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TITLE ANATOMICAL AND EXPERIMENTAL STUDIES ON THE TEMPORAL POLE OF THE MACAQUE

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LOUIS J. POIRIER

1950

ANATOMICAL AND EXPERIMENTAL STUDIES ON THE TEMPORAL POLE OF THE MACAQUE

by

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of the requirements for the degree of
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TABLE OF CONTENTS

	Page
Introduction	1
Material and technique	2
Description of lesions and results	5
Monkey No. 1	5
Summary	5
Monkey No. 2	6
Macroscopic and microscopic anatomy	7
Summary	8
Monkey No. 3	9
Macroscopic and microscopic anatomy	10
Summary	13
Monkey No. 4	15
Macroscopic and microscopic anatomy	17
Summary	22
Monkey No. 5	23
Macroscopic and microscopic anatomy	26
Summary	30
Monkey No. 6	31
Macroscopic and microscopic anatomy	31
Summary	35
Discussion	36
General summary	40
Literature cited	42
Abbreviations for figures	45

INTRODUCTION

This study dealing with the brain of the monkey is part of a research program carried on in the Laboratory of Comparative Neurology at the University of Michigan. The writer wishes to thank the A. B. Brower and E. R. Arn Research and Scholarship Fund, made available through the Dean of the Medical School, for the generous grant which made possible the present work. The author also expresses his sincere gratitude to Professor Elizabeth C. Crosby for her numerous suggestions and her unfailing cooperation. This research work on the temporal pole of the brain was suggested to the author mainly by two series of papers. One of these by C. J. Herrick ('33, p. 13) stressed the importance of the olfactory formations in the function of the nonolfactory cortex: "It is perhaps significant in this connection that in most of the experiments designed to test the part played by the cortex of lower mammals in learning the ablation operations involve only the neopallium, leaving the olfactory cortex intact or but slightly injured."

The second set of papers which influenced the author to study the temporal pole of the brain of macaque are those published by Klüver and Bucy ('37, '38, '39). After extensive removal of the temporal lobes bilaterally, these two experimenters obtained a complete syndrome, which was characterized by "psychic blindness," oral tendencies, hypersexuality, hypermetamorphosis, emotional changes, etc. Such far-reaching

results from injury to this particular area of the brain appeared to the author worthy of further investigation, for it was thought that with smaller and additive lesions some of the specific structures, the destruction of which is responsible for any or all of these symptoms, could be studied microscopically.

MATERIAL AND TECHNIQUE

For this problem on the temporal lobe including the amygdala, the piriform lobe, and the hippocampus, Macaca mulatta was selected. Lesions were placed in the brains of six monkeys under ether anesthesia. The surface cortex was removed with the help of electrocoagulation or with a scalpel. Deeper lesions were made mostly by scooping out the brain tissue, and a few lesions were produced with the help of the stereotaxic instrument of Horsley-Clarke (the McCulloch modification). All of these monkeys except No. 6 were tested for the discrimination of shape and various objects and some for the discrimination of sound, weight, or color.

Discrimination of various objects, including those edible and inedible, was tested according to the "multiple object tests" as devised by Klüver and Bucy ('39). For the discrimination of shape, two boxes similar in size, color, and weight were used. One of the two differed from the other only by presenting along its upper edge a semilunar notch as shown in figure 1. In order to obtain food, the animal had to pull in the box which presented a semilunar edge. Both boxes were placed at a distance of about 8 feet from the cage. When the

animal was able to pull in the correct box directly for twenty trials without error, the test was considered as learned. For the discrimination of weight, sound, or color, the two boxes varied one from the other only by differences in weight, sound, or color, respectively. For the discrimination of weight, food was placed in the lighter of two boxes; for the discrimination of sound, the animal in order to obtain food had to pull in the box which was not connected with a bell. So for these two tests, he had to shift each time before pulling in the right box. For color discrimination metallic gray and white were used. These tests were learned preoperatively after an average of 150 to 200 trials.

The behavior of the animals was also recorded pre- and postoperatively by observing the monkeys in the cages and noting their reactions toward food, toward the experimenter, and toward other animals - in other words, their social behavior. After various lengths of time the animals were killed by overdosage of nembutal, the tissue being perfused with 10% to 15% formalin while the heart was still beating. After removal their brains were fixed for a few days in 10% formalin. Then they were stained with osmic acid according to the Marchi technique. In the case of the brain of monkey No. 6, the slices of brain tissue were placed on a thread, standing upright in the staining fluid, as suggested by J. W. Krieg ('49) and others, and the degenerated myelin was found to be well impregnated by the osmic acid. In other cases an attempt was made to restain with osmic acid some sections in which the

degenerated fibers were rather pale. After mounting individual sections these were run through xylol, alcohol, and distilled water and then placed in the staining solution proposed by Swank and Davenport ('35) for slices of tissue. It was found that the fibers which had been stained weakly appeared darker and sharper after this treatment and could be photographed more easily. Compare figure 21 with figure 21A.

In studying degeneration in the anterior commissure, Fox, Fisher, and Desalva ('48) made the observation that staining with osmic acid was better in this tract after three weeks than after fourteen days. The amount of degenerated myelin in the present material was found to increase between the second and third weeks after the lesion, not only in the anterior commissure but also in the fornix and stria terminalis. Some lesions in this series of cases are older than three weeks, and for this reason some fibers show retrograde degeneration while certain nuclear masses are filled with black granules; this is especially evident in the thalamo-cortical fibers and the thalamic nuclei (figs. 3 and 9).

The brain of monkey No. 1 was studied only grossly. So five series of monkey brains with various lesions were available for microscopical studies. Microphotographs were taken with the generous help of Mr. George Smith, technician in the Laboratory of Comparative Anatomy.

DESCRIPTION OF LESIONS AND RESULTS

Monkey No. 1

This monkey learned preoperatively to discriminate shape by the pulling-in technique; he performed the last 50 trials without error. He could also discriminate various objects placed on a board in front of the cage after only a few trials. A first temporal lobotomy was done November 5, 1948, on the left side. The same tests were repeated a few days after this first lesion, and all the tests that had been learned previously were recalled perfectly. On November 26, 1948, a right temporal lobotomy was produced. In the following days, discrimination of various objects was recalled perfectly, and new objects presented to the animal were quickly learned. Discrimination of shape was nearly as good as before, the animal making only two errors out of 27 trials.

Examination of the brain at autopsy revealed that on both sides the superior, middle, and inferior temporal gyri had been sectioned, the hippocampal gyrus and hippocampus being spared. On the right side the incision corresponded to a line which continues downward from the lower end of the central fissure through the temporal lobe. On the left the incision was about 1/2 centimeter caudal to that on the right.

Summary After bilateral lobotomy of nearly the anterior two-thirds of the temporal lobes, but not involving the hippocampal gyrus and hippocampus, no changes in behavior were observed. Discriminatory tests were performed as well after

this bilateral lesion as preoperatively and the animal learned to discriminate new objects as rapidly as before.

Monkey No. 2

Preoperatively this monkey learned to discriminate shape, showing no errors in the last 18 trials; he could also discriminate between various objects placed on a board in front of him. Through an opening in the left superior temporal gyrus a first lesion was placed in the region of the uncus on January 21, 1949. Postoperative testing did not disclose any loss in the previously learned objects and tests and observation did not show any changes in behavior.

On February 4, 1949, the animal was reoperated on the right side, this lesion involving chiefly the superior, middle, and inferior temporal gyri. Tests for discrimination, on being repeated postoperatively, revealed only a little loss of memory for shape. On 50 trials for shape discrimination the animal made only 8 errors. Discrimination of previously learned objects was as good as preoperatively but this monkey was able to learn to discriminate new objects only after repeated trials. In his behavior he was more tame, having been very wild previous to this last operation. He now could be approached and handled with ease by the experimenter. An attempt was made to have the animal discriminate weight by the pulling-in technique; but after numerous trials he did not show any sign of learning, even when there was a marked difference in the weights.

Macroscopic and microscopic anatomy Study of the brain of monkey No. 2 revealed the following destruction and degeneration. On the left side (first operation) the middle portion of the superior temporal gyrus and a little overlying parietal cortex were destroyed. Deeper, most of the lower half of the insular cortex was involved, together with the claustrum and its two limiting capsules, extrema and externa. The lower part of the putamen was partially affected by the lesion also. Still deeper the instrument severed the tail of caudate and the stria terminalis; forward the uncus and the amygdala were largely involved and also the transverse limb of the anterior commissure and the uncinate fasciculus. Very few degenerated fibers were found in the left temporo-pontine tract, but stria terminalis on this same side showed degenerated fibers throughout its course. On the right side the superior temporal gyrus showed deep destruction in the middle third of its extent and the middle temporal gyrus in its caudal half; also, a large part of the insula, about the lower two-thirds, and the capsula extrema and claustrum were involved, the capsula externa being spared. Very little parietal cortex at the base was destroyed. More medially and deeper the right fasciculus uncinatus was sectioned and about the anterior third of the ventral portion of the right inferior temporal gyrus was completely destroyed.

The right temporo-cortico-pontine tract shows many degenerated fibers in contrast to the fewer seen in the homologous tract on the left side (fig. 2). On the left side a large

part of the superior temporal gyrus was destroyed and the degenerated fibers seen in the left temporo-pontine tract could not be traced from this cortex, but were injured in the putamen through which they run. This fact gives further support to the view that the temporo-pontine tracts have their origin in the middle and inferior temporal gyri (Dejerine, 1895), and in this case the degenerated fibers in the right temporo-pontine tract appear to come chiefly from the right middle temporal gyrus which was injured more caudally than the right inferior temporal gyrus (Crosby and Henderson, '48).

Summary After a left lesion which involved the superior temporal and insular cortices, stria terminalis, and the basal parts of the putamen, the claustrum, and the external and extreme capsules, and which destroyed largely the uncus and left amygdala, this monkey showed no change in behavior and he recalled previously learned tests and objects. A second lesion on the right side destroyed parts of the superior, middle, and inferior temporal gyri, and a large part of the insula in addition to the claustrum and capsula extrema. After this operation the monkey was very tame and he recalled previously learned objects and tests. When a new test (weights) was introduced, however, he could not learn it; and in the case of new objects, he could learn to discriminate them only after multiple attempts. This animal, although much tamer than before, uttered many more sounds than previously.

Monkey No. 3

This monkey learned preoperatively to discriminate shape and weight by the pulling-in technique, making no errors in the last 27 and 21 trials, respectively. After only a few attempts the animal learned to discriminate various objects placed in front of the cage, picking up only those which were edible. On February 25, 1949, a first lesion was placed along the basal and medial surface of the temporal lobe through a small opening in the superior and middle temporal gyri. Following this first lesion, the monkey performed the discrimination tests as well as before and no changes in behavior were observed. On March 4, 1949, a similar lesion was made on the right side, following which the animal showed greater tameness and uttered more sounds than previously, just like monkey No. 2. However, so far as discrimination was concerned, the picture was quite different. Discrimination of weight was perfectly recalled and various objects placed on a board were recognized at once; new objects could be learned and selected after a few trials only. The ability to discriminate by shape, however, was no longer recalled and the animal showed no signs of relearning even after 200 trials. His performance on the "multiple object tests" revealed that no visual impairment was present which could explain his loss of discrimination for shape. On being tested for shape, the animal shifted from one box to the other at each trial before pulling in one; but it appeared

that, although he could see both boxes, he could not, so to speak, "make up his mind" as to which of the two boxes he should pull to obtain food.

A third lesion on March 11, 1949, which destroyed the surface cortex of the temporal lobe around the previous opening in the brain, added nothing more to the last-described picture of the animal. A similar lesion on the right side made a week later (March 18, 1949) was followed by a greater loss. However, weight discrimination was still recalled, but this time not only was the animal unable to discriminate between the shapes of the boxes but also between various objects placed on a board in front of him. He picked up indiscriminately any object offered to him, smelling it and licking it and eating it when it was edible. However he discarded even edible objects of which he was fond, for instance unshelled peatnuts. If the experimenter placed his finger in front of the animal, the animal would grasp it at once like any other object in sight. Vocalization, which was very marked following the second and third operations, disappeared completely and the tameness increased.

Macroscopic and microscopic anatomy Study of this brain reveals that on the left side approximately the middle third of the superior temporal gyrus and about the caudal third of the middle temporal gyrus were destroyed together with the rostral portion of area 19 behind and a little of the lower part of the parietal cortex above. More medially and rostrally this same lesion involved the lateral olfactory tract,

the prepiriform cortex, the anterior limb of the anterior commissure, and the diagonal band of Broca; backward the dorsal part of the amygdala and fasciculus uncinatus were damaged and the capsulae externa and extrema and the claustrum were destroyed at the base of the brain together with part of the transverse limb of the anterior commissure. Still farther back the lesion involved the lower part of the insula and of the putamen, interrupting some of the fibers which run through this latter structure. The caudal end of the lesion included the basal surface of the inferior temporal gyrus and about the lower half of the hippocampus.

On the right side the superior temporal gyrus was destroyed in about the same area as on the left; in addition the lower part of the pre- and postcentral gyri show degeneration. More medially and more rostrally the uncus and amygdala were largely destroyed; the inferior temporal gyrus, especially its ventral portion, and the hippocampal gyrus are deeply disintegrated rostro-caudally together with the rostral portion of the hippocampus. Above this structure stria terminalis and the tail of caudate were encroached upon. More laterally fasciculus uncinatus was separated from the temporal pole and the capsulae extrema and externa show degenerated fibers in their vertical limbs, these fibers having been destroyed at the base of the brain along with the claustrum. The transverse limb of the anterior commissure is also involved at its origin in the temporal pole. Very little of the putamen was affected but many fibers were injured just ventrolateral to this structure.

From these superficially and deeply destroyed structures degenerated fibers can be traced into both medial olfactory tracts (but much more conspicuously into the left), into the left lateral olfactory tract, into the right stria terminalis (fig. 3), and into both fornices. The degenerated fibers in the right stria terminalis can be traced chiefly to the bed nucleus of this tract. Fibers showing Marchi granules are more numerous in the left fornix; some of these fibers can be traced to the left lateral septal nucleus (fig. 4) and others to the ventral half of the left mammillary body. Those in the right fornix, fewer in number, could be traced only to the right lateral septal nucleus (fig. 4). Two other structures showing degeneration are the tubercula olfactoria. Marked degeneration was found in the left temporo-cortico-pontine tract which was partially destroyed in the putamen with a few fibers of the temporo-pulvinar-fasciculus of Arnold and a few fibers of the optic radiations. Other degenerated fibers in the left temporo-pontine tract appear to come from the cortex. The right temporo-cortico-pontine tract shows much less degeneration, only its more ventral fibers having been injured at the base of the putamen with a few fibers of the right temporo-pulvinar fasciculus (fig. 5). On the right side the pulvinar shows black granules in its medial and caudal part (fig. 3); on the left these granules are less in number and occupy the ventral half of the medial part of the pulvinar (fig. 6). This area of the pulvinar in which are seen these black granules (figs. 3 and 6) can be compared quite well to

a similar area shown in figure 25 (section 151) of Walker's The Primate Thalamus ('38). In the part of the pulvinar illustrated in this figure no retrograde degeneration is visible, although the animal had suffered a partial hemidecortication (experiment 6, page 109) which spared the temporal lobe. In the present material the lesion involves chiefly that area which was left intact in his case 6 and it appears that these black granules represent cellular changes following the interruption of thalamo-cortical fibers which have their origin in this particular area of the pulvinar (dorsomedial part). On the basis of the lesions in this case and those to follow, these fibers appear to end along the hippocampal or inferior temporal gyri, behind the level of the amygdala. Both medial geniculate nuclei show also many dark granules, apparently due to involvement of the superior temporal gyri which were injured in about the same area on both sides. The right medial geniculate nucleus is shown in figure 3. Other degenerated fibers are seen in the capsulae externa and extrema of both sides, in the anterior commissure, and in the corpus callosum. A few degenerated fibers are present in the optic radiations and in the ventral components of both divisions of the left internal cortico-tectal tract (Crosby and Henderson, '48) (fig. 6).

Summary This monkey, which had learned to discriminate perfectly shape, weight, and various objects, did not present any changes in discrimination and in behavior following a left-sided lesion which involved, among other structures, a

little surface cortex of the temporal lobe, the lateral olfactory tract, the prepiriform cortex, and only the dorsal part of the amygdala, and which destroyed the base of the claustrum and of the capsula externa and capsula extrema and also a few fibers of fasciculus uncinatus; farther caudally it destroyed much of the temporo-pontine fibers and partially involved the putamen, the temporo-pulvinar fasciculus and the hippocampus. A second lesion on the right destroyed completely the amygdala and uncus, the rostral end of the hippocampus and the hippocampal and inferior temporal gyri, in addition to a little surface cortex. Following this second lesion the monkey could no longer discriminate shape and he showed a greater tameness. Weight and various objects could still be discriminated. The animal presented this same picture after destruction of part of the surface cortex of the temporal lobe on the left side. However, following removal of more cortex of the temporal lobe on the right side, the animal could neither discriminate the shape of the boxes nor recognize various objects placed on a board, although he could still discriminate differences in weight. His tameness had increased. All objects which were presented to him had to be smelled and licked before he ate them, if they were edible, indicating that he could no longer discriminate by sight alone but had to use also his senses of smell and of taste.

Monkey No. 4

This monkey was tested for the discrimination of shape and of various objects before he was operated on May 27, 1949. Through a bilateral opening in the skull over area 6, needles were introduced into the brain substance with the help of the stereotaxic apparatus, the aim of this operation being to destroy the columns of the fornix. No changes in behavior and no loss of discrimination followed this first bilaterally placed lesion.

A week later (June 3, 1949) the external and extremal capsules were destroyed on either side with the help of this same instrument. No changes in behavior were recorded afterwards and all previously learned tests were perfectly recalled; moreover the animal learned quickly to discriminate differences in weight. The animal was reoperated on June 14, 1949, and the rostral half of the left temporal cortex was removed. Postoperative testing disclosed no loss of discrimination and the behavior of the animal seemed normal. Ten days later (June 24, 1949) a lesion was made similar to the last one, but on the right side. Again no changes in behavior and no loss of discrimination were recorded.

On July 1, 1949, a lesion was placed in the left hippocampal gyrus and the surrounding structures. Upon manipulation of the instrument in the medial and ventral region of the temporal pole (apparently the hippocampal gyrus) changes in respiration were noted consisting of an arrest of respiration

followed by a deep inspiration. In spite of all these lesions, the animal could still discriminate very well and appeared normal in behavior.

Finally, on July 8, 1949, the right hippocampal gyrus was destroyed and the same changes in respiration were noted. It was only after this last lesion was made that some loss in discrimination was observed. The animal was tested for the discrimination of weight and this was recalled perfectly. Then he was retested for the discrimination of shape, and it was found that he had forgotten completely what he had previously learned in order to obtain food. He pulled in either box indiscriminately. However, after a few days the animal was able to relearn to discriminate shape; he relearned it, however, only after more trials than were required to learn it the first time. Besides, instead of pulling in the correct box directly as before, he had to shift at each trial. It was thought that the animal might be using other cues than visual to supplement his deficiency of visual discrimination. To eliminate all possible cues other than visual, the boxes were reweighed and found to be of the same weight; to eliminate auditory cues, paper was glued under each box and the tests repeated. Again the monkey could pull in the right box. Then the paper floors were removed, the shape equalized on each box, and it was found that, with only a few errors, the monkey could discriminate between one box and the other by the noise produced by the rubbing of the boxes on the floor. Immediately after the last operation the animal was using auditory cues in

addition to visual cues to select the box which contained food, and that is why he was shifting at each trial. After numerous trials the monkey was able to pull in the correct box directly, showing that he was now able to discriminate between the two boxes upon visual cues alone. On the other hand, he made fewer errors than expected when only auditory cues were present, proving that he had learned these previously and probably was using them immediately following the last operation when he was shifting at each trial.

To complete the information on visual discrimination the animal was tested for the discrimination of light and dark using white and gray. It was only after repeated trials, more than usual, that the animal could discriminate one box from the other. On the other hand, discrimination of sound, using a bell connected with one of the two boxes, was learned much more quickly.

This animal showed no personality changes following all these lesions.

Macroscopic and microscopic anatomy Each lesion could be individualized and most of the degenerated tracts could be traced from a definite lesion and thus correlation between function and structure was possible. The first two lesions were made the same day and as symmetrically as possible, with the help of the Horsley-Clarke instrument. On the right side the structures involved in the lesion were the following: a little surface cortex of area 6, the cingulum, the corpus callosum, the fornix, stria medullaris, and the mammillo-thalamic

tract. On the left side the following structures were involved: a little surface cortex of area 6, the corpus callosum, the head of caudate, the left stria medullaris, the mammillo-thalamic tract, and the anterior limb of the internal capsule, in addition to a few fibers of the ansa lenticularis.

The corpus callosum shows many degenerated fibers (fig. 7) due to the lesions on the surface cortex and in the commissure itself. The degenerated fibers of the right cingulum are numerous rostral to the lesion (fig. 7) decreasing in number as they are followed anteriorly; behind the lesion, fewer fibers show Marchi granules (fig. 8). The degeneration in the right fornix is in the lateral third of this structure (fig. 8); these degenerated fibers can be traced chiefly to the corresponding lateral septal nucleus. Both striae medullares are largely degenerated; only the more medial fibers of the left stria medullaris are intact (fig. 9). These fibers were destroyed at the point where the various components of the stria medullaris join each other; on the left side, the lesion being a little more lateral, the more medial fibers were spared. Apparently the undegenerated fibers come from the medial olfactory area. The degenerated fibers can be traced to the habenulae and are seen decussating in the habenular commissure (fig. 10). The right habenula receives degenerated fibers more medially than the left one, corresponding to the degeneration in the striae medullares. Both mammillo-thalamic tracts show degenerated fibers which can be traced to the anterior thalamic nuclei, these fibers being

more numerous on the left side (fig. 8). The anterior limb of the left internal capsule was destroyed in about its lower third for quite an extent. As a consequence, many degenerated fibers can be traced within the left fronto-pontine tract and interconnections between the thalamus and the frontal cortex show degeneration on the left side; most of these fibers come from or go to the left dorsomedial nucleus of the thalamus (fig. 9) and a few come from and pass to the lateral and anterior thalamic nuclei and among these fibers a few, presumably from the anterior thalamic nucleus, end in the left cingulate gyrus.

The second set of lesions, made with the same instrument, were caudal and lateral to the previous destructions. On the right side the needle went through cortex, corona radiata, the external capsule (dorsally), and the putamen to the lower part of the external capsule; the lesion was placed so that the capsulae externa and extrema and the claustrum were destroyed with a few fibers interconnecting the temporal gyri. On the left side the needle was introduced into the brain a little more laterally than on the right and its course into the tissue can be traced from the cortex through the corona radiata and the insula to the lower part of the claustrum; the lesion destroyed the claustrum and fibers of its two limiting capsules, externa and extrema, just above the transverse limb of the anterior commissure.

The next two lesions, made 10 days apart, involved the lateral surface cortex of both temporal lobes in about their

anterior half. The superior and middle temporal gyri were destroyed rostrally and, in addition, a little surface cortex at the base of the frontal lobe. From these two lesions there resulted a degeneration of the fibers interconnecting the superior, middle, and inferior temporal gyri and also of the fibers of the capsula extrema which interconnect the superior temporal gyri with the overlying cortex. Degenerated fibers probably due to these lesions are seen in both temporo-cortico-pontine tracts.

The last two lesions, one made a week later than the other, involved the undersurface of the temporal lobe, partially destroying, on either side, the ventral part of the inferior temporal gyrus and the hippocampal gyrus. These lesions are separated from the previous ones, except for a small area on the left, by a longitudinal band of tissue which was not encroached upon by the instrument. On the right side the deepest point of the lesion involved a few fibers of the alveus ventrally, and on the left side, the ventrolateral part of the amygdala rostrally. Among the degenerated fibers leaving the inferior temporal gyrus some can be seen to enter the transverse limb of the anterior commissure on either side. Farther caudally, as the anterior commissure appears more dorsally, two major groups of degenerated fibers accumulate below this structure; the more dorsal of these fibers can be traced in large number into the temporo-pontine tracts; the more ventral face, in part, in the temporo-pontine tracts. A number of them accumulate laterodorsal to the tail of caudate,

then, probably as temporo-pulvinar fascicles, can be traced caudally to the caudal and lateral part of the pulvinar. At first these fibers lie laterodorsal to the tail of caudate, but become mediodorsal to this structure as they run caudalward, being separated from the lateral geniculate nucleus by the external cortico-tectal tract which appears intact in this case. Other degenerated fibers pass to the thalamus laterally, but their origin and course cannot be determined in the material. Other fibers can be seen passing caudally through the pulvinar (fig. 11) to the superior colliculus on either side; these fibers, which belong to the ventral components of the internal cortico-tectal tracts, presumably have their origin in the more caudal part of these two last lesions which involved the inferior and the hippocampal gyri far caudally into the occipital lobe. The caudal part of pulvinar on either side shows in its dorsomedial area (fig. 11) a strong concentration of black granules which appear to represent cellular disintegration in relation to destruction of the surface cortex along the basal part of the temporal lobe.

From the lateral and rostral area of the left amygdala, which was partially injured by the instrument, fibers can be traced into the lateral components of the left stria terminalis. As these fibers swing forward with the caudate nucleus, they become ventromedially placed in the stria terminalis (Lauer, '45). These fibers can be traced only to the left stria medullaris, which was injured by a previous lesion; rostral to this structure no degenerated fibers can be seen in the left stria

terminalis, which suggests that the degenerated fibers (lateral component) have passed into the stria medullaris.

On the right side a few fibers of the alveus were severed in the rostral part of the hippocampus ventrally. These few fibers can be traced into the corresponding fornix and some of them end in the right lateral septal nucleus, although others pass into the postcommissural fornix to join the right stria medullaris. A very few fibers of the optic radiations were destroyed on the right side, along with the alveus.

Summary After lesions which involved the striae medullares, the mammillo-thalamic tracts, the external and extreme capsules partially, and most of the interconnections of the left dorsomedial thalamic nucleus with the frontal cortex, in addition to a few fibers of the right fornix and right cingulum, no appreciable personality changes and no loss of discrimination were observed in this animal. Other destructions placed on the surface cortex of the rostral half of each temporal lobe resulted in no changes in behavior. Retesting for discrimination disclosed no loss of memory for previously learned skills.

Only after bilateral destruction of the inferior temporal and hippocampal gyri was added to the previous lesions did the animal present a lack of visual discrimination; however, with the aid of other cues like sound he was able to relearn to discriminate shape; but it took him many more trials than previously. To learn a new test based on visual cues, more than the normal number of trials were required. Tests based on auditory cues were learned very rapidly.

Apart from this temporary loss of memory for shape discrimination and a slowness in relearning or learning for the first time tests based on visual cues, this monkey showed no changes in behavior.

Monkey No. 5

This monkey was tested for the discrimination of shape, sound, and weight. He performed the last 50 trials of the tests for shape without error, pulling in directly the box which contained food. He also learned to discriminate perfectly differences in sound and in weight, shifting at each trial before pulling in the right box. Following these preliminary tests, lesions were placed (July 29, 1949) in the region of the amygdala on either side of the brain. Upon manipulation of the instrument on the deeply situated structures, changes in respiration, similar to those obtained during the operation on monkey No. 4, were observed.

It was surprising, a few hours after the operation when the effect of the ether had surely disappeared, to find the animal apparently sleeping, in a state comparable to the monkeys who were asleep following hypothalamic lesions (Ranson, '39). At first the animal lay on his side, with his eyes half closed (fig. 12). Loud noises or intense light brought only a weak response, the animal opening the eyes and moving the head slightly. He would not eat by himself, so feeding was done intravenously, using a solution of amino acids and dextrose. Rectal temperature taken on the first day indicated 99.7° F. (6 p.m.); respiratory rate was 30 and heart rate 85.

On the second day after the operation, the animal sat most of the time with his head bent forward and the eyelids drooping (fig. 13). Intravenous injection was repeated. When the animal was handled, he responded by jerky movements of the limbs. Rectal temperature remained at 99.7° F. (11 a.m.). On the third day his attitude remained unchanged; he was drowsy most of the time. Intravenous injection was repeated. However, his rectal temperature indicated a rise toward normal, reaching 98.2° F. at 10 a.m. and 100.3° F. at 4.p.m.

On the next day (fourth) the animal began to awaken; he responded to less intense stimuli than on the first day after the operation. At the end of the day he was taking any object which was handed to him, smelling it, and eating it if edible. For instance, he ate pieces of banana, orange, and apple, and a few raisins, but discarded, after smelling them, pieces of bread and casein cubes which were familiar to him prior to the operation. Pieces of bread covered with white sugar, of which monkeys are usually very fond, were presented to the animal; he smelled them and discarded them as being inedible. It seemed that he had to depend at that time entirely upon his sense of smell to discriminate food from other objects, indicating that smell was the first sense to reappear in this animal who was just coming out of a vegetative state. Although he could feed himself, he still had a strong tendency toward the sleeping posture (fig. 14); for instance, he was seen a few times in that typical posture with a piece of banana held to his lips. On a few occasions he picked up various objects

directly with his mouth, using his hands only to smell them.

On the fifth day after the operation the animal began gradually to be more and more active until by the twelfth day he had resumed almost normal activity, eating the usual food, including bread and casein. Even eleven days after the operation he could still be seen sitting down with his head bent forward, especially if it was quiet around him. As the animal became more active a right hemianopsia could be observed, evidenced by the fact that he picked up only the objects which were placed in his left visual field and he circled around to the left when he wished to reach to the right. In addition, observation disclosed a little weakness of his left limbs which disappeared in a few days. He remained very tame and very easy to handle.

Twelve days after the operation the animal was considered normal enough to repeat the discrimination tests. He was retested first for the discrimination of shape. On the first few trials he made many errors, showing a strong tendency to pull the box on the left, as was to be expected with a right hemianopsia. In spite of this visual defect, he managed to relearn the visual test in half as many trials as preoperatively. For instance, he made 21 errors in the first 30 trials, showing a strong tendency to the left; of all the errors made in the following 40 trials, however, only two errors were made in the last 25. It took him only a few trials to carry out the test for weight discrimination as well as preoperatively. After 40 trials the animal chose every

time the lighter of the two boxes to obtain food. Sound discrimination was almost perfectly recalled, the monkey making only a few errors in the first few attempts. He was sacrificed on August 15, 1949, and perfused with 10% formalin.

Macroscopic and microscopic anatomy On the right side the lesion involved the superior temporal gyrus through which the instrument was introduced; this gyrus was destroyed along the middle third of its caudo-rostral extent. Deeper, there is a slight involvement of the insular cortex. Rostrally the lesion included most of the amygdala, only the dorsal part of this structure being spared (fig. 15). The anterior half of the hippocampal gyrus, or its connections, and, caudal to the amygdala, the rostral two-thirds of the hippocampus, together with the fimbria, were destroyed. Laterally the transverse limb of the anterior commissure and the basal part of the capsula extrema were partially severed. Dorsal to the hippocampus the tail of the caudate and a few fibers of the temporo-pontine and temporo-pulvinar tracts and of the optic radiations were injured in the ventrolateral part of the putamen (fig. 16). The caudal part of the lesion involved chiefly the hippocampus and the hippocampal gyrus.

On the left side the instrument was introduced also through the superior temporal gyrus, which was destroyed in about the middle third of its extent; deeper the fibers interconnecting the superior and the middle temporal gyri were interrupted. Rostromedially (fig. 17) the uncus and amygdala were completely destroyed. Rostrolaterally (fig. 17) the instrument severed

the fasciculus uncinatus, the base of the capsula extrema and of the claustrum, the temporal limb of the anterior commissure, and a little more caudally, the transverse limb of this same commissure. Behind the anterior commissure the lesion extended dorsally to the base of the putamen and of the globus pallidus, involving also the ventral part of the ansa lenticularis and, below this structure, fibers of the supraoptic system. Behind the amygdala only the very rostral end of the hippocampus was destroyed, but the fimbria was injured in about the anterior half of its extent (fig. 18). The rostral part of the hippocampal gyrus was likewise injured and farther back its interconnections were severed for quite a distance. As the lesion is followed caudally, it shifts more dorsally; still farther back it extends more medially as well. Above the hippocampus the tail of the caudate and the stria terminalis were transected (fig. 18); dorsal to these structures the globus pallidus and the putamen were destroyed more dorsally and, with this last structure, fibers belonging to the temporo-pontine and temporo-pulvinar tracts (fig. 18). Medial to the putamen the optic tract was severed just before its entrance into the lateral geniculate nucleus (fig. 18). As the lesion is traced still farther back (fig. 19) structures showing destruction can be seen in the following order: the putamen, the posterior limb of the internal capsule, the lateral nucleus of the dorsal thalamus, and finally, at the caudal end of the lesion, the posterior commissure and the commissure of the superior colliculus, all on the left side (fig. 20).

From the two destroyed areas some degenerated fibers can be followed clearly and traced to some precise termination; other degenerated fibers can be traced only for a part of their course. On the left side stria terminalis was transected completely and degeneration can be seen in the fibers of its two components: the medial and the lateral. The degenerated fibers of the lateral component can be traced to the corresponding habenula; the fibers of the medial component distribute largely to the bed nuclei of stria terminalis and of the anterior commissure on the same side (fig. 21); other degenerated fascicles continue ventralward and presumably caudalward, some of them passing in front of the anterior commissure (fig. 22), others behind it. On the right side, corresponding to an involvement of the ventral part of the amygdala, stria terminalis shows degeneration chiefly in the fibers of its lateral component, these passing to the left habenula; only a few fibers of the medial component show degeneration and these can be traced chiefly to the bed nucleus of the right stria terminalis (fig. 21). Degenerated fibers are also seen bilaterally in the fornix; some of these fibers end in the lateral septal nucleus, (fig. 21 and 22) others run in the postcommissural fornix toward the habenula and toward the hypothalamic area. Those fornix fibers ending in the habenula appear to terminate more laterally than those derived from the stria terminalis (fig. 20). Other degenerated fibers, the origin of which cannot be determined, were traced into the preoptic and hypothalamic areas. They form on either side a

group of fine fibers which run ventrally and close to the ventricle. At the level of the mammillary body some of the fibers decussate to the opposite side and are seen dorsolateral to this structure; from this point they become more ventral as the mammillary body disappears and they continue their course behind this nucleus into the basal part of the midbrain where they disappear.

Conspicuous degeneration, especially on the left side, can be seen in the tuberculo-septal fibers from the left tuberculum olfactorium. Among these degenerated fibers a large number can be traced to the rostral area of the lateral septal nucleus (fig. 22). Other degeneration resulting from the rostral part of the lesion is found in the anterior commissure, most conspicuously, and in the left capsula extrema. A little more caudally, degenerated fibers are seen in the supraoptic system and in the left ansa lenticularis, fasciculus lenticularis, and optic radiations. Farther back the temporo-pulvinar fasciculi show fine degenerated fibers, and large degenerated fibers are present in both temporo-pontine tracts but most numerous on the left. The posterior limb of the left internal capsule shows also some degeneration.

Finally, the more caudal structures showing some degeneration, all on the left side, are the following: the external and internal cortico-tectal tracts, the superior collicular and posterior commissures, the medial tecto-spinal tract, and fibers of the mesencephalic root of V (fig. 23). The two last groups of fibers were destroyed in placing the lesion,

since the instrument touched upon the periventricular gray of the midbrain, at the caudal limit of the lesion.

Summary This animal learned preoperatively to discriminate differences in shape, weight, and sound. Lesions were then placed in the temporal poles. Some of the structures involved bilaterally were as follows: the rostral part of the hippocampus and of the hippocampal gyrus or their interconnections, the anterior commissure, the temporo-pulvinar and temporo-pontine fibers, and a little surface cortex of the superior temporal gyrus. Other structures injured more on the left side are the amygdala, putamen, claustrum, and capsula extrema. Finally, the globus pallidus, the ansa lenticularis, the lateral thalamic nucleus, the optic tract, and the internal capsule were destroyed in part on the left side, but not affected on the right side. From these structures degeneration was traced into the several tracts and nuclei.

Following these lesions, the animal was in a state resembling sleep; for the first three days he was sitting down, with his head bent forward and his eyes half closed. During that time the animal had to be fed intravenously and his temperature was subnormal. On the fourth day following the operation, he gradually became more active until on the twelfth day he appeared normal in behavior except for a greater tameness than usual, which persisted. When this animal began to come out of his drowsiness he ate only the food he could discriminate by smell, discarding other food even that of which he was very fond, as for instance white sugar. After a few days his dietary habits became normal.

Retesting was possible twelve days after the operation and no marked loss of discrimination was observed. The animal relearned quickly to discriminate differences in shape in spite of a complete right hemianopsia. Weight discrimination was also relearned after a few trials only. When the discrimination of sounds was tested, it was found that the animal could repeat the test as well after the operation as before, except for a few errors in the first attempts.

Monkey No. 6

No discriminatory tests were carried out on this animal, for the chief interest in the case was the investigation of some of the anatomical structures the destruction of which could cause a sleeping-like state. Lesions were first placed bilaterally in the caudal part of the hippocampus through an opening in the temporal cortex, on September 17, 1949. Using the same bilateral routes, on October 6, 1949, the rostral area of the temporal lobe was injured along its basal surface. During this last operation, changes in respiration similar to those reported for Cases 4 and 5 were observed upon contacting the medial and basal portions of the temporal poles. Following these two bilateral lesions, no changes in behavior were observed, the animal being as wild as ever.

Macroscopic and microscopic anatomy Postmortem study of this brain revealed that on the left side the lesion extended rostrocaudally along the ventrolateral surface of the temporal lobe. Rostrally the cortex was injured where the middle and the inferior temporal gyri meet on the basal surface; caudalward

the lesion extends more laterally and involves the lateral part of the inferior temporal gyrus and, to a lesser extent, the middle temporal gyrus; in the caudal half the injury is entirely along the basal surface of the inferior temporal gyrus and is deeper. In this caudal part of the lesion, the interconnections of the hippocampal and inferior temporal gyri are severed along the ventrolateral part of the alveus. In other words, the lesion extends along areas 20 and 19 rostrocaudally and encroaches upon area 21 rostrally.

On the right side the superior and the middle temporal gyri were partially injured more rostrally than on the left. Deeper, the rostral end of the lesion involved the caudal part of the amygdala and the underlying hippocampal gyrus. Caudal to the amygdala the rostral part of the hippocampus is completely destroyed, and as it is followed caudally more and more of the dorsal and medial parts of this structure are spared. At the caudal end only the basolateral portions of the cornu Ammonis and of the gyrus dentatus were injured. Lateral to the hippocampus, the interconnections of the hippocampal and the inferior temporal gyri are cut together with some fibers of the optic loop.

The anterior commissure shows many degenerated fibers most of which have their origin in the left inferior and the middle temporal gyri (fig. 24), the basal portions of which were injured more rostrally than on the opposite side of the brain. These fibers can be traced on the right side; a large number of the more ventral fibers end in the right, middle,

and inferior temporal gyri and to a lesser extent, in the right hippocampal gyrus; the other, more dorsal, fibers extend farther caudally into the right external capsule. The left fornix presents only a few degenerated fibers due to a small injury of the ventrolateral part of the alveus caudally. Many fibers of the right fornix show some degeneration. The only bundles which are intact are the more lateral and more dorsomedial fascicles within the body of fornix (fig. 25), which arise from the more caudal areas of the gyrus dentatus and the cornu Ammonis. Some of the degenerated fibers of the right fornix can be traced rostrally into the right lateral septal nucleus; others pass to the caudal part of this same nucleus (fig. 26). These last fibers turn off from the postcommissural fornix, which distributes chiefly to the hypothalamic area (fig. 26), particularly to the mammillary body. A few degenerated fibers join the right stria medullaris to end in the corresponding habenula; others pass to the opposite fornix as commissural fibers. Another group, fibers which have their origin in the right gyrus dentatus (Riley, '43), can be traced into the right lateral longitudinal stria. These last decrease in number as they are traced rostrally. The right stria terminalis shows a few degenerated fascicles which run in its medial component to end in the right bed nucleus of this tract.

As the anterior commissure is followed caudalward it decreases in size and moves dorsally. Below it other degenerated fibers can be seen accumulating into two groups: a more dorsal group, the fibers of which cross through the putamen to

pass into the temporo-pontine tract and a more ventral group, the fibers of which enter this same tract and also the temporo-pulvinar fasciculus below the putamen. Other degenerated fibers belonging to the ventral group accumulate medial to the temporo-pulvinar fasciculus above the tail of caudate and constitute the external cortico-tectal tract (fig. 27). The degenerated fibers seen in these three tracts are numerous on the right side corresponding to a larger involvement of the fibers themselves on that side. Although on the left side only the basal part of the inferior temporal gyrus is destroyed in the area in which these tracts have their origin, on the right several bundles coming from the middle and nearly all of the fibers coming from the inferior and hippocampal gyri were injured far caudally. The fibers of the temporo-pontine tract can be seen swinging around the laterodorsal edge of the lateral geniculate body to join the parietal component of the tract. The fibers to the pulvinar accumulate first laterodorsal to the tail of the caudate, caudalward they become more medially placed, and still farther back pass along the lateral edge of the pulvinar to distribute to this structure (fig. 28). The right medial geniculate nucleus receives a few degenerated fibers from the right superior temporal gyrus, which was damaged in front of the auditory cortex. Another tract showing degeneration from the involvement of area 19 is the internal cortico-tectal tract (fig. 28). On both sides, the cortex or the fibers from the basal and lateral part of area 19 were injured. From these destroyed areas, degenerated

fibers pass in the ventral component of the preoccipital division and in the ventral component of the occipital division of the internal cortico-tectal tract on either side to the superior colliculus.

Summary This animal was operated upon twice; a first lesion was placed in the caudal and basal part of the temporal lobe along areas 20 and 19 bilaterally, and a second lesion involved the rostral part of the temporal lobe, also on both sides. In addition, the lateral temporal cortex was partially injured along the superior and middle temporal gyri on the right side and along the middle and inferior temporal gyri on the left side. No changes in behavior were observed following these two sets of lesions.

Apart from the cortex, the main structures destroyed were, on the right side, the caudal part of the amygdala, most of the hippocampus, and certain fascicles from the middle and inferior temporal, and the hippocampal gyri caudal to the amygdala; and, on the left, fibers from the inferior temporal and the hippocampal gyri at the level of area 19. From these superficial and deep lesions a few tracts show degenerated fibers. The anterior commissure presents many degenerated fibers from a left lesion; the temporo-pulvinar, temporo-pontine, and external cortico-tectal tracts are largely destroyed on the right, and to a lesser extent on the left. Cortico-geniculate fibers showing degeneration are present only on the right side. The fornix is largely degenerated on the right and very little on the left. The internal cortico-tectal

tracts of both sides show many degenerated fibers in the ventral components of both the preoccipital and occipital divisions. Finally the right stria terminalis shows a few fibers containing Marchi granules.

DISCUSSION

In this series only one animal (monkey No. 2) showed impairment in weight discrimination; this test, however, which the animal could not learn after repeated trials was introduced postoperatively. Ruch, Fulton, and German ('38) observed that in monkeys discrimination of lifted weights was rapidly relearned after partial lesion of the precentral gyrus or following destruction of the posterior parietal lobe as well as after bilateral extirpation of the postcentral gyrus. Only in one case did they obtain a partial and permanent loss of discrimination for weight following a lesion which involved the posterior partietal lobule together with the postcentral gyrus. In the present material very little of the lower part of the parietal cortex was destroyed, but the insula and many of the interconnections of the parietal cortex were injured on both sides. Since the test was introduced only after bilateral lesions and since similar findings have not been reported in the literature consulted, the author can draw no definite conclusions on the basis of this single result. However, negative results in other cases show that lesions restricted to the temporal lobes do not interfere with the discrimination of weights, as expected.

Two animals presented an impairment of shape discrimination. Case 3 showed a complete loss which was never overcome; case 4 relearned the visual test only after repeated trials and apparently with the help of other cues. Several lesions were placed in the brains of these two animals. However, this loss and this lack of visual discrimination appeared only after destruction along the basal surface of the temporal lobe on either side. In monkeys Nos. 2 and 5 no loss of discrimination was observed following lesions on the basal surface of the brain, but in these animals the lesions did not extend as far caudally as in cases 3 and 4, at least on either side. The apparent discrepancy between these results has probably its explanation in the fact that in monkeys 3 and 4 more of the visual association cortex and of its interconnections were injured. This is particularly evident in the brain of monkey No. 3 in which the lesions were deeper and extended farther caudally. Ades and Raab ('49) observed a permanent loss of form discrimination only when a bitemporal decortication was added to removal of areas 18 and 19. In monkey No. 3 a permanent loss of discrimination for shape was obtained following lesions which interrupted surely many interconnecting fibers from areas 19 and 18 at the base of the brain, but which involved very little of the temporal cortex. However, after decortication of the caudal area of both temporal lobes had been added to the previous lesions, the monkey showed a greater loss of visual discrimination. The animal could no longer discriminate by sight alone and resembled in this

respect the monkeys studied by Klüver and Bucy ('39) which showed "psychic blindness." The production of this visual agnosia appears to depend upon the bilateral destruction of area 19 and may be also of area 18 in addition to the caudal area of the temporal lobe which is much more under the influence of the visual association cortex than its more rostral and dorsal part (Bailey et al '44a; see also McCulloch's diagram, fig. 39, p. 81, in Bonin and Bailey's The Neocortex of Macaca Mulatta, 1947).

The monkeys who were tested for the discrimination of sound recalled the tests following variously placed lesions in the temporal lobes; all these lesions, however, involved only partially the auditory association cortex. The sense of smell appeared to be intact in all cases, even after extensive lesions which included the amygdala, piriform lobe, and hippocampus. These results are in agreement with the findings of Swann ('34) in the rat and with those of Allen ('41) in the dog.

None of the writer's monkeys showed the complete "polysymptomatic picture" described by Klüver and Bucy ('37, '38, '39) following bilateral temporal lobectomy. However, one animal referred to earlier in this discussion presented a visual agnosia which can be compared to the "psychic blindness" of these two authors. It appears to the present author that while the other symptoms of the "bitemporal monkeys" may depend for their production upon complete and bilateral destruction of the temporal lobes, this particular symptom, "psychic

blindness," can be observed apart from the others following lesions which are restricted on both sides to the caudal area of the temporal lobe and which include area 19 together with or without area 18.

Another alteration of normal behavior observed in four of the animals studied was a change toward greater tameness following lesions which involved mainly the rostral area of the temporal lobes including the so-called "olfactory formations" on the medio-basal surface. Other symptoms such as "oral tendency," "hypermetamorphosis," and "hypersexuality," observed by Klüver and Bucy were not seen in the monkeys of this series following differently placed destructions in the temporal lobes. The symptoms failed to appear, probably because the lesions were not sufficiently extensive, as these two last-named authors noted after various subtotal destructions in the temporal lobes (Klüver and Bucy, '39).

Finally, an unexpected result was obtained in monkey No. 5 when this animal showed a state resembling sleep following bilateral lesions in the temporal pole. The chief structures bilaterally destroyed to a considerable extent were the amygdala, the piriform cortex, and the hippocampus. The hypothalamus was entirely spared. To postulate a new center of awakeness on the basis of this single result would be unwise. Further studies need to be made, first to prove that the caudal area of the hypothalamus is either such a center, or a relay center necessary for the state of awakeness, or an area of passage of fibers the destruction of which produce a

sleep-like state. That the structures destroyed in the present case exert a direct influence on the hypothalamus, if it is a center of awakeness, or that they send fibers which pass through the caudal area of this structure, appears to the writer the more plausible explanation of this result. For degenerated fibers, the origin of which, however, cannot be determined exactly in the material available, were found on either side of the hypothalamus, and some of them were seen to bypass the mammillary bodies to reach the midbrain.

GENERAL SUMMARY

This report is concerned with anatomical and experimental studies of the brains of six monkeys in which various lesions had been placed. All of these involved the temporal lobes. Five of these animals were tested pre- and postoperatively for shape discrimination, and some of them for weight and sound discrimination.

Sound discrimination was preserved in all cases. One animal could not learn to discriminate differences in weight postoperatively, following brain lesions which destroyed on both sides many interconnections from the parietal cortex. Another animal had forgotten completely shape discrimination following extensive bilateral injury to the fibers of the visual association cortex. Another monkey could relearn to discriminate shape after a lesion similar to but less extensive than that suffered by the previous animal.

Finally, one monkey was found in a state of drowsiness after a bilateral destruction which involved mainly the medial and basal structures of the temporal poles.

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ABBREVIATIONS FOR FIGURES

AMYG., amygdala

ANT. COM., anterior commissure

ANT. COM. TEMP. L., anterior commissure, temporal limb

ANT. COM. TRANS. L., anterior commissure, transverse limb

ANT. THAL. N., anterior thalamic nucleus

AQ., aqueduct

BED N. + ST. TERM., bed nucleus of stria terminalis and stria terminalis

BR. PONT., brachium pontis

CAUD. N., caudate nucleus

CING., cingulum

CLAUS., claustrum

CORP. CAL., corpus callosum

DOR. MED. THAL. N., dorsomedial thalamic nucleus

EXT. CAP., external capsule

EXT. CORT. TECT. TR., external cortico-tectal tract

FIM., fimbria

FOR., fornix

FOR. BOD., body of fornix

FOR. POSTCOM., postcommissural fornix

GL. PAL., globus pallidus

HAB., habenula

HAB. COM., habenular commissure

HIP., hippocampus

HIP. G., hippocampal gyrus

INF. TEMP. G., inferior temporal gyrus

INS., insula

INT. CAP., internal capsule

INT. CORT. TECT. TR., internal cortico-tectal tract

LAT. GEN. N., lateral geniculate nucleus

LAT. SEPT. N., lateral septal nucleus

LAT. THAL. N., lateral thalamic nucleus

LAT. VENT., lateral ventricle

MAM. THAL. TR., mammillo-thalamic tract

MED. GEN. N., medial geniculate nucleus

MED. TECT. SP. TR., medial tecto-spinal tract

MES. R. V, mesencephalic root of V

MID. TEMP. G., middle temporal gyrus

MOT. N. V, motor nucleus of V

OPT. CH., optic chiasma

OPT. TR., optic tract

POST. COM., posterior commissure

PUL., pulvinar

PUT., putamen

ST. MED., stria medullaris

ST. TERM., stria terminalis

SUP. COLL., superior colliculus

SUP. COLL. COM., superior collicular commissure

SUP. TEMP. G., superior temporal gyrus

TEMP. CORT. PONT. TR., or TEMP. PONT. TR., temporo-cortico-pontine tract

TEMP. PUL. F., temporo-pulvinar fasciculus

TUB. SEPT. F., tuberculo-septal fibers

Figures 1, 12, 13, and 14 are photographs; all the other figures represent microphotographs of sections of the brains of monkeys Nos. 2 to 6; all these sections were stained according to the Marchi technique.

Fig. 1 - Photograph of the boxes used for testing discrimination of shape.

Fig. 2 - Microphotograph of a section of the brain of monkey No. 2. This section which passes through pons shows degenerated fibers in the right temporo-cortico-pontine tract. X15.

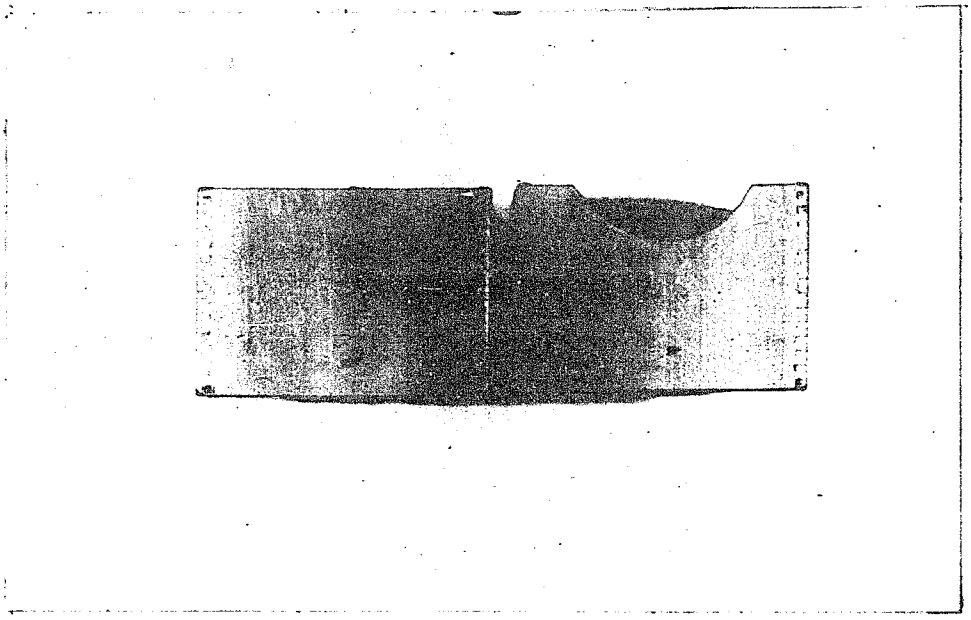


FIG. 1

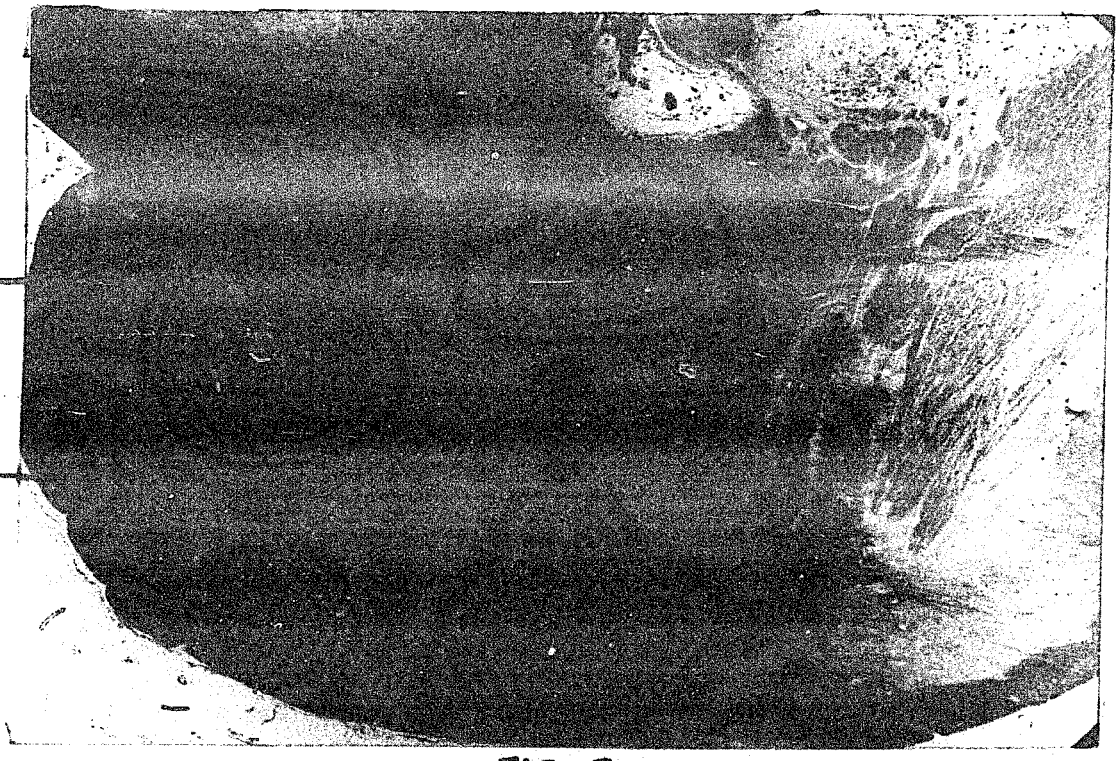


FIG. 2

Fig. 3 - A microphotograph showing degeneration in the right pulvinar, the right medial geniculate nucleus, and the right stria terminalis (monkey No. 3). X15.

Fig. 4 - A microphotograph showing degenerated fibers terminating in the rostral part of the lateral septal nuclei (monkey No. 3). X15.

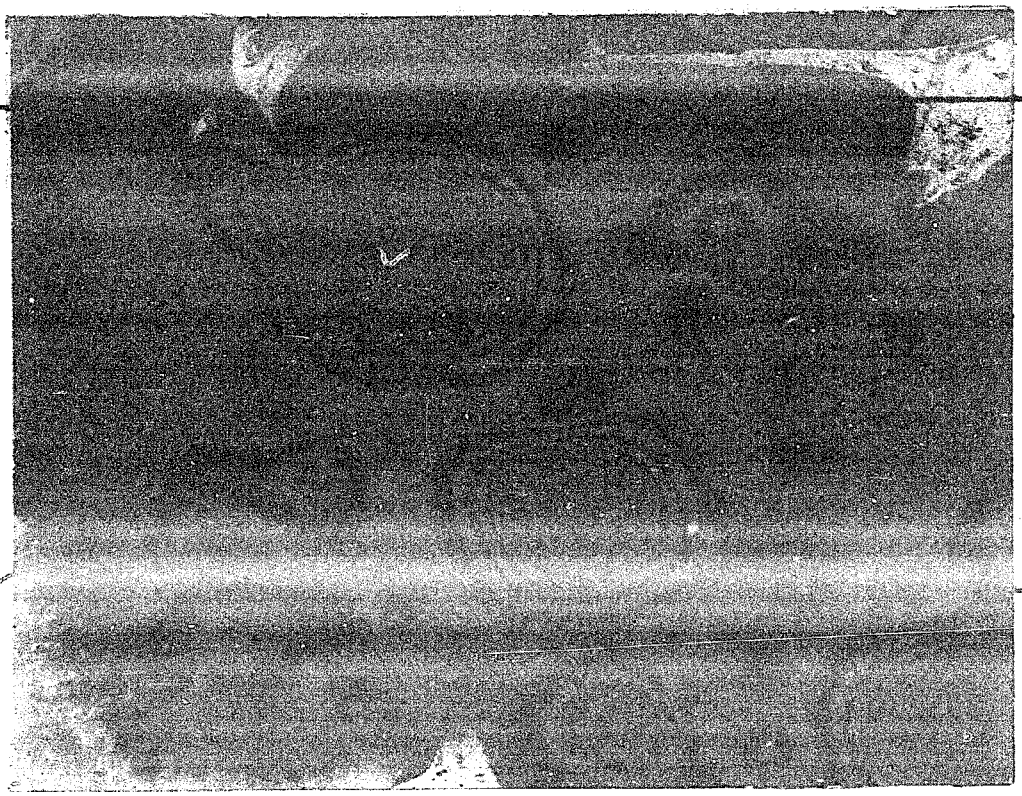


FIG. 3

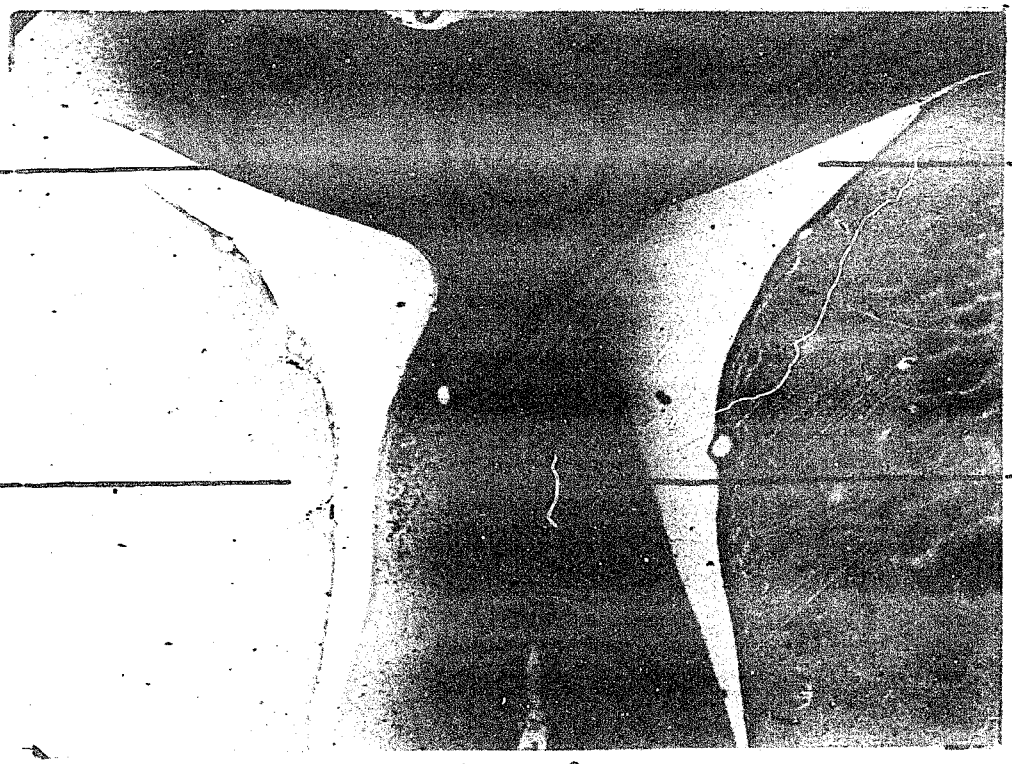


FIG. 4

Fig. 5 - Section of the right side of the brain of monkey No. 3 showing particularly degeneration granules in the hippocampus, the hippocampal gyrus, and the inferior temporal gyrus. X10.

Fig. 6 - This section passes through both pulvinars (monkey No. 3). The right pulvinar contains more black granules than the left, and the left internal corticotectal tract can be seen ending in the superior colliculus. X10.

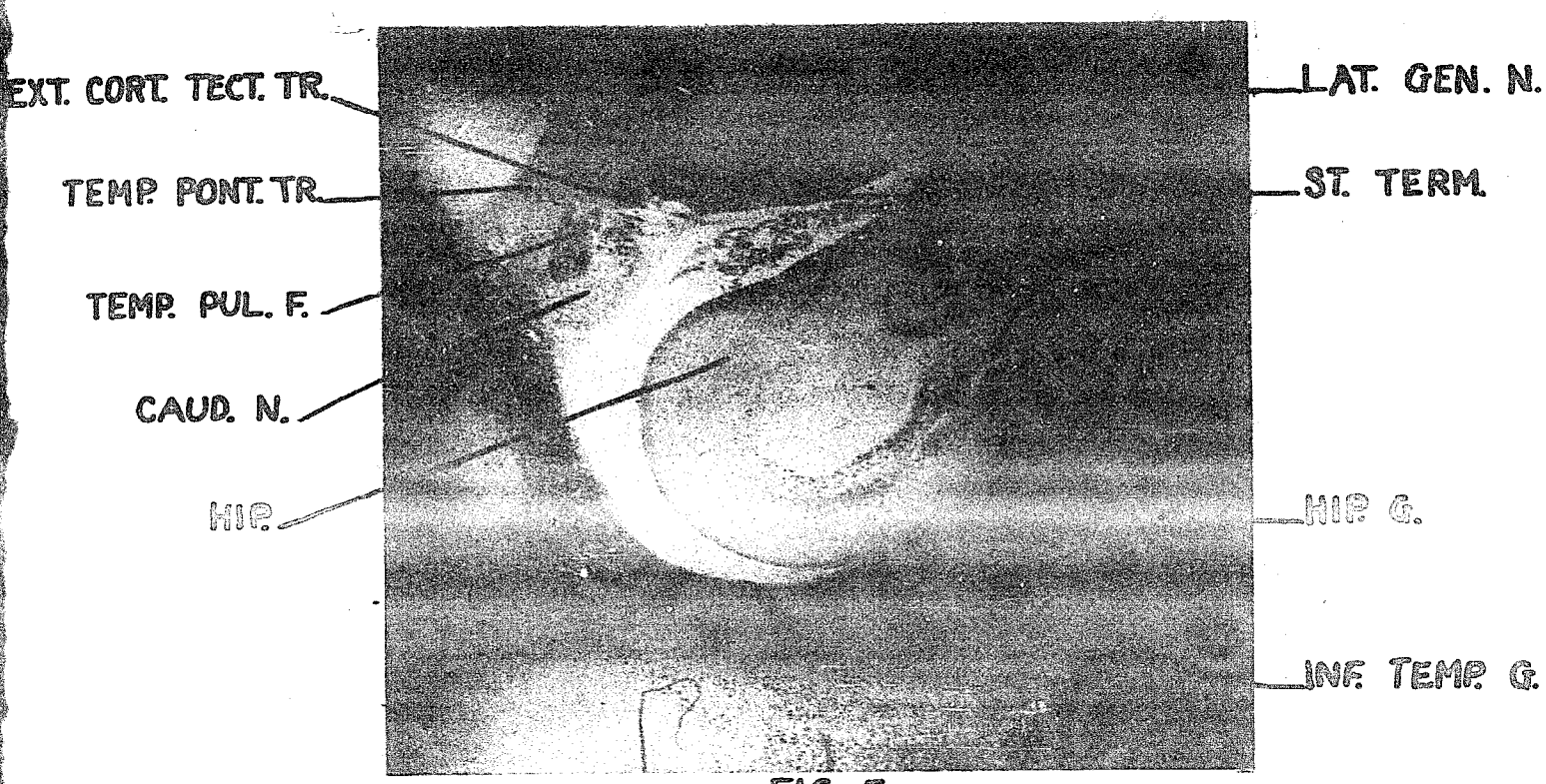

EXT. CORT. TECT. TR.
TEMP. PONT. TR.
TEMP. PUL. F.
CAUD. N.
HIP.
LAT. GEN. N.
ST. TERM.
HIP G.
INF. TEMP. G.

FIG. 5


PUL.
SUP. COLL.
CORP. CAL.
INT. CORT. TECT. TR.

FIG. 6

Fig. 7 - Section of the brain passing through the right cingulum and the corpus callosum (monkey No. 4), both of which show many degenerated fibers. X15.

Fig. 8 - Section of the brain of monkey No. 4 through the anterior thalamic nuclei. Degenerated fibers can be seen in the corpus callosum, the striae medullares, the mammillo-thalamic tracts, the right cingulum, and the fornix. X15.

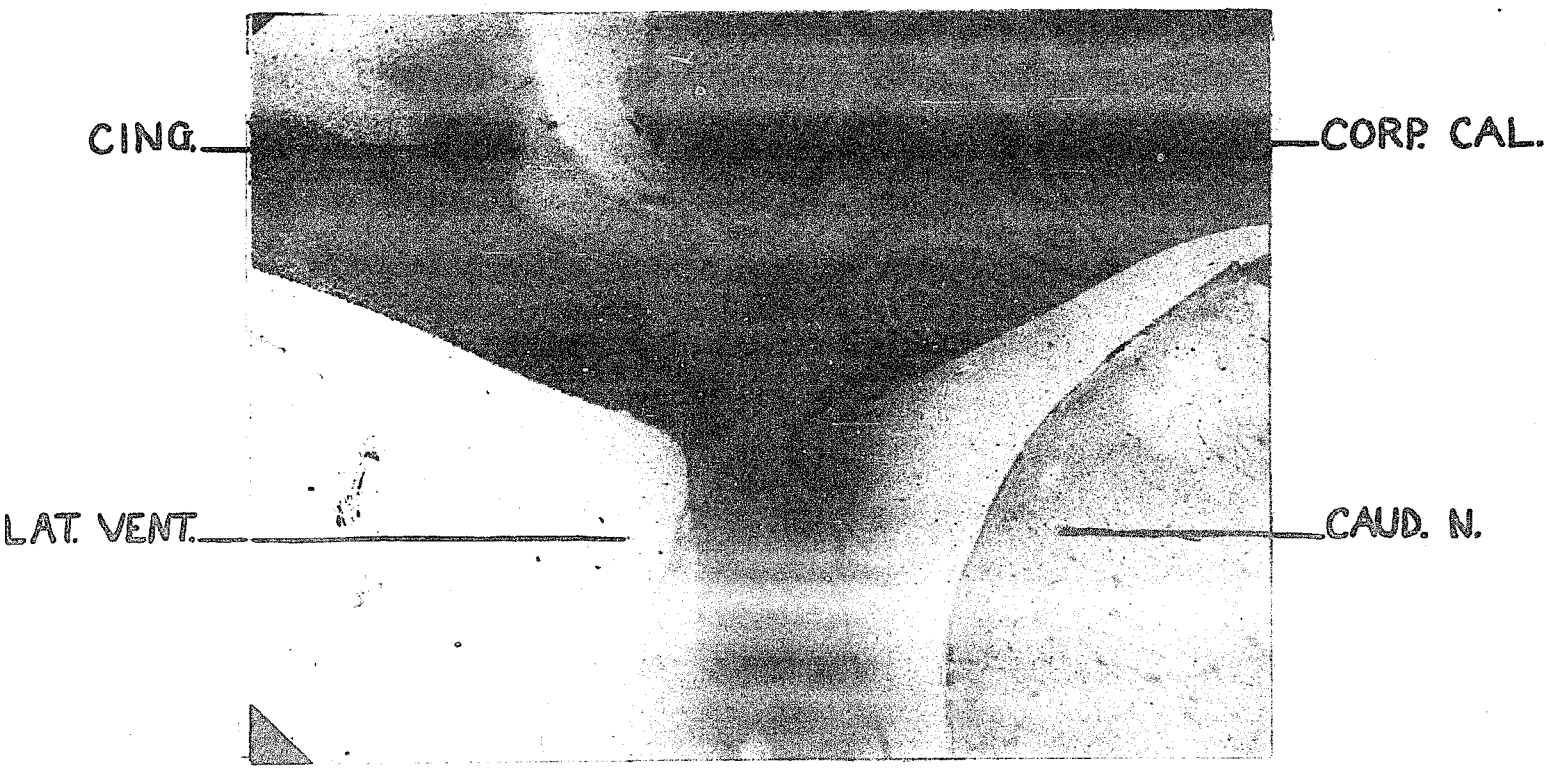

CING.
CORP. CAL.
LAT. VENT.
CAUD. N.

FIG. 7

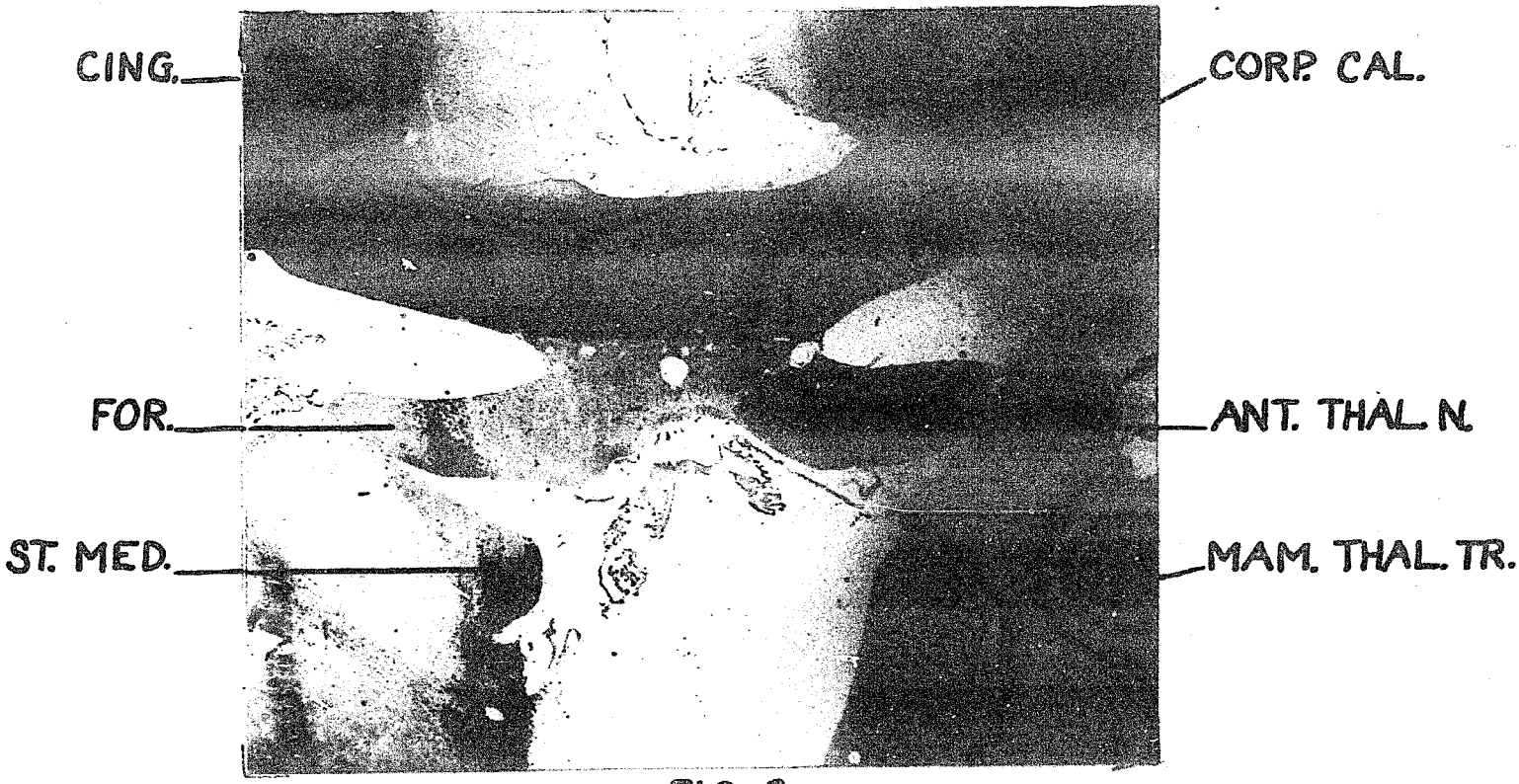

CING.
CORP. CAL.
FOR.
ANT. THAL. N.
ST. MED.
MAM. THAL. TR.

FIG. 8

Fig. 9 - Section of the brain of monkey No. 4 at the level of the dorsomedial nuclei of thalamus. There is conspicuous degeneration in the left dorsomedial thalamic nucleus and both striae medullares. X15.

Fig. 10 - Section of the brain of monkey No. 4 showing mainly a degeneration of fibers of the habenular commissure. X15.

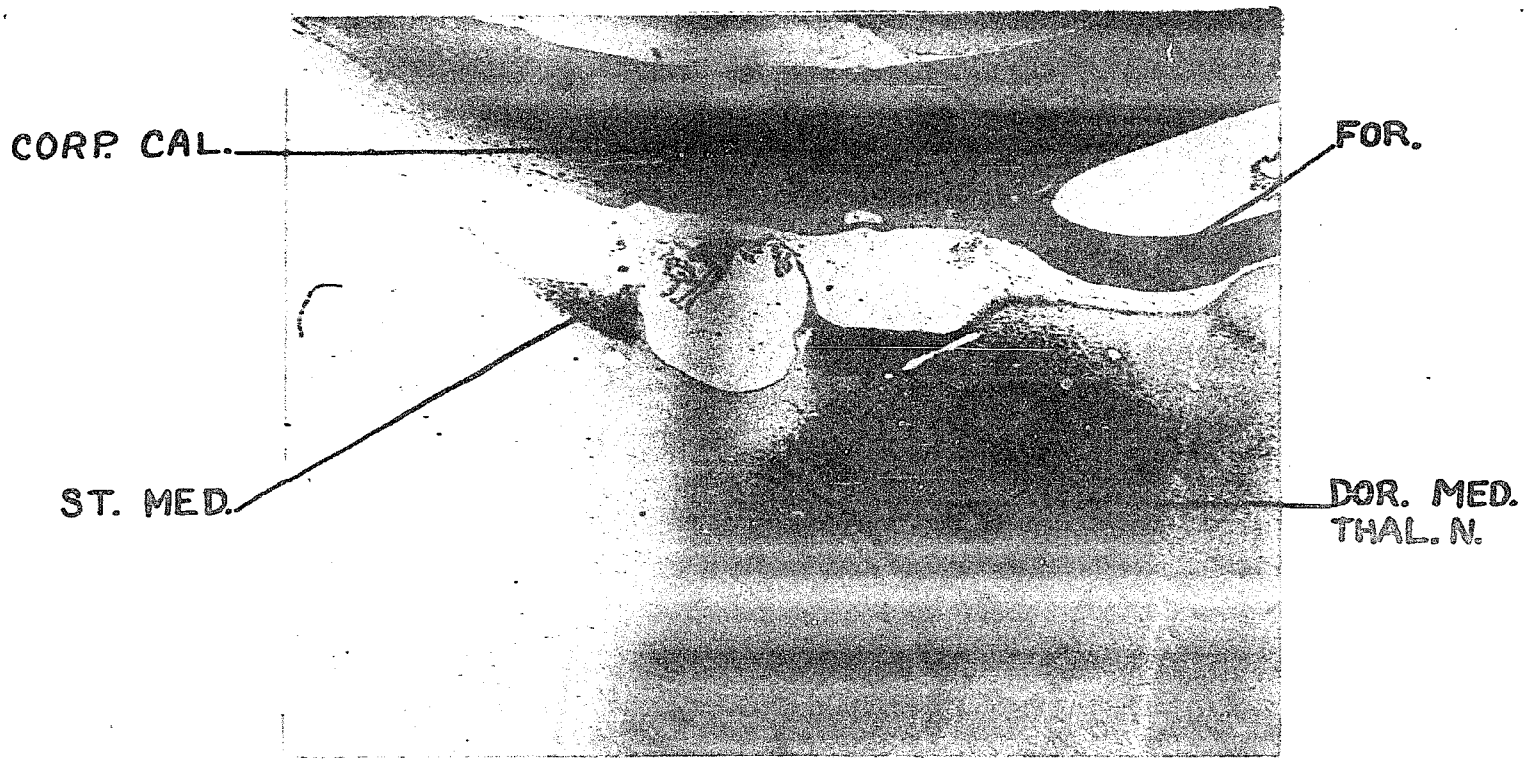


FIG. 9

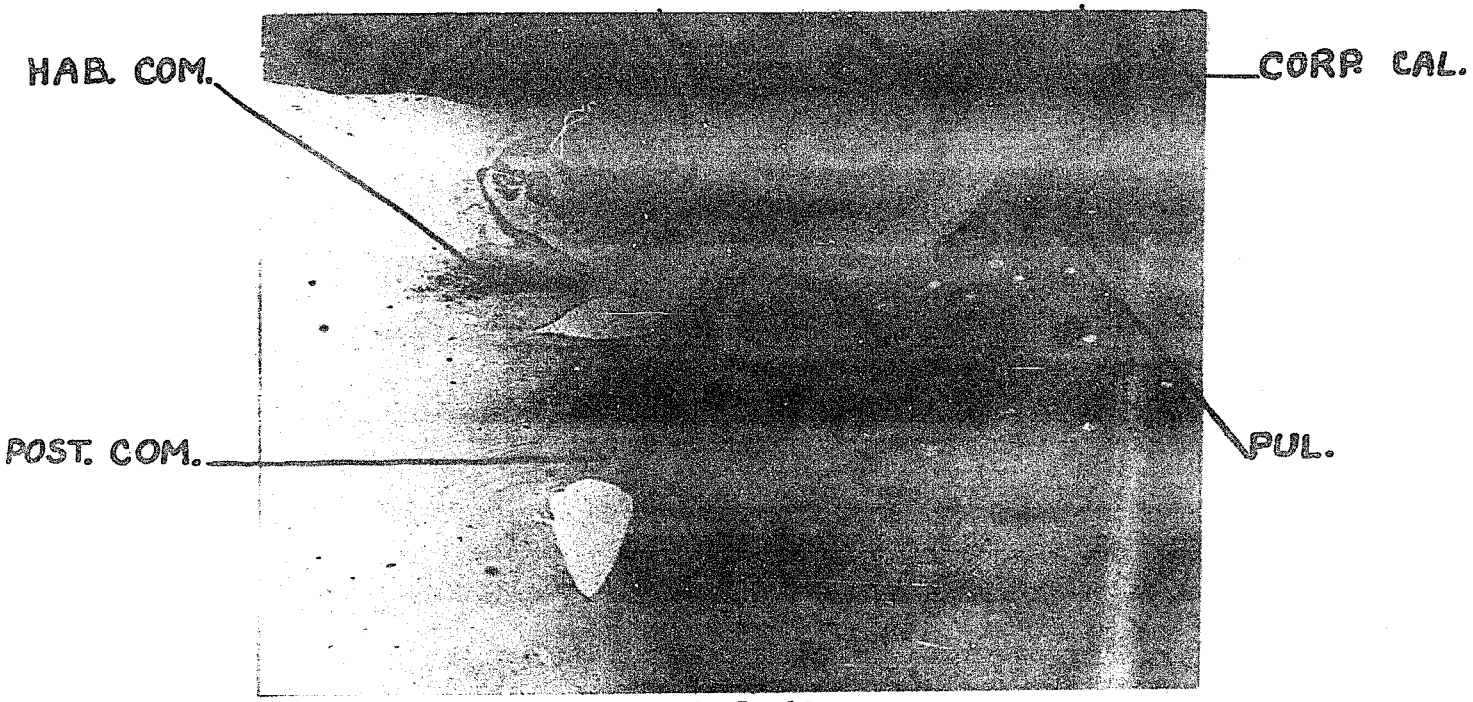


FIG. 10

Fig. 11 - Section of the brain showing Marchi granules in the left pulvinar and left medial geniculate nucleus (monkey No. 4). X15.

Fig. 12 - Photograph of monkey No. 5 a few hours after the operation.

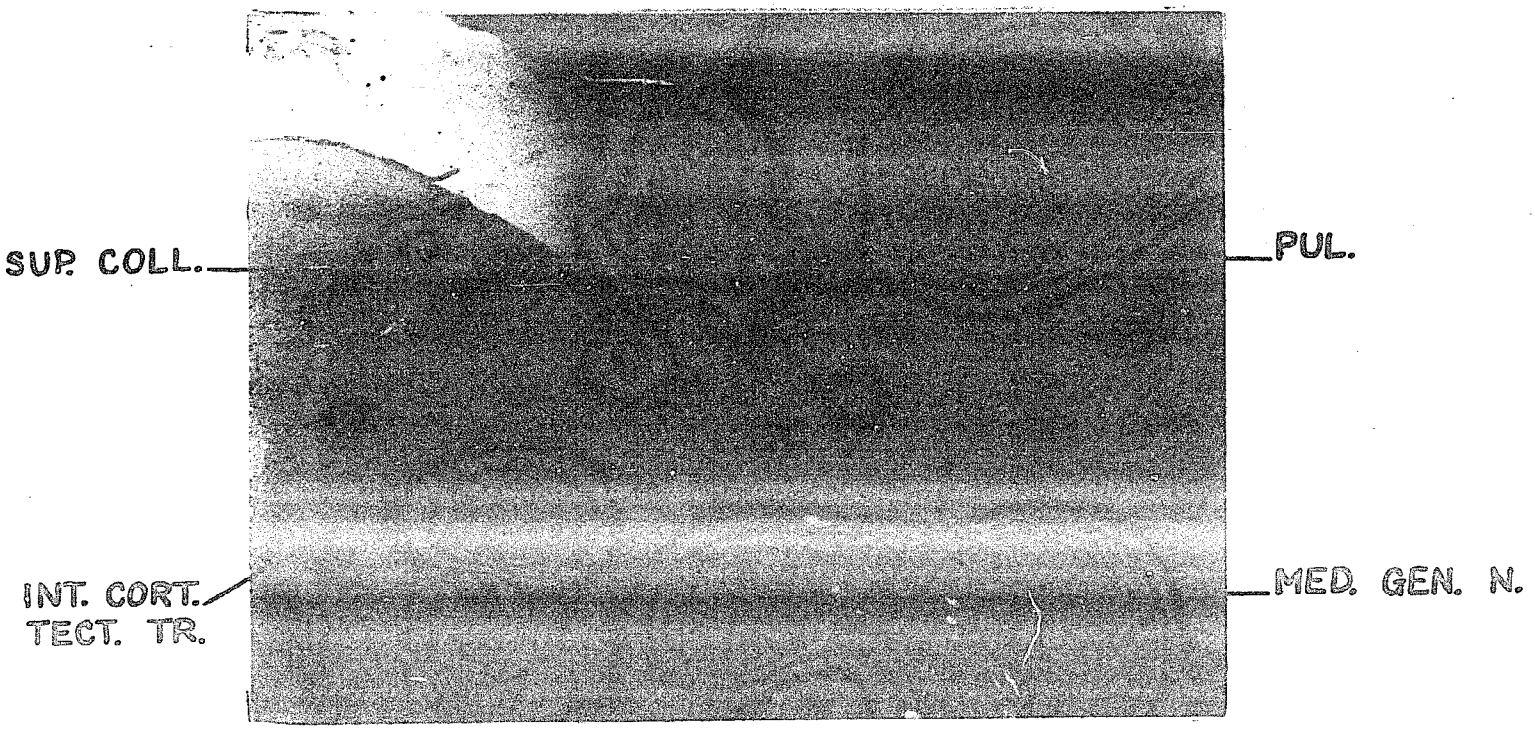


FIG. 11



FIG. 12

Fig. 13 - Photograph of monkey No. 5 on the second day after the operation.

Fig. 14 - Photograph of the same animal two days later.

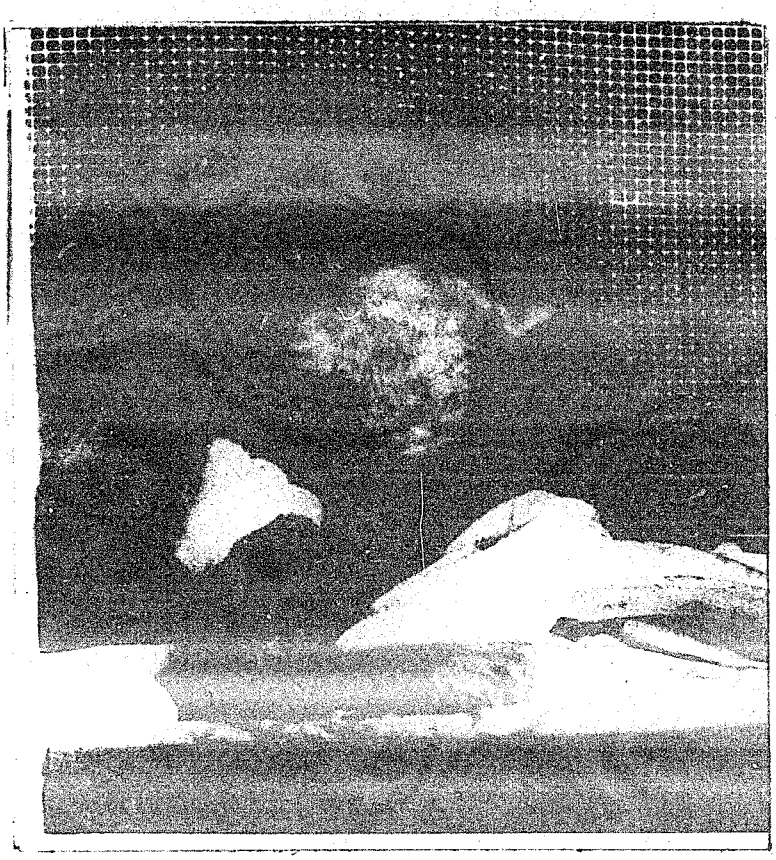


FIG. 13



FIG. 14

Fig. 15 - Microphotograph of a section of the brain of monkey No. 5 showing the rostral portion of the lesion placed on the right side. X15.

Fig. 16 - The more caudal part of the lesion illustrated in the preceding figure. X10.

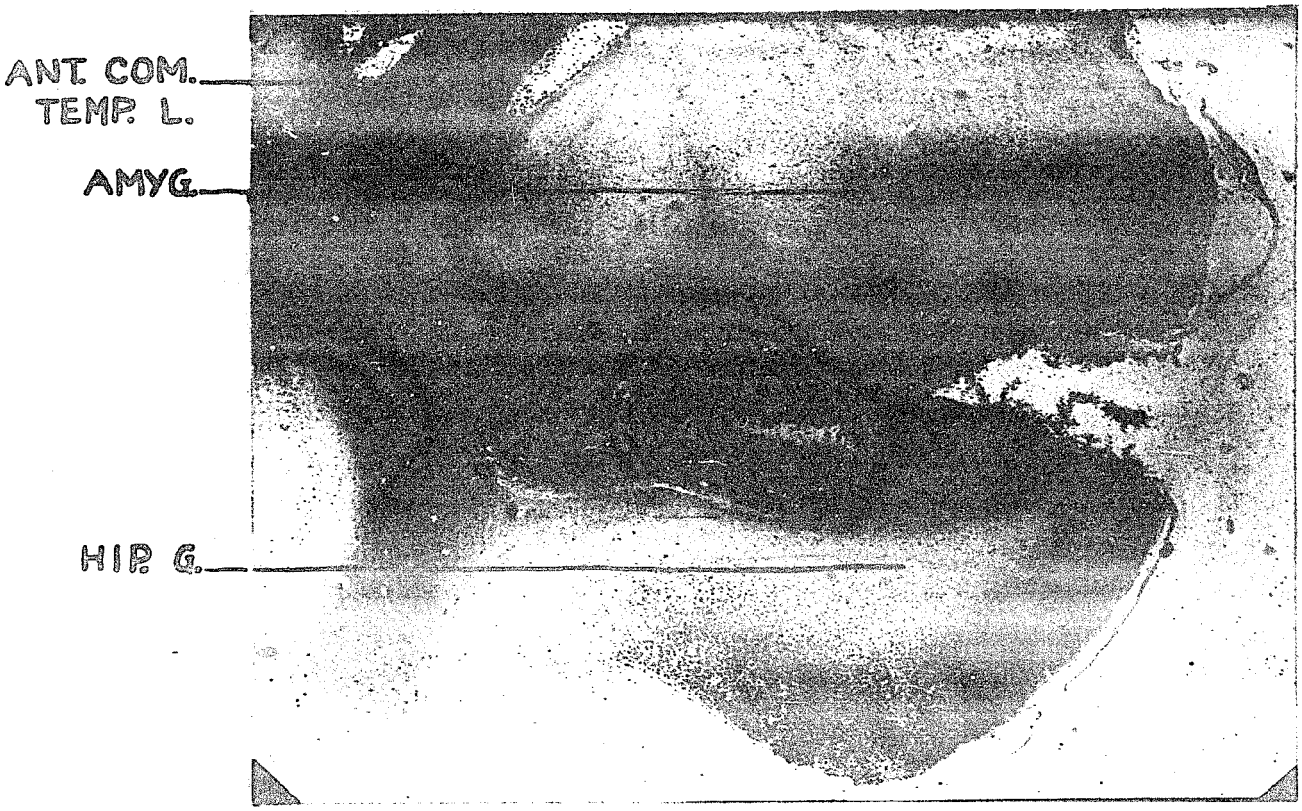


FIG. 15



FIG. 16

Fig. 17 - Section of the brain of monkey No. 5 through the rostral part of the lesion placed on the left side. X4.

Fig. 18 - Section passing through the lesion illustrated in figure 17, but at a more caudal level. X10.

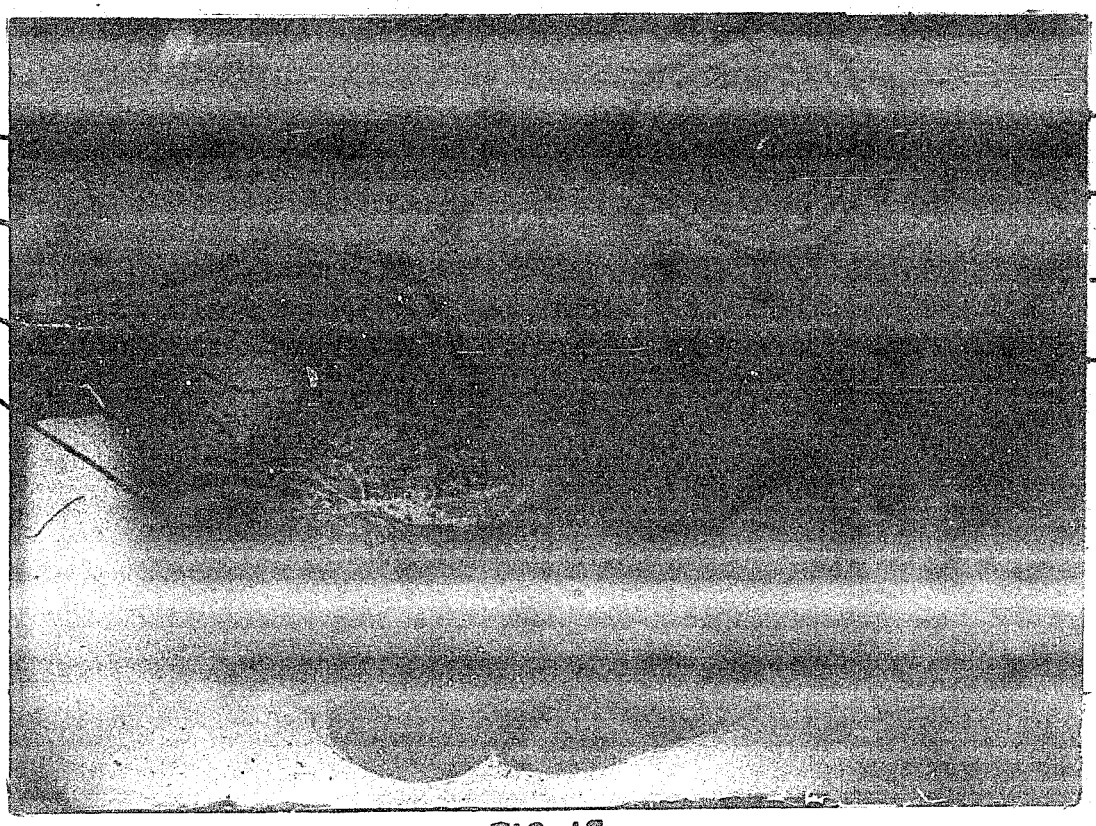

GL. PAL.
ANT. COM.
OPT. CH.
HIP. G.
PUT.
EXT. CAP.
INS.
SUP. TEMP. G.

FIG. 17

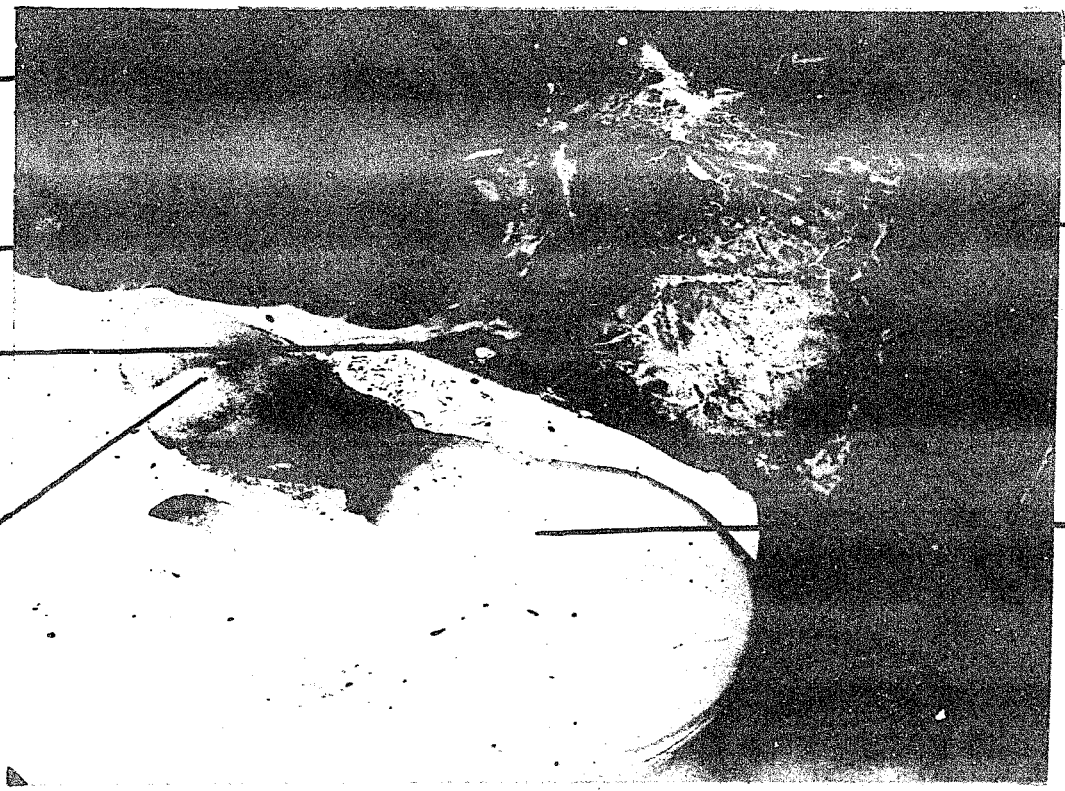

INT. CAP.
OPT. TR.
ST. TERM.
FIM.
PUT.
GL. PAL.
HIP.

FIG. 18

Fig. 19 - Section passing through the lesion illustrated in figures 17 and 18, but caudal to the plane of figure 18. X10.

Fig. 20 - The caudal tip of the lesion illustrated in figures 17 to 19. X15.

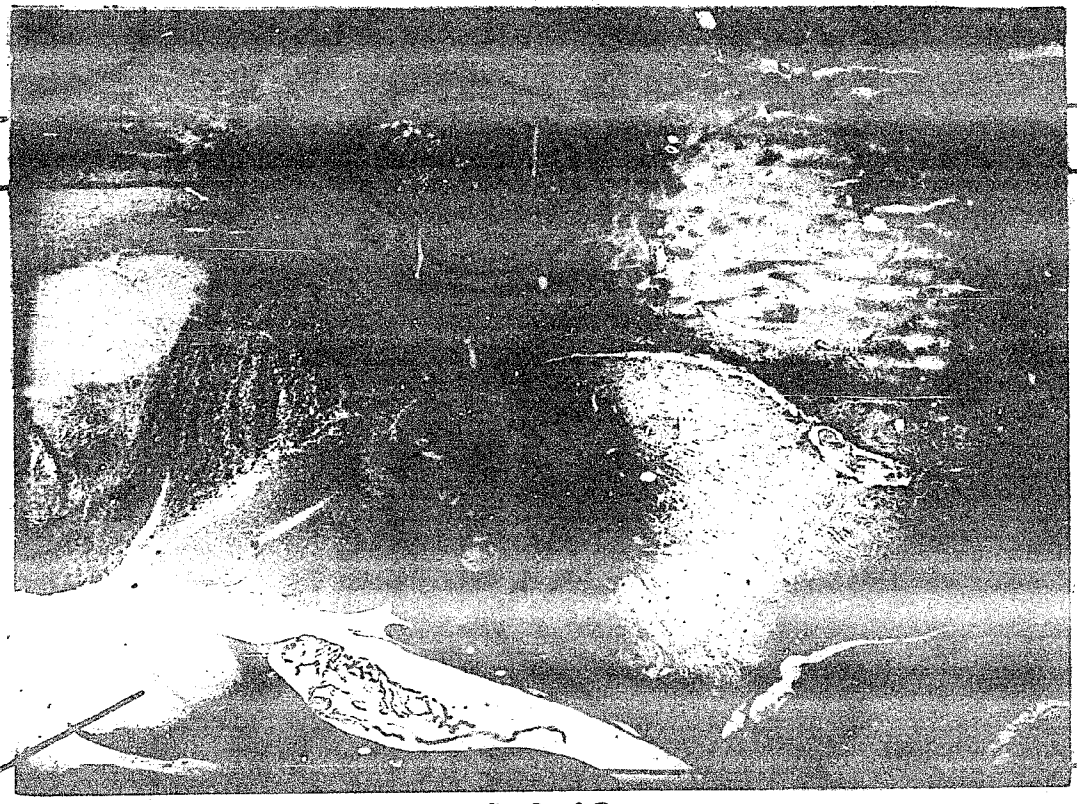

LAT. THAL. N.
INT. CAP.
PUT.
CLAUS.
FIM
HIP.

FIG. 19

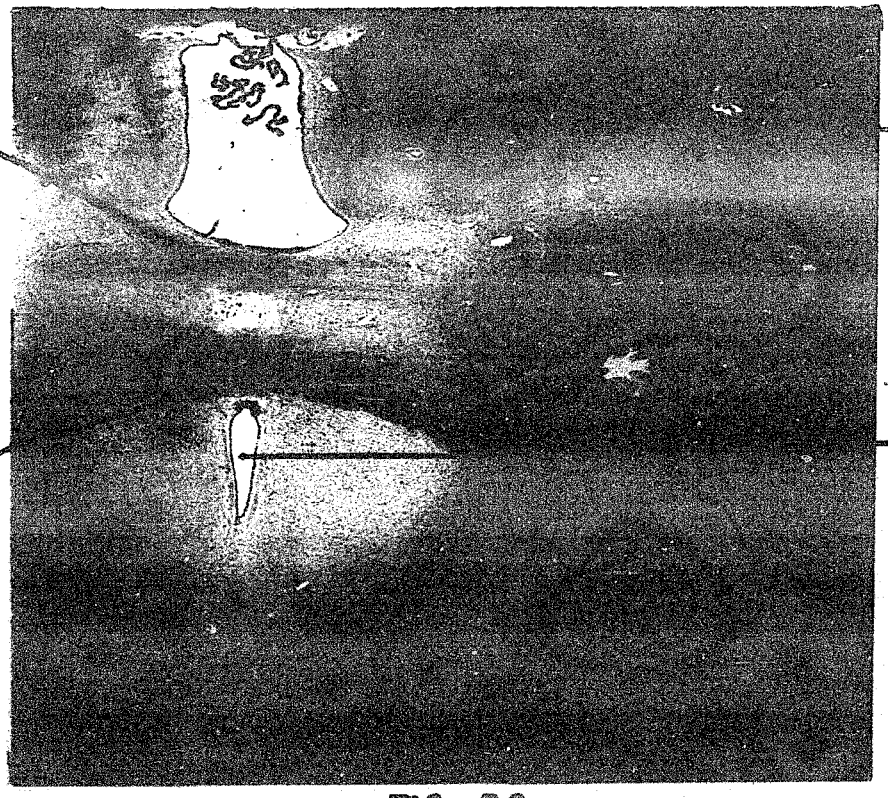

SUP. COLL. COM.
POST. COM.
HAB.
AQ.

FIG. 20

Figs. 21 and 21A - Microphotographs of sections of the brain of monkey No. 5. These sections pass through the lateral septal nuclei which show degeneration. Degenerated fibers can be seen in the left stria terminalis. Figure 21 was restained as described in the text. X10.

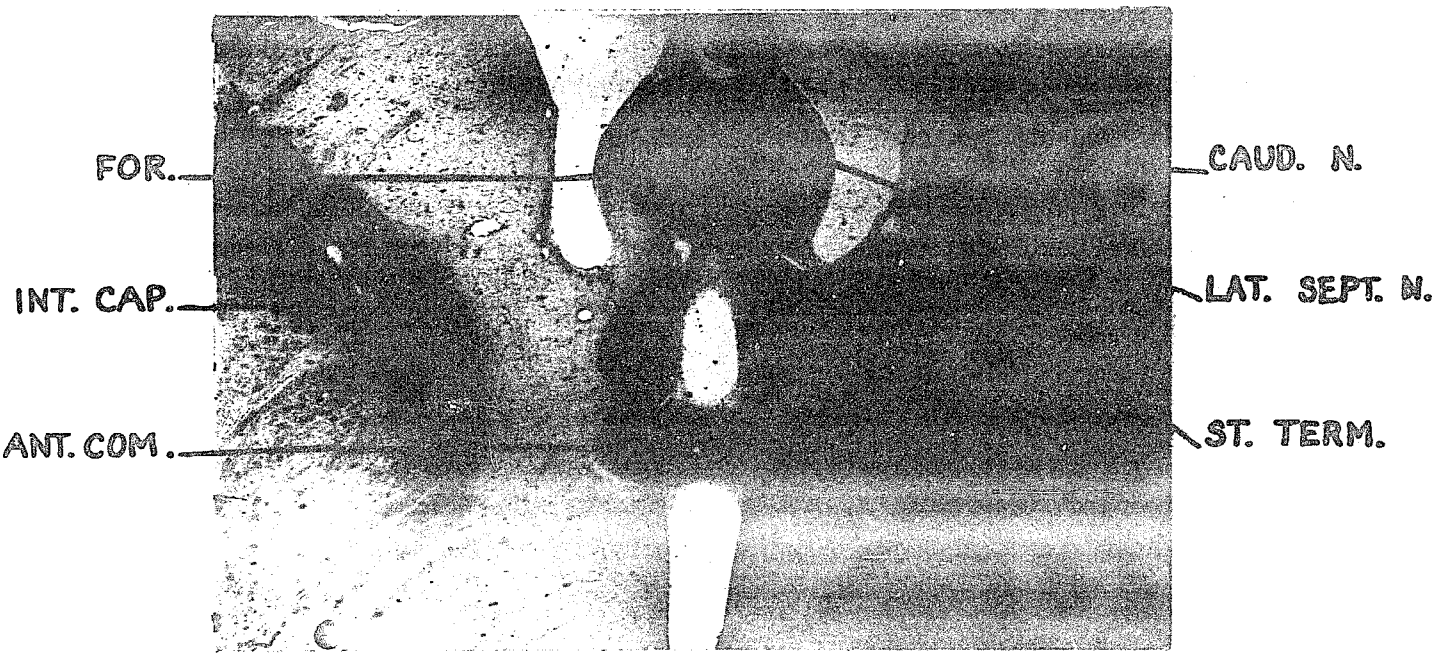


FIG. 21

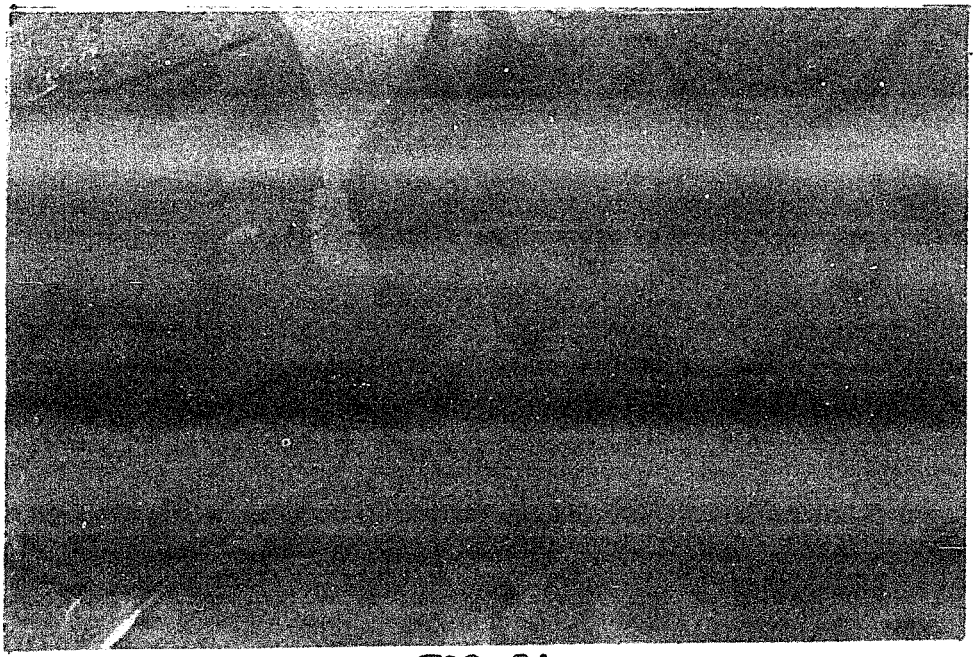


FIG. 21a

Fig. 22 - Section of the brain of monkey No. 5. This section passes through the lateral septal nuclei more rostrally than does that in the preceding figure. X15.

Fig. 23 - This section shows degenerated fibers in the left mesencephalic root of V and in the left medial tectospinal tract. These fibers were injured in placing the lesion illustrated in figure 20. X15.

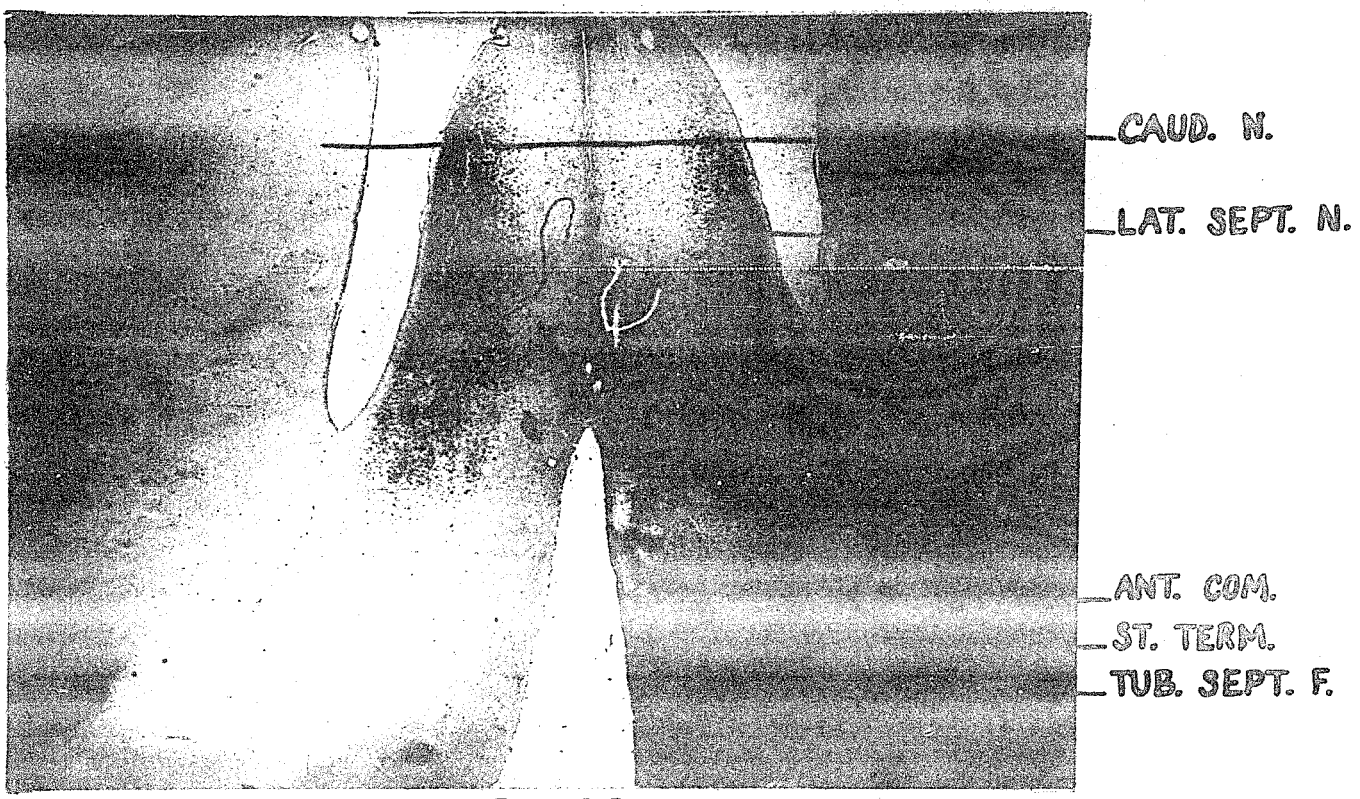

CAUD. N.
LAT. SEPT. N.
ANT. COM.
ST. TERM.
TUB. SEPT. F.

FIG. 22

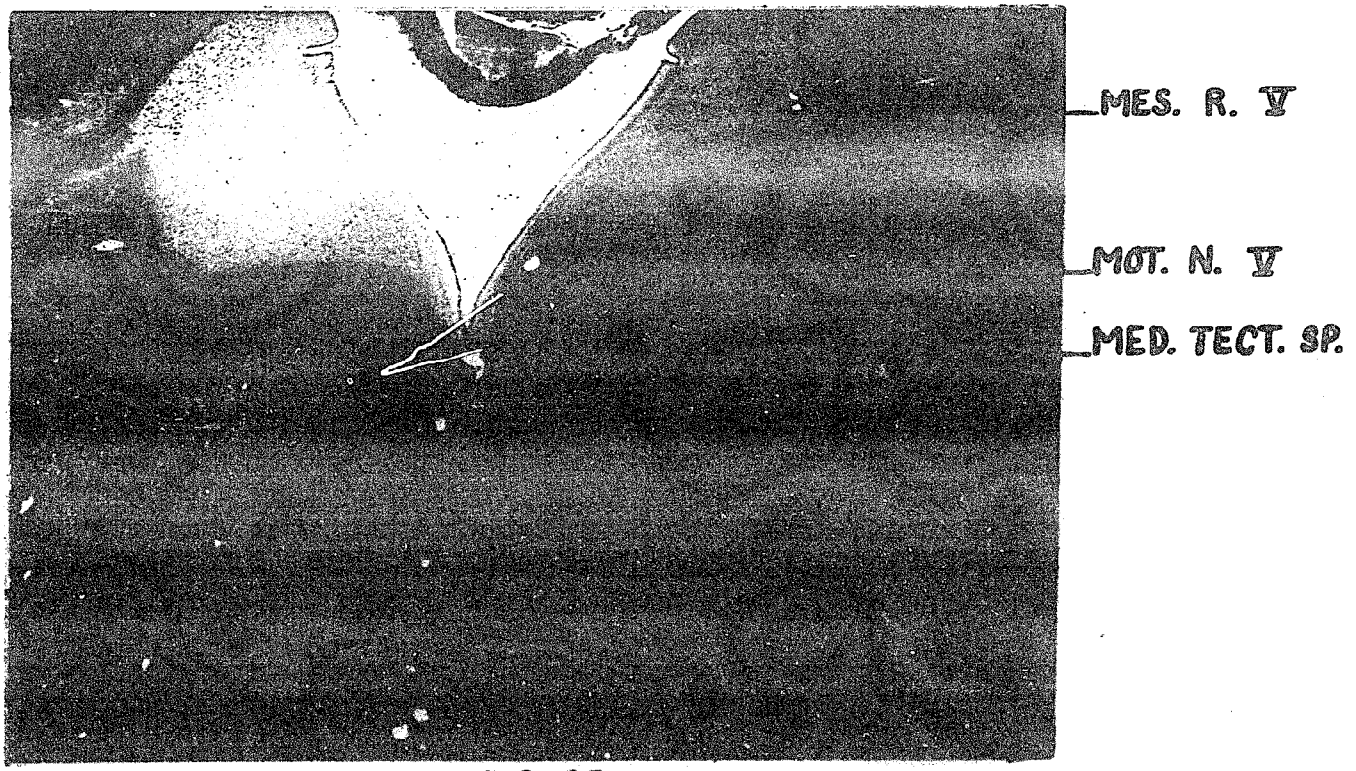

MES. R. V
MOT. N. V
MED. TECT. SP.

FIG. 23

Fig. 24 - This section from the brain of monkey No. 6 shows fibers in the left temporal limb of the anterior commissure which have degenerated as the result of injury to the left inferior and middle temporal gyri. X10.

Fig. 25 - Section through the body of fornix (monkey No. 6) showing many degenerated fibers on the right side. X10.

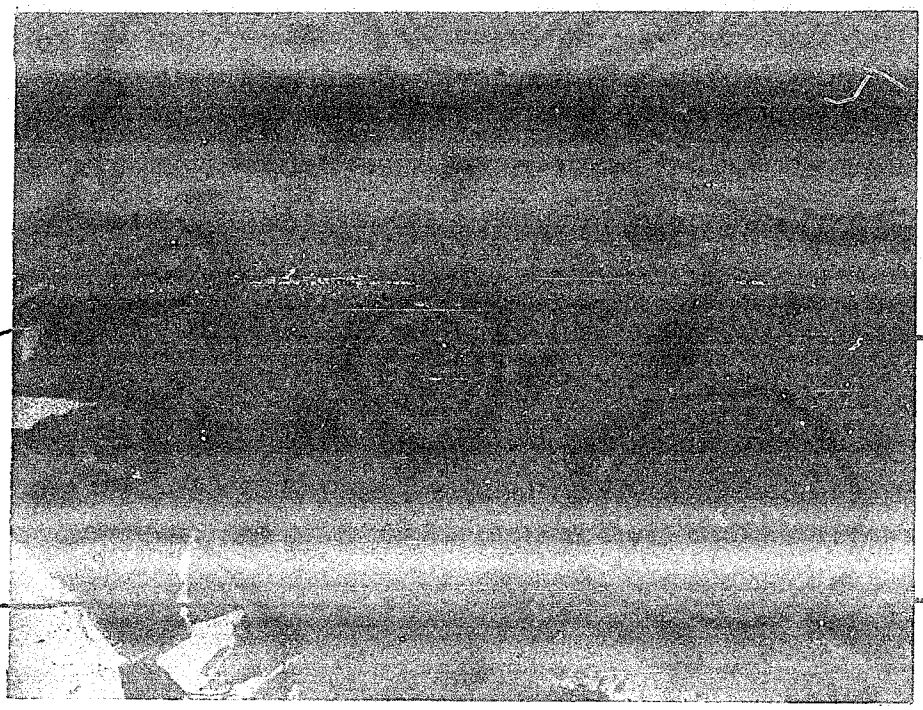

ANT. COM. TRANS. L.
ANT. COM. TEMP. L.
INF. TEMP. G.
MID. TEMP. G.

FIG. 24

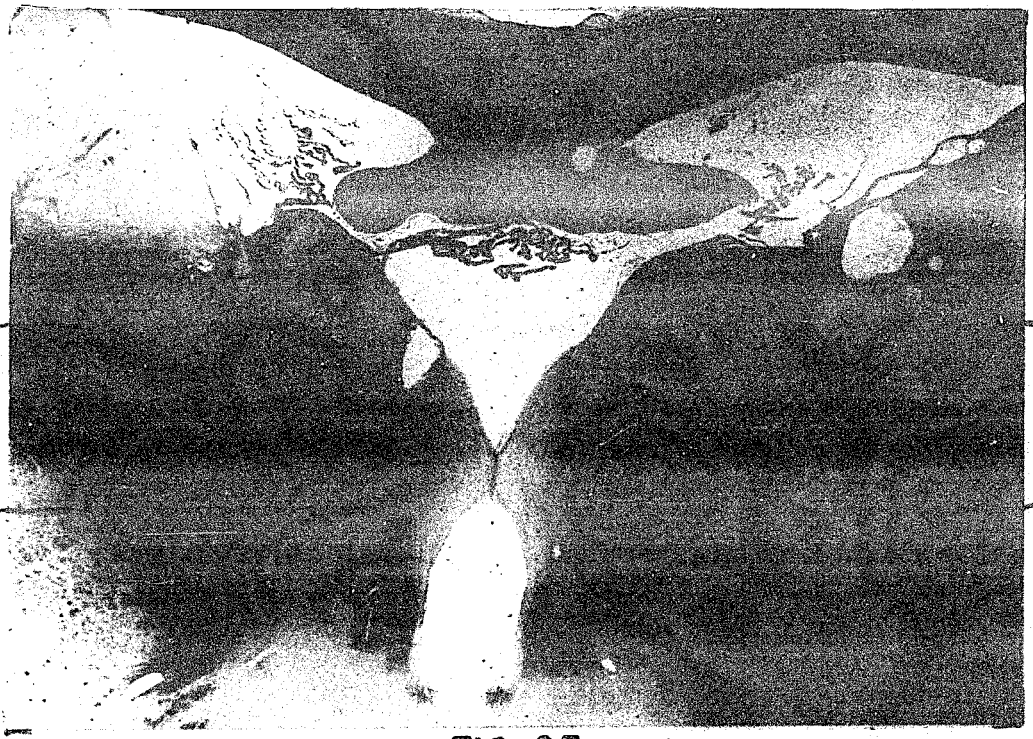

FOR. BOD.
ANT. THAL. N.
INT. CAP.
FOR. POST COM.

FIG. 25

Fig. 26 - Section passing through the rostral part of the brain of monkey No. 6 showing degenerated fibers in the fornix, the anterior commissure, and the lateral septal nuclei. X10.

Fig. 27 - Section passing through the right hippocampus (monkey No. 6) which shows many degenerated fibers at the base of putamen. X15.

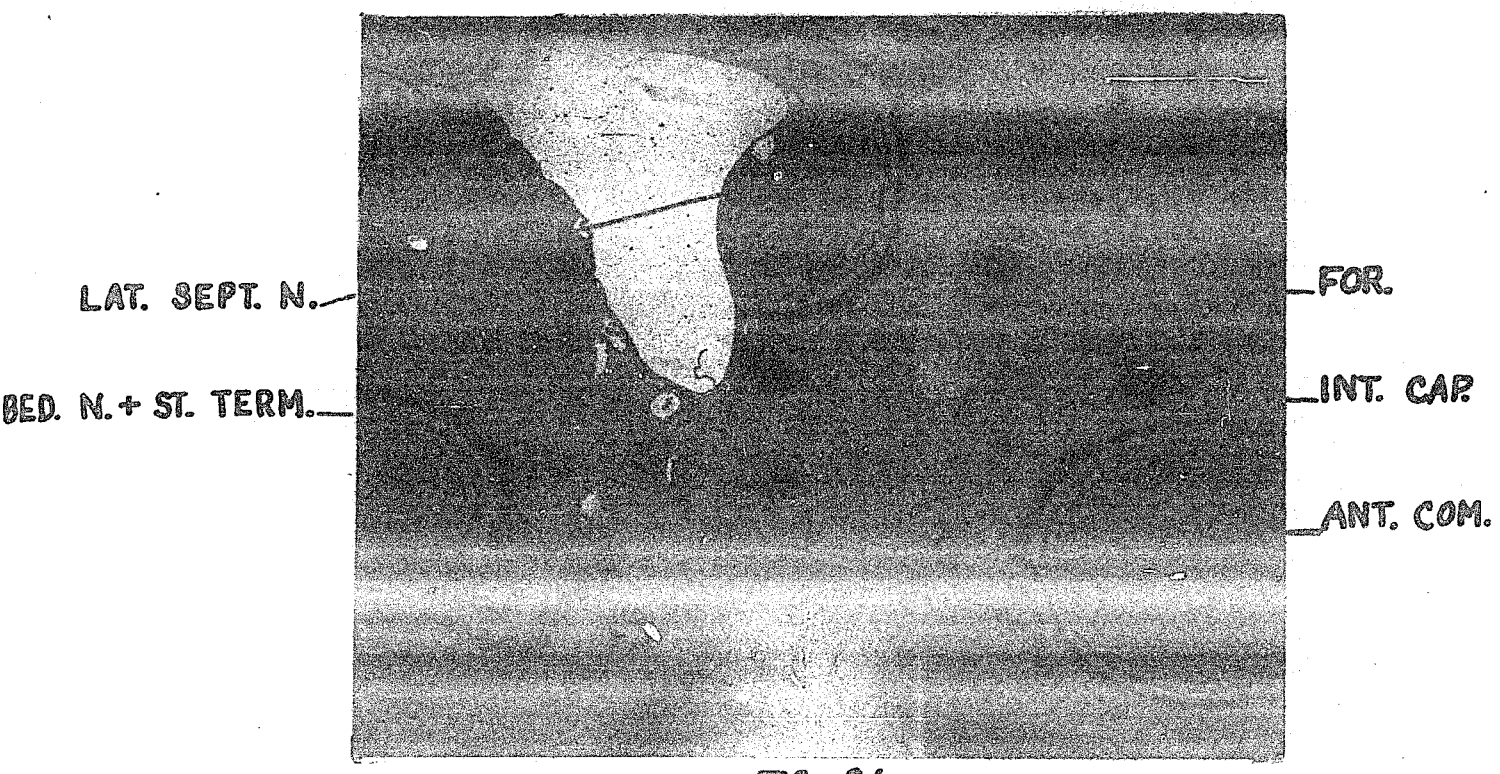

LAT. SEPT. N.
BED. N. + ST. TERM.
FOR.
INT. CAP.
ANT. COM.

FIG. 26

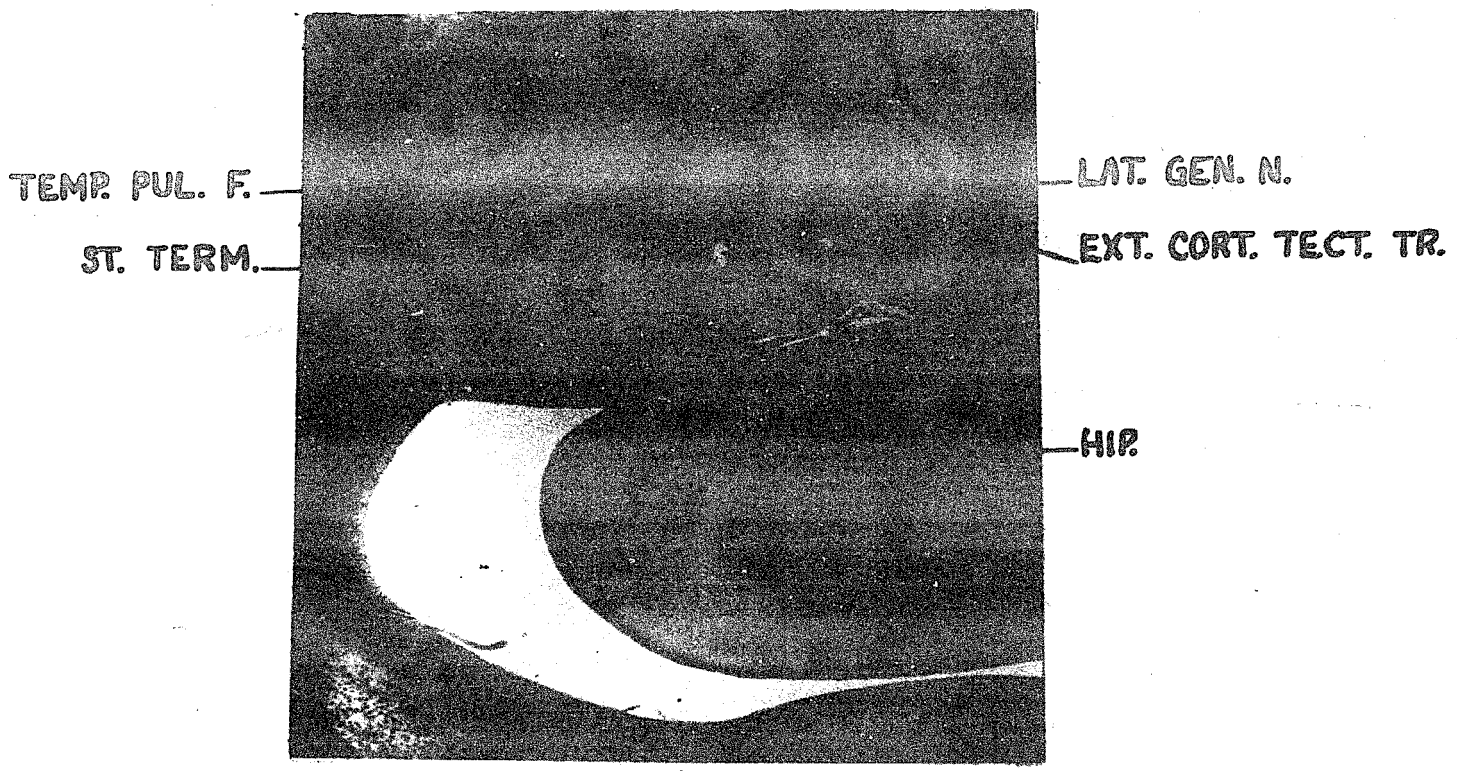

TEMP. PUL. F.
ST. TERM.
LAT. GEN. N.
EXT. CORT. TECT. TR.
HIP.

FIG. 27

Fig. 28 - Section at the level of the caudal part of the left pulvinar of monkey No. 6. Degenerated fibers can be seen especially in the internal cortico-tectal tract, the temporo-pulvinar fasciculus, and the fornix. X10.



FIG. 28