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CORTICOSPINAL FIBERS IN A PROSIMIAN PRIMATE,

GALAGO

By

George Edward Goode

B.A., University of Virginia, 1966

Thesis

submitted in partial fulfillment of the requirements for the
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at the Medical College of Virginia

Health Sciences Division

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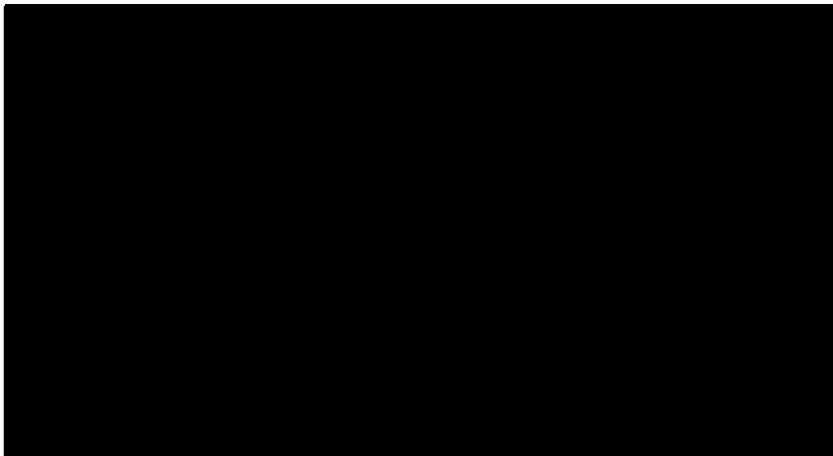
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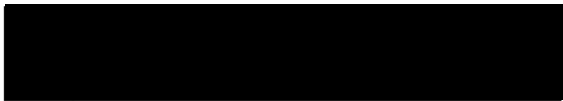
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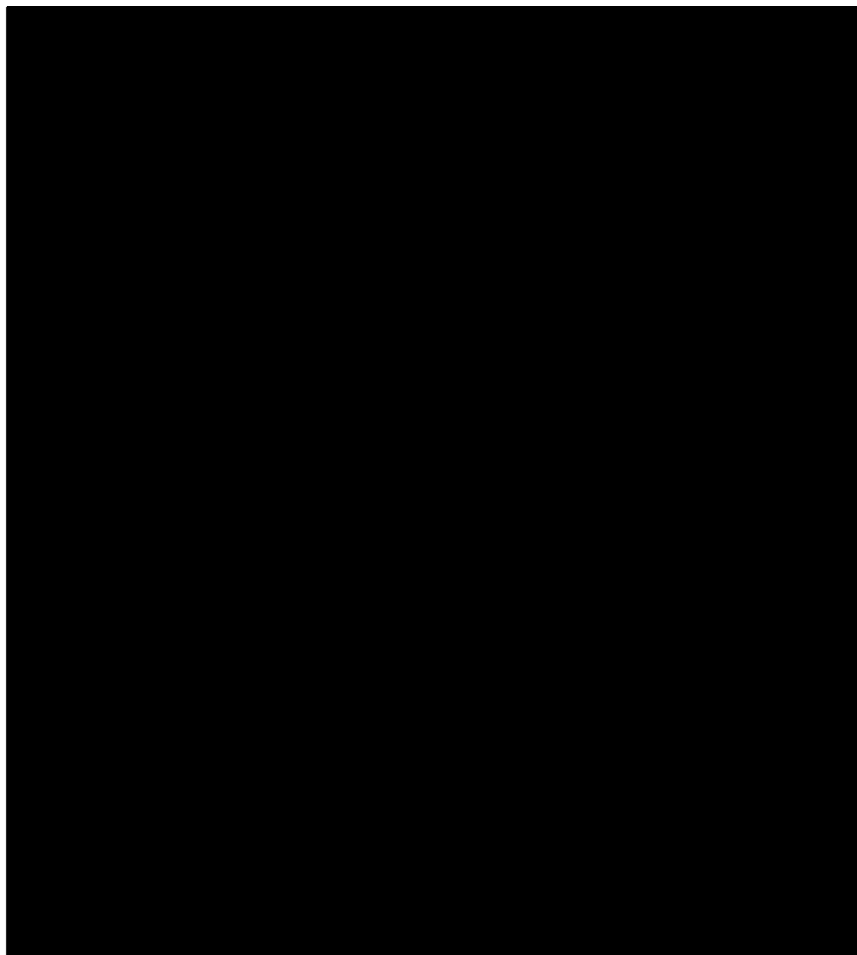


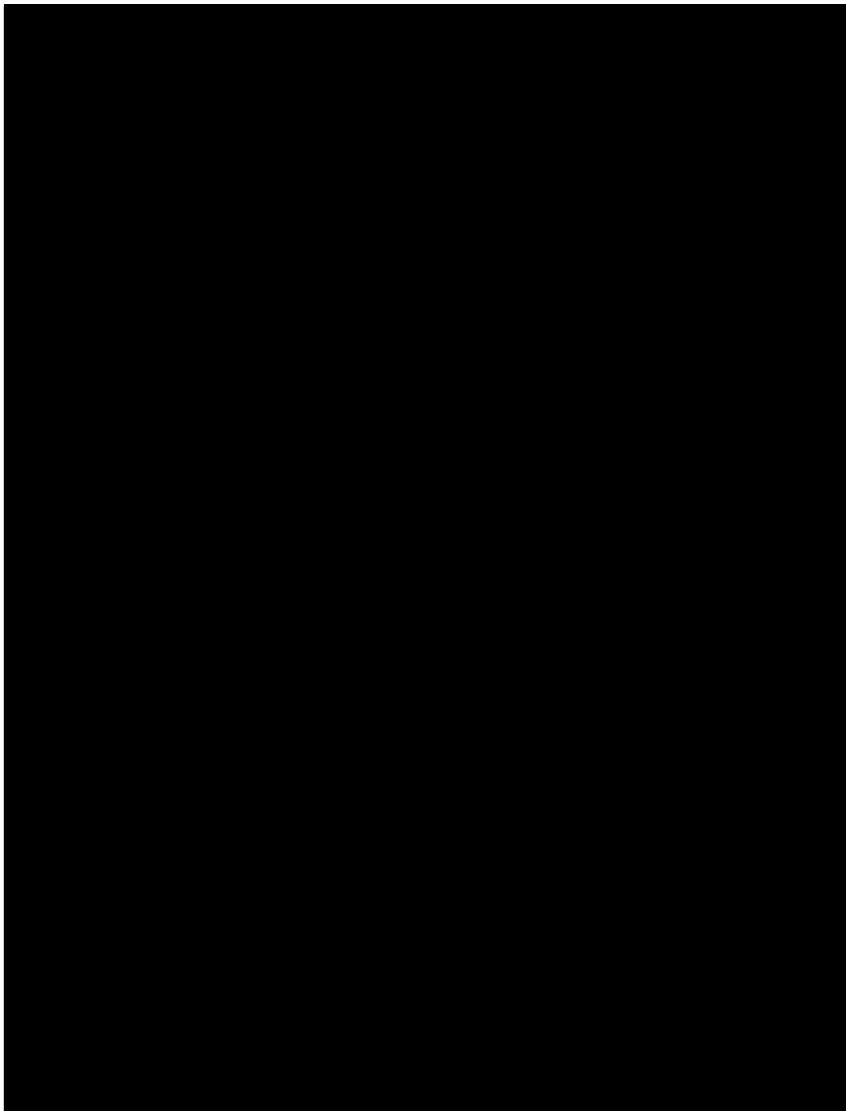
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Dean of the School of Basic Sciences and Graduate
Studies

CURRICULUM VITAE





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Introduction

The function of the central nervous system cannot be understood from inspection of a single region, for each cell and fiber has discrete connections. Therefore, a study of the nervous system requires distinct approaches. One fundamental approach has been the study of comparative neuroanatomy.

In a comparative study of the evolution of the primates and subsequently man, the investigator is confronted with a variety of animal forms. Each form represents an end product of a long vertical line of evolutionary development. The problem is to try to reconstruct the vertical line (ancestral forms) from the horizontal end products (extant forms).

The order Primates has two suborders: (1) the Prosimii - composed of six families - Tupaiidae, Lemuridae, Indriidae, Daubentoniidae, Lorisidae and Tarsiidae and (2) the Anthropoidea - also composed of six families including the Old and New World monkeys, the great apes and man. One group of the suborder Prosimii is the family Lorisidae. The living members of the family are represented by the lorises of India and Southeast Asia

and the galagoes and pottos of Africa. Characters these animals share with the higher anthropoid primates are seen in the osteology of the middle ear and the medial wall of the orbit (Le Gros Clark, 1959). They also have orbits encircled by bone, three kinds of teeth, a well developed caecum, true nails and a pseudo-opposable thumb. In habit, these animals are omnivorous, nocturnal and arboreal. In progression, the lorisooids are less tied to the quadrupedalism of many lemurs (Osman Hill, 1953). The lorises have a slow deliberate mode of hand-over-hand locomotion, their limbs are subequal in length. In contrast, the galagos locomote by a rapid, saltatory behavior and have pelvic limbs much longer than pectoral limbs. Both of these means of progression effect an orthograde (erect or semi-erect) posture of the trunk and a tendency for a different mode of balancing the head on the spine.

Some authors regard the vertical clinging and leaping of galagos as the earliest locomotor specialization of primates (Napier and Walker, 1967; Napier, 1967). From the post-cranial osteology of early Miocene Lorisidae (Walker, 1970) and from a comparative osteological,

behavioral and paleontological study (Napier and Walker, 1967), it appears that this locomotor pattern was present in early Eocene and subsequent Miocene prosimians. These authors conclude that vertical clinging and leaping is the earliest known primate locomotor specialization and preadaptive to some or possibly all subsequent patterns of primate progression-quadrupedalism, brachiation and bipedalism.

Although comparative neuroanatomical investigations have utilized the anthropoid primates, (mainly Macaca) rodents and carnivores (chiefly the cat), the prosimian primates have been relatively ignored. Yet their locomotor behavior and their propensity toward bipedalism make them an interesting model for a study of central nervous pathways related to locomotion.

Statement of Proposal

The present study was undertaken in order to determine: (1) the cortical origin of spinal projections, (2) whether or not the somatotopic organization of the cortex is maintained within the spinal terminations, and (3) the locations of spinal nuclei under direct cortical influence, in a vertical clinging and leaping primate.

Rationale

The utilization of animals other than man for a study of this nature is easily justified on the grounds that man is inaccessible for most experimental approaches. In addition, some investigators expect that the structure of other animals may be simpler and many exemplify man's structural and functional patterns in a less complex form. Some comparative studies even state that certain animal species may be closer to a presumed ancestral state and, therefore, will give information concerning the conditions from which man evolved. This position is exemplified in the search for the ideal archetype from which all present versions of animal features are derived.

Evolutionary principles clarified by Simpson, Grant, Mayr and Gain (Gans, 1969) make it quite clear that present day forms are not to be considered remnants of some past evolutionary state. One must then look at functional and structural patterns of the nervous system and attempt to discriminate between newly evolved and phylogenetically retained conditions. The problem, according to Le Gros Clark (1959) is to separate characters of common inheritance from characters of individual acquisition.

One approach that may solve this problem is the use of divergent forms. The use of divergent forms assumes that different solutions to functional problems will be contrasted on a presumably similar genetic background. Thus, if two closely related forms differ only in limited functional and structural characteristics, the probability increases that a given structural difference may be recognized as being related to an observed difference of function. It is with these considerations that this study was conceived.

Literature Review

Descending central nervous system pathways associated with motorsensory function can be classified as corticospinal and subcorticospinal projections (Kuypers, Fleming, and Farinholt, 1962). Projections from the brainstem (red nucleus, tectum, vestibular nuclei and reticular formation) are examples of the phylogenetically old subcortical motor system. Collectively, these pathways represent the main motor system of non-mammalian vertebrates.

In addition to these subcorticospinal pathways, mammals have a direct corticospinal system. This system is composed of axons originating from motor and sensory cortical neurons. Many of these neurons project their axons ipsilaterally through the brainstem, cross in the caudal medulla, and terminate in the contralateral gray matter of the spinal cord. Cells of the somatosensory cortex project predominantly to sensory nuclei of the brainstem and to cells in the dorsal horn of the spinal cord. Neurons of the somatomotor areas project predominantly to internuncial cells of the spinal cord gray which in turn project onto motor neurons of the

ventral horn. In some carnivores and in most primates there are also direct projections from the motor cortex to dendrites and cell bodies of alpha and gamma motor neurons in the ventral horn of the spinal cord. It is this latter pathway which may provide a means for further refinement and improvement in direction, speed and appropriateness of movements in pectoral and pelvic limbs (Lawrence and Kuypers, 1968 a, b).

Projections from the motor cortex directly to the spinal cord are said to appear first in the class Mammalia¹. As a new acquisition to the mammalian radiation, the corticospinal tracts vary in origin, course and termination between the orders. Yet their anatomy is reported to be fairly constant within each order. Previous studies have emphasized the differences between the orders but little information is available to compare the different genera. In order to clarify this point and to trace the phylogenetic development of the

¹Obersteiner (1896) and Kalischer (1901, 1905) report a corticospinal tract in the parrot. Karten (1969, 1971) found a pyramidal system in the owl and pigeon. Thus, the antiquity of the system is extended from the Triassic to the Carboniferous period (Towe, 1973).

tract, its origin, course and termination within the various orders of the class Mammalia has been reviewed.

In order to describe the terminations of descending projections to the spinal cord several nomenclatures have evolved. Three principle classifications are in use today to subdivide the spinal cord gray matter: (1) a purely descriptive nomenclature based on anatomic regions irrespective of nuclear groups, (2) subdivision by nuclear groups and columns of cells, and (3) the laminar patterns according to Rexed (1952, 1954).

The investigator may be confronted with one or combinations of these classifications in the literature of the last decade. Table 1 is an attempt to organize the different nomenclatures, grouping analogous terms across the table. In the present study a combination of Rexed's lamina and nuclear groups is used (See schematic line drawing which supplements Table I).

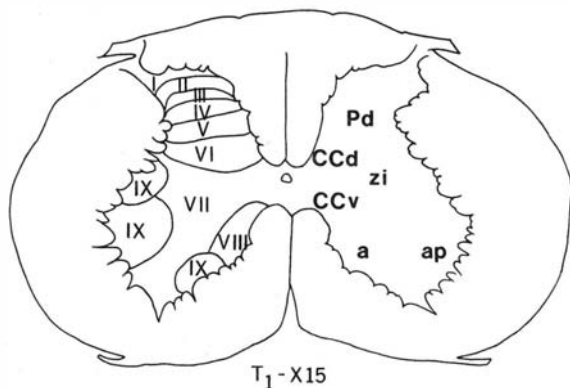
TABLE I. PRINCIPLE NOMENCLATURES OF SPINAL CORD GRAY MATTER

	Rexed's lamina	Nuclear organization	Zones
D.H.	I.-VI.		
	I.	Waldeyer's marginal nuc.	Sulcomarginal
	II.	Substantia gelatinosa	---
	III.	Nuc. proprius cornu dorsalis	
	IV.	" "	
	V.	" "	
	VI.	Nuc. cornu commissuralis dorsalis	Internal and external basilar region
I.Z.	VII.	Clarke's column; medial and lateral intermediate nuclei; internuncial nuclei	zone intermedia
	X.	---	substantia geliosa
V.H.	VII.-IX.		
	VII.	Internuncial nuclei	---
	VIII.	Nuc. cornucommissuralis ventralis medial motor nuclei	
	IX.	Medial and lateral motor nuclei	---

D.H. Dorsal horn - primary sensory and relay centers

I.Z. Intermediate zone - primary relay centers and autonomic

V.H. Ventral horn - primary motor centers



Supplement to Table I

Rexed's laminae are labeled on the left half of a cross section of spinal cord of Galago. The principal nuclear groups are identified on the right half. Pd - dorsal proper nucleus; CCd - nucleus cornucommissuralis dorsalis; CCv - nucleus cornucommissuralis ventralis; zi - zona intermedia; a - axial group of motor neurons, nucleus motorius medialis; ap - appendicular group of motor neurons nucleus motorius lateralis.

A. Prototherian Mammals
Monotremata

Echidna (the spiny anteater)

Goldby (1939a) studied the corticospinal tract of the spiny anteater using the Marchi technique². In a single specimen of Echidna fibers decussated in the anterior pons, coursed through the lateral medulla and entered the lateral funiculus of the cord. The tract descended to at least the twenty-fourth spinal segment (sixteenth thoracic level), but was not followed caudal to this point. Goldby states that the twenty-fourth segment (sixteenth thoracic) is in the lumbosacral enlargement.

²The Marchi procedure (Swank et al., 1935) selectively stains the degenerating myelin of lesioned neurons or fiber tracts. Therefore, the technique is limited to the determination of the origin and course of fiber projections but not their termination because nerve fibers lose their myelin before they terminate. This technique was used extensively in the first half of the present century; therefore, most references prior to 1954 do not include terminations of projection systems.

B. Metatherian MammalsMarsupialia

There have been several investigations which reported the origin, course and termination of the corticospinal tract in the Virginia opossum (Turner, 1924; Ward, 1954; Bautista and Matske, 1965; and Martin and Fisher, 1968).

Turner (1924) reported that the tract decussated in the medulla and descended into the dorsal funiculus of the upper cervical cord. He could not follow the projections further with the Marchi technique. With selective silver techniques the tract was found to originate from neurons around the orbital sulcus, principally from the postorbital cortex (Bautista and Matzke, 1965; Martin and Fisher, 1968). These cells projected through the brainstem to the midventral medulla where a decussation occurred. The major bundle crossed to the central margin of the dorsal funiculus, a lesser bundle crossed to the lateral funiculus. These fibers failed to descend beyond the cervical enlargement and terminated medially in the dorsal horn (laminae III-VI).

Other Marsupialis studied include Pseudochirus peregrinus, (Ziehan, 1899) and Trichosurus vulpecula the phalanger, (Goldby, 1939b; Martin, Megirian and Roebuck, 1970). Corticospinal fibers arose in postorbital and midcortical areas, descended through the brainstem, crossed in the caudal medulla to compose a large tract in the dorsal funiculus and a smaller bundle in the lateral funiculus. Fibers could be traced as far as T10. Terminals were abundant medially in the dorsal horn, laminae III-VI, although some fibers extended ventrally into laminae VII and VIII (Martin, et al., 1970).

Watson (1971a,b) reported the origin and course of the corticospinal tract of the quokka Wallaby (Setonix brachyurus) and the kangaroo (Macropus fulliginosus and Megaliia rufa). The major bundle formed a crossed dorsal tract which extended to T7. Minor bundles were reported in an uncrossed dorsal tract and in crossed and uncrossed lateral funicular tracts. These minor bundles were not found below cervical levels. Terminations were reported in dorsal and intermediate gray of the spinal cord.

Martin, Megirian and Conner (1972) showed in the Tasmanian potoroo (a small hopping marsupial) a crossed dorsal tract (major) which extended to T12 and a crossed

lateral tract (minor) which ended at T8. The somatotopic organization of the cortex was maintained in the corticospinal projection; motor (postorbital) cortex projected to the more ventral laminae (V-VII); projections from lateral parietal cortex (sensory) were confined to the dorsal laminae (III and IV).

C. Eutherian Mammals

Insectivora

The majority of reports of this order deal with Erinaceus, the European hedgehog (Ziehan, 1899; Kotzenberg, 1899; Bischoff, 1900; Edinger, 1904; Draeseke, 1904; van der Vloet, 1906, and Campbell, 1965). Ziehan (1899) and Kotzenberg (1899) reported no corticospinal fibers present in the caudal medulla or spinal cord. Edinger (1904) described an uncrossed tract in the ventral funiculus to the upper cervical cord. Neither van der Vloet (1906) nor Draeseke (1904) reported a pyramidal decussation in the hedgehog or the mole (Talpa).

Linowiecke (1914), using the pyridine silver technique in the mole (Scalopus), traced the tract into the ventral funiculus of the cervical cord; and Campbell

(1965) in a more recent study, using the Nauta-Gygax technique, described a ventral funicular tract to the cervical cord in Erinaceus. He could not locate a decussation in the pons or medulla, not could he find terminals in the spinal gray matter.

Chiroptera

Draeseke (1903), using the bats, Vesperugo serotinus and Pteropus ursinus, found most of the pyramidal fibers ending on the facial nucleus. Those fibers which did reach the cord were found in the dorsal funiculus.

Edentata

Fisher et al. (1969) reported projections from presupraorbital cortex to the lateral cord gray in the armadillo. Much of this study was re-evaluated in a more recent work (Dom et al., 1971). This study is the only available work combining cortical stimulation and cortical ablation to trace the corticospinal tract in the edentate line. Fiber degeneration was present in the contralateral ventral and lateral funiculi to rostral thoracic levels. Terminals were abundant in the

medial dorsal gray, laminae IV-VI, but did not extend into ventral lamina in the cervical enlargement.

Rodentia

Douglas and Barr (1950) studied the rat, golden hamster, Canadian beaver, woodchuck and the thirteen-lined ground squirrel. Previously King (1910) reported the course of the corticospinal tract in the rat; and Simpson (1912a, 1915) reported its course in the striped gopher and the Canadian porcupine. Simpson states that in porcupine a direct uncrossed ventral tract and crossed dorsal tract extended into sacral segments, an unusually well-developed tract for a rodent. Simpson (1914) also studied the tract in the red squirrel and chipmunk; and Reverley (1915) described its course in the guinea pig.

More recently, Goldby and Kacker (1963) reported its extent in the coypu rat (Myocaster coypus), using the Nauta-Gygax technique. The tract is primarily a crossed dorsal projection, although crossed lateral and uncrossed dorsal and ventral projections have been reported in the cervical cord. The main dorsal bundle descended to the lumbar enlargement. The tract terminated in the medial

dorsal horn gray (laminae IV-V). Most recently, Brown (1971) reported the synaptology of the rodent corticospinal system using a combined silver degeneration and electron microscopic technique. Degenerating axons appeared to synapse only with dendrites of neurons in the dorsal most regions of the dorsal horn. No axosomatic or axoaxonal figures were described.

Lagomorpha

The course of the corticospinal tract in the rabbit (Oryctolagus) was investigated by Swank (1936). From the decussation, a crossed tract was followed into the lateral funiculus but ended quickly in the upper cervical cord, short of the enlargement. Evidence such as this may account for the removal of the rabbit from the order Rodentia to be placed in a separate order (Douglas and Barr, 1950).

Proboscidea

The pyramidal system was first studied in elephant by Bregmann (1915). He reported that two-thirds of the bundle was distributed to the facial nucleus (VI), and only one-third descended beyond the decussation in the contralateral ventral funiculus.

In contrast, Verhaart and Kramer (1958) and Verhaart (1963) reported an uncrossed ventral tract which ended in the cervical cord and a crossed dorsal funicular tract that extended into the upper thoracic cord. Verhaart used the non-experimental Haggqvist technique, and the terminations of the tract have not been described.

Artiodactyla

Ziehan (1900) described a crossed dorsal and a lateral funicular tract in the sheep, Ovis. In the same genus, Dexler and Margulies (1906) found, in addition, an uncrossed ventral tract. These authors also described similar findings in the goat, Capra. King (1911) found a small crossed lateral tract which extended to the upper cervical spinal cord in sheep, but no sites of termination have been reported.

Carnivora

The corticospinal pattern of carnivores was reported to be similar to that of the primates, although the ventral funicular components were much reduced or absent. In addition, there were no commissural fibers of passage nor were there terminations upon the nuclei of the ventral

horn (there were two known exceptions - see below) (Simpson, 1912b; Chambers and Liu, 1957; Kuypers, 1958a; Nyberg-Hansen and Brodal, 1963; Buxton and Goodman, 1967; and Petras and Lehman, 1966; Petras, 1969). The major contribution to the cord was located in the lateral funiculus and extended into coccygeal segments. Minor bundles were reported in crossed and uncrossed ventral and uncrossed lateral pathways, although these tracts usually ended in the upper cervical cord. Dense terminal degeneration was reported in the external basilar zones of the dorsal horn and in the underlying zona intermedia. No terminals were reported on appendicular or axial motorneurons in the cat, although occasional fibers were reported among appendicular neurons in the dog (Buxton and Goodman, 1967). In the raccoon and kinkajou, however, corticospinal fibers were reported on the most dorsolaterally located cells of the ventral horn (lamina IX). These dorsolateral cells innervate distal appendicular musculature (Petras and Lehman, 1966; Petras, 1969).

The cortical projections to the cord were also somatotopically arranged as they were in the Primates. Projections from the caudal postsigmoid gyrus terminated

predominantly on the dorsally located sensory nuclei of the brain stem and spinal cord. Projections from the rostral postsigmoid gyrus ended more ventrally along the neuroaxis and terminated on internuncial neurons in the external basilar zone of the cord gray matter (laminae V and VI). These terminations also extended well into the zona intermedia (lamina VII) (Nyberg-Hansen and Brodal, 1963).

Primates

Prosimian- Comparative corticospinal morphology is available in only two prosimian families, the Lorisiidae (slow loris and galago) and Tupaiidae (the Malayan tree shrew). Inclusion of Tupaia into the order Primates has been questioned by Van Valen (1965), Campbell (1966a) and Straus (1949).

The corticospinal system in the Malayan tree shrew has been reported by a number of investigators (Jane, Campbell and Yashon, 1965; Verhaart, 1966; Shriver and Noback, 1967; and Jane, Campbell and Yashon, 1969). Results of cortical mapping in Tupaia followed the general schema found in other small placental mammals. There was a motorsensory amalgam of the frontal lobe with slight separation of motor function toward the rostral pole. Cortical topography (indentations and eminences) appeared related to patterns of localization (Lende, 1970). Projections from the motorsensory cortex to the spinal cord were found contralaterally in the dorsal funiculus. A few fiber bundles were reported in a crossed lateral and in uncrossed ventral and dorsal tracts. The major dorsal bundle descended through thoracic segments; the aberrant

bundles terminated in upper cervical segments. Preterminal and terminal degeneration were confined to the medial portions of the base of the dorsal horn, lamina V and VI. Relatively few fibers projected dorsally to lamina III or ventrally into lamina VII. No degeneration was reported crossing the dorsal or ventral gray commissures.

In slow loris (Nycticebus), Jane et al. (1965) reported a complete decussation of the pyramidal bundle to the contralateral lateral funiculus to course the entire length of the cord. Degeneration was most abundant at the base of the dorsal horn and intermediate gray column. Sparse degeneration was reported in the ventral horn with some fibers recrossing through the dorsal and ventral gray commissures.

Campbell et al. (1966b) reported, in addition, the presence of a small bundle in the ipsilateral lateral funiculus which extended to the lumbar cord and rare fibers in the dorsal funiculus. Campbell also described the terminal degeneration in the ventral horn as most abundant in the medial portions with only occasional terminals located on the large, laterally placed cells of the ventral horn. There was no evidence of a ventral tract.

Ferrer (1971) reported the extent of the tract in greater galago (Galago crassicaudatus). Crossed and uncrossed lateral tracts traversed the length of the cord; and a ventral tract was identified at cervical and upper thoracic levels. Terminations were abundant in mediobasal and laterobasal dorsal horn gray. A few fibers were traced into the medial ventral horn (lamina VIII) contralateral to the lesion. Degeneration was dense at the external basilar dorsal horn and zona intermedia, (laminae IV-VII). Lesions of somatosensory cortex produced degeneration in the more dorsal laminae (laminae III-IV) of the dorsal horn, but no terminals were reported on large motor neurons in the ventral horn.

Anthropoidea - New World Monkeys

Callitrichidae

Shriver and Matzke (1965) described the corticospinal tract in the cotton-top tamarin (Saguinus oedipus). A long major crossed lateral and a short minor uncrossed lateral tract were reported. Degeneration was mainly to the base of the dorsal horn with some terminals found in the lateral aspect of zone intermedia. There were no fibers crossing either gray commissure nor were

there terminals associated with the motor nuclei of the ventral horn.

Cebidae

Harting and Noback (1970) described the corticospinal fibers in the squirrel monkey (Saimiri sciureus). Following lesions of the somatomotor cortex, degenerating debris was found contralaterally in the lateral funiculus with occasional fibers found ipsilateral to the lesion. Degeneration was dense in the external basilar dorsal horn and zona intermedia (laminae IV-VII). Lesions of the somatosensory cortex, however, produced degeneration in the more dorsal lamina (III-IV). No terminals were reported on large motor neurons in the ventral horn.

Anthropoidea- Old World Primates, including Man

Extensive literature is available on the pyramidal system of monkeys and apes. Lassek (1954) reviewed the literature from 1709 to the middle of the present century. The anthropoid corticospinal system may be summarized, as follows: The motor sensory cortex projects its fibers into four spinal pathways forming crossed and uncrossed lateral and ventral tracts. The largest and most consistent tract

descends in the contralateral lateral funiculus coursing the length of the cord.

The ventral tracts are more variable. They terminate in cervical levels but occasionally are reported to descend to lower lumbar segments (Liu and Chambers, 1964; Fulton and Sheehan, 1935; and Verhaart, 1970). Fiber termination is chiefly on cells of the contralateral dorsal horn and intermediate zone. Cortical projections to the dorsolateral ventral horn are also present with an apparent increase in the number of monosynaptic terminals as one ascends the primate series (prosimian-simian-anthropoids).

The projections of the motorsensory cortex to the spinal cord can be organized into a dorsal sensory modulating component (into lamina III-V) and a ventral motor component (into lamina VI-IX). The motor component can be further organized into medial and lateral zones. The medial zone affects proximal limb and axial musculature; the lateral zone affects appendicular musculature, (Liu and Chambers, 1964; Kuypers, 1958a,b; Schoen, 1964; Kuypers and Brinkman, 1970).

Termination of the tract is on internuncial neurons in the basilar zones (medial and lateral) of the dorsal horn as well as throughout the zona intermedia. Terminals in the ventral horn synapse directly with the smaller gamma motor neurons as well as with large alpha motor cells.

The function of this direct monosynaptic pathway and the pyramidal system as a whole is not understood. It may provide a means for refinement or improvement in speed, direction and appropriateness of movement. "The system probably adds the necessary 'readiness to act' that make all the difference in the selective process where speed and appropriateness of action are so important (Towe, 1973)."

Materials and Methods

A total of twelve bushbabys were used in the present study. These members of the family Lorisidae have a unique mode of locomotion that has been classified as vertical clinging and leaping (Napier and Walker, 1967).

Galago senegalensis senegalensis - lesser bushbaby
from East Africa -
seven specimens

Galago senegalensis moholi - lesser bushbaby from
South Africa - three
specimens

Galago crassicaudatus - greater or thicktailed galago
from East Africa - two
specimens

The animals were anesthetized with an intravenous aqueous solution of Diabutal³ (sodium pentobarbital-15mg/kg body weight) and placed on a stereotaxic frame. Ear pins and nasal bars were not used to avoid injury to peripheral branches of cranial nerves. After a midline incision, the superior border of the left temporalis muscle was dissected from its origin and reflected to expose the calvarium. Access to the cranial vault was accomplished

³Diamond Laboratories, Des Moines, Iowa

with a dental drill, rongeurs, and bone cutting forceps. The dura was incised and a lesion was selectively placed in the cerebral cortex by subpial aspiration.

Localization of lesions was aided by the areal maps of von Bonin (1945) and Kanagasuntheram, Leong and Mahran (1966) as well as gross surface anatomy (dimples, grooves and sulci) (Haines et al., 1974). Placement of lesions was confirmed by subsequent cytoarchitectural observations. The dura was then sutured; a bone flap or Gelfoam⁴ was placed over the exposed area; and the temporalis muscle was sutured to the contralateral temporal fascia. The skin was sutured following a subcutaneous application of Furacin⁵ (nitrofurazone). One death occurred 24 hours following a medial hemispheric lesion. The cause of death was due to complications other than the experimental surgery.

Eleven successfully lesioned animals were observed postoperatively for deficits in locomotor skills although no testing was performed. It was felt that survival times

⁴The Upjohn Company, Kalamazoo, Michigan

⁵Eaton Laboratories, Norwich, New York

were too brief to evaluate postoperative motor deficits. After survival times that ranged from 4-12 days, the animals were anesthetized and the abdominal aorta and inferior vena cava exposed and freed. The aorta was cannulated at the level of its bifurcation into the common iliac arteries. The cannula was tied down and 500 units of sodium heparin⁶ (diluted to 1 ml with saline) was injected through the cannula followed by 10 ml of saline. The inferior vena cava was excised several minutes later and the animal was perfused with 200-400 ml of 0.9% saline. The saline was followed by a perfusion with 200-400 ml of 10% formalin.

Three animals were also perfused with a 0.5% glutaraldehyde - 4.0% paraformaldehyde in a 0.2M phosphate buffer with 4.0% sucrose (modified after Karnosky, 1965).

The entire central nervous system was stored in 10% formalin for 1-2 weeks, placed in sugar formalin⁷ for 2-5 days, and serially sectioned at 40 micra on a sliding microtome modified for frozen sections. These sections were kept in serial order in mini-cube icetrays. Serial

⁶Sigma Chemical Company, St. Louis, Missouri

⁷600 gm-Sucrose; 200 ml - formalin; 1450 ml distilled water

order was also maintained during the selective silver impregnation of degenerating axoplasm (Fink-Heimer, 1967) by placing sections in Coors perforated porcelain crucibles⁸ and immersing them in egg trays filled with the appropriate solution. Alternate sections were stained with either a cresylviolet acetate stain or the luxol-fast-blue, cresylviolet technique (Kuver-Barrera, 1953) in order to identify nuclear configurations.

Three normal brains and spinal cords, which were stored in 10% formalin for six months to a year, were utilized for the zinc chromate modifications of the Golgi technique (Fox et al., 1951). Tissue perfused with glutaraldehyde was used in the Golgi-Kopsch technique (Colonnier, 1964). These blocks were either rapidly embedded in paraffin and serially cut on a rotary microtome or frozen and cut on a sliding microtome. Golgi preparations were cut at 150-200 micra and mounted with albumin. Fink-Heimer and nuclear stained material were cut at 40-80 micra and mounted from alcoholic gelatin (Albrecht, 1954).

⁸Scientific Products, McGraw Park, Illinois

Scaled line drawings of gross specimens were made to compliment macrophotographs of normal and lesioned brains. In addition to photomicrographs, projection drawings⁹ were also made of Fink-Heimer, Nissl and Golgi preparations to show fiber tracts and sites of termination as well as nuclear configuration and dendritic arborization of neurons.

⁹Micro-macroprojector, Bausch and Lomb Optical Company, Rochester, New York

Results

A. Cortex

1. External Morphology

Descriptions of the external morphology of the brains of a variety of prosimians are found in the literature. Elliot Smith (1903) reviewed the nineteenth century literature; more recently, the topography of the cortex was reported by Ariens Kappers et al. (1936), Connolly (1950) and Haines et al. (1974).

It was proposed by Abbe (1940) and by Sanides and Krishnamurti (1967) that the sulcal pattern of the primate cortex is based upon the separation of different cytoarchitectural and functional areas. Therefore, in order to place discrete lesions in a presumptive motor-sensory homunculus, a clear understanding of cerebral anatomy is necessary.

The nomenclature of the cerebral sulcal pattern of prosimian primates is varied (Table II). Different terms are given to the same sulcus and different sulci have the same names. In order to establish a nomenclature for this study and to select discrete cortical areas from which to study spinal projections, the external morphology of the

available members of family Lorisiidae was examined (Haines et al., 1974).

The pallium is classically divided into three cortical areas based on phylogenetic and cytoarchitectonic considerations. The oldest midline ring of cortex is the archipallium (archicortex). The lateral cortex, associated with olfactory connections, is the paleopallium (paleocortex). The new cortex, or neocortex, expands dorsally between the older, less developed, archipallium and the paleopallium. The neocortex is separated from the archicortex by the cingulate sulcus and from the paleocortex by the rhinal fissure.

The prosimian neocortex generally follows the concept of gyrification¹⁰ when compared across phylogeny, although this concept cannot be seen within the family Lorisiidae. Whereas the lorisooids (pottos and lorises) and the larger galagos (G. crassicaudatus) are about equal in body size, the neocortical development of the lorisooids is more complex and varied than that of G. crassicaudatus. The prosimian cortex is also less gyrencephalic than the larger

¹⁰The variety and number of grooves and sulci are directly proportional to animal size.

TABLE II

The cerebral cortical nomenclature and abbreviations used in this investigation are listed in the first column on the left. Synonymous terms and their literature origin make up the remainder of the table.

NOMENCLATURE USED IN PRESENT STUDY	G. ELLIOT SMITH (1903)	C. J. CONNOLLY (1950)	OTHER
Sylvian complex - Anthony (1913) sy-cl-	Sylvian fissure (pseudosylvian and suprasylvian)	Sylvian fissure (pseudosylvian and suprasylvian)	Lateral fissure
Orbital sulcus o.	Sulcus orbitalis	Sulcus orbitalis	*Presylvian; precentral, Panach
Sulcus rectus r.	Coronal sulcus	Sulcus rectus	*Infero-frontal, Beddard (1895)
Sulcus "a" a.	Sulcus "x" and sulcus "y"	Sulcus "a"	*Precentral sulcus, Flatou and Jacobsohn (1889)
Sulcus "c" c.	Sulcus "f"	Sulcus "c"	*Supero-frontal sulcus, Flower (1866) Angular sulcus, Beddard (1895) *Presylvian sulcus, Beddard (1895)
Central sulcus ce.	Sulcus "f" joined with sulcus "x" + "y"	Agress with Ziahan	**Sulcus "c" + sulcus "a" = central Ziahan (1896); precentral sulcus, Flatou and Jacobsohn (1889)
Intraparietal sulcus ip.	Lateral sulcus	Intraparietal sulcus	*Angular, Beddard (1895)
Superior temporal sulcus t.s.	Patsylvian sulcus	Superior temporal sulcus Parallel sulcus	*Anterotemporal, Beddard (1895) first temporal sulcus
Middle temporal sulcus t.m.	-----	Middle temporal sulcus	*Inferior temporal sulcus, Ziahan(1896) **Second temporal sulcus, Flatou and Jacobsohn (1889)
Occipito-temporal sulcus oct.	Sulcus "c"	Inferior temporal sulcus occipito-temporal sulcus	Third temporal sulcus
Collateral sulcus col.	Collateralsulcus, sulcus "b"	Collateral sulcus	*Sulcus gamma, Ziahan (1896)
Lunate sulcus l.	Posterior lateral sulcus	Transverse occipital, lunate sulcus	*Lateral parieto-occipital sulcus and similar sulcus, Beddard 1895 **maxiparieto-occipital sulcus
Lateralcalcarinesulcus lc.	Lateral occipital sulcus	Lateral calcarine (Ingalls) external calcarine (Cunningham)	**Occipital diagonal ypsilonformis sulcus, Koppers; triadatus, Landou; superior occipital sulcus, Flatou and Jacobsohn (1889)
Rectus communicating sulcus, Sanides and Krishnamurti (1967) crs.	"x" and "y" joining coronal sulcus	Sulcus "a" joined to sulcus rectus by vascular groove	*Infero-frontal, Beddard (1895)
Diagonal sulcus di.	Diagonal sulcus	-----	Intersomatic sensory sulcus, Krishnamurti(1966)
Cingulate sulcus cg.	Intercalary sulcus	Callaomarginal sulcus	Cingulate sulcus
Genua sulcus g.	Genua sulcus, rostral sulcus	-----	-----
Calcarine sulcus, para- and retrocalcarine sulcus pc. rc.	Calcarine sulcus, para- and retrocalcarine	Calcarine sulcus, para- and retrocalcarine	-----
Sulcus "d" d.	Sulcus "d"	-----	-----
*cited by G. Elliot Smith, 1903 **cited by C. J. Connolly, 1950			

anthropoid primates; however, there is some evidence of specific cortical development.

The family has a distinct cortical sulcal pattern around the Sylvian complex (Fig. 1). This pattern is seen in the development of the intraparietal sulcus and the deep superior temporal groove. A tri-radiate depression is present in the frontal lobe and a transverse groove courses through the occipital lobe (Fig. 2). Essentially the same cortical pattern is seen in the greater galago; however, the individual elements of the pattern are more separate and distinct. On the frontal lobe, there is a distinct sulcus rectus, sulcus "e" and an orbital sulcus. A hint of a "central depression" can also be seen in some specimens. The intraparietal sulcus extends well over the termination of the Sylvian complex and a transverse groove courses the occipital lobe (Fig. 3).

The larger members of the family have a more complex sulcal pattern and, consequently, more variations are seen. Whereas the sulci tend to unite in these larger prosimians, the majority of sulci remain in the sagittal plane, although there are a few located coronally (Figs. 2C, D and 3C, D).

FIGURE 1

Photomacrographs of the brains of (A) the greater galago, Galago crassicaudatus, and (B) the slow loris, Nycticebus coucang. Note the increase in the variety and number of sulci in the hemisphere of the slow loris. The intraparietal (ip) is continuous with the Sylvian complex (Syc) and sulcus "e" has both a horizontal and vertical component. Abbreviations are listed in Table II.

X 3

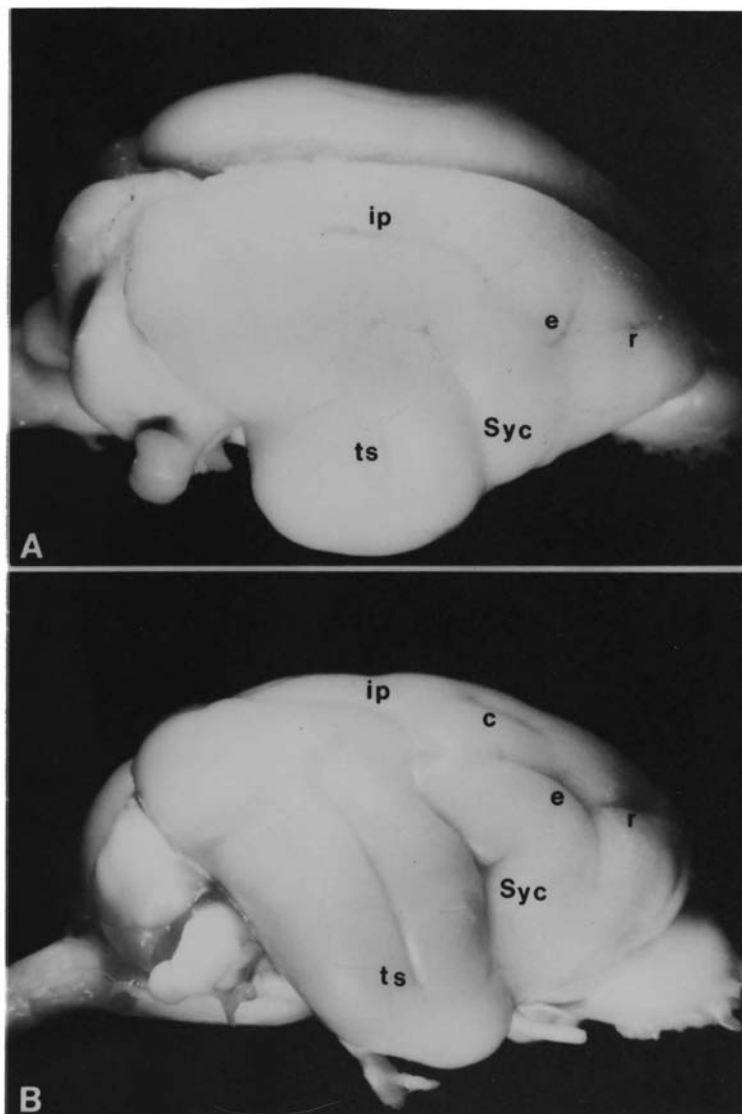
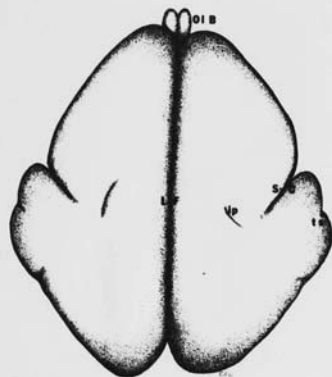
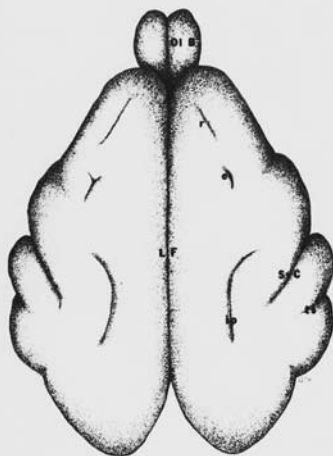


FIGURE 2

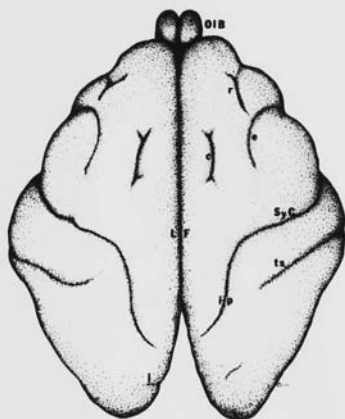
Dorsal views of the cerebral hemispheres of (A) lesser galago, Galago senegalensis, (G.s); (B) greater galago, Galago crassicaudatus (G.c.); (C) slow loris, Nycticebus coucang (N.c.); and (D) the potto monkey, Perodicticus potto (P.p.). Figure abbreviations are explained in Table II. Scale = 0.5 cm.



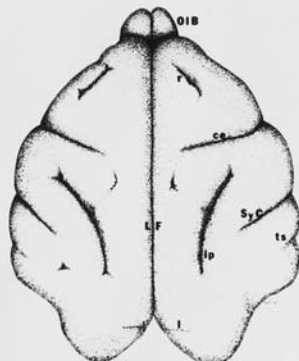
G.s.



G.c.



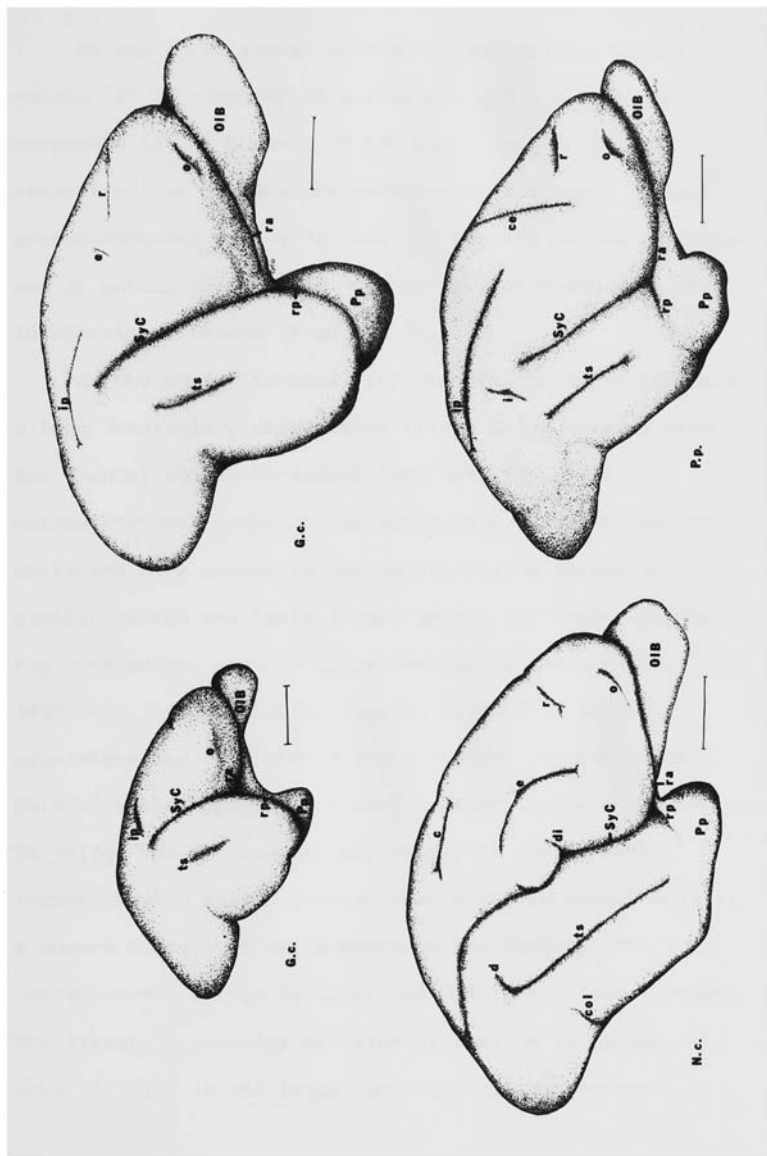
N.c.



P.p.

FIGURE 3

Line drawings to scale of the lateral aspect of the cerebral hemispheres of (A) lesser galago, (G.s.); (B) greater galago, (G.c.); (C) slow loris, (N.c.); and (D) the potto monkey, (P.p.). Note the increase in the number of coronally oriented sulci in loris and potto. In all these animal forms the cortical sulcal pattern defines the somatotopic organization of the cerebral cortex. In the slow loris, sulcus "c" separates the dorsal hindlimb cortex from the more lateral forearm cortical area. The horizontal component of sulcus "e" separates the forearm cortex from the more lateral cortex which represents the face. (Sanides and Krishnamurti, 1967). Abbreviations are listed in Table II. Scale = 0.5 cm.

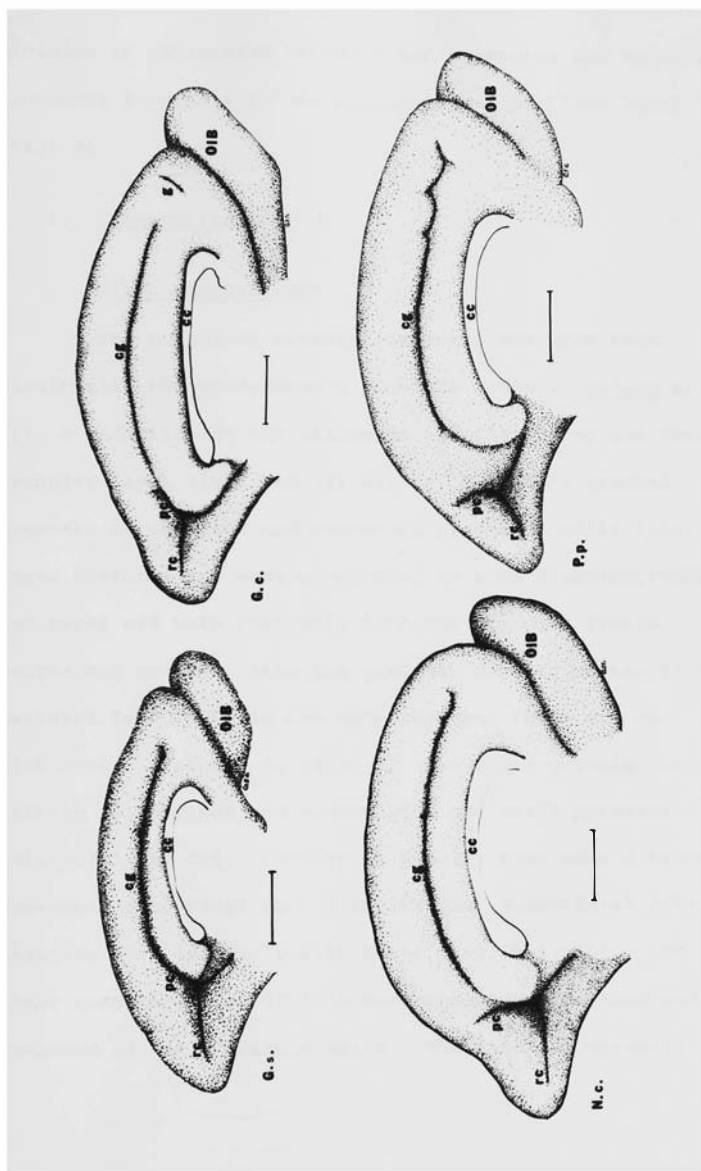


On the dorsolateral surface of the frontal lobe, sulcus "e" is composed of a vertical and a horizontal component in the loris. In the potto monkey, a true central sulcus divides the motor-sensory cortex. Sulcus rectus connects sulcus "e" and the orbital sulcus in loris; and in potto, the Sylvian complex is continuous with the intraparietal sulcus (Figs. 2C,D).

On the mesial cortical surface all the lorisoids have a long intercalary (cingulate) sulcus which extends from the frontal to the occipital lobe (Fig. 4). The sulcus branches rostrally in potto (Fig. 4D), whereas it continues as a groove to the paracalcarine sulcus in greater galago and loris (Figs. 4B,C). In lesser galago the intercalary sulcus joins the paracalcarine directly (Fig. 4A). The calcarine complex is similar in these prosimians and consists of a tri-radiate pattern. The paracalcarine appears as a continuation of the intercalary in Galago but is directly superiorly in loris. The retrocalcarine sulcus extends toward the occipital pole as a common feature in all members of the family. The ventrolateral cortex is interrupted by the rhinal fissure. The fissure's anterior division is shallow in Galago but more definite in the larger animals. The posterior

FIGURE 4

Line drawings to scale of the medial aspect of the cerebral hemispheres of the four Lorisidae shown in Figures 2 and 3. Note the triradiate appearance of the calcarine complex. In the galagoes (upper two figures) the cingulate sulcus (cg) is continuous with the paracalcarine (pc). Abbreviations are listed in Table II. Scale = 0.5 cm.



division is attenuated caudally and separates the temporal neocortex from part of the paleopallium (piriform lobe) (Fig. 2).

2. Cytoarchitecture

Nissl preparations

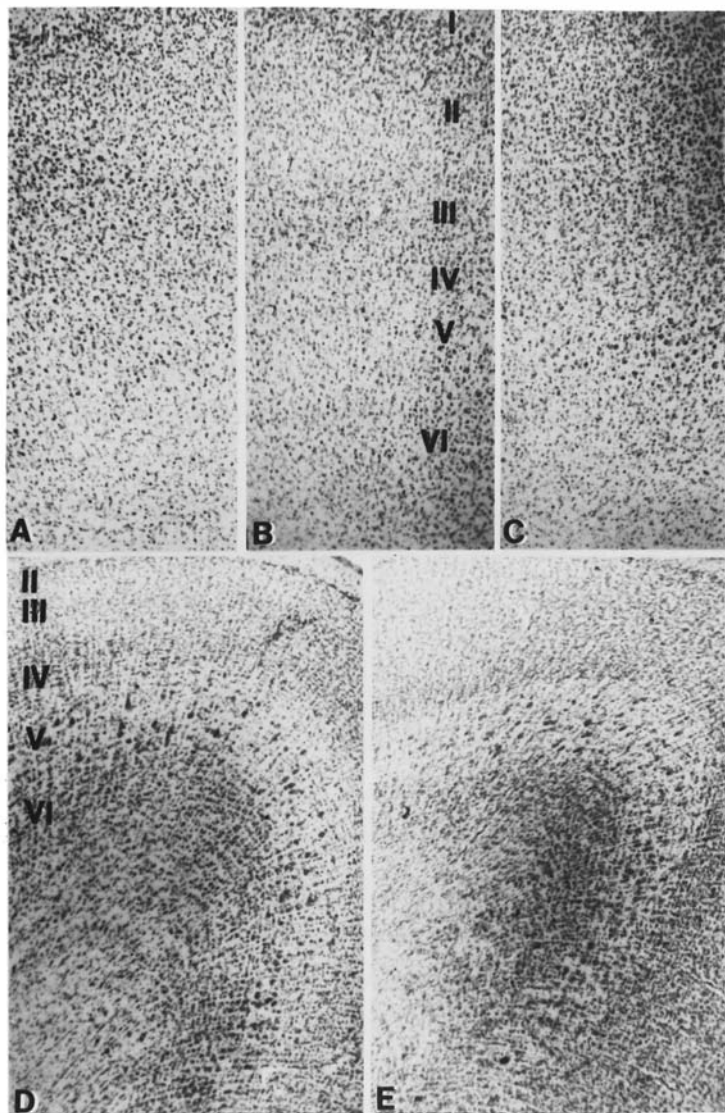
The principal cytoarchitectural features that distinguish the motorsensory cortical areas in Galago are: (1) a reduction in the thickness and clarity of the inner granular layer (IV), and (2) within layer V, a gradual increase in the size and number of pyramidal cells (Fig. 5). These features are most pronounced in area gigantopyramidalis and taper off both rostrally into the granular frontal cortex and caudally into the granular sensory cortex of the parietal lobe. Within the motor cortex, there are no distinctive features in layer I. The outer granular layer (II) is ill-defined and merges with the small pyramidal cells of layer III. Laminas II and III then make a broad homogeneous cortical band with its most superficial cells staining more intensely with basic dyes (Fig. 5D). The inner granular layer (IV) is moderately well defined and is composed of small granule cells. The internal pyramidal

FIGURE 5

Low power photomicrographs of coronal sections through the (A) rostral, (B) middle, and (C) caudal motor cortex (area 6) of the lesser galago, Galago senegalensis. (D) is a section from the rostral motorsensory amalgam (area 4) while (E) is through the caudal motorsensory overlap (area 3-1-2). Throughout the motorsensory cortex note the increase in cell density at the interface of layer I and II and the fusion of laminae II and III. There is a gradual increase in cell size in layer V (A-C) which reaches its maximum in area 4 (D). Although there is a distinct lamina IV in (D), the internal granule cells of layer IV increase significantly in (E), and produce an absolute increase in cortical depth.

I - molecular layer, II - external granular layer,
III - external pyramidal layer, IV - internal granular layer,
V - internal pyramidal layer, VI - fusiform layer. The plane of section for A-E is shown on Figure 8C.

Cresylviolet acetate. X 100.



layer (V) is also well delineated by a lack of stainable cells beneath layer IV superiorly, and inferiorly, by the small pyramidal cells in layer VI (Fig. 5E). The fifth layer (V) is composed of medium to large pyramidal cells with only an occasional giant cell of Betz. The largest cells measure not greater than 50 micra, the majority reaching 35-40 microns (Fig. 6).

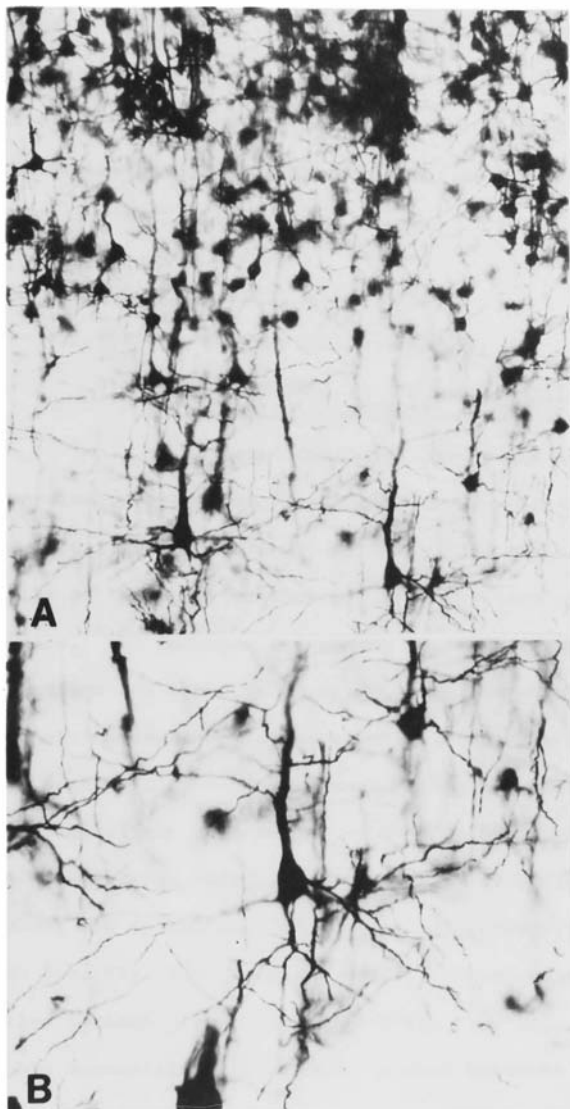
This pattern of cytoarchitecture is carried into the somatosensory cortex in Galago, without any sharp line of demarcation. There is a progressive invasion of granule cells into layer IV, whereas layer V is relatively unchanged. The principal difference is, then, an increase in the cell density in lamina IV resulting in a total increase in cortical thickening.

Golgi Preparations

Studies of material stained with the Golgi-Fox technique reveal the same fusion of supraganglionic layers, seen in the Nissl preparations (Fig. 6). Within layer I, no horizontal cells of Cajal are seen, although vertical and obliquely running fibers enter the layer from lower lamina. Layers II, III and IV are composed of small pyramidal cells with only occasional stellate cells present.

FIGURE 6

High power photomicrographs of Golgi-Fox preparations of the motor sensory cortex in Galago senegalensis. Granule and stellate cells are present in the upper half of the field in (A). X 450 The large pyramidal cells of layer V in (A) are slightly magnified in (B). X 500 Note the long smooth apical dendrite projecting from the top of the cell body and the irregular basal dendritic processes filling the lower half of the field. Zinc-chromate modification of the Golgi method.



In the ganglionic layer (V), large spineless dendrites are found to originate from the base and apex of pyramidal cells (Fig. 7A). Distally, numerous spines appear on these dendrites; the spines increase in number as the dendrites branch (Fig. 7B,C).

B. Cortical Projection to the Cord

1. Lesions (Galago senegalensis)

a. Cortical origin of spinal projections and their course through the brainstem

In order to determine the origin of corticospinal projections in the bushbaby, cerebral cortical lesions were placed over the entire dorsal convexity of the anterior two-thirds of the left cerebral hemisphere. The location and extent of these surgical interventions are shown in Figure 8. Lesions which did not produce stainable degeneration at cord levels are shown in Figures 9 and 11. The motorsensory cortex is, therefore, well defined within the margins of lesions 5-9, 3-4, 4-7, 9-9 and 10-12 (Figs. 10,11). Degeneration is dense throughout the spinal cord from large motorsensory lesions (lesion 1-9, Fig. 10), whereas debris is more moderate from selective lesions (lesion 2-10 and 8-11, Fig. 10). No stainable degeneration is present in cord segments from

FIGURE 7

High power (oil immersion) photomicrographs of the large pyramidal cell in Figure 6,B. The proximal portion of the apical dendrite is smooth (A) in contrast to the basal dendrites which have numerous spiny projections. X 750. Distally, the apical dendrite accumulates projections (B) and the spines on terminal branches acquire bulbous ends (C). X 1000. Zinc-chromate modification of the Golgi method.

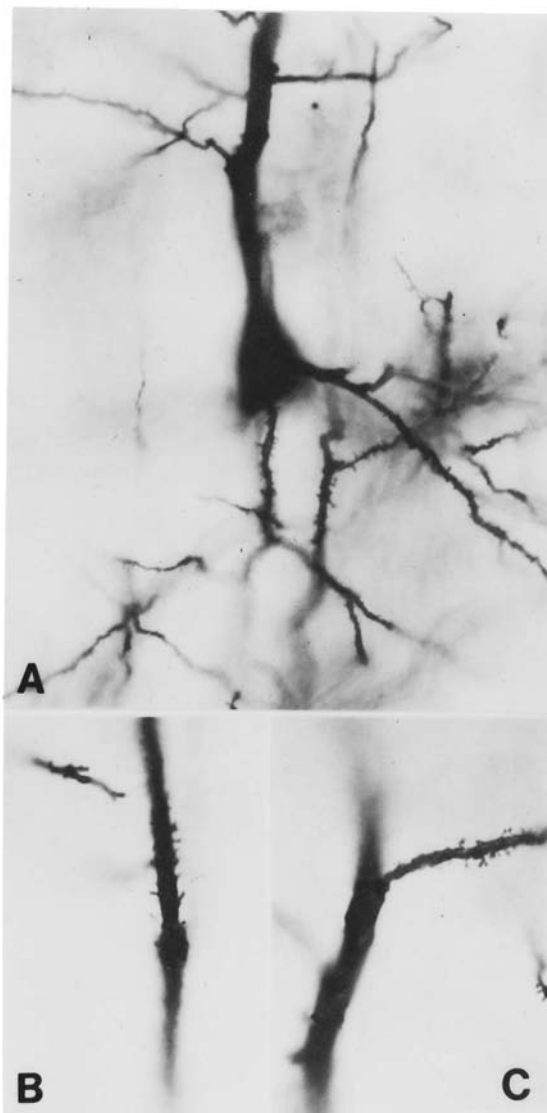
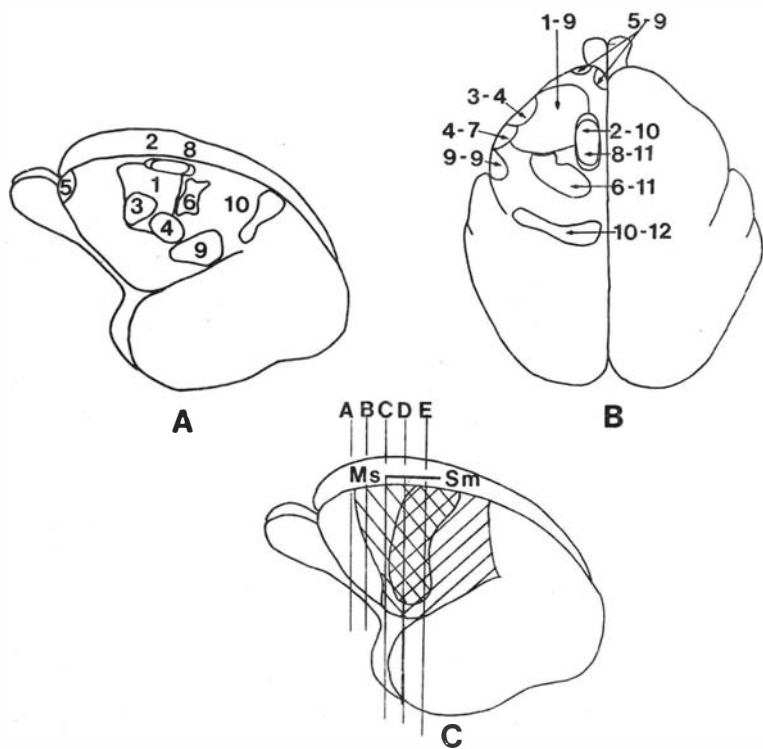


FIGURE 8

Composite drawings of cerebral cortical lesions in Galago senegalensis. (A) dorsolateral view; (B) dorsal view. The second digits in (B) indicate the survival times for each lesion. The schematic diagram (C) is drawn from the cytoarchitectural maps and electrophysiological studies of Von Bonin (1945) and Kanagasuntheram et al. (1966) and the results of the present study. The motorsensory cortex of Galago has a rostral predominantly motor area (Ms) and a caudal somatosensory area (Sm). X 2.6.

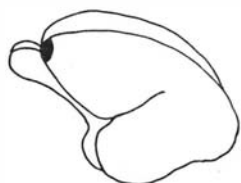


lesions of the frontal pole (lesion 5-9), nor from the dorsolateral margin of the dorsal convexity (lesions 3-4, 4-7, and 9-9, Fig. 9). Lesion 10-12 (Fig. 9) was placed over the dorsal termination of the Sylvian complex in order to determine the caudal extent of the cortex which gives rise to spinal projections. Terminal debris is not found in cord segments from this cortical lesion.

From lesions which produce stainable debris in cord segments, degenerating fibers can be traced through the subcortical white matter to the anterior limb of the internal capsule (Fig. 13A). Corticospinal fibers occupy much of the cerebral peduncle with only smaller non-corticospinal bundles located laterally (Fig. 13B). Debris is not confined to any division of the peduncle, but there is evidence for separate lemnisci and nebulae (Fig. 13B). The debris is then spread over the dorsal half of the basal pontine nuclei before forming a dense core of degeneration in the ipsilateral pyramid which extends to the caudal medulla (Fig. 13C,D,E). The fibers in the pyramid do not surpass four micra in diameter, and most fibers are less than two micra in the lateral funiculus. At the caudal medulla an incomplete decussation occurs. A major crossed component courses dorsolaterally

FIGURE 9

Line drawings that locate the areas of cortical lesions which, although they produce degenerating debris in the brain and brainstem, do not produce degeneration in spinal cord segments. Therefore, these lesions define the limits of the cerebral cortex which gives rise to corticospinal projections in Galago senegalensis. X 1.8



5-9



3-4



4-7



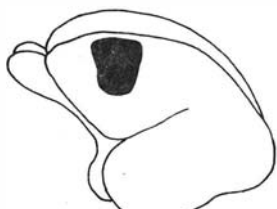
9-9



10-12

FIGURE 10

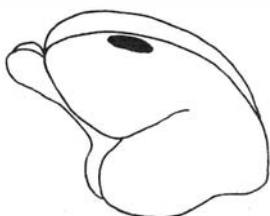
Line drawings of cortical lesions which produce stainable degeneration throughout the spinal cord of Galago senegalensis. Lesion 1-9 involves most of the motorsensory amalgam. Lesions 2-10 and 8-11 involve a dorsomedial area presumed to include the somatotopic hindlimb motor cortex (Ms). Lesion 6-11 involves the forelimb and hindlimb cortex of the somatosensory area (Sm). The animal with cortical lesion 8-11 was also subjected to a peripheral nerve transection of the major terminal branch from spinal cord segments L₅, L₆ and S₁ (the sciatic nerve). X 2.0



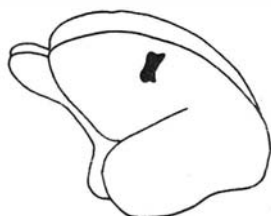
1-9



2-10



8-11



6-11

FIGURE 11

Photomicrographs of lesions in the motorsensory cortex of Galago senegalensis. (A) shows a lesion in the dorsolateral motor cortex, the presumptive face cortical area. (Brain 9-9 of Fig. 9) X 1.5 This lesion did not produce degeneration in the segments of the spinal cord. (B) a lesion of the dorsomedial motor cortex (hindlimb cortex), produces degeneration which terminates predominantly in the lumbosacral enlargement. (Brain 8-11 Fig. 10) X 1.5 The cortical lesion in (C) is an attempt to define the most caudal cortical tissue which projects long descending fibers into the spinal cord. This lesion did not produce degeneration in spinal cord segments. (Brain 10-12 Fig. 9) X 2.2 (D) higher power photomicrograph of a second hindlimb cortical lesion (Brain 2-10, Fig. 10) which also projects selectively to the lumbar intumescence. X 4.7 (E) a lesion in the sensory portion of the motorsensory amalgam (Sm) produces degeneration which is confined to the dorsal nuclei in the dorsal horn of the spinal cord. X 4.7 (F) two distinct lesions of the frontal pole were made in order to avoid the terminal distribution of the anterior cerebral artery (open arrows). The groove, made by the artery, is seen at the solid arrow. X 4.7

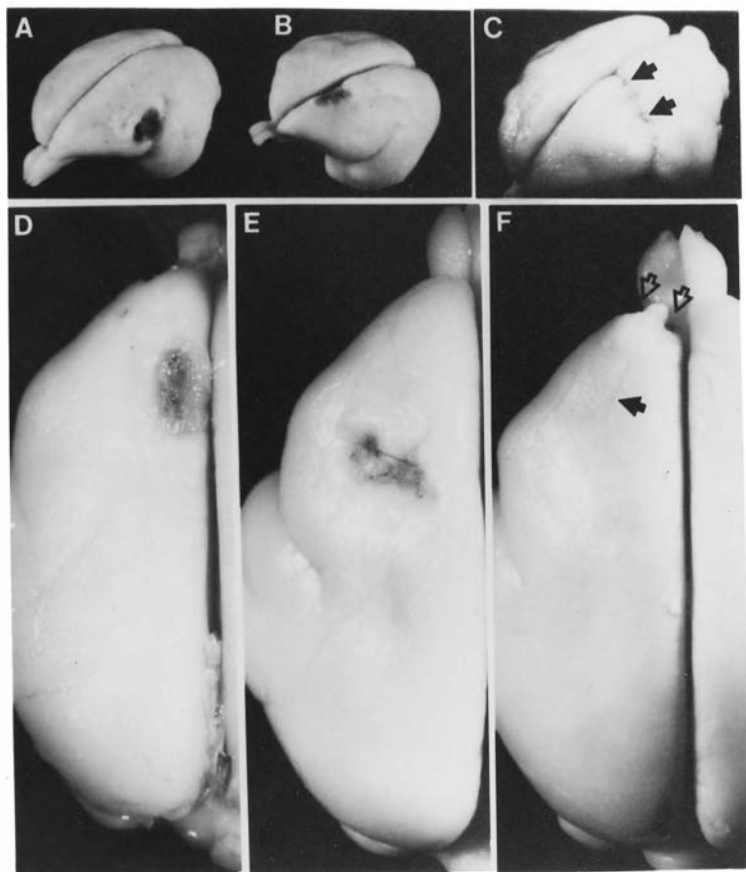


FIGURE 12

Photomicrographs of 40 micra coronal sections through lesions of the motor sensory cortex of Galago senegalensis. Following survival times of (A) 10 days and (B) 11 days, extensive gliosis is seen filling the area where subpial aspiration removed the upper five lamina in (A) and the upper six layers in (B). Note that the lesions destroy the large cells of lamina V, cells which are known to project long descending fibers to the spinal cord. Cresylviolet acetate. X 100

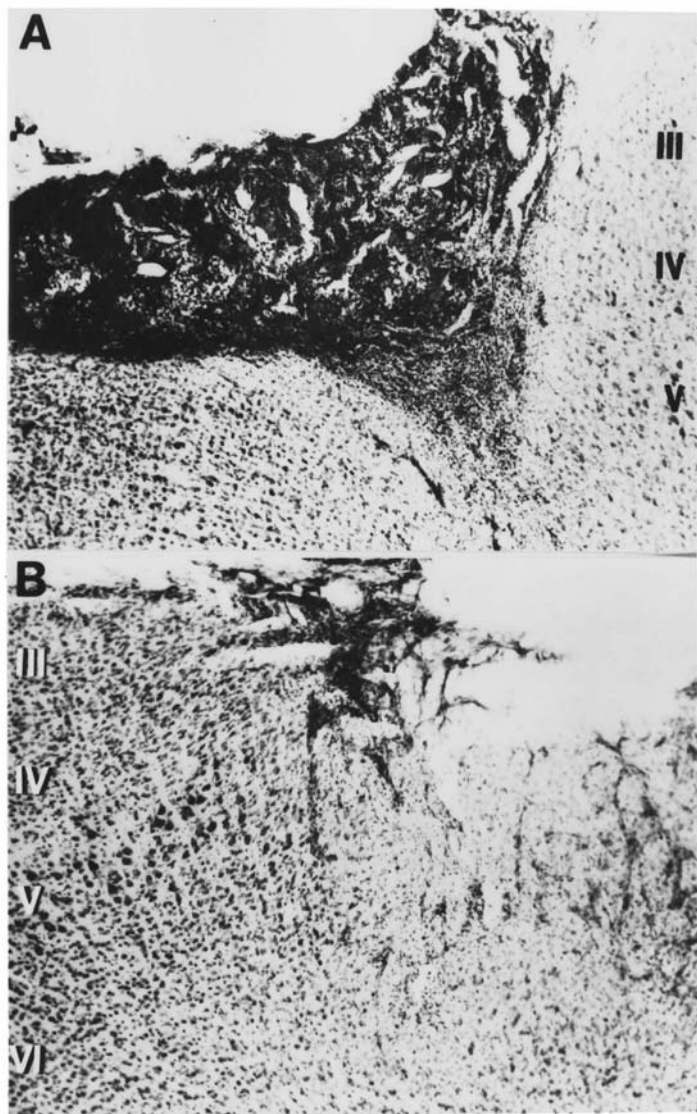
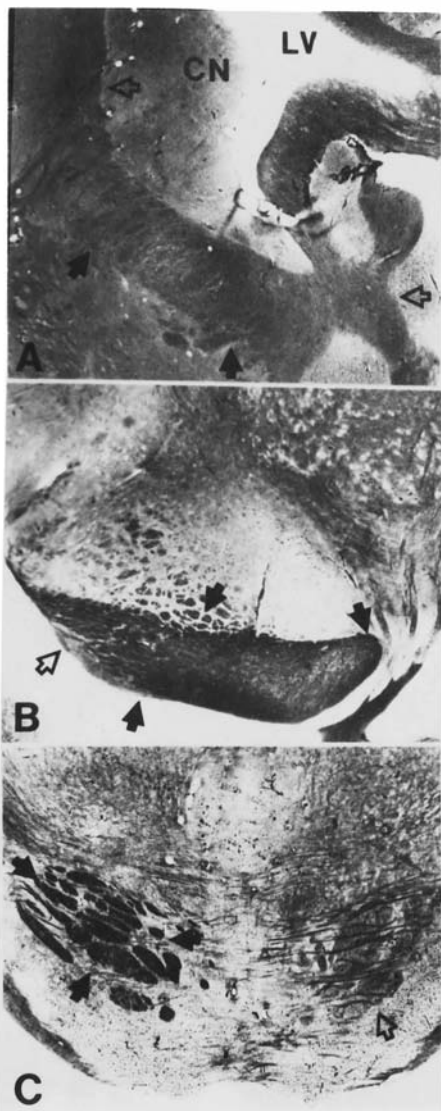
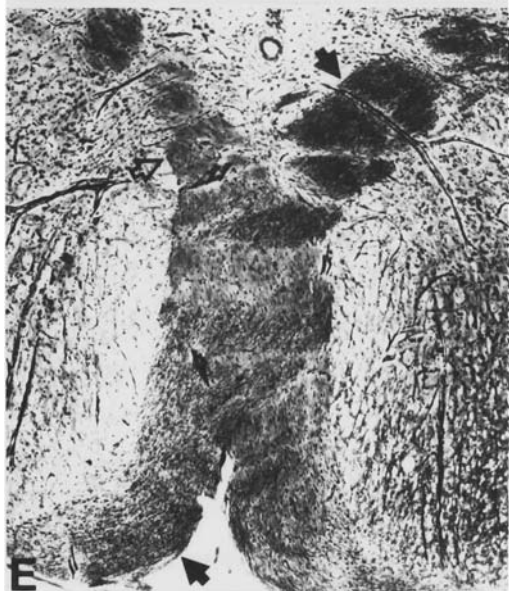
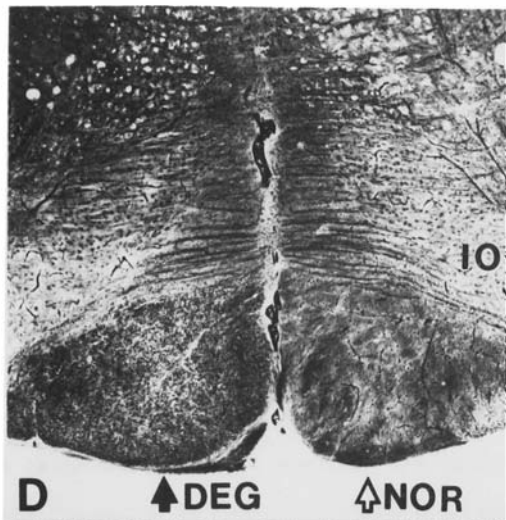


FIGURE 13

Degenerating debris is present in the anterior limb of internal capsule in (A). X 35. CN-caudate nucleus; LV-lateral ventricle. The closed arrows (▲) mark the limits of degenerating fibers of passage; the open arrows point to normal fiber bundles. The same degenerating fibers of passage can be seen filling two-thirds of the cerebral peduncle in (B) and coursing the basilar pons in (C). X 35. The closed arrows delineate the debris in (B) and (C) whereas the open arrows point to normal fiber bundles. The degenerating fibers course the left medullary pyramid in (D) and cross to the contralateral side in the pyramidal decussation of the caudal medulla (E). X 100. IO-inferior olivary nucleus; DEG-degenerating fibers of passage; NOR-normal fiber bundles. Fink-Heimer method.





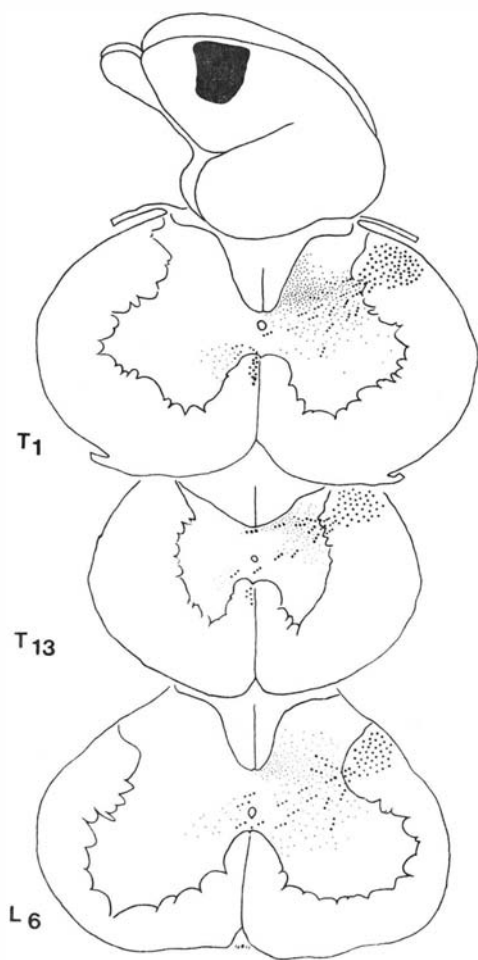
to form a large tract in the dorsal part of the lateral funiculus. A smaller bundle remains ipsilateral to the lesion and descends as a sulcomarginal tract in the ventral funiculus. There is no evidence of ipsilateral lateral or dorsal tracts, nor are intracommissural bundles present.

b. Position, extent and termination of corticospinal fibers

After large lesions of the motorsensory cortex, a large contralateral tract in the dorsal part of the lateral funiculus is found to extend the length of the cord. A smaller ipsilateral tract in the anterior funiculus can be followed into upper lumbar segments (Fig. 14). Contralateral fiber degeneration of the cervical, thoracic, lumbar, and sacral segments is: (1) heaviest in the internal basilar region of the dorsal horn (Figs. 14,15) including nucleus proprius cornu dorsalis and nucleus cornucommissuralis dorsalis (laminae IV, V, VI); (2) moderate in zona intermedia (lamina VII); and (3) sparse in nucleus motorius medialis and lateralis (laminae VIII, IX) (Fig. 14). Moderate debris ipsilateral to the lesion is also found in nucleus motorius medialis and nucleus cornucommissuralis ventralis.

FIGURE 14

Line drawing to illustrate the distribution of degenerating debris in representative spinal cord segments following a lesion of the majority of the motorsensory cortex in Galago senegalensis. Fibers of passage are represented by heavy dots, terminal degeneration by fine stippling. The area of heaviest debris is in the internal basilar region of the dorsal horn. Moderate debris can also be seen in the medial nuclei of the ventral horn ipsilateral to the lesion. Brain X 2.2; Cord segments. X 16



Degenerating fibers reach these ipsilateral nuclei either from the lateral tract, having crossed the ventral gray commissure, or from the ipsilateral ventral tract directly (Fig. 14). There is no evidence of terminations contacting cell soma in Waldeyer's marginal nucleus, substantia gelatinosa, Clarke's column or the intermediate thoracolumbar nuclei.

Discrete cortical lesions near the midline on the dorsal convexity presumptive hindlimb area (lesions 2-10 and 8-11, Fig. 16) produce little or no degeneration in cervical or thoracic gray. Dense terminal degeneration is present only in the segments of the lumbar enlargement at the base of the dorsal horn. Debris is heavy in the medial half of nucleus proprius cornu dorsalis and continues medially into the dorsal commissural nucleus (Fig. 16). Fibers of passage can also be traced across the ventral gray commissure to end in the ipsilateral ventral commissural nucleus and in the medial half of the ventral horn.

Lesions of somatosensory cortex, including parts of both hindlimb and forelimb areas (lesion 6-11, Fig. 18) produce dense degeneration in all cord segments. However, the dense band of degeneration in the dorsal horn is

FIGURE 15

The low power photomicrograph at (A) is the same section (T1) from which the preceding figure was traced (Fig. 14, T1-lesion 1-9) X 50. The box in (A) is magnified at (B) X 160. The medial cells of the dorsal proper nucleus are again shown in (C) X 312. Note the abundant debris throughout the field as well as the apparent terminal debris associated with medium and large neuron cell bodies (indicated by the three open arrows). Fink-Heimer method.

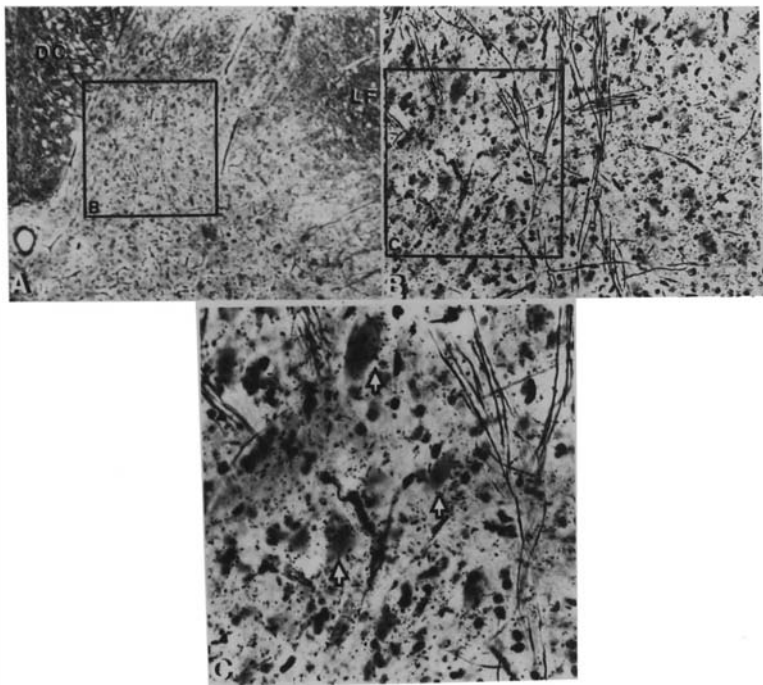


FIGURE 16

Line drawing to illustrate the distribution of degenerating debris in representative spinal cord segments following a lesion of the dorsomedial motor cortex (presumptive hindlimb area) of Galago senegalensis. There is little or no degenerating debris in cervical and thoracic cord segments. Note the pattern of terminal debris which is only seen in the segments of the lumbosacral enlargement (L4, L5, L6 and S1). Brain X 2.2; Cord segments X 16.

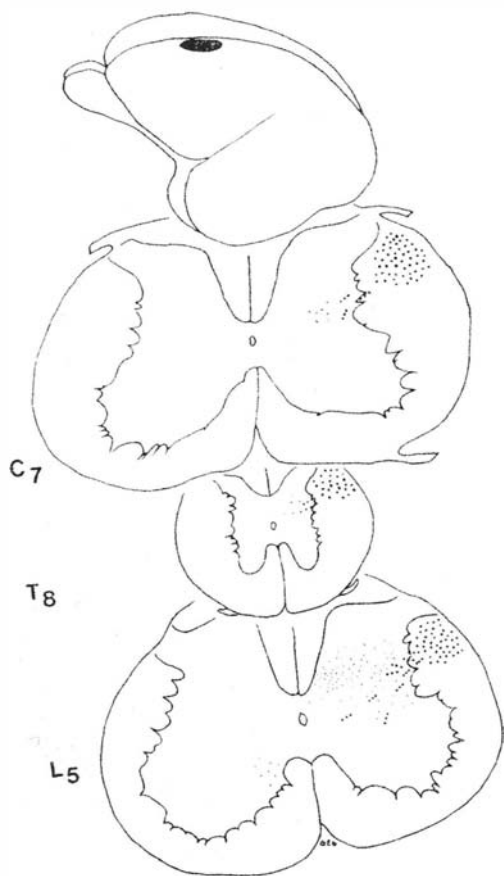
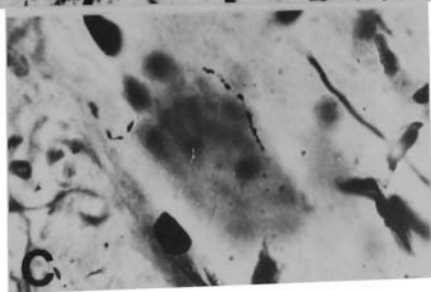
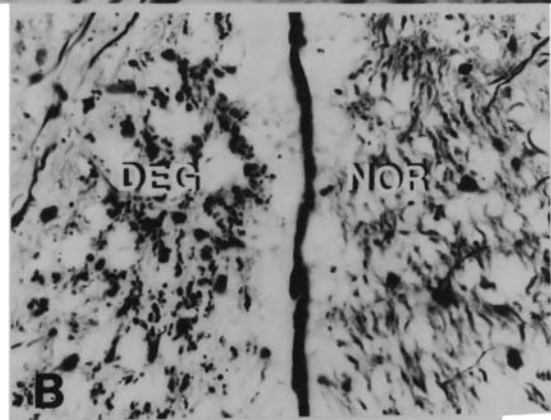
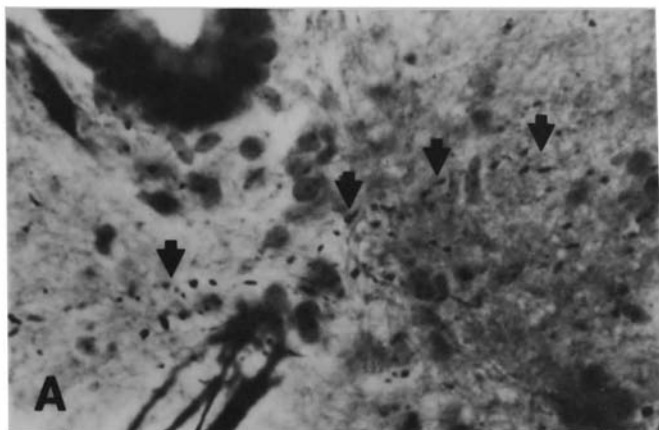


FIGURE 17

Photomicrograph (A) shows fibers of passage coursing through the ventral gray commissure. X 1000. These fibers will terminate in the medial nuclei of the ventral horn ipsilateral to the lesion. These medial nuclei (nuc. cornucommissularis ventralis and nuc. motorius medialis) also receive input from the ipsilateral ventral tract in (B). X 400. Terminal debris can be seen associated with a large motor neuron in nucleus motoris medialis in (C). X 1000. Fink-Heimer method.



shifted dorsally toward substantia gelatinosa (Figs. 18,19). Terminal debris is concentrated in the dorsal regions of nucleus proprius cornu dorsalis (Fig. 19) and extends ventrally only to the dorsal commissural nucleus. Degenerating debris is found in substantia gelatinosa, but the presence of terminals is equivocal. The degeneration from somatosensory cortical lesions does not extend ventrally into the zona intermedia (Fig. 19).

2. Lesions (Galago crassicaudatus)

Selective lesions also were placed in two different cortical areas of the thicktailed bushbaby, Galago crassicaudatus (Fig. 20). Earlier experimental data did not clarify the location of forelimb and hindlimb cortical areas with respect to cortical sulcal patterns (Campos-Ortega and Cluver, 1969). Therefore, lesions were placed either in the midline cortex of the dorsal convexity (presumptive hindlimb area), or on the dorsal bank of sulcus "e" (Fig. 20).

Degenerating debris is found in the contralateral lateral funiculus; however, no ventral tract is found from these lesions. From presumptive hindlimb area lesions, fibers bypass the cervical intumescence and the thoracic

FIGURE 18

Line drawing to illustrate the distribution of degenerating debris in representative spinal cord segments following a lesion of the somatosensory cortex in Galago senegalensis, (lesion 6-11, Fig. 8). Note that the dense band of degenerating debris is shifted to the dorsal regions of the dorsal horn. There is little or no debris in either zona intermedia or in the nuclei of the ventral horn. Brain X 2.2; Spinal cord segments. X 16.

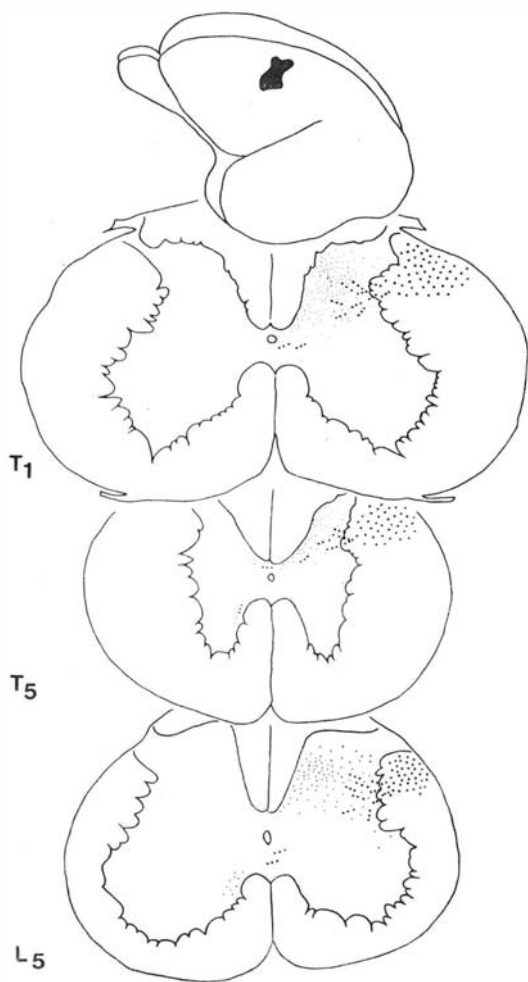


FIGURE 19

The low power photomicrograph at (A) is the same section (T1) from which the preceding figure was traced (Fig. 18, T1-lesion 6-11). X 50 Fink-Heimer. The box in (A) is in the dorsal aspect of the proper dorsal nucleus and just ventral to the substantia gelatinosa. In (B) note the dense preterminal debris in the upper half of the field. X 160. The boxed area in (B) is magnified in (C), X 312, where terminal debris can be seen associated with the cell bodies of small and medium-sized neurons. Fink-Heimer method.

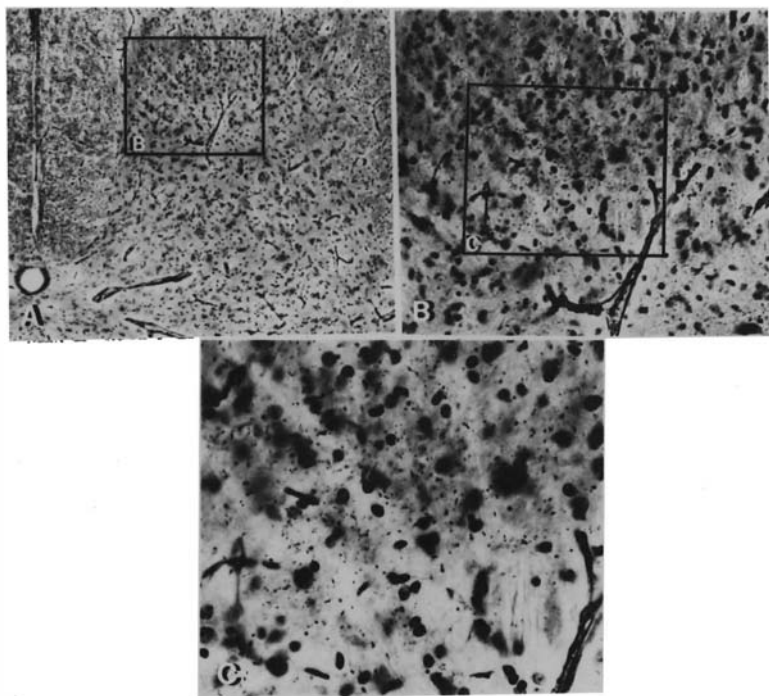
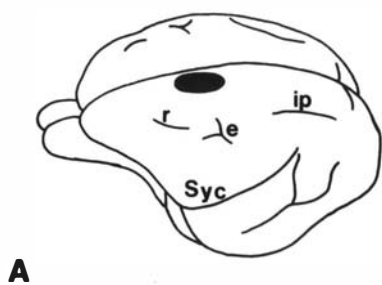


FIGURE 20

Line drawings and photomicrographs of lesions in the thicktailed or greater galago. In (A) and (B) a cerebral cortical lesion can be seen in the dorsomedial, presumptive hindlimb hindlimb area of the greater galago, Galago crassicaudatus. This lesion produced stainable degeneration that was confined to the segments of the lumbar enlargement (see Fig. 21). The lesion, shown in (C) and (D), is on the dorsal bank of sulcus "e". If this sulcus divides the more lateral face cortical area from the forelimb cortex, then this lesion should produce selective degeneration only in the cervical enlargement (see Fig. 22). (A) X 1.5; (B) X1; (C) X 1.5; (D) X 1.4.



gray to end in the segments of the lumbosacral enlargement (Fig. 21). Debris is heaviest in internal base of the dorsal horn and extends well into zona intermedia. Fibers of passage also can be traced through the ventral gray commissure and bilaterally into the medial nuclei of the ventral horn, nucleus cornucommissuralis ventralis and nucleus motorius medialis.

From a lesion in the dorsal bank of sulcus "e", a presumptive forelimb area, fibers terminate only in the segments of the cervical enlargement. No stainable debris is present below the segments of the cervical enlargement. This somatotopic organization is similar to the projections from the forelimb cortical area in the lesser galago (Goode and Haines, 1973). Distribution of pre-terminal and terminal debris is similar to that previously described in the lesser bushbaby (Fig. 22).

C. Termination of cortical projections: special topics

As a corollary to the description of terminals associated with the lamina of the spinal cord or within specific nuclear groups, two additional studies sought to:

- (1) localize specific motor nuclei in the ventral horn by studying chromatolytic effects due to peripheral nerve

FIGURE 21

Line drawing to illustrate the pattern of preterminal and terminal debris in a representative section (L5) from the lumbosacral enlargement, following a dorsomedial cortical lesion (hindlimb area) in Galago crassicaudatus. Fibers of passage are represented by heavy dots, terminal debris by fine stippling. Degenerating debris is concentrated in the medial nuclei of the basilar dorsal horn, nucleus proprius cornu dorsalis and nucleus cornucommissuralis dorsalis. Moderate debris is found in zone intermedia but becomes scattered in the ventral horn contralateral to the lesion. Although there is no degeneration in a ventral corticospinal tract, fibers recross through the ventral gray commissure to innervate the medial nuclei of the ventral horn ipsilateral to the lesion (i.e. ventral commissural nucleus and the ventral motor nuclei). Brain X 1.3; Cord segments X 15.

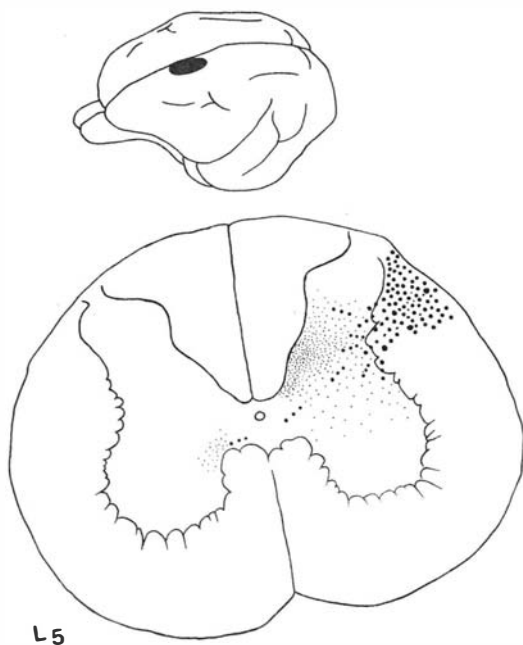


FIGURE 22

Line drawing to illustrate the pattern of degenerating debris found only in the cervical enlargement (C5-T1) following a cortical lesion of the dorsal bank of sulcus "e", Galago crassicaudatus. There was little or no debris in spinal cord segments below C8, indicating that this lesion was placed in the cortical forelimb area of the greater galago. Brain X 1; Spinal cord X 15.

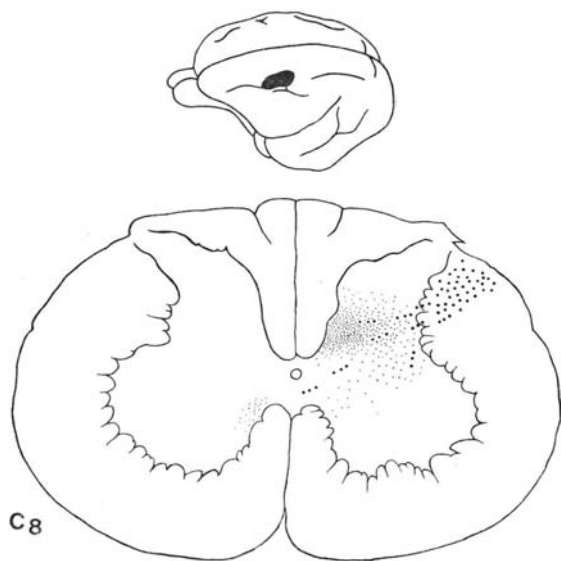
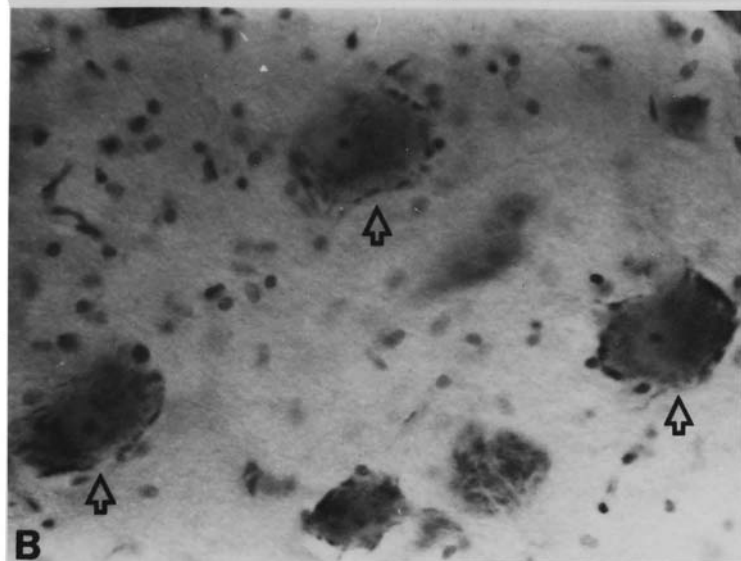
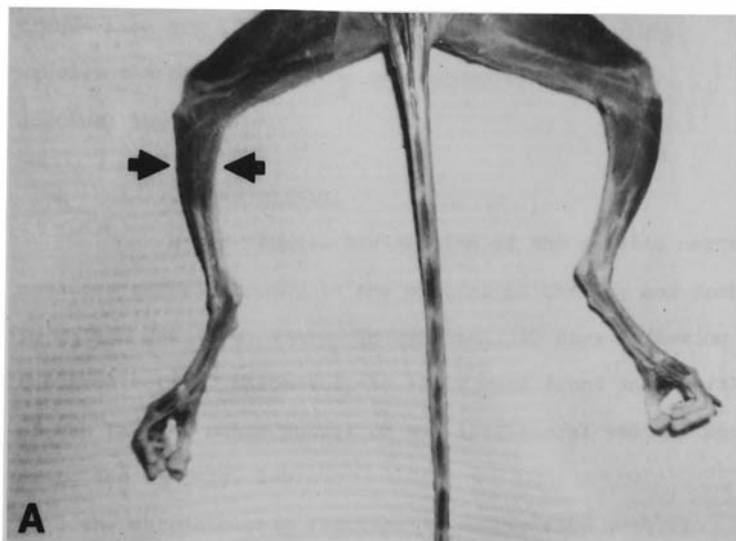


FIGURE 23

Photograph (A) shows the inferior extremities and tail of a lesser galago, Galago senegalensis. A midfemoral transection of the sciatic nerve (in galago, the main contribution is from L5, L6 and S1) produced a flaccid paralysis of the leg and subsequent atrophy of the muscles of the leg and foot which were thereby denervated. This animal was also subjected to a dorsomedial hindlimb cortical lesion fourteen days after the nerve transection. Chromatolytic cells were found in the lateral and dorsolateral motor nuclei of L5 and L6. (B) is a photomicrograph of three neurons from the lateral motor nucleus which display the characteristics of chromatolysis. Cresylviolet acetate. X 1000.



transection and (2) demonstrate by Golgi impregnation studies the dendritic arbor of neurons which receive cortical input.

1. Chromatolysis

A mid-femoral transection of the sciatic nerve produced severe atrophy in the muscles of the leg and foot in galago G8A (Fig. 23A). In addition, 25 days following the transection, chromatolytic cells were found in several of the lateral motor nuclei of the ipsilateral ventral horn of L₅ and L₆ (Fig. 23B).

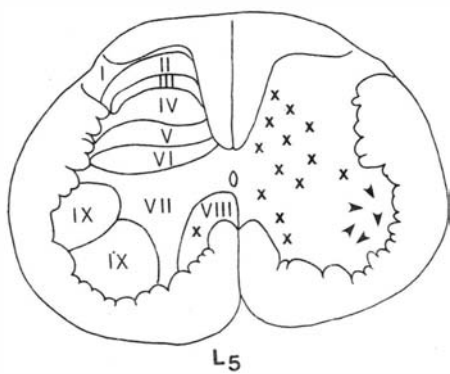
The chromatolytic reaction is represented both by swelling of the neuron cell body with displacement of the nucleus toward the periphery, and by dispersion and dissolution of the Nissl substance, first centrally, then peripherally. Several of these stages are seen in this study (Fig. 23B). The location of these cells is in the ventrolateral and dorsolateral motor nuclei of the ventral horn (Fig. 24). The ventro- and dorsolateral motor nuclei project peripherally to innervate mainly distal appendicular musculature (Sprague, 1948).

In addition to a peripheral nerve lesion, this animal (G8A) was also subjected to a lesion of the cerebral

FIGURE 24

Line drawing of a representative section from the fifth lumbar spinal segment in Galago senegalensis. Rexed's laminae are drawn on the left half of the figure. Lamina VIII contains the ventral commissural nucleus and the medial motor nucleus. Lamina IX contains the lateral motor nuclei. The small cross hatching (X) represent the terminal pattern of corticospinal fibers in Galago. The closed arrows (▲) represent the location of chromatolytic neuron cell bodies in the lateral and dorsolateral motor nuclei.

X 15.



cortex, which, in previous experiments included in this study, produced degenerating debris only in the lumbosacral enlargement. Terminal debris in G8A is also confined to the lumbar enlargement but it is only occasionally associated with nuclei which contain chromatolytic neurons. In contrast, moderate debris is found in the medial nuclei of the ventral horn which give rise to dorsal primary rami that supply axial musculature (Sprague, 1948; Goode and Haines, 1973).

2. Golgi studies

From the Golgi material, fortuitous impregnations were collected for histologic preparation including cells in the base of the dorsal horn, zona intermedia, ventral commissural nucleus, and ventral horn. The location of these cells and the extent of their dendritic arbor were studied. Tracings were made from a camera-lucida and exact line drawings of these cells were produced (Fig. 25).

The dendritic orientation of cells in the cervical and lumbar enlargements reflects the presynaptic patterns that are generated by the lateral corticospinal input. Specifically, the dendrites of cells located in the external

basilar zone of the dorsal horn are oriented mediolaterally in parallel with the fiber projections coming in from the lateral columns (cell-a, in Fig. 25). From the silver degeneration studies, debris is seen to spread medially and become concentrated in a dorsoventral band in the medial side of the dorsal proper nucleus and the dorsal commissural nucleus. The orientation of the dendrites in this region also appears to reflect this same course (Fig. 25 and 26).

Golgi impregnated cells in the medial nuclei of the ventral horn also reflect a dorsoventral orientation of their dendritic tree. In addition, a few long dendrites can be followed dorsomedially and found to cross the ventral midline under the central canal (Fig. 27). This pathway is also followed, but in the opposite direction, by fibers of passage from the lateral corticospinal tract. The Golgi material, then, appears to delineate the terminal course and intramedullary distribution of pre-terminal and terminal debris of corticospinal fibers observed in the Fink-Heimer material.

Golgi studies also demonstrate that the dendrites of spinal neurons extend beyond the lamina to which their cell bodies are confined. Neurons in the internal basilar

FIGURE 25

A composite line drawing of tracings from fourteen fortuitous impregnations of adult spinal cord. The neurons at (a) project their dendritic arbor toward the lateral funiculus, apparently receiving part of their input from it. The neuron at (b) is in the dorsal proper nucleus; the neurons at (c) are in the dorsal commissural nucleus. Their dendritic arbor is directed in a dorsoventral plane and reflect the intramedullary distribution of corticospinal projections into the spinal cord gray matter. The neuron at (d) is in the ventral commissural nucleus. Note that its dendrites extend far from the cell soma, even to cross the midline under the central canal. Corticospinal fibers terminate bilaterally in association with these neurons. Although there is little corticospinal input into lamina IX, in Galago the dendrites of the large ventral horn motor cells (e) extend well into the intermediate zone. Therefore axodendritic association even with these cells cannot be ruled out. Lumbosacral enlargement. Golgi-Kopsch method. X 20.

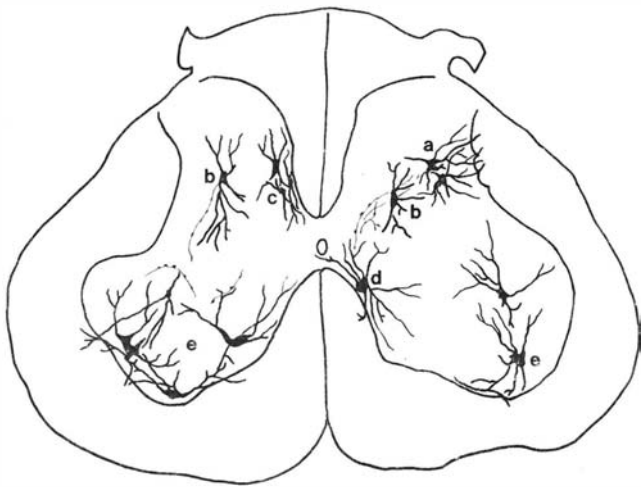


FIGURE 26

Camera lucida tracing of the neuron marked (b) in Fig. 25, from the dorsal proper nucleus. The dendrites of this second order neuron are without spiny projections in contrast with the large pyramidal cells (first order neuron) of the cerebral cortex. Note the direction of the dendritic arbor. The heaviest concentration of terminal debris from the lateral corticospinal tract is associated with the dendrites and soma of such a neuron. L5 Golgi-Kopsch method. X 500.

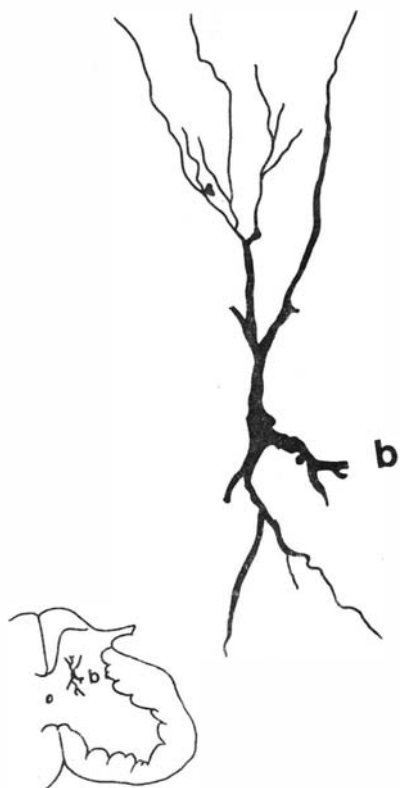
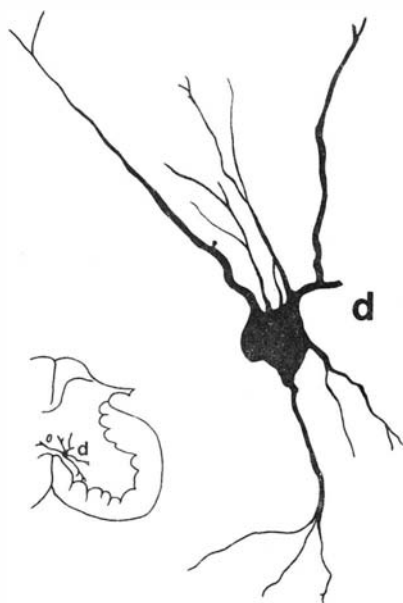


FIGURE 27

Camera lucida tracing of the neuron marked (d) in Fig. 25, from the ventral commissural nucleus. The orientation of the dendrites of this neuron mirror the intramedullary course and part of the terminal distribution of the corticospinal input to the cord gray matter. These neurons are also known to project bilaterally to the medial motor nuclei of the ventral horn (Sterling and Kuypers, 1968). L5 Golgi-Kopsch method. X 500.



nuclei project their dendritic processes from lamina III to lamina VII. Neurons in the ventral laminae (VII, VIII and IX), in addition to sending processes toward each other, also send their dendrites well within the zona intermedia (Fig. 25).

DiscussionA. Motor Cortex

The existence of a motor cortex as a discrete and definable tissue is based primarily on the observation the electrical stimulation of certain areas of the cortical surface produces muscle contraction. These regions more properly can be designated "the electrically excitable motor cortex". Although the electrically excitable motor cortex generally is thought to be limited to the precentral gyrus, in no mammal, including man, is this motor tissue so restricted¹¹. The entire nervous system in a sense, can be conceived of as motor, for it exists fundamentally to generate output.

One fundamental component of the motor cortex is the corticospinal system. Cortical neurons which give rise to spinal projections are concentrated along the border between the frontal and parietal lobes and become more

¹¹Among all the mammals, only the primates, and not all of them, possess a precentral gyrus.

scattered away from this border. In most mammals, there is also a fine topographical organization within the motor region (Woolsey, 1958), and in most primates this organization is reflected in the cortical sulcal pattern (Welker and Campos, 1963; Sanides and Krishnamurti, 1967).

In prosimian primates there is a motorsensory cortical overlap with a rostral strip predominantly motor and a caudal parietal strip predominantly sensory (Kanagasuntheram et al., 1966; Jameson et al., 1963). Large members of the family Lorisiidae have a sulcus which separates primary motor and sensory cortices. The potto monkey has a definite central sulcus, whereas the vertical component of sulcus "e" is the homologue in the slow loris (Sanides and Krishnamurti, 1967; Haines et al., 1974). Three other sulci extend rostrocaudally across the motorsensory amalgam of the prosimian cortex; these sulci are sulcus rectus, the horizontal component of sulcus "e" and sulcus "c". It was shown by electrophysiologic and cytoarchitectural studies (Sanides and Krishnamurti, 1967; Jameson et al., 1963; Kanagasuntheram et al., 1966) that these sulci define the somatotopic limits of the motorsensory cortex, but the anatomic corollary was not confirmed. The present study has shown that: (1) sulcus rectus and the horizontal

component of sulcus "e" do, indeed, separate the dorsomedial forelimb area from the more dorsolateral face cortical area and (2) within the predominantly sensory cortex, sulcus "c" separates the cortical representation of hindlimb from forelimb area. This degree of cortical somatotopic organization was not suspected from earlier studies of corticospinal projections of a prosimian primate (Campbell, 1966b).

Cortical separation of function by cytoarchitectural differences and by cortical sulci becomes more refined as one ascends the phylogenetic scale. This is exemplified in the order Primates. The brains of small primates are lissencephalic except for calcarine, hippocampal, ectorhinal fissures, and an indication of the suprasylvian sulcus. Modern tree shrews have advanced little from this basic pattern (Le Gros Clark, 1924, 1929, 1932).

Tarsius spectrum has only a small suprasylvian element on its orbital surface and a triradiate calcarine complex (Connolly, 1950). The brain of Microcebus murinus, the mouse lemur, although advanced in comparison to Tupaia, is still simple when compared to the other lemurs (Le Gros Clark, 1931; Connolly, 1950; Friant, 1970).

The overall development of the cerebral hemispheres of the Lorisidae is represented by an increase in the number and complexity of neocortical sulci. Although the cortex of Galago is relatively simple, a primate pattern can be distinguished. There is a true temporal pole separated from the frontal cortex by a Sylvian complex and a well developed calcarine area. And, compared with the general mammalian cortex, these lower primates characterize the trends of neocortical evolution seen in the Anthroidea. These trends are represented by an increase in neocortical growth associated with the separation and expansion of the motorsensory cortex and development of visual, temporal and association cortices. These modifications can be correlated with an increase in the number of coronally oriented sulci which in the motorsensory cortex serve to separate somatotopic organization. Cortical separation of function also can be seen in the organization of the long descending fiber systems of the spinal cord, especially the corticospinal projections.

B. Corticospinal Projections

1. Origin

In most nonprimate mammals the corticospinal fibers originate from a motorsensory amalgam. There is little cytoarchitecture difference across the amalgam, and there is no cortical somatotopic organization that is separated by a distinct sulcal pattern. For example, the cortical projections to the spinal cord in carnivores originate mainly from the postsigmoid gyrus, and there is no sulcus which separates the predominantly motor cortex from the somatosensory cortex (Nyberg-Hansen and Brodal, 1963).

In primates, there is a trend toward complete separation of motorsensory cortical topography. At the lowest scale of primate phylogeny, as represented by the extant tree shrews, corticospinal projections originate from the entire frontal lobe including the polar cortex (Jane et al., 1965; Shriver and Noback, 1967). In the prosimian primates, as represented by the family Lorisidae, with the addition of cortical somatotopic organization, the motorsensory cortex is shifted caudally and the prefrontal area including the frontal pole is occupied by a silent granular cortex. Although Campbell

(1966b) reported sparse projections to the spinal cord from frontal pole lesions in the slow loris, these data were not confirmed in the present study. When care was taken to avoid the terminal distribution of the anterior cerebral arteries¹², frontal pole lesions did not produce stainable degeneration in the spinal cord of Galago.

The cortical origin of corticospinal projections in Galago corresponds closely to the area of electrically excitable cortex reported by Mott and Halliburton (1908) in Lemur macaco and in L. catta; by Zuckerman and Fulton (1941) in Perodicticus potto and Galago demidovii; and by Kanagasuntheram et al. (1966) in Galago senegalensis. In contrast, motor responses were not reported from stimulation of somatosensory areas 3-1-2 in Galago (Kanagasuntheram et al., 1966), whereas Woolsey and his coworkers (1958) have recorded motor responses from these areas in both New and Old World monkeys, the absence of these responses in prosimians may be explained by the anatomical data. The cytoarchitecture is similar across

¹² In Galago, the large polar branches of the anterior cerebral arteries loop over the frontal pole and their terminal branches supply the dorsomedial motorsensory cortex.

the motorsensory amalgam in Galago, but there is a substantial increase in the number of granule cells in layer IV of the somatosensory cortex. There is also poor differentiation in the supraganglionic layers with fusion of the laminae II, III and IV, as reported in the slow loris (Sanides and Krishnamurti, 1967) and confirmed in the present investigation. In addition, the somatosensory cortex gives rise to projections which terminate almost exclusively on dorsal nuclei of the dorsal horn where there is little direct or indirect access to the larger motor cells of the ventral horn. This projection is in marked contrast to the distribution of degenerating debris from lesions of somatomotor cortex which may terminate directly upon the motor nuclei of the ventral horn.

In the higher anthropoid primates, with the addition of a complete central sulcus, the majority of corticospinal projections arise from the pre- and postcentral cortex (Liu and Chambers, 1964; Petras, 1969). The somatotopic organization of these projections is also much refined. For example, there are distinct sites on the precentral gyrus of Macaca which project predominantly to the medial internuncial and medial motor nuclei of the spinal cord. There are also selective sites which project

predominantly to the lateral and dorsolateral motor nuclei (Kuypers and Brinkman, 1970).

2. Corticospinal Projections - Position and Extent

One outstanding feature of the corticospinal pattern is its high degree of variation in its location, extent and in its site of termination in the spinal cord. As the tract reaches the cervical cord, it may course in any of the three funicular pathways regardless of the mammalian order examined. In addition, the major tract may extend a variable distance down the cord and differ in its nuclei of termination.

To summarize part of the literature review, the major crossed corticospinal projection is found in the dorsal funiculus in chiropterans, some edentates (armadillo), marsupials and rodents. A ventral tract is reported in elephants, hyracoids, and insectivores. The lateral funiculus contains the major projections in some edentates (sloth) and monotremes and in all ungulates, carnivores, lagomorphs and primates. With few exceptions the tract is well developed throughout the cord, only in the carnivores and primates (for references, see literature review).

Two notable exceptions of corticospinal development are seen in: (1) a rodent, the Canadian porcupine (Simpson, 1912a) and (2) in the hopping and arboreal marsupials (Martin et al., 1970, 1972). Although the rodents in general possess a long crossed dorsal pathway, the projections in the porcupine are significantly different. In addition to the crossed dorsal tract, this animal also has an uncrossed ventral tract that extends to sacral levels and an uncrossed dorsal bundle that ends just short of the lumbar enlargement. A less dramatic modification is seen within the marsupials. Rarely can the corticospinal fibers of marsupials be traced below cervical segments (Bautista and Matzke, 1965; Martin and Fisher, 1968). In contrast, all hopping and arboreal marsupial forms (potoroo, kangaroo and phalanger) have fibers which extend well into the thoracic cord. Some of these fibers terminate just short of the lumbar enlargement (Goldby, 1939; Martin et al., 1970; Watson, 1971a,b). This extension of fibers may be related to the specialized locomotor requirements of these animals.

A similar specialization is seen in Galago. These animals possess corticospinal fibers which extend the length of the spinal cord. The major tract is located in

the lateral funiculus, but there is also a long ventral tract which may extend to the lumbar cord. Fibers from the ventral tract terminate ipsilaterally upon the neurons in the medial nuclei of the ventral horn. In addition, these medial nuclei also receive corticospinal input from cortical areas which do not product degeneration in a ventral tract. In these cases, fibers from the contralateral tract recross the ventral gray commissure to terminate in the medial nuclei of the ventral horn.

3. Sites of Termination of Corticospinal Projections (with special reference to the primates)

The chief site of spinal terminations of cortical projections in nonprimate and primate mammals is to the base of the dorsal horn (laminae IV-VI). This site can be divided into medial and lateral zones. In carnivores, the major projection is reported to terminate in the external basilar region or lateral zone of the dorsal horn. This projection site was confirmed recently by a quantitative electron microscopic investigation (Shapovalov, 1973). In the anthropoid primates, the degenerating fibers to the basilar regions form a dense band of debris across laminae V and VI and are reported

to be more concentrated in the lateral or external basilar zone in investigations which used the Nauta technique (Petras, 1969). This chief projection is supplemented in most primates by additional terminals onto the large motor cells of the ventral horn¹³. In anthropoid primates, the density of these direct projections increases proportionally with animal size and degree of animal dexterity. This direct projection into the ventral horn nuclei is also reported in certain carnivore, specifically the raccoon and kinjajou (Petras and Lehman, 1966; Petras, 1969). In these forms monosynaptic connections are present only in the cervical enlargement; however, in primates the monosynaptic projections are present throughout the spinal cord. The function associated with these direct projections is an increase or refinement of the speed and direction of fine motor movements, especially of the intrinsic muscles of the hand (for review, see Phillips, 1970).

Although these data have gained wide acceptance, there are additional terminal nuclei which receive monosynaptic

¹³This projection into the ventral horn is absent in tree shrew (Jane *et al.*, 1965; Shriver and Noback, 1967), marmoset (Shriver and Matzke, 1965) and the squirrel monkey (Harting and Noback, 1970).

input from the motorsensory cortex. In the prosimian primates, as reported in this investigation and in other studies (Campbell, 1965; Jane et al., 1965; Ferrer, 1971), there are additional projections not only to the internuncial nuclei of lamina VII but also to the larger cells in the medial nuclei of the ventral horn. This site of termination has also been reported in the anthropoid primates, including man (Petras, 1969). To date, this medial organization of corticospinal projections has only been reported in animal forms with semierect or erect posture or in animal forms with the potential for erect posture.

The fibers which innervate the medial nuclei of the ventral horn gain access to their terminal nuclei directly from a long ventral tract or from fibers that recross from the contralateral tract through the ventral gray commissure. This is a constant feature of all primates thus far studied except for the tree shrew, marmoset and squirrel monkey.

The Tupaiidae possess a number of characters which have produced unresolved controversies as to their taxonomic position (for review, see Haines and Swindler, 1972). But regardless of their systematic position, they are the only

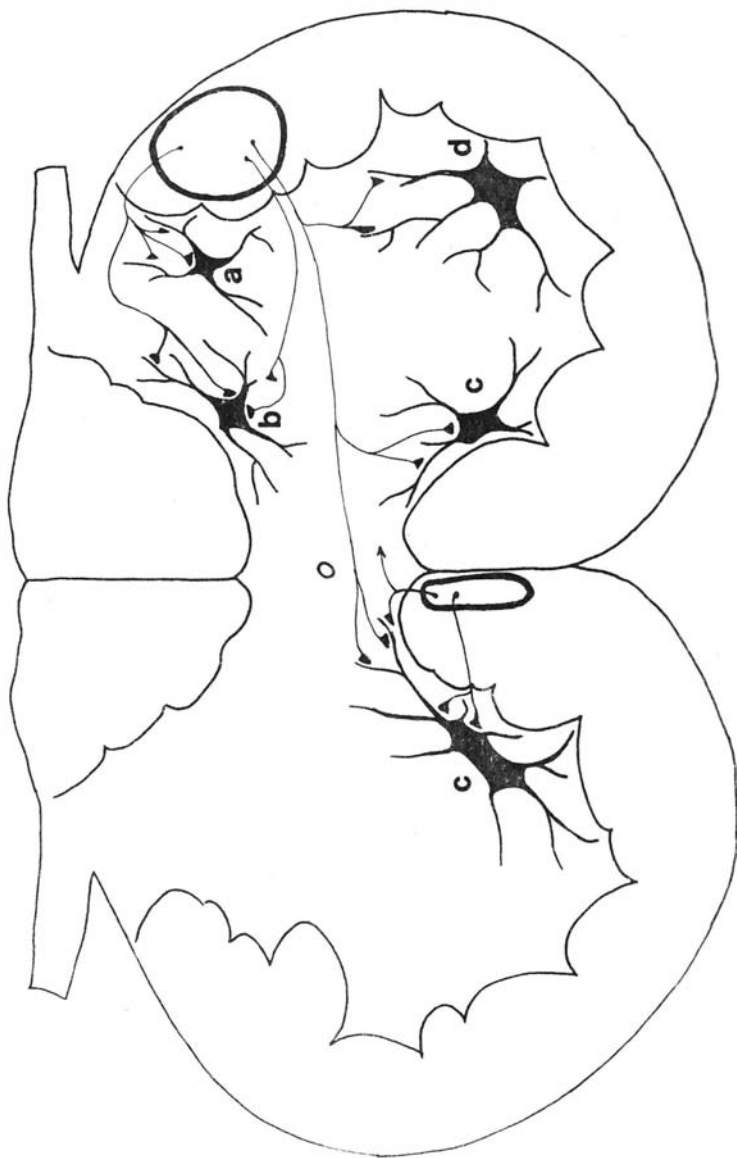
extant forms which are thought to be close to the ancestral stock from which the primates evolved. For this reason, they are useful in an attempt to characterize an evolving primate pattern. Jane et al. (1965) and Shriver and Noback (1967) report that the corticospinal projections in Tupaia glis terminate in the internal basilar region or medial zone of the dorsal horn. This site of termination is also one of the major projection areas within the order Primates. Petras (1969) suggests a heavier concentration of terminal debris in the medial nuclei of the anthropoid apes when compared to the Old and New World monkeys. Kuypers and Brinkman (1973) also report separate cortical areas in Macaca which selectively project to the medial nuclei of the ventral horn.

This medial organization is also well represented in the prosimian primates. The present investigation of Galago, as well as the data reported by Campbell (1966b) on the slow loris show the same medial projections into the nuclei of the dorsal horn. In addition, substantial bilateral projections are directed toward the medial nuclei of the ventral horn.

When these corticospinal projections are compared with the morphology of spinal cord neurons from the Golgi material, the following correlates result: 1) the cells in

FIGURE 28

Schematic line drawing to summarize the synaptic patterns in the terminal nuclei from corticospinal fibers in Galago. This figure is a compositive of material stained with the Fink-Heimer method, for degenerating axoplasm, and the Golgi method. From the lateral corticospinal tract, fibers terminate by axodendritic and axosomatic synapses in (a) nucleus proprius cornu dorsalis, (b) nucleus cornucommissuralis dorsalis and bilaterally in (c) nucleus cornucommissuralis ventralis and nucleus motorius medialis. In addition, the nuclei of the medial ventral horn also receive terminals from the ipsilateral ventral tract. The lateral motor nuclei (d) probably receive monosynaptic input from the motorsensory cortex, but only onto their distal dendrites.



the internal basilar zone receive axosomatic as well as axodendritic input from the motorsensory cortex; 2) neurons in the medial nuclei of the ventral horn also receive axodendritic and axosomatic contact from the corticospinal tracts, and 3) because the dendritic arbor of the lateral motor neurons of the ventral horn extend well into the intermediate zone (lamina VII), they too, probably receive some axodendritic synapses from the motorsensory cortex in Galago (Fig. 28).

Although the synaptology of the descending projections cannot be verified morphologically without the use of the electron microscope, the organization of degenerating debris stained with the Fink-Heimer method has been verified at the ultrastructural level (Heimer and Peters, 1968). Plans are now being completed by this author to combine the silver staining of degenerating axoplasm with electron microscopy to verify the synaptology of the descending cortical and subcortical motor pathways in Galago.

C. Phylogenetic Considerations

Phyletically, it has been suggested that corticospinal pathways evolved independently in each mammalian order (Noback and Shriver, 1966a,b). In the

carnivores and primates such a development has produced both a motor and a sensory component. The sensory component is probably phylogenetically older for it is also present in lower forms, e.g., in the opossum (Martin et al., 1968), an animal which does not have a well developed motor component.

The lorisooids (galagoes and lorises) are a divergent population, and have different locomotor behavior; but the pattern of corticospinal morphology is similar. These data would suggest that the prosimian corticospinal pattern was determined by inheritance from a common stock and was not individually acquired. Thus, when comparing the system across primate phylogeny, the medial organization of the tree shrew is carried into the medial ventral horn in the prosimian stock. Because cells in the medial nuclei of the ventral horn innervate proximal limb and axial musculature, it is proposed that direct cortical influence over the axial musculature provided a selective advantage in the evolution of semi-erect or erect posture. Once this posture was achieved successfully, a continued selective advantage was gained with the freedom of the hands. This manual dexterity is well known in most Old and New World monkeys, the great apes, and in man.

D. Functional Considerations

Observations of terminal input to the spinal cord by corticospinal projections usually concentrate upon the ventral horn nuclei of the cervical and lumbar enlargements. But in many mammalian species, these projections reach neither the cervical enlargement nor the large motor cells of the ventral horn. Yet such mammals possess an electrically excitable cortex and perform motor behavior that appears voluntary (ie, the opossum, the tree shrew).

This apparent contradiction is typical of the misunderstandings of corticospinal function. It has been shown that the corticospinal system may exert both an excitatory and an inhibitory action on its terminal nuclei (Casey and Towe, 1961). Inhibition may be either direct or indirect, such as a presynaptic mechanism. In addition, the system can also be affected by cutaneous, auditory, visual and proprioceptive influences. It was not until the refinements of the staining of degenerating axoplasm (Nauta and Gyax, 1951; 1954; and Nauta, 1957; Fink and Heimer, 1967) and the electron microscopic verification of these techniques (Heimer and Peters, 1968) that the terminal distribution of many brain pathways were known.

Electrophysiological studies, with stimulation and recording of acute and chronic lesioned animals, as well as behavioral studies, have shown that the pyramidal system (corticospinal and corticobulbar pathways) is not the "hot line" from the motor cortex that is responsible for overt motor activity (Tower, 1935; Phillips and Porter, 1964; Liu and Chamber, 1964; Lawrence and Kuypers, 1968a,b; for review, see Wiesendanger, 1969 and Towe, 1973). Its action on the brainstem sensory nuclei and on the sensory nuclei of the spinal cord are not understood (Fetz, 1968). Its action on motor centers is varied. Within the cortex, neurons which project to the cord increase their discharge rates prior to and during movement; whereas, the same projections from the sensory cortex fire during and after the movement (Evars, 1968; 1969; Fetz, 1969; Fetz and Finocchio, 1971). Yet these discharge rates (average 15-35/sec. in primates) fail to achieve a level which can fire motor neurons or potentiate the motor neurons to fire (100/sec). This data makes the "hot line" notion even more untenable. The present concept of corticospinal function is that the projection acts upon its terminal motor nuclei to improve the speed and direction of the action and adds the necessary readiness

to act (Lawrence and Kuypers, 1968a,b; Petras, 1969; Towe, 1973).

Towe (1973) states that the corticospinal system has existed for perhaps 300 million years but only in the last century, was it discovered. From the available data, it is possible to state that any mammal, including man, could survive as an individual without this system. But whether any collection of mammals could survive as a species under such circumstances is quite another matter: it probably could not. The pyramidal system adds the necessary 'readiness to act' that makes the difference in the selective process where speed and appropriateness of action are so important in the survival and subsequent evolutionary development of any mammal.

BIBLIOGRAPHY

- ABBIE, A. A. 1940 Cortical lamination in the monotremata.
J. comp. Neurol., 72:428-467.
- ALBRECHT, M. H. 1954 Mounting frozen sections with
gelatin. 29(2):89-90.
- ARIENS KAPPERS, C. U., G. C. HUBER, and E. C. CROSBY
1936 The Comparative Anatomy of the Nervous System
of Vertebrates, including Man. New York. p. 1517-1713.
- BAUTISTA, N. S., and H. A. MATZKE 1965 A degeneration
study of the course and extent of the pyramidal tract
of the opossum. J. comp. Neurol., 124:367-376.
- BISCHOFF, E. 1900 Beitrag zur anatomie des igelgehirnes.
Anat. Anz., 18:348.
- BONIN, G. von 1945 The Cortex of Galago, University of
Illinois Press, Urbana, 55 pp.
- BREGMANN, L. E. 1915 Neue. untersuchungen zur kennntniss
der pyramidenbahn. Die oblongatopyramide des
elephanten. Anat. Anz., 48:235, cited by Campbell,
1965.
- BROWN, L. T. 1971 Projections and terminations of the
corticospinal tract in rodents. Exp. Brain Res.,
13:432-450.

- BUXTON, D. F., and D. C. GOODMAN 1967 Motor function and the corticospinal tracts in the dog and raccoon. J. comp. Neurol., 129:341-360.
- CAMPOS-ORTEGA, J. A., and P. F. De V. CLUVER 1969 The corticothalamic projections from the sensorimotor cortex of Galago crassicaudatus. J. comp. Neurol., 136:397-418.
- CAMPBELL, C. B. G. 1965 Pyramidal tracts in primate taxonomy. Ph.D. Thesis, University of Illinois.
- CAMPBELL, C. B. G. 1966a The relationships of the tree shrews: The evidence of the nervous system. Evolution, 20:276-281.
- CAMPBELL, C. B. G., D. YASHON, and J. A. JANE. 1966b The origin, course and termination of corticospinal fibers in the slow loris, Nycticebus coucang (Boddaert). J. comp. Neurol., 127:101-112.
- CASEY, K. L., and A. L. TOWE 1961 Cerebellar influences on pyramidal tract neurones. J. Physiol. (Lond), 158:399-410.
- CHAMBERS, W. W., and C. N. Liu 1957 Corticospinal tract of the cat. An attempt to correlate the pattern of degeneration with deficits in reflex activity following neocortical lesions. J. comp. Neurol., 108:23-55.

- COLONNIER, M. 1964 Experimental degeneration in the cerebral cortex. *J. Anat. (Lond)*, 98:47-53.
- CONNOLLY, C. J. 1950 External Morphology of the Primate Brain, Springfield.
- DEXLER, H., and A. MARGULIES 1906 Ueber die pyramidenbahn des Schafes und der Ziege. Morph. Jahrb., 35:413, cited by Campbell, 1965.
- DOM, R., G. F. MARTIN, B. L. FISHER, A. M. FISHER, and J. K. HARTING 1971 Motor cortex and corticospinal tract of the armadillo. *J. Neurol. Sci.*, 14:225-236.
- DOUGLAS, A., and M. L. BARR 1950 The course of the pyramidal tract in rodents. *Rev. Canad. Biol.*, 9:118-122.
- DRAESEKE, J. 1903 Zur mikroskopischen kenntniss der pyramidenkreuzung der chiropteren. *Anat. Anz.*, 23:449-456.
- DRAESEKE, J. 1904 Zur kénntniss des Ruckenmarks und der Pyramidenbahmen von Talpa europaea. *Monatsschr. Psychiat. Neurol.*, 15:401-409.
- EDINGER, L. 1904 Bau der Nervozen Zentralorgane 1:116, cited by Campbell, 1965.

- ELLIOT SMITH, G. 1903 On the morphology of the brain in the mammalia, with special reference to that of the Lemurs recent and extinct. Trans. Linn. Soc. Lond., 8:319-432.
- EVARTS, E. V. 1968 Relation of pyramidal tract activity to force exerted during voluntary movement. J. Neurophysiol., 31:14-27.
- EVARTS, E. V. 1969 Activity of pyramidal tract neurons during postural fixation. J. Neurophysiol., 32:375-385.
- FERRER, N. G. 1971 The pyramidal system of the greater galago. Anat. Rec., 169:314-315.
- FETZ, E. E. 1968 Pyramidal tract effects on interneurons in the cat lumbar dorsal horn. J. Neurophysiol. 31:69-80.
- FETZ, E. E. 1969 Operant conditioning of cortical unit activity. Science, 163:955-958.
- FETZ, E. E., and D. V. FINOCCHIO. 1971 Operant conditioning of specific patterns of neural and muscular activity. Science, 174:431-435.

- FINK, R. P., and L. Heimer 1967 Two methods for selective impregnation of degenerating axons and their synaptic endings in the central nervous system. *Brain Research*, 4:369-374.
- FISHER, A. M., J. K. HARTING, G. F. MARTIN and M. I. STUBER 1969 The origin, course and termination of corticospinal fibers in the armadillo (*Dasytus novemcinctus mexicanus*). *J. Neurol. Sci.*, 8:347-361.
- FOX, C. A., M. UBEDA-PURKISS, H. K. IHRIG, and D. BIAGIOLI 1951 Zinc chromate modification of the Golgi technic. *Stain Technology*, 26:109-114.
- FRIANT, M. 1970 Le cerveau des Lemuriens de Madagascar. *Acta neurol. belg.* 70:439-470.
- FULTON, J. F., and D. SHEEHAN 1935 The uncrossed lateral pyramidal tract in higher primates. *J. Anat.*, 69:181-187.
- GANS, Carl 1969 Some questions and problems in morphological comparison. In: J. M. Petras and C. R. Noback (eds.), *Comparative and Evolutionary Aspects of the Vertebrate Central Nervous System*, Ann. N. Y. Acad. Sci., 167:506-513.

- GOLDBY, F. 1939a An experimental investigation of the motor cortex and the pyramidal tract of Echidna aculeata. J. Anat., 73:509-524.
- GOLDBY, F. 1939b An experimental investigation of the motor cortex and its connections in the phalanger, Trichosurus vulpecula. J. Anat., 74:12-33.
- GOLDBY, F., and G. N. KACKER 1963 A survey of the pyramidal system in the coypu rat, Myocaster coypus. J. Anat., 97:517-531.
- GOODE, G. E., and D. E. HAINES 1973 Corticospinal fibers in a prosimian primate (Galago senegalensis). Brain Research, 60:477-481.
- HAINES, D. E., and D. R. SWINDLER 1972 Comparative neuroanatomical evidence and the taxonomy of the tress shrews (Tupaia). J. Human Evol., 1:407-420.
- HAINES, D. E., B. C. ALBRIGHT, G. E. GOODE, and H. M. MURRAY 1974 The external morphology of the brain of some Lorisidae. In Prosimian Biology (Eds.), R. D. Martin, G. A. Doyle and A. C. Walker. Duckworth Company, Ltd., London, in press.

- HARTING, J. K., and C. R. NOBACK 1970 Corticospinal projections from the pre- and postcentral gyri in the squirrel monkey (Saimiri sciureus). Brain Research, 24:322-328.
- HEIMER, L., and A. PETERS 1968 An electron microscope study of a silver stain for degenerating boutons. Brain Research, 8:337-346.
- JAMESON, H. D., R. KANAGASUNTHERAM, G. E. DECOURSEY, M. MURRAY, G. S. O'BRIEN, and C. N. WOOLSEY. 1963 Cortical localization in Galago senegalensis senegalensis. Neurology, Minneap., 13:352.
- JANE, J. A., C. B. G. CAMPBELL, and D. YASHON 1965 Pyramidal tract: A comparison of two prosimian primates. Science, 147:153-155.
- JANE, J. A., C. B. G. CAMPBELL, and D. YASHON 1969 The origin of the corticospinal tract of the tree shrew (Tupaia glis) with observations on its brain stem and spinal terminations. Brain, Behavior Evolution, 2:160-182.
- KÄLLISCHER, O. 1901 Sitzungab. d. k. preuss. Akad. d. Wissenach. zu Berlin. 1:428-439, cited by Towe, 1973.

- KALISCHER, O. 1905 Abh. preuss. Akad. Wiss., Phys.
Abh. nicht zur Akad. gehor Gelehrter. IV:1-105,
cited by Towe, 1973.
- KANAGASUNTHERAM, R., C. H. LEONG, and Z. Y. MAHRAN 1966
Observations on some cortical areas of the Lesser
Bushbaby (Galago senegalensis senegalensis).
J. Anat. (Lond.), 100:317-333.
- KARNOSKY, M. J. 1965 A formaldehyde glutaraldehyde
fixation of high osmolality for use in electron
microscopy. J. Cell Biol., 27:137.
- KARTEN, H. J. 1969 The organization of the avian
telencephalon and some speculations on the
phylogeny of the amniote telencephalon. In:
Comparative and evolutionary aspects of the
vertebrate central nervous system. J. M. Petras and
C. R. Noback (Eds.). Anns. N. Y. Acad. Sci.,
167:164-179.
- KARTEN, H. J. 1971 Efferent projections of the wulst
of the owl. Anat. Rec., 169:353.
- KING, J. L. 1910 The corticospinal tract of the rat.
Anat. Rec., 4:245.

- KING, J. L. 1911 The pyramidal tract and other descending paths in the spinal cord of the sheep. *Quar. Jour. Exper. Physiol.*, 4:133.
- KOTZENBERG, W. 1899 Untersuchungen uber das Ruckenmark des Ingels. Wiesbaden, p. 19, cited by Campbell, 1965.
- KUYPERS, H. G. J. M. 1958a An anatomical analysis of cortico-bulbar connexions to the pons and lower brain stem in the cat. *J. Anat.*, (Lond.), 92:198-218.
- KUYPERS, H. G. J. M. 1958b Pericentral cortical projections to motor and sensory nuclei. *Science*, 128:662-663.
- KUYPERS, H. G. J. M., W. R. FLEMING, and J. W. FARINHOLT 1962 Subcortical projections in the rhesus monkey. *J. comp. Neurol.*, 118:107-137.
- KUYPERS, H. G. J. M., and J. BRINKMAN 1970 Precentral projections to different parts of the spinal intermediate zone in the rhesus monkey. *Brain Research*, 24:29-48.

- KLÜVER, J., and E. BARRERA 1953 A method for the combined staining of cells and fibers in the nervous system. J. Neuropath. Exp. Neurol., 12:400-403.
- LASSEK, A. M. 1954 The Pyramidal Tract. Charles C. Thomas, Publisher, Springfield, Illinois. 166 pp.
- LAWRENCE, D. G., and H. G. J. M. KUYPERS 1968a The functional organization of the motor system in the monkey. I. The effects of bilateral pyramidal lesions. Brain, 91:1-14.
- LAWRENCE, D. G., and H. G. J. M. KUYPERS 1968b The functional organization of the motor system in the monkey. II. The effects of lesions of the descending brain stem pathways. Brain, 91:15-36.
- LE GROS CLARK, W. E. 1924 On the brain of the tree shrew (Tupaia minor). Proc. Zool. Soc. Lond., 1053-1074.
- LE GROS CLARK, W. E. 1929 The thalamus of Tupaia minor. J. Anat. (Lond.), 63:177-206.
- LE GROS CLARK, W. E. 1931 The brain of Microcebus murinus. Proc. Zool. Soc. Lond., 463-486.
- LE GROS CLARK, W. E. 1932 The brain of the Insectivora. Proc. Zool. Soc. Lond., 975-1013.

- LE GROS CLARK, W. E. 1959 The Antecedents of Man.
Edinburgh University Press, Edinburgh, Scotland. p.3
- LENDE, R. A. 1970 Cortical localization in the tree
shrew (Tupaia). Brain Research, 18:61-75.
- LINOWIECKI, A. J. 1914 The comparative anatomy of the
pyramidal tract. J. comp. Neurol., 24:509.
- LIU, G. N., and W. W. CHAMBERS 1964 An experimental
study of the corticospinal system in the monkey
(Macaca mulatta). The spinal pathways and
preterminal distribution of degenerating fibers
following discrete lesions of the pre- and
postcentral gyri and bulbar pyramid. J. comp.
Neurol., 123:257-284.
- MARTIN, G. F., and A. M. FISHER 1968 A further
evaluation of the origin, the course and the
termination of the opossum corticospinal tract.
J. comp. Neurol., 7:177-187.
- MARTIN, G. F., D. MEGIRIAN, and A. ROEBUCK 1970
The corticospinal tract of the marsupial phalanger
(Trichosurus vulpecula). J. comp. Neurol., 139:
245-258.

- MARTIN, G. F., D. MEGIRIAN, and J. B. CONNER 1972
The origin, course and termination of the
corticospinal tracts of the tasmanian potoroo
(Potorous apicalis). J. Anat., 111:263-281.
- MOTT, F. W., and W. D. HALLIBURTON 1908 Localization
of function in the lemur's brain. Proc. Roy. Soc.
B, 80:136-147.
- NAPIER, J. R. 1967 Evolutionary aspects of primate
locomotion. Amer. J. Phys. Anthrop., 27:333-341.
- NAPIER, J. R., and A. C. WALKER 1967 Vertical clinging
and leaping - A new recognized category of locomotor
behavior of primates. Folia primat., 6:204-219.
- NAUTA, W. J. H., and P. A. GYGAX 1951 Silver
impregnation of degenerating axon terminals in the
central nervous system: (1) Technic, (2) Chemical
notes. Stain Technol., 26:5-11.
- NAUTA, W. J. H., and P. A. GYGAX 1954 Silver
impregnation of degenerating axons in the central
nervous system: A modified technique. Stain
Technol., 29:91-93.

- NAUTA, W. J. H. 1957 Silver impregnation of degeneration axons. In: New Research Techniques of Neuroanatomy, W. E. Windle (Ed.), Thomas Springfield, Illinois, p. 17.
- NOBACK, C. R., and J. E. Shriver 1966a Phylogenetic and ontogenetic aspects of the lemniscal systems and the pyramidal system. In: Evolution of the Forebrain, R. Hassler and H. Stephan (Eds.). Georg Thieme Verlag, Stuttgart, pp. 316-325.
- NOBACK, C. R., and J. E. SHRIVER 1966b The phylogeny of the corticospinal tract. *Anat. Rec.*, 154:479.
- NYBERG-HANSEN, R., and A. BRODAL 1963 Sites of termination of corticospinal fibers in the cat. An experimental study with silver impregnation methods. *J. comp. Neurol.*, 120:369-391.
- OBERSTEINER, H. 1896 Anleitung beim Studium des Baues der nervösen Centralorgane. Deuticke, Leipzig, cited by Towe, 1973.
- OSMAN HILL, W. C. 1953 Primates, Comparative Anatomy and Taxonomy. London, pp.
- PETRAS, J. M., and R. A. W. Lehman 1966 Corticospinal fibers in the raccoon. *Brain Res.*, 3:195-197.

- PETRAS, J. M. 1969 Some efferent connections of the motor and somatosensory cortex of Simian primates and Felid, Canid and Procyonid carnivores. In: J. M. Petras and C. R. Noback (Eds.) Comparative and Evolutionary Aspects of the Vertebrate Central Nervous System. Ann. N. Y. Acad. Sci., 167:469-505.
- PHILLIPS, C. G., and R. PORTER 1964 The pyramidal projection to motoneurons of some muscle groups of the baboon's forelimb. Progress in Brain Research, 12:222-245.
- PHILLIPS, C. G. 1970 Evolution of the corticospinal tract in primates with special reference to the hand. Proc. 3rd int. Congr. Primat., 2:2-23.
- REVELEY, I. L. 1915 The pyramidal tract in the guinea pig (Cavia aperea). Anat. Rec., 9:297-305.
- REXED, B. 1952 The cytoarchitectonic organization of the spinal cord in the cat. J. comp. Neurol., 96:415-495.
- REXED, B. 1954 A cytoarchitectonic atlas of the spinal cord in the cat. J. comp. Neurol., 100:297-379.

- SANIDES, F., and A. KRISHNAMURTI 1967 Cytoarchitectonic subdivisions of the sensorimotor and prefrontal regions and of bordering insular and limbic fields in slow loris, (Nycticebus coucang coucang). J. Hirnforschung, 9:225-252.
- SCHOEN, J. H. R. 1964 Comparative aspects of the descending fibre systems in the spinal cord. In: Organization of the Spinal Cord, J. C. Eccles and J. P. Schade, (Eds.), Elsevier, Amsterdam, pp. 203-222.
- SHAPOVALOV, A. I. 1973 Evolution of neuronal systems of suprasegmental motor control. Neurophysiology, 5:346-359.
- SHRIVER, J., and H. S. MATZKE 1965 Corticobulbar and corticospinal tracts in the marmoset monkey (Oedipomidas oedipus). Anat. Rec., 151:416.
- SHRIVER, J. E., and C. R. NOBACK 1967 Cortical projections to the lower brain stem and spinal cord in the tree shrew (Tupaia glis). J. comp. Neurol., 130:25-54.

- SIMPSON, S. 1912a The pyramidal tract in the Canadian porcupine (*Erethigon dorsatus*, Linn.). Proc. Soc. Exper. Biol. Med., 10:5.
- SIMPSON, S. 1912b The motor cortex and pyramidal tract in the raccoon (*Procyon lotor*, Linn.), Proc. Soc. Exper. Biol. Med., 10:46-47.
- SIMPSON, S. 1914 The pyramidal tract in the red squirrel (*Sciurus hudsonius loquax*) and chipmunk (*Tamias striatus lysteri*). J. comp. Neurol., 24:137-160.
- SIMPSON, S. 1915 The pyramidal tract in the striped gopher (*Spermophilus tridecemlineatus*). Quart. J. Exp. Physiol., 8:383-390.
- SPRAGUE, J. M. 1948 A study of motor cell localization in the spinal cord of the rhesus monkey. Amer. J. Anat., 82:1-26.
- STERLING, P., and H. G. J. M. KUYPERS 1968 Anatomical organization of the brachial spinal cord of the cat. III. The propriospinal connections. Brain Research, 7:419-443.
- STRAUS, W. L. 1949 The riddle of man's ancestry. Quart. Rev. Biol., 24:200-223.

SWANK, R. L., and H. A. DAVENPORT 1935

Chlorate-osmic-formalin method for staining
degenerating myelin. Stain Technol., 10:87-90.

SWANK, R. L. 1936 The pyramidal tract. An

experimental study of the corticospinal and other
components in the rabbit. Arch. Neurol. Psychiat.,
36:350.

TOWE, A. L. 1973 Motor cortex and the pyramidal system.

In: Efferent organization and the integration of
behavior, J. D. Maser (Ed.), Academic Press, New York,
pp. 67-97.

TOWER, S. S. 1935 The dissociation of cortical excitation

from cortical inhibition by pyramidal section, and the
syndrome of that lesion in the cat. Brain, 38:238-
255.

TURNER, E. L. 1924 The pyramidal tract of the Virginia

opossum (Didelphys virginiana). J. comp. Neurol.,
36:387-396.

VAN DER VLCEET 1906 Über den verlauf der pyramidenbahn

bei niederen Säugetieren. Anat. Anz., 29:113, cited
by Campbell, 1965.

- VAN VALEN, L. 1965 Treeshrews, primates and fossils. Evolution, 19:137-151.
- VERHAART, W. J. C., and W. KRAMER 1958 The pyramidal tract in the medulla and the cord of the elephant. Acta. morph. neerl. scand., 2:174-182.
- VERHAART, W. J. C. 1963 Pyramidal tract in the cord of the elephant. J. comp. Neurol., 121:45-49.
- VERHAART, W. J. C. 1966 The pyramidal tract of Tupaia, compared to that in other primates. J. comp. Neurol., 126:43-50.
- VERHAART, W. J. C. 1970 The pyramidal tract in the primates. In: The Primate Brain, C. R. Noback and W. Montagna (Eds.), Advances in Primatology, 1:83-108.
- WALKER, A. 1970 Post-cranial remains of the Miocene Lorisidae of East Africa. Am. J. Phys. Anthrop., 33:249-262.
- WARD, J. W. 1954 The development of the corticospinal tract in the pouch-young of the Virginia opossum, Didelphys virginiana. J. comp. Neurol., 101:483-491.
- WATSON, C. R. R. 1971a The corticospinal tract of the quokka wallaby (Setonix brachyurus). J. Anat., 109:127-133.

- WATSON, C. R. R. 1971b An experimental study of the corticospinal tract of the kangaroo. *J. Anat.*, 10:501.
- WELKER, W. I., and G. B. CAMPOS 1963 Physiological significance of sulci in somatic sensory cerebral cortex in mammals of the family Procyonidae. *J. comp. Neurol.*, 120:19-36.
- WIESENDANGER, M. 1969 The pyramidal tract. Recent investigations on its morphology and function. *Erg. de Physiol., Reviews of Physiology*, 61:72-136.
- WOOLSEY, C. N. 1958 Organization of somatic sensory and motor areas of the cerebral cortex. In: *Biological and Biochemical Bases of Behavior*. H. F. Harlow and C. N. Woolsey, (Eds.), University of Wisconsin, Madison, Wisc., pp. 63-81.
- ZIEHAN, T. 1899 Zur vergleichende anatomie der pyramidenbohn. *Anat. Anz.*, 16:446.
- ZIEHAN, T. 1900 Ueber der pyramidenkreuzung des schafes. *Anat. Anz.*, 17:237, cited by Campbell, 1964.
- ZUCKERMAN, S., and J. F. FULTON 1941 The motor cortex in Galago and Perodicticus. *J. Anat.*, 75:447-456.