Pyramidal and Non-Pyramidal Pathways in Monkeys: Anatomical and Functional Correlation

Abstract. *In monkeys, corticospinal fibers terminate on motoneurons and interneurons. Brainstem fibers, which may be grouped into medial and lateral pathways, terminate on the same interneurons. Observations following bilateral pyramidotomy indicate that motility can be adequately directed by the brainstem systems while cortical connections add speed and the capacity for further fractionating movements. Further experiments suggest that the medial and lateral brainstem pathways primarily direct proximal and distal movements, respectively.*

The pattern of termination of the descending fibers from the cerebral cortex and brainstem to the spinal cord has recently been studied by means of the Nauta-Gygax silver impregnation technique. In the rhesus monkey the cortical fibers terminate in the dorsal horn, the zona intermedia, and the mediodorsal parts of the ventral horn (internuncial zone), the distribution in the ventral horn being in part ipsilateral. In addition, some fibers terminate directly on motoneurons, especially those innervating distal musculature (*1*). In contrast, the long descending fibers from the brainstem which extend throughout the spinal cord terminate primarily in the internuncial zone, as demonstrated by their lumbosacral distribution (*2*). These fibers may be separated into a lateral and a medial group on the basis of their terminal distribution in the spinal gray matter. The lateral group descends in the lateral funiculus and distributes predominantly to the lateral and dorsal parts of the internuncial zone; most of these fibers are derived from the red nucleus but some probably arise from other sources. The medial group descends in the ventral funiculus and ventral parts of the lateral funiculus and terminates predominantly within the ventral and medial parts of the internuncial zone, overlapping to some extent the termination of the lateral group. These fibers are derived principally from the medial bulbar reticular formation, the vestibular complex, and from certain mesencephalic cell groups including the interstitial nucleus of Cajal. Shorter descending brainstem fibers accompany the long descending pathways and terminate in a somewhat similar fashion in the upper parts of the spinal cord.

The descending cortical and subcortical pathways constitute the only routes by which the brain can steer spinal motor mechanisms. It seemed worthwhile, therefore, to investigate, in the *freely moving animal*, the contribution of each of these pathways. We were particularly interested in determining whether the two anatomically separable descending brainstem systems are concerned with directing different movements. In order to disclose the activity of the descending brainstem pathways, however, it was first necessary to abolish the corticospinal influence on the spinal cord. Therefore, in 20 rhesus monkeys (*Macaca mulatta*) the pyramidal tracts were interrupted bilaterally at medullary levels through a hole drilled in the base of the skull. Twelve animals have been killed so far and the lesions studied histologically. The observations in these animals form the basis for this report. In one animal one tract and in eight animals both tracts were interrupted completely, with some additional damage to ventral fibers of the medial lemniscus (Fig. 1*E*). In two others small portions of one or both tracts were left intact and in the remaining animal neither tract was injured, the lesion affecting the pontine gray instead.

Immediately after surgery, the animals with complete interruption of both tracts demonstrated the thalamic posture of Bieber and Fulton (*3*). Within 12 to 72 hours they were able to right themselves from either side to a sitting position with legs and arms extended and head and trunk upright. When the animals were held by the pelvis with the head down, their arms and hands were fully extended; however, when they were brought toward the cage, their arms moved forward and backward at the shoulders with flexion-extension of the elbows (Fig. 1, *C* and *D*).

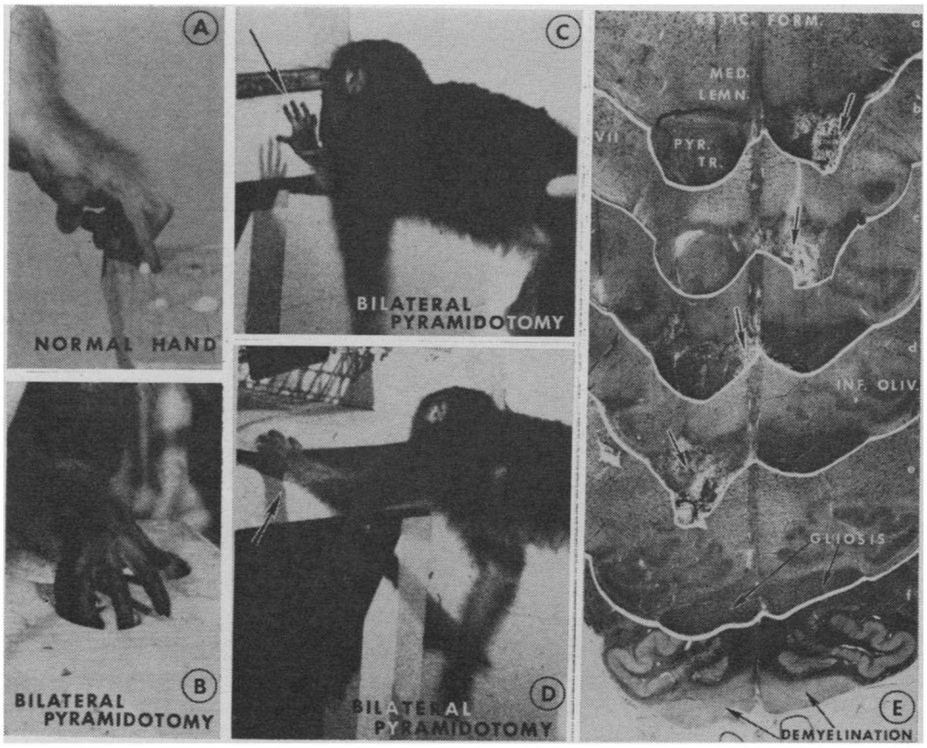

Fig. 1. (*A*) Animal with intact pyramidal tract taking food morsel from an 8-mm hole using index finger alone. (*B*) Animal 2 months after bilateral pyramidotomy was performed, taking food from large hole by moving fingers in concert. (*C* and *D*) Animal reaching for cage 12 days after bilateral pyramidotomy was performed. (*E*) Sections (stained by the Nissl method) (*a* to *e*) through the interruption of the pyramidal tract, from the animal shown in *B* through *D*. Note gliosis of pyramidal tracts in section *e* and demyelination in *f*, a section stained by Weil's method.

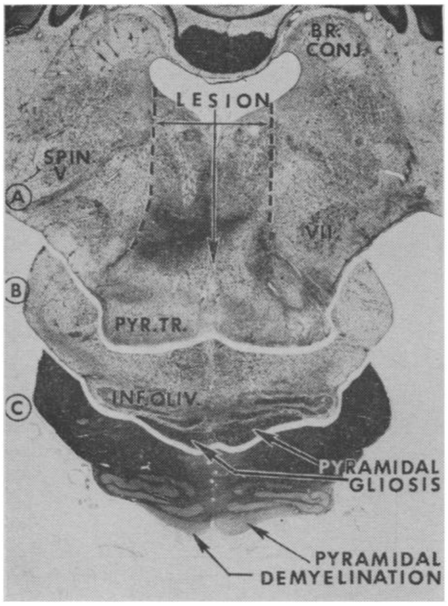

Fig. 2. Sections through brainstem of monkey with bilateral pyramidotomy (not shown) and lesion in the medial medullary tegmentum (incision through floor of fourth ventricle). (*A*) Section (stained by the Nissl method) demonstrating total extent of the tegmental lesion. (*B* and *C*) Sections (stained by the Nissl and Weil methods, respectively) through caudal medulla demonstrating bilateral gliosis and demyelination of both pyramidal tracts.

When close enough to the cage the fingers closed around the bars and held firmly, particularly when traction was applied to the arms. By the 4th to 5th day after surgery the animals were able to stand on all fours with feet and hands prone and to take several steps. In standing, and to a lesser extent in sitting, their limbs showed a bias toward extension which was evident to some degree throughout the period of observation.

Initially the animals had to be fed by stomach tube because of inability to chew and swallow. Within 10 days they were able to feed themselves by bending forward to bite and eat pieces of apple off the cage floor. By the 14th day after surgery most animals could be coaxed into reaching for food held in front of them; subsequently they learned to take food morsels from holes (diameter, 37.5 mm) drilled in a board (Fig. 1*B*).

In doing so, their aim was accurate and they had little difficulty in maintaining a stable posture. In approaching the food, the forearm was held pronated, the wrist slightly dorsiflexed and the fingers semiflexed and abducted. When the food was reached, it was picked up by flexion of all fingers in concert. However, when the food was brought to the mouth, all animals were unable to release their grip.

During the next several weeks further improvement occurred in the rapidity and ease with which all movements were performed. Ultimately, many of the animals were able to snatch food morsels with a rapid movement of arm and hand and to run rapidly across the floor and climb up the pipes and bars to the top of the cage banks (3 m). Yet despite this improvement, independent finger movements never returned, and all movements remained slower and fatigued more rapidly than in a normal animal.

In contrast, the animals with incomplete interruption of a pyramidal tract displayed greater rapidity and agility of movements in the corresponding extremity than the animals described above. At the same time, the capacity for independent finger movement returned to some degree. In the animal in which both pyramidal tracts were spared entirely, no deficiency occurred in its motility.

The only published report of experiments with rhesus monkeys in which complete interruption of both pyramidal tracts was achieved and in which the lesions were verified histologically is that of Tower (*4*). Her observations were made on two animals, one of which was 14 days of age when operated on, while the other was an adult. Our observations of animals with a unilateral interruption of the pyramidal tracts agree well with her description of such animals. However, her description of the defect following bilateral lesions differs from our observations. Thus the persistent axial hypotonia, drooping of the head, slumping of the body, and general passivity which she reports were either absent in our animals or represented transient phenomena. In the final paragraph of her report Tower states that "an impressive capacity for voluntary movement survives the pyramid section, especially if the lesion be bilateral, forcing the issue."

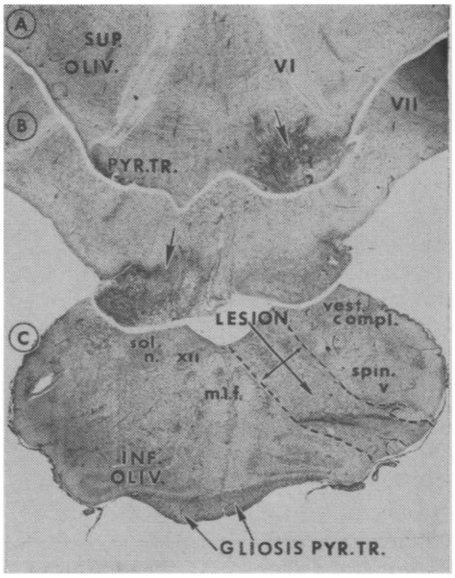

Fig. 3. Sections (stained by the Nissl method) through brainstem of monkey with bilateral pyramidotomy (*A* and *B*) and a lesion (*C*) in the lateral medullary tegmentum (incision through floor of fourth ventricle). Section *C*, cut at an angle to the incision: arrows and dashed lines indicate total extent of the lesion projected upon this level. Note the gliosis in the depths of this area resulting from passage of the instrument.

Our observations suggest a somewhat similar conclusion, which may be summarized as follows. The movements of body and limbs can, to a large degree, be adequately steered by means of the brainstem pathways only. This seems to be supported also by the findings of Liu and Chambers (*5*). The corticospinal pathways add speed and agility to these movements and, in addition, contribute the unique capacity for fractionating movements (*6*), for example, individual finger movements (Fig. 1*A*). This may be considered as the functional expression of the fact that descending brainstem fibers and corticospinal fibers have access to the same interneurons while other corticospinal fibers, in addition, terminate directly upon motoneurons (*7*).

In the cat, electrophysiological evidence indicates that spinal interneurons, similar to motoneurons, display some somatotopic organization (*8*). Thus, interneurons leading primarily to the lateral motoneurons of the ventral horn, which innervate distal musculature, are located laterally in the internuncial zone. It has been suggested, therefore, that the interneurons located ventrally and medially are related principally to medial motoneurons which innervate proximal musculature. In addition, it could be inferred from the work of Lloyd (*9*) that interneurons leading to motoneurons of flexor muscles are located primarily dorsally in the internuncial zone. Their counterparts, leading to motoneurons of extensor muscles, might therefore be located more ventrally.

A comparison of this organization of the internuncial zone with the differential termination of the two descending brainstem systems suggests that these pathways have preferential access to different interneuronal areas. Thus the medial group of fibers would have access principally to interneurons leading to motoneurons of proximal and extensor muscles, while the lateral group would have access primarily to interneurons leading to motoneurons of distal and flexor muscles. The two brainstem systems would therefore appear to be concerned preferentially with steering distal and flexor and proximal and extensor mechanisms. Such an organization seems to be implicit in previous reports (*10*), and has been largely corroborated by experiments with cats (*11*).

An attempt was made to test this hypothesis. After a recovery period of at least 6 weeks following interruption of both pyramidal tracts, lesions were placed medially or laterally in the brainstem at pontomedullary levels. The resulting changes in motility were studied over a period of several weeks. The brains of four animals in which such lesions were made have been studied histologically. Lesions of the medial brainstem pathways (Fig. 2) resulted in a severe impairment of proximal motility (long-lasting deficit in righting and unsteadiness in progression) associated with a flexor bias of the extremities, while distal movements (picking up food) were relatively unaffected.

In contrast, lesions interrupting the lateral brainstem pathways (Fig. 3) had relatively little effect on proximal motility, while distal movements were impaired. The same held true if the lateral lesion preceded the pyramidal interruption. These findings seem to support the hypothesis regarding the functional differences between the two long descending brainstem systems in directing motility.

DONALD G. LAWRENCE
Division of Neurology
HENRICUS G. J. M. KUYPERS
Department of Anatomy,
Western Reserve University,
Cleveland, Ohio 44106

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Somnambulism: All-Night Electroencephalographic Studies

Abstract. *Using special techniques allowing for subject mobility, we obtained continuous electroencephalographic recordings of known sleepwalkers. Somnambulistic incidents occurred during periods of slow-wave sleep. The incidents were not related temporally to dream periods, nor did they affect the total time or the percentage of time spent dreaming during the nights on which the subjects were studied.*

Somnambulism has been the subject of numerous anecdotal and clinical reports based on indirect evidence rather than direct observation. Not infrequently, it has been stated that sleepwalking incidents occur during dreaming and are in fact the acting-out of a dream (*1*). We have studied the relation of sleepwalking to the sleep-dream cycle directly, utilizing Dement and

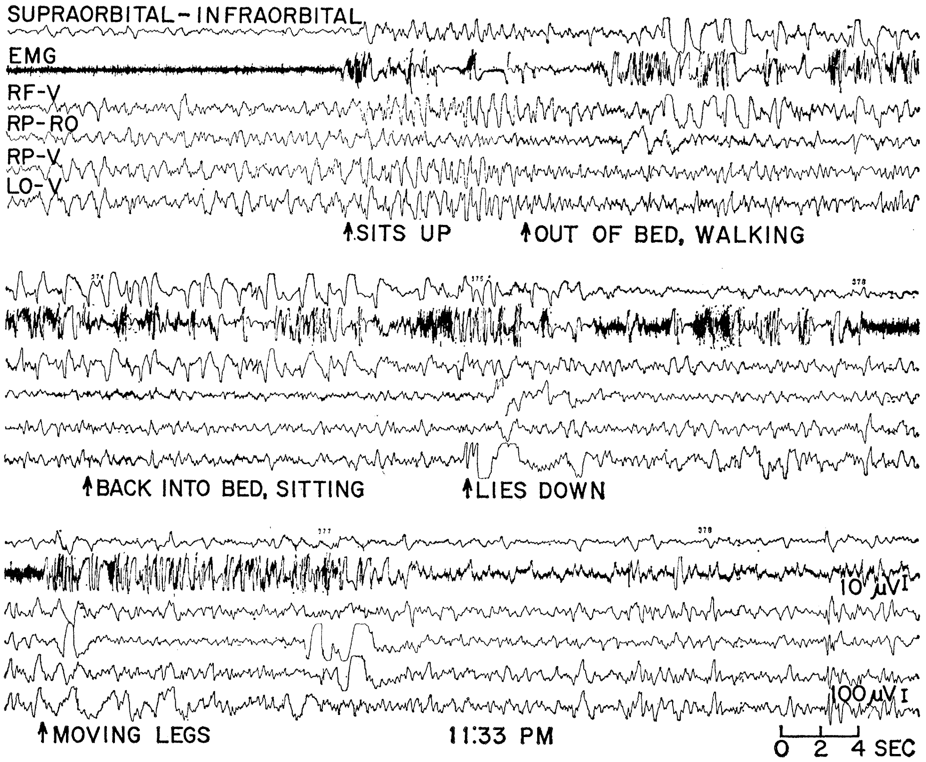

Fig. 1. Sleepwalking incident. The high-voltage slow-wave pattern begins as the subject sits up, and the slow-wave record is maintained throughout most of the incident. Eye movements are recorded by the orbital and frontal electrodes when the subject begins sleepwalking. (*R*, right; *L*, left; *F*, frontal; *P*, parietal; *O*, occipital; *V*, vertex.)