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CYTOARCHITECTURE AND DENDRITIC PATTERNS OF THE DORSAL COLUMN NUCLEI OF THE OPOSSUM

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CYTOARCHITECTURE AND DENDRITIC PATTERNS OF THE DORSAL COLUMN NUCLEI OF THE OPOSSUM

CHAPTER I

INTRODUCTION

The published research of the dorsal column nuclei can be grouped into three categories, viz., (1) that concerned with the nuclei, (2) that concerned with the afferent nerve fiber connections, and (3) that concerned with the efferent nerve fiber connections.

The Dorsal Column Nuclei

In the dorsomedial portion of the medulla, at the level of the obex and the rostral end of the dorsal white columns, three, bilaterally paired nuclei can be found. These paired nuclei comprise the dorsal column nuclei and are designated as the nucleus gracilis (gracile nucleus, nucleus of Goll), the nucleus cuneatus (cuneate nucleus, nucleus of Burdach), and the lateral cuneate nucleus (accessory cuneate nucleus, nucleus corporis restiforme, external cuneate nucleus, nucleus of Clark-Monakow). Of these three nuclei, the nucleus gracilis is the most medial and extends the farthest caudally. In contradistinction, the lateral cuneate nucleus is the most lateral and

extends farthest rostrally. The nucleus cuneatus is interposed between the nucleus gracilis and external cuneate nucleus, extending farther rostrally than the nucleus gracilis, and farther caudally than the external cuneate nucleus.

When using the term "dorsal column nuclei", many authors have reference only to the nucleus gracilis and nucleus cuneatus (Truex and Carpenter, 1964; Crosby, Humphrey and Lauer, 1962). There are several reasons for this exclusive usage of the term "dorsal column nuclei": (1) the nucleus cuneatus and nucleus gracilis are functionally similar while the lateral cuneate nucleus is functionally similar to the nucleus dorsalis (Clarke's column); (2) the fibers of the lateral cuneate nucleus are directed toward the cerebellum, while fibers from the nucleus cuneatus and nucleus gracilis are directed toward the cerebrum via the thalamus, and (3) the lateral cuneate nucleus is a dorsolateral nuclear structure, while the nucleus gracilis and nucleus cuneatus are true dorsal nuclear structures. For these reasons, the term "dorsal column nuclei", as used in this thesis, refers only to the nucleus gracilis and nucleus cuneatus.

In certain mammals either the nucleus gracilis of one side joins that of the other or a separate accumulation of cells occurs in the midline; this is known as the nucleus of Bischoff (1900). Since it receives the most medial and consequently the most caudal fibers of the fasciculus gracilis, it is often considered as being concerned with sensory innervation of the tail.

Its occurrence in rats, shrewmice, kangaroos, great anteaters, opossums and some monkeys appear to support this concept. It is not invariably present in all mammals with well-developed tails (Ziehen, 1899, 1903, 1913). The nucleus of Bischoff is not evident in Ateles and Cebus (Ariëns Kappers, Huber and Crosby, 1960).

No differences between the nucleus gracilis and nucleus cuneatus are seen on a purely cytoarchitectonic basis (Valverde, 1966 [in the rat]). Two general types of neurons are found in these nuclei, the round cell and the irregular cell.

The round cells are characterized by short bushy dendrites (Ramón y Cajal, 1909 [in various animals]), a fine, evenly dispersed, moderately stained, Nissl substance, and a centrally placed nucleus (Taber, 1961 [in the cat]). In primates and cats, these cells are frequently grouped in a circular fashion around a central cell-free area forming cell clusters (Kuypers and Tuerk, 1964) or "cell nests" (Hand, 1965; 1966; Keller and Hand, 1970). In the space between the cell bodies and surrounding them and their dendrites, a dense neuropil is found. This neuropil contains terminal ramifications of collaterals or terminal branches from dorsal column fibers and is named a glomerulus. Similar terminal ramifications exist in the rat (Valverde, 1966), but in this animal the glomerulus of one cell fuses with "glomeruli" of other cells in the cluster. In this manner a larger neuropil, relatively devoid of cell bodies is formed.

The irregular cells are characterized by either a fusiform, triangular, polygonal or multiform cell body, with longer, less profuse dendritic branching (Ramón y Cajal, 1909 [in various animals] ; Ramón-Moliner, 1962 [in various animals] ; Kuypers and Tuerk, 1964 [in cats]). The irregular cells are interspersed between and around the round cell nests (Hand, 1966 [in the cat]) in conjunction with the interlacing fibers of the dorsal white columns (Glees and Soler, 1951 [in the cat]). Of the irregular cells, the fusiform type is somewhat smaller than the round cell while the multiform (polygonal) cell type is somewhat larger (Taber, 1961 [in the cat]).

A cellular gradient along the rostrocaudal axis of the nucleus gracilis has been observed. The caudal portion of the nucleus contains all cell types, but is made up of predominantly round cells. Cranial to the obex toward the rostral pole, the cytoarchitecture consists of mainly small cells, loosely organized with poor delineation (Taber, 1961 [in the cat]). At rostral levels in the rat, the cells of the dorsal column nuclei tend to be disposed more compactly in the ventral limits (pars compacta of Valverde, 1966). The histogenesis of this nucleus (Taber, 1963 [in mice]) reveals a caudal portion older than the rostral portion. This correlates nicely with the two-fold division of the nucleus gracilis (Taber, 1961 [in the cat]).

Hand (1966) confirmed the preceding findings and added certain other details. Accordingly, the nucleus was divided into three cytoarchitecturally distinct regions: (1) an area rostral to the obex, characterized by a loose

organization of small cells (10 X 10 mu) which is similar to the reticular formation and is referred to as the "reticular region"; (2) a middle area caudal to the obex and characterized by larger cells (20 X 20 mu) organized into clusters designated as the "cell nest" region, and (3) a region of the caudal pole, termed the "caudal region", characterized by fewer but larger cells (20 X 30 mu) occurring singly or in small isolated clusters.

A rostocaudal differentiation of the nucleus gracilis into three divisions has been determined electrophysiologically using as a basis the size of the receptive field (Gordon and Paine, 1960 [in cats] ; Gordon and Seed, 1960 [in cats] ; Gordon and Jukes, 1962 [in cats] .; McComas, 1962; 1963 [in rats]). A receptive field is defined as the total area of skin which can be stimulated mechanically to excite a particular cell (McComas, 1963 [in rats]). These three regions correspond nicely with Hand's data in that, (1) the cells with the smallest size receptive field are found in the middle of the nucleus ("cell nest" region of Hand); (2) cells with the largest receptive fields are found in the rostral portion of the nucleus ("reticular region" of Hand), and (3) cells with intermediate size receptive fields are found in the caudal portion of the nucleus ("caudal region" of Hand).

Other investigators, also using electrophysiological methods for the determination of receptor fields, have not found this three part, longitudinal differentiation of the nucleus gracilis (Kruger, Sininoff and Witkovsky, 1961 [in cats] ; Perl, Whitlock and Gentry, 1962 [in cats] ; Winter, 1965 [in

cats] ; Nord, 1967 [in rats]). These investigators (especially Winter, 1965 and Nord, 1967) maintain that the actual relationship is between field size relative to position on the body surface as opposed to field size relative to position in the nucleus.

The cell body types and dendritic structures of cells in the nucleus cuneatus, as previously mentioned, are like those of the nucleus gracilis. The round cells are more numerous and are slightly larger than those of the nucleus gracilis (Taber, 1961 [in cats]). The round cell clusters are most dense in the main body of the nucleus and have a tendency toward lamination in concentric circles (Ferraro and Barrera, 1935a [the Rhesus monkey]). At higher levels the nucleus cuneatus is formed by two portions, a round portion, the pars rotunda, and a triangular portion, the pars triangularis, which is situated between the external cuneate nucleus and the pars rotunda (Ferraro and Barrera, 1935a [in the Rhesus monkey]).

Like the nucleus gracilis, a cellular gradient along the rostrocaudal axis of the nucleus cuneatus has been observed. Thus the nucleus cuneatus can be divided into a rostral and a caudal region on the basis of cell size, morphology, and cellular arrangements as observed in Nissl and silver impregnations (Taber, 1961 [in cats] ; Kuypers and Tuerk, 1964 [in cats] ; Keller and Hand, 1970 [in cats]). The caudal, or "cell nest" region, extends from the caudal limit of the nucleus to slightly above the level of the obex. The cells which comprise the dorsal aspect of the caudal region are large round cells (20 mu X 20 mu). The cell of the ventral aspect of the caudal region are more dissociated and resemble

those cells of the rostral region. The rostral or "reticular" region extends from slightly above the level of the obex to the rostral pole of the nucleus and consists of smaller (12 mu X 8.5 mu) dissociated cells with a few larger cells (23 mu X 15 mu) dispersed throughout the area (Keller and Hand, 1970 [in cats]).

Unlike the nucleus gracilis, the nucleus cuneatus does not appear to exhibit a rostrocaudal differentiation based on receptor field size. However, there is experimental evidence which could warrant division of the nucleus into two parts on the basis of a segregation of modalities. Rosen (1967; 1969 [in cats]) found the group I CTR cells (cuneothalamic cells) are situated in the deep parts (i.e., ventral parts) of the nucleus, whereas, cutaneous CTR cells occupied a superficial (i.e., dorsal) as well as deep (i.e., ventral) parts of the nucleus.

A somatotopic organization with the dorsal column nuclei is manifested as a result of dorsal column projections onto the nuclei. The basic projection of the body surface onto the dorsal column nuclei can be visualized as an upside down figure of the animal projected onto a cross section of the dorsal medulla. The tail of the animal is situated along the midline portion of the nucleus gracilis with more rostral body areas projecting laterally into the nucleus cuneatus. The extremities point toward the dorsal surface of the medulla with the trunk of the animal being adjacent to the reticular formation. The lower extremity is associated with the nucleus gracilis and the upper extremity is associated with the nucleus cuneatus. The head and face have homologus projections in the laterally adjacent

trigeminal nucleus. Most of the body surface is represented at every level throughout the rostrocaudal dimension of the nucleus. Thus, each body area appears as a longitudinal column of cells within the nuclei. There is a considerably greater volume of the dorsal column nuclei devoted to the representation of the distal limbs than that devoted to the proximal limbs and body trunk. The foregoing somatotopic relationships have been found in the cat (Kuhn, 1949; Rustioni and Macchi, 1968; Kruger, Sininoff and Witkovsky, 1961; Hand, 1965; 1966; Keller and Hand, 1970), the rat (Nord, 1967), the alligator (Kruger and Witkovsky, 1961), the sheep (Woudenberg, 1969) and the raccoon (Johnson, Welker and Pubols, 1968).

Afferent Nerve Fiber Connections

The cells of the dorsal column nuclei have two sources of afferent fiber connections: (1) from the dorsal roots through the dorsal funiculus, and (2) from the cerebral cortex through the pyramidal tracts.

Peripheral fibers destined for the dorsal funiculus are relatively large and well myelinated with a rapid conduction rate. These first order neurons, whose large unipolar cell bodies are situated in the dorsal root ganglia, originate from receptors in the skin, muscles and joints. The fibers enter the spinal cord by way of the medial division of the dorsal root. Entering the dorsal funiculus, they bifurcate into ascending and descending fibers, some of which may enter one of the reflex pathways located in the dorsal funiculus (fasciculus interfascicularis or septomarginal fasciculus). Other fibers eventually may effect a reflex connection with neurons in the dorsal and intermediate gray; or, in the case of the myotatic

reflex, they may end directly on the ventral horn cell (Matzke and Foltz, 1967).

About 20% of the ascending fibers contribute to various reflexes and are lost from the dorsal funiculus within the first two or three segments above their segment of entry. About 22% of the remaining ascending fibers continue the entire length of the spinal cord to reach the dorsal column nuclei of the medulla (Glees and Soler, 1951 [in cats]). The ascending fibers maintain an orderly arrangement in the dorsal funiculus in that fibers entering from caudal areas take a medial position along the dorsal median sulcus. More and more fibers from rostral segments are added in successively more lateral positions. Thus, a somatotopic lamination of the dorsal funiculus occurs (Ferraro and Barrera, 1935b [in the Rhesus monkey]; Kodama, 1942 [in cats]; Walker and Weaver, 1943 [in the Macaque monkey]; Chang and Ruch, 1947 [in the Spider monkey]; Glees, Livingston and Soler, 1951 [in cats and rabbits]; Werner and Whitsel, 1967 [in the Squirrel monkey]).

In the mid-thoracic region of the spinal cord, a septum (dorsal intermediate septum) appears which divides each of the dorsal funiculi into two fasciculi. The medial group of fibers is referred to as the fasciculus gracilis and contains ascending fibers from coccygeal, sacral, lumbar and lower thoracic spinal nerves. The lateral group of fibers is referred to as the fasciculus cuneatus and contains ascending fibers from upper thoracic and cervical spinal nerves. As the fasciculus gracilis approaches the nucleus gracilis, the fibers bifurcate into two bundles, a ventrolaterl and a dorsomedial. The ventrolateral bundle contains fibers from the

lumbar, sacral and coccygeal roots (Glees, Livingston and Solar, 1951 [in cats and rabbits]; Glees and Soler, 1951 [in cats]). The fibers then divide into still smaller bundles and intercalate among the cell bodies of the nucleus (Chang and Ruch, 1947 [in the Spider monkey]; Glees and Soler, 1951 [in cats]).

Lesion studies, utilizing the Marchi technique for detection of degenerating myelin, reveal degeneration which can be traced to the dorsal column nuclei (Ferraro and Barrera, 1935b [in the Rhesus monkey]; Walker and Weaver, 1942 [in the Macaque monkey]; Esocolar, 1948 [in cats]; Glees, Livingston, and Soler, 1951 [in cats and rabbits]; Glees and Soler, 1951 [in cats]). Lesion studies, utilizing Nauta and Fink-Heimer techniques for detection of degenerating axons, reveal fiber terminals which appear to enter into synaptic contact with the round cell populations. These terminations are primarily within the clusters of round cells of the intermediate portion of the nucleus gracilis (Kuypers and Tuerk, 1964 [in cats]; Hand, 1965; 1966 [in cats]; Petras, 1965 [in cats]; Sovoskina and Skibo, 1969 [in cats]; Jane and Schroeder, 1971 [in the hedgehog]). In the nucleus cuneatus, dense terminal degeneration can be traced to the caudal "cell nest" region, with more diffuse degeneration in the rostral "reticular" region (Keller and Hand, 1970 [in the cat]). By light microscopy, only axo-somatic connections are observed. They appear as large terminal boutons against the postsynaptic cell (Glees and Soler, 1951 [in cats]; Rozsos, 1958 [in cats]). However, electron microscopy reveals that both axo-somatic and axo-dendritic connections occur, with the axo-dendritic connections being greater

by a ten to one ratio (Valverde, 1966 [in rats] ; Walberg, 1966a; 1966b [in cats]).

The dorsal column nuclei also receive corticofugal fibers from the somatosensory cortex of the cerebrum. Passing through the internal capsule to become part of the pyramidal tracts, these fibers enter the dorsal column nuclei where they bifurcate into numerous collaterals which spread over wide areas within the nuclei (Chambers and Liu, 1957 [in cats] ; Walberg, 1957 [in cats] ; Kuypers, 1958a [in cats] ; 1958b [in man] ; Magni, Melzack, Moruzzi and Smith, 1959 [in cats] ; Levitt, Carreras, Chambers and Liu, 1960 [in cats] ; Kuypers, Hoffman and Beasley, 1961 [in cats] ; Levitt, Carreras, Liu and Chambers, 1964 [in cats] ; Zimmerman, Chambers and Liu, 1964 [in cats] ; Bautista and Matzke, 1965 [in the opossum] ; Petras, 1965 [in rats] ; Valverde, 1966 [in rats]). These corticofugal fibers appear to be preferentially distributed to those nuclear areas in which there is a predominance of irregular cells (i.e., multipolar, triangular, fusiform, and polygonal). The nuclear areas containing round cell populations receive only sparse numbers of corticofugal fibers (Kuypers, Hoffman and Beasley, 1961 [in cats] ; Kuypers and Tuerk, 1964 [in cats]).

A finding of considerable interest with respect to dorsal column nuclei function is that of presynaptic inhibition. Recent physiological studies have demonstrated a depression of synaptic transmission occurring in the dorsal column nuclei following simultaneous stimulation of peripheral nerves and cerebral sensorio-motor cortex. This depression of synaptic transmission is due, at least in part,

to presynaptic depolarization (Andersen, Eccles, Oshima and Schmidt, 1964 [in cats]; Andersen, Eccles, Schmidt and Yokota, 1964a, 1964b, 1964c [in cats]). These findings extended the previous observations (Wall, 1968 [in cats]; Towe and Jabbur, 1961 [in cats]; Guzman-Flores, Buendia, Anderson and Lindsley, 1962 [in cats]; Andersen, Eccles and Schmidt, 1962 [in cats]) that presynaptic inhibition occurs on the synaptic relays of the dorsal column fibers in the nucleus gracilis and included the nucleus cuneatus. The presynaptic inhibition was theorized to be mediated via interneurons whose axon terminals were believed to be in synaptic contact with the nerve terminals of the fibers of the dorsal funiculus (Andersen, Eccles, Schmidt and Yokota, 1964b [in cats]).

Anatomical verification of the above physiological findings came when synaptic relationships of small terminal boutons upon larger terminal boutons were observed in electron micrographs of the nucleus cuneatus (Walberg, 1965 [in cats]; Valverde, 1966 [in rats]). The larger boutons are those which degenerate following section of the posterior columns. In contradistinction, the small boutons, which synapse on the large ones, do not degenerate following section of either the corticofugal pyramidal tract fibers or the dorsal column fibers. It was thus concluded that the small boutons which formed axo-axonic synapses with dorsal column boutons originated from interneurons. Further, these axo-axonic synapses were assumed to form the morphological stratum responsible for the presynaptic depolarization (inhibition) observed in the nucleus cuneatus by various neurophysiologists (Walberg, 1965 [in cats]).

Other neurophysiologists have found facilitatory influences upon the dorsal column nuclei from stimulation of various brain loci: (1) the nucleus ventralis posterolateralis of the thalamus (Guzman-Flores, Gault, Anderson and Lindsley, 1963 [in cats]); (2) the sensorimotor cortex and other motor cortex (Jabbur and Towe, 1961 [in cats]; Carreras, Levitt, Chambers and Liu, 1960 [in cats]).

Efferent Nerve Fiber Connections

The major neural output from the dorsal column nuclei is through the medial lemniscus. Efferent fibers reaching the medial lemniscus originate from the round cell populations within the cell clusters (Ferraro and Barrera, 1935b [in the Rhesus monkey]; Kuypers and Tuerk, 1964 [in cats]; Gordon and Seed, 1961 [in cats]). Arising from the cell body or from one of the dendritic trunks (Valverde, 1966 [in rats]), these axons sweep ventrally and medially from the nuclei of both sides, forming an inverted arc of interlacing fibers. They are known as internal arcuate fibers and make up the sensory decussation of the medulla. These axons may give off one or more collaterals which may return to the same or adjacent cells within the dorsal column nuclei (Valverde, 1966 [in rats]). After crossing to the contralateral side, these fibers turn rostrally and ascend in the ventral brain stem just dorsal to the pyramidal tracts (Ranson and Ingram, 1932 [in cats]; Ferraro and Barrera, 1936a [in the Rhesus monkey]). Within the medial lemniscus, there is not an obvious lamination (Matzke, 1951 [in cats]). However, the topological relations of the dorsal white columns and dorsal column nuclei are maintained.

Discrete lesions of the dorsal column nuclei reveal the following: (1) At the level of the sensory decussation, fibers from the gracile nuclei are caudal and dorsal, while the fibers from the cuneate nuclei are rostral and ventral. (2) At the more rostral interolivary level, the gracile fibers are situated just dorsal to the pyramidal tracts, with the cuneate fibers just dorsal to the gracile fibers. Throughout the medulla, the medial lemniscus is seen to be compressed from side to side along the midline, dorsal to the pyramids. Its greatest diameter is in the dorsoventral plane of the midline. (3) In the pons, the medial lemniscus begins to migrate laterally so that its greatest diameter comes to lie in a horizontal plane. (4) With this shift, the gracile fibers become displaced laterally with the cuneate fibers situated dorsomedial to them. (5) As the lemniscus continues rostrally through the pons toward the mesencephalon, it shifts laterally and dorsally between the red nucleus and medial geniculate body. (6) The lemniscal fibers terminate in the posteroventral lateral nucleus of the thalamus (Ranson and Ingram, 1932 [in cats]; Ferraro and Barrera, 1936b [in the Rhesus monkey]; Rasmussen and Peyton, 1948 [in man]; Glees, Liddell and Phillips, 1951 [in cats]; Matzke, 1951 [in cats]; Verhaart, 1955 [in various animals]; Bowsher, 1958; 1961 [in the Macaque monkey]; Truex and Carpenter, 1964; Matzke and Foltz, 1967; Crosby, Humphrey and Lauer, 1962).

There has been considerable controversy in association with the medial lemniscus. One such controversy involves the question of complete or partial decussation of the medial lemniscal fibers. A second such controversy involves the question of the projection of the medial lemniscus to areas other than the ventrobasal thalamus.

Several electrophysiological investigations demonstrate contralateral as well as some ipsilateral conduction through the medial lemniscus toward the posterolateral ventral nucleus of the thalamus or toward higher centers (Berry, Karl, and Hensey, 1947 [in cats]; Hunt and O'Leary, 1952 [in cats]; Bohm, 1953 [in cats]; Bohm and Petersen, 1953 [in cats]; Gaze and Gordon, 1952, 1954 [in cats]; Cohen, 1955 [in cats]; Harwood and Cress, 1954 [in cats]; Cooper and Williams, 1963 [in cats]). It is interesting to note that in all the above reports concerning ipsilateral conduction in the medial lemniscus, not one report involved direct stimulation of the dorsal column nuclei with measurement of impulses directly in the medical lemniscus. Only one such experiment using direct stimulation has been done (Berry, Karl, and Hinsey, 1950 [in the cat and monkey]). In this study it was found that stimulation of the dorsal column nuclei with greatly increased stimulus strength, resulted in only contralateral impulses in the medial lemniscus.

The majority of fiber degeneration studies reveal only contralateral fibers entering the medial lemniscus from the dorsal column nuclei (Ferraro and Barrera, 1936b [in the Rhesus monkey]; Ranson and Ingram, 1932 [in cats]; Rasmussen and Peyton, 1946, 1948 [in man]; Matzke, 1951 [in cats]; Bowsher, 1958, 1961 [in the Macaque monkey]; Hand and Liu, 1966 [in cats]). One exception to this strict contralateral projection has been reported. In the marsupial phalanger, some degeneration on the ipsilateral side at inferior olivary levels suggest a small component of uncrossed fibers (Clezy, Dennis and

Kerr, 1961).

In reviewing the controversy of complete or partial decussation of the medial lemniscus, Allen C. Norton (1969) summarized as follows:

> . . . there is a complete decussation of those medial lemniscus fibers which originate in the dorsal column nuclei. There are, however, alternate pathways (other than through the DCN) from the spinal cord to the thalamus. The fibers of these alternate pathways may travel in the medial lemniscus, and there certainly is bilateral projection in some of these alternate pathways. It is suggested that the electrophysiological studies reporting ipsilateral conduction in the medial lemniscus did not account, or provide the proper controls, for all such possible alternate routes; thus they cannot be used as proof that there is incomplete decussation of those medial lemniscal fibers arising from the DCN (Norton, 1969, p. 21).

Norton later states: "Most of these electrophysiological studies merely show pathways (other than the dorsal column system) from the periphery to the midbrain which have bilateral representation" (Norton, 1969, p. 78).

The question of the projection of the medial lemniscus to areas other than the ventrobasal thalamus presents controversies similar to those of ipsilateral conduction. In reviewing the controversy, Matzke (1951) offered the following comments in his historical summary:

> While there seems to be general agreement as to the course and termination of the majority of the fibers arising from the posterior column nuclei, the connections of these nuclei with the cerebellum and many other nuclei throughout the brain stem have been the subject of much controversy . . .
>
> The fibers of the medial lemniscus apparently have their principal origin from the opposite gracile and cuneate nuclei. Following lesions of these nuclei or the medial

> lemniscus, degenerating fibers have been traced by various workers into the inferior olivary nucleus, reticular nuclei, red nucleus, corpora quadrigemina, substantia nigra, subthalamic nucleus, hypothalamus and globus pallidus. These connections have at one time or another been affirmed and denied (Matzke, 1951, p. 439).

In his own experimental work, Matzke (1951 [in cats]) found only contralateral degeneration of the medial lemniscus with termination in the postero-ventral nucleus of the thalamus. He surmised that the earlier findings which demonstrated various terminations of the medial lemniscus could be due to any one of the following: (1) failure to distinguish between those fibers which arose from the dorsal column nuclei as opposed to those fibers which arose from other areas but merely coursed near or with the medial lemniscus; (2) utilization of a wide variety of experimental animals and techniques; (3) and faulty interpretation of the Marchi stained material (e.g., "Since the myelin sheath is lost a variable distance from the fiber's termination, it is dangerous to conclude that the presence of Marchi granules in a nucleus indicates a functional connection between the nucleus and degenerated fibers or that the fibers actually terminate there (Matzke, 1951, p. 449).

Using the Nauta technique, which demonstrates degenerating axons to their terminations, Bowsher (1958 [in the Macaque monkey]) substantiated Matzke's findings and added one minor additional area of fiber termination: the nucleus paralemniscalis, a small triangular nuclear area in the rostal mesencephalon situated between the medial lemniscus and cerebral peduncles.

Subsequent Nauta and/or Fink-Heimer studies reconfirm that the fibers

of the medial lemniscus have their principle origin from the opposite gracile and cuneate nuclei and subsequent termination in the posteroventral lateral nucleus of the thalamus (Bowsher, 1958, 1961 [in the Macaque monkey]; Hand and Liu, 1966 [in cats]; Lund and Webster, 1967 [in rats]; Ebbesson, 1968 [in cats]; Schroeder and Jane, 1971 [in the tree shrew]). However, these studies also indicate a diffuse fiber component which has been observed to terminate in various nuclei. Among these are: (1) the dorsal accessory nucleus of the inferior olive; (2) the pars medialis or magnocellularis of the medial geniculate body; (3) the regions of the collicular plate; (4) the zona incerta; (5) the pontine gray; (6) the posterior thalamic complex, and (7) the red nucleus (Bowsher, 1958, 1961 [in the Macaque monkey]; Hand and Liu, 1966 [in cats]; Lund and Webster, 1967 [in rats]; Ebbesson, 1968 [in cats]; Schroeder and Jane, 1971 [in the tree shrew]). Some of the diffuse fiber components are ipsilateral terminations in the external nucleus of the inferior colliculus (Schroeder and Jane, 1971 [in the tree shrew]) and the spinal trigeminal nucleus (Hand and Liu, 1966 [in cats]).

Research Rationale

From the foregoing synopsis, one can readily see that the dorsal column-medial lemniscal system is not as simple as is indicated in some of the current neuroanatomy textbooks. There is much controversy and uncertainty related to the finer details of this system, and anatomical study of any of its aspects is readily warranted. Any such anatomical study would necessarily involve any one of three

different aspects: (1) the dorsal column fibers and their connections; (2) the medial lemniscal fibers and their connections, or (3) the dorsal column nuclei. In order for fiber degeneration studies to be undertaken, a detailed knowledge of the dorsal column nuclei would be a necessary prerequisite. Precise afferent terminations would be hampered without a knowledge of the intra-nuclear arrangements and their dendritic patterns. Then, too, efferent fiber studies would be greatly facilitated by a detailed knowledge of the cytoarchitecture of these nuclei. For this reason, a detailed study of the cytoarchitecture and dendritic patterns was decided to be expedient.

Selection of Experimental Animal

From the historical synopsis, one readily can see that the experimental animals of choice have been almost exclusively the cat, the rat, or the monkey. Very few studies have been done on other animals. No detailed study of the dorsal column nuclei of the opossum has been done. Verification of the two basic cell types is given in two small paragraphs by E. Oswaldo-Cruz and C. E. Roch-Miranda (1968) in their stereotaxic atlas, and minor descriptions of the component nuclei is made by Ariëns Kappers, Huber and Crosby (1960); but little else has been done. This seems relatively strange in view of the opossum's phylogenetic status. The opossum is a marsupial and a relatively primitive mammal. For these reasons the opossum would be an excellent experimental animal for comparative neuroanatomical studies.

Anatomical Correlates for Electrophysiological Division into Subnuclei

In the historical review it was suggested that division of the nucleus gracilis and nucleus cuneatus seemed possible on the basis of electrophysiological studies. This concept was somewhat confirmed by detailed anatomical studies which involved cytoarchitectural differences. Further confirmation seems necessary and the primitive opossum would be an excellent animal for comparative study. Then, too, this question arises: If the cytoarchitecture reveals subnuclei, do differences in the total dendritic patterns disclose yet another anatomical basis for division of nuclei?

Uniqueness of Dehdritic Patterns

In describing the dendritic patterns within the nucleus gracilis and nucleus cuneatus, mention was made of a unique "glomerular" arrangement in the rat as opposed to primates and cats. Being a marsupial and a primitive mammal, it seems probable that a different dendritic pattern could exist in the opposum.

Most dendritic studies involve individual neurons rather than total dendritic patterns. Interest is focused on an isolated cell and its arborizations. Interest also needs to be focused on the total dendritic pattern or patterns. The individual dendritic patterns for round cells and irregular cells have been described in other species, but not in the opposum. The total dendritic pattern or patterns of all the round cells and all the irregular cells as group entities has not been described. This information could supply an anatomical basis which would

correlate with the type of afferency (i.e., touch as opposed to proprioception) or with the origin of the afference (i.e., fibers from the spinal cord might enter into those areas where a certain dendritic pattern exists, while fibers from the cerebrum might enter those areas where a different dendritic pattern exists). Knowledge of the total dendritic patterns would supply precise information as to synaptic possibilities existing within the nuclei.

The Interneuron

Mention was made of electrophysiological evidence for presynaptic inhibition and an interneuron was hypothesized as causing this inhibition. The synaptic part of this inhibition was verified anatomically by electron microscopy when small terminal boutons were identified on larger terminal boutons. Anatomical verification of the source cell for this presynaptic inhibition is as yet unknown. Two cell sources are possible, the round cell and irregular cell. The possibility also exists that a collateral axon could be the source for the presynaptic inhibition. Determination of the source cell can only be verified with a detailed anatomical study of the neuron fibers.

Mensurational Data

Almost no mensurational data is given on the dorsal column nuclei. Neuron size and rostrocaudal extent are the two categories of data which are commonly given. Other mensurational data is sadly lacking and would seem necessary. For example, knowledge about the total cell population and how and

where these cells are distributed within the nuclei could supply information relative to afferency and efferency. Round cells supply the efferent fibers to the medial lemniscus. Knowing the number of round cells as opposed to the number of lemniscal fibers would give information as to how many irregular cells contribute to the lemniscal system, and/or how many other fibers might come from other nuclear sources. From this, one could approximate the number of irregular cells that distribute fibers to other areas or act as interneurons.

From the preceding paragraphs, it seems apparent that a detailed study of the cytoarchitecture and dendritic patterns of the dorsal column nuclei in the opposum is warranted.

CHAPTER II

MATERIALS AND METHODS

This study is based upon the neuroanatomical investigation of 30 specimen of the Virginia opposum, Didelphis marsupialis virginiana. Eighteen of the animals were adults, four of the animals were approximately four to six months old, and eight of the animals were approximately six to 12 weeks old. The animals of each age group were evenly divided by sex. The 18 adult animals were anesthestized by an intraperitoneal injection of diabutol (1 cc/5 lbs. body weight). The animals then were infused with a physiological saline solution introduced directly into the left ventricle. Fixation followed with a 10% formalin-saline solution. The brains were then removed in toto and fixed in a 10% formalin solution for several weeks to insure adequate fixation. Because of their small size, the 12 younger animals were not infused; rather, their brains were removed in toto and fixed in 10% formalin. The infratentorial brain stem, cerebellum and upper cervical cord of each specimen were removed by a transverse cut just below the level of the inferior colliculus. The cerebellum was partially or completely removed and the remaining brain stem and cervical spinal cord was divided into three pieces: (1) cervical spinal cord; (2) lower medulla below the obex, and (3) upper medulla (open medulla) above the obex.

Specimens from five adult animals, and one each of the two younger groups were embedded in paraffin utilizing the alcohol-xylol technique. Specimens from three adult and two younger animals were cut transversely in a plane at right angles with the floor of the fourth ventricle. Of the two remaining adult animals, one specimen was sectioned in a plane horizontal to the floor of the fourth ventricle, and the other was sectioned in a plane parasagittal to the midline raphe. The brain stems were sectioned at 15 micra, mounted on glass and every fifth section in serial order was stained using a luxol fast blue-basic fuchsin procedure (a modification of Szabo, 1965). The luxol fast blue component of this stain technique stains myelin blue while leaving nuclear areas unstained. This allows for easy determination of nuclear areas. The basic fuchsin component of this stain technique stains neuron cell bodies red while leaving the myelin unstained. This gives cytological details of the neuron and allows for easy determination of cell populations.

From the remaining 23 opossum brain stems stained, 18 were stained in block utilizing a modified Golgi technique (Anderson, 1954) and the remaining specimens stained via the Ranson-pyridine silver technique (Davenport, 1960). These silver impregnation methods were utilized for determination of neuron dendritic and axonal processes. The stained blocks were embedded in paraffin and sectioned at 50 microns. Every section was mounted in serial order, deparaffinized in xylol and covered utilizing permount and glass cover slips.

On one adult specimen, serial sections were prepared in which three

different stains were employed. One series (sections 5, 10,15, etc.) was stained using the luxol fast blue-basic fuchsin method. An adjacent series (sections 6, 11, 16, etc.) was stained with thionin. The next adjacent series (sections 7, 12, 17, etc.) was stained with a Bodian stain (protargol-silver technique, Davenport, 1960). These differentially stained series facilitated comparison of different neuronal characteristics on adjacent slides.

In comparing the slides from one specimen with those of another specimen, the obex was the common point of reference. Sections equidistant from the obex were always compared regardless of the stain employed. In comparing data in the tables, for example, slide 25 is the obex for animals #1 and #2, while slide 21 is the obex of animal #3. These slides are comparable. Similarly, the next slide either rostrally or caudally represents an equidistant spacing from the obex. In tabulating the average cell populations and average nuclear areas, slides equidistant from the obex were averaged.

All mensurational data was taken from adult animals stained with luxol fast blue-basic fuchsin or thionin stained sections and are given in the text or in various tables and graphs found in the Appendix. This mensurational data includes: (1) range in sizes of round cells and irregular cells; (2) numbers of round cells and irregular cells found in various sections throughout the rostrocaudal extent of the dorsal column nuclei; (3) ratio of round cells to irregular cells throughout the rostrocaudal length of the nuclei; (4) maximum rostrocaudal extent, maximum medial to lateral width and maximum dorsal to ventral thickness; (5) nuclear area

Specimens from five adult animals, and one each of the two younger groups were embedded in paraffin utilizing the alcohol-xylol technique. Specimens from three adult and two younger animals were cut transversely in a plane at right angles with the floor of the fourth ventricle. Of the two remaining adult animals, one specimen was sectioned in a plane horizontal to the floor of the fourth ventricle, and the other was sectioned in a plane parasagittal to the midline raphe. The brain stems were sectioned at 15 micra, mounted on glass and every fifth section in serial order was stained using a luxol fast blue-basic fuchsin procedure (a modification of Szabo, 1965). The luxol fast blue component of this stain technique stains myelin blue while leaving nuclear areas unstained. This allows for easy determination of nuclear areas. The basic fuchsin component of this stain technique stains neuron cell bodies red while leaving the myelin unstained. This gives cytological details of the neuron and allows for easy determination of cell populations.

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On one adult specimen, serial sections were prepared in which three

of every tenth section throughout the rostrocaudal extent of the nuclei, and (6) volume of each nucleus.

Whenever possible, measurements were taken directly from the slides. To facilitate these measurements, a reticle graduated in millimeters was placed in the eye piece of a microscope. The reticle was then calibrated against a stage micrometer which was also graduated in millimeters. In this way, true cell sizes, dorsal to ventral depth and medial to lateral width could be directly measured. The rostrocaudal length of both the nuclei was determined by taking the total number of sections and multiplying by the thickness of the section.

Area determinations for each of the nuclei were taken from each section in the following manner. First the entire section was photographed. The lens system used produced a negative which gave a mangification of 13 diameters. The negative was then projected through a lens system which gave an additional magnification of 6 diameters. This represents a total magnification of 78 diameters. Tracings of each nuclear area were made from the negatives and their boundaries verified by microscopic examination. The nuclear areas were then measured with a planimeter and corrected to their real values by dividing the total magnification of 78 diameters. Tracings of each nuclear area were made from the negatives and their boundaries verified by microscopic examination. The nuclear areas were then measured with a planimeter and corrected to their real values by dividing the total magnification squared into the magnified areas. Graphic representation of the areas throughout the rostrocaudal extent of each nucleus is given in the Appendix.

The volume of each of the nuclei was determined in conjunction with the area determinations. As mentioned previously, the area occupied by each of the nuclei on the magnified tracings was measured with a planimeter. Three measurements of each tracing were made and the average values plotted on a graph. Utilizing the planimetric measurement of the "area under the graph" method (Dornfeld, et al., 1942) the volumes were computed by the following mathematical formula:

$$V = \frac{(xyt)}{m^2} p$$

where V = the volume of the organ in cubic millimeters; p = the planimeter reading of the area below the graph in millimeters squared; x = the number of sections per horizontal millimeter; y = the number of millimeters squared per vertical millimeter; m = the linear magnification; and t = the thickness of the sections in millimeters.

Cell counts were accomplished by means of a special microscope with a motor-driven stage which scanned the nucleus in which the cells were counted. A hair lined reticle was placed in the microscopic eye piece and each cell type was counted as it passed the hair line. An electronic digital counter recorded the numbers of cells as they were counted. Tabulations of the results as well as graphic representation are found in the Appendix.

All the figures are un-retouched photomicrographs printed from 35 mm negatives of pantomic X film. The microscopic optical systems were varied in order to best reproduce those aspects of the nuclei which were of special interest. All photomicrographs are found in the Appendix.

CHAPTER III

OBSERVATIONS AND DESCRIPTIONS

Nucleus Cuneatus

The nucleus cuneatus of the opossum exists as a rounded column of neurons extending from the upper cervical spinal cord to about the middle of the medulla. The caudalmost portions of the nucleus are relatively uniform in diameter. However, as the nuclear column extends rostrally toward the obex, the circular diameter of the column gradually increases from 0.2 mm to its maximum diameter of 0.8 mm. From the obex rostrally, the nucleus gradually bends from a medial position to a more lateral position. The angle of deflection is approximately 60^{0} from the original rostrocaudal axis of the nucleus. There is also a very slight deviation dorsally (3^{0} to 4^{0} from the original axis). Concurrent with this lateral deviation, the nucleus diminishes in diameter from 0.8 mm at the obex to 0.3 mm at the rostral pole. From the obex, the nucleus extends 3.9 mm caudally and 1.5 mm rostrally. The total rostrocaudal dimension is thus 5.4 mm. If the nucleus continued in a straight line instead of deviating laterally, the true length of the nucleus would probably be increased to about 7.0 mm.

About 0.2 mm caudal to the obex, a thin plate-like nuclear bridge connects the ventromedial portion of the nucleus cuneatus with the ventrolateral

portion of the nucleus gracilis (Figures 20, 21). This plate-like nuclear bridge exists until the rostral termination of the nucleus gracilis. The caudal edge of the bridge is relatively thick (0.1 mm) while the rostral edge of the bridge is relatively thin (0.03 mm).

The fasciculus cuneatus covers the dorsal half of the nucleus cuneatus throughout the rostrocaudal extent of the nucleus. The ventral half of the nucleus is adjacent to the cells of the reticular formation throughout this same rostrocaudal extent. About 0.5 mm from its rostral pole, the dorsolateral surface of the nucleus lies adjacent to the lateral cuneate nucleus (Figure 21). Its ventromedial relationship with the nucleus gracilis was described in the preceding paragraph in conjunction with the nuclear bridge.

Cell Types

The cells of the nucleus cuneatus correspond with those described in other animals. There are two general types of cells, the identification of which is based on the general shape of the cell body. Thus there are round cells and irregular cells.

The round cell, as its name implies, has a cell body which is characteristically round. This multipolar cell has an extremely convex surface between its dendrites which gives it a general rounded appearance (Figures 1-4). The roundness of the cell body is further accentuated by its extremely large, round nucleus (Figures 2, 4). The nucleolus is very distinct within the clear nucleus (Figures 2, 4). The cytoplasm exhibits a fine, evenly dispersed Nissl material

with only an occasional occurrence of tigroid bodies (Figures 2, 4). Cell size varies from 20 mu to 30 mu in diameter.

The irregular cell, as its name implies, has a cell body that exhibits a variety of shapes. Three types were commonly found in the opossum: (1) triangular; (2) multipolar, and (3) fusiform. The triangular irregular cell exhibits a plane surface between its dendrites in assuming its characteristic triangular shape. This cell is usually quite small (8 mu to 10 mu in diameter), with an indistinct nucleus and nucleolus. The multipolar irregular cell exhibits a plane or concave surface between its dendrites which easily distingish it from the multipolar round cell which has a convex surface between its dendrites. This cell is usually quite small (8 mu to 10 mu in diameter) but many are quite large (25 mu to 35 mu in diameter). The larger multipolar irregular cell characteristically has a large clear nucleus with a distinct nucleolus (Figures 5, 6). The fusiform irregular cell is spindle-shaped with the central portion of the cell being ovoid or ellipsoid. The nucleus is similarly shaped and usually contains a distinct nucleolus (Figures 5, 6). These cells range from 10 mu to 15 mu in diameter.

Cellular Arrangements

A cellular gradient along the rostrocaudal axis of the nucleus cuneatus occurs in the opossum. This gradient is characterized by three cytoarchitecturally distinct regions: (1) a central region extending rostrally and caudally about 0.6 mm on either side of the obex; (2) a region rostral to this central region,

and (3) a region caudal to the central region.

The area rostral to the obex is characterized by small round cells (20 mu in diameter) and irregular cells (8-10 mu in diameter) randomly dispersed throughout the region. The irregular cells outnumber the round cells by an approximate ratio of three or four to one (Tables 1-4, Graph I).

The obex region is also characterized by small round cells (20 mu in diameter) and small irregular cells (8-10 mu in diameter). However, several distinctive features help differentiated this region from the other two regions. First, the round cells tend to be arranged in small, isolated clusters of four to eight cells. These cells also occur singly in a random fashion throughout the region. Second, the irregular cells, while still outnumbering the round cells, have a diminished ratio of two to one. This is considerably less than the cellular ratios of the other two regions. Third, the irregular cells, while randomly dispersed throughout the area, are frequently found near and between clusters of round cells.

The caudal region is characterized by a sparse population of rather large round cells (25 mu to 35 mu in diameter) randomly dispersed throughout the region. The small irregular cells (8-10 mu in diameter) also are scattered randomly in this region and grossly outnumber the round cells by about a six to one ratio (Tables 1-4, Graph I).

Cell counts of the cuneate nucleus throughout its rostrocaudal extent (Tables 1-4, Graph I) demonstrate definite trends relative to the two types of

cells and their distribution. In general, there is an increase in the numbers of round cells and irregular cells from the caudal pole to a point about 0.6 mm rostral to the obex. From this point to the rostral pole, the numbers of each cell type gradually decrease. Concomitant with the increase of cell numbers from the caudal pole to the obex, there is a decrease in the ratio of irregular cells to round cells. Similarly, the ratio of irregular cells to round cells increase as the rostral pole is approached.

As mentioned in the chapter on materials and methods, the sections from which the cell counts were made were also used to determine nuclear areas throughout the rostrocaudal extent of the nucleus cuneatus. In this manner, direct comparison of cell populations and nuclear areas could be made on a slide by slide basis. The individual area determinations for each experimental animal and their averages are given in Tables 5-8 in the Appendix. A rostrocaudal plot of the averages of the three areas is given in Graph II, also in the Appendix.

From the tables, and particularly from the graph, the following general observations can be made: (1) a gradual increase in the size of the nucleus cuneatus occurs from the rostral pole to the obex. This increase in the diameter of the nucleus was previously mentioned (see page 28). (2) A gradual decrease in the size of the nucleus cuneatus occurs from the obex to the rostral pole. This too, correlates with other mensurational data previously given concerning the diminution of nuclear diameter. (3) The rostrocaudal length of the nucleus is readily apparent, as was mentioned in the chapter on materials and methods.

(4) A direct comparison of the nucleus cuneatus with the other dorsal column nuclei easily is made relative to areas, volumes and rostrocaudal extent.

Dendritic Patterns

The isolated round cell of the nucleus cuneatus exhibits rather sparse dendritic arborizations. Several dendritic trunks usually arise from the cell body (Figures 9-16) and these dendritic trunks usually give rise to secondary dendrites which in turn give rise to tertiary dendritic branches (Figures 9, 10, 12, 13, 14, 15). Quaternary dendritic branching was not observed. Small dendritic spines or gemmules were almost always present (Figure 10). The round cell was characterized by dendritic patterns of the radiate type as described by Ramón-Moliner (1962). The dendrites also appeared slightly wavy as they project outwardly from the cell body (Figures 9, 15). Dendritic branching of the round cell occurred in every direction (i.e., dendrites extended dorsally, ventrally, medially, rostrally, etc.). Such dendritic patterns are described as being multiplanar.

The individual dendritic pattern of the round cell within the round cell cluster was similar to that of the isolated round cell. The combined arborizations of the cells within the cluster gave a dendritic pattern in which the dendrites projected toward the imaginary center of the cluster. Other dendrites of each of the cells within the cluster projected in a direction outward from the cluster (Figures 11, 14). The combined dendritic pattern of the round cell clusters was very dense centrally, and less dense outward from the center of the cluster.

The dendritic pattern of the irregular cell was demonstrated by only a few cells, and these were, at best, poor examples. No examples of multipolar or triangular irregular cells were seen. Only irregular cells of the fusiform type were seen. In this cell, long radiating dendrites on each end, with one or two secondary dendrites, typified the pattern (Figure 9). Of the few fusiform cells observed, each appeared to be oreinted in only one direction. Any one cell might be oriented in a rostrocaudal direction, while another cell might be oriented in a dorsoventral direction, while still another cell might be oriented in a medial to lateral direction. Such cells are described as being planar in orientation.

The total rostrocaudal dendritic pattern of the cuneate nucleus appeared thicker at the margin of the nucleus where it merged with the fasciculus cuneatus. The ventral margins of the nucleus appeared rather sparse of dendrites. Then, too, the total dendritic pattern rostral to the obex became less dense as the rostral pole was reached.

Axon Patterns

Axons of the round cell are not easily distinguishable from dendrites. In Golgi stained materials, axons are characteristically longer, thinner and of more uniform diameter throughout their central to distal length. Multiple branching of axons rarely occurs and when branching does occur, the fiber that branches is of the same diameter as the trunk from which it originated. Dendrites, on the other hand, exhibit large, thick, trunk-like origins that gradually become thin as the dendrite radiates peripherally. Then, too, multiple branching of dendrites

is common.

Two types of axons were observed arising from round cells. One type, which was by far the most common, originated from the cell body of the round cell (Figures 9, 10). The second axon type originated from the dendrite of a round cell (Figures 11, 12, 13). Axons from round cells were directed either ventrally or medially. No axons were observed projecting dorsally or laterally from a round cell. No collateral axons were observed.

Other axons in the nucleus cuneatus were commonly observed. Axons from the fasciculus cuneatus entered the nucleus cuneatus as three or four large fascicular bands (Figure 24). These thick bands gradually branched into smaller fascicles as they penetrated ventrally into the nucleus. Axons projecting through the cuneate nucleus from the fasciculus cuneatus were less numerous in sections caudal to the obex (Figure 8). Axons projecting from the fasciculus cuneatus in the region of the obex were definitely more numerous than in any other region of the nucleus cuneatus.

Axons comprising the internal arcuate fibers (Figure 25) appear as thin, attenuated fascicles projecting ventromedially from the nucleus cuneatus. The decussation of internal arcuate fibers occurs at the same level as does the pyramidal decussation, but has a greater rostral extent than the pyramidal decussation.

The pyramidal decussation occurs in the caudal regions of the cuneate nucleus and has the same rostrocaudal extent as does the nucleus of Bischoff

(Figures 22, 23). At their decussation, the pyramidal fibers consist of thick, bulky fascicles which project to a position just ventral and lateral to the nucleus cuneatus. Some of the fibers appear to enter the nucleus cuneatus from its ventralmost aspect (Figures 22, 23).

In one of the Golgi preparations, axons entering the nucleus cuneatus ventrally were seen to come into synaptic contact with a round cell (Figures 14-16). Because of their direction of entry in the nucleus, these axons were probably pyramidal fibers.

Nucleus Gracilis

The nucleus gracilis of the opossum exists as a rounded column of neurons situated medial to the nucleus cuneatus. The caudalmost portions of the nucleus are relatively uniform in diameter. As the nuclear column extends rostrally toward the obex, the circular diameter increases from 0.1 mm to its maximum diameter of 0.6 mm. This greatest diameter occurs at a point 0.75 mm caudal to the obex. From this point rostrally, the nucleus gradually diminishes in size until a rostral pole diameter of 0.15 mm occurs. The nuclear column extends 3.3 mm caudally from the obex and 0.9 mm rostrally from the obex. The total rostrocaudal length is 4.2 mm. About 2.1 mm from the caudal pole, the nuclear column undergoes a 60^{0} angle bend laterally. Concurrent with this lateral deviation is a very slight dorsal deviation (3^{0} to 4^{0} from the original rostrocaudal axis). If the nucleus continued in a straight line instead of bending laterally, the true length of the nucleus would probably be increased to about

4.5 mm. A nuclear bridge exists between the cuneate and gracile nuclei and has already been described.

The fasciculus gracilis is directly incorporated with the nucleus gracilis throughout the caudal half of the nucleus. This being the case, the caudal half of the nucleus gracilis is reticular and indistinct as a nuclear entity (Figures 17, 18). Rostral to the halfway point of the nucleus, the fasciculus gracilis becomes incorporated with the medial portions of the fasciculus cuneatus, and the nucleus gracilis becomes a distinct nuclear entity (Figures 19-21).

Cell Types

The cell types of the nucleus gracilis are morphologically similar to those described with the nucleus cuneatus.

Cellular Arrangements

A cellular gradient along the rostrocaudal axis of the nucleus gracilis occurs in the opossum. This gradient is characterized by two cytoarchitecturally distinct regions: (1) a caudal region, and (2) a rostral region. The two regions are approximately the same size and shape and have the same rostrocaudal dimensions.

The caudal region is composed of large round cells (25 mu to 30 mu in diameter) and small irregular cells (8-10 mu in diameter). Both cell types are randomly scattered throughout the rostrocaudal extent of the region. Only occasionally do four or five round cells form a cell cluster (Figures 17, 18). The caudal region has a rather sparse neuron population.

The rostral region is composed of small round cells (20 mu in diameter) and small irregular cells (8-10 mu in diameter). The round cells occur singly and in small clusters of four to five cells, which tend to be located in the central portions of the region. The irregular cells are randomly scattered throughout the region with a moderate tendency to be situated along the periphery of the nucleus. The rostral region has the greatest neuron populations (see Tables 1-4).

Cell counts of the nucleus gracilis throughout its rostrocaudal extent (Tables 1-4) demonstrate definite trends relative to the two types of cells and their distribution. In general, the number of round cells in the caudal half of the nucleus remains fairly constant with only a very slight increase in numbers rostrally. The number of irregular cells gradually increases from the caudal pole rostrally. The ratio of irregular cells to round cells remains constant at approximately five to one.

The rostral half of the nucleus gracilis demonstrates a definite increase in the numbers of both round and irregular cells (Tables 1-4). The peak number of round cells and irregular cells occurs about the midpoint of the rostral region (about 0.75 mm caudal from the obex). Despite the increase in cell numbers, the ratio of irregular cells to round cells remains constant at about five to one throughout the rostral region. In fact, the ratio of irregular cells to round cells remains constant at five to one throughout the entire rostrocaudal extent of the nucleus (see Table 4).

Dendritic and Axon Patterns

Unfortunately, none of the silver impregnations rendered discernable results relative to the dendritic and axonal patterns of the nucleus gracilis. All the impregnations were too intense and background precipitation clustered and obscured the pattern of distribution. The literature has reported similar dendritic and axonal patterns for the nucleus gracilis and nucleus cuneatus in several species (Valverde, 1966 [in the rat]; Ramon y Cajal, 1909 [in various animals]). Similar dendritic and axonal patterns are assumed to exist in the opossum.

Nucleus of Bischoff

The nucleus of Bischoff in the opossum is a plate-like lamina of neurons situated on the midline between the right and left gracile nuclei. This rectangular lamina is 0.06 mm thick (medial to lateral), 0.4 mm high (dorsal to ventral), and 2.85 mm long (rostrocaudal dimension). The nucleus extends about 150 mu farther caudal than the nucleus gracilis and does not reach the obex rostrally.

Cell Types

The cell types composing the nucleus of Bischoff are similar to those described in the nucleus cuneatus.

Cellular Arrangements

A cellular gradient along the rostrocaudal axis of the nucleus of Bischoff

does not occur in the opossum. The nucleus appears homogeneous throughout its rostrocaudal extent. Small round cells (20 mu in diameter) and irregular cells (8-10 mu in diameter) occur in a random fashion throughout the nucleus. The round cells exhibit no tendency toward clustering. A slight increase in the numbers of round cells occurs from the caudal pole toward the rostral pole of the nucleus. The irregular cells are equally distributed throughout the nucleus (Tables 1-4). Caudally, the ratio of irregular cells to round cells is approximately six to one. This ratio changes rostrally to about four to one. The nucleus ends abruptly at both the caudal and rostral ends.

Dendritic and Axon Patterns

As with the nucleus gracilis, the nucleus of Bischoff was impregnated with too much silver. Since the nucleus of Bischoff is considered to be a specialized portion of the nucleus gracilis, it is assumed that its dendritic and axonal patterns would be similar to those of the nucleus gracilis. This being the case, its dendritic and axonal patterns also would be similar to those of the nucleus cuneatus.

CHAPTER IV

DISCUSSION AND CONCLUSIONS

From the foregoing observations and descriptions of the dorsal column nuclei of the opossum, it is apparent that there are many points of similarity in the component nuclei. However, it is also evident that numerous differences also occur. Points of similarity and dissimilarity are noticed when comparing the opbssum with other species reported in the literature.

Cell Types

The two basic cell types, round cells and irregular cells, were found in each the nucleus cuneatus, nucleus gracilis and nucleus of Bischoff. These cell types appear to correlate with other descriptions of the cell types found in other animals reported in the literature (see Chapter I, Introduction). The range in size for the round cells (20 mu to 30 mu in diameter) and for the irregular cells (8-10 mu in diameter) also closely corresponds with that given in the literature.

Cellular Arrangements

Nucleus Cuneatus

The cellular gradient along the rostrocaudal axis of the nucleus cuneatus of

the opossum is different from that reported for other animals. Previous investigations have reported a rostrocaudal gradient which divides the nucleus cuneatus into two regions, a rostral region, and a caudal region. In the opossum, as opposed to the cat, there is a threefold division of the nucleus cuneatus into a rostral region, an obex region and a caudal region. Similarities between the cellular regions of the cat and opossum cuneate nuclei are as follows: (1) the size of the round cells is similar; (2) "cell nests" (Hand, 1966) in the caudal region of the cat are comparable to the clustering of round cells in the obex region of the opossum, and (3) the "reticular" region of the cat compares to the rostral region of the opossum.

On the other hand, the cellular gradient of the nucleus cuneatus reported in this study compares rather closely with the cellular gradient reported in Hand's study of the nucleus gracilis of the cat. The two descriptions agree in that (1) both nuclei are divided into three similar regions: rostral, obex and caudal regions in the opossum; "reticular", "cell nest" and "caudal" regions in the cat; (2) the three regions contain similar arrangements of cells (e.g., clusters of round cells found in the "cell nest" region compared to clusters of round cells found in the obex region); and (3) the cell sizes were comparable (slightly larger in the cat). A minor difference occurs in that the "cell nest" region is caudal to the obex in the cat, while the comparable region of the opossum is at the level of the obex and extends a short distance in both rostral and caudal directions.

In the literature review, the nucleus gracilis of the cat was reported to be divided into three regions on an electrophysiological basis relative to the size of

receptive fields. It is possible that an electrophysiological study on the nucleus cuneatus of the opossum might yield comparable results.

Nucleus Gracilis

The cellular gradient along the rostrocaudal axis of the nucleus gracilis of the opossum is different than the rostrocaudal cellular gradient described in the cat. Three regions are reported in the cat: the "reticular", the "cell nest", and the "caudal" regions. Only two regions exist in the opossum, the rostral and the caudal regions. In describing these regions, mention was made that the caudal regions of the nucleus were incorporated with the fibers of the fasciculus gracilis creating a reticulated, indistinct nuclear entity. In contradistinction, the rostral region is a distinct nuclear entity. Histogenesis of the nucleus gracilis (Taber, 1963 [in mice];) reveals a caudal portion older than the rostral portion. This small bit of supportive evidence tends to substantiate the division of the nucleus into two regions.

This indistinct caudal region causes one to ponder the possibility that this region is more primitive and less organized than the rostral region. Phylogenetic comparison of this nucleus with those of more primitive animals might reveal a nucleus with an even larger reticulated caudal portion. Perhaps the entire nucleus might exist in the reticulated form exhibited by the caudal region of the opossum. If the cat is considered to be more advanced phylogenetically, then the division of its nucleus into three regions might represent an evolutionary trend toward specificity of this nucleus in regard to both function and appearance. For these

reasons, more comparative studies over a wider range of animals would seem to be warranted.

In comparing the nuclear areas and/or volumes of the nucleus gracilis with that of the nucleus cuneatus, it is obvious that the nucleus cuneatus is much larger than the nucleus gracilis (Graph II). Cell counts reveal a much greater cell population for the nucleus cuneatus than for the nucleus gracilis (Tables 1-4). The greater size and cell population of the nucleus cuneatus would seem to indicate a more prominent functional role for this nucleus. The smaller, less cellularly populated nucleus gracilis might be indicative of a less prominent functional role. Behavioral observations of opossum in the wild and in captivity indicate that the forepaw or "hand" is used quite extensively. For example, the opossum frequently grasps food with the "hands" and holds it while eating. Then, too, when climbing trees, the "hands" are used much more extensively for climbing and grasping than are the "feet". The "hands" are used in grasping persimmons when in the tree feeding. When rummaging through the dump, the "hands" are used to turn items over for inspection. This prominent usage of the upper extremity would seemingly necessitate a larger nucleus with a greater cell population.

Reports in the literature also indicate a correlation of nuclear size to functional usage of the extremities. Ariëns Kappers, Huber and Crosby (1960) report: " . . . in cetaceans the nucleus gracilis is very small, as is to be expected in a form lacking posterior extremities and with such poorly developed skin sensibility. Nucleus cuneatus, although not large, is better developed in these animals,

a fact associated with the presence of anterior extremities." These authors also report that (1) in the seal the nuclei of the dorsal funiculi are more highly developed than in cetaceans; (2) in endentates both nuclei are highly developed, and (3) in Atelidae and Cebidae the greatest development of the nuclei of the dorsal funiculi is found. In these monkeys, the large size of the nucleus gracilis is associated with the lower extremity and tail and their role in their arboreal life.

In man both nuclei are well developed. Although the nucleus gracilis extends to the first cervical segment, it is smaller than is the same nucleus in the monkey. The predominant usage of the upper extremities with its highly developed skin sensibility contribute to the larger size of the nucleus cuneatus in man, (Yoshida, 1924; Ariëns Kappers, Huber and Crosby, 1960).

Nucleus of Bischoff

Very little concerning the nucleus of Bischoff can be found in the literature (Ariëns Kappers, Huber and Crosby, 1960; Bischoff, 1900). The literature shows that this nucleus is a specialized portion of the nucleus gracilis which is believed to be associated with those animals having a prehensile tail. This certainly seems true for the opossum. The opossum uses the tail as an additional grasping appendage when climbing trees. The infant opossum readily demonstrates the prehensibility of its tail by wrapping its tail around one's finger. That the nucleus of Bischoff is, in fact, associated with prehensile tails has not been substantiated directly. The opossum would be a good candidate for degeneration studies to confirm or refute this fact.

Because of the paucity of the literature, the information concerning the nucleus of Bischoff reported in this study may be the first detailed descriptions of this nucleus. Although the cell types have been reported (Ariën Kappers, Huber and Crosby, 1960; Bischoff, 1900), the cell counts, area measurements and other mensurational data are thought to be original.

The Role of the Irregular Cell

In correlating the information gained in this study with that of the literature, one question kept recurring: "What is the functional role of the irregular cell?" The literature does not designate a function for the irregular cell. As a matter of fact, this cell has been largely ignored in preference to the larger, more readily apparent round cell. The various published studies have designated the round cell as being the cell that gives rise to fibers destined for the medial lemniscus. The functional role of the round cell would be the rostral conduction of those impulses which deal in the eventual perception of descriminatory touch and proprioception. No role is assigned to the irregular cell.

The cell count data (Tables 1-4, Graph I) indicate an increase in the number of round and irregular cells from the caudal pole to a point just above the obex, with a subsequent diminution of cells occurring toward the rostral pole. At either pole, the ratio of irregular to round cells is greater than at the obex region. At no location throughout the rostrocaudal extent of the dorsal column nuclei does the number of round cells exceed the number of irregular cells. A greater ratio of irregular cells to round cells always occurs.

Mention has been made that the pyramidal fibers decussate at the same level at which the caudal regions of the nucleus cuneatus exist and that some of these fibers enter the nucleus. The literature also gives evidence for pyramidal fibers entering the nucleus cuneatus (the nucleus gracilis as well). Reports also indicate that the pyramidal fibers enter into synaptic relation with the irregular cell populations. It is interesting to note that the caudal regions of both the nucleus cuneatus and nucleus gracilis, were the irregular cells predominate, are at the same level of the pyramidal decussation. This seems to indicate pyramidal input in nuclear areas heavily populated with irregular cells.

Electrophysiological experiments have indicated the presence of presynaptic inhibition in the dorsal column nuclei, and have suggested that an interneuron is responsible for this inhibition. Electron microscopy has demonstrated small boutons synapsing on larger boutons and has indicated a strong possibility that this is the anatomical entity that functions in inhibition. The literature also mentions the existence of facilitatory input into the dorsal column nuclei.

Previously, mention was made that the fusiform cells exhibit a planar dendritic arrangement, while the round cells exhibit a multiplanar dendritic tree. A planar dendritic pattern means that the dendrites are orientated in one plane. A multiplanar dendritic arrangement means that the dendrites are oriented in every plane. The planar dendritic arrangement would probably limit the number of synaptic contacts on such a cell. The multiplanar dendritic pattern would tend to facilitate a greater number of synapses since it is oriented in a multiple number of planes.

The central region of the cell clusters present an excellent site in which a single cell could make multiple contacts with a number of round cells. The irregular cells are located around and in between the cell clusters.

A sequential listing of the certain observations facilitates a hypothesis as to the functional role of the irregular cell:

(1) Round cell axons are distributed to the medial lemniscus.

(2) No distribution of irregular cell axons is given.

(3) Dorsal column fibers synapse on round cells.

(4) Pyramidal fibers synapse on irregular cells.

(5) The number of round cells is greater in those regions where the pyramidal decussation occurs.

(6) Irregular cells are more numerous than round cells.

(7) Dendritic patterns of round cells create a large probability of greater numbers of synaptic contacts.

(8) Irregular cells are frequently found near round cell clusters.

(9) Presynaptic inhibition occurs in the dorsal column nuclei and is hypothesized as being induced by an interneuron.

(10) Facilitatory mechanisms reportedly exist in the dorsal column nuclei.

From the foregoing evidence one can speculate that the functional role of the irregular cell might be that of controlling and modifying input and output of the dorsal column nuclei. As an interneuron, the irregular cell could easily inhibit or facilitate the round cell.

In Chapter I, rationale for this study was given. This same rationale serves as a justification for the future study of additonal species. Comparative anatomical studies relative to the dorsal column-medial lemniscal system are sadly lacking. Furthermore, the lack of mensurational data makes for a formidable task when one tries to compare those species which have been studied. More investigations with more complete mensurational data are needed.

The exact functional role of the irregular cell has not been definitely determined. Such a task remains to be done and most definitely is warranted.

CHAPTER V

SUMMARY

The cytoarchitecture and dendritic patterns of the dorsal column nuclei in the opossum, Didelphis marsupialis vriginiana, have been described. Detailed morphological descriptions of the cells, their individual and total dendritic patterns also have been completed.

The following mensurational data have been obtained: (1) area distribution of the component nuclei throughout their rostrocaudal extent (Tables 5-8, Graph II); (2) rostrocaudal length and diameter measurements of each component nucleus; (3) volume of each nucleus; (4) cell populations of round cells and irregular cells throughout the rostrocaudal length of each component nucleus (Tables 1-4, Graph I), and (5) cell size relative to the two types of cells and where they are located.

Comparison among the various component nuclei with that of animals reported in the literature has been made in the following categories: (1) cell types; (2) cellular arrangements; (3) cellular distributions; (4) dendritic patterns; (5) cell numbers; (6) nuclear areas; (7) nuclear dimensions, and (8) nuclear volumes.

The functional role of the irregular cell has been hypothesized as being an interneuron which modifies the input and output of the round cells.

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APPENDIX

TABLE 1

CELL POPULATIONS OF DORSAL COLUMN NUCLEI

Caudal Pole to Rostral Pole Sequence
Left Side Nuclei of Animal #1

Slide No.*	Nucleus Gracilis		Nucleus of Bischoff		Nucleus Cuneatus	
	Round	Irregular	Round	Irregular	Round	Irregular
1					5	27
2					7	52
3			0	7	7	40
4	0	5	1	10	8	55
5	0	5	2	15	6	62
6	Slide Missing: No cell counts					
7	0	5	2	20	12	75
8	0	4	2	22	8	85
9	Poorly stained		Poorly stained		10	51
10	2	14	1	21	Torn out	
11	0	16	3	11	21	61
12	2	16	5	26	20	51
13	4	20	4	26	14	65
14	5	28	3	26	18	75
15	5	23	2	18	21	75
16	11	25	5	13	25	66
17	10	38	7	18	24	78
18	15	42	Nucleus not present		32	85
19	12	59			30	90
20	19	67			31	70
21	20	80			35	114
22	11	75			39	91
23	11	59			38	104
24	11	61			42	117
25	12	58			62	130
26	10	50			61	100
27	8	42			63	107
28	5	38			73	113
29	Nucleus not present				63	108
30					35	114
31					30	103
32					15	50
33					6	36
34					0	12

*Distance between slide numbers is 150 micra.

TABLE 2

CELL POPULATIONS OF DORSAL COLUMN NUCLEI

Caudal Pole to Rostral Pole Sequence
Left Side Nuclei of Animal #2

Slide No.*	Nucleus Gracilis		Nucleus of Bischoff		Nucleus Cuneatus	
	Round	Irregular	Round	Irregular	Round	Irregular
1					0	31
2					7	31
3			0	5	5	65
4.	0	3	2	12	10	58
5	0	11	3	15	10	62
6	1	8	3	18	9	60
7	0	7	3	20	6	65
8	3	13	4	23	7	71
9	2	12	3	22	12	62
10	0	13	3	21	18	62
11	0	19	3	21	15	73
12	5	13	5	25	18	87
13	4	15	5	21	11	92
14	4	24	3	26	14	90
15	4	18	3	22	26	86
16	6	25	5	19	22	61
17	10	46	9	23	31	69
18	14	57	8	17	34	102
19	16	50	3	11	32	109
20	22	69	Nucleus not present		39	103
21	22	91			28	124
22	12	62			31	100
23	10	57			44	110
24	12	52			45	114
25	12	56			46	100
26	10	50			82	115
27	5	35			70	111
28	5	32			100	130
29	0	28			78	103
30	Nucleus not present				29	120
31					25	100
32					18	47
33					0	31
34					0	15

*Distance between slide numbers is 150 micra.

TABLE 3

CELL POPULATIONS OF DORSAL COLUMN NUCLEI

Caudal Pole to Rostral Pole Sequence
Left Side Nuclei of Animal #3

Slide No.*	Nucleus Gracilis		Nucleus of Bischoff		Nucleus Cuneatus	
	Round	Irregular	Round	Irregular	Round	Irregular
1	0	8	0	8	5	26
2	2	10	0	11	6	30
3	0	8	3	16	8	38
4	2	13	5	20	8	39
5	5	21	4	18	8	41
6	0	18	1	15	12	55
7	4	22	3	19	15	48
8	2	15	2	16	17	61
9	4	27	1	18	16	63
10	3	21	3	18	21	68
11	2	19	5	20	17	62
12	4	20	3	15	17	60
13	4	15	0	12	23	69
14	5	31	6	17	25	73
15	17	44	6	26	29	83
16	19	38	Nucleus not present		37	77
17	15	43			46	89
18	12	49			53	102
19	10	41			50	97
20	13	38			65	104
21	14	40			60	107
22	9	33			63	106
23	10	27			67	96
24	4	22			55	88
25	Nucleus not present				45	85
26					27	71
28					17	66
29					5	30
30					3	26

*Distance between slide numbers is 150 micra.

TABLE 4

AVERAGE CELL POPULATIONS OF DORSAL COLUMN NUCLEI

Caudal Pole to Rostral Pole Sequence
Left Side Nuclei of Animals #1, #2, & #3

Slide No.	Nucleus Gracilis		Nucleus of Bischoff		Nucleus Cuneatus	
	Round	Irregular	Round	Irregular	Round	Irregular
1					3	29
2					7	42
3			0	6	6	53
4	0	4	1	11	9	56
5	0	8	2	13	7	47
6	1	9	1	10	8	45
7	0	7	3	19	9	66
8	2	10	4	22	8	65
9	3	16	3	13	10	51
10	1	15	2	19	15	58
11	1	16	3	17	17	64
12	3	15	4	22	18	66
13	4	21	3	22	14	73
14	4	24	3	23	18	78
15	4	20	3	20	21	74
16	7	23	4	16	21	62
17	8	53	5	18	26	72
18	11	43	7	17	30	87
19	15	51	4	18	30	94
20	20	58	Nucleus not present		36	83
21	16	71			36	109
22	12	62			41	98
23	10	32			44	104
24	12	30			51	112
25	13	51			56	112
26	10	44			69	107
27	8	35			67	105
28	5	31			76	110
29	0	28			62	99
30	Nucleus not present				30	102
31					24	89
32					13	42
33					3	31
34					0	14

AVERAGE CELL POPULATIONS

Caudal Pole to Rostral Pole Sequence

NUCLEUS CUNEATUS

GRAPH I

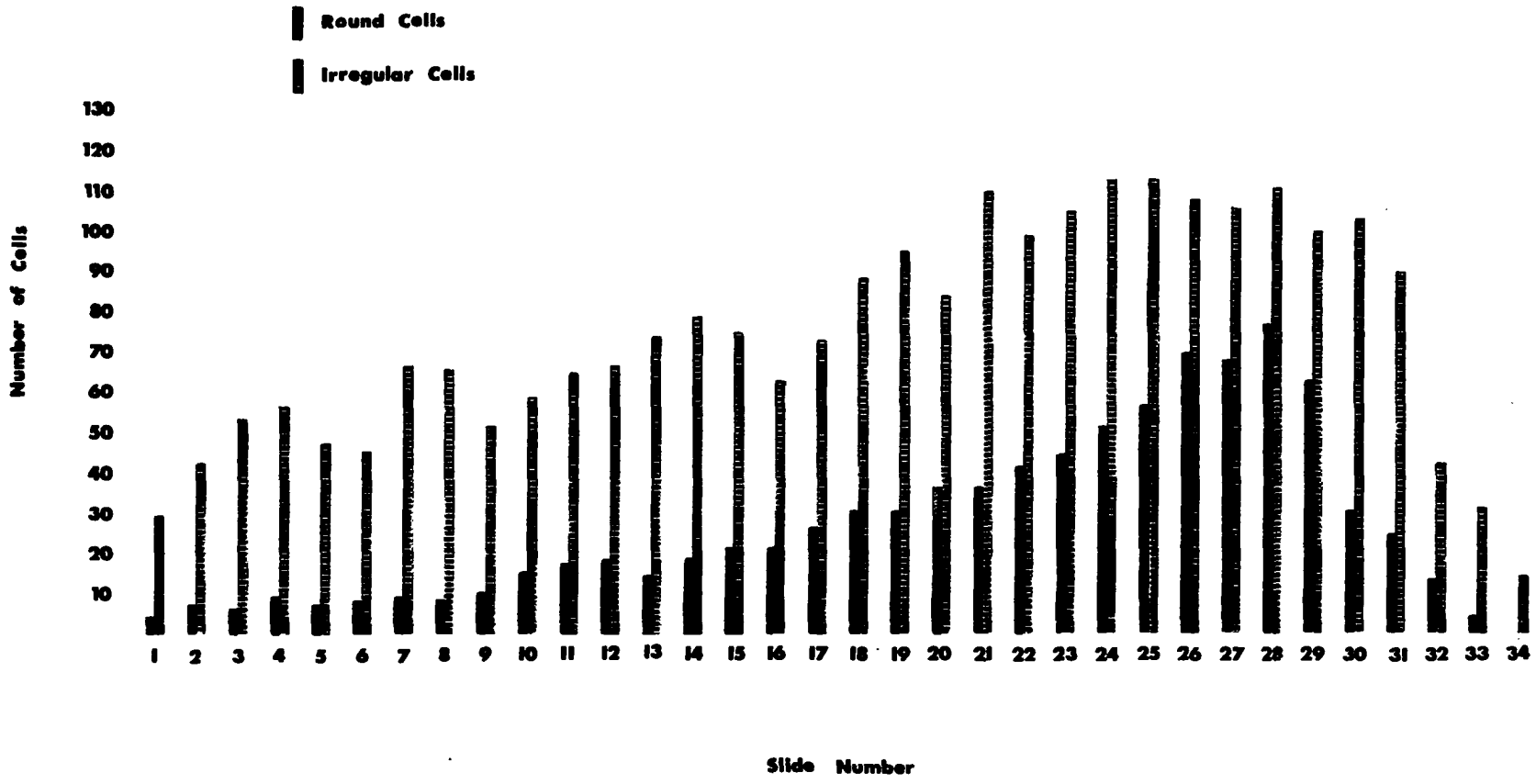


TABLE 5

NUCLEAR AREAS OF DORSAL COLUMN NUCLEI*

Caudal Pole to Rostral Pole Sequence
Left Side Nuclei of Animal #1

Slide No.	Nucleus Gracilis	Nucleus of Bischoff	Nucleus Cuneatus
1			3.8
2			3.8
3		0.2	3.7
4	0.4	0.4	4.1
5	0.6	0.6	4.4
6	Slide Missing: No area determination		
7	0.3	0.4	5.5
8	0.4	0.4	5.3
9	Poorly stained	Poorly stained	5.3
10	0.6	1.2	Torn out
11	1.0	1.2	6.4
12	1.1	2.0	5.8
13	1.1	1.3	5.3
14	2.5	2.7	7.3
15	1.8	2.2	9.3
16	2.2	2.5	9.2
17	4.5	1.2	8.1
18	6.1	Nucleus not present	10.0
19	7.2		14.7
20	8.1		16.3
21	8.4		21.1
22	6.2		18.5
23	5.5		16.1
24	4.1		16.8
25	3.9		17.8
26	3.2		18.7
27	2.1		18.2
28	3.0		19.6
29	Nucleus not present		15.8
30			15.8
31			13.1
32			4.8
33			4.2
34			1.1

*Measurements in square centimeters (78 X magnification).

TABLE 6

NUCLEAR AREAS OF DORSAL COLUMN NUCLEI*

Caudal Pole to Rostral Pole Sequence
Left Side of Nuclei of Animal #2

Slide No.	Nucleus Gracilis	Nucleus of Bischoff	Nucleus Cuneatus
1			2.5
2			3.0
3		0.2	3.6
4	0.4	0.5	3.8
5	0.6	0.7	4.0
6	0.5	0.5	4.0
7	0.5	0.2	4.0
8	0.3	0.4	4.2
9	1.0	0.6	4.5
10	1.1	1.0	5.8
11	1.0	1.0	7.1
12	1.0	1.3	7.9
13	0.9	1.3	8.8
14	1.4	1.8	9.6
15	1.9	2.2	10.9
16	2.3	2.4	10.6
17	4.3	2.4	10.6
18	6.6	2.0	9.7
19	7.1	1.6	16.3
20	7.4	Nucleus not present	17.1
21	7.4		19.4
22	6.1		19.0
23	5.7		19.4
24	3.9		18.1
25	4.3		17.3
26	3.0		16.3
27	2.5		15.2
28	2.1		16.5
29	1.0		8.4
30	Nucleus not present		8.4
31			4.5
32			3.6
33			3.6
34			2.8

*Measurements in square centimeters (78 X magnification).

TABLE 7

NUCLEAR AREAS OF DORSAL COLUMN NUCLEI*

Caudal Pole to Rostral Pole Sequence
Left Side Nuclei of Animal #3

Slide No.	Nucleus Gracilis	Nucleus of Bischoff	Nucleus Cuneatus
1	0.9	1.2	3.2
2	0.8	2.5	4.0
3	0.8	1.6	4.7
4	0.7	1.2	6.7
5	1.0	1.3	5.4
6	0.9	1.0	4.5
7	1.0	0.9	5.1
8	1.1	0.9	5.7
9	1.0	0.9	5.9
10	0.9	0.9	6.2
11	1.1	1.0	5.2
12	1.3	1.1	4.3
13	1.8	1.1	7.0
14	2.3	1.1	9.7
15	2.7	1.1	10.1
16	3.1	Nucleus not present	12.5
17	2.4		11.2
18	1.8		11.0
19	1.8		10.3
20	1.9		10.5
21	1.3		9.4
22	0.8		9.2
23	0.4		8.3
24	0.4		8.8
25	Nucleus not present		7.4
26			4.8
27			6.3
28			5.9
29			5.6
30			2.6

*Measurements in square centimeters (78 X magnification).

TABLE 8

AVERAGE NUCLEAR AREAS OF DORSAL COLUMN NUCLEI*

Caudal Pole to Rostral Pole Sequence
Left Side Nuclei of Animals #1, #2, & #3

Slide No.	Nucleus Gracilis	Nucleus of Bischoff	Nucleus Cuneatus
1			3.1
2			3.4
3		0.2	3.6
4	0.6	0.7	3.7
5	0.7	0.9	4.1
6	0.7	1.0	4.4
7	0.5	0.9	5.4
8	0.6	1.0	4.9
9	0.9	0.8	4.8
10	0.9	1.0	5.5
11	1.0	1.0	6.4
12	1.0	1.4	6.5
13	1.0	1.2	6.8
14	1.0	1.8	7.4
15	1.3	1.8	8.2
16	1.7	2.0	8.9
17	2.1	1.6	9.3
18	3.7	2.5	9.9
19	5.1	1.6	14.5
20	5.8	Nucleus not present	11.6
21	6.2		17.2
22	5.8		12.6
23	4.7		15.3
24	4.4		14.8
25	3.1		14.8
26	3.0		14.4
27	2.2		14.1
28	1.3		14.5
29	1.7		9.7
30	1.0		10.2
31	Nucleus not present		7.8
32			4.7
33			3.5
34			2.0

*Measurements in square centimeters (78 X magnification).

AVERAGE NUCLEAR AREAS

Caudal Pole to Rostral Pole Sequence

(Magnification Factor X 68)

GRAPH II

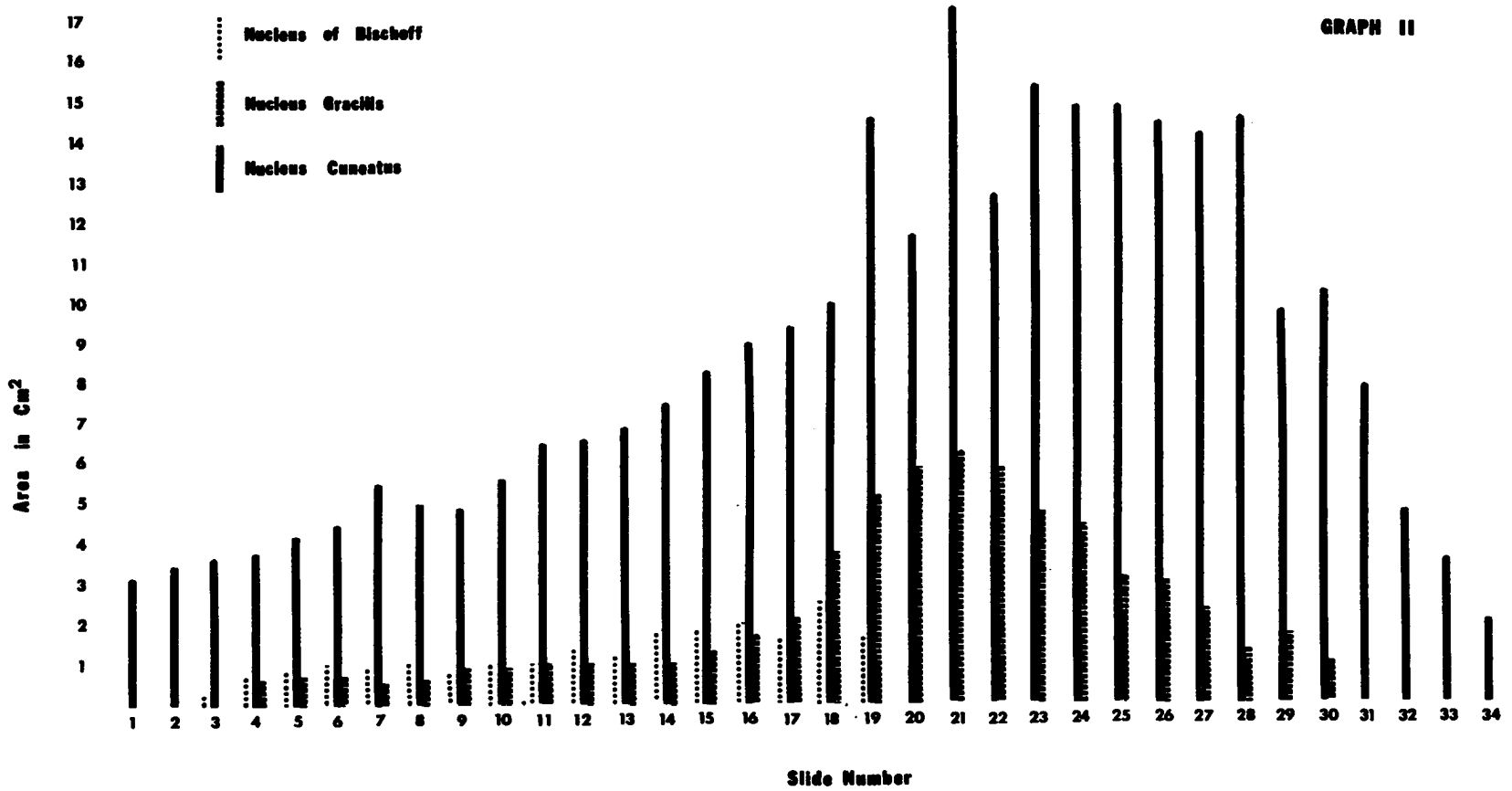


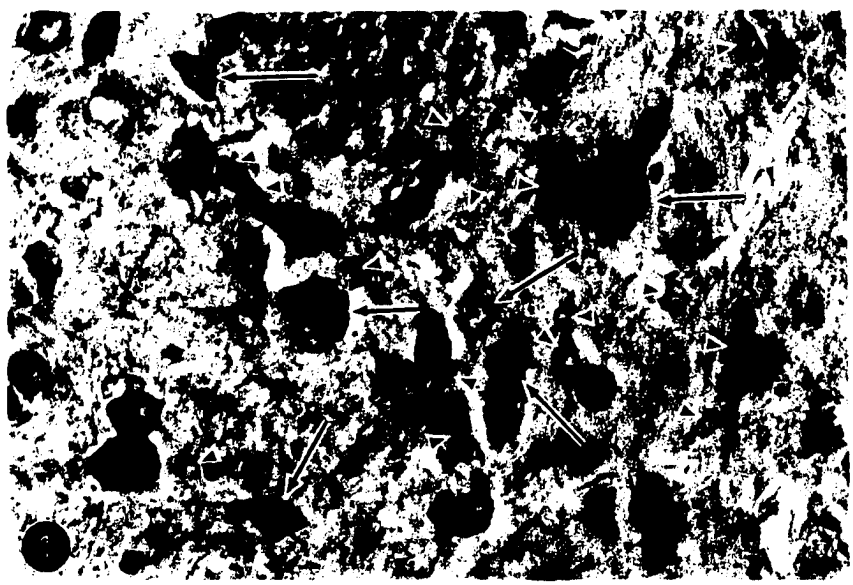
PLATE I

Luxol Fast Blue - Basic Fuchsin Stain

Figure 1. A cross section through the caudal portion of the Nucleus Cuneatus. Typical round cells (arrows) and irregular cells (arrowheads) can be seen. 300 X.

Figure 2. Higher magnification of the central cells of Figure 1. Note the distinct nucleolus (n) within the cell nucleus (N) of the large round cells. The round cells (arrows) are obviously larger than the irregular cells (arrowheads). 600 X.

PLATE I



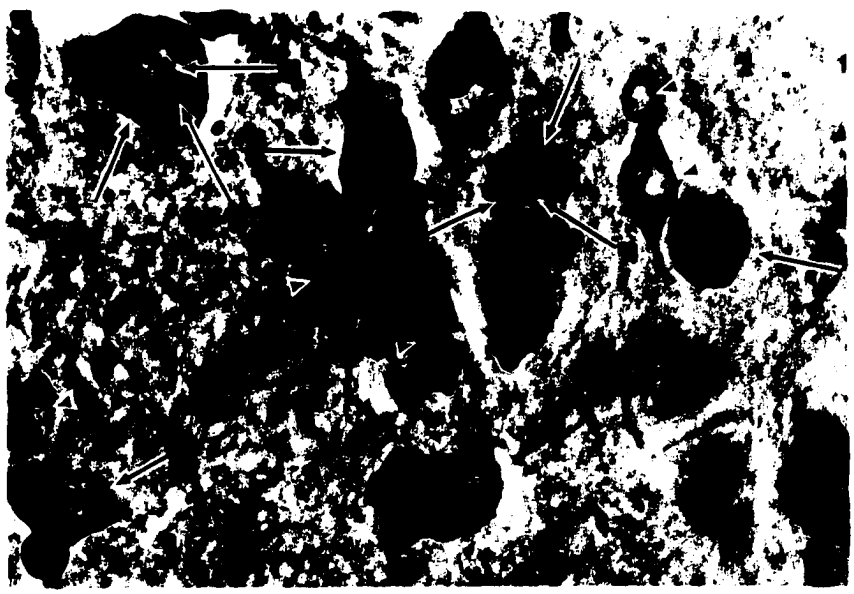


PLATE II

Luxol Fast Blue - Basic Fuchsin Stain

Figure 3. A cross section through the Nucleus Cuneatus at the level of the obex. Note the clustering of the larger round cells (arrows) in a circular fashion. Note also the smaller irregular cells (arrowheads) randomly dispersed throughout the nucleus. 300 X.

Figure 4. Higher magnification of a round cell cluster from the central portion of Figure 3. Observe the contrast in size between the larger round cells (arrows) and the smaller irregular cells (arrowheads). 600 X.

PLATE II

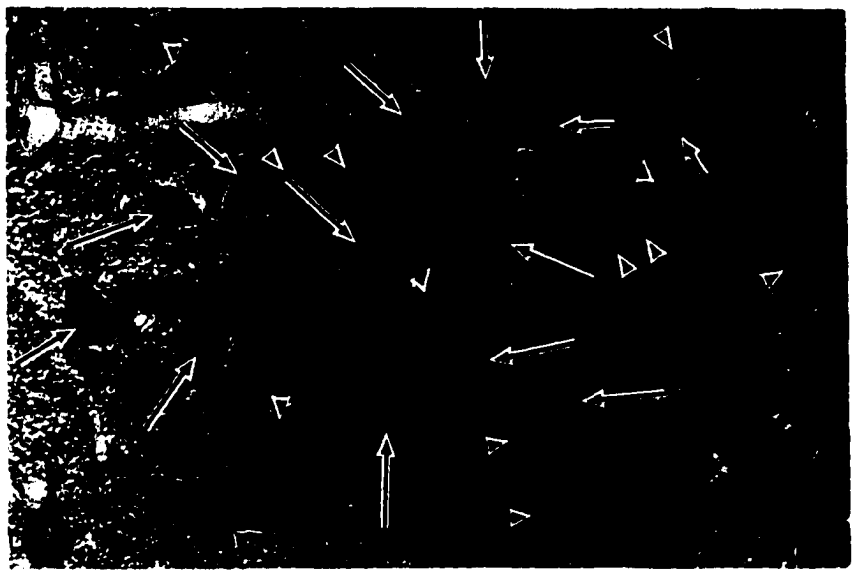


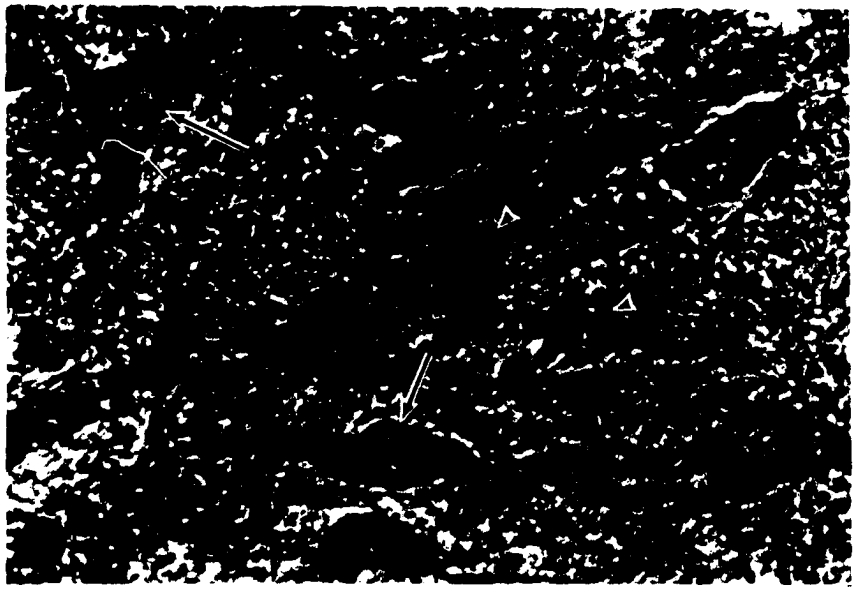
PLATE III

Luxol Fast Blue - Basic Fuchsin Stain

Figure 5. Cross section through the Nucleus Cuneatus at the level of the obex. Note the typical irregular cells (arrows). Their multipolar and fusiform cell bodies readily distinguish them from the rounded cell bodies of the round cells (arrowheads). 600 X.

Figure 6. Multipolar shaped irregular cell demonstrating a distinct nucleolus (n) within a clear nucleus (N). A fusiform irregular cell (arrow) and several round cells (arrowheads) are also present. 600 X.

PLATE III



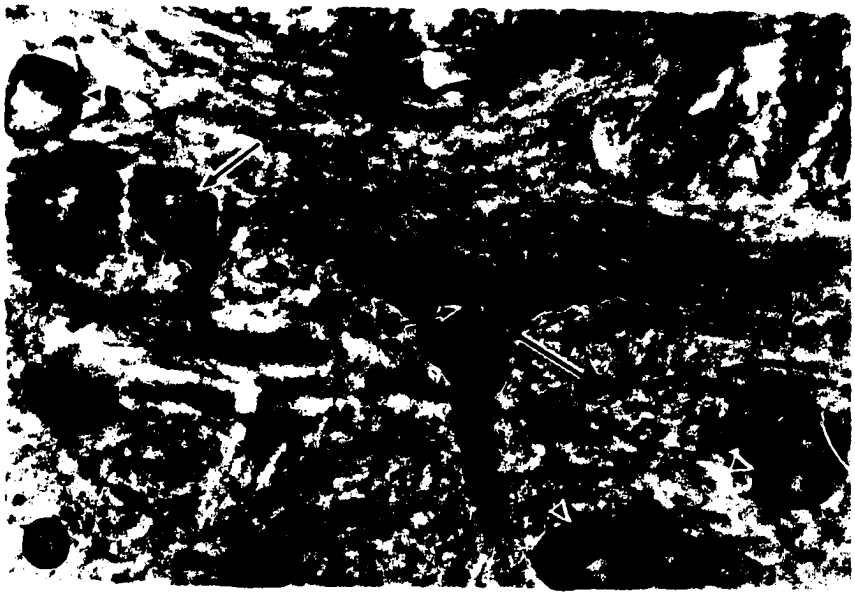


PLATE IV

Golgi Silver Impregnation

Figure 7. Cross-section through the Nucleus Cuneatus just rostral to the obex. Small diameter axons (arrowheads) can be seen coursing through the nucleus in a dorsal to medial direction. These axons originate from the fasciculus cuneatus or cells within the nucleus. 150 X.

Figure 8. Cross section through the caudal portion of the Nucleus Cuneatus. Axons (arrowheads) through caudal sections are not as numerous as those around the obex. Contrast with Figure 7. 150 X.

PLATE IV

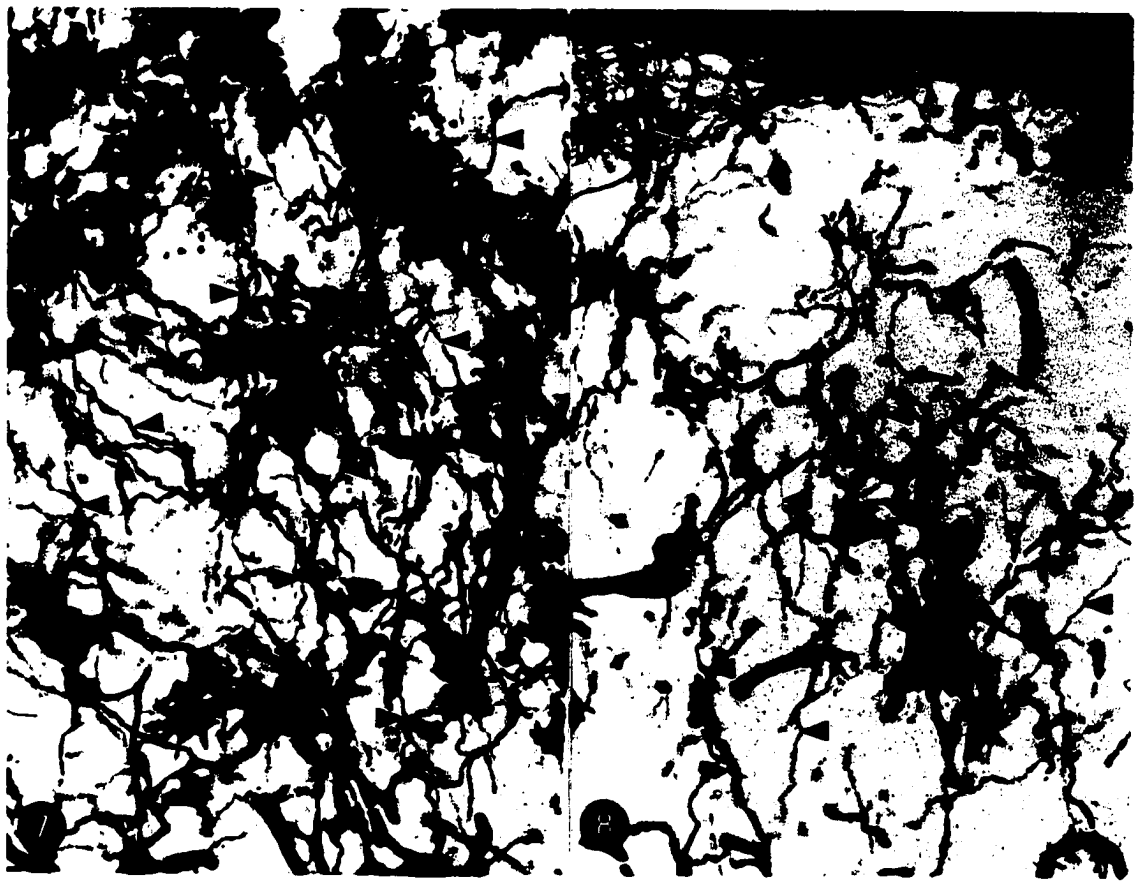


PLATE V

Golgi Silver Impregnation

Figure 9. Typical round cell of the Nucleus Cuneatus. The thick dendrites (arrowheads) branch, becoming smaller as they extend distally from the cell body. The single axon (arrow) is thin with a relatively uniform diameter throughout its length. 150 X.

Figure 10. Higher magnification of Figure 9. Observe the ventrally directed axon (arrow) and the branching dendrites (arrowheads). Dendritic spines or gemmules (lines) can be observed on the dendrites. 300 X.

PLATE V

PLATE VI

Golgi Silver Impregnation

Figure 11. Cross section through the Nucleus Cuneatus demonstrating a round cell with its axons (arrow A) branching from a dendrite (arrowhead). A cluster of round cells (black arrows) can be observed also. The dendrites of this cluster project toward the center of the cluster as well as outward from the center. 150 X.

Figure 12. Higher magnification of the round cell in Figure 11. Notice (1) the extreme length of the medially directed axon (arrow); (2) the relatively uniform diameter of the axon (arrow) in contrast to the bulky, trunk-like dendrite (arrowhead), and (3) the absence of branches along the axon (arrow) in contrast with the dendritic trunk (arrowhead). 300 X.

Figure 13. Higher magnification of the same cell. Observe the three dendritic branches (arrowheads) of the main dendritic trunk (double arrowhead). 600 X.

PLATE VI

PLATE VII

Golgi Silver Impregnation

Figure 14. Cross section of the Nucleus Cuneatus just caudal to the obex. A cluster of round cells (black arrows) have dendritic patterns which are directed toward the center of the cluster as well as directed outward. A round cell with three small afferent axons (arrowheads) is located toward the bottom of the figure. 150 X.

Figure 15. Higher magnification of the round cell in Figure 14. The three afferent axons (arrowheads) are seen to come into synaptic contact with the round cell. Only two of these contacts (arrows) can be focused. 300 X.

Figure 16. Higher magnification of the same cell. Synaptic clefts can be observed as small spaces at the ends of the arrows. 600 X.

PLATE VII

PLATE VIII

Luxol Fast Blue - Basic Fuchsin Stain

Figure 17. Cross section through a caudal portion of the Nucleus Gracilis (NG). Observe the thin Nucleus of Bischoff (NB) between the two portions of the Nucleus Gracilis. Round cells (arrows), irregular cells (arrowheads), and a round cell cluster can also be observed. The intermingling of the Fasciculus Gracilis causes the nuclei to appear indistinct. 90 X.

Figure 18. Higher power magnification of the round cell cluster (arrows) of Figure 17. Notice the irregular cells (arrowheads) scattered throughout the nuclei. 300 X.

PLATE VIII

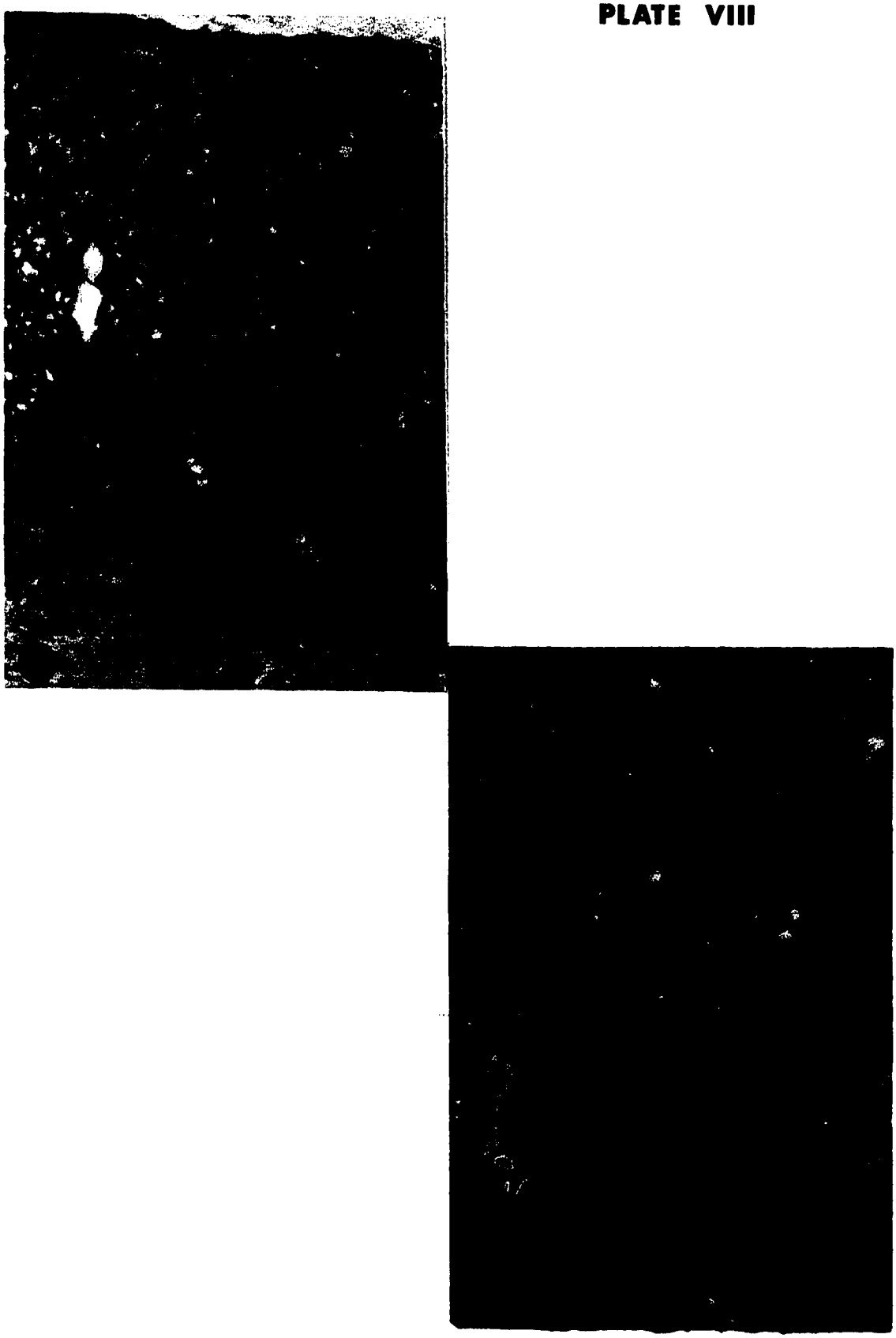


PLATE IX

Luxol Fast Blue - Basic Fuchsin Stain

Figures are in a Caudal-to-Rostral Sequence

Figure 19. Cross section through the Nucleus Gracilis (NG) just caudal to the obex. The nucleus has become distinct (compare with Figure 17) and the Nucleus of Bischoff is no longer present. 90 X.

Figure 20. Cross section through the Nucleus Gracilis (NG) and Nucleus Cuneatus (NC) just caudal to the obex. A thin nuclear connection (arrows) extends between the two nuclei. 90 X.

Figure 21. A cross section rostral to the obex through the Nucleus Gracilis (NG), Nucleus Cuneatus (NC) and Lateral Cuneate Nucleus (LC). Observe the following: (1) the Nucleus Gracilis (NG) has diminished in size from Figures 19 to 21; (2) the nuclear bridge between the Gracile and Cuneate Nuclei is thinner (arrows), and (3) the caudal beginning of the Lateral Cuneate Nucleus (LC). 90 X.

PLATE IX

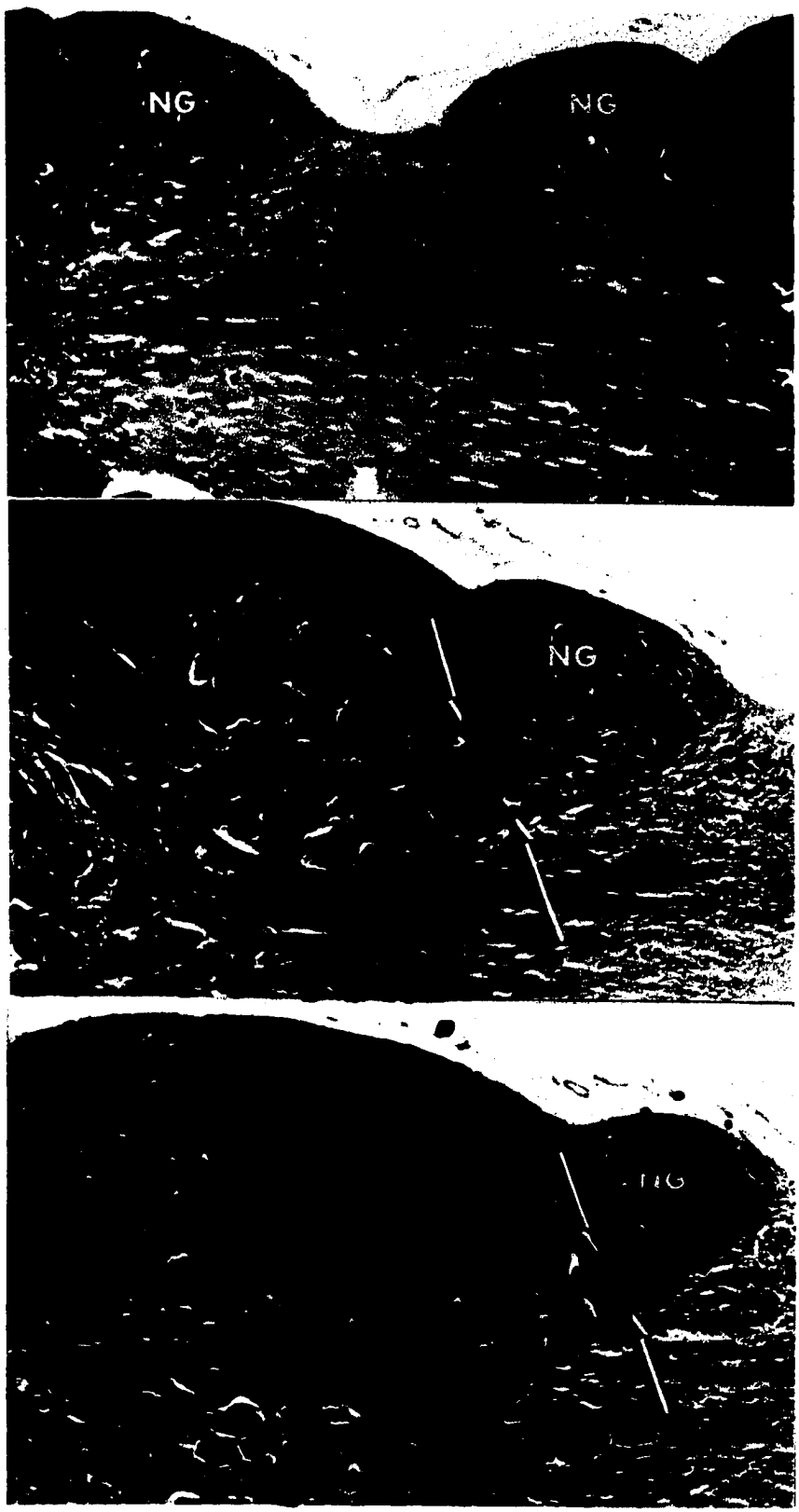


PLATE X

Luxol Fast Blue - Basic Fuchsin Stain

Figure 22. Cross section through the medulla caudal to the obex. Pyramidal fibers (arrowheads) are seen decussating across the midline from the Pyramids (P). The Pyramidal fibers (arrowheads) are directed dorsolaterally to a point just ventral and lateral to the Nucleus Cuneatus (NC). 90 X.

PLATE X

PLATE XI

Bodian Protargol-Silver

Figure 23. Cross section through the medulla caudal to the obex. Pyramidal fibers (arrowheads) are seen in relationship to the Nucleus Cuneatus (NC) and Nucleus Gracilis (NG). 90 X.

PLATE XI

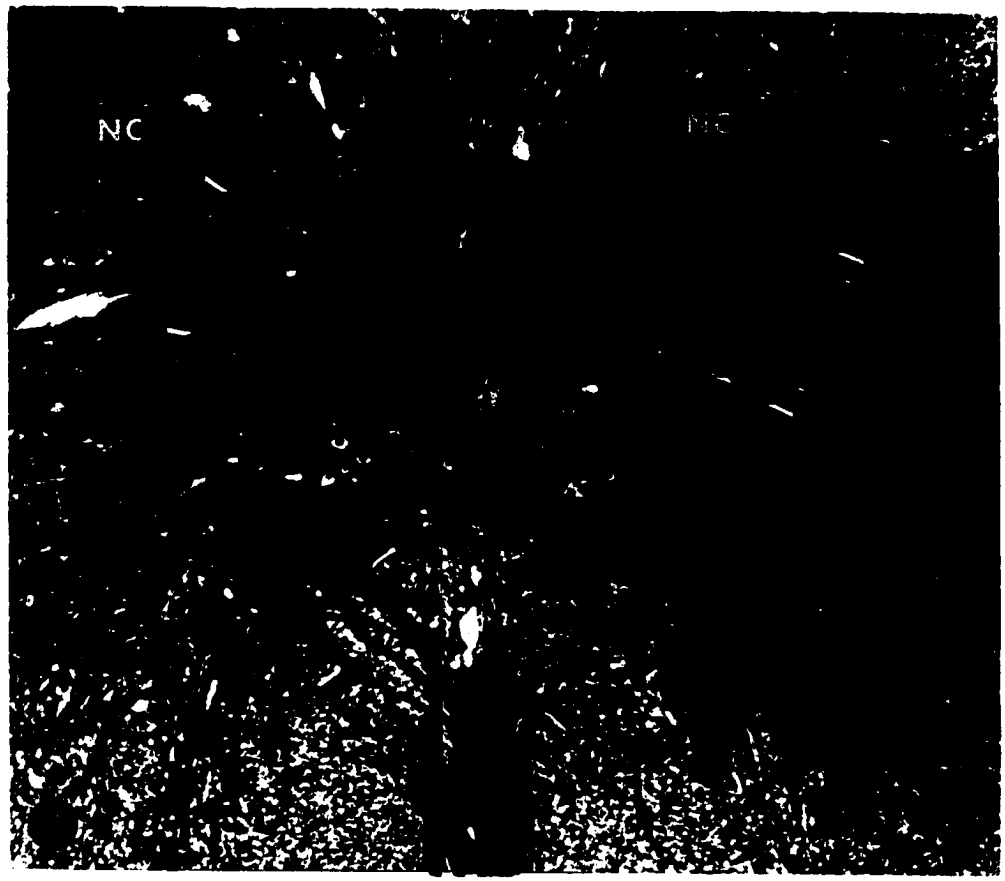


PLATE XII

Bodian Protargol-Silver

Figure 24. Cross section through the Nucleus Cuneatus (NC) at the level of the obex. Observe the fascicles (arrowheads) from the Fasciculus Cuneatus (FC) projecting ventrally into the Nucleus Cuneatus (NC). 150 X.

Figure 25. Internal arcuate fibers (arrowheads) coursing through the ventral medulla. They appear thin and attenuated in comparison to the pyramidal fibers (arrowheads) of Figures 22 and 23. 150 X.

PLATE XII