An Investigation Concerning the Restitution of Motor Function Following Injury to the Spinal Cord

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The nearly complete restitution of motor function that is observed in a wide range of experimental animals including rodents,¹⁷ carnivores,¹ and primates¹⁰,¹⁴ following lateral hemisection of the spinal cord has prompted study of the mechanisms and pathways that are responsible. Two major features of this recovery remain obscure. First, what motor fibers are involved? The corticospinal tract and reticulospinal and propriospinal system represent two possible and not necessarily mutually exclusive ways in which efferent impulses may be carried to the limbs ipsilateral to the hemisection. Second, does the functional connection between the sides of the cord take place between each segment or at one specific location?

Mettler¹⁴ has approached these problems by performing cervical hemisections and allowing recovery to take place. Cortical ablations were then performed on the side contralateral to the cord lesion. A hemiparesis contralateral to the cortical lesion and on the same side as the cord lesion was attributed to late crossing pyramidal fibers. Lassek and Anderson's¹⁰ investigation was based upon crossed hemisection in 7 Macaca mulatta, of which none showed significant recovery.

In the present study crossed hemisection, i.e. left lateral section at one level and right lateral section at another, were made in a series of 19 cats, 7 of whom showed considerable restitution of motor function (Figs. 1 and 2). This paper reports these results and their implication for spinal-cord function, particularly recovery of function, based upon histological examination of the cord lesions.

Materials and Methods

A total of 19 cats was used. The hemisection or sections were lateral, being achieved through a standard laminectomy of one to three vertebrae. The dura mater was left open and Gelfoam was placed in the lesion. Three to 8 weeks were allowed for recovery from the first hemisection. The second hemisection was then performed. In most preparations the higher section was performed as

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Fig. 1. E5 shown walking on to a ledge. Some atrophy of the extremities is apparent.

Fig. 2. E5 assuming fairly normal posture while feeding.
Ordinarily began within 1 week of the second procedure.

Seven cats recovered function to the extent of being able to walk and climb up on a 10" ledge and jump from it (Figs. 1, 2 and 3). These animals showed residual weakness which was more severe distally. It was necessary to express their bladders manually 1 to 3 times each day.

3. Before perfusion was carried out in these animals that had recovered, a complete transection of the spinal cord was performed just above the highest lesion. This was done to rule out the possibility that the motor function observed was produced by the spinal cord alone and was a form of "spinal walking." In each case paraplegia resulted from transection, indicating that supraspinal structures were involved in the recovery of function. These animals were observed from 1 to 3 days during which time no recovery was apparent. Another indication that the function was under supraspinal control is furnished by experiments to be reported in which cortical sensorimotor ablations were made following crossed hemisections. A predominantly crossed paresis resulted from these cortical lesions, again implicating supraspinal control of motor function.

Summary of Results and Interpretation of Histology

1. A single hemisection at the cervical or thoracic level is followed by nearly complete recovery.

2. A second hemisection performed 3 to 14 segments below or above the first but on the opposite side is followed by bilateral paralysis.

3. Function is not recovered if at either level of section the ventral columns are interrupted on both sides.

Discussion

In order to explain recovery in the bilateral crossed hemisections the remaining nervous tissue in the cord must have the following characteristics. First, there must be a diffuse system with frequent crossings capable of

Fig. 3. Reconstruction of cord lesions of those animals that recovered function.
functioning between the crossed sections. Second, this system is probably located principally in the ventral columns since bilateral interruption of the ventral columns is not compatible with recovery.

The known properties of the propriospinal system of the cord would fulfill both requirements and it is proposed that the ventral component of this system is especially important in the recovery of function seen in the above experiments. The propriospinal system consists of fibers arising and terminating within the cord itself. As described by Tower et al. and discussed by Nathan and Smith, these fibers are most dense immediately about the central grey matter. Sherrington and Laslett considered this system to be composed of both long and short axons and divided it into dorsal, lateral, and ventral components. These early workers thought that only the ventral fibers crossed over. Lloyd's work has indicated that reticulospinal and propriospinal fibers form a continuous network stretching from brain stem through the cord and that discharge of anterior horn cells is accomplished by interaction between the pyramidal and propriospinal systems.

More recent studies by Gernandt and Megirian have shown the important function of the descending propriospinal system in the phasic control of lumbar activity. Gernandt and Shimamura and Livingston have distinguished two systems, spinobulbospinal and propriospinal, as important in spinal-cord function. They have demonstrated by electrophysiological methods that only the propriospinal system is characterized by frequent crossings in the cord. With regard to these two systems, they felt that “both normally apparently occupy widespread ascending and descending pathways along the spinal cord.” The present experiment suggests that the propriospinal fibers important in recovery of voluntary motor function are those fibers that are located principally in the ventral columns, their site of crossover being in the anterior white commissure.

Apparently the relative importance of the

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**Fig. 4.** Reconstruction of cord lesions of those animals that did not recover function.
efferent propriospinal system, much like diffuse sensory systems, decreases through phylogeny. Thus Ingebritsen has described virtually complete recovery following crossed cervical hemisection in the rat. Because of the primitive median dorsal position of the corticospinal tract in the rat, it is somewhat difficult to be sure that all fibers were severed. In the cat with lateral corticospinal tracts the results here reported show that fair recovery is possible without long tracts. In *Macaca mulatta*, whose spinal cord is much like that of the cat anatomically, Lassek and Anderson and Turner have shown that no useful function returns after crossed hemisections.

These findings indicate that a major physiological difference in the function of the long tracts occurs in phylogeny and that this change is unaccompanied by a major morphological development. It is interesting that although there is a marked difference between the anatomy of the spinal cord of the rat and the cat, in that the rat possesses a dorsal corticospinal tract, lying beneath the gracile and cuneate fasciculi, the differences between the efferent systems of the cat and monkey are much less striking. The cat possesses only a small ventral corticospinal tract which ends in the cervical region while in the monkey this tract is fairly well developed. Also, there is an increase in relative size of the pyramidal system in the monkey.

We are now pursuing this line of inquiry and are attempting to determine where in the insectivore-primate line the cortical spinal system becomes essential for function. We shall report the effect of crossed hemisections in more primitive primates (marmosets and tree shrews).

The recovery from single hemisection takes place in a different way from that described above for bilateral hemisections. Since the second hemisection results in bilateral paralysis whether performed 3 or 14 segments from the first, it is necessary to assume that the responsible efferent system on the intact side interacts with the side of the hemisection at or near the level of the lumbosacral outflow. The alternative explanation would be that the interaction takes place near the level of the first hemisection. If this alternative was correct the second hemisection performed some distance away from the first would not interrupt this interaction and would result only in a unilateral paralysis. Since bilateral paralysis is the consequence of the second hemisection we must conclude that restitution of function is mediated at or near the lumbosacral outflow by either the propriospinal system or long tracts.

In opposition to this reasoning, it might be argued that the second hemisection results in a state of spinal shock which would be bilateral. But this supposition is not supported by the results of hemisections performed below the first but on the same side. If the bilateral paralysis which results initially from the second crossed hemisection were caused by general dysfunction of the cord then a second hemisection not crossed but performed on the same side as the first should also give bilateral paralysis. In a group of 6 cats hemisection of the cord was performed, recovery took place and a second hemisection was performed on the same side as the first. Bilateral paralysis did not result. This finding indicates that spinal shock or general dysfunction are not factors in the bilateral paralysis seen after crossed hemisection.

The questions asked in the beginning of this paper concerning the recovery of function following hemisection may be partially answered in the following way. First, considering the diffuse nature of the ventral propriospinal tract and the major termination of the corticospinal tract in the lumbosacral enlargement we may only speculate that the latter system would more likely be involved in restitution of function following single hemisection. However, the ventral propriospinal system probably mediates recovery in the double hemisection preparations. Second, the site of functional crossover in the single-hemisection preparation is probably mainly at the lumbosacral outflow. It should be emphasized that this applies to the lower extremity for, as Gernandt and Gil-
man² have shown, the physiology of the cervical and lumbar cord may be quite different.

Summary

1. In the cat, function is recovered following spaced contralateral hemisection, if the ventral columns are not destroyed bilaterally at either section.

2. This recovery may be mediated by the ventral propriospinal tract.

3. The recovery of the lower extremities from single hemisection is probably mediated by connections established at the lumbo-sacral outflow.

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References


