# EXPERIMENTAL STUDIES OF THE CONNECTIONS OF THE FORNIX AND SEPTUM IN THE CAT

by

Keith Davis Holmes, B.A.

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# INTRODUCTION

Descriptions of the fornix and septum have always appeared as a part of the olfactory system and as such their morphology has been classically described by several investigators in a number of mammals and reptiles (10, 25, 27, 44, 46, 53, 72, 73, 91). All of these studies were made from normal material. Only a few morphologic studies in this area were carried out by the experimental method (24, 71, 30, 6), and in these investigations the Marchi or retrograde degeneration methods were utilized with their inherent deficiencies.

Ramon y Cajal (72) indicated that there were no direct morphologic connections between the olfactory bulb and the hippocampus. However, it remained the opinion of most students in the field that the hippocampus and its associated structures were primarily olfactory in function. Evidence has mounted in the past thirty years against these areas being primarily olfactory in nature. Swann (83, 84), in rats, found olfactory discrimination to be unaffected by lesions in various parts of the rhinencephalon including the hippocampus and fornix. Allen (4, 5), in dogs, found no change in olfactory conditioned reflexes when the greater part of the hippocampus was removed. The possibility of a direct projection from the olfactory bulb to the hippocampus was

tested anatomically by Clark and Meyer (20) in the rabbit by the experimental method and using a silver staining technique. They found that the fibers from the olfactory bulb ended principally in the olfactory tubercle, the prepyriform area and certain amygdalloid nuclei. Their results were confirmed in the monkey by Meyer and Allison (62) and in the marsupial by Adey (1) using similar techniques. Electrophysiologic studies with stimulation of the olfactory bulb of the cat by Rose and Woolsey (74), Berry et al. (12), Fox et al. (29), and by Kaada (47) have given a distribution of recorded potentials which agrees closely with the above morphologic studies. Berry, Hagamen, and Hinsey (12), in cats, recorded potentials in the hippocampus, fornix, and septum but the magnitude of the potentials was low and the latent period between stimulation and evoked potential was slow. These authors conclude that if stimuli from the olfactory bulb do reach the hippocampus and septum it must be through multisynaptic pathways entering the entorhinal area to the hippocampus or via the olfactory tubercle to the septum.

In 1937 Papez (65), on the basis of neuronal connections and clinical studies proposed his theory of emotion. He considered the hippocampus, fornix, mammillary body, anterior thalamic nuclei, and the gyrus

cinguli to constitute an integrated circuit controlling emotion. This gave impetus to numerous investigators who have since attempted to find functions for various parts of this circuit and its associated nuclei.

In recent years there has been a great deal of investigation of these rhinencephalic areas as they pertain to affective, autonomic, somatic, and emotional functions as well as to their part in psychomotor epilepsy. These studies are multitudinous and have been excellently reviewed by several authors (16, 55, 56, 57, 58, 47, 66, 23, 2).

Studies of function which are limited to the fornix (and hippocampus from which it arises) and septum have been fewer in number. Spiegel et al. (77) elicited rage reactions in cats and dogs with bilateral lesions in the fornix-hippocampal region and found these reactions to be more severe when the septum was involved. Bard and Mountcastle (11) were not able to produce rage in cats with a bilateral removal of the hippocampus and fornix. These latter conflicting results were also obtained by Rothfield and Harman (75) in cats.

Recent studies by several investigators (14, 15, 51, 85) have shown changes in behavior following septal and fornix lesions in the rat. Bond et al. (13) saw these changes also but their lesions involved the thalamus.

Votaw (88, 89) reported similar behavioral changes but emphasized that large bilateral ablations of the septal area were necessary to bring about such reactions. These changes in affective behavior were not noted by Wheatley (90), Harrison and Lyon (40, 41), Simpson (76), and Allen (5, 8) in a variety of mammals with lesions of septal and hippocampal areas. Cairns and Mosburg (19) noted no behavior changes in the human following bilateral fornicotomy. Electrical stimulation of the hippocampus and fornix has been carried out with consistent behavioral changes in unanesthetized cats (48).

Somatic motor movement has been elicited in cats with stimulation of the hippocampus by Votaw (88, 89). Hodes et al. (43) achieved similar results when stimulating septal areas. Kaada (47) denied any motor response in the cat by stimulation of these areas and he is supported in this result by Penfield (67) in the human.

Green and Arduini (33) noted a definite pattern of electrical activity in the hippocampus of rabbits, cats, and monkeys. This pattern was altered with arousal of the animal and he could repeat this arousal pattern by stimulation of various areas including the fornix and septum.

Kabat, Magoun, and Ranson (50), Kabat (49), Hodes and Magoun (42), and Gloor (31) have elicited a variety

of autonomic responses from stimulation of the septum.

Considerable recent interest has centered around the possibility that the septum and hippocampus may be associated with temporal lobe seizures. Green and Shimamoto (35) and Andy and Akert (8) by means of stimulation in animals have shown a low seizure threshold in the hippocampus and that these seizures spread rapidly to the rest of the limbic lobe. These results were confirmed by MacLean (57) in stimulation of conscious cats. Andy, Chinn, and Bonn (9) have achieved similar results by stimulating the septum of the cat, while Green, Clemente, and DeGroot (34) were able to produce epilepsy with a lesion of the hippocampus in a cat. The pathways involved in these seizures have been studied with repetitive stimulation and measurement of the resulting after-discharge by Ajmone-Marsan and Stoll (3) in the monkey.

The many studies involving function of the fornix and septum have not all been proved morphologically. They did give impetus to the anatomists and as a result many experimental studies have come forth in recent years (64, 86, 60, 61, 37, 45). Several electrophysiological studies have also appeared which have contributed to the evaluation of the connections of these areas (79, 12, 21).

These recent morphologic and electro-physiologic studies, as well as the aforementioned studies of function in the fornix and septum, have been clouded with many conflicting results in their anatomic content. The extent and complexity of the connections of the fornix and septum and the conflicting opinions as to their presence are numerous and will be covered in the discussion section of this paper.

It is the purpose of this investigation to attempt to resolve some of the above conflicts in morphology of the septum and fornix by the experimental method.

## MATERIAL AND METHODS

The material studied comprised the brains of forty three healthy young adult cats weighing between 1.6 and 2.0 kg. Electrocoagulative lesions were made with a Johnson-Krieg modification of the Horsley-Clark stereotaxic instrument under light intraperitoneal Nembutal anesthesia. Lesions were unilateral or bilateral and involved the following areas: the hippocampus and fimbria at various levels and to a varying extent, the body of the fornix complete and partial, the ventral hippocampal commissure, the column of the fornix, the septal area in a variety of positions and varying in extent, the anterior commissure, the stria terminalis, the thalamus, and the stria medullaris.

Degeneration was allowed to continue for six to thirteen days, the optimum period for recognition of primary neuronal and terminal degeneration. The animals were then sacrificed by means of intraperitoneal Nembutal followed by immediate thoracotomy and intracardiac perfusion with a solution of 15% formalin to insure the quick and adequate fixation which is necessary for the preservation of intact synaptic terminals. The brains were removed and immersed in 15% formalin for a period of four or more weeks for further fixation. Following dehydration a series of

every fifth or tenth section was mounted and stained by a modification of the intensified protargol method as described by Stotler (80, 82). The blocks were cut in the transverse plane.

Two normal cats were carried as controls and prepared by the same method for comparison with experimental material.

In many of the studies mentioned previously the accepted Weigert, Marchi, and Nissl procedures have been relied on for analysis of the material. In his investigations of the normal nervous system, Ramon y Cajal (72) made use of silver staining techniques. In their studies of the optic, auditory, and other major fiber systems Glees and Clark (32), Brodal (17), Sprague and Meyer (78), Stotler (81), and Nauta (64), have found silver techniques to be the most reliable and precise method of studying fiber degeneration in the central nervous system. This superiority in the demonstration of degenerated axones, fine preterminal endings, and terminal endings has led us to use silver techniques in this study.

Histologic study of all silver preparations was carried out by observing fiber degeneration which was either primary to a direct lesion of the tract or secondary to destruction of their cells of origin.

Degenerating fibers appear markedly argyrophilic with gross fragmentation and swelling. Small preterminal fibers when degenerated appear as a finely granular argyrophilic debris. Degenerating terminals appear as black swollen boutons. The degenerated areas having all been carried seven to ten days show a rather marked clearing of fragmented fibers and terminal debris. This results in a conspicuous loss of pericellular neuropil in the areas which are involved.

A histologic analysis of fifteen cats will be presented to demonstrate the findings in this study.

## RESULTS

A review of the literature dealing with the fornix and septum reveals many discrepancies in nomenclature of their subdivisions. Terms used by one author to describe an area will often be used by others to denote an entirely different structure. Many of these structures have been endowed with a multiplicity of terms. For this reason a description of the fornix and septum with the nomenclature to be used in this paper would seem necessary before describing the results. A diagrammatic summary of the results of this study is shown in Figure 13.

The hippocampus in the cat begins ventrally and somewhat posterior along the lateral wall of the lateral ventricle and extends dorsally and then anteriorly. For purposes of this paper it can be divided into two major subdivisions. The first is an antero-dorsal portion lying in the dorsal wall of the lateral ventricle, between the dorsal surface of the thalamus and midbrain ventrally, and the corpus callosum above. The most medial anterior portion of this structure is in contact with the superior fornix above. The remainder of the hippocampus will be referred to as the ventro-postero-lateral portion. This lies as it is named in the lateral ventricle between the brainstem medially and the temporal lobe laterally.

The hippocampal commissure or psalterium has been

described in many ways. In the cat there are two commissural structures. The dorsal hippocampal commissure lies below the superior fornix and extends between the medial parts of the fornix at the level of the anterior extremity of the antero-dorsal hippocampus. The ventral hippocampal commissure is much larger and lies in the posterior part of the septum, dorsal and just posterior to the anterior commissure, and caudal to the descending column of the fornix.

The fornix is divided into three parts.

1. The dorsal fornix, also known as the stria of Lancisi, extends over the top of the corpus callosum to the genu and then ventrally into the lateral septal area.
2. The medial fornix arises along the superior surface of the antero-dorsal hippocampus between this structure and the corpus callosum dorsally. Rostrally it lies on either side of the midline. At the level of the post commissural septum it curves ventrally as the column and pillar of the fornix and then descends posteriorly through the hypothalamus as the descending column of the fornix. The medial fornix can be subdivided into two divisions. The first, the medial component,

is a distinct bundle of fibers lying on either side of the midline, which descends in the column of the fornix. This is referred to as the superior fornix. The second, lateral component, lies immediately lateral to the first and is a group of fibers which arise in the antero-dorsal hippocampus, but appear to pass forward contiguous to the lateral fornix. These fibers take part in the dorsal hippocampal commissure and join the opposite superior fornix to form the contralateral component of the column of the fornix. The superior fornix does not take part in the dorsal hippocampal commissure.

3. The lateral fornix arises primarily in the ventro-postero-lateral part of the hippocampus. It is the largest division and contributes to the ventral hippocampal commissure. It also supplies afferents to both pre and post commissural septal nuclei.

The septum includes the basal area of the hemisphere lying beneath the corpus callosum in the antero-medial wall of the hemisphere. It extends laterally as far as the lateral ventricle, antero-posteriorly from the frontal cortex to the ventral hippocampal commissure

and ventrally to the diagonal band of Broca, tuberculum olfactorium and the preoptic area of the hypothalamus. The septum is divided into two major subdivisions.

1. The medial septum begins anteriorly at the posterior border of the anterior olfactory nucleus as the anterior continuation of the hippocampus or subcallosal area. From the posterior edge of this nucleus the medial septal nucleus begins and continues posteriorly to the ventral hippocampal commissure. The medial septal nucleus will include the nucleus septo-hippocampalis and nucleus septalis triangularis. Ventral to the medial septal nucleus in the region of the tuberculum olfactorium is the nucleus of the diagonal band. This nucleus extends ventrolaterally beneath the olfactory tubercle.
2. The lateral septum will be described as just the lateral septal nucleus. The nucleus accumbens is often described with this area anteriorly but this represents a medial extension of the caudate nucleus. The lateral septal nucleus includes the bed nucleus of the anterior commissure as well as the nucleus septalis fimbrialis which lies

just lateral to the column of the fornix.

The fornix and septum will be described as pre commissural and post commissural with reference to their relationship to the anterior commissure.

Cat DW-90. Unilateral lesion; Eight day degeneration.

The lesion and resulting degeneration in this case are summarized in Figure 1. The main body of this lesion lies in the antero-dorsal hippocampus, however, it extends ventrally to involve the entire fimbria in the most dorsal part of the ventro-postero-lateral hippocampus. The superior fornix and small areas of the corpus callosum, gyrus cinguli, and the optic radiation were also within the confines of the lesion. A small area of destruction was found in the most ventral portion of the ventro-postero-lateral hippocampus. The thalamus was invaded by a separate narrow lesion which cut directly through the pulvinar.

Complete degeneration of fibers occurs rostral to the lesion in both the medial and lateral fornix on the side of the lesion (Fig. 14). Degenerated fibers can be seen crossing in the dorsal hippocampal commissure and terminal degeneration is noted at this level in both the polymorphic and pyramidal layers of the antero-dorsal hippocampus of the opposite side. Normal fibers from the

fornix of the side without a lesion can be seen crossing in the dorsal hippocampal commissure and entering the degenerated alveus over the antero-dorsal hippocampus on the side with the lesion. Rostral to the antero-dorsal hippocampus a few degenerated fibers can be seen passing forward in the medial fornix on the normal side.

At the level of the ventral hippocampal commissure many degenerated fibers can be seen entering the lateral fornix on the opposite side. These degenerated fibers are not seen in the undegenerated fornix posterior to the commissure and they can be followed into the lateral septal area (Fig. 16). The fragmented argyrophilic fibers of the lateral fornix on the side of the lesion can be followed easily into the lateral septal nucleus, both pre and post commissural, where there is rather marked terminal degeneration with clearing of the neuropil throughout (Fig. 15). Terminal degeneration was noted in the lateral septal nucleus of the opposite side but not to the extent with which it occurs on the side of the lesion.

Degenerated fibers are seen passing through the medial septal nucleus (Fig. 17) and the nucleus of the diagonal band bilaterally with a small amount of terminal degeneration in the medial septal nucleus of both sides. These degenerated fibres appear to pass

above the nucleus of the diagonal band and then curve laterally dorsal to the diagonal band (Fig. 22) where degenerated terminals were noted around the cells of the islands of Calleja in the tuberculum olfactorium bilaterally (Fig. 24). The fibers of the diagonal band were not degenerated. Argyrophilic debris was also present in the lateral preoptic area (Fig. 21).

The degenerated superior fornix on the side of the lesion is joined laterally, where it passes ventrally as the column of the fornix, by several normal fibers from the lateral division of the medial fornix. These are fibers that have crossed in the dorsal hippocampal commissure. At the same position on the opposite side degenerated fibers can be seen joining the normal column of the fornix. As the degenerated column passes behind the anterior commissure it is joined medially by a group of undegenerated fine fibers which appear to curve dorsally over the descending column of the fornix to join its medial side (Fig. 18). The descending column of the fornix then passes through the hypothalamus to the mammillary body where rather marked terminal degeneration and gliosis is noted in the lateral part of the medial mammillary nucleus. There is also fiber and terminal degeneration in the area between the mammillary bodies and the supramammillary decussation

but no degenerated fibers could be followed caudal to the mammillary bodies. A few degenerating terminals were seen in the opposite mammillary body.

Many degenerating fibers and terminals were present in the posterior thalamic nuclei but they could be followed easily to the lesion in the pulvinar.

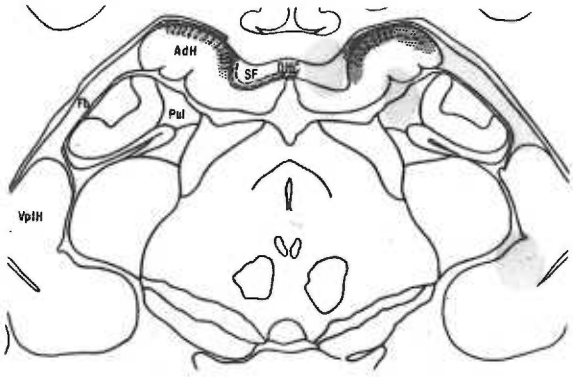
It is interesting to note that with this complete unilateral loss of the fornix that a thorough examination revealed no degeneration in the stria medullaris (Fig. 20), the habenula, the anterior thalamic nuclei, the extreme anterior septal areas, and the hypothalamus other than in the mammillary bodies and the lateral preoptic area.

Cat DW-87X. Bilateral lesion; Thirteen day degeneration.

The lesion and resulting degeneration in this case are summarized in Figure 2. This is a lesion of the fornix at the level of the ventral hippocampal commissure. The fibers entering this commissure are completely destroyed bilaterally.

On one side the entire lateral and medial fornix with the column are destroyed as they enter the post commissural septum. The lesion extends somewhat to involve the superior part of the lateral postcommissural septum and a small amount of the superior medial and lateral precommissural septum. The lesion

Figure 1. A series of six drawings illustrating representative sections of cat DW-90. The extent of the lesion is shown in 1, 2, and 3 (shaded area). Note heavy terminal (coarse stipple) and fiber (interrupted lines) degeneration on the homolateral side rostral to the lesion (1-6) and moderate degeneration of terminals (fine stipple) and fibers (interrupted lines) on the contralateral side (1-6). Note degeneration of the dorsal hippocampal commissure (2) and ventral hippocampal commissure (4). Degeneration of terminals and fibers in the thalamus are shown in 2 and 3.

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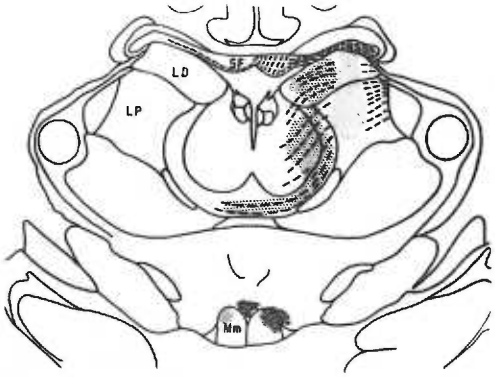


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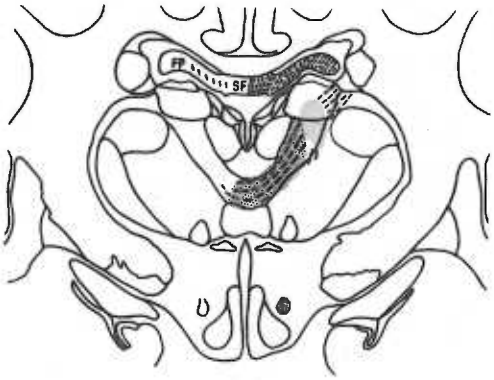


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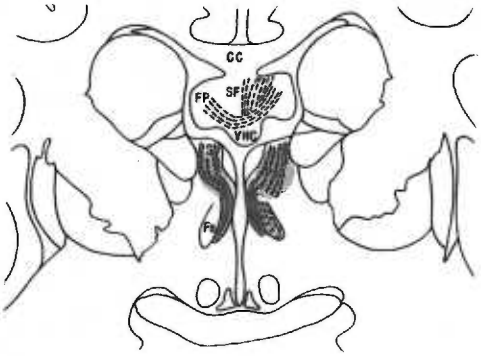


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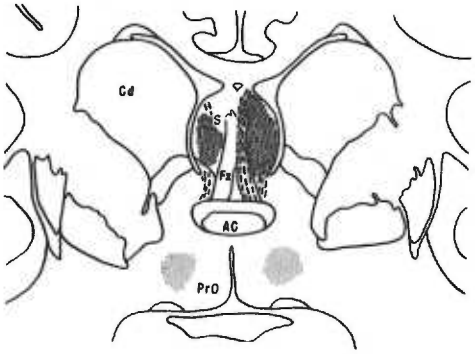


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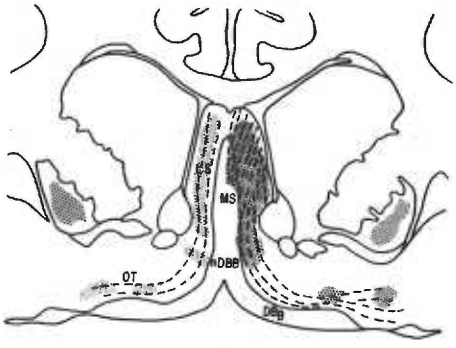


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also involves the corpus callosum.

The lesion of the other side was similar except that the superior fornix and column were spared. However, the fibers which join the column from the lateral division of the medial fornix were involved in the lesion as was the stria terminalis and the medial edge of the caudate nucleus.

The side which had a lesion of both the lateral and the medial fornix shows rather widespread degeneration. The descending column of the fornix in the hypothalamus is completely degenerated but is joined medially by partially degenerated fibers passing over it dorsally just posterior to the anterior commissure (Fig. 19). These fibers appear to arise from the lateral post commissural septum in the same area from which the stria medullaris arises. The descending column of the fornix ends in the lateral superior part of the medial mammillary nucleus where a marked gliosis and clearing of neuropil are present. Considerable fragmented argyrophilic debris is again seen in the immediate supramammillary region below the decussation but none can be followed into lower areas of the brainstem. No degenerated fibers or terminals were found in the midline hypothalamic nuclei or in the perifornical region. Many argyrophilic preterminals and

terminals were noted in the lateral preoptic area of the hypothalamus.

The post commissural septum on this side shows considerable terminal debris throughout but marked clearing has taken place. The pre commissural septum has many fragmented fibers coursing through it with a marked gliosis. Terminal debris is widespread in the lateral septal nucleus but there has been considerable clearing of the degenerated neuropil. The fragmented fibers can be followed ventrally in the lateral septal area where they course laterally above the diagonal band and enter the islands of Calleja of the tuberculum olfactorium where many swollen boutons and argyrophilic preterminals are noted. The medial septal nucleus and ventrally the nucleus of the diagonal band are spared as is the diagonal band.

The stria medullaris on this side was partially degenerated throughout its course with terminal degeneration noted in the habenular nucleus in its lateral part.

A thorough search of the anterior thalamic nuclei revealed no degeneration.

Posterior to the lesion considerable degeneration of the medial and lateral fornix were noted but this disappeared at a level just behind the dorsal hippocampal

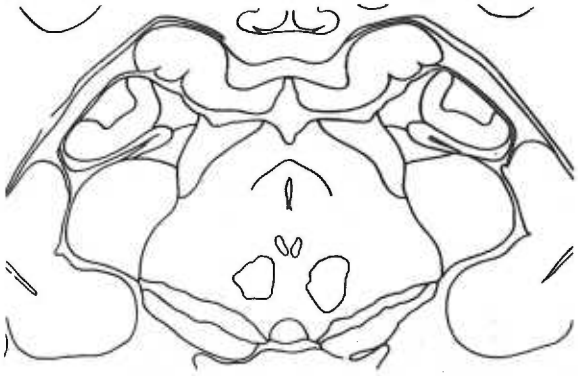
commissure. No degenerated fibers were found crossing in the dorsal hippocampal commissure and no degenerated fibers or terminals could be seen entering the antero-dorsal or ventro-postero-lateral hippocampus.

The side in which the column of the fornix was spared along with the stria medullaris shows somewhat the same pattern of degeneration. It differs in that the descending column of the fornix shows only a few degenerated fibers which entered it from the lateral division of the medial fornix at the level of the ventral hippocampal commissure. There is only slight degeneration in the mammillary body of the homolateral side. A few fragmented fibers can be seen crossing in the habenular commissure to enter the habenula on this side. The degenerated stria terminalis can be followed in the medial preoptic area where it terminates.

Cat DW-93. Bilateral lesion; 7 day degeneration.

The lesion and resulting degeneration in this case are summarized in Figure 3. The lesion is approximately the same on both sides. It involves the antero-dorsal hippocampus and the alveus on its superior surface, lateral to the most posterior part of the superior fornix. Most of the corpus callosum and a small part of the gyrus cinguli were also involved in the lesion. The ventral, medial, and most anterior parts of the antero-dorsal

Figure 2. A series of six drawings illustrating representative sections of cat DW-87X. The extent of the lesion is shown in 4 and 5 (shaded area). Note the heavy terminal degeneration (coarse stipple) of the septum (4) and fine terminal degeneration (fine stipple) in the lateral preoptic area and olfactory tubercle. The stria medullaris and habenula are degenerated, (2, 3, 4). Note almost total loss of fibers of the column of the fornix on one side and slight loss on the other in 4 (interrupted lines). Lesion of the stria terminalis is shown (4) with resultant degeneration of terminals (fine stipple) in the medial preoptic area (5). Note degeneration of the fornix caudal to the lesion (3).



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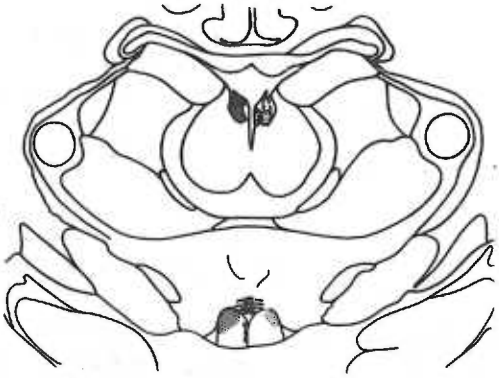

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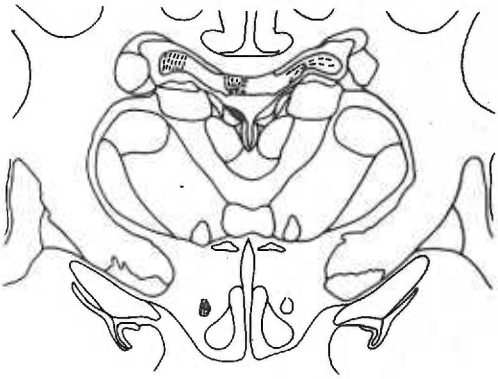

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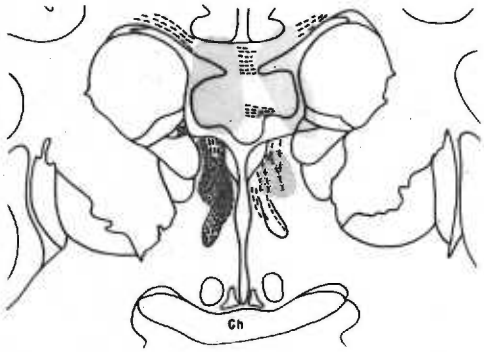


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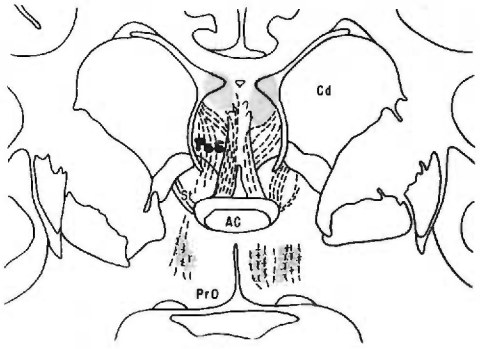


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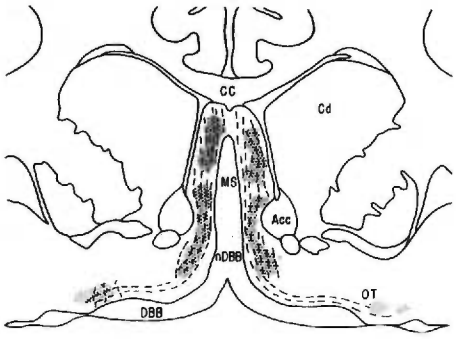


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hippocampus were not destroyed.

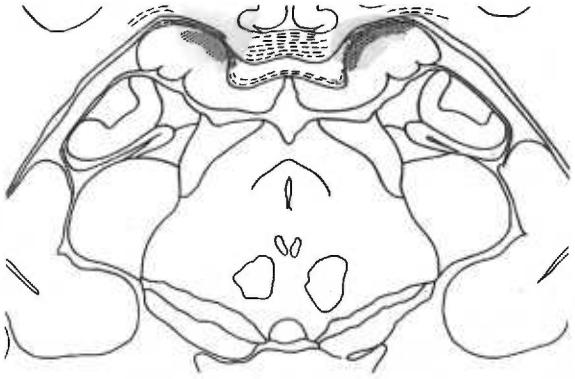
The pattern of degeneration is the same on the two sides. Anterior to the lesion the fibers crossing in the dorsal hippocampal commissure are completely degenerated (Fig. 25). Degenerated fibers can be seen entering the antero-dorsal hippocampus and considerable terminal debris is noted around the pyramidal cells of the polymorphic and pyramidal layers (Figs. 46, 47, 48). In front of the dorsal hippocampal commissure degenerated fibers can be seen in the lateral division of the medial fornix. These fibers join the column of the fornix and pass through the hypothalamus to the mammillary bodies where a small amount of degeneration is noted in the medial mammillary nucleus. A rather marked amount of debris is noted in the supramammillary area with many apparently crossing fragmented fibers.

Thorough examination reveals no degeneration in the habenula, anterior thalamic nuclei, medial or lateral septum, preoptic and other areas of the hypothalamus. There was no degeneration in the diagonal band or tuberculum olfactorium (Fig. 23). The ventro-postero-lateral part of the hippocampus is normal in all layers.

Cat K-15. Unilateral lesion; eight day generation.

The lesion and resulting degeneration in this case are summarized in Figure 4. The lesion is confined

Figure 3. A series of five drawings illustrating representative sections of cat DW-93. A bilateral lesion of the anterodorsal hippocampus is shown in 1 (shaded area). Note degenerated fibers (interrupted lines) of the lateral division of the medial fornix (2, 3, 4) and moderate terminal degeneration (fine stipple) in the mammillary body and supramammillary area (2).



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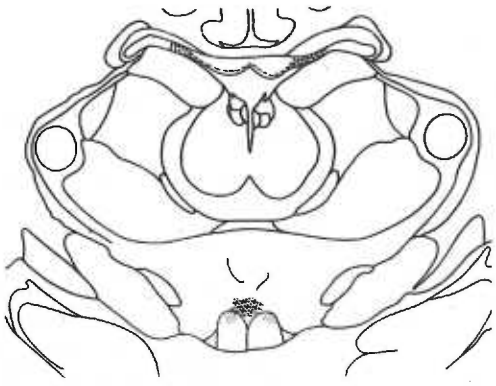

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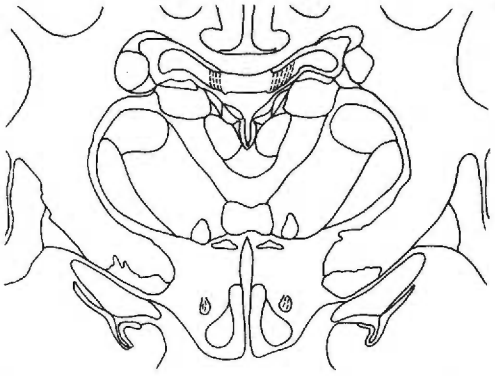

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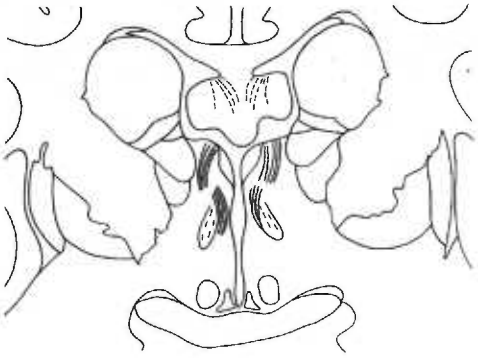

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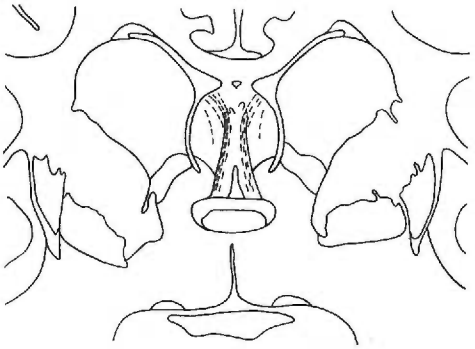

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mainly to the superior part of the ventro-postro-lateral area of the hippocampus. It involves the whole width of the hippocampus in this area including the alveus and fimbria. The only other areas of destruction involved small portions of the temporal lobe and the optic radiation.

Degenerated fibers were noted in the fimbria above the area of the lesion. At the level of the fornix the degenerated fibers were limited to the lateral fornix. No degenerated fibers could be found in the medial fornix, or in the dorsal hippocampal commissure. All layers of the antero-dorsal hippocampus of both sides were free of degenerating terminals and the ventro-postro-lateral hippocampus of the opposite side is free of any involvement.

At the level of the ventral hippocampal commissure many degenerated fibers from the lateral fornix are seen crossing to a similar position on the opposite side. These degenerated fibers of both sides can be followed into the lateral septum both pre and post commissural. None of these fibers can be found in the fornix of the opposite side posterior to the commissure.

Many swollen, argyrophilic fragments of fibers can be seen coursing through the lateral pre and post commissural septum of both sides (Figs. 27, 28). These

are far greater in number on the side of the lesion (Fig. 27). A great many swollen boutons are noted in the lateral septal nuclei and there is a rather marked gliosis and clearing of pericellular neuropil in these areas. Only a slight amount of terminal degeneration was noted in the medial septal nucleus. The diagonal band and nucleus of the diagonal band show no degeneration. There is a very moderate amount of terminal degeneration in the lateral preoptic area bilaterally.

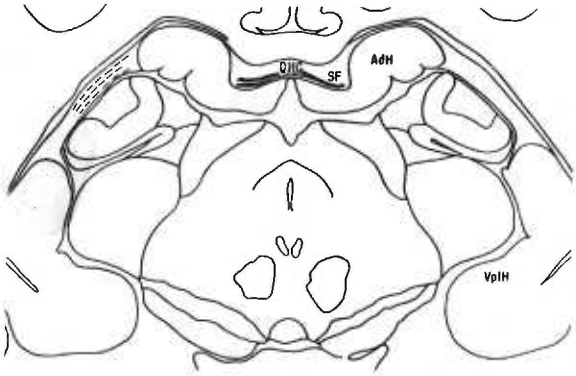
Degenerated fibers pass through the lateral septal nucleus, curve medially and then laterally above the diagonal band to terminate in the islands of Calleja in the olfactory tubercle (Fig. 26). Again this is more marked on the side of the lesion.

The medial fornix was intact bilaterally throughout its course. No areas of degeneration were found in or near the mammillary body. The anterior thalamus, other regions of the hypothalamus, stria medullaris, habenula, and the extreme anterior septal areas were free of degeneration bilaterally.

Cat K-9. Unilateral lesion; seven day degeneration.

The lesion was small and localized in the ventro-postero-lateral hippocampus without involving the alveus. No other nearby structures were involved

Figure 4. A series of six drawings illustrating representative sections of cat K-15. The lesion of the ventro-postero-lateral hippocampus is shown in 1 (shaded area). Degenerating fibers (interrupted lines) are shown in the lateral fornix (2, 3) and ventral hippocampal commissure (4). Note heavy degeneration of terminals (coarse stipple) on the side of the lesion and light terminal degeneration (fine stipple) on the contralateral side. Note intact dorsal hippocampal commissure (uninterrupted lines (2).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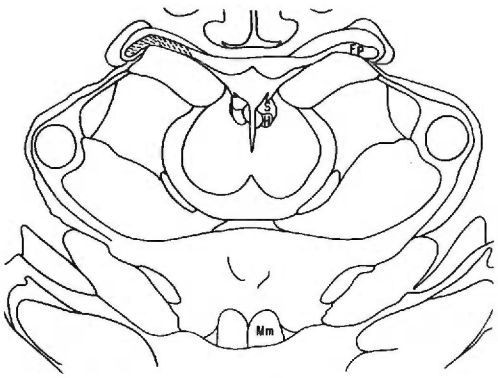
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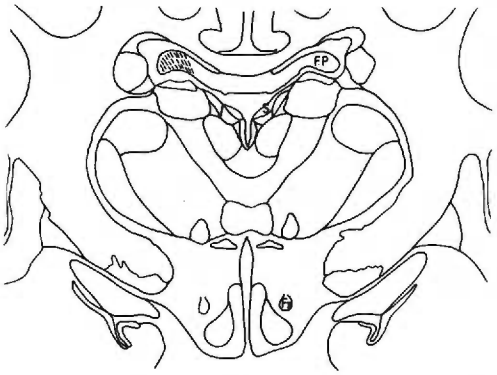
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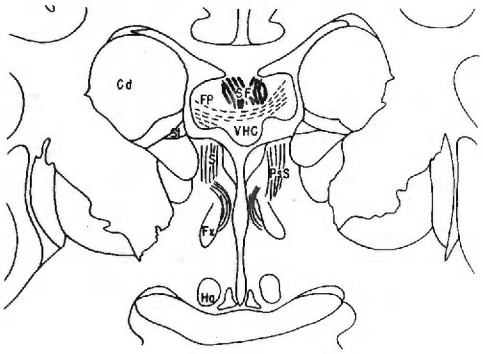
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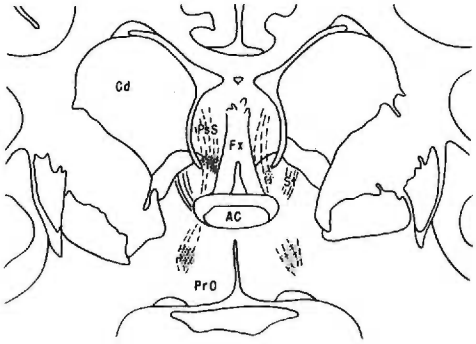
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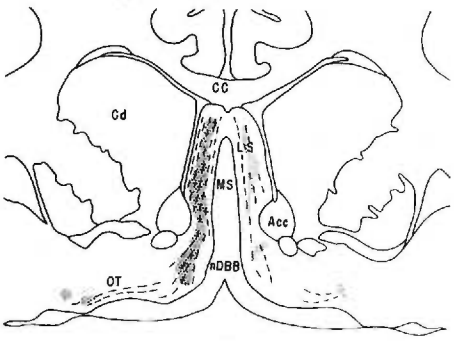
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in this lesion.

Degeneration occurred forward in a very narrow area of the lateral part of the lateral fornix. The pattern of degeneration was identical to that present in cat K-15 but on a much smaller scale.

Cat DW-77. Unilateral lesion; eight day degeneration.

The lesion and resulting degeneration in this case are summarized in Figure 5. The lesion in this animal destroyed the superior fornix posteriorly, the superior surface of the antero-dorsal hippocampus, and a part of the most dorsal portion of the ventro-postero-lateral hippocampus. Incidental involvement occurred in the splenium of the corpus callosum and the superior colliculus of that side.

The superior fornix is degenerated in front of the lesion, as it lies between the antero-dorsal hippocampus and the corpus callosum. As it passes forward normal fibers appear to join the superior fornix from the antero-dorsal hippocampus. At the level of the dorsal hippocampal commissure the superior fornix appears to be about two thirds degenerated. There are no degenerated fibers in the alveus over the superior surface of the antero-dorsal hippocampus at this level and the dorsal hippocampal commissure is made up of normal fibers. The partially

degenerated superior fornix can be followed into the column of the fornix where it is joined on its lateral side by normal fibers from the lateral division of the medial fornix. The column then curves posteriorly in the hypothalamus and the mammillary bodies show the same pattern of degeneration as seen in DW-90 and DW-87X (Figs. 29, 30).

Degenerated fibers are present in the medial half of the lateral fornix posteriorly (Figs. 31, 32, 33). These fibers course to the post commissural septum where many of them cross to the opposite side in the ventral hippocampal commissure. Others can be seen descending and terminating in the lateral septal area just above and posterior to the anterior commissure. This is the region from which the stria medullaris appears to take origin. Other degenerated fibers pass to the pre commissural septum and their degenerated terminals can be seen in the medial septal nucleus and the medial part of the lateral septal nucleus. The degenerated fibers could not be followed as far as the tuberculum olfactorium.

Again no degenerated terminals or fibers were found in the thalamus, hypothalamus with the exception of the mammillary bodies, stria medullaris, or habenula. No degeneration was noted in the preoptic area of the

hypothalamus and there was no apparent degeneration behind the lesion in any part of the hippocampus.

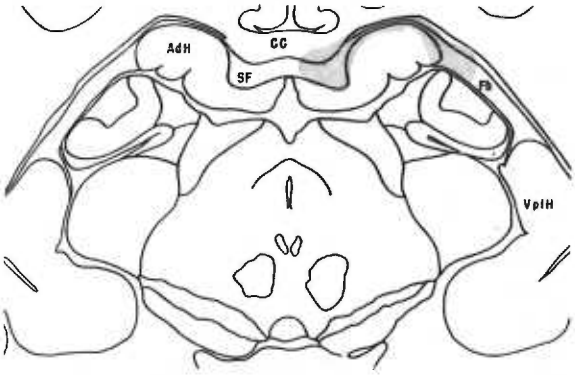
On the side which had no lesion, degeneration was limited to those fibers entering it in the ventral hippocampal commissure. These fibers appear to follow the same pathway noted in the septal area of the opposite side. The terminal degeneration was not as great in extent as on the side of the lesion. No degenerated fibers were found in the fornix posterior to the ventral hippocampal commissure.

Cat DW-88. Bilateral lesion; eight day degeneration.

The lesion and resulting degeneration in this case are summarized in Figure 6. The lesion in this animal was large. It begins posteriorly where it destroys the superior fornix and a part of the fimbria at the superior end of the ventro-postero-lateral hippocampus. As the lesion extends forward the dorsal hippocampal commissure is involved. The superior border of the antero-dorsal hippocampus is coagulated. Anterior to the most rostral level of the hippocampus the medial fornix is destroyed along with the medial one half of the lateral fornix. A large area of corpus callosum and gyrus cinguli were included in the area of the lesion. The lesions on the two sides were identical.

Anterior to the lesion the fibers of the medial

Figure 5. A series of six drawings illustrating representative sections of cat DW-77. The lesion of the superior fornix and superior surface of the antero-dorsal hippocampus is shown in 1 (shaded area). Resulting degeneration (interrupted lines) is shown in the fornix and ventral hippocampal commissure (4). Moderately heavy terminal degeneration is shown (coarse stipple) in the homolateral mammillary body and septum (2, 4, 5, 6). Moderate degeneration of the contralateral septum (fine stipple) is present in 5 and 6. Note no degeneration of stria medullaris or septo-mammillary tract (4). The terminal degeneration in the pre commissural septum is mainly in the medial part of this structure (6).

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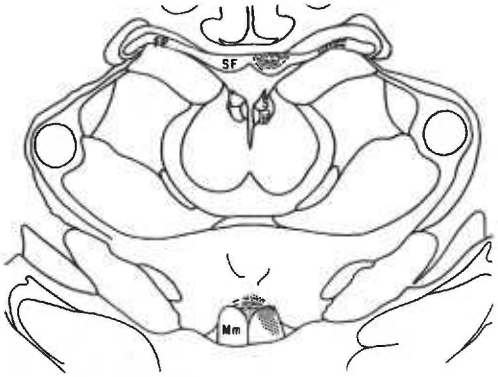


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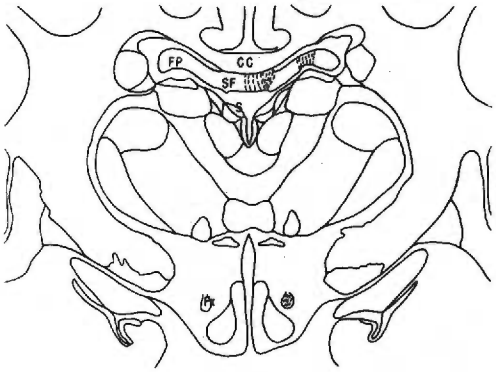


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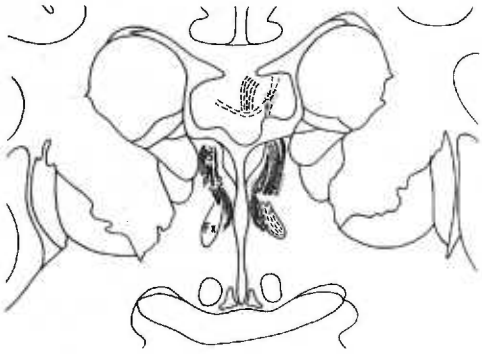

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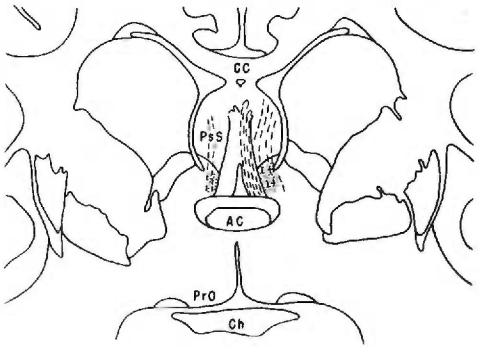


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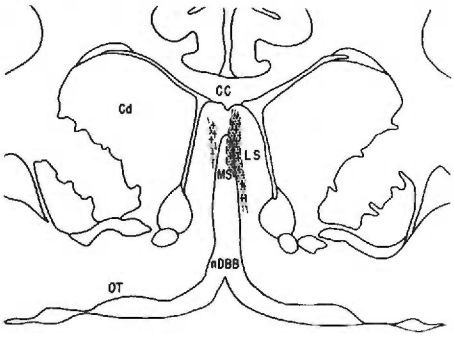


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fornix and the medial one half of the lateral fornix are entirely degenerated (Figs. 34, 35). No degenerating terminals could be found in any part of the ventro-postero-lateral hippocampus. The antero-dorsal hippocampus could not be examined due to its involvement in the lesion.

Anteriorly the columns of the fornix are completely degenerated. They can be followed post commissurally where they are joined medially by normal fibers which appear in the post commissural septum in the area from which the stria medullaris appears to arise. As the descending columns pass through the hypothalamus none of the fornix fibers can be seen entering the hypothalamus. Degenerating terminals are spread throughout the lateral part of the medial mammillary nucleus. Again considerable argyrophilic debris is noted in the supramammillary area. These fibers could not be followed into the tegmentum.

The degenerated fibers of the medial one half of the lateral fornix can be followed into the post commissural septum where a few of the degenerated fibers cross in the superior portion of the ventral hippocampal commissure. It appears however, that at least 80% of the commissure is not degenerated and is made up of normal fibers from the lateral one half of the lateral fornix.

Rather widespread terminal degeneration was noted

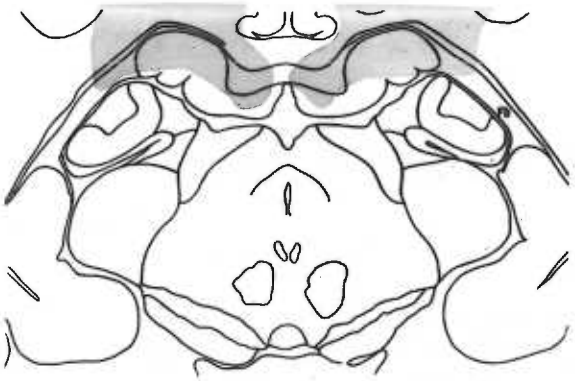
in the medial and lateral septal areas both pre and post commissural. This appears to be more marked in the medial septal nucleus and the medial one half of the lateral septal nucleus (Fig. 37). There is a large amount of gliosis and many fragmented swollen fibers can be seen coursing through the septum. Many of these fibers appear to pass laterally above the diagonal band. A few degenerated terminals were seen in the islands of Calleja of the olfactory tubercle. The diagonal band and the nucleus of the diagonal band show no evidence of degeneration. Very little terminal degeneration was noted in the post commissural septum.

Numerous degenerated terminals and fibers were found in the posterior thalamic nuclei. These fibers could be followed into the white matter of the lateral part of the hemisphere. No degenerated material could be found in the anterior thalamic nuclei and no degeneration was noted in the stria medullaris (Fig. 36) or habenula.

Again swollen terminals and argyophilic debris were noted in the lateral preoptic area of the hypothalamus. The rest of the hypothalamus and the epithalamus were free of involvement.

The stria of Lancisi or dorsal fornix can be seen entering the lateral septum anteriorly. The fibers are

Figure 6. A series of six drawings illustrating representative sections of cat DW-88. The extent of the lesion is shown in 1 and 2 (shaded area). Fiber degeneration (interrupted lines) is represented in the medial fornix and medial half of the lateral fornix bilaterally. Note the lack of fiber degeneration in the lateral half of the lateral fornix (3), the ventral hippocampal commissure (4) and the lateral part of the septum (6). Note also moderate degeneration of terminals (fine stipple) in the lateral preoptic area (5) and olfactory tubercle (6). The stria medullaris (3, 4) and habenula (2) are free of degeneration. Note the degeneration in the thalamus (2) due to the lesion in parietal white matter (1).



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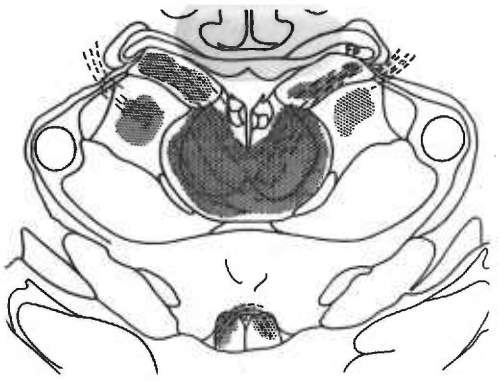

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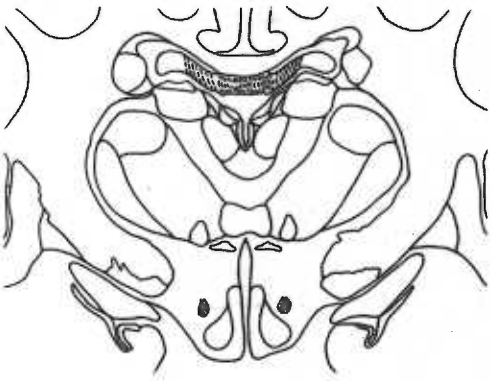

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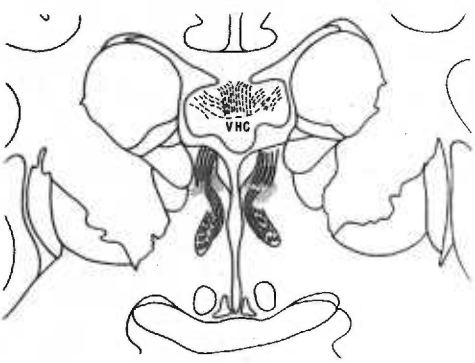


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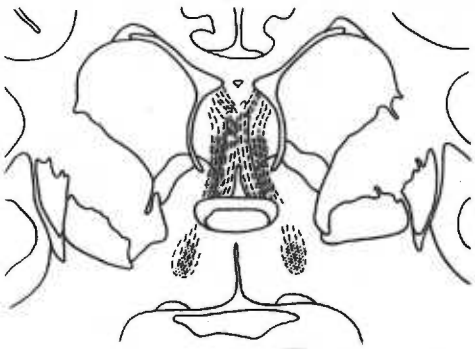

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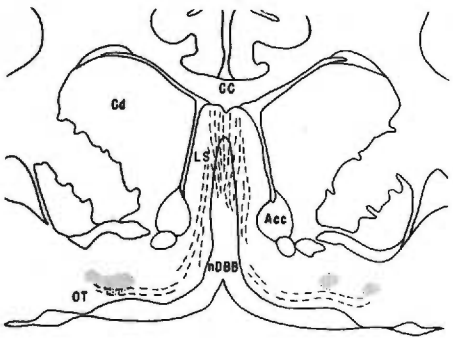


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degenerated bilaterally and considerable terminal debris can be seen in the lateral septal nucleus. There is no terminal degeneration in the anterior continuation of the hippocampus.

Cat DW-94. Bilateral lesion; eight-day degeneration.

The lesion and resulting degeneration in this case are summarized in Figure 7. The lesion is somewhat posterior at the level of the rostral end of the artero-dorsal hippocampus. The lesion on one side destroyed the whole superior fornix, the dorsal surface and alveus of the artero-dorsal hippocampus, and a very small part of the fimbria in the superior extremity of the ventro-postero-lateral hippocampus. The lesion of the other side only destroyed a few of the dorsal fibers of the superior fornix and the alveus and superior border of the antero-dorsal hippocampus. The corpus callosum was involved slightly on both sides.

On the side in which the entire superior fornix and a small amount of the superior fimbria were involved forward degeneration was found in the medial fornix (Fig. 38). Degeneration in the column and the mammillary body were nearly the same as that in DW-77 and DW-88.

On the side in which the superior fornix was only slightly involved there was only minimal

degeneration noted in the columns of the fornix.

The dorsal hippocampal commissure was partially degenerated (Fig. 38). Argyrophilic terminal debris was noted in the polymorphic and pyramidal layers of the antero-dorsal hippocampus bilaterally. No degeneration was found in the ventro-postero-lateral hippocampus of either side.

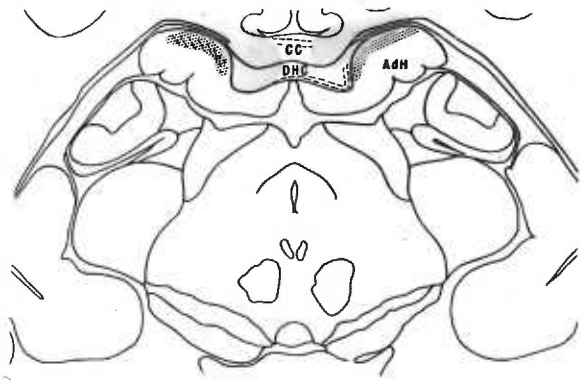
It was interesting that no degenerated fibers could be found entering the pre commissural septum, the post commissural septum, the stria medullaris, the hypothalamus other than the mammillary bodies, nor the anterior thalamic group of nuclei.

Cat K-11. Unilateral lesion; eight day degeneration.

In this cat the lesion was limited to the medial fornix and a small amount of the antero-dorsal hippocampus and the alveus lying over it.

Degeneration occurred in the same pattern as was present in cat DW-94 on the side with the lesion of the superior fornix. In this animal a few degenerated fibers were noted crossing in the dorsal hippocampal commissure and a small amount of terminal degeneration could be found at this level in the opposite hippocampus around the pyramidal cells. No degeneration was found in the homolateral hippocampus in front of the lesion. Many normal fibers could be

Figure 7. A series of five drawings to illustrate representative sections of cat DW-94. The extent of this lesion is represented in 1 (shaded area). Note fiber degeneration (interrupted lines) of the medial fornix on the left, the lateral division of the medial fornix on the right, and the dorsal hippocampal commissure. Terminal degeneration (course stipple) occurred in the antero-dorsal hippocampus (1) and mammillary bodies (2). Note fibers of the lateral division of the medial fornix joining the column on the right (4, 5). Note also the lack of degeneration in the ventral hippocampal commissure (4), preoptic area (5) stria medullaris (4) and septum.

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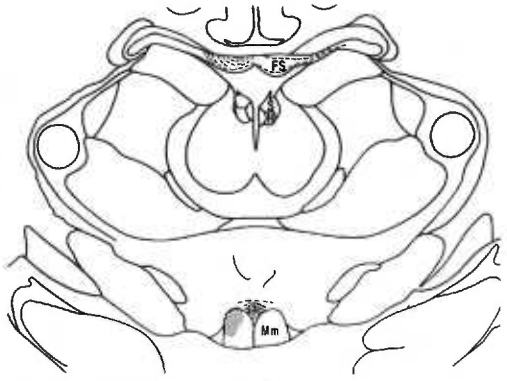


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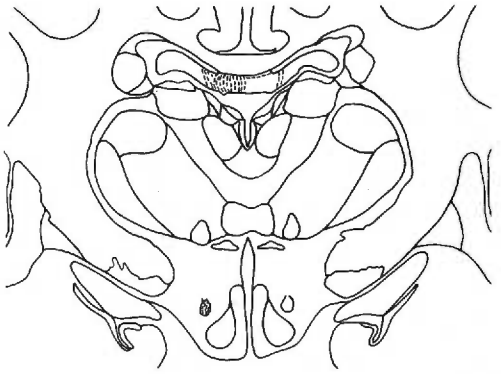

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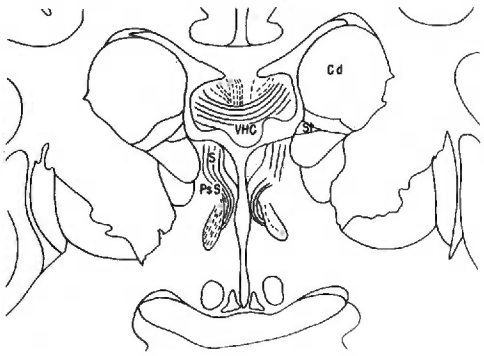


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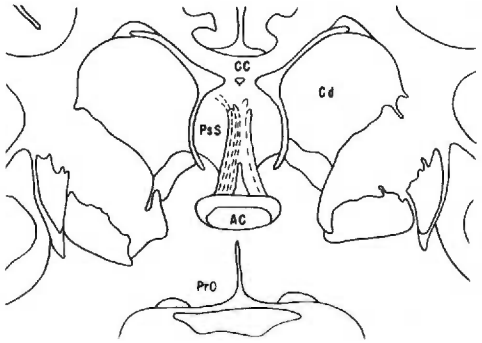


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seen entering the degenerated alveus on the side of the lesion at the level of the dorsal hippocampal commissure.

Cat K-14. Unilateral lesion; six day degeneration.

The lesion and resulting degeneration in this case are summarized in Figure 8. The lesion in this animal was large but only involved the septal area. The area of destruction begins posteriorly in the post commissural septum just below the ventral hippocampal commissure and above the anterior commissure. The pillar of the fornix is destroyed along with the septum above and on the lateral side of the pillar. This region of the septum is where the stria medullaris and fibers which join the fornix medially are usually noted to take origin. The anterior commissure is not included in the lesion but the stria terminalis is destroyed at this level.

The pre commissural lesion includes the fibers from the lateral fornix as they enter the septum at this level. The medial and lateral septal nuclei are destroyed for some distance anteriorly. The superior medial part of the diagonal band and the nucleus of the diagonal band are also incorporated in the lesion.

The descending column of the fornix in the hypothalamus appears to be completely degenerated. Terminal degeneration appearing in the mammillary

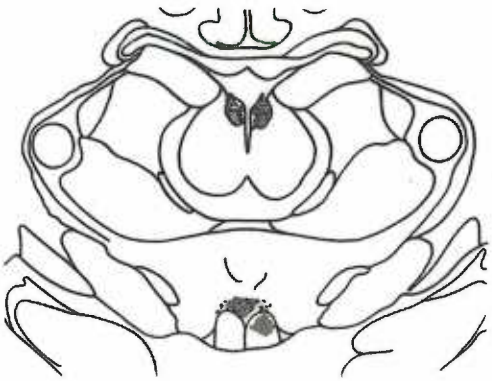
body and supramammillary area on the side homolateral to the lesion was the same as was found with lesions of the antero-dorsal hippocampus and superior fornix in cats DW-90, DW-87X, DW-88, DW-94, and K-11. The normal fibers which joined the fornix medially in the post commissural septum in the above cats were reduced to fragments of argyrophilic material in this preparation (Figs. 41, 42, 43).

The fibers of the stria medullaris are completely degenerated (Figs. 44, 45) and terminal degeneration is present in the lateral part of the habenular nucleus. Some degenerated fibers can be seen crossing in the habenular commissure to terminate in the medial habenular nucleus of the opposite side.

Rather marked gliosis and degeneration of fibers and terminals were noted in the medial and lateral septal nuclei ventral to the lesion. Terminal degeneration was found in the nucleus of the diagonal band and a few of the fibers of the diagonal band appear fragmented. Again degenerated fibers could be seen moving laterally above the diagonal band toward the islands of Calleja where some terminal debris was noted. The extreme anterior extent of the septum is free of degeneration and the stria of Lancisi is intact.

Posterior to the lesion there was no degeneration in any part of the fornix, the hippocampus, or in the

Figure 8. A series of five drawings to illustrate representative sections of cat K-14. A lesion of the post commissural septum and the pillar of the fornix is represented in 3, 4, and 5 (shaded area) with resulting fiber degeneration (interrupted lines) in the stria medullaris thalami (1-3) and fibers of the septum joining the fornix on its medial side. The lesion in the stria terminalis is shown in (4) with terminal degeneration (stipple) in the medial preoptic area (4). The lesion extends to include the whole pre commissural septum and nucleus of the diagonal band in 5. Degeneration of terminals (coarse stipple) is shown in the olfactory tubercle and nucleus of the diagonal band (5). Note degeneration in habenula bilaterally (1).



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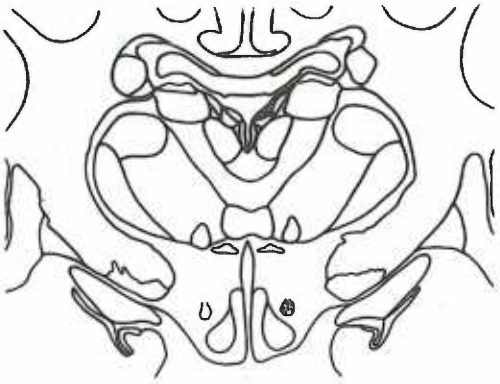

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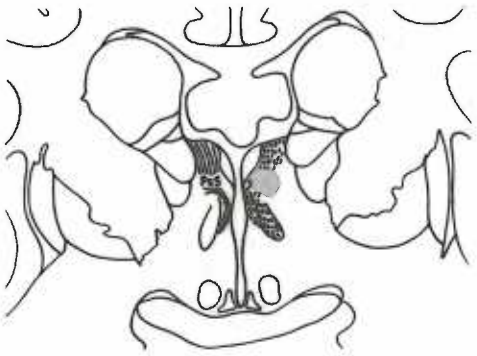

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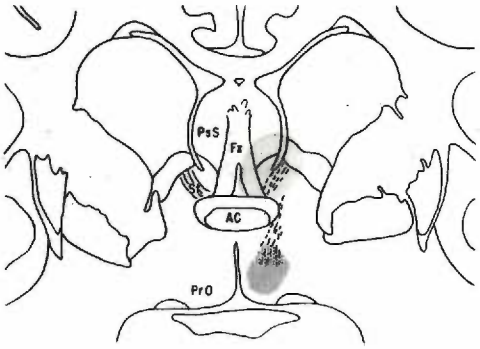


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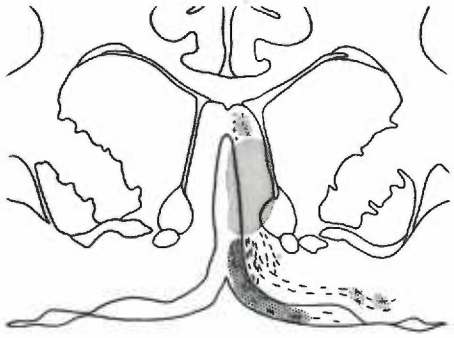

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dorsal and ventral hippocampal commissures.

The degenerated fibers of the stria terminalis could be followed into the medial preoptic area. There was no other evidence of degeneration in any part of the hypothalamus. The anterior thalamic nuclei showed no abnormality.

Cat DW-89. Unilateral lesion; twelve day degeneration.

The lesion and resulting degeneration in this case are summarized in Figure 9. The lesion began in the post commissural region where it destroyed a small portion of the ventral hippocampal commissure, the anterior commissure, and the superior preoptic area. Approximately one half of the pillar of the fornix was involved along with a part of the septal area lateral to it as in Cat K-14. In the pre commissural septum the lesion involved the medial septal area in its whole dorso-ventral extent including the diagonal band and the nucleus of the diagonal band. The lateral septal area and stria terminalis were spared in this lesion.

The pattern of degeneration was identical to that in Cat K-14 except that the lateral septal nucleus, islands of Calleja and medial preoptic area were spared of degeneration. The diagonal band in this lesion was degenerated for only a short distance beyond the lesion.

A small lesion was noted in the ventral portion of

the corpus callosum, just above the septum. From this lesion degenerated fibers could be seen terminating in the medial septum anteriorly but none could be followed into the corpus callosum behind the lesion (Figs. 49, 50, 51).

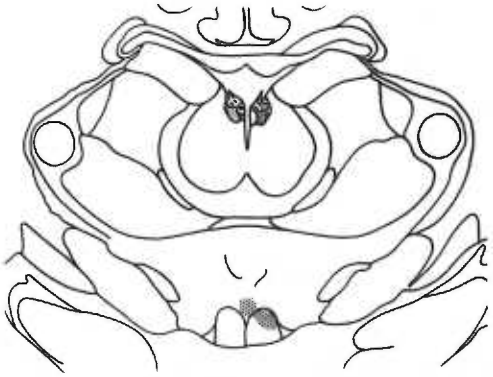
Cat K-18; Cat DW-165. Unilateral lesion; ten day degeneration.

The lesion and resulting degeneration in these cases are summarized in Figure 10. The lesion in these two animals involved the lateral pre commissural septum superiorly. The lesion was just in front of the anterior commissure and involved none of the post commissural septum. The pre commissural fibers of the lateral fornix were destroyed.

On the side of the lesion there was a marked clearing of fibers and debris in the lateral septal nucleus but a large amount of argyrophilic debris nevertheless remained throughout. A few degenerated fibers which appear to come from the lateral septal area could be followed laterally above the diagonal band. There was some clearing of neuropil and terminal degeneration in the islands of Calleja.

There was no degeneration behind the lesion in any part of the fornix or hippocampus. The epithalamus, thalamus, and hypothalamus were free from any abnormality.

Figure 9. A series of five drawings to illustrate representative sections of cat DW-89. A lesion is shown of the post commissural septum, column of fornix, and a small part of the anterior commissure and dorsal preoptic area (4) (shaded areas). The lesion extends to the medial pre commissural septum (5). Degeneration of fibers (interrupted lines) is shown in the stria medullaris thalami and descending column of the fornix (1-3). Note terminal degeneration (stipple) in the homolateral lateral habenula and contralateral medial habenula.



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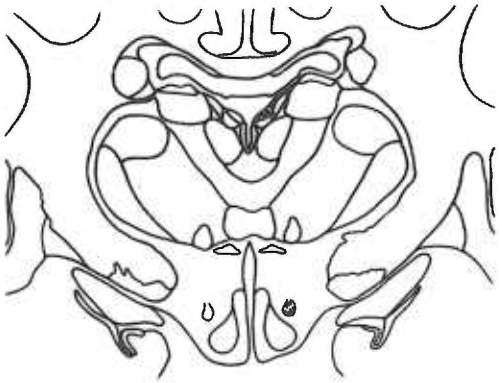

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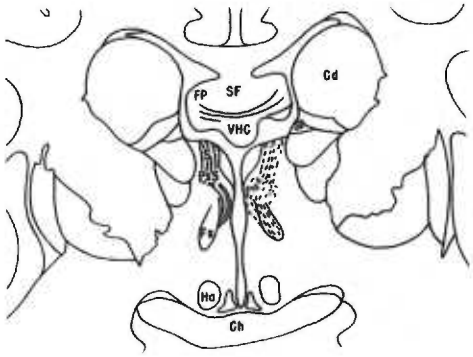


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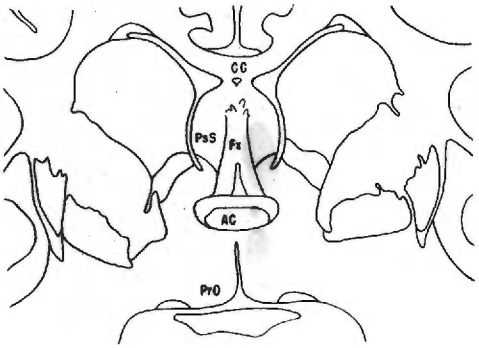


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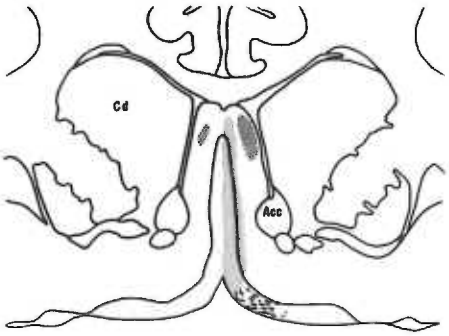


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Cat K-5. Unilateral lesion; seven day degeneration.

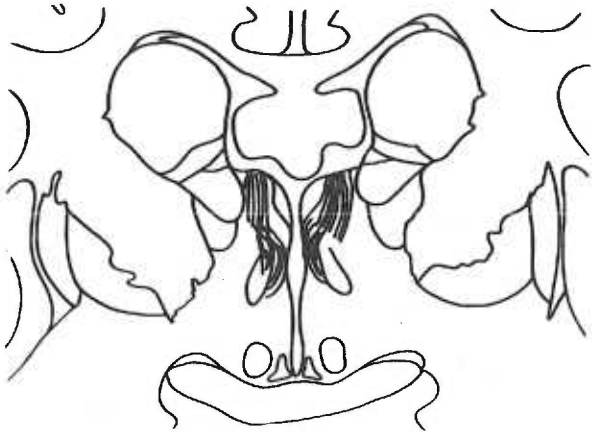
The lesion was confined to the lateral pre commissural septum in its whole dorso-ventral extent from the anterior commissure to, but not including, the nucleus accumbens. There was a small lesion in the lateral pre commissural fornix.

Technical difficulty prevented any evaluation of the degeneration in the lower half of these sections. The lesion was significant, however, in that there was no degeneration in any part of the fornix or hippocampus behind the lesion. Another important finding was a lack of degeneration in the stria medullaris, habenula, and thalamus.

Cat K-16. Unilateral lesion; eight day degeneration.

The lesion and resulting degeneration in this case are summarized in Figure 11. This lesion was limited to the post commissural septum and the ventral hippocampal commissure. It involved the whole lateral fornix as it entered the post commissural septum, thereby cutting all of the fibers of the ventral hippocampal commissure. About two thirds of the medial fornix was destroyed as it descends ventrally as the column of the fornix. The majority of the post commissural septum was destroyed. None of the lesion extended to the pre commissural septum. The corpus callosum and gyrus cinguli were

Figure 10. A series of three drawings to illustrate sections of cats K-18 and DW-165. The lesion is shown in the superior part of the lateral pre commissural septum (shaded area). Degeneration of terminals (stipple) occurs in the medial and lateral pre commissural septum below the lesion (3) and in fibers (interrupted lines) coursing above the diagonal band (3). Note the terminal degeneration in the islands of Calleja of the olfactory tubercle (3). Note also the undegenerated stria medullaris and fibers joining the fornix on its medial side (1).



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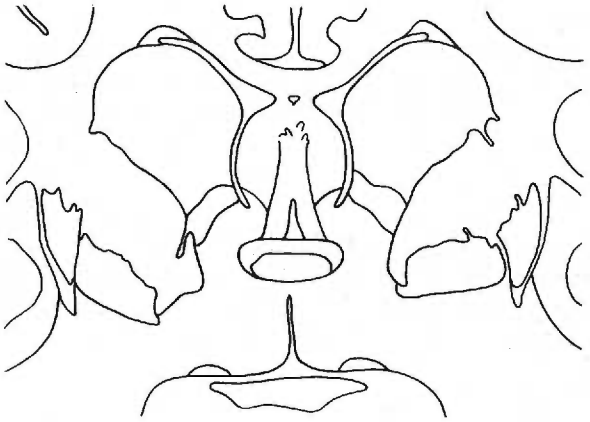

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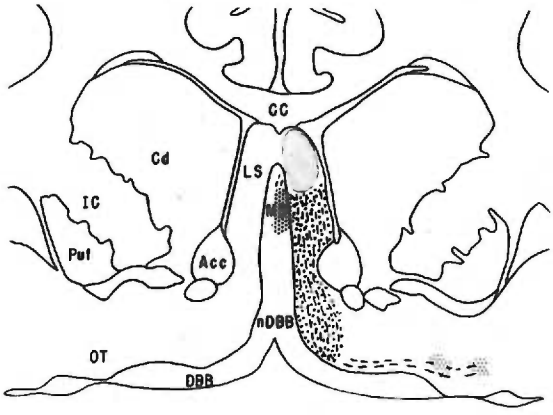


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involved slightly but no other structures were injured.

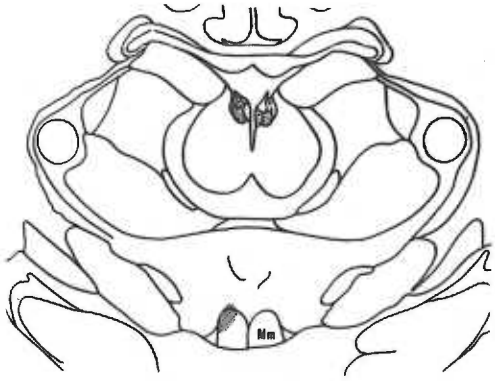
The descending column of the fornix and its afferent terminals in the mammillary body on the side of the lesion were degenerated as in cat K-14 and others. Degenerated fibers could be seen crossing to the normal side in the ventral hippocampal commissure. These crossed fibers could not be followed in the fornix caudal to the lesion and examination of the entire hippocampus on the normal side revealed no abnormality.

Degeneration of fibers and terminals occurred in the lateral septal nucleus and islands of Calleja bilaterally, and there was a slight degeneration in the medial septal nuclei. The degeneration here was the same as in cat K-18.

A striking finding in this animal was the nearly complete degeneration of the stria medullaris with terminal degeneration in both habenular nuclei. The fibers which have been described in previous lesions (K-14) as joining the medial side of the descending column of the fornix after passing over it dorsally, are also completely degenerated in this cat.

Again no degeneration was noted behind the lesion in the fornix and hippocampus. The thalamus and hypothalamus, other than the lateral preoptic area and mammillary bodies were free of degeneration.

Figure 11. A series of five drawings to illustrate representative sections of cat K-16. The extent of the lesion is shown in 3 and 4 (shaded area). Note fiber degeneration (interrupted lines) in the ventral hippocampal commissure (3) and stria medullaris (3). The fibers joining the fornix column on its medial side are also degenerated (3). Terminal degeneration (stipple) of the septum (5), olfactory tubercle (5), lateral preoptic area (4), and habenula (1) are shown.

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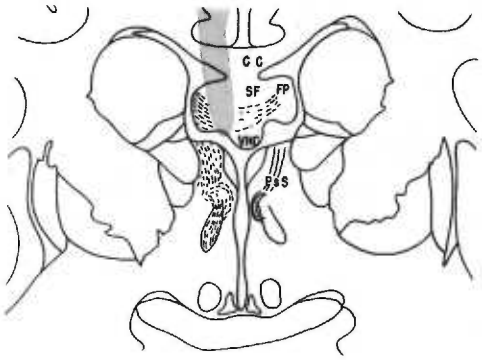


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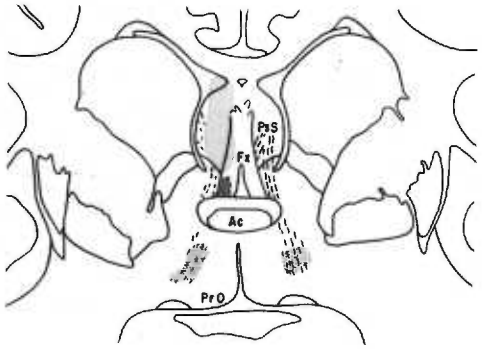


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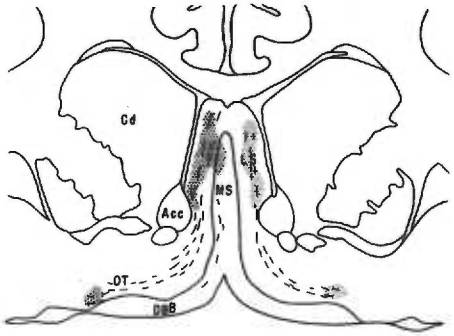


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Cat DW-146. Unilateral lesion; six day degeneration.

The lesion and resulting degeneration in this case are summarized in Figure 12. This was a remarkable lesion in that it appeared to follow the path of the inferior thalamic peduncle. The area of destruction began posteriorly just lateral to the descending column of the fornix and then extended forward and upward to reach the third ventricle at a level just posterior to the anterior commissure (Fig. 39). Throughout its course the lesion remained lateral to the post commissural fornix and septum. The stria terminalis was destroyed on the side of the lesion along with a small area of the dorsal preoptic area ventrally. The lesion also included the mammillothalamic tract.

Rather marked degeneration was noted in the anterodorsal, anteroventral, and anteromedian thalamic nuclei (Fig. 40).

A remarkable finding was the complete lack of degeneration in the stria medullaris (Fig. 39) and habenula as well as in the fornix and hippocampal areas. No degeneration was found in any part of the septum or basal olfactory areas.

The fragmented fibers of the stria terminalis could be followed into the medial preoptic region where a moderate amount of argyrophilic terminal debris was noted.

Figure 12. A series of three drawings to illustrate representative sections of cat DW-146. The lesion of the medial thalamus involves most of the inferior thalamic peduncle (1-3) (shaded area). Degeneration occurs in the anterior thalamic nuclei (1, 2) (stipple). Note that there is no degeneration of the stria medullaris (1, 2).


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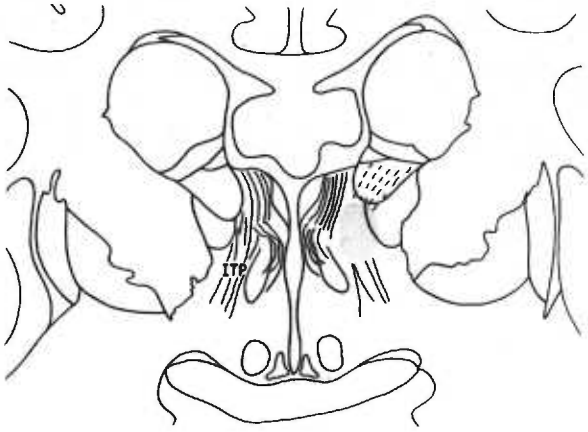


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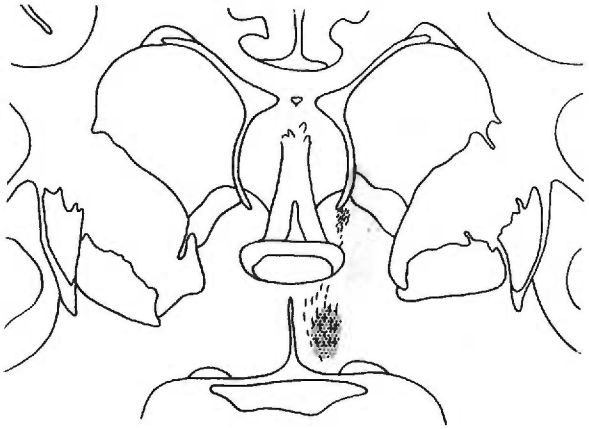

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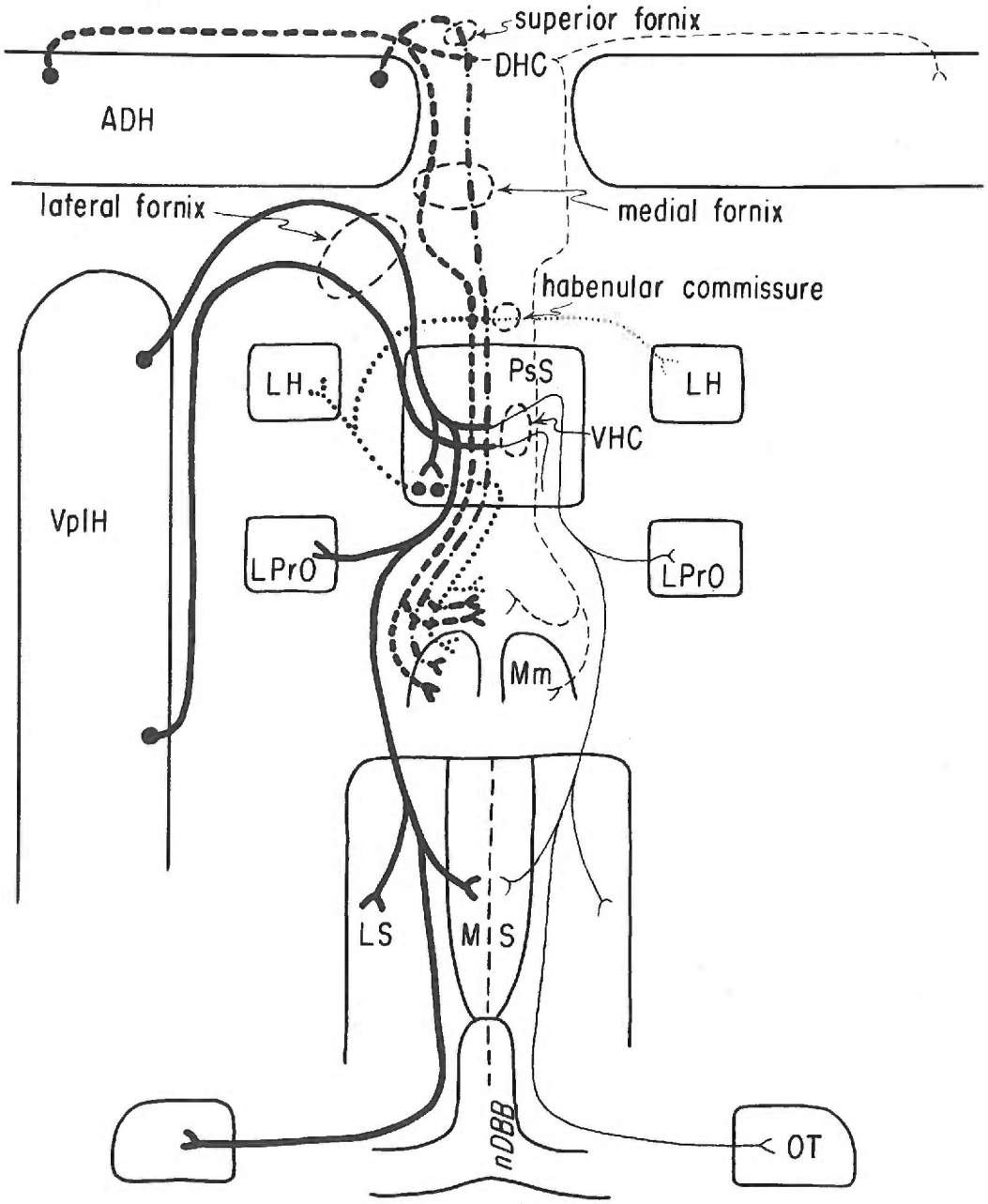
Figure 13. A schematic diagram representing a partial summary of the connections of the fornix and septum in the cat. Heavy lines represent a large amount of fibers and fine lines small contributions of fibers.


superior fornix
DHC
ADH
lateral fornix
medial fornix
habenular commissure
LH
PsS
LH
VHC
VpIH
LPrO
LPrO
Mm
LS
MS
nDBB
OT

# DISCUSSION

## Origin of the Fornix

The origin of the fornix from the pyramidal cells in the stratum lucidum of the hippocampus was described in the early literature by Ariëns Kappers, Huber and Crosby (10), Ramon y Cajal (72), and Lorente de Nó (54). More recently Allen (6), in Nissl preparations of the dog brain following section of the fornix, found complete chromatolysis of the pyramidal cells of the hippocampus. Allen also noted chromatolysis in a number of cells of the polymorphic layer of the dentate gyrus.

Daitz and Powell (22) noted a complete absence of any demonstrable change in the cells of the hippocampus in Nissl preparations after complete section of the fornix in the rat, rabbit, and monkey. They used both short and long term experiments with the same results. These investigations have been repeated with similar results in monkeys by McLardy (60) and Simpson (76).

Whatever the cellular origin of these fibers it is generally accepted that axons from the hippocampus reach the alveus. Daitz and Powell (22), in their studies of retrograde degeneration following lesions of the fimbria alone, noted degeneration of the alveus over the ventral surface of the hippocampus as well as

the lateral two thirds of the dorsal surface. With lesions that involved the superior fornix, as well as the fimbria, the whole alveus appears degenerated.

Simpson (76), while working with monkeys, described a topographical relationship between the fibers of the fornix and their origin in the hippocampus. He found that the alveus of the anterior part of the hippocampus projects to the lateral fornix while the more posterior alveus projects to the medial fornix. Support for this was shown, also in the monkey, by Bucy and Klüver (18). Nauta (64) and Valenstein and Nauta (86) confirmed these results in the guinea pig, cat, monkey, and rat. Using silver techniques they noted that lesions in the more distal parts of the hippocampus cause degeneration in the more lateral parts of the fornix while those of the proximal hippocampus result in degeneration of the medial fornix.

No cellular studies were carried out in this paper but several relatively discrete lesions were made in various parts of the hippocampus which gave indications of a distinct topographical organization of the fornix and hippocampus. In cat DW-90 a lesion of the antero-dorsal hippocampus and the fimbria of the ventro-postero-lateral hippocampus resulted in

complete degeneration of both medial and lateral fornix. Lesions which involve mainly the antero-dorsal hippocampus (DW-93, DW-77, DW-88, DW-94) show antegrade degeneration of the medial fornix while lesions of the ventro-postero-lateral hippocampus as is K-15 and K-9 resulted in degeneration of the lateral fornix. The lesion in cat DW-77 was interesting in that although the lesion involved the superior fornix posteriorly, normal fibers entered this bundle as it proceeded anteriorly above the antero-dorsal hippocampus. By the time it reached the septum the superior fornix was comprised of predominantly normal fibers which would indicate that these take origin from the antero-dorsal hippocampus.

Hippocampal Afferents in the Fornix

Ramon y Cajal (72) and Lorente de Nó (54) noted in normal material that the fornix was entirely efferent in relation to the hippocampus. More recently Allen (6), in Marchi studies of dogs following transection of the fornix, concluded that the fornix was a centrifugal tract emanating from the pyramidal cells of the hippocampus.

Ariëns Kappers, Huber, and Crosby (10), in mammals, described a septo-hippocampal pathway and

later Gerebtzoff (30), using Marchi studies in the rabbit, found degeneration in the hippocampus following lesions of the basal septal area. Sprague and Meyer (78), using silver techniques in the rabbit, found degeneration of the superior fornix posterior to lesions of the fornix. They were able to follow these fibers through the corpus callosum to the deep layers of the cingulum and thence to the hippocampus. McLardy (61) described these fibers and indicated that they terminated in the temporal lobe.

Morin (63), using the Marchi technique in guinea pigs, noted that lesions in the septum resulted in degenerated fibers in the ventral hippocampal commissure and the fimbria while Daitz and Powell (22), after sectioning the fimbria of the rat, rabbit, and monkey, noted massive retrograde degeneration in the neurons of the medial septal nucleus as well as partial degeneration of the neurons in the nucleus of the diagonal band. Their findings in the medial septal nucleus were confirmed in the monkey by McLardy (60) using a similar technique. The above anatomic results have been supported by several electrophysiologic studies (3, 79, 33, 21, 88, 89).

In the present studies nearly all of the lesions involved either the septum or fornix. Yet, only one

of the animals, cat DW-87X, shows degeneration of the fornix or hippocampus posterior to the lesion (Fig. 2). This cat was allowed the longest term of degeneration in this study (13 days) and it may be that this was retrograde degeneration. Though the degeneration appeared to move for a short distance in a caudal direction, the fornix had a normal appearance at the level of the dorsal hippocampal commissure.

Following lesions of the septum no degenerating fibers could be found piercing the corpus callosum. It is evident that in the cat this study cannot support the existence of hippocampal afferents in the fornix.

The Hippocampal Commissures

von Kolliker (52), in his studies on the rabbit, describes a dorsal and a ventral psalterium. Ramon y Cajal (72), in normal rodents, indicated a dorsal psalterium connecting the temporal lobe of one side with the contralateral hippocampus. He also observed a ventral psalterium which was an inter-hippocampal path but noted that some of these fibers went forward into the septum. Ramon y Cajal further designates a group of fibers crossing above the ventral psalterium carrying fibers from the supracallosal part of Ammon's horn. Ariëns Kappers,

Huber, and Crosby (10) indicate that the posterior psalterium lies between the posterior pillars of the fornix and carries inter-hippocampal fibers while an anterior psalterium in the region of the anterior commissure carries fibers from the hippocampus to the opposite mammillary body.

McLardy (61), using the Glees technique in monkeys, described an "anterior psalterium" at the junction of the body and pillar of the fornix. He indicated that fibers from the isocortex of the temporal pole crossed in this region in their path toward the septum. Sprague and Meyer (78), using retrograde cell degeneration methods, noted that the ventral hippocampal commissure was not a pathway for decussating projection fibers but was entirely inter-hippocampal in its connections.

Powell and Cowan (69) could trace no fibers beyond the ventral hippocampal commissure in rats with lesions of the fimbria and fornix. They did note in monkeys some fibers crossing between the two subcallosal fornices which persisted after complete unilateral fimbrial section. Daitz and Powell (22) transected the fimbria of one side and saw no degeneration of the opposite fimbria so they concluded that no inter-hippocampal fibers existed.

Electrophysiologic experiments in the monkey by Ajmone-Marsan and Stoll (3) indicated a bilateral connection between the septum and temporal pole which is carried in the fornix. Simpson (76), working with monkeys, noted bilateral degeneration in the ventromedial hypothalamus with lesions of the fornix and hippocampus.

In this study of the cat several points can be noted with reference to the hippocampal commissure. The commissure in this animal can be divided into a dorsal hippocampal commissure and a ventral hippocampal commissure as described in an earlier section.

In lesions involving the antero-dorsal hippocampus of one side, degeneration is seen in the dorsal hippocampal commissure (cats K-11 and DW-94). These fibers can be followed into the superior alveus of the antero-dorsal hippocampus of the opposite side and degenerating terminals are seen around the pyramidal cells of the pyramidal and polymorphic layers. In cat DW-77 the lesion involved the superior fornix of that side and resulted in no degeneration of the dorsal hippocampal commissure. In cat DW-93 a bilateral lesion of the superior part of the antero-dorsal hippocampus was made. This resulted in bilateral degeneration in the polymorphic and pyramidal layers

of the hippocampus ahead of the lesion and complete loss of the dorsal hippocampal commissure. Lesions of the ventro-postero-lateral hippocampus or of the lateral fornix cause no degeneration in the dorsal hippocampal commissure (cat K-15).

It would appear from these findings that fibers arising in the antero-dorsal hippocampus pass forward as the lateral division of the medial fornix. Some of these fibers cross in the dorsal hippocampal commissure to the opposite antero-dorsal hippocampus. Neither the superior fornix or the lateral fornix takes part in this commissure. Some of these crossed fibers appear to go forward on the opposite side and join the superior fornix in the descending column to terminate in the mammillary body.

The ventral hippocampal commissure appears degenerated when any part of the lateral fornix is involved in a lesion (cats K-15, K-9, DW-77, DW-86, DW-90). Lesions of the antero-dorsal hippocampus elicit no degeneration of this commissure.

The more dorsal lesions of the ventro-postero-lateral hippocampus appear to have little effect on the ventral hippocampal commissure (DW-88), while in cats K-15 and K-9, with small lesions of the more ventral parts of the hippocampus, degeneration of

the lateral end of the lateral fornix results in marked degeneration occurring in the commissure. In a unilateral lesion of the commissure (K-16) no degeneration can be found posterior to the lesion in the lateral fornix or hippocampus of the opposite side. Anterior to the lesion on the opposite side degeneration was noted in the pre and post commissural septum, the lateral preoptic area, and the tuberculum olfactorium. In lesions of the medial fornix with complete degeneration of the column of the fornix no degeneration was noted in the ventral hippocampal commissure.

In summary the ventral hippocampal commissure of the cat is derived from fibers arising in the ventro-postero-lateral hippocampus which run in the lateral fornix. The fibers to the opposite side all project forward in the contralateral fornix and none are inter-hippocampal in nature.

Hippocampo-Mammillary Tract

Forel (26), as quoted from Nauta, indicated that the fornix formed a loop in the mammillary body and continued on in the mammillothalamic tract to the anterior thalamus. In his studies on the mouse Ramon y Cajal (72) noted that the part of the fornix

that descended in the hypothalamus was distinctly separate from that which entered the commissure. He indicated that the latter group of fibers originated from the more superior regions of the hippocampus, was totally post commissural, and the terminals were in the medial mammillary nucleus. The termination of this tract in the medial mammillary nucleus has also been described in normal and experimental material by several investigators (10, 78, 69) while Allen (6), Guillery (37), and Nauta (64) have in addition described a few fibers to the lateral mammillary nucleus.

Most of the above authors considered this projection to arise from both the medial and lateral fornix. Nauta (64), in his studies on the rat, noted abundant degeneration in the column of the fornix with lesions of the caudal hippocampus. Valenstein and Nauta (86) in the guinea pig, cat, and monkey achieved similar results. It was interesting to note in the latter study that guinea pig case GPS 3 with a lesion involving the entire septum and column of the fornix on one side and just the medial part of the superior fornix on the other, shows an equal amount of degeneration in the column of the fornix and mammillary body of the two sides. These

workers also noted that many fibers from the superior fornix terminated in the pre commissural septum. Powell and Cowan (69), in their studies on the rat, rabbit, and monkey, noted that two thirds of the descending column of the fornix remained intact following lesions of the fimbria which spared the dorsal fornix. Sprague and Mayer (78), using the silver technique in rabbits, noted no degeneration in the mammillary body on sectioning the superior fornix.

Guillery (37) noted that the mammillary fibers of the fornix arise in the dorsal fold of the alveus and travel in the superior fornix.

Powell et al (1957) in electrophysiologic studies on the cat noted that following stimulation of the antero-dorsal hippocampus the greatest activity was recorded in the mammillary body, while stimulation of the ventro-postero-lateral hippocampus did not elicit activity in this area.

In the present experimental studies the lesions which involve only the ventro-postero-lateral hippocampus with resultant degeneration in the lateral fornix and ventral hippocampal commissure show no degeneration in the column of the fornix or mammillary body (cats K-15, K-9). Cat DW-93 with a lesion bilaterally in the antero-dorsal

hippocampus shows degeneration of the dorsal hippocampal commissure and the lateral division of the medial fornix bilaterally. These fibers can be seen joining the undegenerated superior fornix and passing to the mammillary body where a small amount of terminal degeneration is present. No degeneration occurred in the pre or post commissural septum.

Cat DW-94 on one side had a lesion of the entire medial fornix at the rostral end of the antero-dorsal hippocampus but none of the lateral fornix. Complete loss of the column of the fornix occurs exclusive of a few fibers which join it in the septal region and will be described later in the paper. It would appear that in the cat the fibers from the antero-dorsal hippocampus pass into the medial fornix and descend as the column of the fornix to the mammillary body. No contribution from the lateral fornix enters the mammillary body. No fibers from the medial fornix, following lesions which involved them, were noted to enter the pre commissural septum and it is apparent in these studies that this is an entirely post commissural tract.

Mammillary Decussation of the Fornix

Fibers decussating above the mammillary body to the medial mammillary nucleus of the opposite side were

described by Edinger and Wallenberg (24) in the rabbit. These findings were confirmed by Nauta in the rat (64) and by Valenstein and Nauta in the cat (86). They thought that this was quite a large connection in the cat. These findings were also supported by Guillery (37) in the rat. Ariëns Kappers, Huber, and Crosby (10) noted this decussation and they indicated that these fibers went to unknown terminations in the mesencephalon. This decussation was not seen by Simpson (76) in the monkey, by Sprague and Meyer (78) in the rabbit, nor by Allen (6) in the dog.

In this study degenerated fibers could be seen crossing above the mammillary body in every lesion that involved the medial fornix. However, no conclusion could be drawn as to the termination of these fibers, except that it appeared to be in the overlying tegmental area.

Tegmental Overshoot of the Fornix

Ramon y Cajal (72) in his description of the fornix indicated that in the mouse the largest segment of the fornix bypassed the mammillary body after giving a few fibers to it and travelled on into the midbrain tegmentum and pons where he was unable to follow it further. Sprague and Meyer (78) were able to follow these fibers to the region of the oculomotor nucleus

but were unable to determine their termination point. They were using the silver technique in rabbits. Guillery (37) agreed with these findings using the Nauta technique in rats.

Nauta (64) and Valenstein and Nauta (86) noted a fornix bundle bypassing the mammillary body in the guinea pig, rat, cat, and the monkey. They indicated that these fibers proceed mainly to the central grey of the rostral midbrain and that some of the fibers appeared to decussate but most did not. They noted also in the studies on the guinea pig and monkey that some of these fibers went to the subthalamic nucleus.

Rioch (73) was unable to see these structures in his studies on normal dogs and cats, nor was Simpson (76) able to find them in experimental studies on monkeys. In the present study fibers could not be followed beyond the level of the mammillary bodies in any of the cats. Degenerated terminals and fibers were noted in the supra-mammillary region of the tegmentum below the subthalamico-tegmental tract but none of these could be followed in a caudal direction.

Hippocampo-Septal Projection

Ramon y Cajal (72) noted that fimbrial fibers destined for the ventral hippocampal commissure as well as those destined for the column of fornix give

rise to collaterals which terminate in the septal nuclei. He indicated that many of these fibers were not collaterals but rather direct projection fibers. He concludes that this is the reason for the rather marked diminution in size of the fornix as it descends behind the anterior commissure. These fibers were also noted by Ariëns Kappers, Huber, and Crosby (10). Fox (28), using cats, made lesions in the most anterior inferior part of the hippocampus next to the amygdalla. Using the Marchi method he traced degenerated fibers into the lateral extremity of the fornix and noted their terminations in the lateral septal nucleus and nucleus accumbens. Sprague and Meyer (78), using a silver technique in rabbits, noted that the pre commissural fornix terminated in the medial and lateral septal nuclei, as well as in the nucleus accumbens. They achieved these results with lesions of the fimbria.

Simpson (76) from fiber counts in the monkey indicated that the pre commissural projection of the fornix was greater in size than that to the mammillary body. However, following lesions of the fornix or hippocampus only moderate degeneration was found and it was limited to the lateral septal nucleus. Similar findings were reported by Daitz and Powell (22) in the rat, rabbit, and monkey using retrograde cell studies.

Powell and Cowan (69) noted, in protargol preparations of the rat, rabbit, and monkey, that lesions of the fimbria alone caused degeneration of all pre commissural fibers to the septum as well as of some fibers which join the column of the fornix. Powell, Guillery, and Cowan (70), in fiber counts, noted that in the monkey, human, and probably also in the rat, rabbit, and cat, the fornix decreases to half its former size as it passes through the septum.

Nauta (64), in rats, noted degeneration in all of the septal cell groups including the nucleus of the diagonal band. It was indicated that these fibers came from both the pre and post commissural fornix.

Electrophysiologic studies in monkeys (3) and in cats (79) have indicated connections between the temporal pole and the septum in these animals.

The studies reported here indicate that no fibers from the medial fornix or antero-dorsal hippocampus project to the septum. Cat DW-94, and DW-93 with lesions of the superior fornix and antero-dorsal hippocampus show degeneration in the column of the fornix but none in the septal region.

Unilateral lesions involving the ventro-postero-lateral hippocampus result in bilateral degeneration of both the medial and lateral septal nuclei pre and

post commissural (K-9, K-15, DW-77). The degeneration in the septum is much more marked on the side of the lesion. It can be seen from these studies that there is some topographic localization of the terminals within the septum. Lesions in the more ventral parts of the ventro-postero-lateral hippocampus degenerate fibers of the more lateral part of the fornix and result in terminal degeneration in the more lateral parts of the septum while those from the superior ventro-postero-lateral hippocampus result in terminal degeneration within the medial septal nucleus and the medial part of the lateral septal nucleus (DW-77). None of the fornix or hippocampal lesions show degeneration in the nucleus accumbens or nucleus of diagonal band. Unilateral lesions of the ventral hippocampal commissure and of components of the lateral fornix entering it, result in the same pattern of degeneration noted in the lesions of the ventro-postero-lateral hippocampus (cat K-16).

In cat K-14 a lesion which was produced in the superior supra-commissural septum in front of the ventral hippocampal commissure resulted in terminal degeneration in the medial and lateral pre commissural septum on the ipsilateral side.

Hippocampo-Habenular Connections

In his studies on the rat, Gurdjian (39) described the medial cortico-habenular tract arising from the lateral side of the column of the fornix in the region of the anterior commissure and bending dorsally to enter the stria medullaris. In studies of a variety of animals several investigators have described this tract (73, 91, 44, 10, 59). Gerebtzoff (30) in Marchi experiments noted this tract in guinea pigs and rabbits.

Ramon y Cajal (72), in his normal preparation of the mouse, was unable to demonstrate this tract. Sprague and Meyer (78), in experimental studies on rabbit using silver techniques, could find no fornix fibers to the habenula. Numerous other workers have denied the existance of this tract in experimental material from many species (64, 76, 69, 37, 38, 86).

In the studies presented here lesions were placed in nearly every area of the hippocampus and fornix (K-15, DW-93, DW-88) without resultant degeneration in the stria medullaris. It was only when the fornix was coagulated along with the post commissural septum that degeneration was noted in the stria medullaris.

Hippocampo-preoptic Projection

Fibers passing from the pre commissural fornix

to the lateral preoptic region via the medial forebrain bundle have been described by Nauta (64) in the rat, and in the guinea pig, cat, and monkey by Valenstein and Nauta (86). This group of fibers was denied by Sprague and Meyer (78) in their studies of the rabbit and by Daitz and Powell (22) in the rat, rabbit, and monkey.

The present studies would indicate that the lateral fornix sends terminals to the lateral preoptic area. In cats with lesions of the antero-dorsal hippocampus or medial fornix no degeneration was noted in the preoptic area (DW-93 and DW-94). Those animals with lesions of the ventro-postero-lateral hippocampus, lateral fornix, or ventral hippocampal commissure exhibited bilateral degeneration in the lateral preoptic area. This was always more marked on the side of the lesion, (K-15, K-9, K-16). It was interesting that in those cats with lesions of the stria terminalis degeneration was noted also in the medial preoptic area (DW-146).

Hippocampo-Hypothalamic Projection

Ramon y Cajal (72) described two groups of fibers leaving the fornix to enter the hypothalamus. The first he described as the "cornual band of the tuber cinereum" which separates from the medial side of the pillar of the fornix and passes to the tuber cinereum. The other

he describes as a collateral from the descending column of the fornix as it passes through the hypothalamus. Ariëns Kappers, Huber, and Crosby (10), in normal material, describe a medial cortico-hypothalamic tract from the fornix to the tuber cinereum.

Allen (6), in Marchi studies of the dog, noted dorsal and ventral branching of the descending column of the fornix but could not follow these fibers to their termination. Several experimental studies have shown fibers from the fornix to the dorsal and ventral periventricular areas and the perifornical area (76, 64, 86). These fibers were identified in the rat and guinea pig by Valenstein and Nauta (86), but could not be found in the cat or monkey. In all of these animals the aforementioned authors noted fibers to the lateral hypothalamus emanating in the caudal third of the hippocampus. They were supported in this finding by the electrophysiologic studies in the cat of Powell et al. (68).

Powell and Cowan (69) noted degeneration in the medial cortico-hypothalamic tract following lesions of the fimbria and dorsal fornix in the rat. They attributed this to the fibers of the column that are derived from the fimbria. Guillery (37) noted a similar pattern of degeneration in the hypothalamus.

Sprague and Meyer (78) denied any contribution of the fornix to the hypothalamus except for fibers which terminate in the perifornical area.

The present study would indicate that no direct fibers from the hippocampus or fornix pass to the hypothalamus either as a medial cortico-hypothalamic tract or in the form of fascicles from the descending column of the fornix. It appears from these studies that the fibers of the medial cortico-hypothalamic tract may well be the septo-mammillary tract noted in these studies on the cat. These fibers will be described in a later section.

Hippocampo-Thalamic Projection

This pathway was originally described by Gudden (56) in the normal rabbit. Vogt (87) followed large numbers of fornix fibers to what were probably the anteroventral and anteromedian nuclei of the thalamus. He indicated that these originate entirely in the septal region. Ramon y Cajal (72) describes a group of collaterals separating from the superior aspect of the fornix, after it passes behind the anterior commissure, which ascend into the anterior thalamic area.

Nauta (64) noted that in the rat this tract

begins in the hippocampus and passes to the anterior part of the post commissural fornix, terminating in both the anteroventral and anteromedial thalamic nuclei but predominantly in the former. These results were confirmed for the rat by Guillery (37) who indicated that this projection was bilateral via the commissure of the anteromedian nucleus. Valenstein and Nauta (86) indicated a similar distribution of terminals in the monkey, but in the cat and guinea pig they noted terminals in the intralaminar cell group between the anterior and ventral anterior thalamic nuclei.

Hippocampal projections to the thalamus were denied by Daitz and Powell (22) in experimental studies on the rat, rabbit, and monkey. This connection, furthermore, was not noted by Sprague and Meyer (73) in the rabbit or Simpson (76) in the monkey.

The indication from the present study was that no projection occurs from the hippocampus to any part of the thalamus. A thorough search of the thalamus in all of the cats with lesions of the hippocampus or fornix affords no indication of degeneration in any of the anterior thalamic nuclei. In one animal, degeneration of the posterior thalamus was noted but these fibers could be traced to a large lesion of the parietal cortex and pulvinar (DW-88). In cat DW-146

a lesion just lateral to the post commissural fornix and septum resulted in massive degeneration of the anterior thalamic nuclei. This could be attributed to the destruction of fibers in the inferior thalamic peduncle and mammillothalamic tract.

Hippocampo-Olfactory Tubercle Projection

Fox (27) described fibers from the fornix coursing through the lateral septum and running with the diagonal band to the olfactory tubercle in normal cats. Valenstein and Nauta (86) note that in lesions of the fornix some of the degenerated fibers extended into the diagonal band.

In the present study lesions of the antero-dorsal hippocampus or medial fornix result in no degeneration within the olfactory tubercle. However in lesions which involve the ventro-postero-lateral hippocampus, the lateral fornix, or the hippocampal commissure unilaterally, a few degenerated fibers could be followed through the septum. At the base of the septum they curve medially around the nucleus accumbens and then laterally above the diagonal band to terminate in the islands of Calleja of the olfactory tubercle. This occurred bilaterally but was more marked on the side of the lesion. Lesions of the septum in front of the

ventral hippocampal commissure result in degeneration of the homolateral side only.

Septo-Hippocampal Pathways

These fibers have been discussed in detail in a preceding section of this paper. Fibers arising in the septum and passing toward the hippocampus or to the temporal pole via the fornix have been described by Morin (63), Sprague and Meyer (78), Daitz and Powell (22), and McLardy (60, 61). They have been supported by the electrophysiologic studies of Stoll, Ajmone-Marsan and Jasper (79), Ajmone-Marsan and Stoll (3), Green and Arduini (33), and Votaw (88, 89).

As mentioned previously, lesions of the septum and fornix resulted in no degeneration of the fornix or hippocampus caudal to the lesion. It would appear then that if these connections exist as suggested by electrophysiologic methods they are mediated by some tract other than the fornix.

Septo-Habenular Projection

Fibers projecting from the septum to the habenula via the stria medullaris have been described in normal material by several investigators. These studies by Loo (53) in the opossum, Ariëns Kappers, Huber, and

Crosby (10) in mammals, Rioch (73) in carnivores, and Marburg (59) in humans, have variously described this tract as originating in the medial septal nucleus, lateral septal nucleus, nucleus of the diagonal band, or the nucleus of the anterior commissure. Fox (27), in the normal cat, described the origin of this projection in the nucleus septo-fimbrialis which is the lateral post commissural septal nucleus of this study.

Nauta (64) destroyed the supra-commissural septum in rats and noted degeneration in the stria medullaris and medial habenular nucleus bilaterally. Valenstein and Nauta (86) destroyed the post commissural septum of the guinea pig, cat, and monkey and noted degeneration of the ipsilateral stria medullaris and in the medial habenular nucleus bilaterally. Their lesions of the hippocampus had resulted in no degeneration of the stria medullaris or habenula and it was suggested that the medial cortico-habenular tract which had been described by many investigators was actually a septo-habenular tract.

In this study lesions of the post commissural septum resulted in homolateral degeneration of the stria medullaris and lateral habenular nucleus. Degenerated fibers could be followed across the habenular commissure to a termination in the

contralateral medial habenular nucleus, however, the degeneration was far greater in extent on the ipsilateral side (cats DW-87X, DW-89, K-14, and K-16). Lesions of the fornix or hippocampus without involvement of the septum as previously mentioned resulted in no degeneration in these areas. Lesions of the pre commissural septum without involvement of the post commissural septum did not show degeneration of the stria medullaris or in the habenula (cats K-5, K-18, and K-165). It would appear that the stria medullaris arises from the post commissural septum in the region often called the nucleus septo-fimbrialis.

Septo-Tubercular Projection

In normal material Ariëns Kappers, Huber, and Crosby (10) in mammals, Fox (27) in cats, and Johnson (45) in the mole, have described fibers from the pre commissural septum running dorso-ventrally to the olfactory tubercle.

In the preparations presented here (cats K-5, K-18, and DW-165), degeneration was noted in the olfactory tubercle following lesions of the pre commissural septum, however these lesions also involved the pre commissural fornix fibers some of which were previously noted entering the olfactory

tubercle. Because of this we would be unable to determine if degeneration in these studies was due to the lesion in the pre commissural fornix or septum. No difference in degree of degeneration in the olfactory tubercle was noted in these two types of lesion.

Septo-Hypothalamic Projection

Morin (63), from his Marchi studies on the guinea pig, noted degenerated fibers joining the post commissural descending column of the fornix following lesions of the pre commissural septum. Powell and Cowan (69) studying the rat, rabbit, and monkey noted that even with complete bilateral section of the fimbria and fornix an undegenerated group of fibers on either side of the midline joined the descending column of the fornix. Powell et al. (68) stimulated the septum and evoked no response in the mammillary body and from this concluded that such a pathway does not exist.

In the studies presented here a distinct group of fibers was seen in normal material arching dorso-medially over the pillar of the fornix from the post commissural septum and continuing with the descending column of the fornix (Fig. 53). These fibers are of a smaller diameter than those of the majority of the fibers of the fornix and are comparable to the fibers

of the stria medullaris. In animals with lesions of the post commissural septum (cats DW-89, DW-87X, K-14 K-16) these fibers were degenerated and could be followed as they joined the fornix, but could not be followed to their destination as in all of these lesions the pillar of the fornix was incidentally involved. It was noted that these fibers arise in the same area from which the stria medullaris originates. In lesions in which the fornix was degenerated prior to entering the septum, the undegenerated fibers from the post commissural septum could be followed into the degenerated fornix column (cat DW-90). Lesions of the pre commissural septum did not result in degeneration of these fibers (cat DW-165, K-18, K-5).

Fibers projecting from the septum to the hypothalamus via the medial forebrain bundle have been described by several authors in normal material from a variety of animals (45, 10, 27, 73).

No evidence of degeneration in any hypothalamic nuclei or in the medial forebrain bundle was seen following discrete septal lesions in this study. However, the medial forebrain bundle of the cat is difficult to follow and degeneration of its fibers would be difficult to evaluate.

The Stria Medullaris

As mentioned previously in the description of the experimental material the stria medullaris appears to arise from the lateral post commissural septum. It has been shown in this paper that in the cat no hippocampo-habenular tract could be found.

Fibers of the stria terminalis arising from the amygdalla which enter the stria medullaris and project to the habenula have been described in normal material by numerous investigators (10, 27, 44, 45, 91). On the basis of information from his experimental studies in cats, Fox (28) rescinded his previous contention adduced from normal material and said that cutting the stria terminalis resulted in no degeneration of the habenula.

In cat DW-146 and in a series of animals studied but not reported in this paper, lesions of the stria terminalis resulted in no degeneration in the habenula.

An even more striking finding in the above mentioned cat was that a lesion of the inferior thalamic peduncle, which nearly isolated the origin of the stria medullaris from the thalamus and hypothalamus, resulted in no degeneration in the stria medullaris (Fig. 39). At the same time lesions of the post commissural septum in other animals resulted in complete degeneration of

the stria medullaris. It would appear from these studies that the post commissural septum is the sole contributor to the stria medullaris in the cat.

## SUMMARY AND CONCLUSIONS

The fiber connections of the fornix and septum have been studied in the cat brain by the experimental method. Lesions were produced in various sectors of the hippocampus, fornix, septum, and paraseptal areas. Following a survival period of six to thirteen days the animals were sacrificed and sections were prepared for histologic study by the intensified protargol method.

Analysis of histologic preparations yielded the following results:

1. On the basis of origin and termination the fornix has been divided into a medial portion arising from the antero-dorsal hippocampus and terminating primarily in the hypothalamus, and a lateral fornix arising from the ventro-postero-lateral hippocampus and terminating principally in the septum. The medial fornix is further subdivided into a medial division or superior fornix, and a lateral division.

2. Lesions of the antero-dorsal hippocampus produce degeneration in the medial fornix. A lesion of the superior fornix results in degeneration of the majority of the fibers in the column of the fornix, and terminal neuropil of the medial mammillary nucleus and supramammillary area. The termination of the medial fornix is entirely post commissural. A lesion

of the lateral division of the medial fornix results in degeneration of the fibers in the dorsal hippocampal commissure and terminal degeneration in the opposite antero-dorsal hippocampus as well as a small amount of degeneration in the column of the fornix, mammillary body, and supramammillary area.

3. Lesions of the ventro-postero-lateral hippocampus result in homolateral degeneration of the lateral fornix and the ventral hippocampal commissure; with degeneration of the terminal neuropil of the medial and lateral pre and post commissural septal nuclei, partial degeneration of the terminal afferents of the lateral preoptic area of the hypothalamus, and degeneration of a small component to the tuberculum olfactorium of the same side. A small contralateral degeneration of terminals occurred in corresponding areas of the septum, preoptic area, and tuberculum olfactorium derived from degenerated fibers of the ventral hippocampal commissure. A topographical organization is suggested, in that, the more ventral lesions of the ventro-postero-lateral hippocampus result in degeneration of the lateral areas of the fornix, ventral portions of the ventral hippocampal commissure, and terminal degeneration in the more lateral areas of the septum. No degeneration was

produced in the contralateral hippocampus.

4. Lesions of the fornix in any position show no degeneration posterior to the lesion. The fornix in the cat is entirely an efferent tract from the hippocampus.

5. The dorsal hippocampal commissure is interhippocampal and carries fibers from only the lateral division of the medial fornix. There is a small projection element through this commissure to the column of the fornix on the contralateral side.

6. The ventral hippocampal commissure is made up entirely of fibers from the lateral fornix and projects only to the contralateral lateral preoptic area, septum, and olfactory tubercle. No projection to the contralateral hippocampus occurs here.

7. No fibers of the column of the fornix could be seen caudal to the mammillary body in lesions of the medial fornix or post commissural septum.

8. Lesions of the fornix result in no degeneration of the diagonal band, nucleus of the diagonal band, and nucleus accumbens.

9. Lesions of the hippocampus and fornix result in no degeneration of the stria medullaris, nor areas of the hypothalamus not definitely mentioned above. No degeneration was noted in the thalamus in these

lesions.

10. Lesions of the post commissural septum result in complete degeneration of the stria medullaris and bilateral degeneration of afferent terminals to the lateral habenular nucleus. Degeneration is also noted in a group of fibers joining the fornix on its medial side in these lesions. The post commissural septum is the origin of the stria medullaris and of a septo-mammillary tract.

11. Lesions of the pre commissural septum result in degeneration of terminals and fibers in the areas of the medial and lateral septal nuclei that are not involved in the lesion as well as in the olfactory tubercle. Degeneration in these areas also occurs following lesions of the pre commissural fornix which is necessarily also involved in this lesion. A consequence of these lesions not noted in lesions of the lateral fornix was the degeneration of fibers in the diagonal band and of terminals in the nucleus of the diagonal band. These lesions result in no additional degeneration of the hypothalamus, fornix, or hippocampus.

12. Lesions of the stria terminalis produce no degeneration in the stria medullaris.

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# TABLE OF ABBREVIATIONS

| | |
|---|---|
| AC | Anterior Commissure |
| Acc | Nucleus Accumbens |
| AD | Anterodorsal Thalamic Nucleus |
| AdH | Antero-dorsal Hippocampus |
| AV | Anteroventral Nucleus of the Thalamus |
| CC | Corpus Callosum |
| Cd | Caudate Nucleus |
| Ch | Optic Chiasm |
| DBB | Diagonal Band of Broca |
| DHC | Dorsal Hippocampal Commissure |
| Fb | Fimbria |
| FP | Lateral Fornix |
| Fx | Column of the Fornix |
| H | Habenular Nucleus |
| Ha | Anterior Hypothalamic Nucleus |
| IC | Internal Capsule |
| ITP | Inferior Thalamic Peduncle |
| LD | Dorsolateral Nucleus of Thalamus |
| LP | Lateral Posterior Nucleus of Thalamus |
| LS | Lateral Septal Nucleus-pre commissural |
| Mm | Medial Mammillary Nucleus |
| MS | Medial Septal Nucleus-pre commissural |

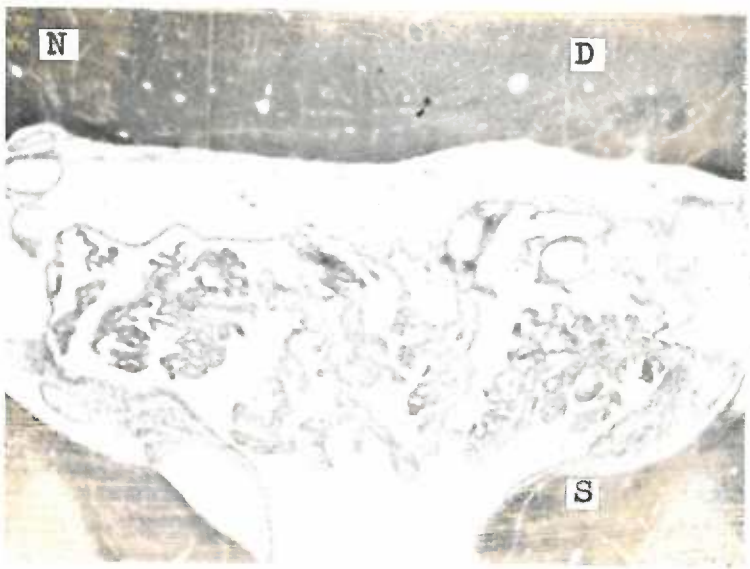
| | |
|---|---|
| nDBB | Nucleus of the Diagonal Band of Broca |
| OT | Olfactory Tubercle |
| PrO | Preoptic Area of Hypothalamus |
| PsS | Post Commissural Septum |
| Pul | Pulvinar |
| Put | Putamen |
| S | Stria Medullaris Thalami |
| SF | Superior Fornix |
| St | Stria Terminalis |
| VHC | Ventral Hippocampal Commissure |
| VplH | Ventro-postero-lateral Hippocampus |

PLATE I.

Figure 14. Cat DW-90. Photomicrograph showing degenerated fornix (D) of one side and normal fornix (N) of the opposite side following a lesion of the antero-dorsal hippocampus and the fimbria of the ventro-postero-lateral hippocampus. Note presence of the undegenerated stria medullaris (S) bilaterally. Low power. Intensified protargol stain.

Figure 15. Cat DW-90. Photomicrograph of the lateral septal nucleus showing degeneration of fibers and terminals (D) following a unilateral lesion of the fibers from the entire hippocampus. Oil immersion. Intensified protargol stain.

14.

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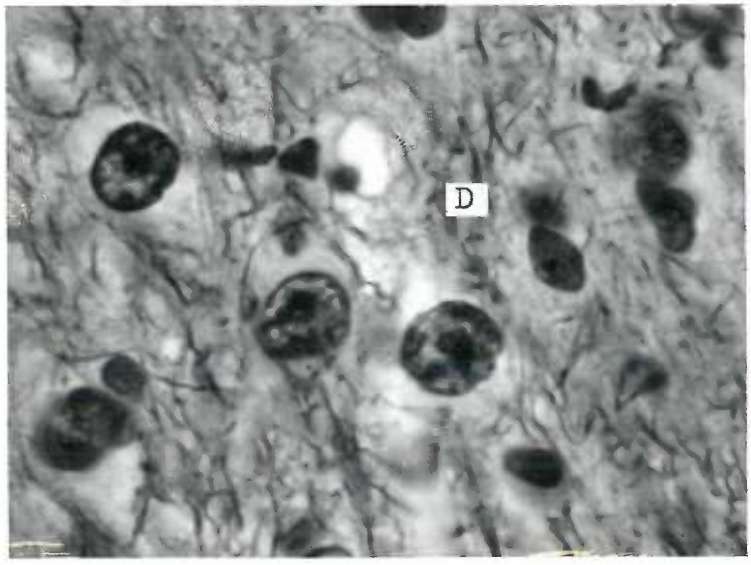
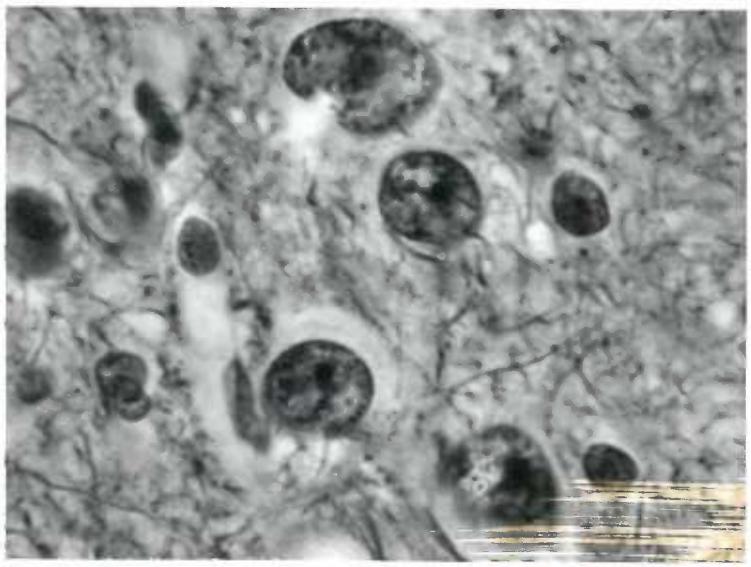


PLATE II.

Figure 16. Cat DW-90. Photomicrograph of the lateral septal nucleus of the side opposite a lesion of the complete hippocampal outflow. Note that degeneration of fibers and terminals is less marked than that in Figure 15. Oil immersion. Intensified protargol stain.

Figure 17. Cat DW-90. Photomicrograph of the medial septal nucleus on the side of the lesion described in Figure 15. Note slight degeneration of fibers in this area (D). Oil immersion. Intensified protargol stain.

16.



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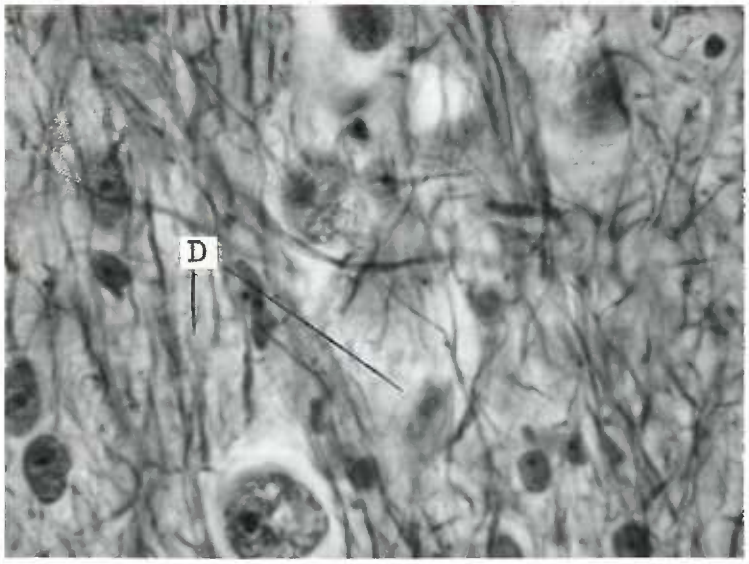
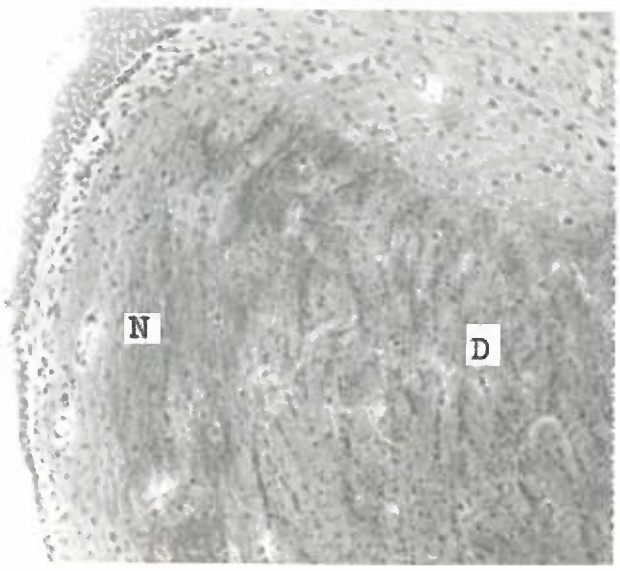


PLATE III.

Figure 18. Cat DW-90. Photomicrograph of the degenerated descending column of the fornix (D) being joined on the medial side by normal fibers (N) from the post commissural septum. Low power. Intensified protargol stain.

Figure 19. Cat DW-87X. Photomicrograph showing degenerated fibers from the post commissural septum (D) joining the degenerated fornix column (F) following destruction of the post commissural septum and fornix. Low power. Intensified protargol stain.

18.

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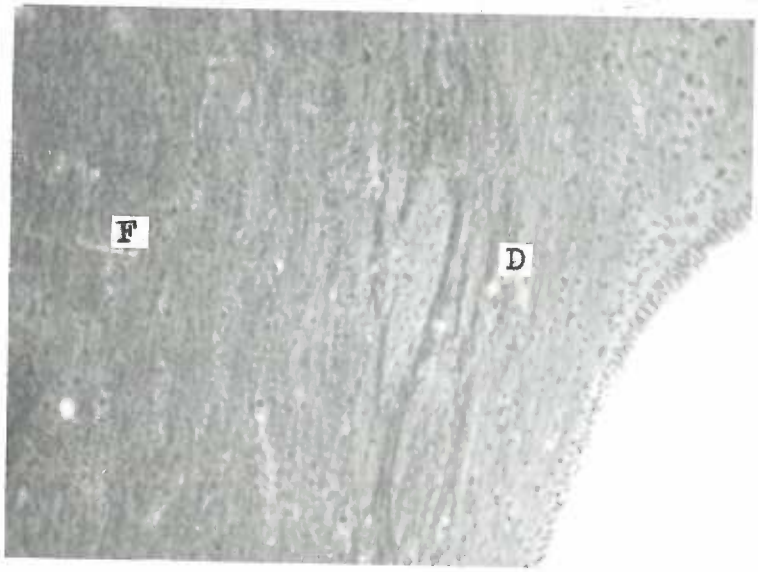
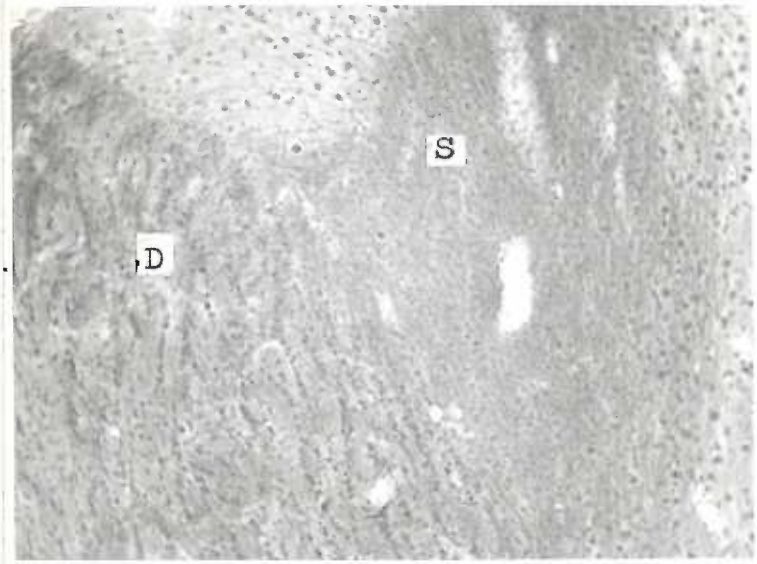


PLATE IV.

Figure 20. Cat DW-90. Photomicrograph showing the undegenerated stria medullaris (S) arising in the post commissural septum lateral to the degenerated column of the fornix (D). Lesion involved the entire hippocampal outflow in this side. Low power. Intensified protargol stain.

Figure 21. Cat DW-90. Photomicrograph showing degeneration and clearing of fibers and terminals in the lateral preoptic area following the lesion described in Figure 20. Oil immersion. Intensified protargol stain.

20.

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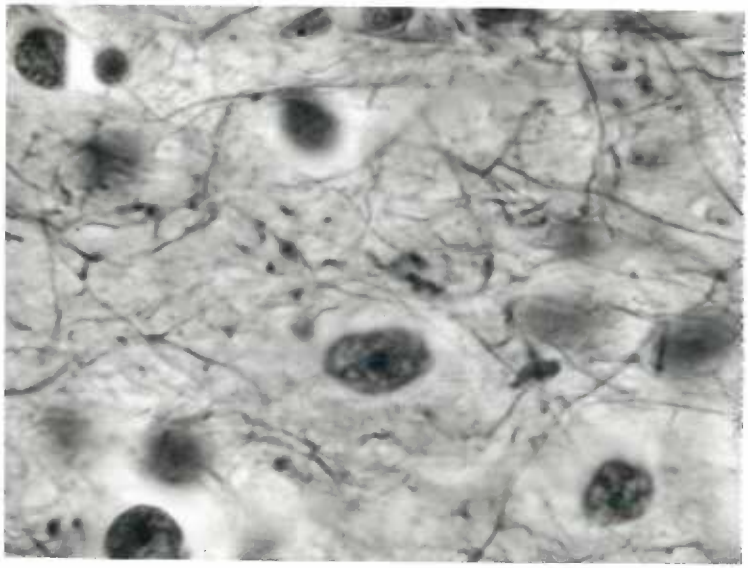
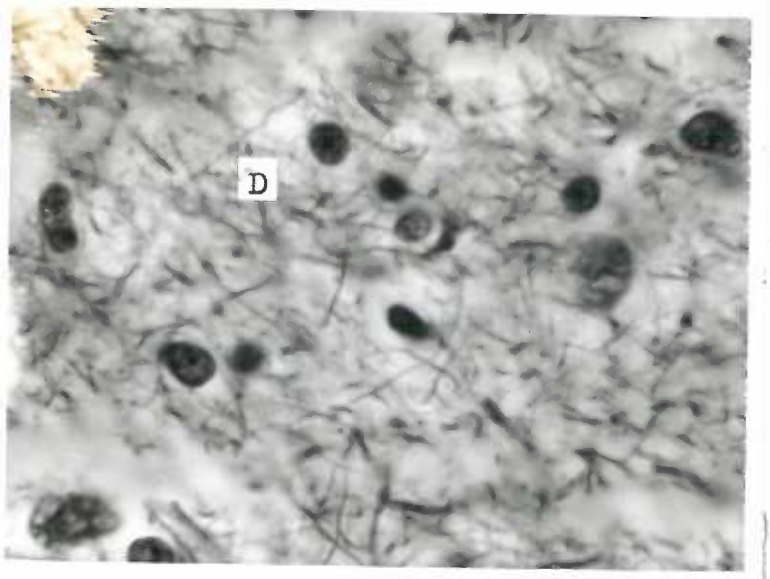


PLATE V.

Figure 22. Cat DW-90. Photomicrograph showing degeneration of fibers (D) passing above the diagonal band toward the olfactory tubercle in a lesion of the entire outflow of the hippocampus. Note loss of fibers compared with Figure 23. Oil immersion. Intensified protargol stain.

Figure 23. Cat DW-93. Photomicrograph of normal fibers (F) running above the diagonal band in an animal with no lesion of the ventro-postero-lateral hippocampus or lateral fornix. Oil immersion. Intensified protargol stain.

22.

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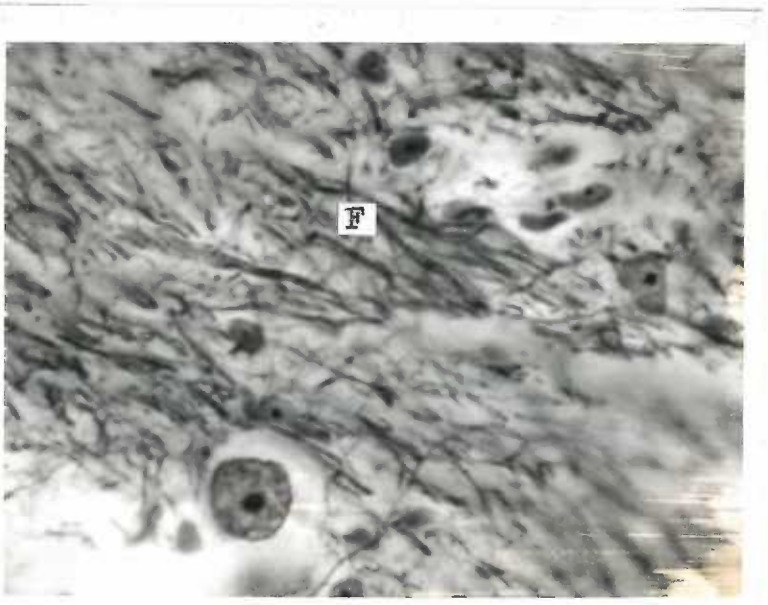
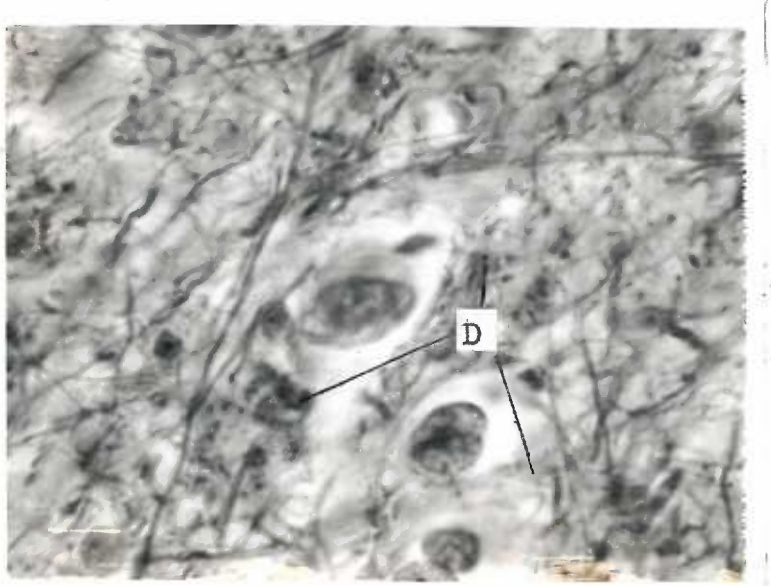


PLATE VI.

Figure 24. Cat DW-90. Photomicrograph showing degeneration of terminals (D) around cells of the olfactory tubercle in a lesion of the entire outflow of the homolateral hippocampus. Oil immersion. Intensified protargol stain.

Figure 25. Cat DW-93. Photomicrograph showing degenerated fibers (D) in the dorsal hippocampal commissure. Bilateral lesion of the antero-dorsal hippocampus. Low power. Intensified protargol stain.

24.

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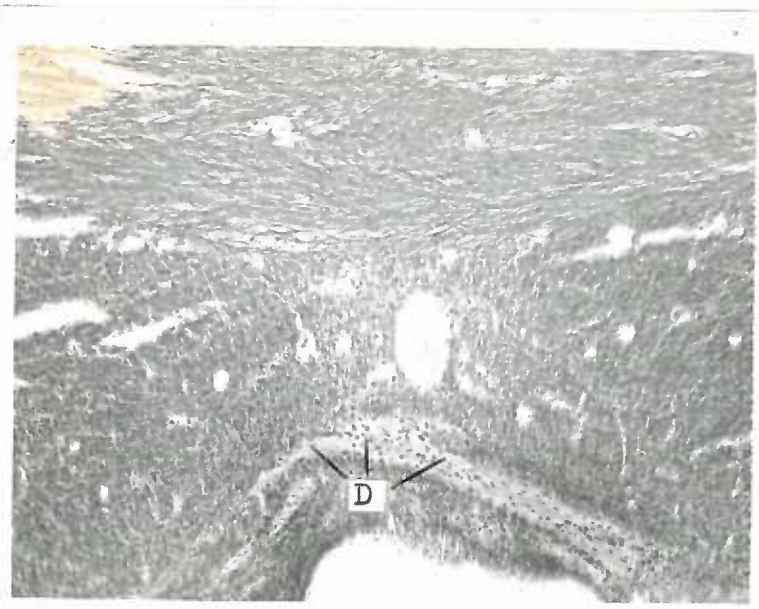
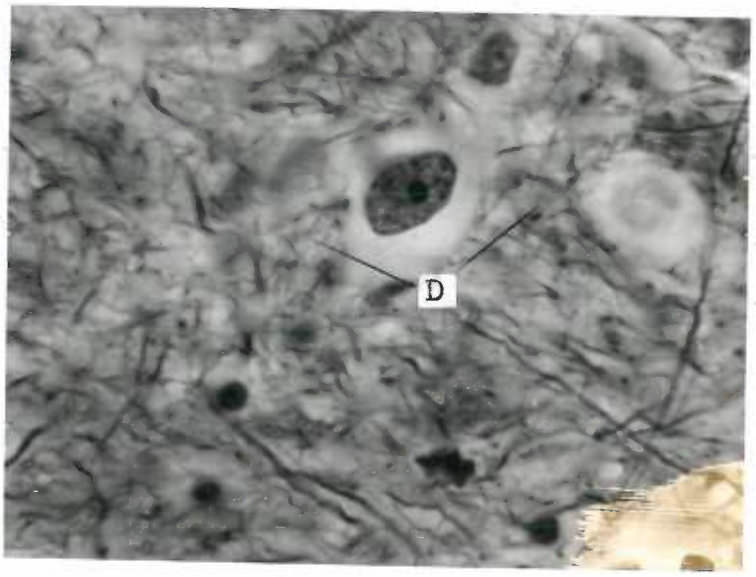


PLATE VII.

Figure 26. Cat K-15. Photomicrograph showing moderate degeneration of terminals around cells of the olfactory tubercle (D). Lesion is of the ventral hippocampal commissure and lateral fornix. Oil immersion. Intensified protargol stain.

Figure 27. Cat K-15. Photomicrograph showing degeneration of fibers (F) entering the lateral septal nucleus. Note considerable clearing of fibers. Lesion of ventro-postero-lateral hippocampus. Oil immersion. Intensified protargol stain.

26.

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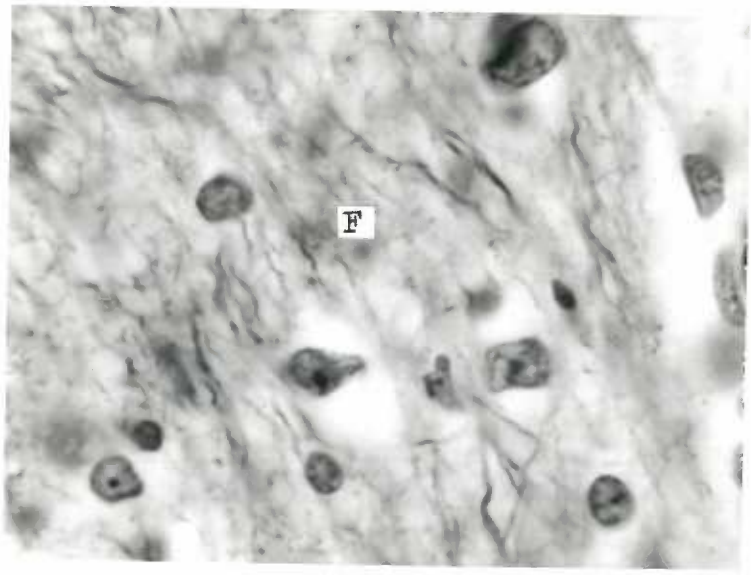
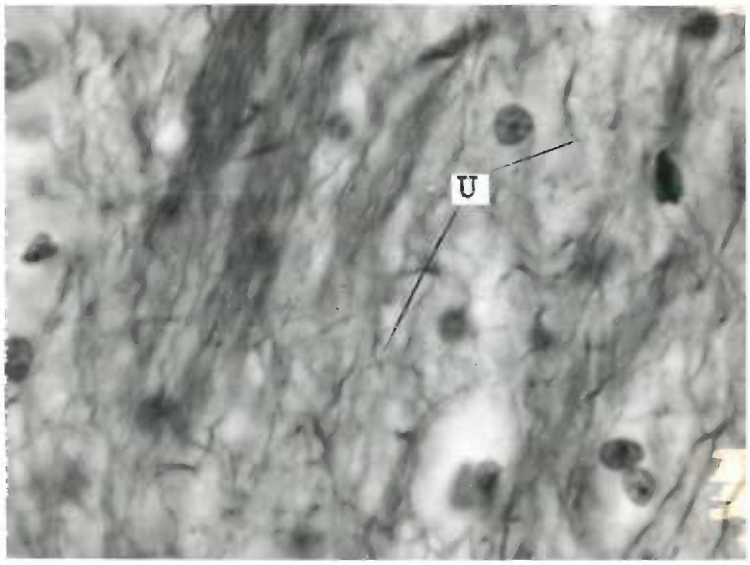


PLATE VIII.

Figure 28. Cat K-15. Photomicrograph of the lateral septal nucleus of the side opposite that in Figure 27. Note slight degeneration of fibers (U). Oil immersion. Intensified protargol stain.

Figure 29. Cat DW-77. Photomicrograph showing degeneration of terminals in the lateral part of the medial mammillary nucleus. Lesion of the superior fornix. Oil immersion. Intensified protargol stain.

28.

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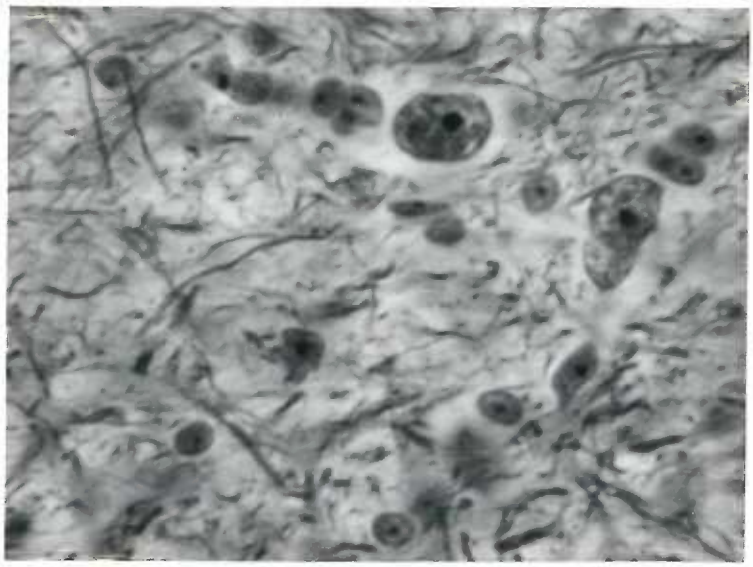
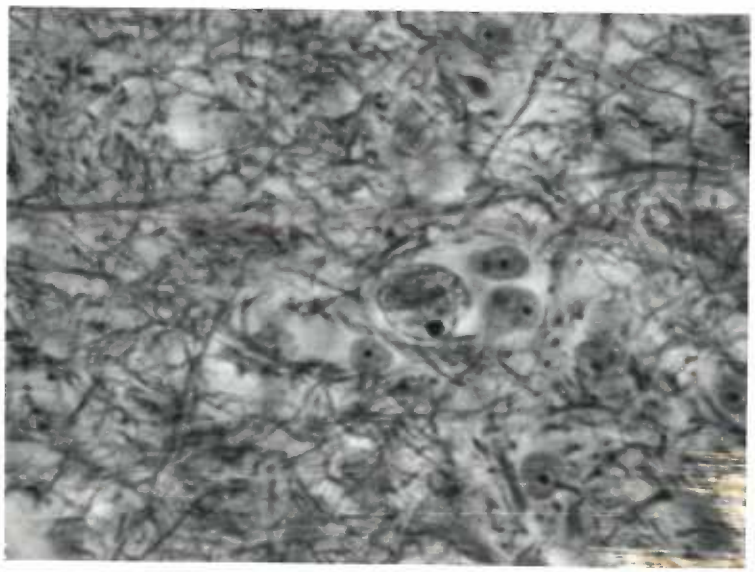


PLATE IX.

Figure 30. Cat DW-77. Photomicrograph of the normal lateral part of medial mammillary nucleus of the side opposite the lesion in Figure 29. Oil immersion. Intensified protargol stain.

Figure 31. Cat DW-77. Photomicrograph showing degenerated fibers (F) in the medial half of the lateral fornix. Lesion involving the most dorsal portion of the ventro-postero-lateral hippocampus. Compare with Figures 32 and 33. Oil immersion. Intensified protargol stain.

30.



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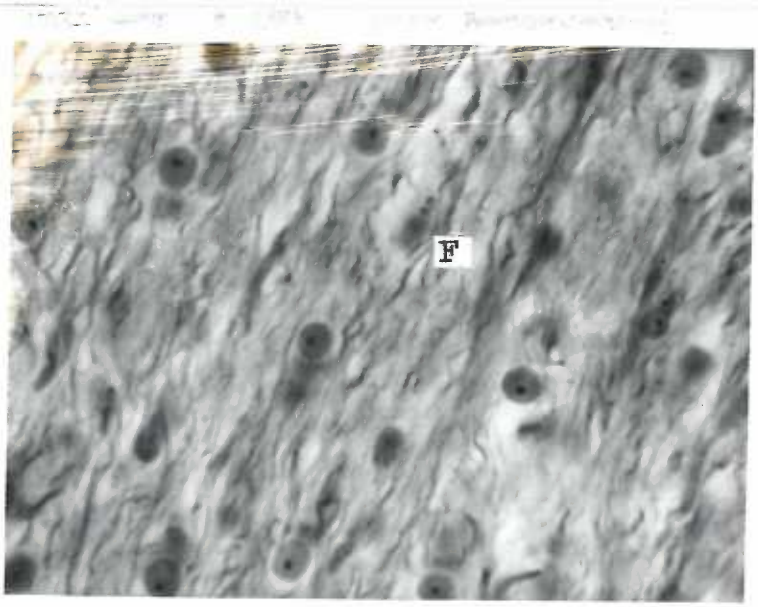
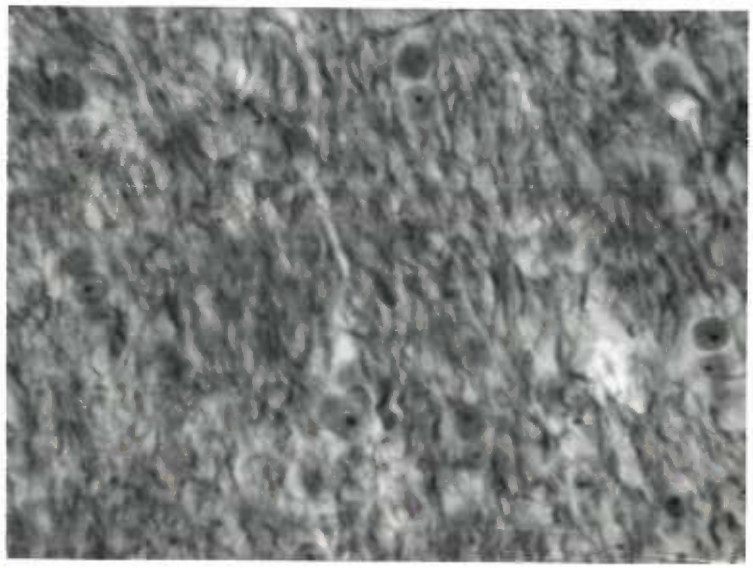


PLATE X.

Figure 32. Cat DW-77. Photomicrograph of the undegenerated medial half of the lateral fornix on the side opposite the lesion in Figure 31. Oil immersion. Intensified protargol stain.

Figure 33. Cat DW-77. Photomicrograph showing the normal fibers of the lateral half of the lateral fornix in the lesion noted in Figure 31. Oil immersion. Intensified protargol stain.

32.



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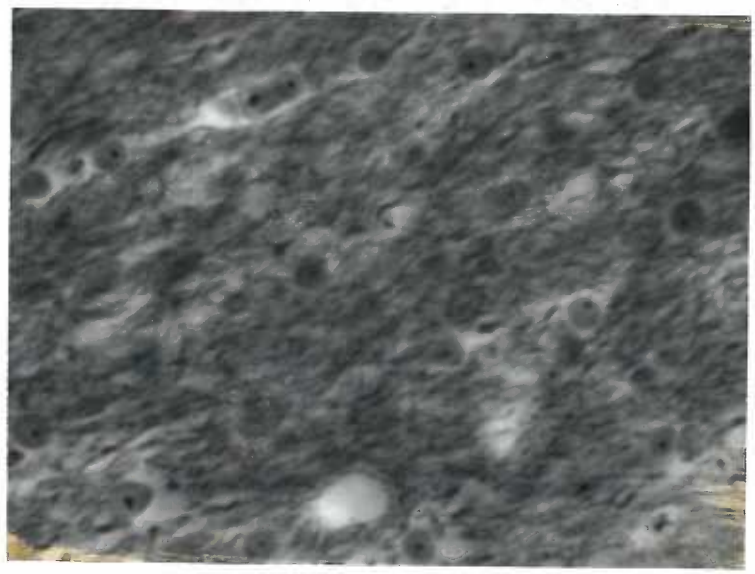
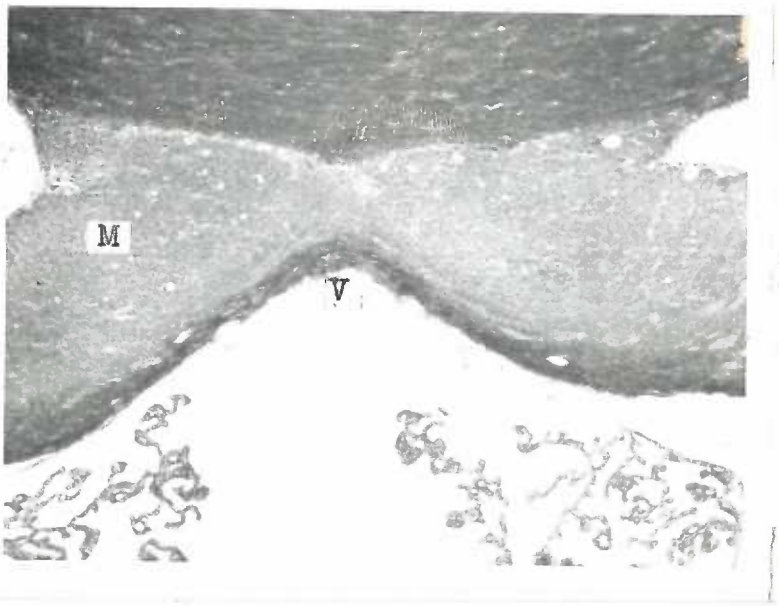


PLATE XI.

Figure 34. Cat DW-88. Photomicrograph showing the degenerated medial fornix (D) above the undegenerated superior part of the ventral hippocampal commissure (V). Bilateral lesion of the medial fornix and dorsal hippocampal commissure. Low power. Intensified protargol stain.

Figure 35. Cat DW-88. Photomicrograph showing degenerated fibers of the medial fornix (M) and undegenerated fibers of the lateral fornix (L). Note fibers from lateral fornix passing medially to ventral hippocampal commissure (V). Lesion as in Figure 34.

34.

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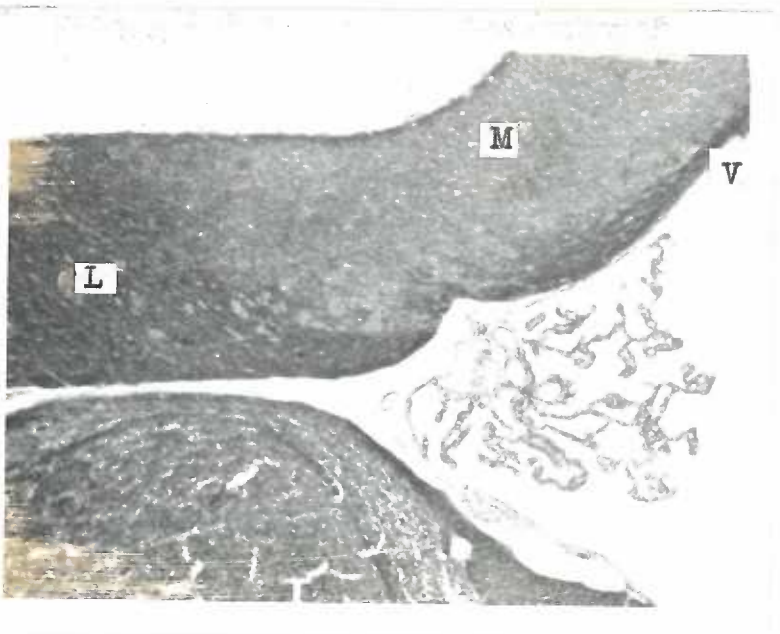
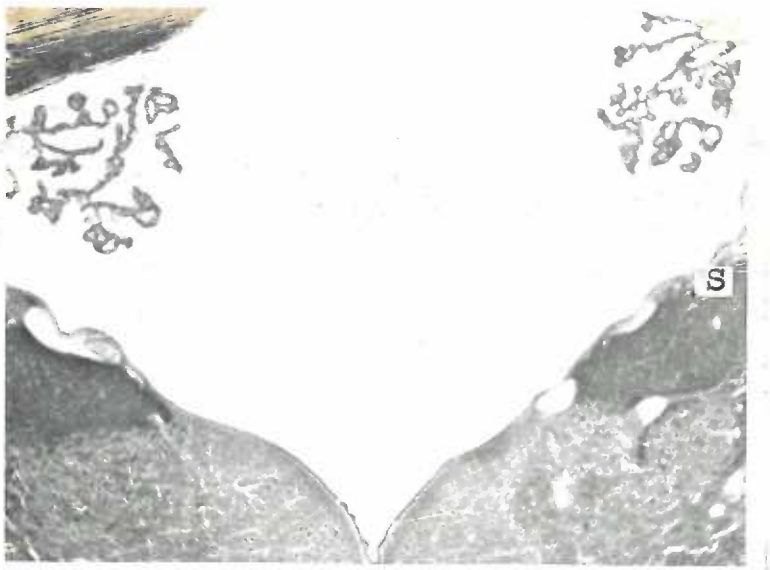


PLATE XII.

Figure 36. Cat DW-88. Photomicrograph showing the undegenerated stria medullaris (S) following complete bilateral lesion of medial fornix. Low power. Intensified protargol stain.

Figure 37. Cat DW-88. Photomicrograph showing degeneration in the medial septal nucleus following lesion involving the most superior part of the ventro-postero-lateral hippocampus of that side. Oil immersion. Intensified protargol stain.

36.

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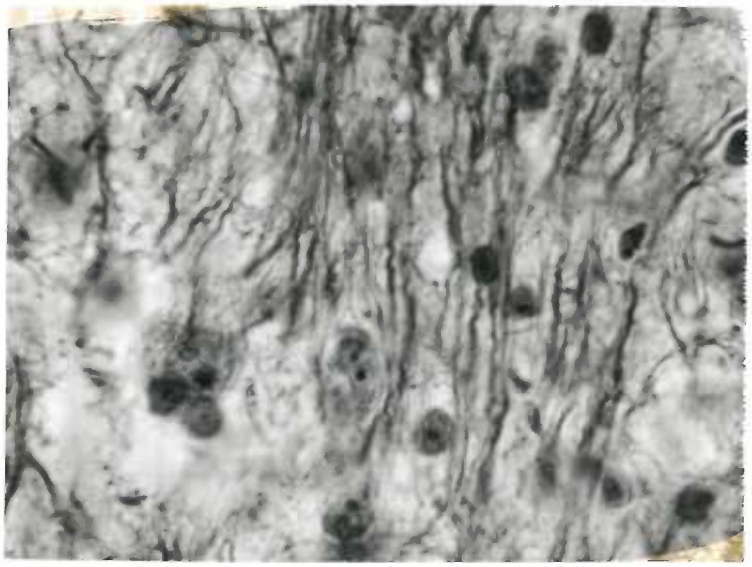
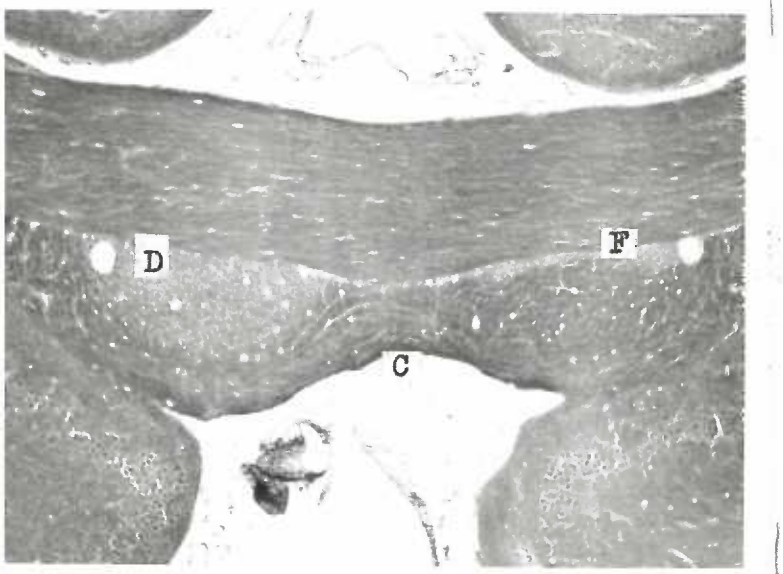


PLATE XIII.

Figure 38. Cat DW-94. Photomicrograph showing unilateral degeneration of the medial fornix (D) after coagulation of the superior fornix and superior border of the antero-dorsal hippocampus posteriorly. Note the partially degenerated dorsal hippocampal commissure (C). Note slight degeneration of the superior fornix of other side (F) due to small lesion of that area. Low power. Intensified protargol stain.

Figure 39. Cat DW-146. Photomicrograph showing lesion (L) of the inferior thalamic peduncle lateral to the stria medullaris (S). Note that there is no degeneration in the stria medullaris. Low power. Intensified protargol stain.

38.

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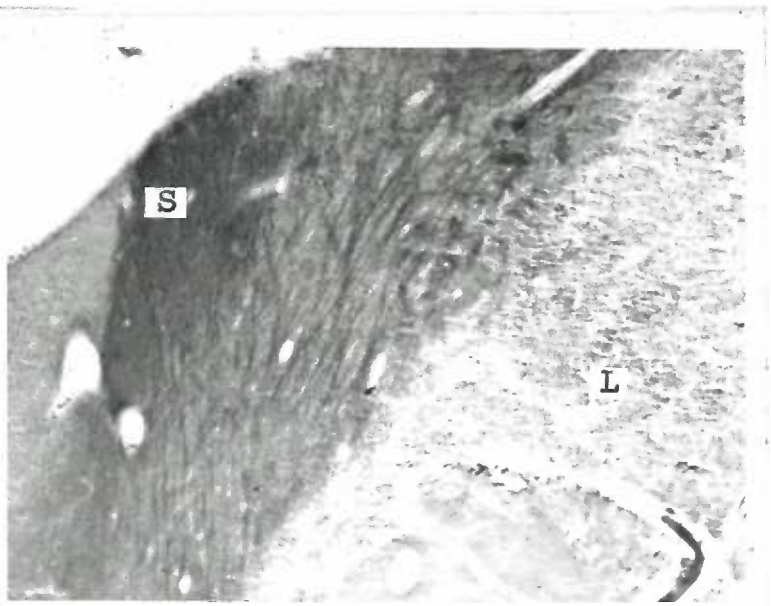
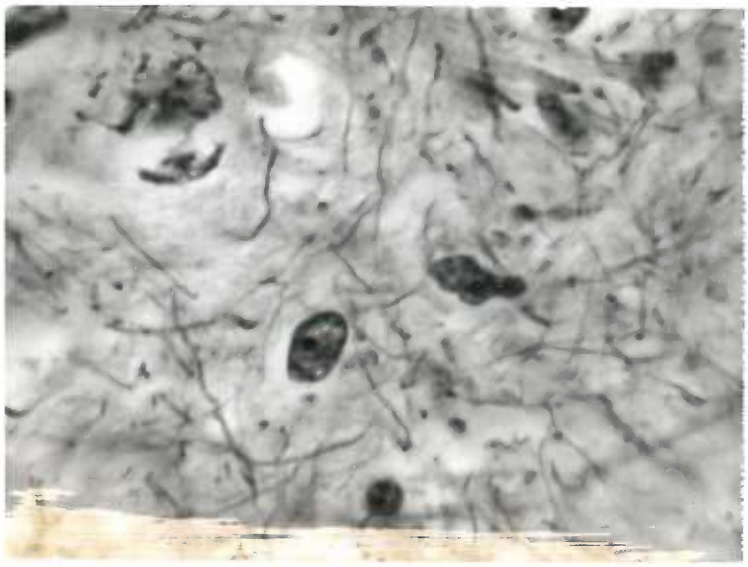


PLATE XIV.

Figure 40. Cat DW-146. Photomicrograph showing degenerated terminals and clearing of neuropil in the anteroventral thalamic nucleus following a lesion of the mammillo-thalamic tract and the inferior thalamic peduncle shown in Figure 45. Oil immersion. Intensified protargol stain.

Figure 41. Cat. K-14. Photomicrograph showing fibers from the post commissural septum joining the column of the fornix (F). Lesion is of the post commissural septum unilaterally. Note degeneration (D) of these fibers joining the fornix on the side of the lesion and lack of degeneration (U) on opposite side. Low power. Intensified protargol stain.

40.



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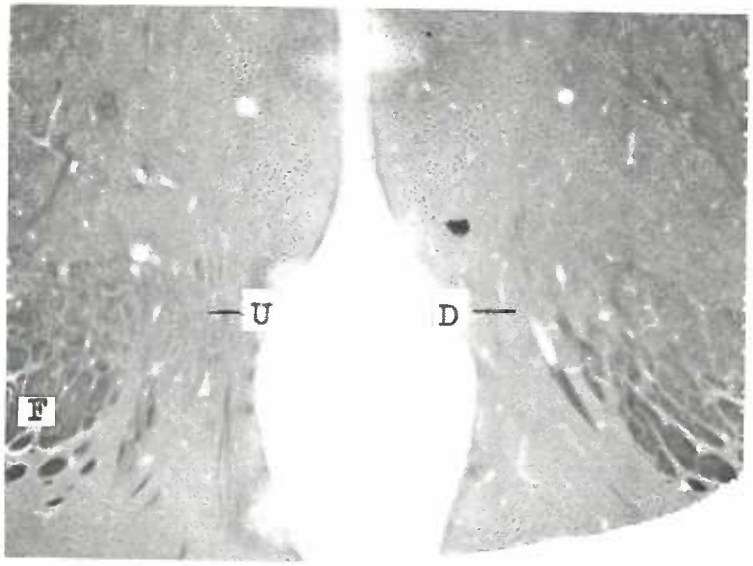
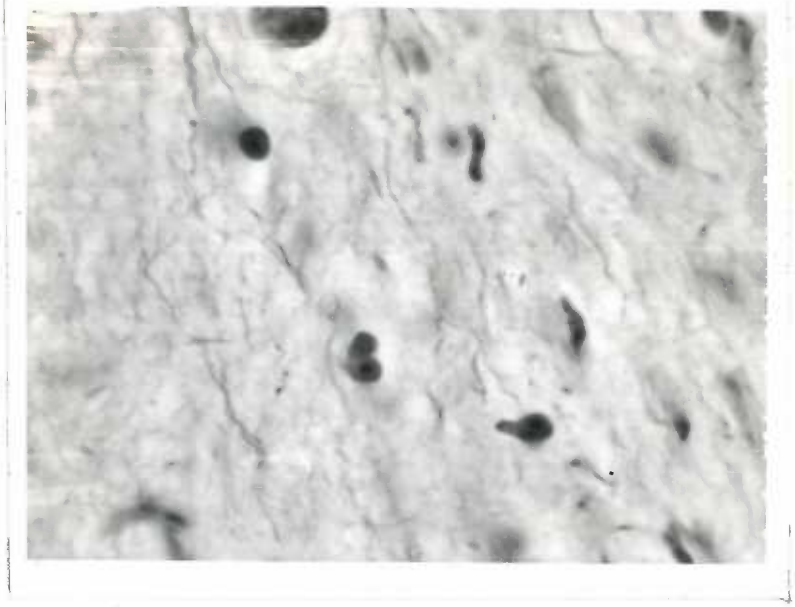


PLATE XV.

Figure 42. Cat K-14. Photomicrograph showing the degenerated fibers from the post commissural septum joining the fornix. The lesion is described in Figure 41. Compare with normal side (Fig. 43). Oil immersion. Intensified protargol stain.

Figure 43. Cat K-14. Photomicrograph showing normal fibers joining fornix on the side opposite the lesion in Figures 41 and 42. Oil immersion. Intensified protargol stain.

42.



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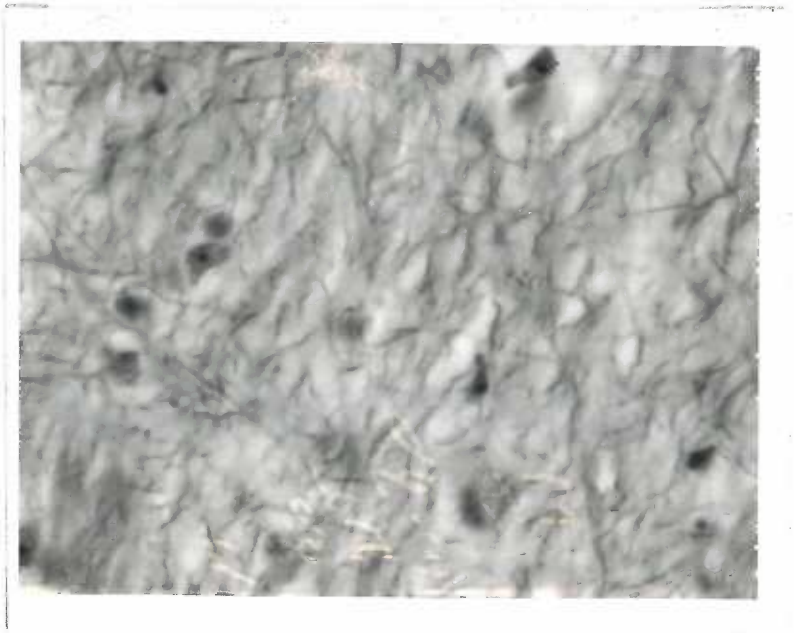
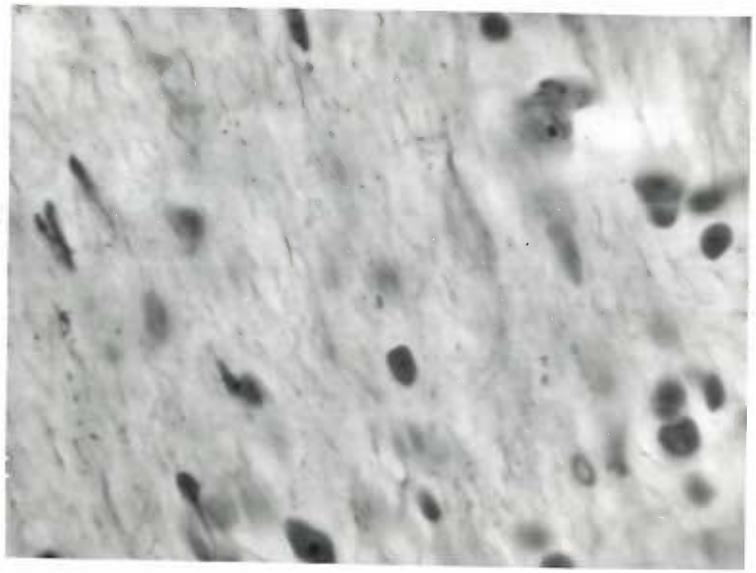


PLATE XVI.

Figure 44. Cat K-14. Photomicrograph showing degenerated fibers of the stria medullaris thalami on the ipsilateral side of a lesion in the post commissural septum. Compare with Figure 45. Oil immersion. Intensified protargol stain.

Figure 45. Cat K-14. Photomicrograph showing the normal stria medullaris thalami on the side opposite the lesion in the post commissural septum. Oil immersion. Intensified protargol stain.

44.



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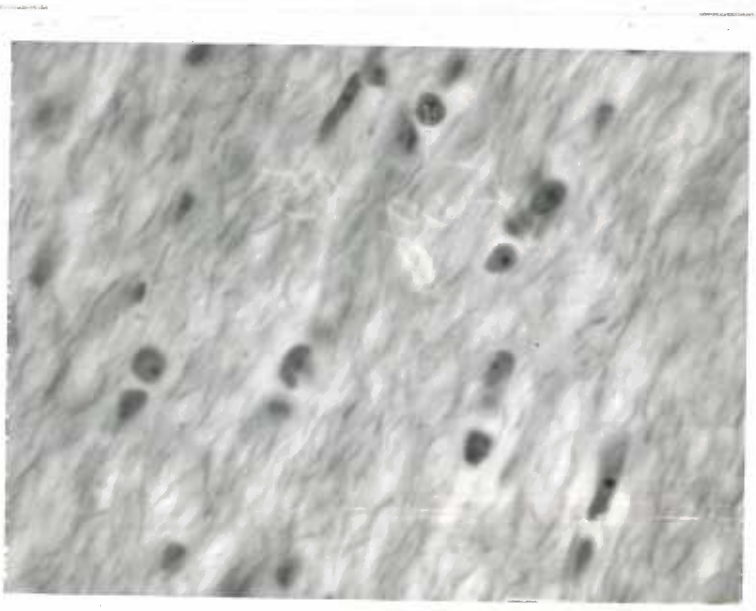


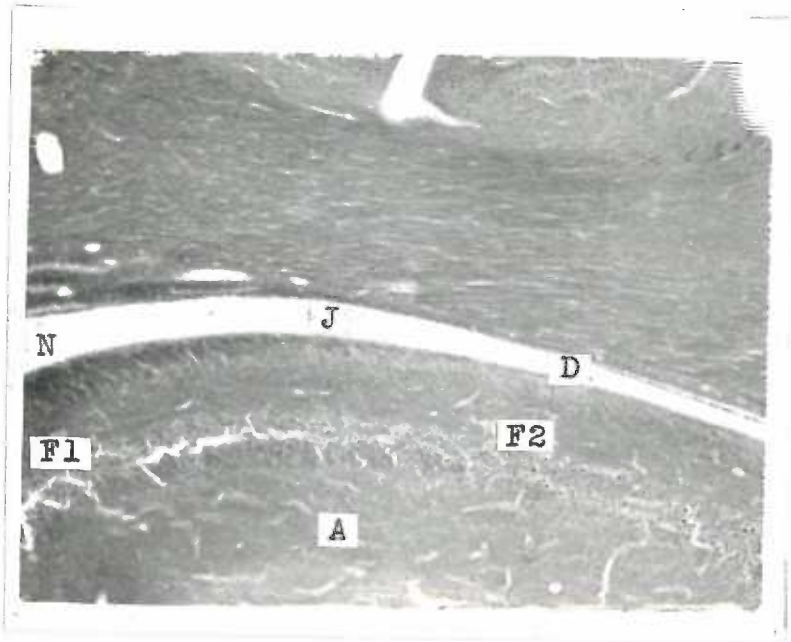
PLATE XVII.

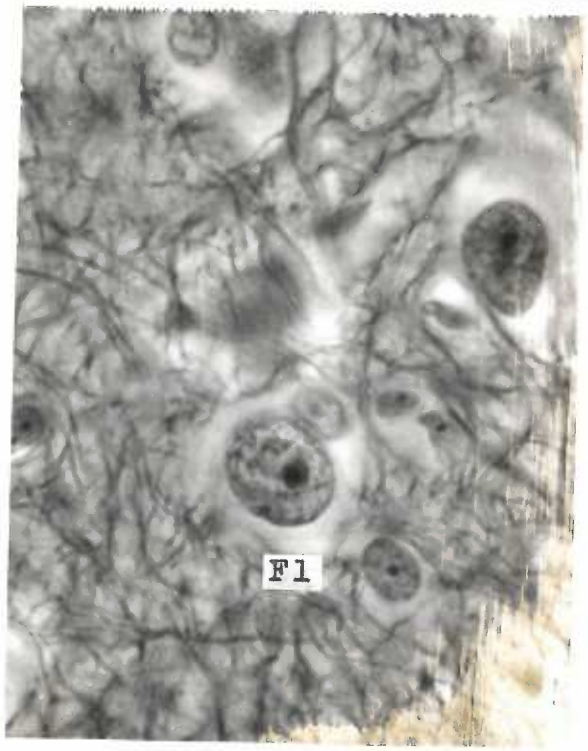
Figure 46. Cat DW-93. Photomicrograph of antero-dorsal hippocampus (A) anterior to a lesion of this area. Note junction (J) of the degenerated (D) and normal fibers (N) of the alveus. Low power. Intensified protargol stain.

Figure 47. Cat DW-93. Photomicrograph showing normal fibers and terminals in the polymorphic layer of the antero-dorsal hippocampus in an area shown in Figure 27 (F1). Oil immersion. Intensified protargol stain.

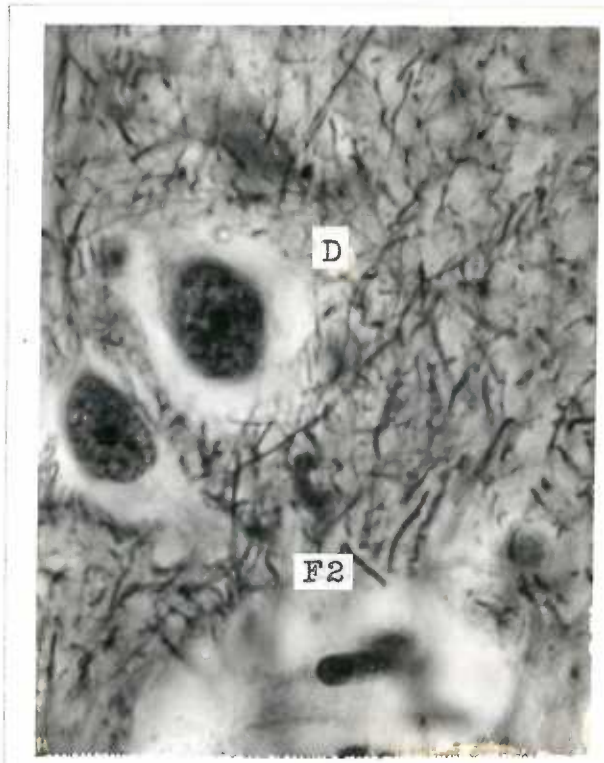
Figure 48. Cat DW-93. Photomicrograph showing degeneration of terminals and fibers (D) around the pyramidal cells of the polymorphic layer of the antero-dorsal hippocampus following lesion of antero-dorsal hippocampus of the opposite side. Taken from area shown in Figure 46 (F2). Oil immersion. Intensified protargol stain.

46.




47.




48.

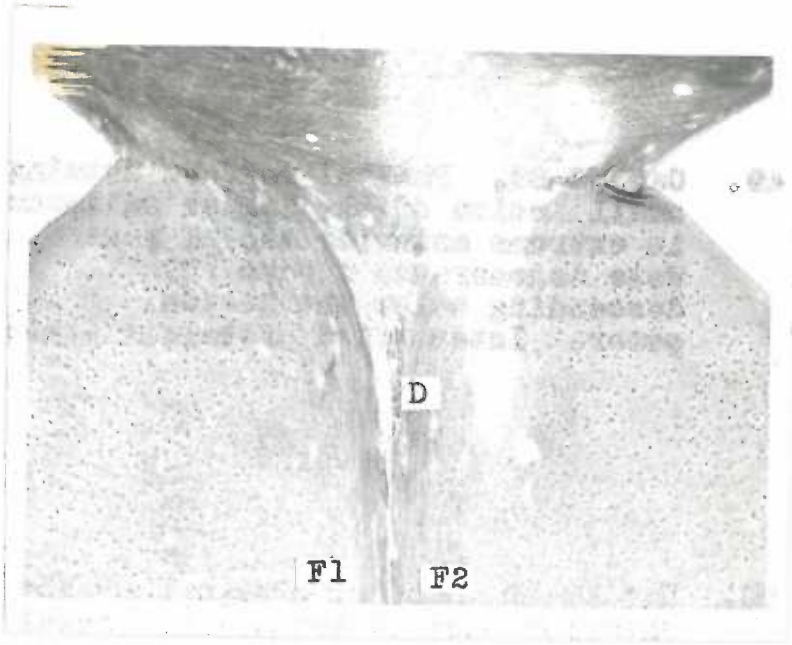
PLATE XVIII.

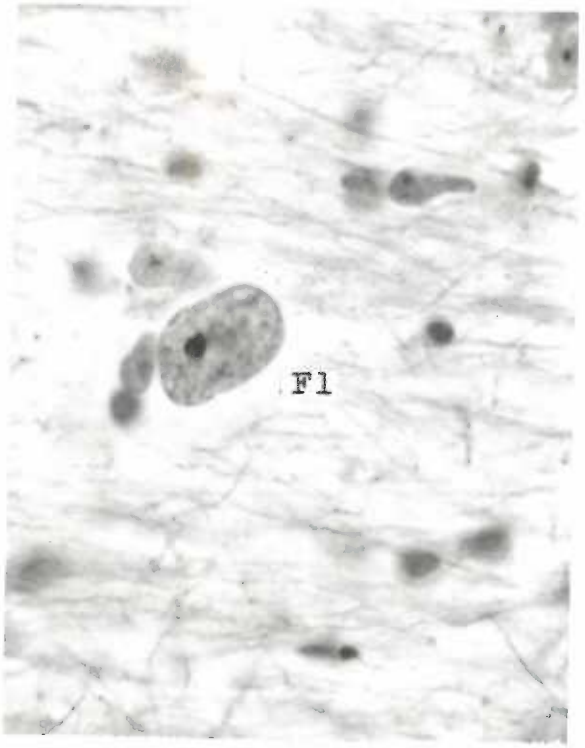
Figure 49. Cat DW-89. Photomicrograph showing small lesion of the corpus callosum in extreme anterior septal region. Note degenerated fibers (D) descending below the lesion. Low power. Intensified protargol stain.

Figure 50. Cat DW-89. Photomicrograph of the anterior part of the medial septal nucleus on the side opposite the lesion in Figure 49 (F1). Note that there is no degeneration as in Figure 51. Oil immersion. Intensified protargol stain.

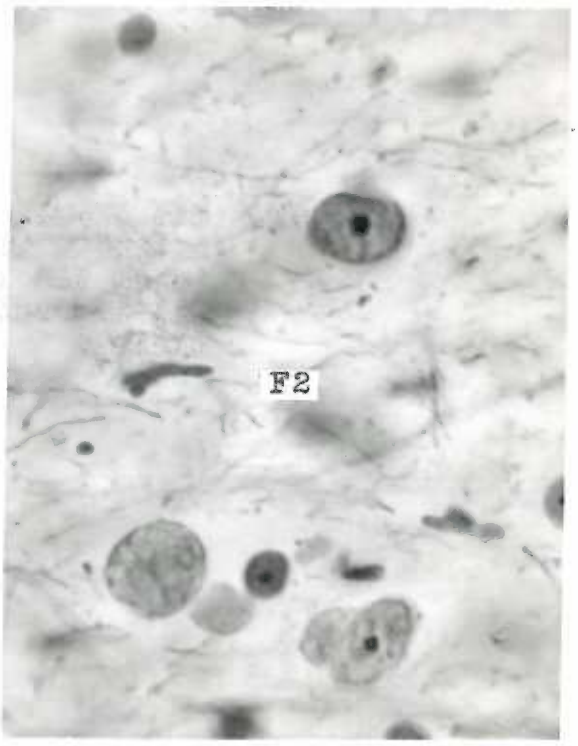
Figure 51. Cat DW-89. Photomicrograph of anterior part of medial septal nucleus below the lesion in Figure 49 (F2). Oil immersion. Intensified protargol stain.

49.




50.




51.

PLATE XIX

Figure 52. Cat DW-99. Photomicrograph of a normal animal showing the origin of the stria medullaris thalami (S), and fibers (F) joining the medial side of the column of the fornix (C). Low power. Intensified protargol stain.

52.