothalamic tract which also is thought to arise from the cells of the nucleus posterioris cornu proprius. Both paths would presumably be involved with relay of "protopathic touch sense and pressure sense". These authors did not study the chief sensory nucleus of V.

Experimental studies published in abstract form by Smith and Mehler (1971) on the ascending fiber projections from the chief sensory nucleus of V in the rat and in the monkey by Smith (1972) have recently been published in detail by Smith (1973). Unilateral pontine level lesions involving the chief sensory nucleus of V were made stereotaxically in twenty-eight adult rats. Fifteen brains acceptable for study were processed with a variety of modifications of the Nauta (1957) method and the Fink-Heimer (1967) method. Two fiber systems were described proceeding from the chief sensory nucleus of V. One of these corresponded to the well-known ventral secondary ascending tract of V and was referred to as the trigeminal lemniscus. In two guinea pigs Smith (1973) also observed totally crossed secondary trigeminal fibers with an ascending course and pattern of termination in the thalamus equivalent to that demonstrated in the rat.

Another fiber system described by Smith (1973) in the rat was called the intertrigeminal system. This system was thought to arise from the parvicellular reticular formation between the chief sensory nucleus of V and the motor nucleus of V. These fibers were described as passing dorsally from the region of the lesion and terminating on the cells of the ipsi- and contralateral motor V nuclei and adjacent contralateral parvicellular reticular formation. This author was unable to produce any evidence supporting the existence of an uncrossed chief sensory trigeminothalamic pathway in the rat even after lesions of the dorsal and rostral portions of the chief sensory nucleus of V. Smith (1973), however, was able to demonstrate in the monkey some ipsilaterally ascending fibers. Unilateral stereotaxic lesions had been made in fourteen monkeys of the same extent as described for the rat. The fibers in the monkey which form the dorsal trigeminothalamic component were found to arise chiefly from the dorsal part of the chief sensory nucleus of V. They were found to ascend with the central tegmental tract on the same side as their lesion of origin to enter the ventral posteromedial nucleus of the thalamus in its pars magnocellularis via the internal medullary lamina and to terminate discretely in its dorsomedial part.

C. Clinical Documentation

Spitzer (1899) studied the brain of a patient with a pontine tumor after the brain had been treated by the Marchi method. Clinically the patient showed no disturbances attributable to this pontine mass. Spitzer (1899) was able to follow two tracts through the brain stem and into the thalamus. His ventral bundle followed that path traditionally ascribed to the ventral secondary ascending tract of V. A dorsal bundle was also described which ran in the lateral "Haubenbahn" (tegmental bundle) beneath the brachium conjunctivum and terminated in the arcuate nucleus of the thalamus. This path was thought to be crossed and presumably represented a crossed dorsal secondary ascending tract of V.

Wallenberg (1904) studied a Marchi stained brain from a patient with a pontine hemorrhage and described an uncrossed tract from the frontal part of the nucleus of the spinal tract of V. This path terminated mainly in the medial part of the arcuate nucleus and in the centromedian nucleus of the thalamus. Passing through the dorsolateral part of the reticular substance beneath the brachium conjunctivum, this tract entered the posterior part of the internal medullary lamina to reach the thalamus.

Another human case with a lesion in the pons yielded information regarding the dorsal secondary tract of V. Von Economo (1911) employed the Marchi method to study this path and found a path from the most medial part of the chief sensory nucleus of V which he felt was involved with taste. This uncrossed path traveled through the lateral tegmental region just ventral to the brachium conjunctivum and terminated in the medial part of the arcuate nucleus of the thalamus.

Based upon his analysis of clinical and pathological material available from three patients, Smyth (1939) suggested that there was no information in these cases in favor of the existence of a dorsal quintothalamic tract. He did observe an entirely crossed ventral quintothalamic tract which ascends through the medial lemniscus to assume a close relationship with the fibers of the spinothalamic tract in the rostral pons.

MATERIALS AND METHODS

The animal used in this study was the common squirrel monkey, *Saimiri sciureus*. The reasons for choosing this animal were as follows:

1. The squirrel monkey has a relatively large brain (26.0 gm ± 1.7 in the adult) with many of the distinctive features of the primate cortex and thalamus.

2. The semilissencephalic cortex of its brain is easily accessible for intracerebral stimulation and recording studies as well as multilead monitoring of electrical activity.

3. Squirrel monkeys, when kept under proper conditions, develop good resistance to disease, and their tolerance of intracranial surgery for acute and chronic experiments is excellent.

4. Because of their small size they can be handled easily.

5. The costs of purchase and care are relatively low.

6. Two excellent stereotaxic atlases (Gergen and MacLean, 1962; Emmers and Akert, 1963) of the brain of this monkey are available, using the Horsley-Clarke coordinate system.

This study was carried out in the following manner using the described techniques.

A. Anatomical Studies

Histological preparations of five normal squirrel brains were prepared for study of the anatomical features of the dorsal secondary ascending tract of V. Brain stem and diencephalic structures related to this tract were studied in serial sections cut perpendicularly to the plane of the brain stem in two of these brains. One of these brain stem series was stained with the Holmes (1943) modification of Bielschowsky's pyridine silver technique to further define the normal anatomical appearance of this fiber system. The other brain stem series was cut serially and stained alternately with the Weil modification of the Weigert method for myelin sheaths or the cresyl violet technique for normal cell studies. A third brain was cut in the sagittal plane using the previously described stains for additional study of the normal anatomy of this pathway as it appears in this plane.

The other two brains were cut serially in the frontal plane and sections stained alternately with the thionin method for cell studies or the Weil (1928) modification of the Weigert method for fiber studies. These five brains cut as described and properly stained provided sufficient anatomical information for studying the normal relations of the dorsal secondary ascending tract of V in the squirrel monkey.

B. Experimental Studies

Seven adult male squirrel monkeys were used in this study, all with body weights between 700-800 gm. In each case the animals were anesthetized with Vetalar (Ketamine HCl - Parke-Davis). The dosage used was 30 mg/kg which provided sufficient anesthesia for the entire surgical procedure. After the animal was anesthetized, his head was completely shaved and then scrubbed with surgical soap. The animal's head was then placed in a Lab-Tronics Stereotaxic Instrument. Because sterile techniques were to be used, the instrument had been sterilized by soaking in a non-corrosive germicidal solution. With the exception of a small area of the head, the entire animal and instrument then were draped with sterile drapes. The animal's head was then sterilized. A 3 cm incision was then placed in the animal's scalp on the left side at coordinates AP 0.0. The incision was U-shaped with the base of the U at the vertex of the skull and the limbs of the U extending toward the animal's ear. The scalp flap was sutured back and the underlying bone was then scraped thoroughly. After determining the desired exact point of entry of the electrode a 5 mm burr hole was placed in the skull at that point. The exposed dura was then gently incised with a scalpel blade.

Unipolar electrodes were used for both stimulation and for making lesions. These electrodes were made from enamel coated nichrome alloy wire. Electrodes were drawn from this wire and coated to insure adequate insulation. Only the electrode tip was bare after it had been ground to a sufficient point. Once placed in the electrode holder of the stereotaxic apparatus, the electrode was connected to a Grass stimulator (model S4). A second lead was connected to the animal's skin.

The initial target chosen in all cases was the motor nucleus of V at coordinates AP 0.0, L 3.0, H -3.5 to -4.0 according to the Emmers and Akert (1963) stereotaxic atlas of the squirrel monkey brain. A stimulus of 1.75 volts at 40 peaks per second was delivered to this target in an attempt at eliciting an appropriate motor response. This usually consisted of opening and closing movements of the mandible as in mastication. Once this motor response was elicited the electrode was then withdrawn from the brain and the electrode carrier moved .5 mm laterally. Upon stimulation at this coordinate a weak motor response was usually elicited. The electrode was again withdrawn and reintroduced at an additional .5 mm distance lateral to that previously used, that is, at coordinates AP 0.0, L 3.5 to 4.0 and H -4.0. Upon stimulation at this point no motor response was evident in which case a lesion was placed at this point using a current of 3 milliamps for 30 seconds.

In order to insure a lesion of sufficient size the electrode was then withdrawn and reintroduced at a level .5 mm posterior to the original lesion. At these coordinates, that is, at P 0.5, L 4.0 and H -3.0, a second lesion was placed again using a current of 3 milliamps for 30 seconds.

After the appropriate lesions were made, the electrode was withdrawn and the area of the burr hole washed with sterile saline solution and then the original incision site sutured to close the wound. The wound was then covered with a 5% celloidin solution to protect the sutures and prevent the animal from disturbing them.

Post-operatively the animals were observed to note any neurological deficits. A slight weakness in chewing movements on the side of the lesion was the most consistently observable post-operative deficit. Because prior dietary measures were taken to insure elevated levels of vitamin C to aid in wound healing and resistance to surgical stress, no post-operative administration of antibiotics or vitamins was carried out. This routine culminated in no loss of life to any of the monkeys used in this study due to operative complications.

After a survival period of from 11 to 14 days the animals were anesthetized and sacrificed by perfusion-fixation utilizing the vascular tree. The ascending aorta was cannulated through an incision made in the left ventricle and the physiological approach to perfusion-fixation by Koenig, Groat and Windle (1945) was employed.

Immediately after perfusion-fixation, the calvaria was removed and the dura incised over the hemispheres. The brains were stored in 10% formalin-NaCl for 24 hours. They were then completely dissected and placed in fresh 10% formalin-NaCl for an additional 48 hours.

To insure complete fixation the brains were then placed in fresh 10% formalin-NaCl for an additional four week period. After this time the brains were blocked at coordinates A 12.0, P 5.0 and L 10.0 leaving the thalamus and brain stem intact as well as overlying cortical areas. After blocking, the brains were placed in 30% sucrose in 10% formalin-NaCl for one week. Upon removal from this formalin-sucrose solution, the brains were frozen with crushed dry ice and sectioned serially in a plane transverse to the brain stem and diecephalon. The sections were cut at 30 microns and stored in a 2% formalin solution until staining.

The Fink-Heimer (1967) silver method for impregnation of degenerating nerve fibers and their synaptic endings in the central nervous system has become widely accepted in experimental neuroanatomy. In order to impregnate degenerating axons and axon terminals in the central nervous system of the monkey, Wiitanen (1969) has suggested adjusting the Fink-Heimer II schedule by changing the staining times as well as the concentrations of several solutions. A slight modification of Wiitanen's (1969) modification was used in this study on the squirrel monkey.

Every other section was impregnated using the above procedure. The extent and location of the lesion were verified histologically and compared to similar levels of the squirrel monkey brain stem cut in the same plane and stained with the thionin method.

The impregnated sections were examined microscopically and the lesion and zones of degeneration plotted onto drawings made of the appropriate levels of the nervous system. The drawings of the brain stem and the diencephalon were prepared by projecting the impregnated sections with a Bausch and Lomb Trisimplex projection apparatus. Line drawings were then made and the degeneration present was entered in the drawings and pertinent finer detail added upon microscopic examination. The degenerated fiber patterns resulting from the lesions were traced by microscopic examination of these serial sections. Using these drawings as a convenient reference point, photomicrographs were then prepared to document precise lesion levels and demonstrate the resulting degeneration. A Leitz Orthoplan research microscope with an Orthomat W microscope camera was used to make these photomicrographs. The film used was Kodak photomicrography monochrome film SO-410.

The terminology and the abbreviations used here in labeling the nuclei and fiber systems of the brain stem and thalamus are those of Emmers and Akert (1969).

Although some would argue that degenerating end structures cannot be identified with certainty using the light microscope, the present author assumes responsibility for his own interpretation of what constitutes terminal arborization as it appears in the available material.

RESULTS

Pertinent protocol concerning operative procedures as well as the results of stimulations will be given for each animal used in this study. In addition, the post-operative observations will be reported as will be a description of the lesion and a description of the resulting degeneration from these lesions.

Monkey #700 (Mich)

Protocol. 2-10-72. Under Ketamine anesthesia and sterile conditions an incision was made just lateral to the midline on the left side at coordinates AP 0.0 and a burr hole 5 mm in diameter was placed at that point. An electrode was introduced at coordinates AP 0.0, L 3.5 to a depth of H -3.5. Upon stimulation using a current of 2.5 volts at 40 peaks per second (pps), the animal's mouth was observed to close. After moving the electrode laterally .5 mm, the same stimulus yielded a slight movement of the jaw. Further lateral movement of .5 mm led to no movement upon stimulation. A lesion was made at these coordinates: AP 0.0, L 4.5 and H -3.5. A current of 3 milliamps (ma) for 30 seconds was used to make the lesion. The electrode was then moved posteriorly .5 mm and a second lesion made after stimulation showed no movement. The coordinates for the second lesion were P 0.5, L 4.5 and H -3.0 and again the current used was 3 ma for 30 seconds.

Post-operative observations. The animal showed no apparent effects of the surgical procedure and/or the lesion.

Protocol. 3-2-72. A second operation was performed on squirrel monkey #700 on this date. Using sterile techniques and Ketamine anesthesia, a similar operation was performed on the right side. A burr hole was placed on the right side at coordinates AP 0.0 and L 3.5. The electrode was advanced to these coordinates and lowered to a depth of H -3.5. Upon electrical stimulation at this point, using a current of 1.75 volts at 40 pps, a jaw movement was observed. The electrode was then removed and lowered into the brain stem at coordinates A 3.0, L 1.5 and H +3.0. Stimulation at this point yielded weak elevation of the mandible. These coordinates approximate upper midbrain levels at which some cells of the mesencephalic nucleus of V are known to be present. Moving the electrode back to coordinates AP 0.0, L 3.5 and down to a depth of H -3.0, a jaw movement was obtained upon stimulation. The electrode tip was thought to be in the motor nucleus of V at this point. The electrode was then removed and reinserted at coordinates AP 0.0, L 2.5 and H -2.5. These coordinates were considered to be halfway between the motor nucleus of V and the locus caeruleus such that the fibers of the mesencephalic root of V would be involved in the lesion. Upon stimulation at these coordinates a weak elevation of the mandible was noted. A lesion was then placed at this point using a current of 3 ma for 30 seconds. The electrode was then raised .5 mm and a second lesion made at coordinates AP 0.0, L 2.5 and H -2.0 using the same strength of current as before.

Post-operative observations. Although the animal showed no effects of the first operation, there seemed to be some evidence of difficulty in chewing after the second operation. However, this weakness was in no way debilitating to the animal. He was able to eat as he had prior to the operation. Examination of this squirrel monkey one week post-operatively showed the jaw muscles to be equal in strength and movements. Eleven days after the second operation the animal was sacrificed under Ketamine anesthesia by perfusion-fixation through the left ventricle as described in the Materials and Methods.

Description of the lesion. No evidence could be found of a lesion on the left side of the brain stem as a result of the first operation on 2-10-72. This was attributed to technical difficulties in the use of the electrical apparatus.

A distinct lesion was found on the right side of the brain stem as a result of the second operation. The location of the lesion is indicated in figure 1. The lesion lies dorsomedial to the chief sensory nucleus of V and the motor nucleus of V and appears to involve fibers which have passed between these two nuclei and toward the ventrolateral border of the periventricular gray. Thus the mesencephalic root of V is primarily involved in the lesion.

Description of the resulting degeneration. One of the most conspicuous features of the degeneration which resulted from a lesion of the mesencephalic root of V in this case was the degeneration of some of these root fibers into the chief sensory nucleus of V on the same side as the lesion. This can be seen in figure 2 which shows the most rostral portion of the chief sensory nucleus of V of squirrel monkey #700.

A few degenerated fibers of the mesencephalic root of V were observed in the decussation of the velum at inferior collicular levels of the midbrain. These fibers can be seen in figure 3. Although only a small number of degenerated root fibers could be seen decussating at this level, a few of these fibers could be traced into the contralateral motor nucleus of V.

As a result of section of the mesencephalic root of V in monkey #700 at pontine levels, some degeneration was noted in the mesencephalic root of V at superior collicular levels of the midbrain. Degeneration is evident in the mesencephalic nucleus of V in figure 4 from animal #700. In particular, the cells situated dorsolaterally or the intermediate group are affected. It is suggested that these cells of the intermediate group are related to the trigeminal nerve.

In addition to the degeneration already described, it was possible in this animal to trace some degenerating fibers into the cerebellum. These fibers entered the cerebellum via the juxtarestiform body. It was not possible to determine the precise termination in the cerebellum of these degenerating fibers.

Monkey #710 (Mike)

Protocol. 5-11-72. After the animal was anesthetized with Ketamine and draped using sterile techniques, a 5 mm burr hole was placed on the left side at coordinates AP 0.0 and L 3.5. The electrode was then introduced at this level and lowered to H -3.5. Electrical stimulation using a current of 1.75 volts at 40 pps yielded a positive response of jaw movement. When the electrode was raised .5 mm the same response was observed upon stimulation. The electrode was moved laterally 1.0 mm and a lesion placed at coordinates AP 0.0, L 4.0 and H -3.0 using a current of 3 ma for 60 seconds.

Post-operative observations. This animal did not show any neurological effects of the operation. Fourteen days after the operation the animal was prepared for perfusion-fixation and sacrificed under Ketamine anesthesia. Because the Marchi method was to be used in this case the animal was perfused with a 5% solution of magnesium sulfate combined with a 3% solution of potassium dichromate.

Description of the lesion. Both the position of the lesion and the quality of the staining in this animal were very poor. The lesion was located in the most lateral edge of the middle cerebellar peduncle and in no way involved any of the components of the trigeminal complex. For that reason no further description of the lesion or the resulting degeneration will be given.

Monkey #720 (Max)

Protocol. 5-11-72. A burr hole 5 mm in diameter was made on the left side in this animal after Ketamine anesthesia and under sterile conditions. At the time of the operation the skull was noted to be somewhat irregular along the sagittal suture. Because of this it was decided that some sort of correction should be attempted to compensate for this irregularity in the skull. For this reason the burr hole was made at coordinates AP 0.0 and L 6.5. On the basis of stimulation of the motor nucleus of V, corrected coordinates were made for what was thought to be the location of the chief sensory nucleus of V. A lesion was then placed at coordinates AP 0.0, L 6.5 and H -3.0 using a current of 3 ma for 60 seconds. The electrode was moved anteriorly and a second lesion was made at coordinates A 0.5, L 6.5 and H -3.0. The same current was used as before to make the lesion.

Post-operative observations. The day following the operation some difficulty in chewing was noted in this animal. The difficulty persisted up until the day on which the animal was sacrificed. On 5-22-72 the animal was prepared for perfusion-fixation. On that day the animal looked very skinny and was somewhat weak. It is not known whether the animal began to lose weight prior to the operation or as a direct result of the surgical procedure.

Description of the lesion. In spite of attempts to compensate for irregularities in the alignment of the calvaria in this animal the lesion which resulted involved only the motor nucleus of V on the left side as shown in figure 5. A partial unilateral destruction of this nuclear group with sparing of the chief sensory nucleus of V and incoming fibers of the trigeminal nerve was the end result of our efforts.

Description of the resulting degeneration. The degeneration which resulted from partial unilateral destruction of the motor nucleus of V can be seen in figure 6. This figure shows the degenerated commissural fibers which pass between both motor nuclei of V. This finding may afford some evidence of the existence of a few crossed as well as many uncrossed fascicles in each motor root of V.

Monkey #730 (Pat)

Protocol. 6-2-72. As had been our practice in the past, Ketamine anesthesia was used and sterile techniques employed in this the fifth operation of the series. A burr hole 5 mm in diameter was made on the left side at coordinates overlying the motor nucleus of V. The coordinates for the motor nucleus of V were determined and at coordinates AP 0.0, L 3.5 and H -3.5 the electrode was inserted. Jaw movement was observed upon stimulation at this point using a current of 1.75 volts at 40 pps. The electrode was then removed and advanced laterally in .5 mm increments and stimulation was carried out to attempt to more precisely locate the lateral limit of the motor nucleus of V. A current of 3 ma for 30 seconds was used to make a lesion at coordinates AP 0.0, L 5.5 and H -3.0. These coordinates were thought to approximate the location of the chief sensory nucleus of V. A second lesion was made after the electrode was moved posteriorly .5 mm to coordinates P 0.5, L 5.5 and H -3.0.

Post-operative observations. Three days after the operation the animal exhibited signs of some chewing difficulty. This was thought at the time to be not so much a motor weakness, as was observed in monkey #720, but rather a problem in reflex chewing. The animal was anesthetized and sacrificed by perfusion-fixation fourteen days after the operation.

Description of the lesion. The lesion in this squirrel monkey involved the chief sensory nucleus of V on the left side as well as the rostral pole of the subnucleus rostralis and the rostral portion of the spinal tract of V. Numerous sections throughout all levels of the brain stem of this animal were stained to show the lesion. These sections were then carefully studied. It was not possible to find the typical appearance of the previous lesions. That is, it was not possible to demonstrate the site of the lesion in the brain stem due to the electrical current used. Figures 7 and 8, however, show the resulting degeneration at levels through the rostral pole of the subnucleus rostralis and the spinal tract of V and through the chief sensory nucleus of V. Clearly there is degeneration present which gives some indication as to the location of the lesion. No explanation can be given by the author as to the reasons why a lesion as found in previous cases could not be found in this animal also.

Description of the resulting degeneration. Degeneration was present in the rostral pole of the subnucleus rostralis, the chief sensory nucleus of V and the upper portion of the spinal tract of V as shown in figures 7 and 8. However, above the level of the chief sensory nucleus of V no degeneration could be observed in any of the secondary ascending trigeminal paths. This failure to observe distinct degeneration above the level of the chief sensory nucleus of V could be attributed to several features of the staining technique. Throughout this study it was observed that the degeneration varies greatly in its time course and that all axons do not go through the same sequence of degenerative changes. Knowledge of the rates at which nerve fibers degenerate is of particular interest in choosing the best survival period for staining degenerating fibers in a particular tract. This animal was allowed to survive fourteen days for degeneration to occur. Since this time should have been sufficient, some other source of error was considered. Suppression times in the potassium permanganate treatment during the staining procedure have an important role in determining which fibers will impregnate. A final possible source of error may have been the location of the lesion. As has been pointed out, no lesion as such was found within the brain stem in this animal although degeneration was seen in the nucleus of the spinal tract of V and the chief sensory nucleus. It thus seems likely that the lesion may have involved the main sensory root of V at its entrance to the pons. Unfortunately the sensory root of V was transected at the pons in removing the brain from the skull.

Monkey #740 (Prancer)

Protocol. 12-19-72. This animal was anesthetized using a 30 mg/kg dose of Ketamine and was then placed in the stereotaxic apparatus. Sterile techniques were used throughout the entire procedure. A burr hole of 5 mm diameter was then placed on the left side at coordinates AP 0.0 and L 3.5. A bipolar electrode was then inserted into the brain at these coordinates at a depth of H -3.5 and a current of 1.75 volts at 40 pps was used for stimulation. A motor response was observed which consisted of movement of the mandible such as that which accompanies the act of chewing. The electrode was then moved laterally and raised .5 mm and a lesion placed at coordinates AP 0.0, L 4.0 and H -3.0 using a current of 3 ma for 60 seconds. The electrode was then withdrawn and reintroduced at coordinates slightly anterior to those described previously, that is, at coordinates A 0.5, L 4.0 and H -3.0. Stimulation at this point yielded no response and a second lesion was then made using a current of 3 ma for 30 seconds.

Post-operative observations. The most conspicuous observation post-operatively was a great tendency of the animal to fall backward and to be severely unbalanced. It was thought initially that this was due to swelling in and around the vestibular nuclei. The notion was also entertained at that time that the vestibulocerebellar fibers may have been involved in the lesion. The following day the animal was more alert but continued to be unbalanced with some involuntary movements of the right upper limb and some nystagmus. On the same day (12-21-72) the animal began to exhibit signs of respiratory difficulty with respiratory retractions observed to be present. Antibiotic therapy was immediately instituted due to the animal's deteriorating respiratory condition. It was felt that aspiration of food had occurred and that possibly pneumonia had developed. Although the animal improved considerably over the next twenty-four hours and began to show normal respirations, he expired rather unexpectedly the evening of 12-23-72.

Because the animal lived only four days after the operation it was determined that sufficient degeneration had not occurred in the fiber system under study. This animal was considered to be unsuitable for further study using silver methods for the impregnation of degenerating axons.

Post-operative examination of the brain of monkey #740 revealed that death was due to a very prominent intraventricular hemorrhage.

Monkey #750 (Rudolph)

Protocol. 12-19-72. Ketamine anesthesia was employed in this the seventh operation in the series. Under sterile conditions a burr hole .5 mm in diameter was placed on the left side at coordinates AP 0.0 and L 3.5. The electrode was then lowered to a depth of H -3.5 and stimulation at this point carried out. Using a current of 4.0 volts at 40 pps a slight jaw movement was observed with involvement of the lower lip. The electrode was then removed and inserted at coordinates AP 0.0, L 4.0 and H -3.0. No movement was obtained upon stimulation at this point. A lesion was then placed at these coordinates using a current of 3 ma for 60 seconds. The animal squealed during the entire time that the current for the lesion was turned on. No explanation can be given for this occurrence. The electrode was then moved to coordinates P 0.5, L 4.0 and H -3.0 and a lesion made at this point using a current of 3 ma for 60 seconds. It was noted that the current flow was extremely variable at the time the second lesion was being made.

Post-operative observations. Although the animal showed some problem maintaining his balance, the day following the operation he soon regained his normal state of balance and seemed to be entirely normal and quite active. Two weeks after the operation the animal was sacrificed using the method of perfusion-fixation under Ketamine anesthesia. The perfusion went very well with some 600-700 milliliters of perfusion fluid being used.

Description of the lesion. The lesion was confined to the chief sensory nucleus of V on the left side with some involvement of the rostral tip of the motor nucleus of V. The precise level of the lesion and its involvement of the structures mentioned can be seen in figure 9.

Description of the resulting degeneration. As shown in monkey #700, degeneration could be observed in this animal to enter the cerebellum via the juxtarestiform body. It was not possible to determine the precise termination of this degeneration in the cerebellar nuclei.

A very conspicuous group of degenerating fibers was found in this animal to pass from the side of the lesion to the position occupied by the ventral secondary ascending tract of V on the contralateral side. Degeneration in the ventral secondary ascending tract of V is shown in figure 10. The degenerated path lies just dorsal to the medial lemniscus.

Some degenerating fibers are seen in figure 11 passing from the region just rostral to the tip of the chief sensory nucleus of V and crossing the midline. These fibers are seen crossing beneath the medial longitudinal fasciculi to take up a position on the contralateral side as a rather indistinct bundle medial to the brachium conjunctivum and ventrolateral to the mesencephalic root of V.

In sections through the inferior collicular level of the midbrain, as shown in figure 12, degeneration is seen bilaterally in the deep tegmental gray. This degeneration represents the dorsal secondary ascending tract of V and is more prominent on the right side.

Figure 13 shows the dorsal tract of V in monkey #750 as it appears at the superior collicular level of the midbrain. This path is seen just dorsal to the red nucleus.

The uncrossed bundle of the dorsal secondary ascending tract of V could be traced to thalamic levels where it terminated in the ventral posteromedial nucleus of the thalamus as shown in figure 14. The crossed component of the dorsal tract of V in monkey #750 became difficult to trace as thalamic levels were approached. It is not possible to determine the termination of the crossed bundle in figure 14.

Monkey #760 (Dancer)

Protocol. 3-7-73. This was the eighth operation in this series. Using sterile techniques and under Ketamine anesthesia, a burr hole 5 mm in diameter was made in the calvaria at coordinates AP 0.0 and L 3.0. The electrode was inserted in the brain at these coordinates and lowered to a level of H -3.5. A stimulus of 0.6 volts resulted in a jaw closure movement. The electrode was then moved posteriorly 0.5 mm and a stimulus of 0.6 volts applied at coordinates P 0.5, L 4.0 and H -3.0. No jaw movement was observed at this level upon stimulation so a lesion was made at this point using a current of 3 ma for 30 seconds.

Post-operative observations. The animal looked quite active the day following the operation. He remained active for the next two weeks and appeared essentially normal. Perfusion-fixation was used on the fourteenth day following the operation as a means of sacrificing the animal. The animal had been anesthetized with Ketamine prior to perfusion.

Description of the lesion. The lesion which resulted from this procedure is shown in figure 15. The lesion is dorsal to the motor nucleus of V and involves the medial aspect of the chief sensory nucleus of V. Fibers leaving this nuclear mass and passing toward its medial side would certainly be involved in such a lesion.

Description of the resulting degeneration. The degeneration which resulted from the lesion shown in figure 15 is very similar to that observed in monkey #750 although it is not as extensive. In figure 16 degenerated fibers which are leaving the rostral tip of the chief sensory nucleus of V on the side of the lesion can be seen crossing the midline. These degenerated fibers then take up a position ventrolateral to the mesencephalic root of V and remain medial to the brachium conjunctivum. The relationship of the crossed dorsal tract of V to the structures mentioned is shown in figure 16.

As inferior collicular levels of the midbrain are approached, degeneration was observed bilaterally deep in the tegmental gray. The uncrossed component of the dorsal tract of V is more conspicuous than its partner as shown in figure 17.

Upon reaching the rostral levels of the midbrain, the dorsal tract of V is found closely related to the red nucleus. In particular, as shown in figure 18, the dorsal tract of V is found dorsolateral to the red nucleus at the superior collicular level of the midbrain. Again the uncrossed degenerated path is more apparent than the crossed component.

At the level of the thalamus the degeneration which resulted from the lesion placed in animal #760 could be traced to its apparent point of termination in the nucleus ventralis posteromedialis. It was very difficult to determine the precise point of termination of the crossed degenerated fibers. Figure 19 shows a transverse section through the thalamus of monkey #760 showing the nuclear region in which the degenerated dorsal tract of V terminated.

DISCUSSION

The nuclear groups and fiber connections of the trigeminal complex in vertebrates including primates and man have been considered frequently in the literature. The present discussion is an attempt to correlate the findings in this study with those of other investigators. In particular, attention is paid to the relationships of the chief sensory nucleus and its fiber connections.

Anatomically the trigeminal complex consists of its peripheral branches, a large trigeminal ganglion, a motor, a sensory and an intermediate root, the spinal tract of V and its nucleus (with three subdivisions), the motor and the chief sensory nuclei of V and the mesencephalic nucleus of V with its associated mesencephalic root. From the trigeminal sensory nuclei impulses are relayed to higher centers over secondary ascending tracts which also constitute part of the trigeminal complex.

The peripheral branches of the trigeminal nerve either carry afferent impulses of an exteroceptive or a proprioceptive nature to the central nervous system or provide a means for efferent impulses to reach the muscles of mastication. Sensory information of a proprioceptive nature comes into the central nervous system with these motor fibers in the squirrel monkey as it does in many other mammals and in other primates including man.

The distribution of the sensory fibers of the trigeminal nerve in man was described by Bolk (1898-1900). From the definitive course, the relations, the branches and the communications of the trigeminal nerve in the baboon, Gasser and Wise (1972) concluded that the trigeminal nerve in this primate has many similarities to that of man.

The cells of origin for fibers carrying exteroceptive impulses to the central nervous system reside in the Gasserian or semilunar ganglion. The central processes of these cells pass toward the pons forming the rather large sensory root of V or portio major. The motor fibers which travel in the mandibular division of V form a distinct motor root of V or portio minor from the ganglion to the pons. In addition to these motor and sensory roots, the present investigator (Augustine, Vidić and Young, 1971), in a previous study, described an intermediate root of the trigeminal nerve in the dog thus confirming the results of Jannetta and Rand (1966), who identified five or more accessory fibers in man between the major sensory and motor roots.

From the trigeminal ganglion to the pons a significant shift occurs in the relations of the trigeminal branches. The ophthalmic portion, which peripherally maintains a somewhat dorsal and superior position, enters the central nervous system at the midpons and takes up a ventral position in the spinal tract of V. This ventral relationship of the ophthalmic branch of the trigeminal nerve in man was shown by van Valkenberg (1911). The practical application of this information would reside with the neurosurgeon in performing trigeminal rhizotomies or trigeminal tractotomies on human patients. In this regard a knowledge and an understanding of the relations of the trigeminal branches along their entire course would be advantageous.

The position and appearance of the motor nucleus of V in the squirrel monkey are essentially similar to those relations and characteristics in most mammalian forms and will not be described here. However, reference to the motor nucleus of V has been made repeatedly during the experimental procedures because of its use as a landmark in approaching the chief sensory nucleus. Electrical stimulation of the motor nucleus of V was carried out after the coordinates for the nucleus had been determined by using the stereotaxic atlas of the squirrel monkey brain by Emmers and Akert (1963). Proper stimulation of this motor nucleus yielded obvious movements of a chewing nature. Since the chief sensory nucleus of V in the squirrel monkey is dorsolateral to the motor nucleus, it was then necessary to move the electrode laterally beyond the root fibers of V to locate the chief sensory nucleus. Electrical stimulation of the chief sensory nucleus of V led to no observable changes. The motor nucleus of V was thus an excellent landmark for the location of the chief sensory nucleus.

The pattern on the motor nucleus of V obtained by study of the responses of individual muscles of mastication to stimulation of specific portions of this nuclear mass as shown in the cat by

Szentágothai (1949) has not been studied in the present paper. However, it is interesting that partial unilateral destruction of this nucleus produced some difficulty in chewing bilaterally. Possibly this was due to the interruption of commissural fibers between the motor V nuclei of the two sides. This finding may afford some evidence of the existence of a few crossed as well as many uncrossed fascicles in each motor root of V, a condition existing in some animals according to Ariëns Kappers, Huber and Crosby (1936) and possibly in man according to Villiger (1925).

Three types of sensory neurons have been described for the semilunar or trigeminal ganglion. Large sensory neurons with much coiled glomeruli and heavily myelinated axons send their axons into the central nervous system to terminate only in the chief sensory nucleus of V as described by Windle (1926). These non-bifurcating fibers are believed to mediate the most discriminatory types of sensibility such as two-point tactile sensibility from special regions of the face. A second type of sensory neuron in the trigeminal ganglion, somewhat smaller than the previously described type, also has myelinated axons although they are less heavily myelinated than those just described. The fibers of the second type bifurcate after entering the brain and one branch of each axon enters the chief sensory nucleus of V and the other descends in the spinal tract of V. This second type of neuron carries a wide range of impulses set up in tactile endings other than the most highly discriminatory type. Darian-Smith, Proctor and Ryan (1963) have reported that these fibers are involved in the more general types of tactile sensibility such as moving of a hair and light mechanical stimulation.

It can thus be seen that the chief sensory nucleus of V receives impulses from specialized tactile receptors including those which permit the distinction of two points closely situated as well as those receiving impulses from other specialized tactile endings. Possibly the chief sensory nucleus of V or the more rostral subdivision of the nucleus of the spinal tract of V, or both nuclear groups, receive impulses activated from the specialized temperature receptors. However, evidence for such termination is as yet lacking. The remainder of the tactile projection, as well as impulses set up by pain and temperature stimuli, are projected to the nucleus of the spinal tract of V as pointed out by Crosby and Yoss (1954), Humphrey (1969) and many others. A discussion of these fibers and their functional nature is outside the special interests of this paper and will not be considered further at this time.

The chief sensory nucleus of V in the squirrel monkey lies lateral to the motor nucleus of V, separated from it by root fibers of the trigeminal nerve. This nucleus forms the scoop of an ice cream cone-shaped structure with the nucleus of the spinal tract of V or the descending root of V forming the cone portion. The further connections of the chief sensory nucleus, as demonstrated in the available material, will be considered immediately, beginning with those of proprioceptive function.

Since the time of May and Horsley (1910) the proprioceptive component of the peripheral roots of V has been known to accompany the motor root of V in the cat and in the monkey. McIntyre and Robinson (1959) have documented like relations for man. In addition to the motor nucleus of V and the nuclei of reception of the exteroceptive types of sensory impulses, the trigeminal complex has cells of origin for its proprioceptive component. These cells of origin are in the brain stem and are referred to as the nucleus of the mesencephalic root of V. Johnston (1909) was one of the first to describe the cells of this nucleus in normal material of the mammalian brain and of that of the human embryo. The presence of cells of the mesencephalic nucleus at various levels of the brain stem from midpons to superior collicular levels as noted by Johnston (1909), Weinberg (1928), Corbin and Harrison (1940), Crosby and Yoss (1954) and many others was also observed in the available squirrel monkey material. This relationship is illustrated although not described in the Emmers and Akert (1963) atlas, picturing sections of the brain of the squirrel monkey. The nucleus extends forward from the levels of entrance of the trigeminal roots at midpons levels. It remains close to the outer border of the periventricular and periaqueductal gray to levels approaching the posterior commissure. In the squirrel monkey, as in many other forms, the mesencephalic nucleus of V is not evenly distributed. There is a collection of its cells at, and just rostral to, the entrance of the trigeminal roots, where it is somewhat intermingled with the locus caeruleus.

The cells of the mesencephalic nucleus of V are differentiable from the locus caeruleus because of neurons of the unipolar ganglion type associated with the mesencephalic root as compared with the smaller, multipolar and pigmented cells of the locus caeruleus. A second condensation of cells of the mesencephalic nucleus of V occurs near the decussation of the trochlear root. These cells are quite probably associated with proprioceptive functions of the trochlear nerve. At inferior collicular levels in the squirrel monkey a few scattered cells of the mesencephalic nucleus of V can be seen in the chief nucleus of this collicular area. The chief nucleus of the inferior colliculus is a derivative of the periventricular gray as noted by Huber and Crosby (1943). Superior collicular levels in the squirrel monkey show the typical midline, intermediate or dorsolateral and scattered ventral grouping of the cells of the mesencephalic nucleus of V characteristic of mammalian and some submammalian forms as noted by Weinberg (1928) and others. All of these cell groups are interconnected by scattered cells of this mesencephalic nucleus.

From the various neurons of the mesencephalic nucleus most of its root fibers, often intermingled with its cells, extend backward along the edge of the periaqueductal and periventricular gray. The fibers join the root fibers of the trigeminal nerve and emerge as a component of the nerve. Some of the cells of the mesencephalic nucleus of V are believed to contribute proprioceptive components to various other cranial nerves.

Although the cells of the mesencephalic root of V located very near to or within the oculomotor nucleus in some mammals, as noted by Weinberg (1928), quite probably provide a proprioceptive component for the oculomotor nerve, the present findings suggest that the more dorsolaterally situated or intermediate group at superior collicular levels are a trigeminal nerve component. This is indicated in figure 4 of the mesencephalic root of V at trigeminal levels in monkey #700, in which the degeneration is evident. That the cells of the intermediate group are related to the trigeminal nerve was also indicated when this dorsolaterally situated cell group of the mesencephalic nucleus was stimulated. In monkey #700 an attempt was made to destroy stereotaxically cells of the mesencephalic root of V rostral to the motor and sensory trigeminal nuclei. As a part of this experiment the electrode was introduced into the region occupied by the cells and fibers of the mesencephalic nucleus of V located at tectal levels. Stimulation of these midbrain mesencephalic fibers and cells of V yielded movements of the mandible which suggested that in the squirrel monkey, the most dorsolateral cells of the mesencephalic nucleus of V are located at the level of the oculomotor nucleus project to the motor nucleus of V. They fire the motor V nucleus as indicated by the jaw movement.

Our findings in the squirrel monkey agree with that of Jerge (1963) who used microelectrode recording methods to localize muscle spindle afferents from the masseter, the temporalis and the medial pterygoid muscles throughout the rostrocaudal extent of the pterygoid muscles throughout the rostrocaudal extent of the mesencephalic nucleus of V. There was no pattern apparent to Jerge (1963) in either the rostrocaudal extent or the dorsoventral direction. Using large electrodes, Corbin and Harrison (1940) had previously reported that in the cat the mesencephalic nucleus of V can be activated by proprioceptors distributed throughout its length. It seems apparent, then, that this mesencephalic nucleus of V in the squirrel monkey and in the cat is concerned with proprioceptive modalities of sensation set up by stimulation of appropriate sensory endings in the muscles of mastication.

A transverse section through the inferior collicular level of the midbrain from monkey #700 showed the generally accepted distribution of degenerated root fibers to the homolateral trigeminal root as noted by Ramón y Cajal (1909-1911) and Willems (1910). Moreover, as the mesencephalic root passed toward its emergence from the brain, a small number of degenerated root fibers was apparent which decussated at inferior collicular levels in the so-called decussation of the velum. These could be traced into the contralateral motor nucleus of V. Such crossed fibers are relatively few in number but they have been seen in this region in various other animals by Weinberg (1928) and are believed by Crosby, Humphrey and Lauer (1962) to be present in man. It is interesting that Smith, Marcarian and Niemer (1967) have recently reported that, in the cat and in the monkey, evoked potentials set up by passive opening of the mouth can be recorded simultaneously from the right and the left mesencephalic nuclei suggesting the existence of crossed as well as uncrossed fibers in the mesencephalic root. The existence of a few crossed and many uncrossed fibers of the mesencephalic root terminating in the motor nucleus of V accord very well with the idea that a few crossed as well as many nondecussating fibers constitute the motor root of V.

Fibers of the mesencephalic root of V also enter the chief sensory nucleus of V, particularly its more rostral portions, (including its smaller cells at the dorsorostral tip) in the squirrel monkey. The chief sensory nucleus of V is not only a region of termination for finer tactile but also for proprioceptive impulses relayed over the trigeminal nerve. It is then a major region of synapse for the projection of such impulses from face areas to higher centers. It should also be mentioned that short intrinsic or internuclear fibers were traced, in the normal material available of the squirrel monkey and in some of the material prepared following brain lesions involving the chief sensory nucleus, between this nucleus and the motor nucleus of V. Other fibers spread out through the reticular gray either to end there or pass to the contralateral motor nucleus of V.

Trigeminocerebellar fibers, sometimes called nucleocerebellar fibers, from the chief sensory nucleus of V and from the rostral end of the nucleus of the spinal tract of V were demonstrated in the present material where lesions were made in the sensory trigeminal nuclei. These nucleocerebellar fibers entered the cerebellum by way of the juxtarestiform body. This finding documents connections which have been described by many observers such as Weston (1936), Larsell (1936 and 1970), Woodburne (1936), Crosby and Yoss (1954), Humphrey (1969) and many others in submammalian and mammalian forms.

Trigeminocerebellar connections have been suggested by many authors since the early experimental work of Wallenberg (1904). He noted that in the dove some fibers of the mesencephalic root of V enter the cerebellum and presumably end in the medial cerebellar nucleus. These mesencephalo-cerebellar connections have been documented by other authors in mammals and in human fetal material by Pearson (1949) where they were followed into the area between the dentate and emboliform nuclei. Recent experimental work by Brodal and Saugstad (1965) failed to demonstrate the termination of mesencephalic fibers in the cerebellum. In squirrel monkey #700, in which the mesencephalic root of V was involved in the lesion, some degeneration was traced into the cerebellum but it was not possible to determine its precise termination.

Secondary trigeminal fibers, both crossed and uncrossed, from the nucleus of the spinal tract of V have been described by Crosby and Yoss (1954), Larsell (1970) and various other authors. Perhaps also cerebellotrigeminal paths are reocgnizable in the mammalian nervous system. However, there is some disagreement in the literature about the existence of these fibers. The present study has nothing to contribute to this matter at the present time.

Secondary ascending fibers from the chief sensory nucleus to higher centers in mammals have presented many problems to observers working on thalamic projections. A ventral secondary ascending tract of V to the thalamus with origin not only in the contralateral nucleus of the spinal tract of V but also in the chief sensory nucleus of V has been rather generally accepted. It has been described many times in various animals including the monkey by Walker (1938). In the present study the fascicles from the chief sensory nucleus of V and the rostral end of the nucleus of the spinal tract of V (which was included in some of the lesions) are easily demonstrated in the silver impregnated material and their course forward in close relation to the medial lemniscus is very evident.

The review of the literature in the present paper (pp. 4-33) gives ample evidence for the existence of an uncrossed dorsal secondary ascending tract of V. This has been shown in both experimental and anatomical studies. The Fink-Heimer stained material provided by this study documents very well the findings described by other observers. The presence of the dorsal tract of V is indicated in figures 11-14 and 16-19.

With regard to the existence of a crossed dorsal secondary ascending tract of V, there has been less general agreement (see Literature in this paper). Such a tract degenerated in the brain of the squirrel monkeys in which lesions were placed in the chief sensory nucleus of V. Following such a lesion and proper processing of the material by the Fink-Heimer method, fibers could be traced from the site of the injury across the midline and forward in a small but distinct bundle through the dorsal tegmental area of the pons and upper brain stem toward the thalamus. The crossed bundle is smaller than the uncrossed tract but clearly evident. Either the timing used in the Fink-Heimer preparation was not quite right or the bundle lost fibers in course since the termination in the medial part of the ventral posterior thalamic nucleus was meager in this material, although evident. As further evidence for the bilaterality of the projection from the chief sensory nucleus to the thalamus is the fact that the animals in this study with a unilateral lesion in the chief sensory nucleus of V showed no change in their behavior, no difference in response to stimulation of the lips or nose, and no modifications of jaw movements on the two sides of the face. This finding in the squirrel monkey correlates well with the common clinical finding that unilateral lesions of the brain stem which involve one dorsal secondary ascending tract of V do not result in a loss of finer tactile sensibility on either side of the face. However, bilateral lesions of the tract result in bilateral loss of such types of sensation.

It is interesting to speculate on certain likeness in function and relations between the projections of the chief sensory nucleus of V and those of the nucleus gracilis and nucleus cuneatus. The chief sensory nucleus of V is an area related to the reception of more discriminatory types of tactile and proprioceptive sensibility from the face; the nucleus gracilis and nucleus cuneatus serve similar functions for the discriminatory tactile and proprioceptive terminations on trunk and limbs. Both have crossed ascending connections to the thalamic nucleus ventralis posterior, with terminations corresponding to the parts of the body represented or to the face. An uncrossed ascending system is easily demonstrable from the smaller-celled rostral end of the chief sensory nucleus of V and evidence is gradually accumulating that a similar path is present, perhaps with synapse in reticular gray in course, in the smaller-celled rostral end of the nucleus gracilis and the nucleus cuneatus.

SUMMARY

From this experimental study of the relations and connections of the chief sensory nucleus in the brain of the squirrel monkey the following results were obtained:

1. Projection to the chief sensory nucleus of V from the cells of the mesencephalic nucleus of V has been established.

2. Internuclear connections between the chief sensory nucleus of V and the homolateral and contralateral motor nucleus of V and the pontine reticular gray were demonstrated.

3. Trigeminocerebellar projections through the juxtarestiform body were identified but not traced to their cerebellar termination.

4. Secondary ascending connections from the chief sensory nucleus of V and the rostral part of the nucleus of the spinal tract of V were traced across the midline into the ventral secondary ascending tract of V. The degenerated fibers of this bundle could be followed forward as an accompaniment of the medial lemniscus to the nucleus ventralis posteromedialis of the dorsal thalamus.

5. Crossed and uncrossed dorsal secondary ascending trigeminal tracts were identified and traced forward to the nucleus ventralis posteromedialis of the dorsal thalamus. The uncrossed bundle was the more conspicuous and more easily followed. The

crossed bundle became difficult to trace as thalamic levels were approached.

6. Attention has been called to certain likenesses in function between the chief sensory nucleus of V on the one hand and the nucleus gracilis and nucleus cuneatus on the other.

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ILLUSTRATIONS

LIST OF FIGURE ABBREVIATIONS

BC	Brachium conjunctivum
BP	Brachium pontis
CC	Corpus callosum
CI	Capsula interna
CeM	Nucleus centralis medialis thalami
CoI	Colliculus inferior
CoS	Colliculus superior
DBC	Decussatio brachii conjunctivi
FLM	Fasciculus longitudinalis medialis
LC	Locus caeruleus
LM	Lemniscus medialis
Mv	Nucleus motorius n. trigemini
Niii	Nucleus n. oculomotorii
Niv	Nucleus n. trochlearis
NMv	Nucleus tractus mesencephalici n. trigemini
NR	Nucleus ruber
NSv	Nucleus tractus spinalis n. trigemini
niii	Nervus oculomotorius
Py	Tractus pyramidalis
Pv	Nucleus principalis n. trigemini
PC	Pedunculus cerebri

List of Figure Abbreviations (continued)

TDv	Tractus dorsalis n. trigemini
TMv	Tractus mesencephalicus n. trigemini
TVv	Tractus ventralis n. trigemini
VPM	Nucleus ventralis posterior medialis
iv	Ventriculus quartus

PLATE 1

Figure 1. Photomicrograph of a transverse section through the middle third of the pons of monkey #700. Note the location of the lesion. Fink-Heimer preparation. X 10.

Figure 2. Photomicrograph of the rostral portion of the chief sensory nucleus of V of monkey #700. This is a higher power photomicrograph of the square outlined in figure 1. Note the degeneration of some of the mesencephalic root of V fibers into the chief sensory nucleus of V. Fink-Heimer preparation. X 100.

PLATE I

①

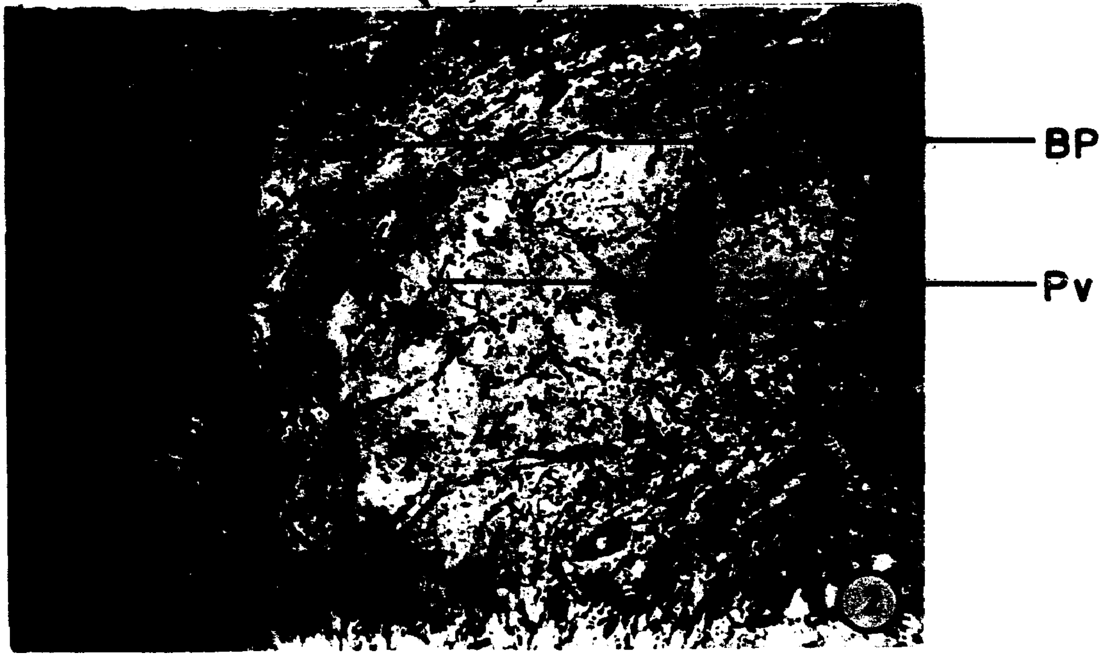

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PLATE 2

Figure 3. A. Photomicrograph of a transverse section through the inferior collicular level of the midbrain of monkey #700. Fink-Heimer preparation. X 10.

B. Photomicrograph of the area outlined in A. Note the presence of a few degenerated fibers of the mesencephalic root of V in the anterior medullary velum. Fink-Heimer preparation. X 40.

PLATE 2

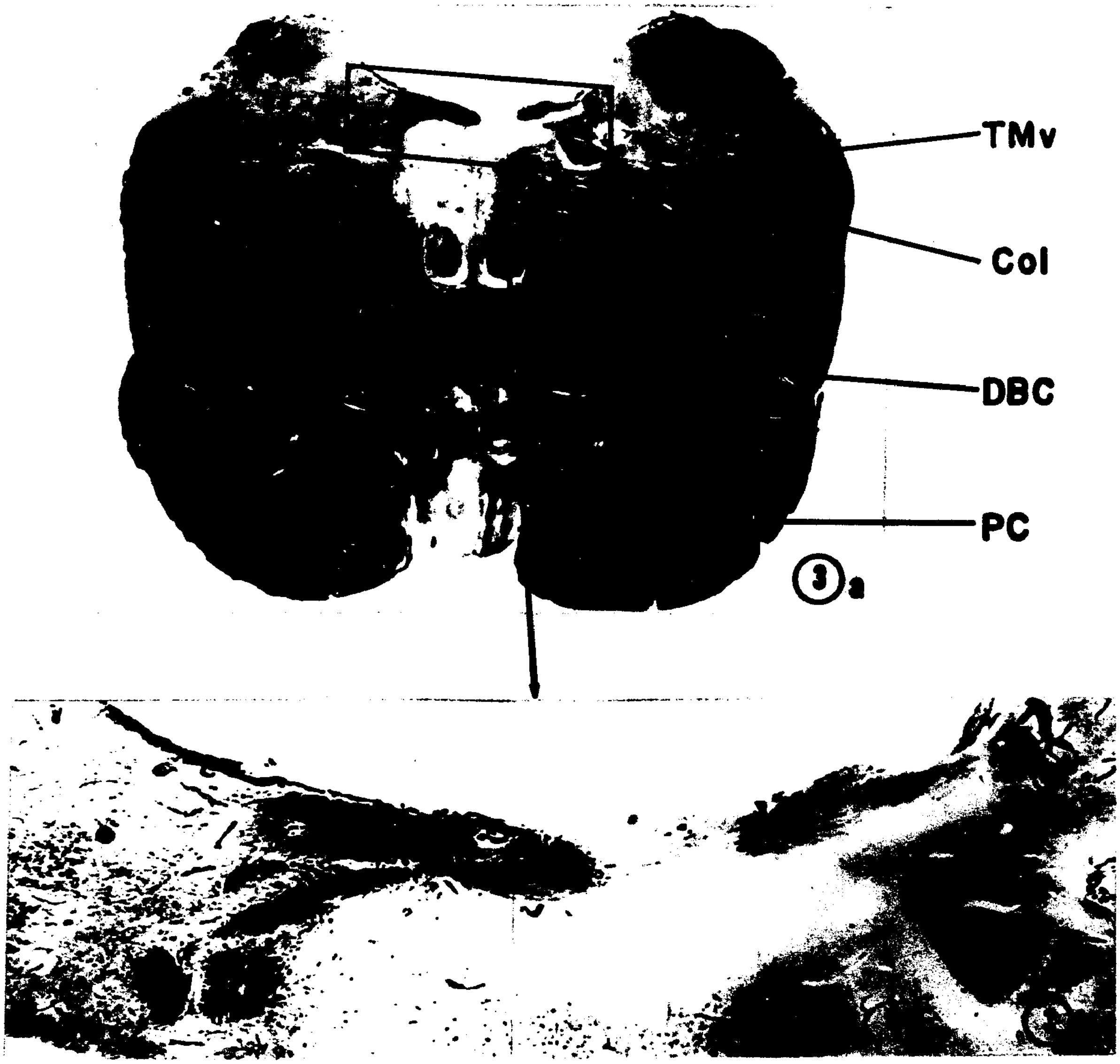

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PLATE 3

Figure 4. A. Photomicrograph of a transverse section through the superior collicular level of the midbrain of monkey #700. Fink-Heimer preparation. X 10.

B. Photomicrograph of the area outlined on the left in A. Note the normal appearance of the mesencephalic root of V and its associated nucleus. Fink-Heimer preparation. X 100.

C. Photomicrograph of the area outlined on the right in A. Note the complete absence of the dorsolaterally situated cells and the degeneration present in the mesencephalic root of V. Fink-Heimer preparation. X 100.

PLATE 3

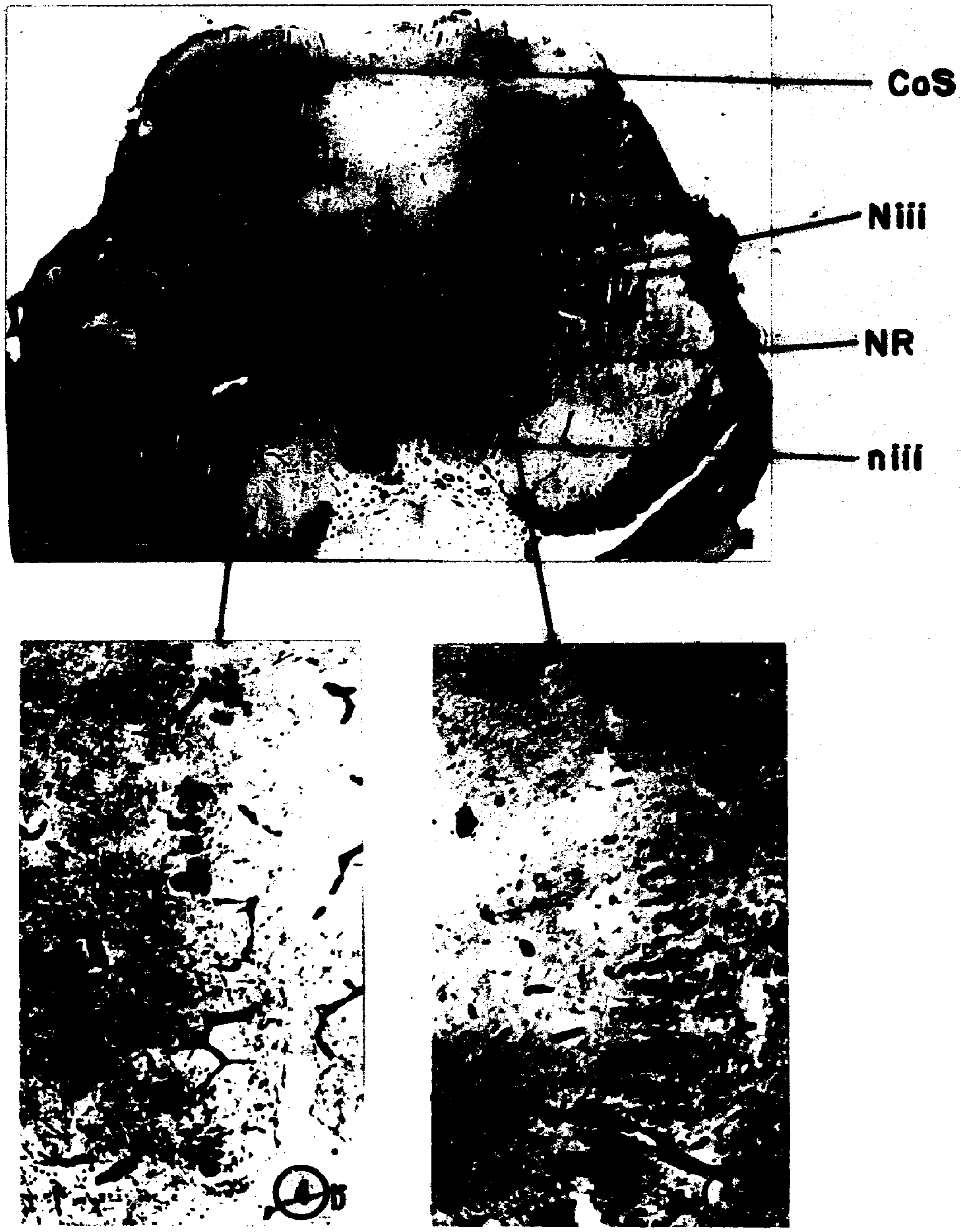

PLATE 4

Figure 5. Photomicrograph of a transverse section through the middle third of the pons of monkey #720. Note the location of the lesion involving almost the entire motor nucleus of V. Neither the chief sensory nucleus of V nor the incoming fibers of V are involved in the lesion. Thionin preparation. X 10.

Figure 6. Photomicrograph of a transverse section through the middle third of the pons of monkey #720. This is a higher power photomicrograph of the region corresponding to that outlined in figure 5. This section is 30 microns rostral to that in figure 5 and has been treated to show degenerated fibers. Note the degenerated fibers which have crossed the midline and are passing toward the motor nucleus of V contralateral to the lesion. Fink-Heimer preparation. X 40.

PLATE. 4

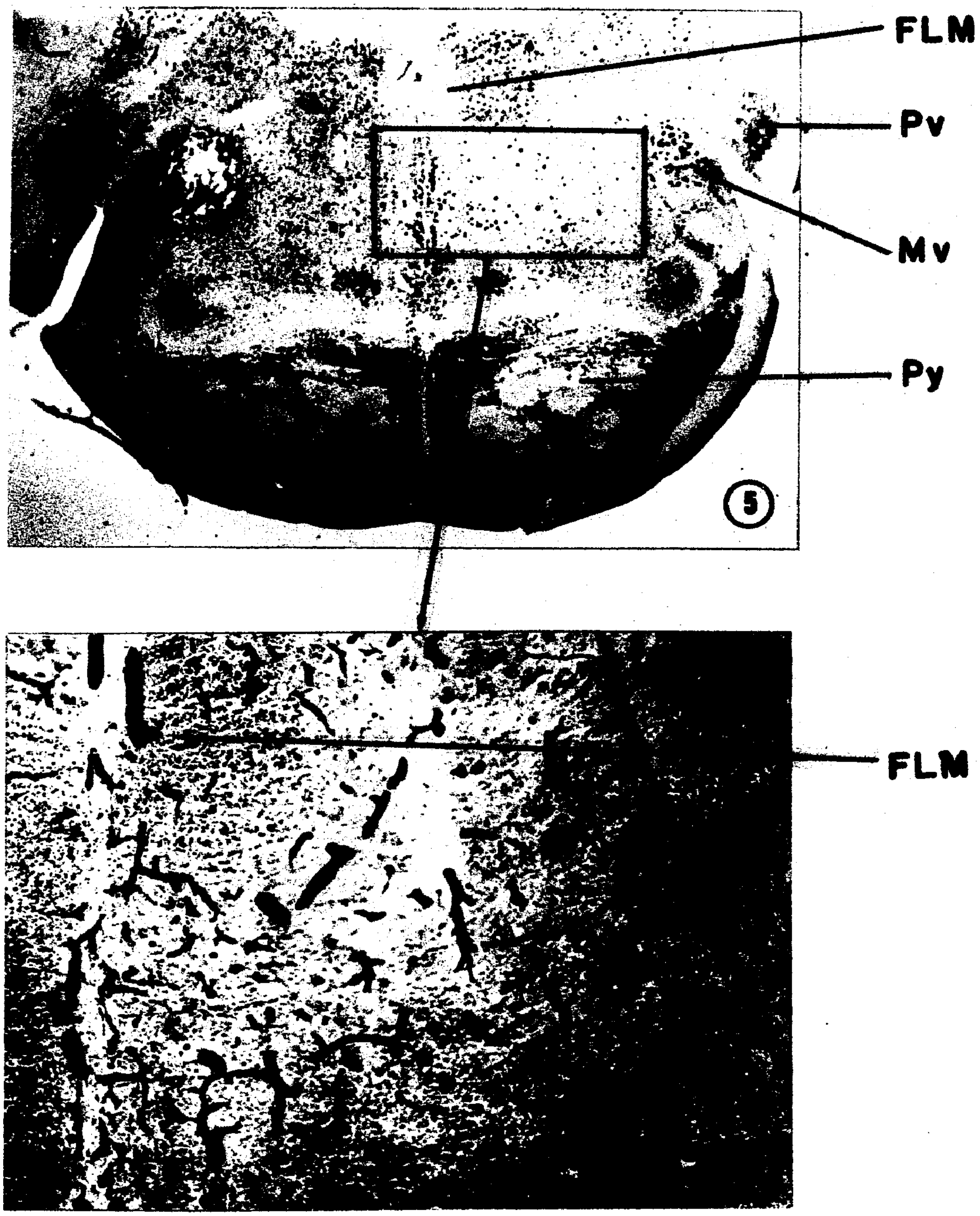

PLATE 5

Figure 7. A. Photomicrograph of a transverse section through the lower third of the pons of monkey #730. Fink-Heimer preparation. X 10.

B. Higher power photomicrograph of the area outlined in A. Note the presence of degeneration in the rostral pole of the nucleus of the spinal tract of V. Fink-Heimer preparation. X 40.

PLATE 5

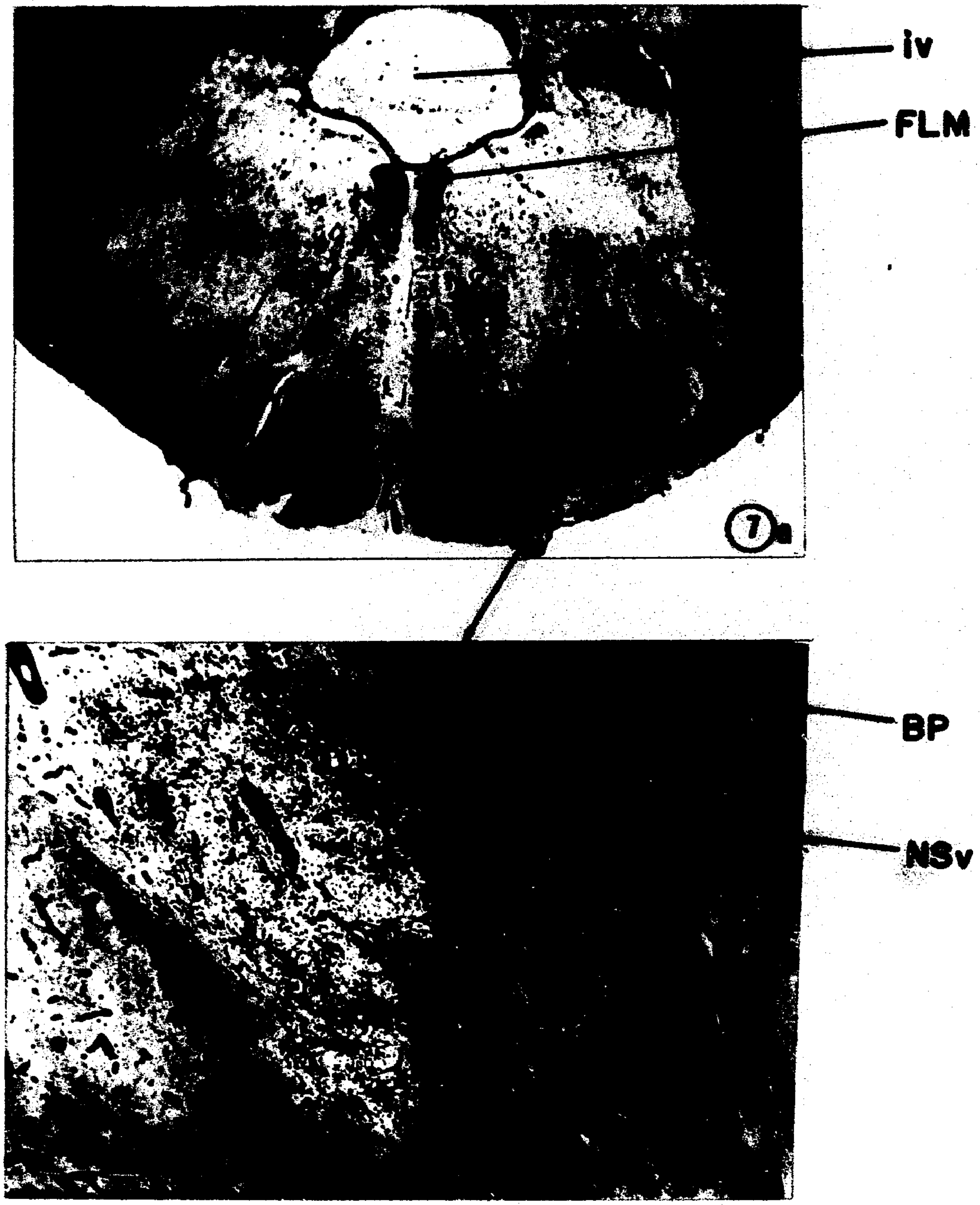

PLATE 6

Figure 8. A. Photomicrograph of a transverse section through the middle third of the pons of monkey #730. Fink-Heimer preparation. X 10.

B. Higher power photomicrograph of the area outlined by the square in A. Degeneration is particularly apparent in the chief sensory nucleus of V. Fink-Heimer preparation. X 63.

PLATE 6

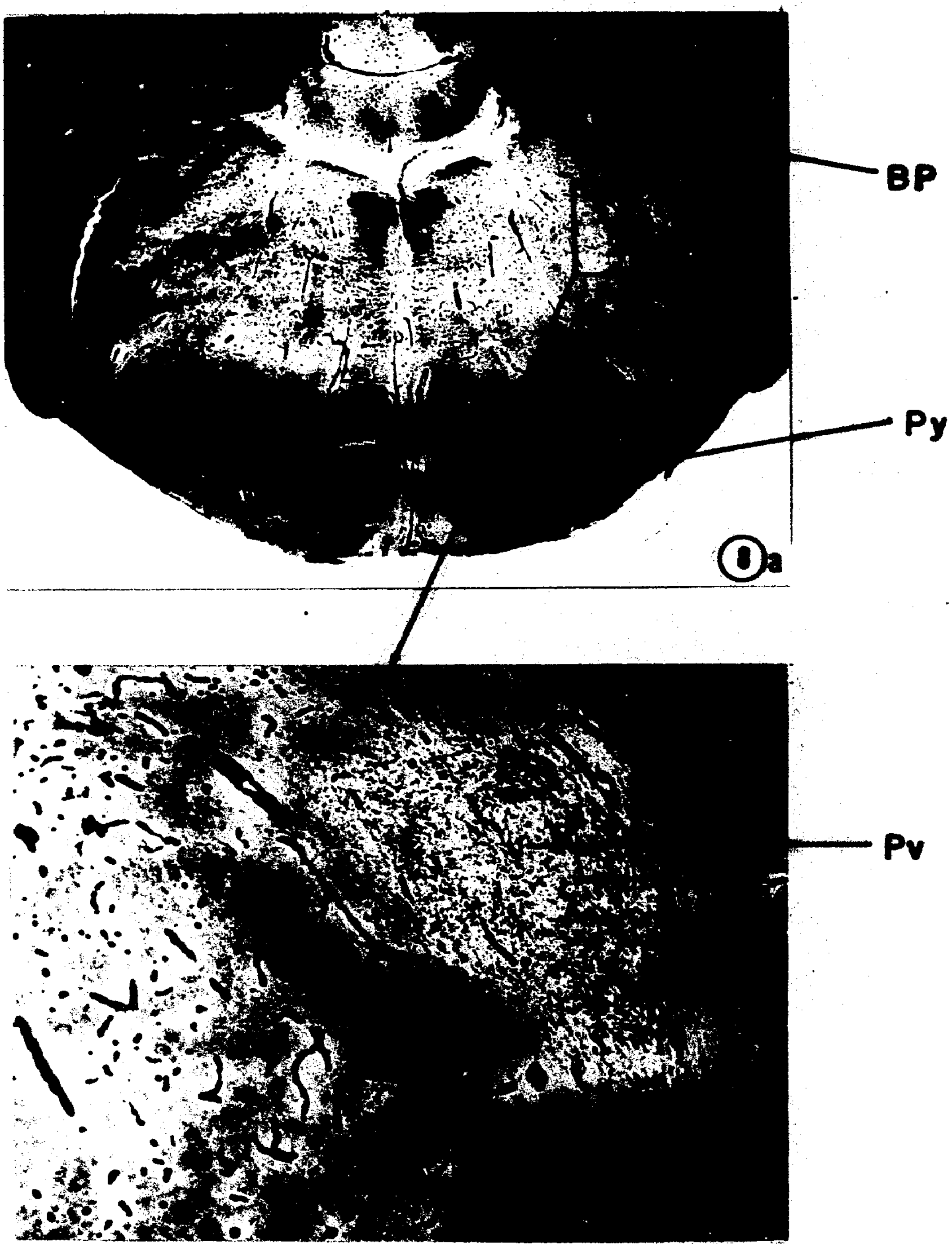

PLATE 7

Figure 9. Photomicrograph of a transverse section through the middle third of the pons of monkey #750. The lesion involves the entire chief sensory nucleus of V and also the motor nucleus of V. Thionin preparation. X 10.

Figure 10. Photomicrograph of a transverse section through the upper third of the pons of monkey #750. This is a higher power photomicrograph of the region corresponding to the area outlined by the square in figure 9. This section is rostral to that shown in the previous figure and has been treated to show degenerated fibers. Note the degenerated fibers of the ventral secondary ascending tract of V crossing the midline to take up a position dorsal to the medial lemniscus. Fink-Heimer preparation. X 40.

PLATE 7

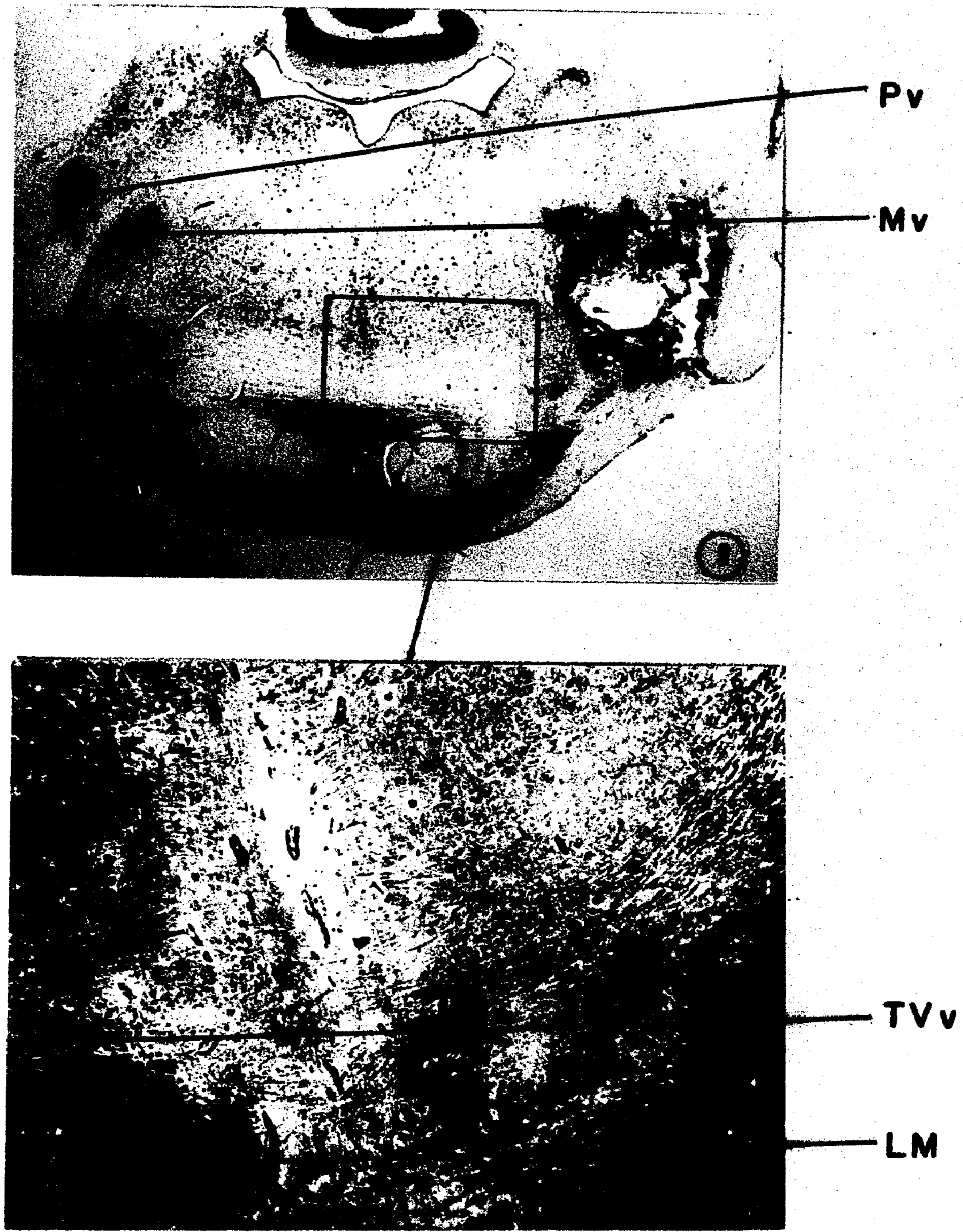

PLATE 8

Figure 11. Photomicrograph of a transverse section through the upper third of the pons of monkey #750. Degenerated fibers of the dorsal tract of V which have left the chief sensory nucleus are crossing the midline to take up a position ventrolateral to the mesencephalic root of V and its nucleus. Fink-Heimer preparation. X 12.

Figure 12. Photomicrograph of a transverse section through the inferior collicular level of the midbrain of monkey #750. Degeneration is present bilaterally in the deep tegmental gray. The arrows indicate the location of the dorsal tract of V. Fink-Heimer preparation. X 10.


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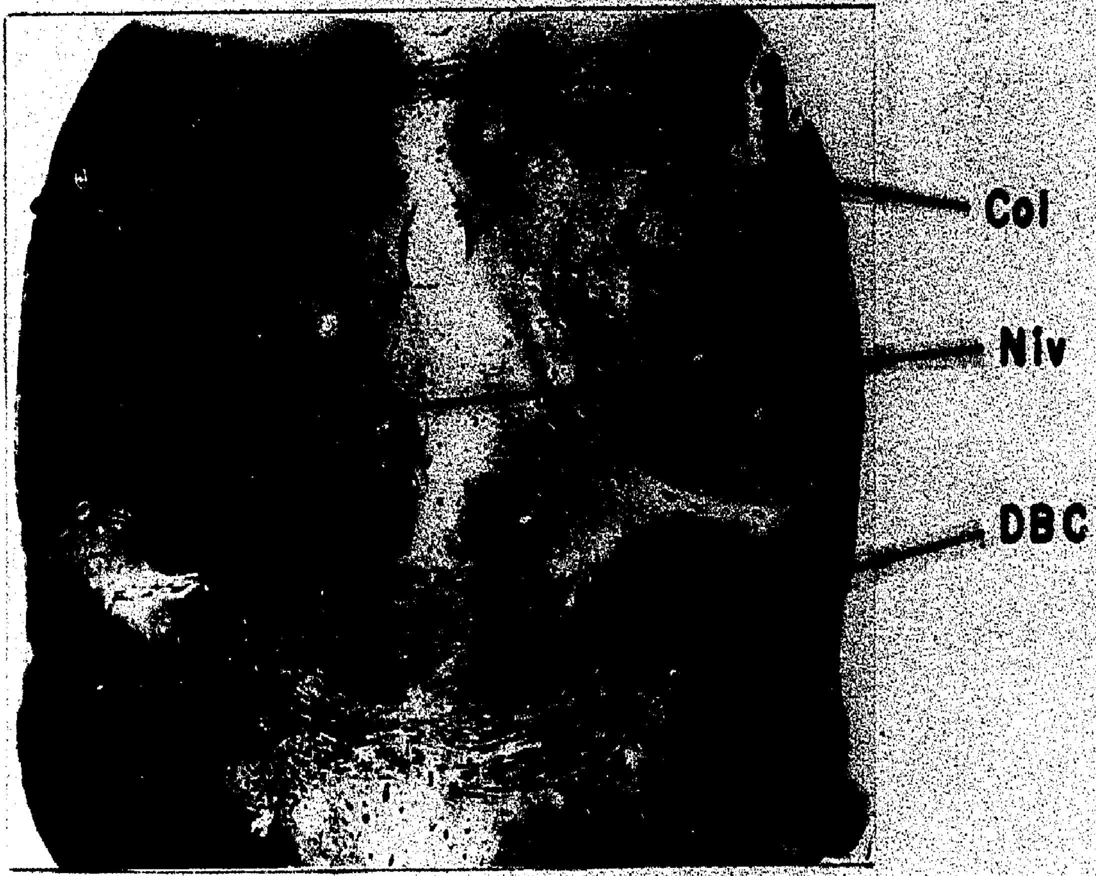
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PLATE 9

Figure 13. Photomicrograph of a transverse section through the superior collicular level of the midbrain of monkey #760. The arrows indicate the location of the dorsal tract of V. The uncrossed path was more conspicuous at this level. Fink-Heimer preparation. X 10.

Figure 14. A. Photomicrograph of a transverse section through the thalamus of monkey #760. Terminal degeneration was present in the nucleus ventralis posteromedialis. This area is indicated by the arrow. Fink-Heimer preparation. X 10.

B. Higher power photomicrograph of the area at the tip of the arrow in A. Note the presence of terminal degeneration around the cells of the nucleus ventralis posteromedialis. Fink-Heimer preparation. X 400.

PLATE 9

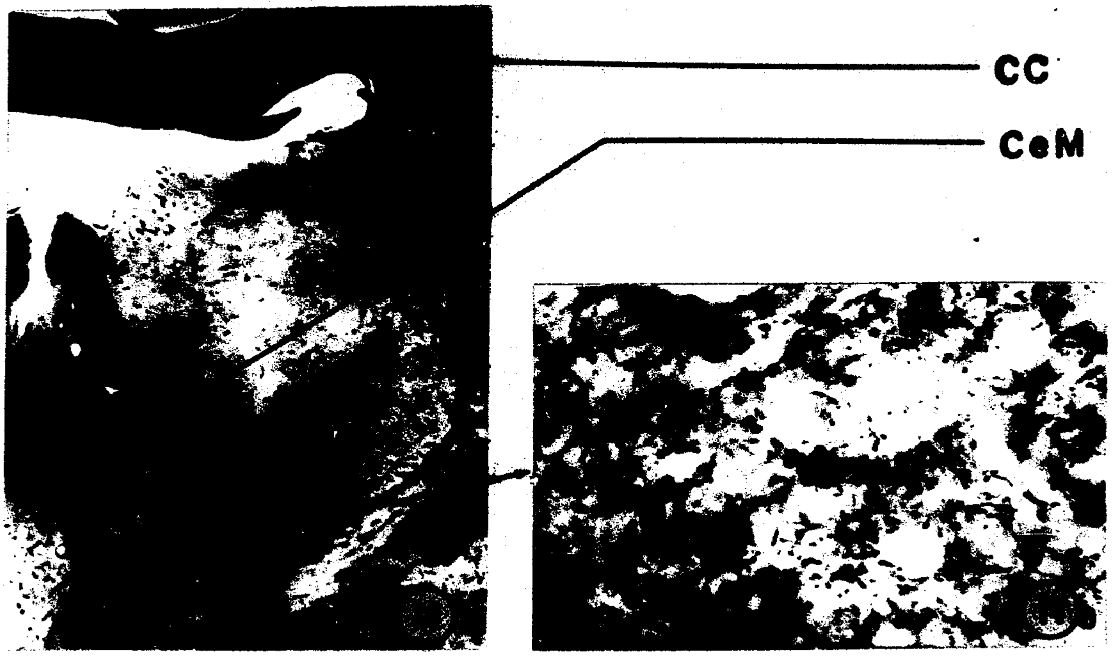


PLATE 10

Figure 15. Photomicrograph of a transverse section through the middle third of the pons of monkey #760. The lesion is indicated by the arrows. Thionin preparation. X 10.

Figure 16. Photomicrograph of a transverse section through the upper third of the pons of monkey #760. Degenerated fibers which have left the chief sensory nucleus are crossing the midline to take up a position ventrolateral to the mesencephalic root of V and its nucleus. The arrow indicates the position of the crossed dorsal tract of V. Fink-Heimer preparation. X 40.

PLATE 10

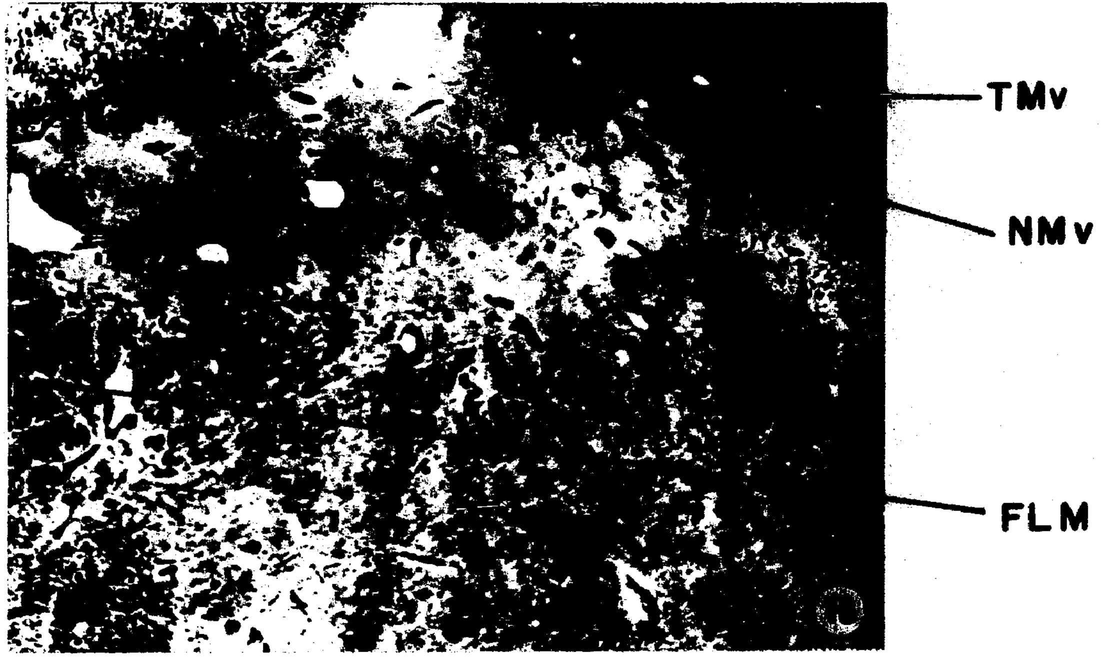


PLATE 11

Figure 17. Photomicrograph of a transverse section through the inferior collicular level of the midbrain of monkey #760. The dorsal tract of V is indicated by the arrows. This degenerated path is more conspicuous on the right side. Fink-Heimer preparation. X 40.

Figure 18. Photomicrograph of a transverse section through the superior collicular level of the midbrain of monkey #760. The location of the dorsal path is indicated by the arrows. Fink-Heimer preparation. X 40.

PLATE II

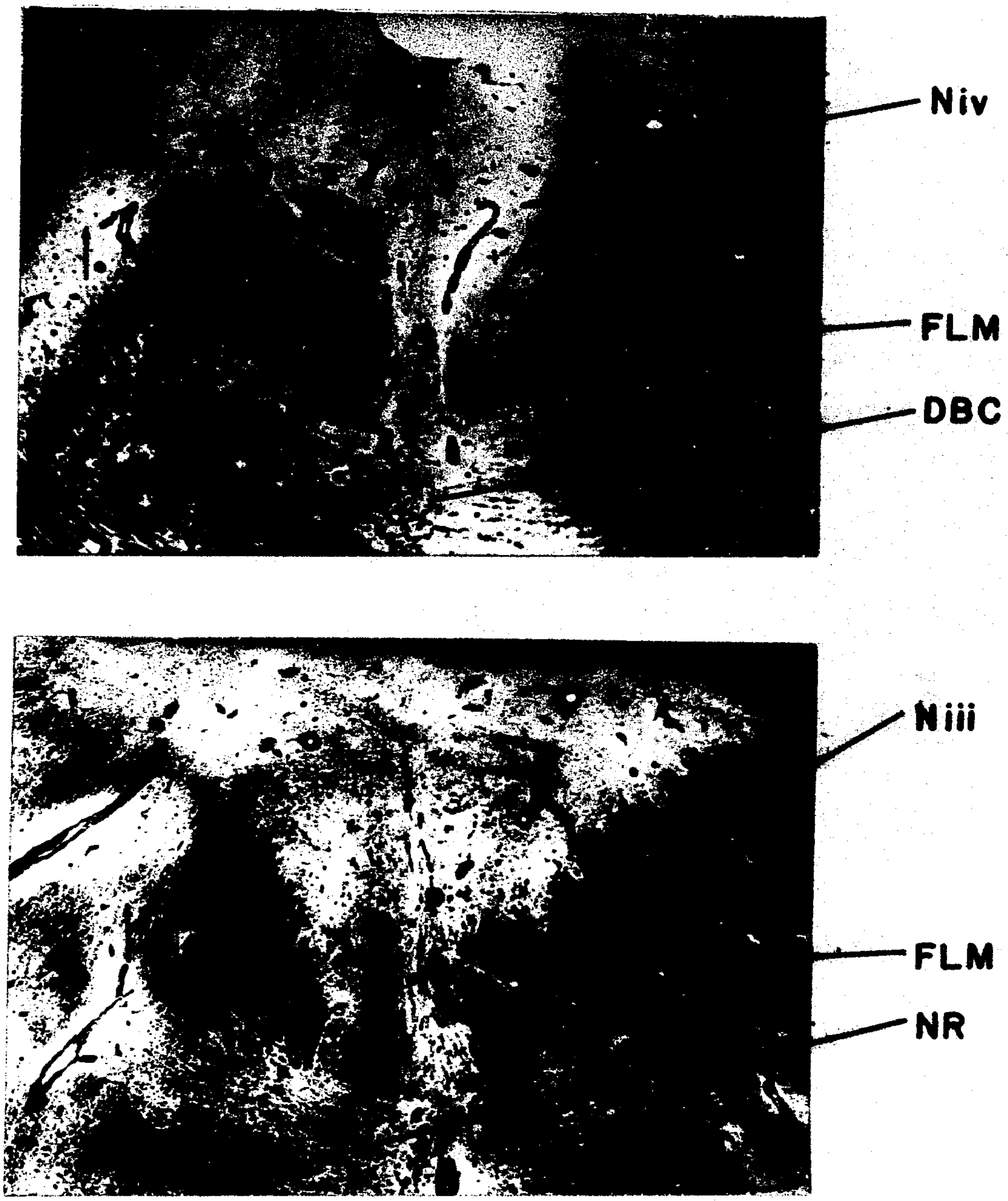
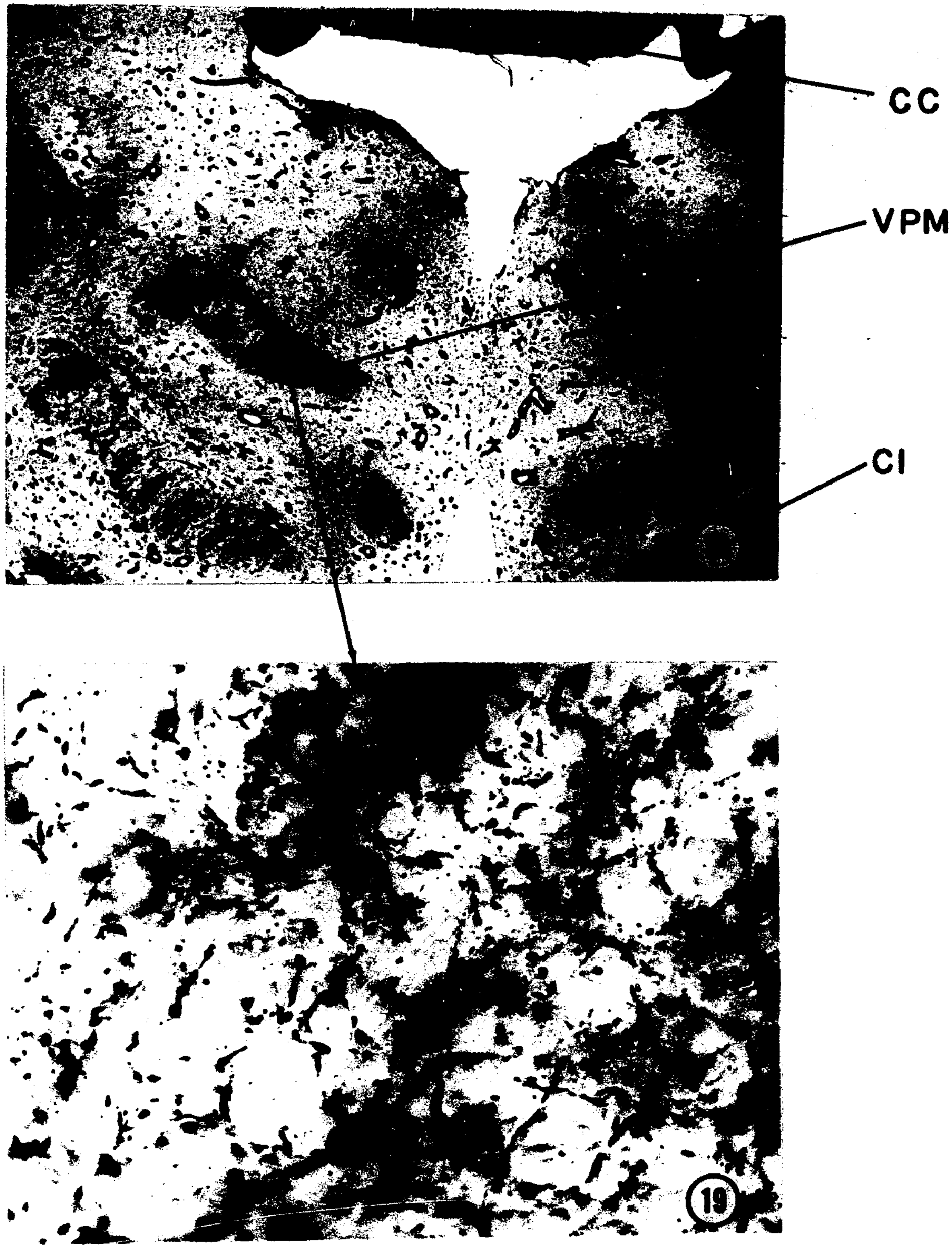


PLATE 12

Figure 19. A. Photomicrograph of a transverse section through the thalamus of monkey #760. Degeneration was found in the medial portion of the nucleus ventralis posterior. The arrow indicates the area of termination of the dorsal tract of V. Fink-Heimer preparation. X 10.

B. Higher power photomicrograph of the area in A at the tip of the arrow. Note the presence of terminal degeneration around the cells of the nucleus ventralis posteromedialis. Fink-Heimer preparation. X 400.

PLATE 12



GRADUATE SCHOOL
UNIVERSITY OF ALABAMA IN BIRMINGHAM
DISSERTATION APPROVAL FORM

Name of Candidate James Robert Augustine

Major Subject Anatomy

Title of Dissertation Certain Experimentally Demonstrated Connections of the Chief Sensory Trigeminal Nucleus in the Squirrel Monkey, Saimiri Sciureus.

Dissertation Committee:

Earl G. Hamel Jr., Chairman

Jerry W Brown

Elizabeth Crosby

Thomas E Hunt

Director of Graduate Program Earl G Hamel Jr

Dean, UAB Graduate School S B Barker

Date 24 August 1973