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Central Gustatory Pathways In The Monkey: An Experimental Study.

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CENTRAL GUSTATORY PATHWAYS IN THE MONKEY:

AN EXPERIMENTAL STUDY

by

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INTRODUCTION

Relatively little research has been completed to determine and document the central (neural) gustatory pathways in primates and man. This is surprising in view of the obvious importance of taste. The loss of taste or one of the gustatory sensations (such as the ability to recognize salty, sweet, sour or bitter substances) may, if no peripheral lesion can be located, be indicative of a lesion within the central nervous system. If the pathways involved in transmitting gustatory impulses to higher centers, including the cerebral receptive and association cortices for the cortical recognition of taste, are known, then the loss of taste or better still the loss of one of the modalities of taste will give the clinician a clue as to the possible level of the lesion.

The cell bodies of gustatory fibers are found in the geniculate ganglion of the facial nerve, the inferior (or petrosal) ganglion of the glossopharyngeal nerve, and the inferior (or nodose) ganglion of the vagus nerve. The central processes of these fibers enter the brain stem (at pons and medulla levels) and synapse, at or near their level of entrance, in the nucleus (dorsal visceral gray) of the tractus solitarius (Schwartz, Roulhac, Lam and O'Leary, 1951). This level of synapse is in contrast to the manner of distribution for the general visceral afferent components of the facial, glossopharyn-

geal and vagus nerves, the central processes of which enter the brain stem, pass inferiorly in the tractus solitarius and synapse in the nucleus of the tractus solitarius caudal to their level of entrance into the brain stem. The secondary projections to higher centers from the nuclei of the tractus solitarius which together receive both special and general visceral afferent fibers are not well documented.

It has been reported that some secondary fibers concerned with taste relay by way of the contralateral medial lemniscus in guinea pig (Allen, 1923b) to the most medial portion of the nucleus ventralis posteromedialis of the dorsal thalamus and thence by thalamic sensory radiations to the cerebral cortex (von Bechterew, 1908-1911). Penfield and Rasmussen (1950) traced gustatory impulses to the base of the central fissure (in both precentral and postcentral gyri) and to the opercular surface of this area for the cortical recognition of taste. Gorschkow (1901) a student of von Bechterew, carried gustatory impulses to the potential island region in the dog.

In its passage rostrally to the dorsal thalamus the medial lemniscus has been said to contribute fibers at midbrain levels to the mammillary peduncle (Papez, 1923). Other investigators traced secondary gustatory fibers rostrally through the dorsal longitudinal fasciculus in cat (Fox, 1941) and in the opossum (Thompson, 1942). Fox observed that these fibers terminated in the ventral tegmental nucleus of isthmus levels. Crosby, Humphrey and Lauer (1962) stated that

> From the ventral tegmental nucleus, bundles have been traced ventromedialward through the tegmental gray to the rostral end of the ventral tegmental area of Tsai, where they join the other fascicles of the mammillary peduncle that have ascended through the medial lemniscus, and, as common bundles pass forward to the mammillary body.

Norgren and Leonard (1973) described, in the albino rat, an ipsilateral secondary gustatory pathway originating from the region of the nucleus of the tractus solitarius which receives primary facial afferent fibers. This pathway ascends to a secondary "pontine taste area" for synapse. Degenerating fibers from lesions placed in this "pontine taste area" were traced forward bilaterally to the nucleus ventralis posteromedialis as well as to the subthalamus, the dorsolateral hypothalamus, and the subpallidal gray in the ventral forebrain.

In addition to problems encountered in following central gustatory pathways to higher centers the question also arises as to the identification of specific levels within the central nervous system at which gustatory impulses come into consciousness. Bradley (1963) performed a number of experiments on monkey (Macaca mulatta) which involved the removal of cortical areas and the placing of lesions in thalamic and superior collicular levels. The monkeys operated upon were given banana sprinkled with quinine both preoperatively and postoperatively. Following removal of the cortex at the base of the central fissure the monkeys continued to respond to the quinine but did so more slowly than previously observed. With lesions involving the superior colliculus of the midbrain there was a great reduction in response but again the animal rejected the quinine. This would indicate, perhaps, that awareness of bitter gustatory sensation comes into consciousness at some level other than those ablated by Bradley.

There are only a few reported clinical cases which support the available anatomical evidence for the central gustatory pathways in man. Adler (1934) reported a case in which a patient had a glioblastoma of the third ventricle which initially involved the most rostral medial portion of the nucleus ventralis posteromedialis of the dorsal thalamus. Contralateral to the side of the lesion the patient had a loss of all gustatory sensation except a slight recognition of bitter. Shenkin and Lewey (1943) reported a case in which the patient had epileptic seizures preceded by an aura in which he experienced a sour-bitter taste. At operation a vascular anomaly was discovered in which the vessels located in the lateral fissure were greatly dilated, the point of greatest dilation being over the most inferior portion of the postcentral gyrus. The patient had a loss of sweet perception over the entire side of the tongue contralateral to the lesion. While the above two clinical cases concur with the available information on the central connections of secondary and tertiary gustatory pathways, it is apparent from the literature that further documentation for these pathways is necessary. A more complete review of the pertinent literature is included in the Discussion.

MATERIALS AND METHODS

Normal Material

A large portion of the brain stem of monkey NR 7749 was used to study the normal configuration of the fiber connections and nuclear groups extending from caudal medullary levels to rostral inferior collicular levels. The brain stem was embedded in paraffin and cut transversely on a rotary microtome at twenty microns. Alternating sections were stained by the Weil-Weigert technique for myelinated fibers and with thionin for the nuclear groups. (Monkey NR 7749 is also referred to on pages 12 and 13.)

Experimental Material

One green monkey (Cercopithecus aethiops), weighing 5.6 kilograms, and eight rhesus monkeys (Macaca mulatta), ranging in weight from 2.9 kilograms to 7.5 kilograms, were used in the experimental studies. Sour and bitter were the taste modalities tested. Each monkey was tested several times both preoperatively and postoperatively after having fasted for a minimum of twelve hours. Initially, when testing for the ability to recognize sour substances a piece of banana which had been soaked for a minimum of twelve hours in reconstituted lemon juice ("ReaLemon") was offered to each animal. Subsequently a piece

of lemon treated banana or a slice of lemon was given to each animal when testing his responses to sour substances. A piece of banana with quinine sulfate powder sprinkled within its center was offered to each monkey to test his ability to recognize bitter substances. The responses to the sour and bitter substances of each monkey were consistent with those reported on particular days in the Results section. Records were kept of the responses of the monkeys to these two substances and whenever possible responses were documented photographically with an eight or sixteen millimeter camera.

Prior to surgery each animal was anesthetized by an intramuscular injection of 25 milligrams/kilogram of ketamine hydrochloride. Additional injections of small amounts of ketamine hydrochloride were administered whenever necessary to maintain the proper level of anesthesia throughout surgery. The head of the anesthetized animal was secured in a Lab-tronics Stereotaxic Instrument and the extremities were fastened to the surgical table with straps. The monkey's head was then shaved, scrubbed with surgical soap and rinsed with merthiolate tincture.

Sterile technique was employed throughout surgery. The monkey's body was covered with sterile drapes. A drape with an opening in its center, so that the area of skin to be incised was left exposed, was sutured to the animal's scalp. A "U" shaped incision of approximately eight centimeters was made with the base of the "U" approaching the midline of the skull. The skin was reflected and the bone was thoroughly scraped to remove the connective tissue. In order to

approach successfully the frontal and the parietal cortices at the base of the central fissure and the opercular surfaces of these two cortical areas it was necessary to reflect the temporalis muscle. A three millimeter opening was drilled through the bone to the dura overlying the appropriate cortical area. The burr hole was enlarged with rongeur forceps to give adequate visibility of the cortical area of surgical interest or the cortical area through which an electrode would be passed during stereotaxic procedures. The dura was carefully excised with a cutting needle and then reflected with a scapel. Cortical lesions were made by cauterization or by suction.

In the development of stereotaxic techniques for locating the nucleus of the tractus solitarius, it was considered essential, as an important anatomical landmark, to locate the motor nucleus of the facial nerve. Once stereotaxic placement of the electrode in this nucleus was verified by appropriate response to electrical stimulation the electrode was moved laterally (0.1-0.5 millimeters) and superiorly (1-2 millimeters) to the approximate anatomical location of the nucleus of the tractus solitarius (dorsal visceral gray) which receives those primary special visceral afferent fibers for taste which enter the brain stem in the facial nerve. Using a unipolar electrode, an electrolytic stereotaxic lesion was placed at this point. This area is continuous longitudinally with those parts of the nucleus of the tractus solitarius which receive primary gustatory fibers entering the brain stem by way of the glossopharyngeal and vagus nerves. These coordinates were then transposed

caudally and longitudinally within the pons and the medulla to coincide with the known anatomical relationships of the nucleus of the tractus solitarius at these levels. Lesions were placed in the nucleus of the tractus solitarius at the level of entrance of the glossopharyngeal nerve in the medulla. Originally, in attempting to locate the motor nucleus of the facial nerve, the stereotaxic coordinates [Posterior (P) 2.5, Left (L) 3.5 and Horizontal (H) -7.5] based on the atlas of Snider and Lee (1961) were used with unsuccessful results. Subsequently other coordinates [Anterior (A) 0.7, L 5 and H -13, based on the figures of Atlas and Ingram (1937] were used and found to be more accurate with respect to the monkeys used in these studies.

The shaft of the unipolar electrode was made from 22 gauge stainless steel hypodermic tubing. The tip of platinum was electropolished to a diameter of 25 microns. The platinum tip was crimped to one end of the shaft of the electrode and an amphenol connector was attached to the other end of the electrode. With the exception of the amphenol connector, the electrode was dipped in epoxylite and then baked at 150 degrees centigrade for one half hour. The electrode was redipped and rebaked for another half an hour. The distal one millimeter of the tip was exposed by placing it in a heating coil. The electrode was placed in the electrode carrier of the Lab-tronics Stereotaxic Instrument and inserted into the brain at the selected coordinates. The grounded unipolar electrode was attached to a Grass stimulator (model S4). To complete the electrical circuit, a second lead, attached to a probe, was inserted into the anus of the monkey.

Originally, the electrolytic lesions were placed using a direct current of 4-8 volts for 30 to 60 seconds. After observing that lesions placed in this manner could not be seen either grossly or histologically, an ammeter was inserted into the electrical circuit to assure that lesions were being placed with a current of 3-5 milliamps.

Bleeding which occurred during surgery was controlled by cauterization or with absorbable gelatin sponge (Gelfoam, Upjohn) and/or cotton and suction. Bone bleeding was controlled with bone wax. Before closing the wound, the surgical area was washed with sterile normal saline. When possible the muscle was sutured to any available connective tissue. To aid in the prevention of infection and to protect the wound from the monkey's interference, the surface of the incision was covered with a coating of 6% celloidin.

Following surgery, 300,000 units of sterile procaine penicillin G suspension were administered intramuscularly for a period of five days to minimize further the possibility of infection. Postoperatively the monkeys were not tested for their responses to the sour and bitter substances until the period of antibiotic therapy was completed.

Immediately upon recovery from surgery, and thereafter until the time of sacrifice, any behavioral changes or neurological deficits present were recorded. With the exception of two animals, monkey NR 7742 and monkey NR 7749 which were employed to help develop stereotaxic procedures, each monkey was not sacrificed for a minimum of fourteen days postoperatively which is the time lapse necessary to allow for a sufficient amount of degeneration of the pathways affected.

Prior to perfusion-fixation each animal was anesthetized with ketamine hydrochloride and his anterior chest wall incised to expose the pericardial cavity. The left ventricle was cannulated and 0.9% saline followed by 10% formalin buffered with calcium carbonate or cacodylate buffered formalin was gravity fed through the cardiovascular system. Immediately following perfusion-fixation the brain was removed and placed in 10% formalin buffered with calcium carbonate or cacodylate. The formalin was replaced with fresh formalin every twelve hours for the first forty-eight hours. Each brain was left in the formalin for a minimum of four weeks to assure proper fixation. The locations of cortical lesions were determined on postmortem. The locations and extents of electrolytic stereotaxic lesions were determined histologically by the Fink and Heimer silver impregnation technique (1967), the De Olmos and Ingram silver impregnation technique (1971) and the use of thionin stain for cellular and nuclear configuration.

Variations of the described surgical procedure, of the placement of cortical and stereotaxic lesions and of the amount of current used in stimulations and in placing electrolytic lesions will be described when reviewing the Operative Protocol of each animal.

The operative protocols of each monkey are discussed in chronological order so that various difficulties encountered during the development of the experimental aspects of this study and their consequent solutions are presented sequentially.

RESULTS

Monkey NR 7742

Operative Protocol: Male. Weight - 6.9 kg. 24 June 1974. An attempt was made to locate stereotaxically the motor nucleus of the facial nerve. An electrode was inserted through the cortex of the left cerebral hemisphere at the coordinates: P 2.5, L 3.5 and H -7.5, based on the atlas of Snider and Lee (1961). A current of two to eight volts at forty pulses per second produced no response. A current of fifteen volts at forty pulses per second, however, did produce some movement of the right lower extremity. Many coordinates (Table 1, page 12), in the vicinity of the original coordinates, were tried with unsuccessful results. A lesion was placed at the coordinates: P 2.5, L 3.5 and H -7.5 with a direct current of eight volts for one minute.

Sacrificed: 24 June 1974

Note: The brain was removed immediately following perfusion-fixation and placed in 10% formalin buffered with calcium carbonate. The formalin was changed every eight hours for seventy-two hours, after which the brain was sufficiently hardened to be sliced. The brain was sliced with a brain knife. It was thought if the lesion could

Table 1

The stereotaxic coordinates and volts used and the response of the monkeys listed in table one refer to the operation on Monkey NR 7742, to the operation on Monkey NR 7749, and to the first operation on Monkey NR 7744.

Stereotaxic Coordinates	Volts at 40 pulses/sec.	Response by the Monkey to the electrical stimulation
P 2.5, L 3.5, H -7.5	2 - 7	None
P 2.5, L 4.5, H -7.5	2 - 8	None
P 4.5, L 4.5, H -9.5	2 - 8	None
P 3.5, L 4.5, H -9.5	2 - 8	None
P 3.5, L 4.5, H -6.0	2 - 8	None
P 2.5, L 3.5, H +7.5	2 - 8	Bilateral movement of legs, hips and feet
P 2.5, L 3.5, H +9.5	2 - 8	Bilateral movement of legs, hips and feet
P 6.5, L 3.5, H -7.5	2 - 8	None
P 6.5, L 3.5, H -10.0	2 - 8	None
P 8.5, L 5.0, H -7.5	2 - 8	None
P 8.5, L 5.0, H -10.0	2 - 8	None
P 8.5, L 5.0, H -9.0	2 - 8	None
P 8.5, L 5.0, H -8.0	2 - 8	None
P 8.5, L 5.0, H -7.0	2 - 8	None
P 3.5, L 4.5, H -10.5	2 - 8	None
P 1.5, L 4.5, H -7.5	2 - 8	None
P 1.5, L 4.5, H -8.5	2 - 8	None
P 2.5, L 4.5, H -7.5	2 - 8	None
P 2.5, L 3.5, H -7.5	15	Slight movement of right lower extremity
P 2.5, L 3.5, H -5.5	15	Slight movement of right lower extremity
P 2.5, L 3.5, H -1.5	2 - 15	Slight movement of right lower extremity

be seen grossly there would be some indication as to the anatomical relationships of the coordinates used in placing the lesion. The lesion could not be found.

Monkey NR 7749

Operative Protocol: Male. Weight - 6.0 kg. 26 June 1974. The surgical procedure which was performed on monkey NR 7742 on 24 June 1974 was repeated on this monkey. The electrode was inserted at the same coordinates (Table 1, page 12) producing the same results. A lesion was placed at coordinates: P 2.5, L 3.5, and H -7.5.

Sacrificed: 26 June 1974.

Note: A large portion of the brain stem of this monkey, from the inferior level of the decussation of the pyramids to the rostral level of the inferior colliculus was used to study the normal configuration of the fiber connections and nuclear groups. The lesion which was placed at coordinates: P 2.5, L 3.5, and H -7.5 could not be found histologically by using light microscopy.

Monkey NR 7744

Operation NR One

Preoperative Testing: 5 August 1974. Monkey NR 7744 was given a piece of lemon treated banana which he hesitantly rejected after having tasted it. He was also offered a piece of quinine treated banana which he expectorated immediately upon tasting the quinine.

Operative Protocol: Male. Weight - 7.0 kg. 6 August 1974. A left craniotomy was performed in which a hole was drilled at the stereotaxic coordinates: P 2.5 and L 3.5. After enlarging the burr hole with rongeur forceps it was discovered that the superior sagittal sinus deviated to the left of the midline. In selecting stereotaxic coordinates it was necessary to compensate for both the location of the superior sagittal sinus and the size of the monkey. The electrode was inserted through the left cerebral hemisphere at the coordinates: P 2.5, L 3.5 and H -7.5, based on the atlas of Snider and Lee (1961). The coordinates which were used on monkey NR 7742 and monkey NR 7749 were used on this monkey (Table 1) with similar results. Many attempts were made to locate stereotaxically any definitive neuroanatomical landmark. None were successful. An electrolytic stereotaxic lesion was not made.

Note: The monkey fully recovered from this operation with no apparent neurological deficits.

Operation NR Two

Preoperative Testing: 3 January 1975. Monkey NR 7744 was tested for taste. He reacted exactly as he had done previously. He hesitantly rejected the lemon soaked banana after he tasted it. He dropped the piece of lemon as soon as he tasted it. He expectorated the quinine treated banana as soon as he had tasted the quinine.

Operative Protocol: 4 January 1975. An incision of approximately six centimeters slanting posterior superiorly to anterior inferiorly was made above the left ear. It was necessary to excise a large portion of the temporalis muscle in order to have an adequate visual field. As much bone as possible was removed overlying the left temporal lobe and the inferior aspects of the rostral parietal lobe and the caudal frontal lobe. The dura was incised with a cutting needle and reflected with a scapel to expose the lateral fissure and the superior, middle and part of the inferior temporal gyri of the left temporal lobe.

In an attempt to remove the island and the gustatory association areas a large portion of the temporal lobe was removed with suction. Little bleeding occurred. The wound was packed with Gelfoam and was closed as soon as the surgical area was dry.

Postoperative Notes: 5 January 1975. The monkey was eating, taking water and sitting erect. By January 31, 1975 the monkey's incision was completely healed and he appeared to have no neurological deficits following the last operation.

Description and Location of the Lesion: Figure 1 shows the location and extent of the lesion which was made on 4 January 1975. As can be observed the lesion included a large portion of the postcentral gyrus and its opercular surface as well as the middle one third of the superior and middle temporal gyri.

Operation NR Three

Preoperative Testing: 2 February 1975. Monkey NR 7744 was tested for his responses to sour and bitter substances. The animal did not, as had been previously observed, find the slice of lemon objectionable for he ate the entire slice. He rejected the quinine treated banana but did so slightly more slowly and with less vehemence than had been observed prior to his operation of 4 January 1975.

Operative Protocol: 3 February 1975. The skin and temporalis muscle were reflected on the right side. A hole was drilled through the bone overlying the base of the central fissure and enlarged with rongeur forceps. The dura was excised and the cortex at the base of the precentral gyrus and at the base of the postcentral gyrus and the opercular surfaces of these two gyri was removed with an electric cautery. Little bleeding occurred. The wound was packed with Gelfoam and was closed as soon as it was dry.

Postoperative Notes: 4 February 1975. Monkey NR 7744 was sitting erect, eating and taking water. On 7 February 1975 monkey NR 7744 sustained a seizure during which he repeatedly struck his head against the cage resulting in hemorrhage and edema. On 8 February 1975 monkey NR 7744 was neither eating nor taking water. He appeared to be completely blind. As he moved around his cage he continually walked into its sides.

Sacrificed: 12 February 1975. There had been no change in the behavior of this monkey since his seizure of 7 February 1975. The animal did not recover sufficiently to be tested for taste. Monkey NR 7744 was sacrificed on this date.

Note: The locations of the cortical lesions were confirmed on postmortem.

Cercopithecus aethiops

Operation NR One

Preoperative Testing: 12 August 1974. Cercopithecus was offered a piece of quinine treated banana which he expectorated as soon as he tasted the quinine. Following his rejection of the quinine banana Cercopithecus did not hesitate to eat a piece of untreated banana. He was then offered a piece of lemon treated banana which he smelled, dropped, then tasted and finally rejected.

Operative Protocol: Male. Weight - 5.6 kg. 13 August 1974. The skin and temporalis muscle were reflected on the left. A left craniotomy was performed in which the bone and dura overlying the base of the central fissure were removed. The cortex at the base of the precentral gyrus and at the base of the postcentral gyrus and the opercular surfaces of these two cortical areas was removed by cauterization in the left cerebral hemisphere.

Postoperative Notes: Cercopithecus fully recovered from this operation with no permanent neurological deficit. For the first two weeks following surgery a slight paresis of the right upper extremity was evident.

Operation NR Two

Preoperative Testing: 26 November 1974. Cercopithecus was given a piece of lemon soaked banana which he sniffed, tasted, then dropped and finally ate. The monkey was then offered a piece of quinine treated banana which he expectorated immediately upon tasting the quinine.

Operative Protocol: 27 November 1974. The skin and temporalis muscle were reflected on the right. A right craniotomy was performed in which the bone and dura overlying the base of the central fissure were removed. By cauterization a large lesion was placed in the cortex at the base of the precentral gyrus and at the base of the postcentral gyrus and also the opercular surfaces of these two gyri. There occurred a large amount of hemorrhage due to involvement of branches of the middle cerebral artery. The bleeding was controlled with Gelfoam, cotton and suction. The wound was packed with Gelfoam and soon as the surgical area was dry the wound was closed.

Postoperative Notes: 10 December 1974. Cercopithecus was tested for taste. He did not hesitate, as had been previously observed, to eat the lemon treated banana. Cercopithecus did reject the quinine treated banana, but did so more slowly than had been previously

observed. His behavior indicated that there had been a loss of some taste discrimination following the removal of the cortices at the base of the central fissure and of the opercular surface of this area bilaterally.

Sacrificed: 11 December 1974.

Note: The locations of the cortical lesions were confirmed on post-mortem and are shown in Figure 2 and Figure 3.

Monkey NR 025

Preoperative Testing: 27 December 1974. Rhesus monkey NR 025 was offered a piece of quinine treated banana which he expectorated immediately upon tasting the quinine. He bit into but did not continue to eat a slice of lemon. Unlike Cercopithecus and the older rhesus monkey NR 7744, both of whom had initially rejected, rather hesitantly, the banana which had been soaked for twelve hours in reconstituted lemon juice, the young rhesus did not hesitate to eat the lemon treated banana.

Operative Protocol: Male. Weight - 2.9 kg. 30 December 1974. The skin and temporalis muscle on the left were reflected. A left craniotomy was performed in which the bone and dura overlying the base of the left central fissure were removed. Cauterization was utilized to remove the cortex at the base of the central fissure and the opercular surface of this area. Little bleeding occurred. As soon as the surgical area was dry the wound was closed.

Postoperative Notes: Monkey NR 025 recovered from this operation with no apparent neurological deficits. On 2 February 1975 monkey NR 025 was tested for his responses to sour and bitter substances. He expectorated the quinine treated banana as soon as he tasted the quinine. He bit into but did not continue to eat a piece of lemon. He did not hesitate to eat a piece of lemon treated banana.

On 5 February 1975 monkey NR 025 was stricken with shigellosis and on 14 February died from complications arising from shigellosis. His brain was removed and placed in 10% formalin buffered with calcium carbonate. Figure 4 shows the location and extent of the cortical lesion in the left hemisphere.

Monkey NR 8349

Preoperative Testing: 1 May 1975 and 2 May 1975. Monkey NR 8349 was tested for taste on each of the dates listed. The monkey did not hesitate to eat the piece of lemon. The monkey was slower to reject the quinine treated banana than had normally been observed in other monkeys tested preoperatively. However, once it became apparent that the monkey had tasted the quinine, the quinine treated banana was expectorated.

Operative Protocol: Male. Weight - 4.5 kg. 3 May 1975. Two holes were drilled through the bone to the dura at the stereotaxic coordinates: P 2.6 and L 7, and P 2.6 and R 7, based on the figures of Atlas and Ingram (1937). The electrode was inserted through the cortex and with a current of 3 ma electrolytic lesions were placed for a

period of 30 seconds at the stereotaxic coordinates: Lesion 1, P 2.6, L 7 and H -12 and H -13, and Lesion 2, P 2.6, R 7 and H -12 and H -13. These coordinates correspond to the nucleus of the tractus solitarius at the level of entrance of the glossopharyngeal nerve into the brain stem.

Postoperative Notes: The monkey recovered completely from this operation with no apparent neurological deficits.

Postoperative Testing: 10 May 1975. The monkey did not hesitate to eat the piece of lemon. As had been observed preoperatively, the monkey was slow to reject the quinine treated banana.

Sacrificed: 17 May 1975.

Description of stereotaxic lesions and resulting degeneration: Frozen sections of the brain stem of this monkey were cut in a transverse plane at 25 microns on a sliding microtome. Every fifth section was stained with the Fink and Heimer silver impregnation technique. Histologic examination revealed two lesions in the brain stem of this monkey; one was located in the reticular formation of the caudal pons just medial to the right motor root of the facial nerve. This lesion extended from caudal to rostral pontine levels and is shown in Figure 5. The second lesion was located in the left internal capsule at the level of the superior colliculus (Figure 6). From the level of the pontine lesion a fairly large bundle of degenerating fibers could be followed contralaterally to a position just dorsal to the medial lemniscus (Figures 7 and 8). This bundle had an extension

which was located medial to the medial lemniscus. The lesion did not directly involve either the nucleus of the tractus solitarius or the nucleus of the spinal tract of the trigeminal nerve. However, from the location of the degenerating axons on the contralateral side of the brain stem it appeared likely that efferent fibers from both these nuclei were interrupted in their passage across the midline. Terminal degeneration was observed in the nucleus ventralis posteromedialis of the dorsal thalamus (Figures 9 and 10). Unfortunately the lesion of the left internal capsule resulted in the degeneration of many axons which also terminated in the nucleus ventralis posteromedialis. Consequently it was impossible to differentiate the terminal degeneration of the axons from the two lesions.

Monkey NR 8501

Preoperative Testing: 20th, 21st and 22nd of May 1975. The monkey was slower to reject the quinine banana than had been observed in other monkeys prior to their operative procedures. She did not hesitate to eat a slice of lemon.

Operative Protocol: Female. Weight - 4.5 kg. 23 May 1975. The skin and underlying connective tissue were reflected from the superior medial aspect of the left side of the head. A burr hole was drilled through the bone to the dura at the stereotaxic coordinates: A 0.7 and L 5. The electrode was inserted through the cortex of the left cerebral hemisphere at the stereotaxic coordinates: A 0.7, L 5 and H -12. A stimulus of 0.1 volt produced ipsilateral movement of the

muscles of the lower face at the corner of the mouth confirming that the tip of the electrode was in the motor nucleus of the facial nerve. Four electrolytic stereotaxic lesions with a current of 3.5 ma for a period of 30 seconds were placed at the following coordinates: Lesion 1, A 0.7, L 4.5 and H -10; Lesion 2, A 0.7, L 5.0 and H -10; Lesion 3, P 2.6, L 3.5 and H -13 and Lesion 4, P 2.6, L 4.5 and H -12 and H -13.

Postoperative Notes: Immediately upon recovery from anesthesia the monkey exhibited a rotary nystagmus which lasted for approximately twenty-four hours and it held its head at an angle toward the side of the lesion until the time of sacrifice. The monkey continually held on to the side of the cage from the time of recovery from the anesthesia until its demise.

Postoperative Testing: The monkey responded exactly as she had done preoperatively. She responded slowly to the quinine-banana, nevertheless she did reject the quinine treated banana. The monkey did not hesitate to eat the slice of lemon.

Sacrificed: 6 June 1975.

Description of stereotaxic lesions and resulting degeneration: The brain stem of this monkey, from caudal medullary levels through rostral thalamic levels, was frozen with solid carbon dioxide and sliced on a sliding microtome at 25 microns. Every fifth section was stained with the De Olmos and Ingram (1971) silver impregnation method for degenerating axons. Adjacent sections through the levels of the

lesions and through the thalamus were stained with thionin. Light microscopy revealed that lesions 1 and 2 (Figure 11) were placed at the level of the entering rootlets of the facial nerve in the caudal one-third of the pons. The lesions involved the superior vestibular nucleus at this level and extended from the floor of the fourth ventricle superiorly to the middle of the lateral reticular formation inferiorly. The lesion did not directly involve the nucleus of the tractus solitarius at this level; however, the lesion was so extensive that any secondary gustatory fibers which may have crossed to the opposite side were most probably interrupted in their contralateral passage and indeed the secondary gustatory tract which had been traced from medullary levels was observed to become larger and more discrete at this level (Figure 12).

Lesions 3 and 4 were placed at rostral glossopharyngeal levels in the medulla. Lesion 3 (Figure 11) involved the deep white matter of the cerebellum and degenerating axons were traced into the left superior cerebellar peduncle. Lesion 4 (Figure 13) was seen to involve the middle, lateral and inferior vestibular nuclei as well as the nucleus of the tractus solitarius (dorsal visceral gray) at the level of the most rostral portion of the glossopharyngeal nerve.

A small, finely medullated bundle of degenerating fibers was observed at the level of the lesion in the medulla to lie just dorsal to the medial lemniscus. At caudal pontine levels this same bundle becomes larger and more discrete (Figure 11). It is assumed that in its rostral projection to the contralateral side the secondary gustatory tract crosses primarily at an oblique angle to reach its

destination just dorsal to the medial lemniscus, for only a few fine fibers can be traced directly across the midline. As the medial lemniscus assumes its characteristic horizontal plane in the rostral pons, the secondary gustatory fibers are seen to maintain their medial and dorsal position in relationship to the medial border of the medial lemniscus (Figure 14 and Figure 15). At rostral inferior collicular levels (Figure 16) degenerating axons of the secondary gustatory tract (Figure 17) are still dorsal to the medial border of the medial lemniscus in close relationship with the ventral secondary ascending tract of the trigeminal nerve. However, at this level the secondary gustatory fibers also lie in close relationship to the ventral portion of the central tegmental bundle within which there is a small degenerating descending component which represents a path resulting from the lesion of the left brachium conjunctivum.

At the junction between the inferior and superior colliculus (Figure 18) secondary gustatory fibers interdigitate with the most lateral portion of the decussating degenerating ascending axons of the brachium conjunctivum (primarily dentatorubrothalamic tract) from which they cannot be clearly distinguished (Figure 19) until their respective terminations within the dorsal thalamus. Many fibers of the ascending component of the brachium conjunctivum terminate within the rostrally located small-celled portion of the red nucleus, whereas other components within this bundle project directly to the nucleus ventralis of the dorsal thalamus. Within the medially and rostrally located parvocellular portion of the nucleus ventralis posteromedialis (arcuate nucleus of many authors) of the dorsal

thalamus terminal degeneration of the secondary ascending gustatory fibers was observed.

The level of termination within the dorsal thalamus of ascending degenerating axons of the secondary gustatory tract is shown in Figure 20. Terminal degeneration within the most rostral portion of the nucleus ventralis posteromedialis pars parvocellularis is seen in Figure 21; and terminal degeneration of the ascending component of the brachium conjunctivum in the nucleus ventralis lateralis can be observed in Figure 22.

Monkey NR 020

Operation NR One

Preoperative Testing: 27 April 1975 and 28 April 1975. Monkey NR 020 ate the lemon soaked banana without hesitation. The animal bit into but did not continue to eat a piece of lemon. The monkey immediately rejected the quinine treated banana upon tasting the quinine.

Operative Protocol: Male. Weight - 3.0 kg. 29 April 1975. The skin and temporalis muscle were reflected on the left side of the head. A left craniotomy was performed and the bone and dura overlying the base of the central fissure and the superior and middle temporal gyri were removed. A large lesion which involved the base of the precentral gyrus, the base of the postcentral gyrus, the adjacent superior temporal gyrus and a small portion of the middle temporal gyrus (Figure 23) was placed with surgical suction. Massive bleeding of the middle cerebral artery resulted. The bleeding was

controlled with Gelfoam and as soon as the surgical area was dry the wound was closed.

Postoperative Notes: The monkey showed a marked paralysis of the entire right side of the body. However, by 29 July 1975, this monkey had apparently fully recovered from his paralysis. The monkey was tested for his responses to quinine and bitter substances on this date. The monkey rejected the quinine treated banana more slowly than prior to surgery and he no longer found the slice of lemon objectionable, for he ate the entire slice without hesitation.

Operation NR Two

Operative Protocol: Male. Weight - 2.9 kg. 19 August 1975. A right craniotomy was performed and the bone overlying the base of the central fissure and the adjacent superior temporal gyrus was removed. The dura was incised with a cutting needle and reflected. Using a micropipette for surgical suction, the cortex at the base of the central fissure, its opercular surface and the adjacent superior temporal gyrus were removed. Little bleeding occurred and the wound was closed.

Postoperative Notes: The monkey fully recovered from this operation with no apparent neurological deficits. Following this second operation little difference could be detected in the taste responses of this monkey. The response to the quinine treated banana was the same as had been observed following the first operation in that the monkey still rejected the quinine more slowly than had been observed prior to any surgical procedure and he still ate the slice of lemon.

The location and extent of the lesions in both hemispheres are seen in Figures 23 and 24.

Sacrificed: 1 September 1975.

Description of resulting degeneration from the lesion in the right cerebral hemisphere: The right cerebral hemisphere of monkey NR 020 was sliced in a coronal plane on a sliding microtome at 30 microns after having been frozen with solid carbon dioxide. Every fifth section was stained by the De Olmos and Ingram (1971) silver method for impregnating degenerating axons. Adjacent sections were stained with thionin.

The level of the lesion at the base of the central fissure can be observed in Figure 25. The base and the inferior portion of the opercular surface were ablated as well as the adjacent portion of the superior temporal gyrus. From the lesion in the frontal and parietal operculum fine degenerating axons can be traced which course through the extreme capsule to end in the dorsal anterior island (Figure 26) thus linking the bases and opercular surfaces of the pre- and postcentral gyri to the island by short association bundles. Degenerating axons from the frontal and parietal lesions can also be traced to the nucleus ventralis posteromedialis of the dorsal thalamus (Figure 27 and Figure 28). These axons course dorsal to the claustrum, and, accompanying the thalamocortical sensory radiations (Figure 29) pass through the posterior limb of the internal capsule to gain the thalamus. Terminal degeneration is abundant in the nucleus ventralis posteromedialis (as described by

Olszewski, 1952) with only a few fine fibers terminating in the nucleus ventralis posteromedialis parvocellularis. Cytolysis of the cells of the nucleus ventralis posteromedialis as well as massive gliosis is clearly evident thus indicating retrograde degeneration from the cortical lesions. Even though degenerating axons could be traced to the parvocellular portion of the nucleus ventralis posteromedialis little if any retrograde degeneration is observable in this portion of the nucleus.

Monkey NR 8373

Preoperative Testing: 19 June 1975. Monkey NR 8373 immediately expectorated the quinine treated banana but she did not hesitate to eat a piece of lemon.

Operative Protocol: Female. Weight - 4.7 kg. 20 June 1975. The skin and underlying connective tissue were reflected from the superior medial aspect of the left side of the head. A burr hole was drilled through the bone to the dura at the stereotaxic coordinates A 0.7 and L 5. The electrode was inserted through the cortex of the left cerebral hemisphere at the stereotaxic coordinates A 0.7, L 5 and H -12. A stimulus of 1 volt produced movements of the lower face at the corner of the mouth indicating that the tip of the electrode was in or near the motor nucleus of the facial nerve. An electrolytic lesion (lesion 1) with a current of 3.5 ma for a period of 30 seconds was then placed at the coordinates A 0.7, L 5 and H -9.5. The electrode was then moved caudally to coincide with the level of

the entering rootlets of the glossopharyngeal nerve and two stereotaxic electrolytic lesions were then placed at the selected coordinates (Lesion 2, P 2.6, L 3 and H -11.5 and Lesion 3, P 2.6, L 4 and H -12.5).

Postoperative Notes: This monkey exhibited no apparent neurological deficits upon recovery from surgery.

Postoperative Testing: 27 June 1975. The monkey's responses to quinine and bitter substances were the same as they had been prior to surgery. She immediately rejected the quinine treated banana upon tasting the quinine; she did not hesitate to eat the slice of lemon.

Sacrificed: 4 July 1975.

Description of the stereotaxic lesions and resulting degeneration: The brain stem of this monkey was sliced in a transverse plane at 25 microns on a sliding microtome after having been frozen with solid carbon dioxide. Every tenth section was stained by the De Olmos and Ingram (1971) method for impregnating degenerating axons with silver. Adjacent sections through the sites of the lesions were stained with thionin. Lesion 1 (Figure 30) was a small lesion involving portions of the superior and middle cerebellar peduncles. Lesion 2 (Figure 31 and Figure 32) was a rather large lesion which interrupted, primarily, the rootlets of the glossopharyngeal nerve as they enter the ventrolateral aspect of the nucleus of the tractus solitarius (nucleus parasolitarius). The most ventrolateral portion of this nucleus was slightly involved as well. The rostral projection of this lesion involved the dorsal aspect of the spinal tract of the trigeminal

nerve. Lesion 3 (Figure 32) was a lesion of the ventral cochlear nucleus. Degenerating axons of the glossopharyngeal nerve can be observed to enter directly into the tractus solitarius and terminal degeneration is present throughout the nucleus of the tractus solitarius (dorsal visceral gray) at the level of the lesion involving the rootlets of the glossopharyngeal nerve. A few degenerating axons of the glossopharyngeal nerve ascend a short distance within the tractus solitarius but most end at their level of entrance into the brain stem (Figure 33).

Just rostral to the caudal extent of the lesion which interrupted the glossopharyngeal nerve, a small bundle of degenerating axons accumulate in the most medial aspect of the medial lemniscus. Degenerating fibers forming this bundle are most prominent in the ipsilateral medial lemniscus, but there are a few degenerating axons located in the same position in the contralateral medial lemniscus. These degenerating axons can be traced with certainty only through the most rostral levels of the pons (Figures 34 and 35). Throughout their passage to the rostral pons the degenerating axons maintain their relationship with the medial lemniscus.

The cumulative results of the cortical and stereotaxic lesions defining the central gustatory pathways in the monkey are illustrated in Figure 36. The normal left cerebral hemisphere of Macaca mulatta is shown in Figure 37 and is contrasted with the same cerebral hemisphere, Figure 38, in which the fronto-parietal operculum and the temporal operculum have been dissected to demonstrate their relationships with the Island of Reil.

DISCUSSION

Cortex

Throughout the first part of this century, it was believed by most observers that the cortical localization for gustatory impulses was in the temporal lobe in close association with afferent olfactory impulses. Ferrier (1886) concluded in experimental procedures on two monkeys that bilateral lesions of the lower temporo-sphenoidal lobe resulted in abolition of smell and taste over the entire tongue. Ferrier thus felt "...the gustatory centres are situated at the lower extremity of the temporo-sphenoidal lobes in close relation with those of smell." Ferrier failed to mention, however, that the adjacent parietal lobe had also been damaged in his experiments, as is shown in Figure 101 of his book. The significance of this fact was also noted by Börnstein (1940a). Kennedy (1911) considered gustatory auras and olfactory hallucinations to be important tools in diagnosing uncinate fits and temporal lobe lesions, linking gustatory impulses with olfactory impulses in the temporal lobe. Cushing (1922) discussed ten of fifty-nine clinical cases in which there were temporal lobe lesions. Of these only two patients had gustatory auras; one patient thought he had smelled and tasted peaches on one occasion and insisted that he smelled and tasted roasted peanuts on another, and another

patient complained of gustatory sensations which were peppermint in nature. Villiger (1925) stated "...the gustatory center has not been definitely located but probably adjoins that for smell," and Grinker (1937) considered the hippocampal formation to have both olfactory and gustatory functions.

Börnstein (1940a) in an extensive paper, reviewed the clinical and experimental evidence for the temporal lobe theory for the cortical localization of taste and concluded that there was insufficient evidence to support this theory. Three clinical cases each one of which was the result of a bullet wound to the left parietal bone were discussed by Börnstein (1940b). The first case resulted in a lesion of the middle third of the pre- and postcentral gyri. The patient had an ageusia for sweet, sour, salty and bitter on the contralateral side of the tongue except for hypogeusia for salty substances on the contralateral tip. Taste was intact or only slightly impaired on the ipsilateral side of the tongue. The second case resulted in a lesion which was located in the face and tongue areas of the pre- and postcentral gyri, i.e., the upper border of the posterior frontal operculum and the parietal operculum. The patient exhibited an ageusia for sweet, sour and weak bitter solutions on the contralateral border of the tongue with slight hypogeusia for salty. On the contralateral tip there was a hypogeusia for sweet, salty and sour and on the contralateral base only sour and sweet were impaired. The third patient developed a parietal opercular syndrome not from the bullet wound itself but rather from the transplantation

of a bone graft over the pre- and postcentral gyri which resulted in a subdural hematoma over this area. There was a hypogeusia for sweet, salty and bitter and a slight hypogeusia for sour on the contralateral side of the tongue. The border of the tongue on the contralateral side was chiefly involved. Gustatory disturbances were slight on the ipsilateral side of the tongue. Shenkin and Lewey's clinical case (1943) in which there was an involvement of the most inferior portion of the postcentral gyrus also indicated this area as a possible site for the cortical localization of gustatory sensations.

Gorschkow (1901) postulated that gustatory impulses were localized in the potential island region in the dog. Adler (1935) gave support to the possibility that the island may be the cortical area responsible for the cortical recognition of gustatory impulses. She discussed a case in which a tumor grew into the island from the superior temporal lobe. The patient had a hypogeusia on the tongue contralateral to the cortical lesion. Penfield and Erickson (1941) cited a clinical case in which the patient had seizures preceded by a gustatory aura of an indescribably disagreeable nature. "This patient had a well circumscribed slowly growing astrocytoma of the island of Reil." Penfield and Erickson concluded that taste was probably represented cortically at the base of the pre- and postcentral gyri in close association with the cortical areas for the jaws and the tongue. Penfield and Jasper (1954), based on their observations of clinical cases, stated "...gustatory sensation has a representation in the cortex which seems to be closely related to

salivation, to the alimentary system, and to second sensory representation. It is located beneath the fissure of Sylvius and within the circular sulcus." Gustatory impulses have been localized in the opercular insular junction and in the floor of the anterior island by Penfield and Rasmussen (1950).

Ruch and Patton (1946) concluded in a series of cortical ablation experiments on monkeys and chimpanzees that taste deficits only occurred when the buried cortex of the fronto-parietal operculum was invaded. After recognizing that Gerhardt had described an area of granular cortex of sensory type in the chimpanzee which was located deep in the frontal operculum bordering on the circular gyrus, Patton and Ruch (1946) attempted destruction of this area. Successful ablation was achieved in only one monkey resulting in a severe taste impairment in regard to bitter solutions. Patton and Ruch (1946) expanded their previous conclusions by stating that taste is localized in the parainsular operculum.

Bagshaw and Pribram (1953) observed a lowering in quinine acceptance thresholds in monkeys in which the anterior insula or both the anterior island and the anterior supratemporal plane had been surgically ablated. Lesions of the anterior island plus operculum resulted in moderate decreases in quinine thresholds. Lesions of the insula, the operculum and the anterior supratemporal plane together resulted in marked and prolonged ageusia.

Bradley (1963), in his experiments on macaques, considered the cortex at the base of the central fissure and the opercular surface

of this area to be important for normal taste discrimination. He, furthermore, suggests from his experiments that taste may have a representation at mid-brain levels.

Bilateral cortical representation in the squirrel monkey for all three nerves innervating the tongue, that is, the chorda tympani branch of the facial nerve, the lingual-tonsilar branch of the glossopharyngeal nerve, and the lingual branch of the trigeminal nerve, was demonstrated by Benjamin et al. (1968) by the utilization of evoked potential techniques. The cortical area found to be responsive to electrical stimulation was in somatic sensory area I at the base of the pre- and postcentral gyri. The major projection, however, of the chorda tympani and lingual-tonsilar nerves was found to be ipsilateral. In a related study which also utilized evoked potential techniques, a responsive locus for taste was located in the most anterior opercular-insular cortex (Benjamin and Burton, 1968). Only stimulation of the ipsilateral chorda tympani nerve and the ipsilateral lingual-tonsilar nerve was effective.

Chemical stimulation of the tongue and/or electrical stimulation of the ipsilateral chorda tympani nerve produced evoked potentials in neurons of the nucleus ventralis posteromedialis pars parvocellularis in the rat and marmoset (Ganchrow and Erickson, 1972). Antidromic stimulation of these same cells by electrical stimulation of the cortical projection area of the chorda tympani nerve indicated direct thalamocortical projections of taste neurons and direct projections from the cortex to the cells of the thalamus which receive gustatory impulses.

Based on cytoarchitectural studies in the squirrel monkey, Sanides (1968) concluded that there was a surface cortical gustatory area in somatic sensory area I and also a deep pure gustatory area located in the frontal operculum and bordering on the insula.

In cat, Patton and Amassian (1952) reported a bilateral cortically responsive area to electrical stimulation of the chorda tympani nerve which was superior to the rhinal fissure and rostral to the anterior ectosylvian fissure. The insula as well as other cortical areas were unresponsive to the stimulation. Ruderman et al. (1972) obtained responses of neurons in the nucleus ventralis posteromedialis pars parvocellularis of the cat while stimulating the anterior portion of the tongue with citric acid solutions. Light brush strokes of various facial regions resulted in evoked potentials which were recorded from electrolytes in the nucleus ventralis posteromedialis. Electrolytic lesions of the nucleus ventralis posteromedialis pars parvocellularis resulted in cortical degeneration in either the lateral or both banks of the presylvian sulcus. Electrolytic lesions placed in the nucleus ventralis posteromedialis resulted in cortical degeneration in the coronal gyrus. Thus separate cortical projection areas for taste and facial tactile impulses were delineated. The cortical area responsive to mechanical stimulation of the ipsilateral chorda tympani nerve in the cat was located by Burton and Earls (1969) in an area which extended from the coronal gyrus anteriorly to the orbital sulcus posteriorly and lay dorsal to the rhinal fissure. This active surface cortex was located within somatic sensory area I for the tongue.

Cohen et al. (1957) explored the cortical projection area of the tongue (orbital surface of the cerebral hemisphere) in cat, with recording electrodes. This area was responsive to electrical stimulation of the chorda tympani and lingual nerves and also to thermal, mechanical and gustatory stimulation of the tongue. Some cortical cells were responsive to electrical stimulation of both chorda tympani and lingual nerves. Cortical cells which responded to mechanical stimulation did not respond to gustatory or thermal stimulation. Evoked potentials were recorded from five cortical cells which responded only to gustatory stimuli, but their response was not specific for a particular taste modality. Zotterman (1958) also reported evoked potentials from single cortical cells in the cat which responded only to gustatory modalities, but again the cells were not specific in their response to particular gustatory sensations. Landgren (1957) reported 27 single cortical cells (out of 101 cortical cells from which evoked potentials were recorded) which responded to more than one type of sensory stimulation. Cells were found which responded to combinations of touch, stretch, cooling, warming and various gustatory stimuli. Various sensory modalities including taste, therefore, were seen to converge on single cortical cells.

Evoked potential studies were utilized by Benjamin and Pfaffmann (1955) to locate the cortical receptive zones for the glossopharyngeal and chorda tympani nerves in the rat. The chorda tympani nerve was found to be represented bilaterally in the cerebral cortex whereas the glossopharyngeal nerve only had a contralateral cortical

representation. Bilateral ablations of this cortical area resulted in permanent taste deficits. The authors stated that the boundaries of the lesions included the anterior insular cortex as delimited by Krieg in the rat.

Bilateral removal of a small area of cortex in the rat just dorsal to the rhinal fissure in somatic sensory area I produced partial taste deficits (Benjamin and Akert, 1959). Inclusion of an adjacent fringe area in bilateral ablations caused severe gustatory impairments. This cortical area corresponded to the cortex which was responsive to stimulation of the glossopharyngeal and chorda tympani nerves as determined by evoked potential techniques. Ablation of all neocortex with the exception of this focal gustatory area had no effect upon the taste discrimination of the animals.

Electrical stimulation of the chorda tympani, glossopharyngeal and lingual nerves in rabbits (Yamamoto and Kawamura, 1975) demonstrated a primarily ipsilateral responsive area in the insular cortex for the chorda tympani nerve, a primarily contralateral response in the same cortical area for the glossopharyngeal nerve and predominantly contralateral projection in somatic sensory area I for the lingual nerve. All projections, however, were bilateral. The cortical projection area for the chorda tympani nerve was found rostral to the projection for the glossopharyngeal nerve and partially overlapped it and the lingual nerve projection area partially overlapped the dorsal aspect of the chorda tympani projection area.

The possible existence of a subcortical and even subthalamic localization of taste responses in carnivores was demonstrated by Macht (1951). Mesencephalic and bulbospinal cat preparations rejected quinine, saline and acetic acid treated substances at the same concentrations as normal rejection thresholds.

In the present study lesions of the cortex at the base of the central fissure and its opercular surface resulted in taste deficits. A unilateral destructive lesion of this area resulted in a definite slowing of the taste responses of one monkey and a loss of some discrimination in regard to sour substances in two out of three monkeys. Destructive lesions placed bilaterally in the cerebral cortex at the base of the central fissure and extending into the opercular surfaces of the precentral and postcentral gyri resulted in a slowing of the response to quinine in one monkey. More importantly the loss of a more delicate type of discrimination, in regard to sour substances, was observed with Cercopithecus aethiops following bilateral ablation of this area.

It is evident from the work of others and from my own work that the cortex at the base of the central fissure extending into the fronto-parietal operculum is of particular importance in the reception of gustatory modalities and, being directly continuous with primary sensory cortex, represents primary receptive sensory cortex for taste. The functional significance of this area as it relates to the anterior island has, however, remained somewhat obscure. Experimental observations have repeatedly shown that

the anterior island in primates and man is involved in the recognition of gustatory modalities. The coronal sections of monkey NR 020 indicate that the cortex at the base of the central fissure and continuing into the fronto-parietal operculum is linked to the dorsal anterior island by short association bundles which course through the extreme capsule. These short association bundles, then, relate gustatory modalities from their primary receptive cortex to the association cortical areas involved in the recognition of gustatory impulses, that is the anterior dorsal part of the Island of Reil.

Elliot Smith (1907) traced, in man, fibers from the lateral olfactory tract into the anterior island. Crosby, Humphrey and Lauer (1962) stated that "The olfactory stalk has been traced into the frontal end of the island on the pyriform side. This relation is seen in the His embryological models." Thus, the anterior island, which receives both olfactory and gustatory impulses, is a correlative cortical area for special visceral afferent sensations and allows for subjective discrimination in regard to these sensations. Special visceral sensations are in turn correlated with other known general visceral functions of the island. Penfield and Rasmussen (1950) elicited a number of visceral sensations upon electrical stimulation of the insula in awake patients. Upon stimulation of various locations within the insula, patients reported a curious disagreeable taste, the sensation of nausea, vomiting, a feeling of illness, an aura of attack with swallowing and mouth opening and the desire to defecate. Kahn et al. (1969) discussed several clinical

cases involving the insula. One patient complained of a bitter taste in his mouth which preceded convulsions. The patient had a tumor of the anterior island. Another patient had had a four-year history of convulsions during which he complained of nausea and often vomited. At operation an arteriovenous malformation was discovered which had a focal point in the parietal operculum and the posterior island. A third patient had auras of abdominal pain which frequently preceded convulsions. A right temporo-parietal cyst was found at operation. The location of the lesion suggested that stimulation in the posterior island region resulted in abdominal pain.

Kahn et al. (1969) suggested that there is some evidence that primary gustatory cortex is connected to the uncus region by fascicles which pass through the island. Such connections could account for reported cases (Kennedy, 1911 and Cushing, 1922) in which gustatory auras preceded convulsions which were the result of lesions located primarily in the temporal lobe. Uncinate fits which are preceded by auras of an olfactory nature are the result of lesions located primarily in the region of the amygdala; or along the lateral olfactory tract and perhaps the anterior perforated space. However, uncinate fits which are preceded by gustatory auras might result from lesions located largely in the anterior island but which involve those fascicles which connect the island with the uncus region.

Thalamus

Adler's clinical case (1934) indicated the nucleus ventralis posteromedialis pars parvocellularis as the thalamic reception nucleus for secondary ascending gustatory pathways. Walker (1938) concluded, from the available clinical and experimental information, that this nucleus was the most likely area of thalamic termination for gustatory modalities.

Walker (1934) demonstrated thalamocortical connections to the central operculum from the nucleus ventralis posteromedialis pars parvocellularis (arcuate nucleus) in the macaque. A large lesion of the fronto-parietal operculum resulted in complete retrograde degeneration of this thalamic nucleus. Retrograde degeneration in the parvocellular portion of the nucleus ventralis posteromedialis was also reported by Le Gros Clark (1937) following the cortical ablation of a large area which included the cortex at the base of the central fissure.

Bilateral stereotaxic lesions of the nucleus ventralis posteromedialis and/or the parvocellular portion of this nucleus in the macaque resulted in varying degrees of taste deficits dependent upon the extent of damage to the nucleus (Blum, Walker and Ruch, 1943, Patton, Ruch and Walker, 1944).

Chow and Pribram (1956) reached the conclusion, based on retrograde degeneration studies following the placing of lesions at various cortical locations in the macaque, that the nucleus ventralis posteromedialis projected to the operculum and to the anterior island.

Using evoked potential techniques (Blomquist, Benjamin and Emmers, 1962) the dorsal thalamus in the squirrel monkey was explored bilaterally with recording electrodes for responses to electrical stimulation of the chorda tympani nerve, the lingual-tonsilar branch of the glossopharyngeal nerve and the lingual nerve. The responses of the two nerves relaying gustatory modalities were reported to be largely ipsilateral with meager contralateral projections, whereas the lingual nerve was reported to have a mainly contralateral projection. The responses of the three nerves were also reported to be in the posterior portion of the nucleus ventralis posteromedialis subjacent to the centromedian nucleus. The chorda tympani was represented rostral to the lingual-tonsilar branch of the glossopharyngeal nerve and the lingual nerve was found to be more laterally located within the ventromedial complex than either of the two "taste" nerves.

Roberts and Akert (1963) performed a series of experiments on rhesus monkeys in which insular and opercular lesions were made. The workers stated that retrograde degeneration in the nucleus ventralis posteromedialis pars parvocellularis was present in all cases where there was injury to both operculum and insular cortex. The authors reported, however, that lesions of the operculum were not necessary for retrograde degeneration within this nucleus, for they presented one example in which the opercular areas were completely removed without resulting damage to the nucleus ventralis posteromedialis pars parvocellularis. It was, therefore, concluded

that it was the anterior island which received primary afferent connections from the nucleus ventralis posteromedialis pars parvocellularis and not the fronto-parietal operculum. Locke (1967), however, reported retrograde degeneration in the rhesus monkey within the nucleus ventralis posteromedialis pars parvocellularis when the white matter of the parietal or frontal operculum was invaded. Lesions restricted to the insula in which the overlying operculum was not damaged showed no retrograde cell changes within the thalamus.

Electrical stimulation of the nerves transmitting gustatory modalities produced evoked potentials in the cerebral cortex of the squirrel monkey (Benjamin et al., 1968). This cortical area, located in the surface cortex in somatic sensory area I, was bilaterally ablated. There resulted no retrograde degeneration within the nucleus ventralis posteromedialis pars parvocellularis; however, when an additional ablation was made in the anterior opercular insular cortex retrograde degeneration was observed within the ventromedial complex of the dorsal thalamus. The authors stated "...thus the taste system has no 'essential' connections to neocortex in the squirrel monkey." They concluded that there are only sustaining projections to somatic sensory area I in the squirrel monkey in regard to gustatory pathways.

Benjamin and Burton (1968) removed the opercular-insular cortex which was responsive to gustatory stimulation, with minimum damage to somatic sensory area I, in three squirrel monkeys. No observable

retrograde degeneration was found within the nucleus ventralis poeteromedialis pars parvocellularis. However, when somatic sensory area I was included in the lesions retrograde degeneration was reported within the nucleus ventralis posteromedialis pars parvocellularis. These investigators also concluded that there were only sustaining connections to the neocortex of the squirrel monkey from the nucleus ventralis posteromedialis pars parvocellularis.

Ables and Benjamin (1960) placed stereotaxic lesions in the thalamus of the albino rat. Lesions of the most medial portion of the subnucleus of the ventralis resulted in permanent taste deficits. The authors concluded that this nucleus represents the thalamic relay for taste in the albino rat.

Wolf (1968) traced degenerating fibers from lesions of the medial subnucleus of the ventral nuclear thalamic complex in rat. Degenerating axons were traced rostrolaterally from this nucleus through the thalamus, internal capsule, globus pallidus and striatum, and were observed to terminate in the insular and parietal cortices around the region of the middle cerebral artery. Cortical lesions of the area of termination of the thalamocortical fibers resulted in the degeneration of axons which accompanied the thalamocortical fibers and which terminated in the dorsal thalamus just dorsal to the medial subnucleus.

Considering the available literature, there can be little question that the nucleus ventralis postermedialis pars parvocellularis receives secondary gustatory projections from that part of the

nucleus of the tractus solitarius (dorsal visceral gray) which is found at the level of the facial and glossopharyngeal nerves in the pons and medulla. In the present study such projections were confirmed by the rostral projection of secondary gustatory fibers to the contralateral nucleus ventralis posteromedialis pars parvocellularis in monkey NR 8501 and were indicated by the presence of terminal degeneration in this nucleus in monkey NR 8349 in which the ascending gustatory and ventral secondary trigeminal paths were interrupted in their passage to the contralateral side of the brain stem.

The neurophysiological evidence for the ipsilaterality, contralaterality or bilaterality of the secondary projections of the dorsal visceral gray is conflicting. Terminal degeneration within the most rostral portion of the nucleus ventralis posteromedialis pars parvocellularis in monkey NR 8501 from a lesion of the contralateral nucleus of the tractus solitarius at rostral glossopharyngeal levels is in accord with the observations that the lingual-tonsilar nerve has a primarily contralateral cortical (and therefore thalamic) projection (Benjamin and Pfaffmann, 1955, Yamamoto and Kawamura, 1975). Certainly the clinical evidence overwhelmingly favors thalamic and cortical projections of gustatory modalities which are primarily contralateral in termination.

Whether there are direct fiber connections from the nucleus ventralis posteromedialis pars parvocellularis of the dorsal thalamus to the anterior insular cortex is questionable. Recent studies by

Roberts and Akert (1963), Benjamin et al. (1968) and Benjamin and Burton (1968) question the direct projection of fibers from the nucleus ventralis posteromedialis pars parvocellularis to somatic sensory area I at the base of the central fissure in monkey. These authors concluded that there were only sustaining axons to both the taste area in somatic sensory I and the anterior island and that both areas must be surgically ablated to result in retrograde degeneration within the nucleus ventralis posteromedialis pars parvocellularis. Locke (1967), however, reported retrograde degeneration within this nucleus following ablation of the fronto-parietal operculum as did Walker (1934) and Le Gros Clark (1937).

It is likely (as is indicated from the observations of slides from monkey NR 020) that the relationship between the primary receptive sensory cortex for taste in somatic sensory area I (located at the base and opercular surfaces of the pre- and post-central gyri) and the anterior island is one in which the two cortical areas are linked by short intra- and intercortical association fibers. Certainly they differ in function.

Pons and Medulla

The organization of and contributions to the fasciculus solitarius are well known and well documented (Allen, 1923a, Ariens Kappers et al., 1936, Nageotte, 1906, Schwartz et al., 1951 and Rhoton et al., 1966). Generally, the rootlets of the facial, glossopharyngeal and vagus nerves carrying primary special visceral

afferent fibers enter the brain stem at their respective levels, contribute to the fasciculus solitarius and synapse in the nucleus of the tractus solitarius (dorsal visceral gray) at or about their level of entrance into the brain stem. The greatest contribution to the tractus solitarius lies opposite the entrance of the sensory root of the glossopharyngeal nerve (Allen, 1923a).

Several investigators (Nageotte, 1906, Schwartz et al., 1951 and Rhoton, 1968) described an ascending component of the fasciculus solitarius from the facial nerve which terminated on the prefacial portion of the solitary nucleus.

Electrical stimulation of the chorda tympani nerve in the middle ear of the cat was employed by Bernard and Nord (1971) to report (by the use of recording depth electrodes) a "pontine taste area." This taste area was located dorsolateral to the sensory trigeminal nucleus.

Degenerating fibers from lesions of the nucleus of the tractus solitarius at the level of the facial nerve in the rat were traced rostrally to an ipsilateral termination in an area ventral to the brachium conjunctivum as it enters the pons (Norgren and Leonard, 1973). Degenerating fibers from lesions placed in this "pontine taste area" were traced forward bilaterally to the nucleus ventralis posteromedialis as well as to the subthalamus, the dorsolateral hypothalamus, and the subpallidal gray in the ventral forebrain.

Norgren (1974) described degenerating axons from the "pontine taste area" which terminated not only in the medial extension of the

ipsilateral ventrobasal complex (nucleus ventralis postermedialis) in the rat but also in the substantia innominata. Antidromic activation of the cells of the substantia innominata and the thalamic taste receptive nucleus resulted in activation of cells in the "pontine taste area" as determined by recording electrodes.

This same "pontine taste area" was injected with tritiated proline in the albino rat (Norgren, 1976). Primarily ipsilateral projections were traced autoradiographically which collect in the central tegmental tract and ascend to their termination in the dorsal thalamus. Other projections were traced to the amygdala and the hypothalamus.

Degenerating fibers from lesions of the cephalic half of the nucleus of the tractus solitarius (except for its most extreme cephalic portion) were traced into the medial aspect of the contralateral medial lemniscus in the guinea pig (Allen, 1923b). These fibers maintained their relationship with the medial lemniscus throughout their rostral projection to their termination in the rostral medial portion of the nucleus ventralis posteromedialis of the dorsal thalamus.

In the material reported in the present study a lesion of the glossopharyngeal nerve rootlets (monkey NR 8373) resulted in terminal degeneration of these fibers in the nucleus of the tractus solitarius at or about their level of entrance into the brain stem. A few degenerating axons were observed to ascend for a short distance within the fasciculus solitarius before their level of termination.

Degenerating fibers from the lesion of the tractus solitarius at rostral glossopharyngeal levels (monkey NR 8501) were traced to the contralateral side of the brain stem. Terminal degeneration of this secondary gustatory tract was observed only in the contralateral nucleus ventralis posteromedialis pars parvocellularis.

CONCLUSIONS

1. The cortex at the base of the central fissure, that is the fronto-parietal operculum, and its opercular extension represent primary sensory receptive cortex for gustatory modalities.
2. This primary receptive cortex for taste is linked to the anterior Island of Reil by short inter- and intracortical association fibers. Thus the anterior island is a gustatory association area involved in the subjective recognition of gustatory modalities.
3. The nucleus ventralis posteromedialis pars parvocellularis of the dorsal thalamus is the thalamic receptive nucleus for gustatory impulses in the macaque.
4. Fibers which originate at rostral glossopharyngeal levels from the dorsal visceral gray terminate in the contralateral nucleus ventralis posteromedialis pars parvocellularis.

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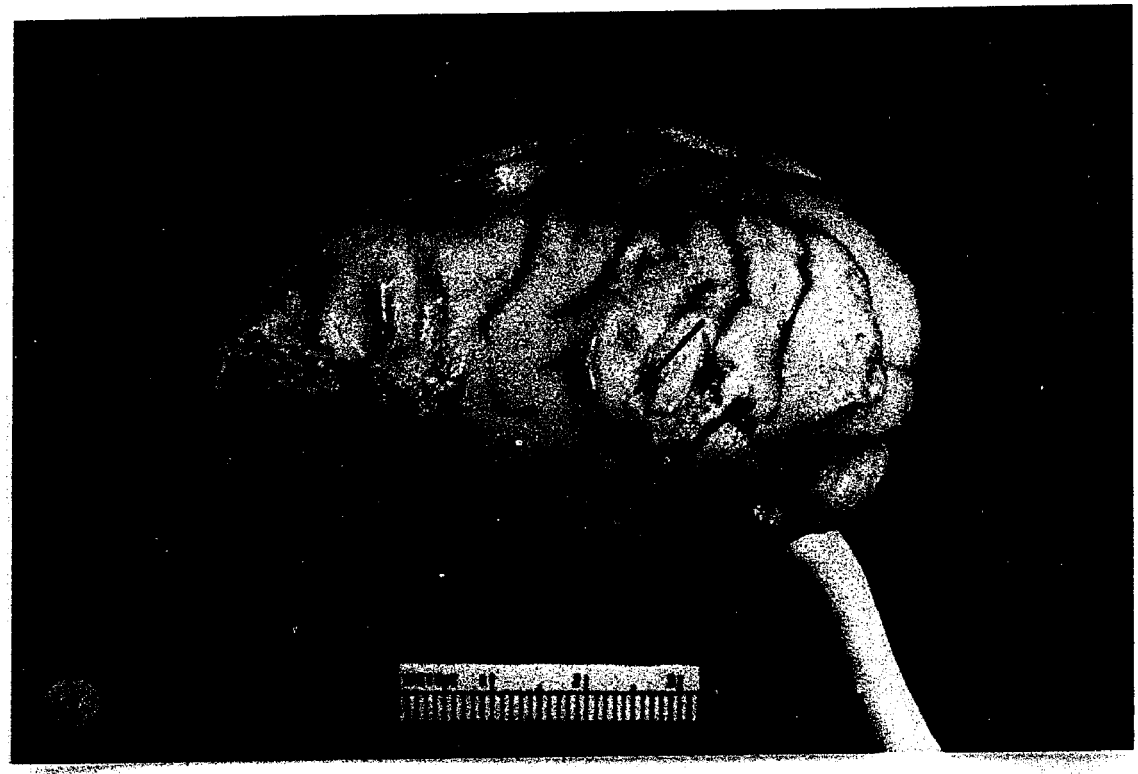
PLATES

Plate 1

Explanation of Figures

1. The left cerebral hemisphere of Monkey NR 7744. The arrow indicates the lesion of the postcentral gyrus and its opercular surface.

2. The left cerebral hemisphere of Cercopithecus aethiops. The cortical lesion at the base of the pre- and postcentral gyri is clearly evident. Arrow indicates the central fissure (CF).



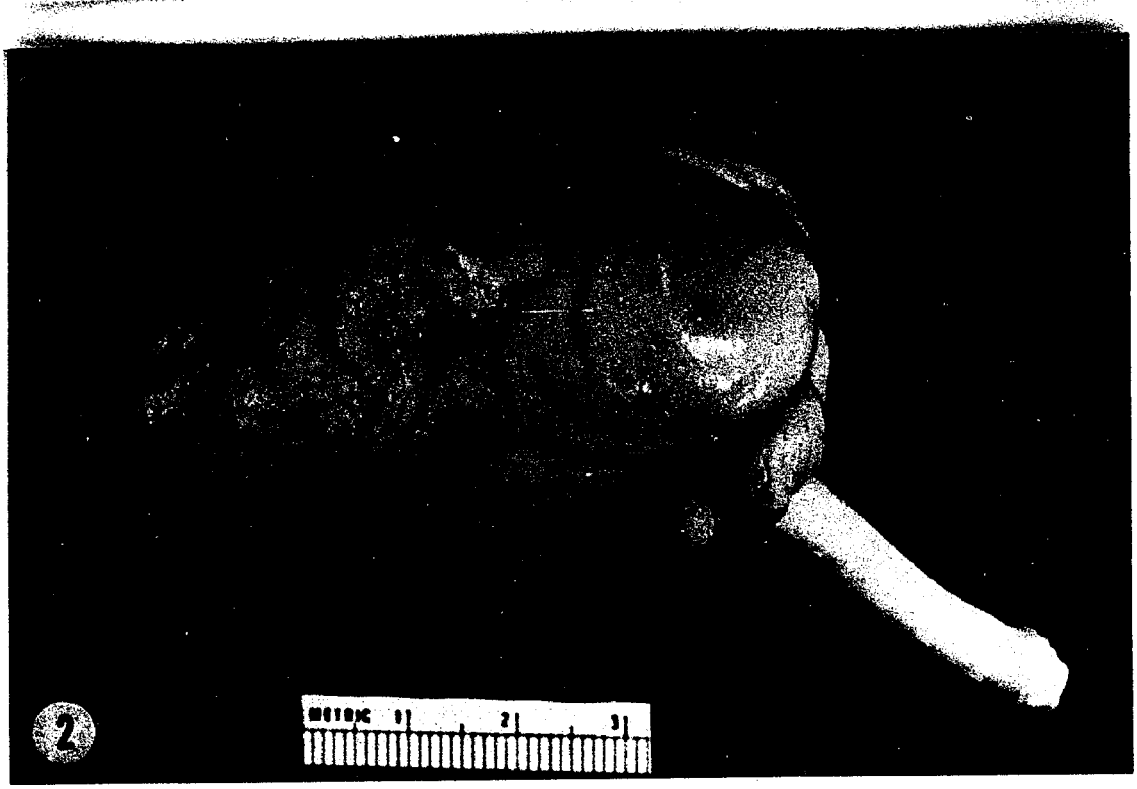

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Plate 2

Explanation of Figures

3. The right cerebral hemisphere of Cercopithecus aethiops. The cortical lesion at the base of the pre- and postcentral gyri, which also included the adjacent superior temporal gyrus, is clearly evident.

4. The left cerebral hemisphere of Monkey NR 025. The cortical lesion at the base of the central fissure and the adjacent superior temporal gyrus is clearly shown.

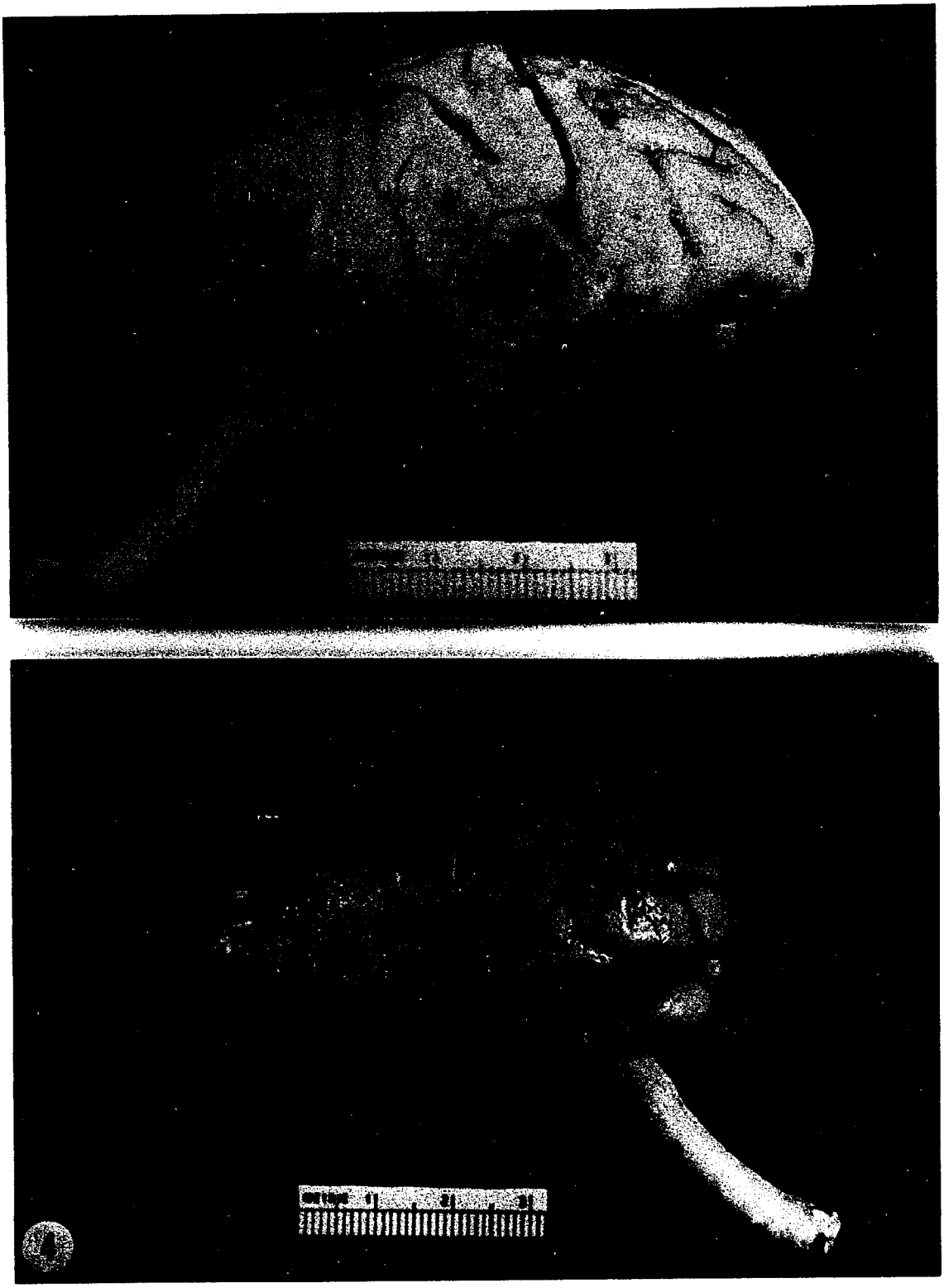


Plate 3

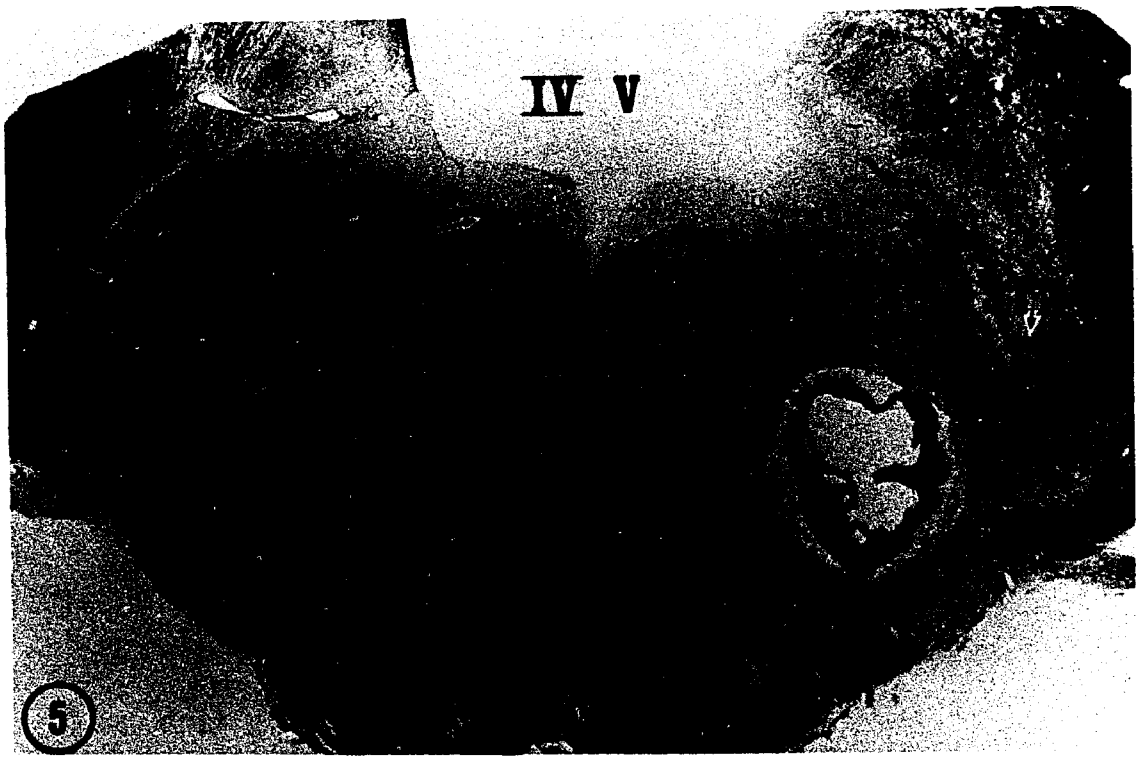
Explanation of Figures

5. Photomicrograph of a transverse section through the caudal one-third of the pons of Monkey NR 8349 illustrating the electrolytic stereotaxic lesion in the right half of the pons.
Fink and Heimer preparation. X 6.3

6. Photomicrograph through the level of the stereotaxic electrolytic lesion in the posterior limb of the internal capsule on the left side in Monkey 8349. The arrow indicates the site of the lesion.
Fink and Heimer preparation. X 8

List of Abbreviations Used in Plate 3

CA	Cerebral Aqueduct
CP	Cerebral Peduncle
DLF	Dorsal Longitudinal Fasciculus
ML	Medial Lemniscus
NSTN V	Nucleus of the Spinal Tract of the Fifth (Trigeminal) Cranial Nerve
Pyr	Pyramid
RN	Red Nucleus
TraF	Trapezoid Fibers
IV V	Fourth Ventricle


IV V
5

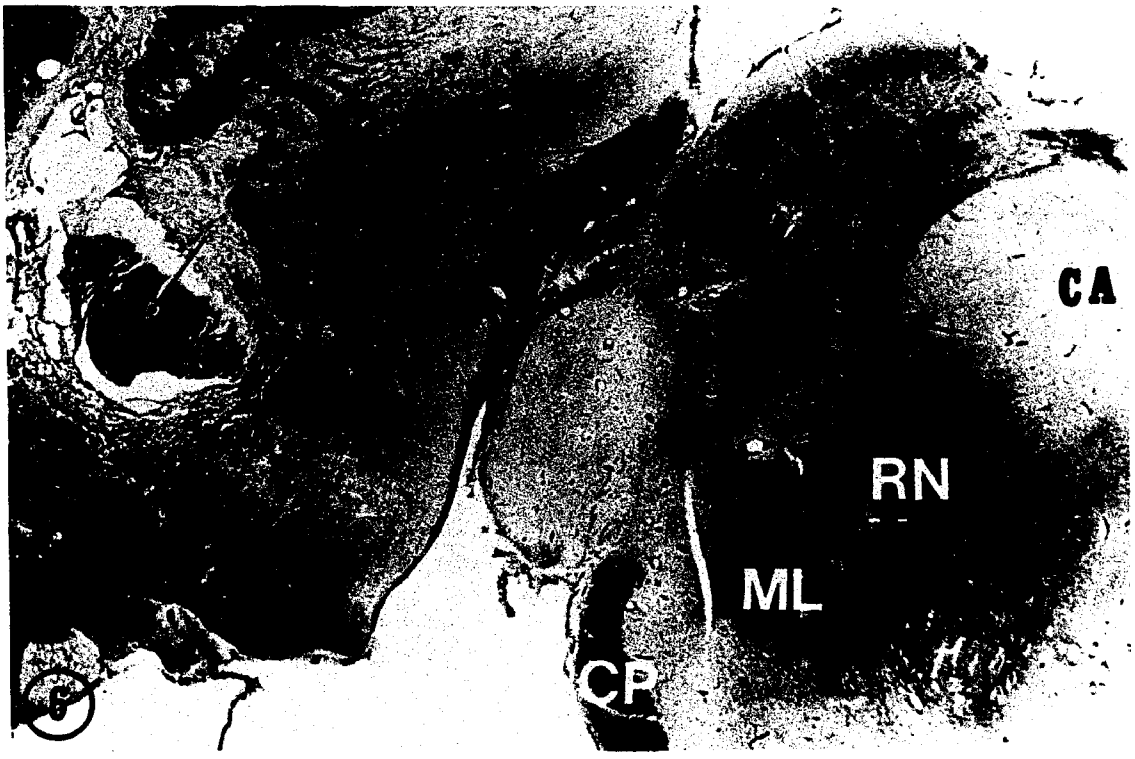

CA
RN
ML
CP
6

Plate 4

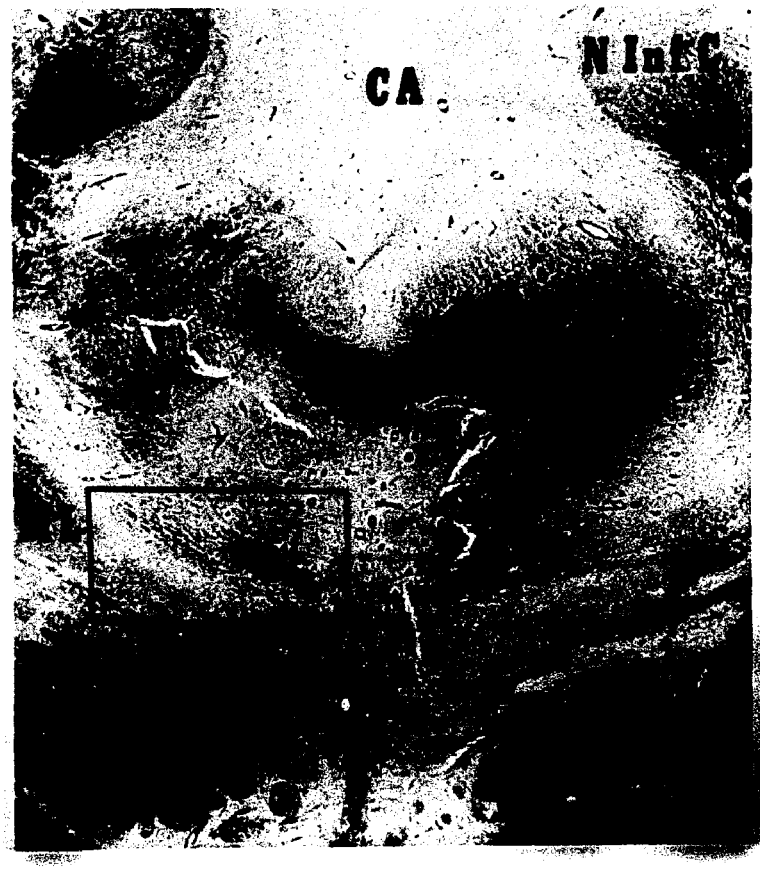
Explanation of Figures

7. Photomicrograph of a transverse section through the level of the inferior colliculus of Monkey NR 8349. The area enclosed in black in the lower left quadrant of the photomicrograph (shown at higher magnification in Figure 8) illustrates the relationship of the degenerating fibers, which originated from the contralateral pontine lesion, to the medial lemniscus. X 8

8. Photomicrograph at a higher magnification of the area enclosed in black in Figure 9. The arrows indicate the degenerating axons from the contralateral pontine lesion in Monkey 8349. X 40

List of Abbreviations Used in Plate 4

CA	Cerebral Aqueduct
DBC	Decussation of the Brachium Conjunctivum
ML	Medial Lemniscus
NInfC	Nucleus of the Inferior Colliculus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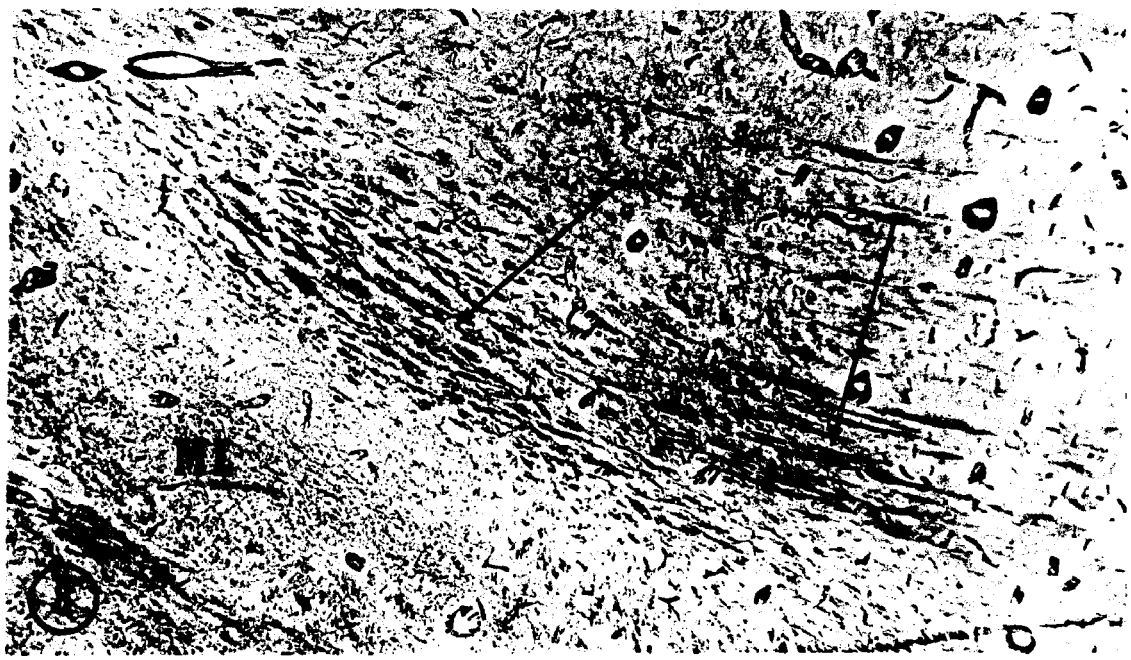


Plate 5

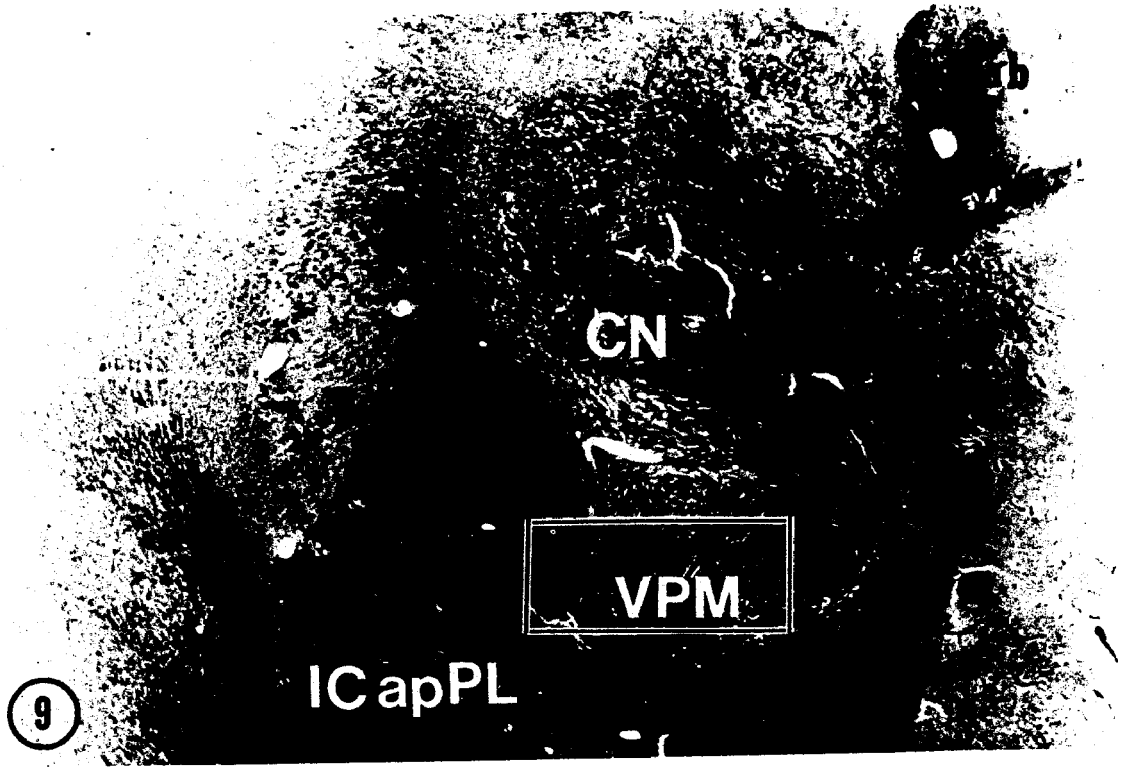
Explanation of Figures

9. Photomicrograph of a transverse section through the dorsal thalamus of Monkey NR 8349. The area enclosed is the nucleus ventralis posteromedialis of the dorsal thalamus. Fink and Heimer preparation. X 8

10. Photomicrograph of the enclosed area in Figure 9. Terminal and preterminal degeneration can be observed throughout the nucleus ventralis posteromedialis. X 80

List of Abbreviations Used in Plate 5

CN	Centromedian Nucleus
Hab	Habenula
ICapPL	Internal Capsule Posterior Limb
VPM	Nucleus ventralis posteromedialis



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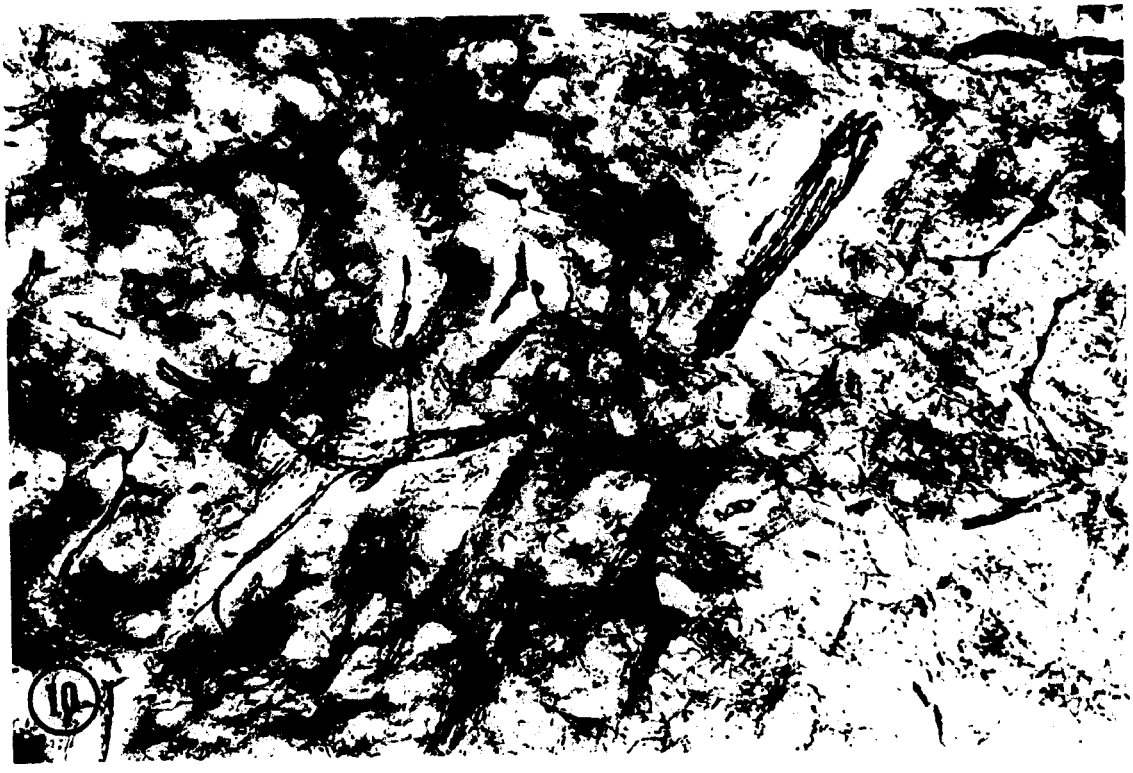

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Plate 6

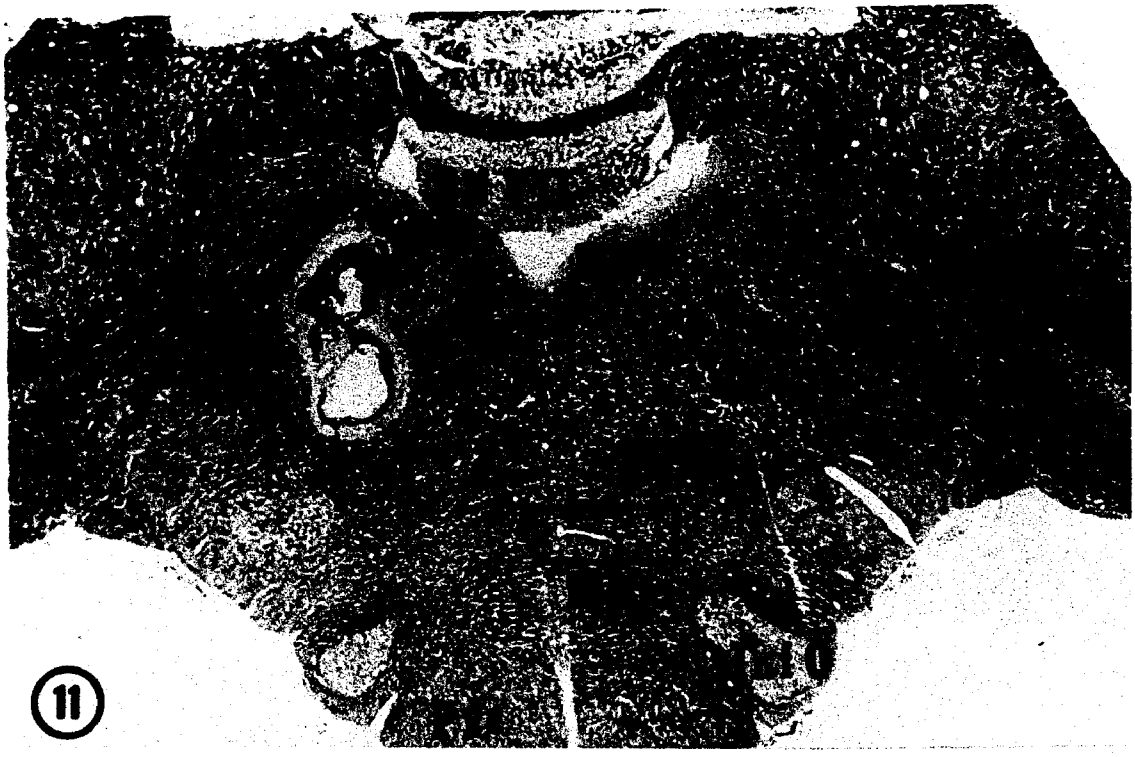
Explanation of Figures

11. Photomicrograph of a transverse section through the caudal one-third of the pons of Monkey NR 8501. Stereotaxic electrolytic lesions 1 and 2 at the level of the entering rootlets of the facial nerve on the left side are clearly evident. The arrow in the upper left quadrant of the photomicrograph indicates the position of stereotaxic electrolytic lesion number 3 which involved the deep white matter of the cerebellum. The area enclosed in black (shown at a higher magnification in Figure 12) indicates the position of the secondary ascending gustatory tract just dorsal to the medial lemniscus.
De Olmos and Ingram preparation. X 6.3

12. Photomicrograph of the area outlined in black in Figure 11. The arrows point to some of the degenerating axons of the secondary ascending gustatory tract. The secondary ascending gustatory tract passes in a rostral longitudinal direction through the brain stem and the degenerating axons are therefore cut transversely. X 32

List of Abbreviations Used in Plate 6

GN VII	Genu of Seventh (Facial) Cranial Nerve
InfO	Inferior Olive
ML	Medial Lemniscus
MLF	Medial Longitudinal Fasciculus
Pyr	Pyramid
SGTr	Secondary Gustatory Tract



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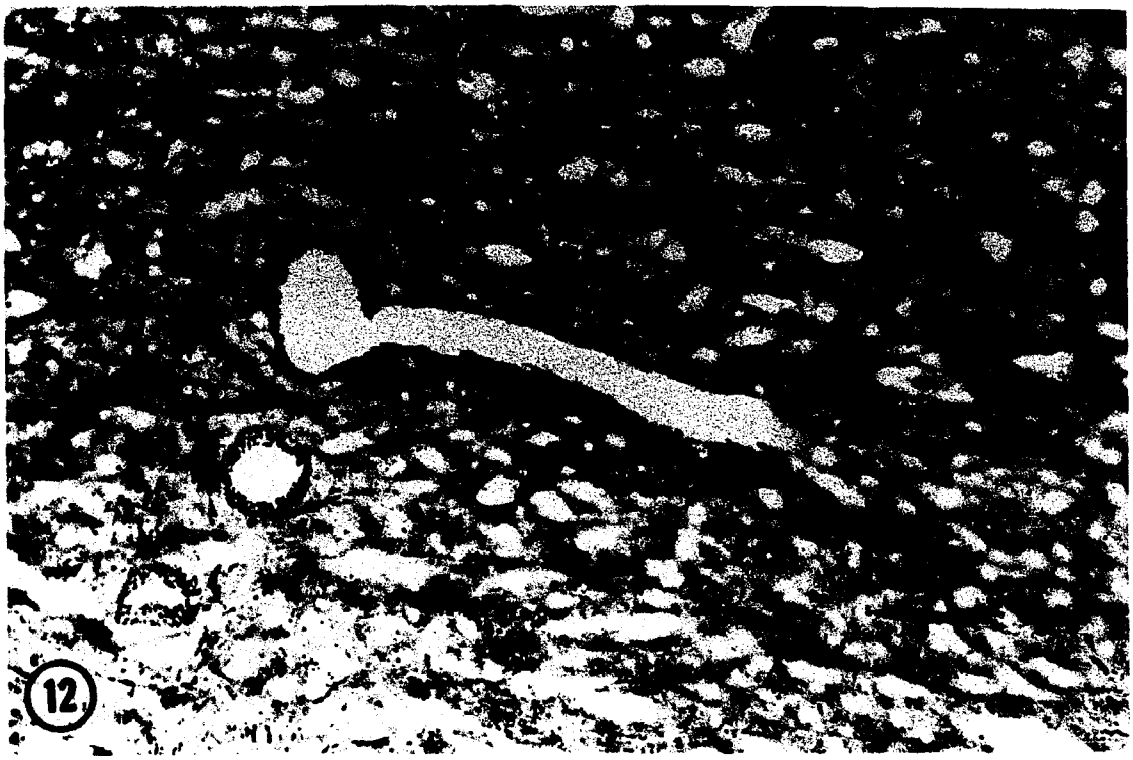

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Plate 7

Explanation of Figure

13. Photomicrograph of a transverse section through the rostral medulla of Monkey NR 8501. The size, relationships and extent of the fourth stereotaxic electrolytic lesion placed in Monkey NR 8501 are clearly evident.
De Olmos and Ingram preparation. X 6.3

List of Abbreviations Used in Plate 7

InfO	Inferior Olive
ML	Medial Lemniscus
MLF	Medial longitudinal fasciculus
NTS	Nucleus of the tractus solitarius
NIX	Ninth (Glossopharyngeal) Nerve
Pyr	Pyramid
SGTr	Secondary Gustatory Tract
IV V	Fourth Ventricle

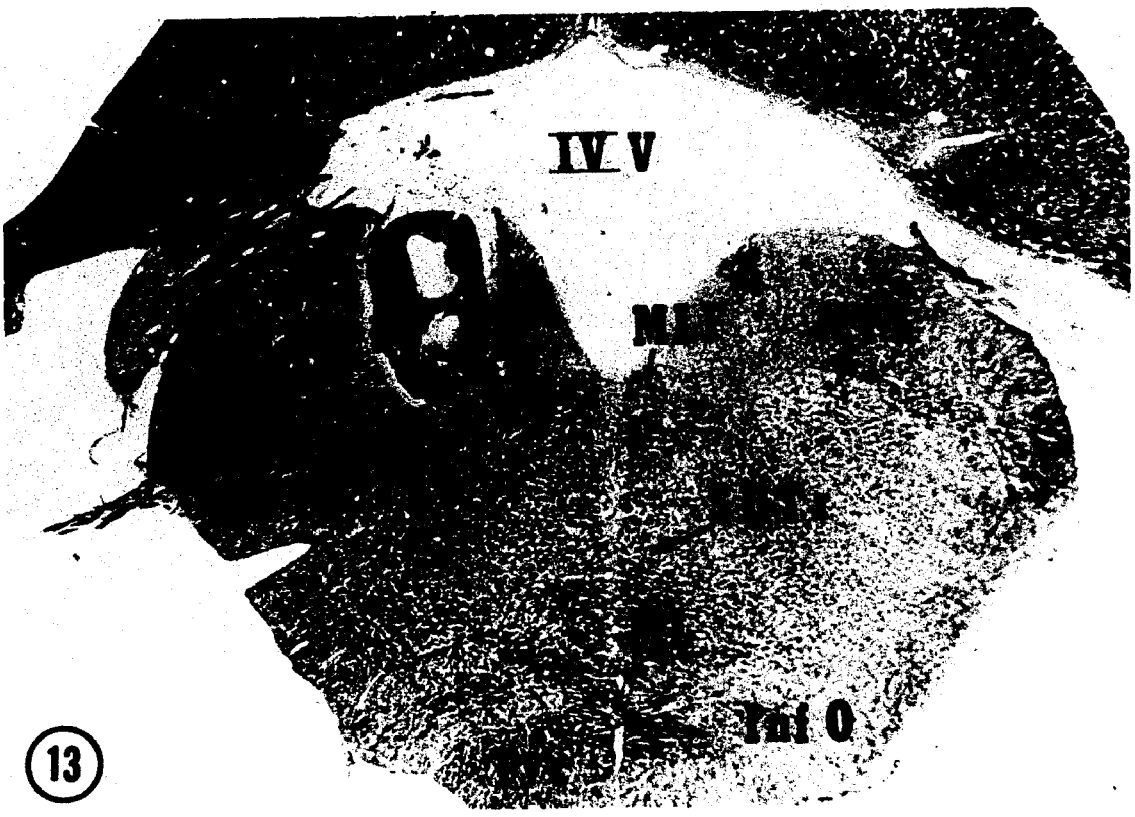
IV V
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Plate 8

Explanation of Figures

14. Photomicrograph of a transverse section through the rostral pons of Monkey NR 8501. The area outlined in black (shown at a higher magnification in Figure 15) illustrates the location of the secondary gustatory tract just dorsal to the medial extent of the medial lemniscus at rostral pontine levels.
De Olmos and Ingram preparation. X 6.3

15. Photomicrograph at a higher magnification of the area outlined in black in Figure 14. The arrows indicate some of the degenerating axons of the secondary gustatory tract which are cut in a transverse plane and are scattered throughout the field. X 80

List of Abbreviations Used in Plate 8

BC	Brachium Conjunctivum
BP	Brachium Pontis
ML	Medial Lemniscus
MLF	Medial Longitudinal Fasciculus
Pyr	Pyramid
SGTr	Secondary Gustatory Tract

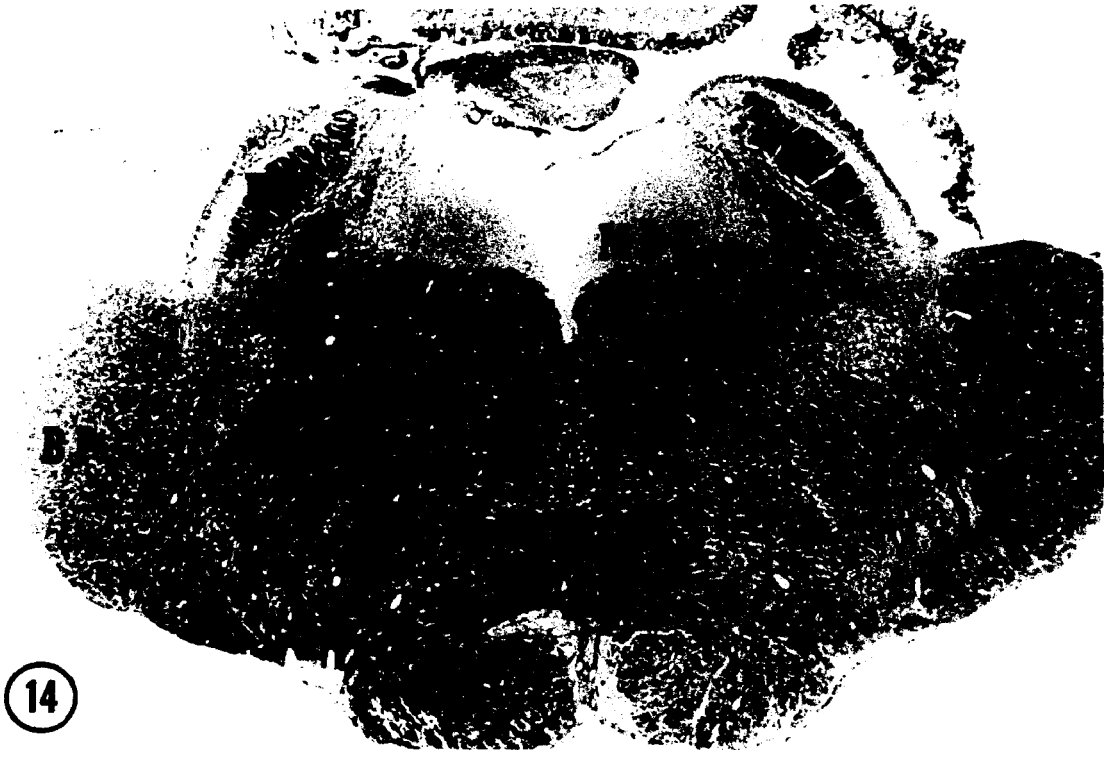

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Plate 9

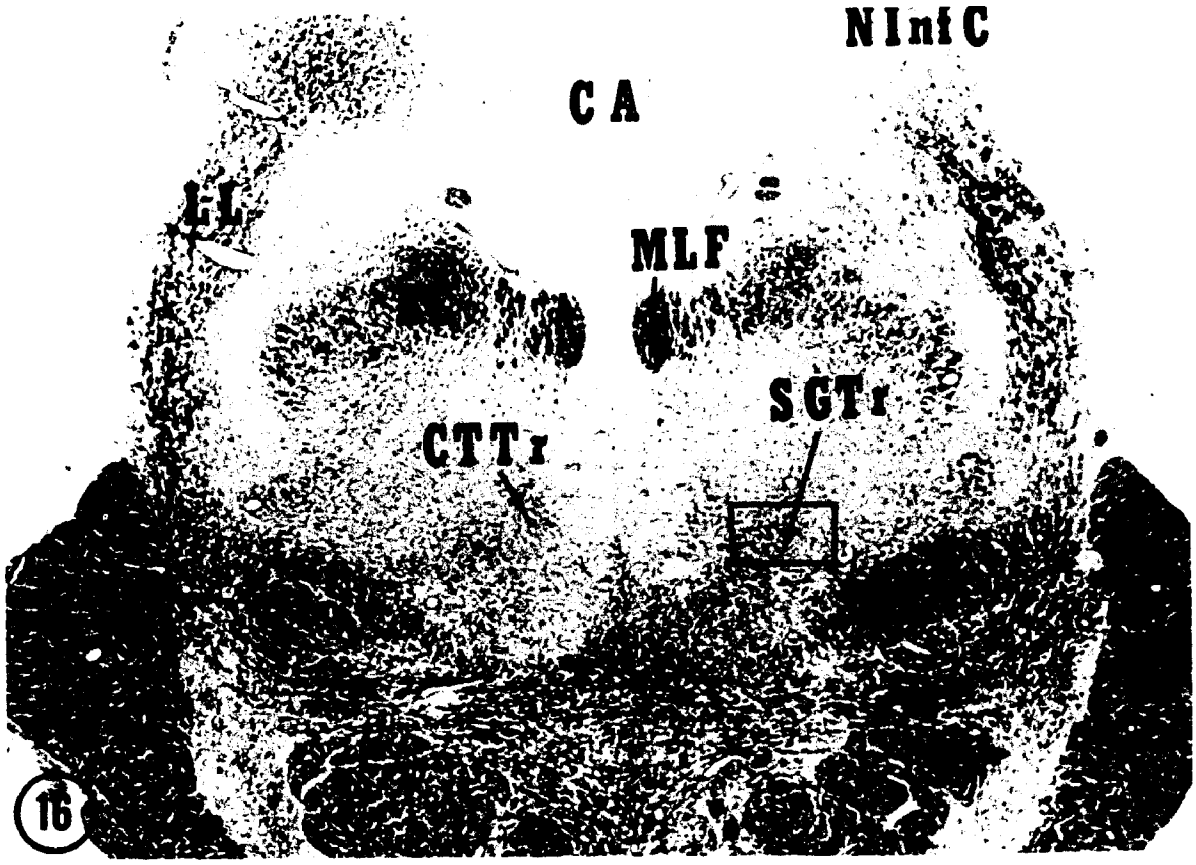
Explanation of Figures

16. Photomicrograph of a transverse section through rostral inferior collicular levels of Monkey NR 8501. The secondary gustatory tract (shown at a higher magnification in Figure 17) is located medially and slightly dorsally to the medial extent of the medial lemniscus and is also related to the ventral portion of the central tegmental tract.
De Olmos and Ingram preparation. X 6.3

17. Photomicrograph of the area enclosed in black in Figure 16. Degenerating axons of the secondary gustatory tract cut transversely are scattered throughout the field. X 80.

List of Abbreviations Used in Plate 9

BC	Brachium Conjunctivum
BP	Brachium Pontis
CA	Cerebral Aqueduct
CTTr	Central Tegmental Tract
LL	Lateral Lemniscus
ML	Medial Lemniscus
MLF	Medial Longitudinal Fasciculus
NInfC	Nucleus of the Inferior Colliculus
SCTr	Secondary Gustatory Tract


NInIC
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SGTr
CTTr
16


17

Plate 10

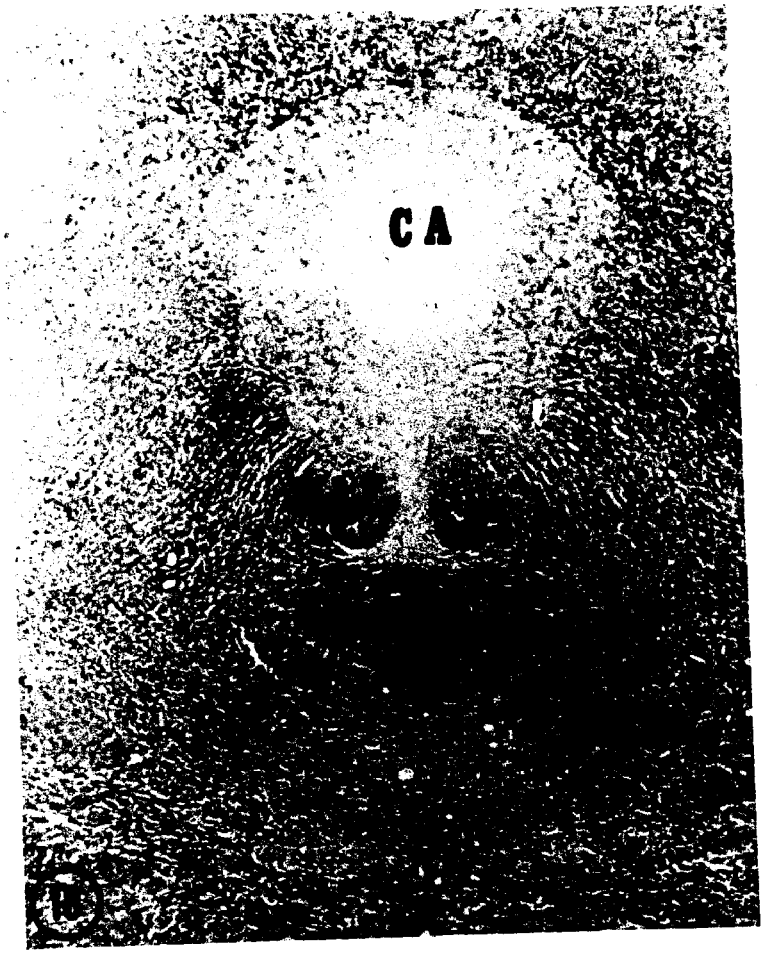
Explanation of Figures

18. Photomicrograph of a transverse section through the junction between the inferior and superior colliculi of Monkey NR 8501 at the level of the decussation of the brachium conjunctivum. The area outlined in black indicates the position of the secondary gustatory tract at this level.
De Olmos and Ingram preparation. X 6.3

19. Photomicrograph at a higher magnification of the area enclosed in black in Figure 18. The secondary gustatory tract interdigitates with degenerating fibers of the decussating brachium conjunctivum and cannot be distinguished from them until their respective levels of termination within the dorsal thalamus. The arrows indicate some of the fibers of the secondary gustatory tract as they swing superiorly to interdigitate with the fibers of the brachium conjunctivum. X 100.

List of Abbreviations Used in Plate 10

CA	Cerebral Aqueduct
DBC	Decussation of the Brachium Conjunctivum
MLF	Medial Longitudinal Fasciculus
SGTr	Secondary Gustatory Tract


CA
18


DBC
SCTr
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Plate 11

Explanation of Figures

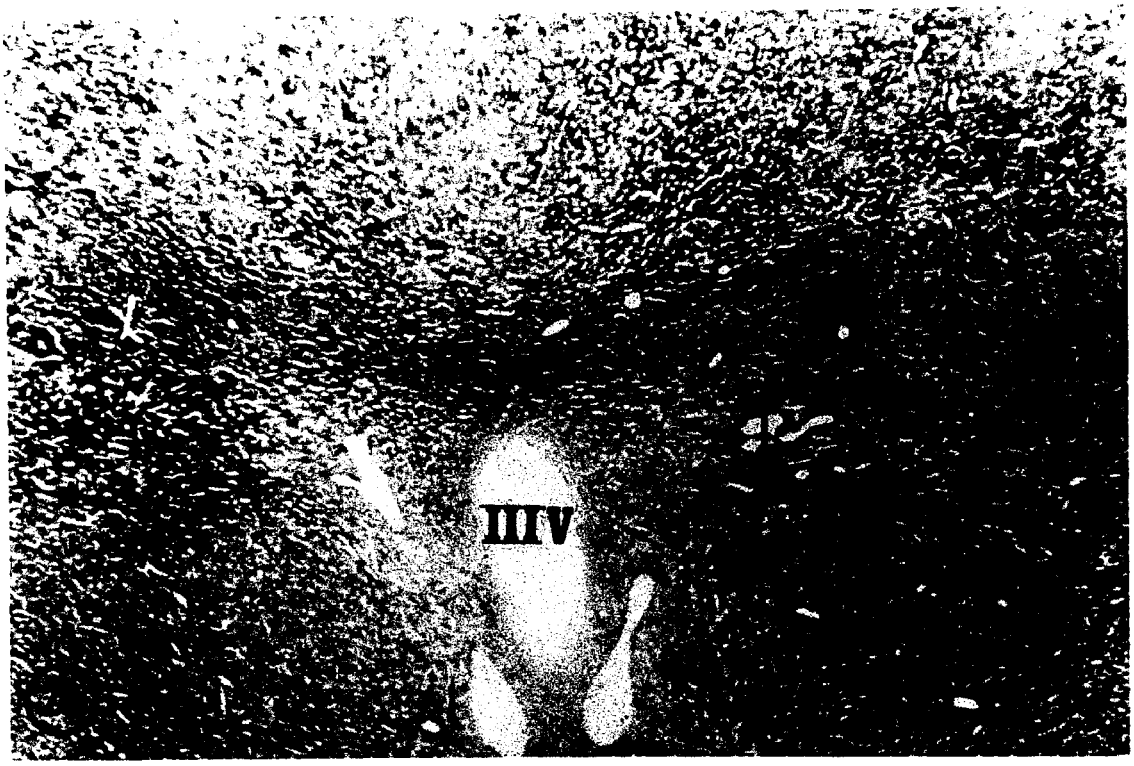
20. Photomicrograph of a transverse section through the dorsal thalamus at the most rostral level of the nucleus ventralis posteromedialis pars parvocellularis of Monkey NR 8501. Terminal degeneration within the nucleus ventralis posteromedialis pars parvocellularis (outlined in black) of the secondary gustatory tract is shown at a higher magnification in Figure 21. Terminal degeneration of the brachium conjunctivum (dentatorubrothalamic tract) in the nucleus ventralis lateralis is outlined in black and shown at a higher magnification in Figure 22.
De Olmos and Ingram preparation. X 6.3

21. Photomicrograph of the nucleus ventralis posteromedialis pars parvocellularis (outlined in Figure 20) demonstrating terminal degeneration of the secondary gustatory tract. X 32

22. Photomicrograph of the nucleus ventralis lateralis (outlined in Figure 20) of the dorsal thalamus illustrating terminal degeneration of the ascending component of the brachium conjunctivum. X 32

List of Abbreviations Used in Plate 11

CN	Centromedian Nucleus
VL	Nucleus Ventralis Lateralis
VPMpc	Nucleus Ventralis Posteromedialis pars parvocellularis
III V	Third Ventricle



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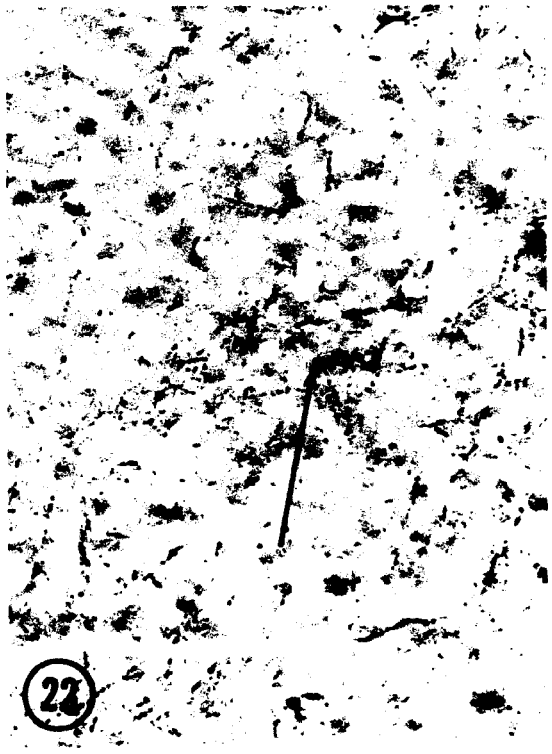

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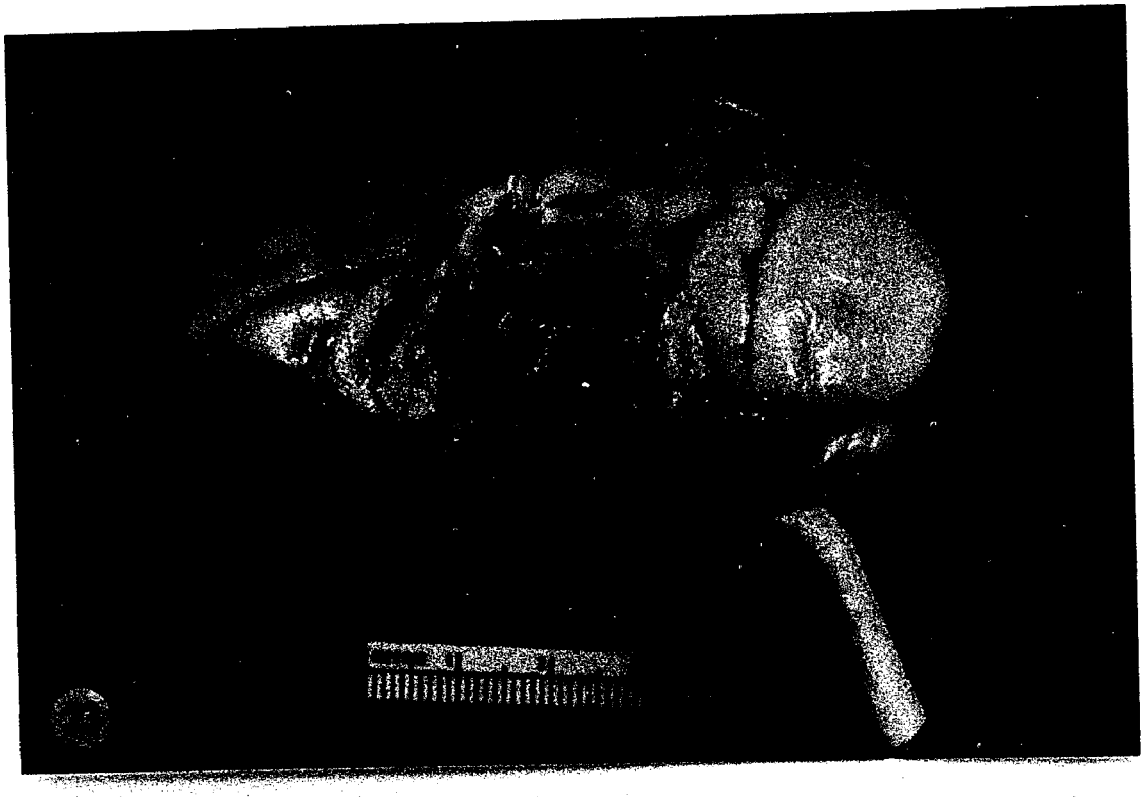
Plate 12

Explanation of Figures

23. Left cerebral hemisphere of Monkey NR 020. The large cortical lesion which involved the bases of the pre- and postcentral gyri and the adjacent superior and middle temporal gyri is clearly apparent.

24. Right cerebral hemisphere of Monkey NR 020 illustrating the cortical lesion which involved the fronto-parietal operculum at the base of the central fissure (CF), its opercular surface and the adjacent portion of the superior temporal gyrus.



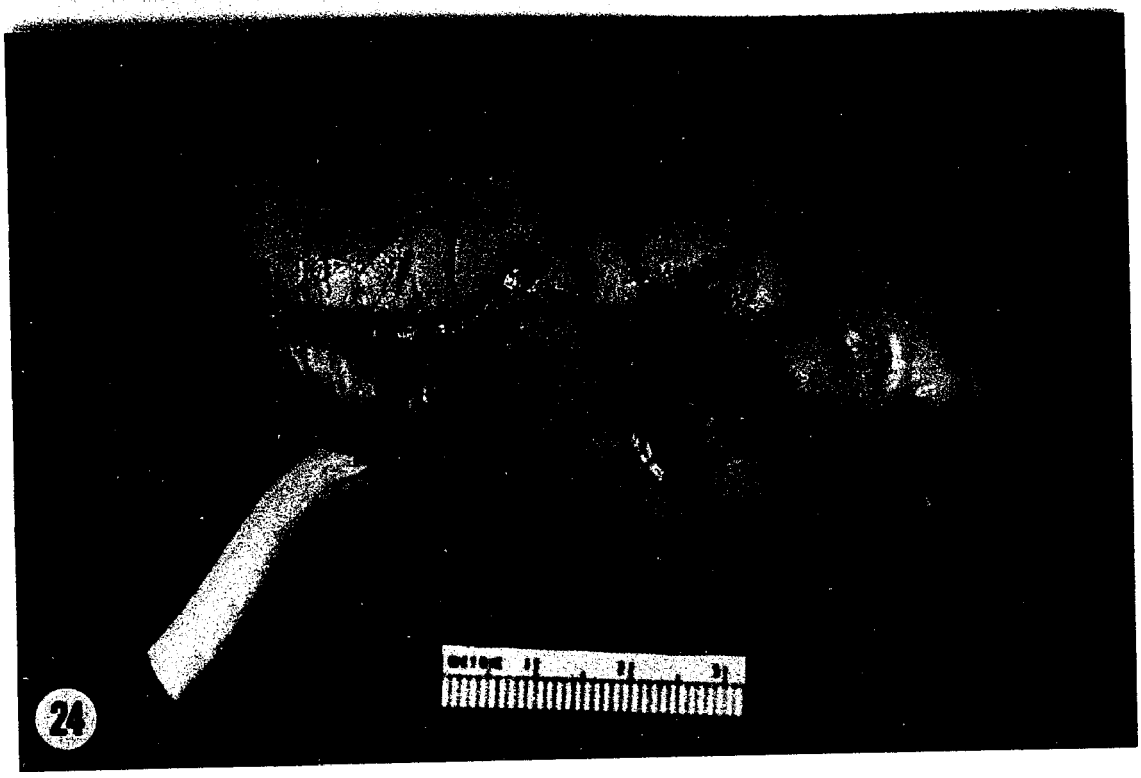

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Plate 13

Explanation of Figures

25. Photomicrograph of a coronal section through the level of the right cortical lesion of Monkey NR 020. As can be observed, the deep white matter of this cortical area as well as the fronto-parietal operculum was involved in the lesion. Fine degenerating axons can be traced through the extreme capsule into the dorsal anterior part of the Island of Reil. De Olmos and Ingram preparation. X 6.3

26. Photomicrograph at a higher magnification of the area outlined in black in Figure 25. Preterminal and terminal degeneration can be observed throughout the field. X 250

List of Abbreviations Used in Plate 13

Cl	Claustrum
Ext Cap	External Capsule
Extr Cap	Extreme Capsule
FPO	Fronto-Parietal operculum
LF	Lateral Fissure
Is	Island of Reil
STG	Superior Temporal Gyrus

LF

40

Plate 14

Explanation of Figures

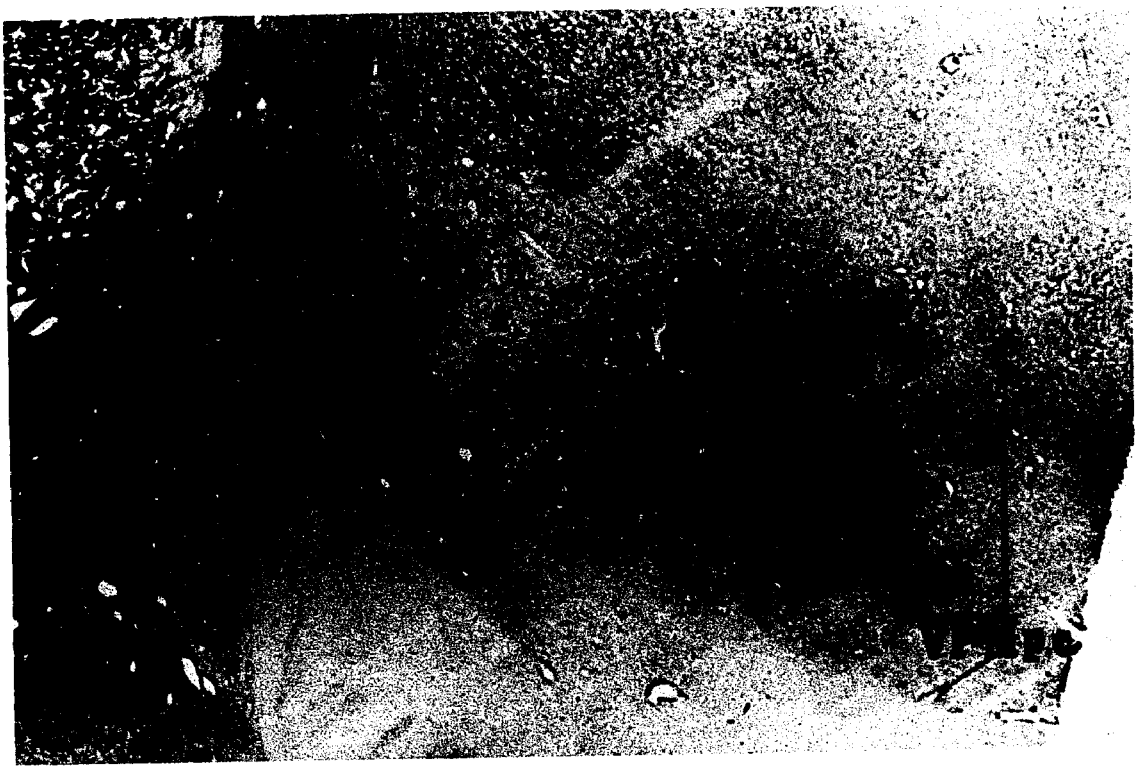
27. Photomicrograph of a coronal section through the dorsal thalamus of Monkey NR 020. Terminal degeneration from the lesion in the fronto-parietal operculum can be observed within the nucleus ventralis posteromedialis and a few fine fibers can be traced to the parvocellular portion of this nucleus.
De Olmos and Ingram preparation. X 6.3

28. Photomicrograph at a higher magnification of the area outlined in black in Figure 27. Massive terminal degeneration can be seen in the nucleus ventralis posteromedialis. The arrows indicate the terminal degeneration of a few fibers within the parvocellular portion of the nucleus ventralis posteromedialis.
X 21.6

29. Photomicrograph of degenerating corticothalamic fibers which accompany the sensory radiations (thalamocortical fibers) as they pass through the posterior limb of the internal capsule to gain entrance to or exit from the dorsal thalamus.
De Olmos and Ingram preparation. X 32

List of Abbreviations Used in Plate 14

Cn	Centromedian nucleus
CT	Corticothalamic fibers
ICapPl	Internal Capsule Posterior Limb
VPM	Nucleus Ventralis Posteromedialis
VPMpc	Nucleus Ventralis Posteromedialis pars parvocellularis



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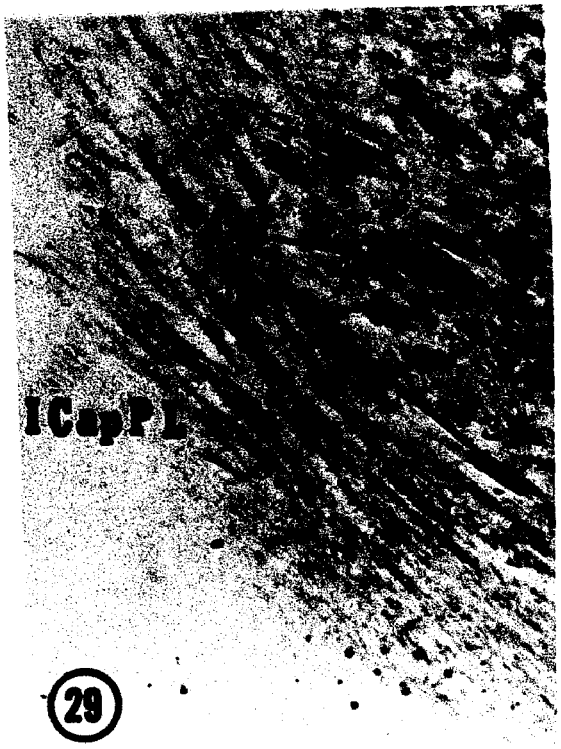

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Plate 15

Explanation of Figures

30. Photomicrograph of a transverse section through the caudal pons of Monkey NR 8373. The arrow in the upper left quadrant shows the position of stereotaxic electrolytic lesion 1 of this monkey.
De Olmos and Ingram preparation. X 6.3

31. Photomicrograph of a transverse section through the medulla of Monkey NR 8373. The large lesion (lesion 2) interrupting the rootlets of the glossopharyngeal nerve as they enter the nucleus of the tractus solitarius is clearly delineated.
De Olmos and Ingram preparation. X 6.3

List of Abbreviations Used in Plate 15

BP	Brachium Pontis
ML	Medial Lemniscus
N VII	Seventh (Facial) Cranial Nerve
N IX	Ninth (Glossopharyngeal) Cranial Nerve
NTS	Nucleus of the Tractus Solitarius
Pyr	Pyramid

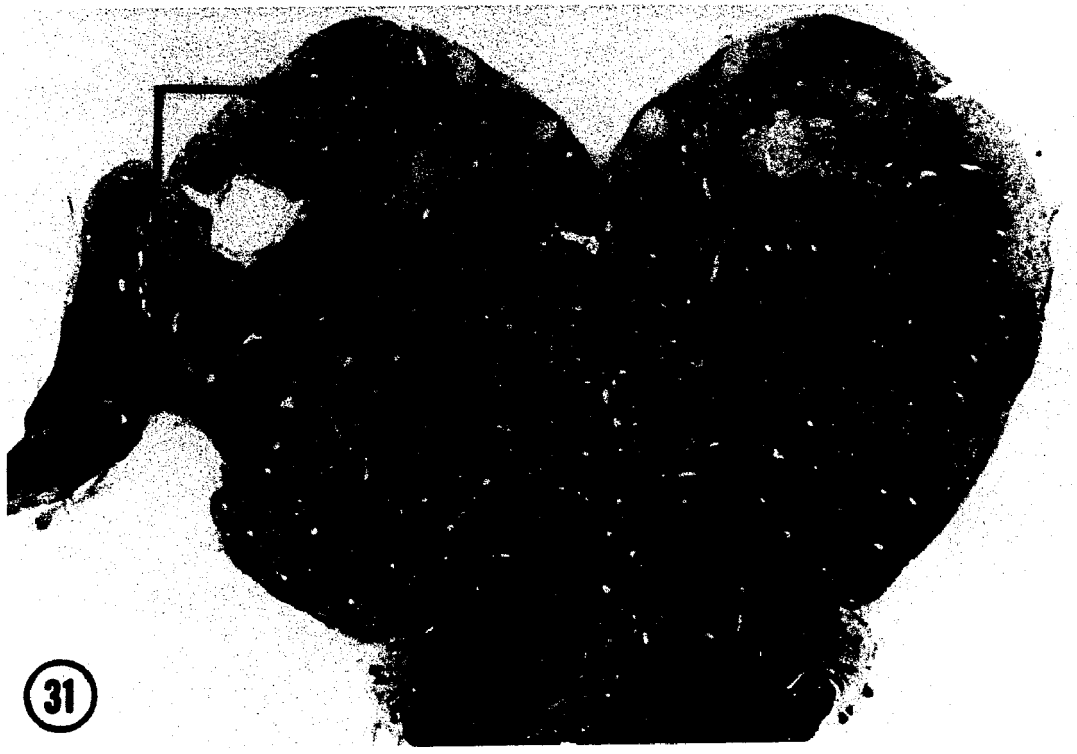

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Plate 16

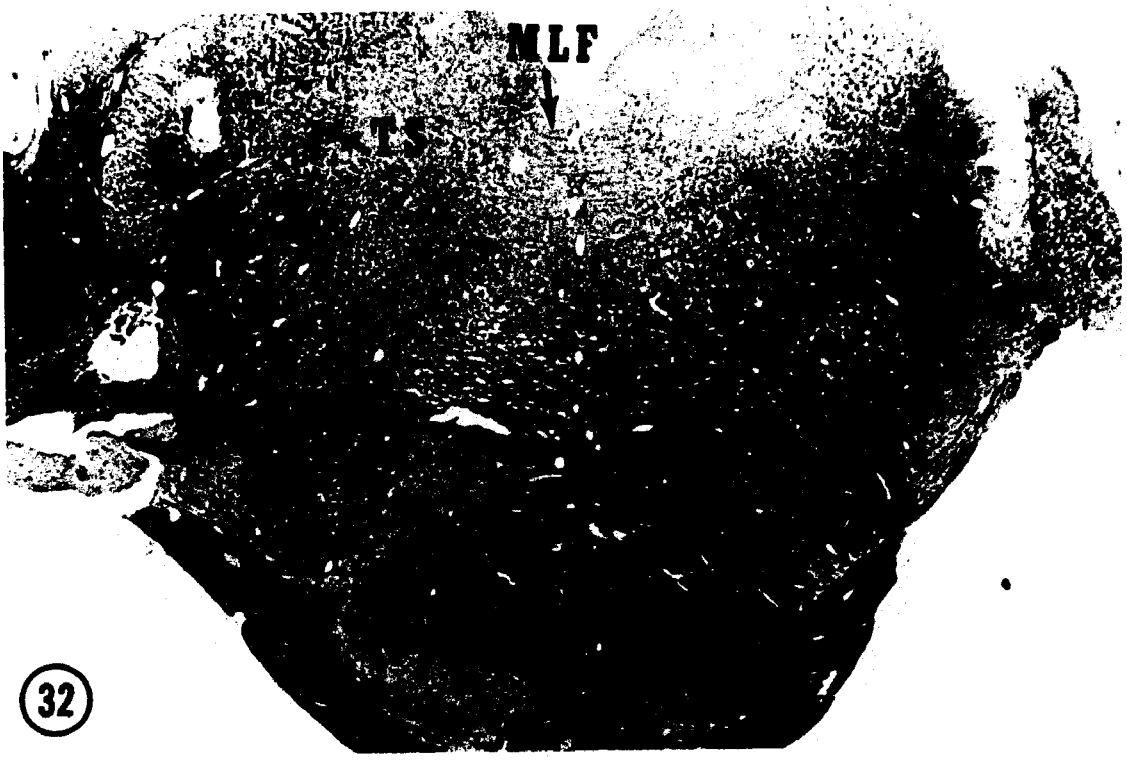
Explanation of Figures

32. Photomicrograph of a transverse section through the most rostral portion of the medulla of Monkey NR 8373 at the level of the lesion of the ventral cochlear nucleus. The rostral continuation of the lesion which involved the glossopharyngeal nerve is shown in the upper left portion of the section.
De Olmos and Ingram preparation. X 6.3

33. Photomicrograph at a higher magnification of the area outlined in black in Figure 31. Degenerating axons of the glossopharyngeal nerve can be seen entering the nucleus of the tractus solitarius and terminal degeneration is seen in the nucleus of the tractus solitarius.
De Olmos and Ingram preparation. X 25.2

List of Abbreviations Used in Plate 16

BP	Brachium Pontis
MLF	Medial Longitudinal Fasciculus
NTS	Nucleus of the Tractus Solitarius
N IX	Ninth (Glossopharyngeal) Cranial Nerve
TraF	Trapezoid Fibers
TS	Tractus Solitarius
VCN	Ventral Cochlear Nucleus



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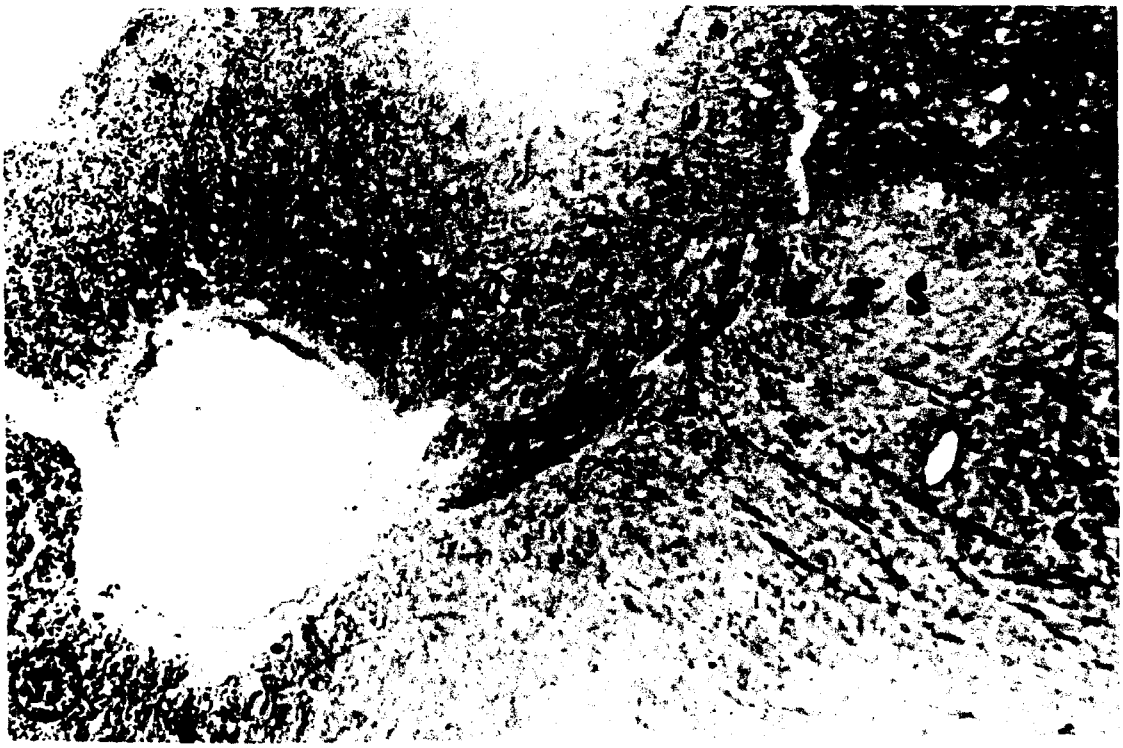

Plate 17

Explanation of Figures

34. Photomicrograph of a transverse section through the rostral pons of Monkey NR 8373. The area outlined in black indicates the position within the most medial portion of the medial lemniscus of degenerating fibers which originated from the lesion of the nucleus parasolitarius. De Olmos and Ingram preparation. X 6.3

35. Photomicrograph at a higher magnification of the area outlined in black in Figure 34. X 80

List of Abbreviations Used in Plate 17

BC	Brachium Conjunctivum
CS	Corticospinal Fibers
ML	Medial Lemniscus

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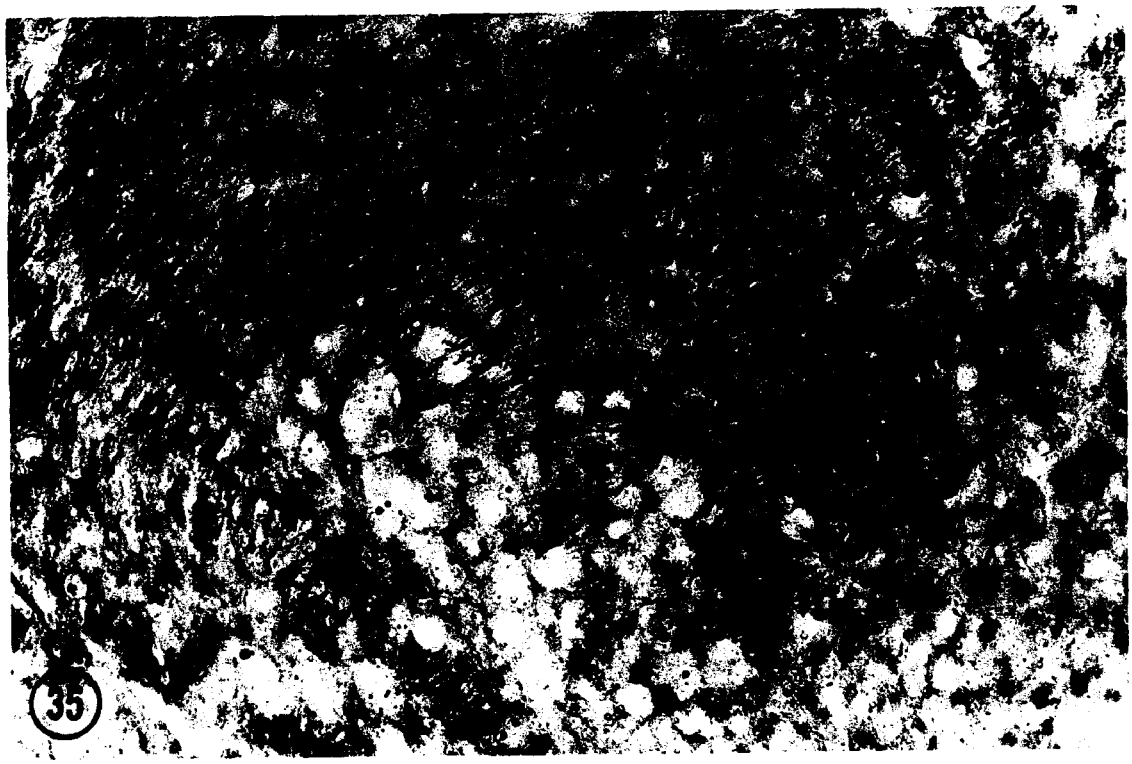

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Plate 18

Explanation of Figure

36. Diagram illustrating the cumulative results of the cortical and stereotaxic brain stem lesions, thus defining the central gustatory pathways in the monkey.

List of Abbreviations Used in Plate 18

BC	Brachium Conjunctivum
BP	Brachium Pontis
CA	Cerebral Aqueduct
DBC	Decussation of the Brachium Conjunctivum
FPO	Fronto-Parietal Operculum
I	Island of Reil
I CapPL	Internal Capsule Posterior Limb
InfO	Inferior Olive
ML	Medial Lemniscus
NInfC	Nucleus of the Inferior Colliculus
NTS	Nucleus of the Tractus Solitarius
N IX	Ninth (Glossopharyngeal) Cranial Nerve
PG	Petrosal Ganglion
Pyr	Pyramid
RB	Restiform Body
SGTr	Secondary Gustatory Tract
VPMpc	Nucleus Ventralis Posteromedialis pars parvocellularis

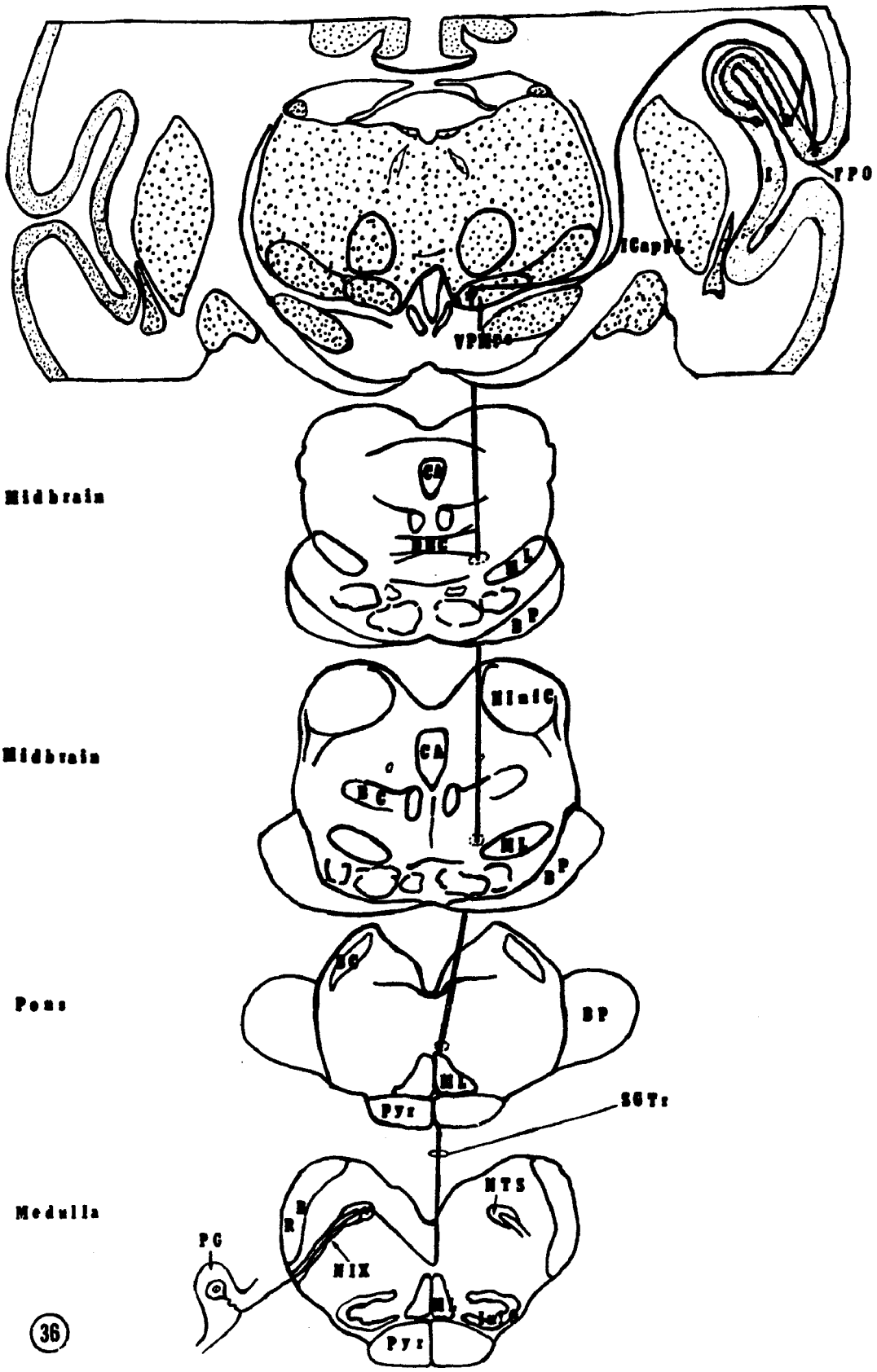
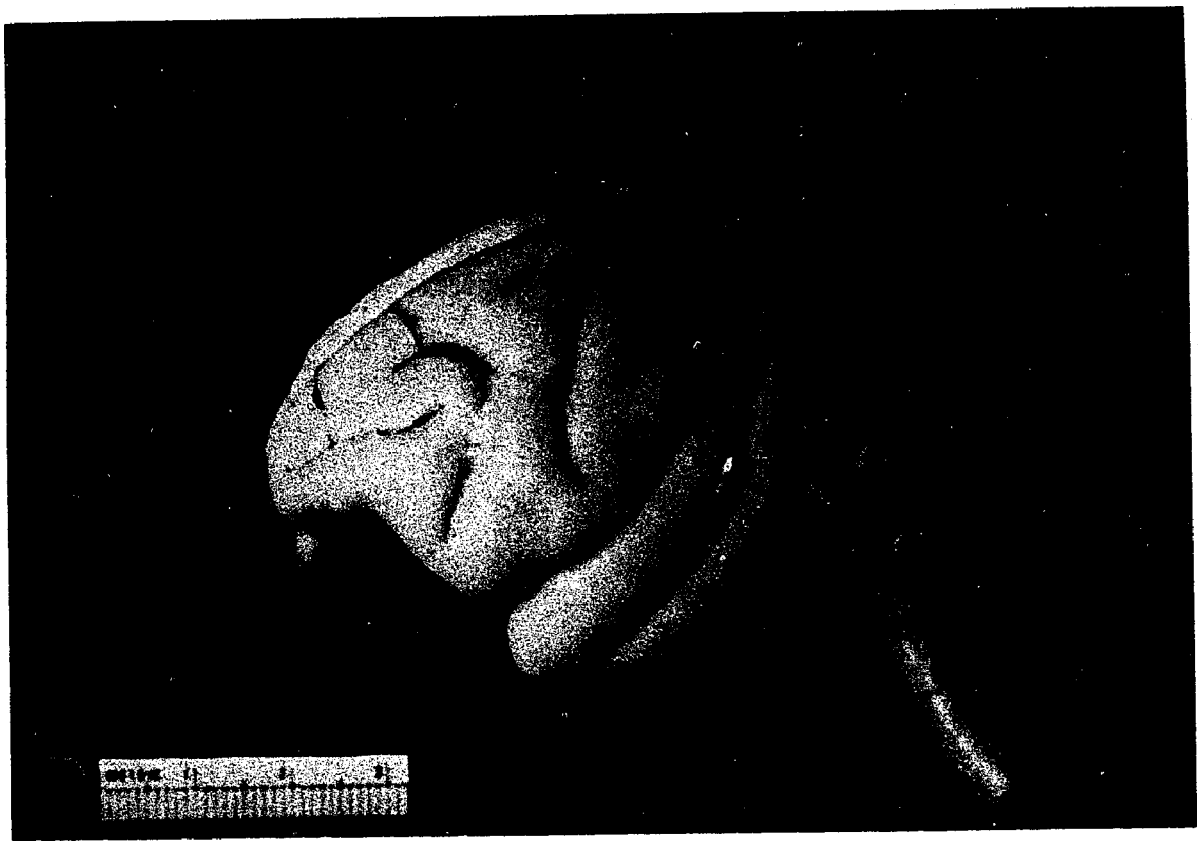

VPO
VPMpc
Midbrain
Midbrain
Pons
Medulla
SGTr
NTS
PG
NIX
Pyr

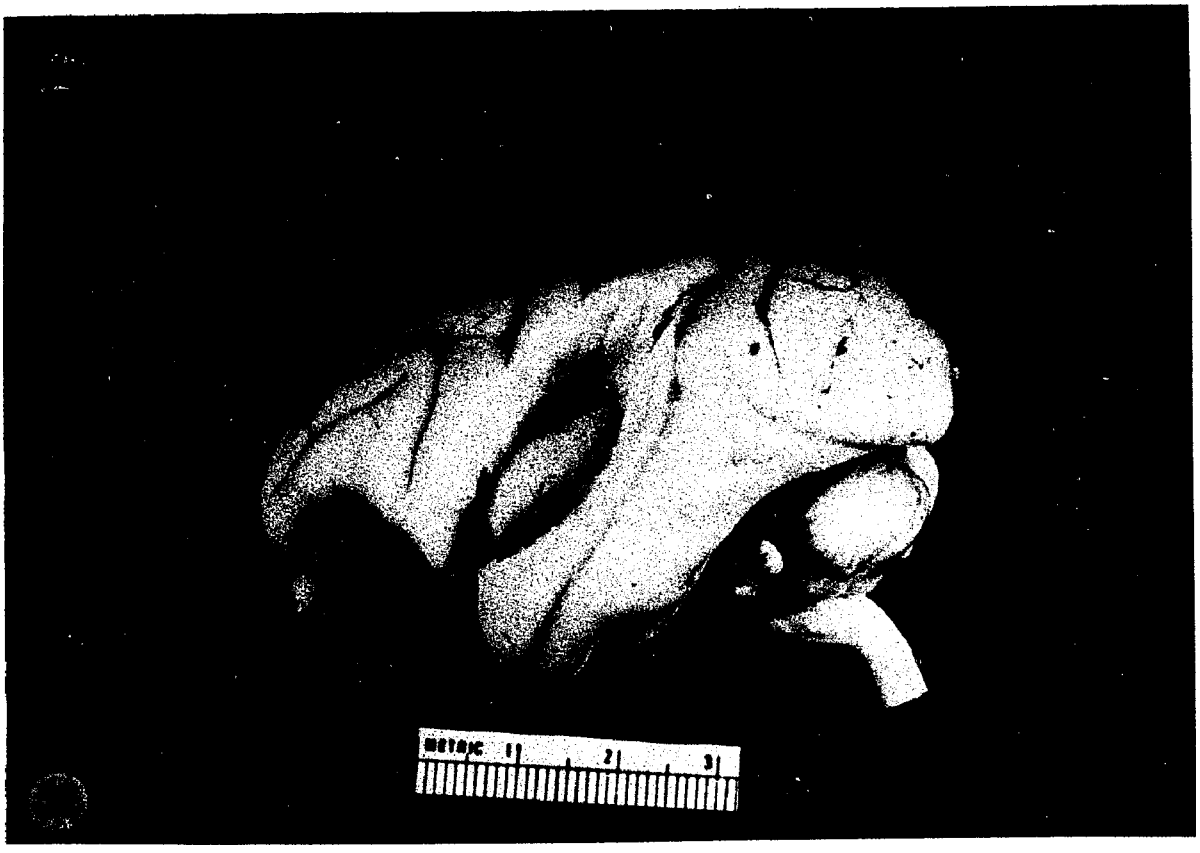
Plate 19

Explanation of Figures

37. The left normal cerebral hemisphere of a Macaca mulatta.

38. The left cerebral hemisphere of a Macaca mulatta in which the fronto-parietal operculum and the temporal operculum have been dissected to demonstrate their relationships with the Island of Reil.

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