Studies on Lower Motor Neurons

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Concluding Remarks

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As indicated in the *Introduction*, the goal of this symposium was to consider the lower motor neuron (LMN), the basic structural and functional substrate for behavioral expression, in terms of those segmental and suprasegmental influences which govern its activity. Our purpose has been fulfilled by a group of papers addressing a wide variety of neuronal systems in vertebrate species which exhibit real behavioral diversity. From the stereotyped swimming teleost or wriggling Tegu lizard, to the shuffling opossum and the vertical leaping of the bushbaby, a spectrum of distinctive patterns of locomotor behavior is displayed. Motor control can and has been profitably analyzed by looking carefully at some of its structural substrates in these selected forms.

The four general areas considered in these reports include: (1) the morphology and relations of the spinal LMN; (2) the influence of peripheral input (i.e. primary afferent fibers) on the LMN; (3) the input from subcortical centers, and (4) input from the cerebral cortex. Consideration of the first of these points, including sizes, shapes, arrangements and especially dendritic orientation and extent of motoneurons, has been emphasized here by CRUCE, MARTIN *et al.*, GOODE and HAINES, and SCHNITZLEIN and BROWN. These authors have shown that direct observation of LMN architecture and its afferent synaptology permits suggestions regarding the origin of various synaptic influences as well as their potential mode of action (i.e. chemical vs electrotonic). In addition, many neural systems, while not terminating in the immediate vicinity of motoneuron cell bodies, clearly end within the dendritic fields of these large cells.

A second question concerning the influence of peripheral input (primary afferent fibers) upon the LMN} is considered by CULBERSON and

KIMMEL for the opossum and is mentioned briefly in SCHNITZLEIN and BROWN'S report on the goldfish. Two points warrant some emphasis; first, the extensive longitudinal influence of primary afferent fibers entering at single spinal segments in mammals demands careful consideration concerning the specificity of these projections. Those fibers which extend to the most distant portions of the spinal grey, end in spinal relay nuclei which are known to convey postural sensory data to higher centers (e.g., nucleus dorsalis). Second, the presence of monosynaptic afferent-efferent coupling in the teleost spinal cord extends this direct influence to a wide range of vertebrate forms. The limited data available on the distribution of peripheral afferent fibers points to a real need for more experimental studies of such fibers, especially in non-mammalian forms.

A third general question concerns the origin, course and pattern of termination of fibers from subcortical centers which alter the action of the LMN. Can we gain insight into motor regulation by observing variations in, and distribution of subcorticospinal pathways within a spectrum of species characterized by behavioral differences? This question is addressed most directly here by CRUCE in his elegant analysis of fiber system-behavior correlation in species with clear-cut locomotor differences. MARTIN and colleagues provide a comprehensive summary of the descending fiber systems in the opossum and MURRAY and HAINES describe the rubrospinal tract in a prosimian primate. With the exception of tectospinal and cerebellospinal fibers (in opossum) subcorticospinal pathways descend the length of the cord and contribute numerous fibers to interneuronal pools of laminae V—VII. There is, however, evidence for some monosynaptic input to motor neurons (e.g., vestibulospinal tract). Even though there are obvious behavioral differences between the opossum and bushbaby, the pattern of termination of jffibrospinal fibers is strikingly similar, within medial and lateral laminae V-SI. The small number of specimens in the report by MURRAY and HAINES places some limitation on direct comparison; greater numbers of specimens may provide detail and/or differences not presently apparent. However, the general pattern of distribution of these fibers (including somatotopy of origin, course and termination) is clearly similar to other mammals.

A fourth question concerns the direct corticospinal influence on the LMN and is here discussed by MARTIN and colleagues for the opossum and by GOODE and HAINES for a primate. In this system there are marked differences in the pattern of termination in the spinal grey. In the quadrupedal opossum, corticospinal fibers do not extend beyond low thoracic

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levels and their endings in spinal grey are mainly in laminae III-VI. In the primate considered here, projections extend throughout the cord from the motor portion of the motor-sensory amalgam and generate a somatotopic distribution into the cord, mainly in laminae V-VII, clearly within the dendritic realm of the LMN. Motoneurons in the opossum receive indirect cortical input even at those levels where the tract is present, while in the bushbaby the correlation between motor control and organization of the corticospinal system appears more obvious.

Many areas requiring further study have been recognized in the present set of papers. All of the fiber systems described here terminate partially, or exclusively, in pools of interneurons about which we know very little. What is the action of specific populations of interneurons on the LMN? What are the dendritic fields of specific groups of spinal interneurons within the spinal grey and the effect of their axons in the white matter? It is clear that before we can understand well the afferent regulation of motoneuronal activity, it is essential that we learn more concerning the connectivity and functional characteristics of spinal interneurons. This dismaying lack of data on interneuronal anatomy and connectivity remains a major obstacle to a more refined concept of motoneuronal control.