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SIGNED: Sharyn Vander Ploeg
to my brother, Doug, who
was killed during my Ph.D. sojourn . . .
ACKNOWLEDGMENTS

This document represents my first endeavor at the research process. Many people assisted and/or guided this process. All receive my thanks. Tops on my list, I thank Dr. Douglas G. Stuart for the opportunity of working with him. I greatly appreciated his educational thrust encompassing the how-to's of experiments as well as the roles and responsibilities of a scientist/academician in today's society. He is to be commended for supporting a lab atmosphere which is conducive to the "healthy exchange and debate of ideas".

Projects such as mine require a significant amount of effort from others. Special recognition and thanks go to Dr. Thomas M. Hamm for his intellectual guidance, total support in all phases of the project and many, many long nights. Other members of the lab receiving thanks include: Bob Reinking for his guidance and assistance in using the equipment; Pat Pierce for her assistance with surgery and illustrations, Chun-Su Yuan for his surgical assistance and Cindy Rankin for her moral support. In addition, Dr. Walter Koelher, a visiting scientist from West Germany, participated in early experiments.

Members of my dissertation committee were also active in my educational program. I am grateful for their participation: Drs. Jay B. Angevine, Jr. (Anatomy, "editor extraordinaire"), Robert W. Lansing (Psychology), Ziaul Hasan (Physiology) and Robert W. Gore (Physiology). Special thanks goes to Dr. Felix E. Zajac III, who served as the
external examiner for my dissertation defense. As my first examiner, he "set the tone" for the exam—challenging yet friendly. In addition, the presentation of my results in this document and other publications has been strengthened considerably due to the thoughtful critiques of Drs. Marc Binder and John Munson.

Within the Department of Physiology, other faculty and staff have expended time and effort on my behalf. I especially appreciate the spirit with which this assistance was given. I thank Lela Aldrich for her ability to get things done and for her sensitivity which brought me much support during difficult times. I thank Mildred Long for her caring nature and tremendously efficient work skills. She truly is our most valuable resource in the temporary buildings.

Fellow students have become valued friends. I thank Cindy Rankin, Mary Moon, Jim Lechleiter, Ursula Hauser and Rob Brinton for their commiseration and continuing support.

Within my personal and professional life, many special people deserve mention. My deepest admiration continues for my "guiding lights": Dr. Jo Jones RN, PhD; and PT-PhDs: Dr. Mary Clyde Singleton, Dr. Suzann Campbell, Dr. Pat Yarbrough and Dr. Russell Davis. I appreciate all their efforts on my behalf.

My Chapel Hill days with Sandy Radtka, Suzanne Parrish Gordon, Dr. Jan Gwyer, Marti Probst, Dr. Geoff Gordon and Susan Attermeier provided me with a necessary and supportive peer group. Our long hours of discussion helped to shape this present reality. I thank them all for always "being there".
In Tucson, a number of people have facilitated my continued involvement in health care and physical therapy practice. I especially thank Bob Burtch, Kiki Gekas, Deb Mager and Carol Burtch for their friendship and commitment to improving the quality of life for the elderly.

Finally, I thank my family—my parents for always supporting my right to make choices and Karyn, Bobbi and Don for always "pushing" and never settling for "what is". Our bond remains my foundation of strength throughout this life.

This work was supported in part by Achievement Rewards for College Scientists, Inc. and the Foundation for Physical Therapy.
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ABSTRACT

In the field of spinal-cord neurophysiology, the nature of and the rules which govern the strength of functional connections between muscle afferents and motoneurons supplying the same muscle are important to delineate. This study addressed a facet of this issue by testing the possibility that the strength of the spindle Ia-motoneuronal connections is stronger (as demonstrated by the differing amplitudes of the mean maximum composite Ia EPSPs) if both neurons supply the same sub-volume of the muscle, providing the various sub-volumes of the muscle are capable of independent action.

Intracellular recordings were made of the Ia EPSP responses of semimembranosus (SM) and lateral gastrocnemius (LG) motoneurons in anesthetized low-spinal cats to electrical stimulation (Group I range) of nerve branches supplying different parts of the homonymous muscle, as well as different heteronymous muscles.

For study of SM motoneurons, stimulated nerve branches included those supplying the anterior (SMa) and posterior (SMp) heads of the SM muscle and three providing heteronymous input from the anterior (BFa) and posterior (BFp) parts of biceps femoris and the distal part of the semitendinosus (STd) muscle. Ia EPSPs were partitioned such that stimulation of the SMa nerve branch produced significantly larger EPSPs in SMa motoneurons than in SMP cells; likewise, stimulation of the SMP nerve branch produced larger EPSPs in SMP motoneurons than in SMa cells.
Study of the differences in the strength of heteronymous Ia input (i.e., from BFa, BFp and STd) between the SMa and SMp cell groups correlates with the different actions reported previously for the two heads of the SM muscle.

For study of LG motoneurons, the stimulated nerve branches were those supplying the four neuromuscular compartments of the LG muscle (LG1, LG2, LG3 and LGm) and the nerve to a heteronymous muscle, soleus (SOL). In all five instances, partitioned Ia effects were evident.

An association is suggested between the present results and previous electromyographic studies. The previous studies have shown that the muscle heads (SM) or neuromuscular compartments (LG) under consideration in this study are capable of somewhat separate actions.

The present study also included assessment of the relative extent to which the partitioned Ia effects could be attributed, in part, to one or two developmental factors, topographic specificity and species specificity. The analysis suggested that both factors were potentially implicated, with species specificity somewhat predominant over topographic specificity.
CHAPTER 1

PREAMBLE TO PROJECT

The central nervous system (CNS) is capable of elaborating a variety of movements ranging from gross whole-limb movements to exquisitely delicate activities, such as threading a needle. The elaboration of each movement requires fine control of the relevant structures—to ensure precise timing of muscle forces and appropriate joint movements. Presumably, this fine control of movement is facilitated by sensory feedback from a number of receptors. However, although much effort has gone into the study of spinal reflexes in motor control, our knowledge of the transducing properties of muscle receptors, their spinal connections and reflex effects on muscle, are still at a primitive stage (Binder, Houk, Nichols, Rymer & Stuart, 1982). For example, it is still not known if the CNS can control separate regions within a single muscle. This issue is addressed in the present project, by considering the possibility that the CNS can achieve independent control in one selected case. The case examined is the monosynaptic pathway between the Ia afferent axons of muscle spindles and their homonymous motoneurons.

Among the receptors, the muscle spindle is of particular interest, because of its unusually complex structure, presence in large numbers and efferent control by the CNS (Matthews, 1972; Hasan & Stuart, 1984). The monosynaptic connection from spindle Ia afferents to
motoneurons is also of particular interest because it is relatively recent in the phylogenetic (Angevine & Cotman, 1981) and ontogenetic (Landmesser, 1976) sense and because the spindle is the only muscle receptor providing a monosynaptic effect onto motoneurons.

In 1977, this laboratory introduced the partitioning hypothesis (Binder, Smith, Reinking & Stuart, 1977; Stuart & Binder, 1977) which addresses both peripheral neuromuscular ("sensory partitioning") and spinal ("central partitioning") aspects of the design and function of short-latency proprioceptive reflexes. Muscle receptors were proposed to accomplish a sensory partitioning of their muscle by responding with greater sensitivity to changes in the length-tension status of muscle units within their immediate locale than to the status of more distant units or to changes of whole-muscle status (Cameron, Binder, Botterman, Reinking & Stuart, 1981). This concept appears well accepted in the motor-control literature, even though it requires further experimental support.

Sensory partitioning may represent a functional as well as design feature of the segmental motor control system if it is correlated with a central partitioning in the homonymous motor nucleus. Such partitioning would be manifest if each motoneuron received stronger sensory input from muscle-receptor afferents supplying the same part of the muscle as that motoneuron than from muscle-receptor afferents supplying other parts of the muscle.

This study provides information on central partitioning by analysis of the monosynaptic effects from Ia spindle afferents within
selected spinal motor nuclei. Recently, a partitioning of Ia excitatory postsynaptic potentials (EPSPs) in a spinal motor nucleus has been referred to as a "localization" of these effects (Botterman, Hamm, Reinking & Stuart, 1983a,b). For clarity, the term localization is restricted in this report to describe the segmentation of reflex effects within a muscle (e.g., localization of the stretch reflex, intramuscular reflex localization).

Partitioning of the monosynaptic component of spindle Ia reflex effects has been demonstrated in selected motor nuclei. In these nuclei, the spindle Ia afferents from the homonymous muscle have been shown to make stronger (as demonstrated by the differing amplitudes of the mean maximum composite or single-axon Ia EPSPs) connections with their "own" motoneurons, i.e., those that supply the same region of the muscle in which the afferent's receptors are located, than with other motoneurons supplying other regions of the muscle.

When partitioning of Ia effects is present, developmental factors also present include a tendency toward somatotopy (i.e., topographic specificity) and some type of afferent-to-cell recognition (i.e., species specificity). Recently, this laboratory has used the term "neuronal recognition" (Botterman et al., 1983a,b,) as a synonym of species specificity. This practice is discarded here because recognition refers to a specific developmental process (i.e., "a specific recognition of one nerve cell by another in order to form a synaptic connection"; Jacobson, 1976) which may or may not be responsible in part for the observed species specificity.
Other evidence has suggested that not all motor nuclei show a partitioning of monosynaptic Ia EPSPs. This situation may be brought about by a lack of topographic and/or species specificity during development.

**Aim of Study**

Monosynaptic Ia EPSP effects appear to be partitioned to different degrees in different spinal motor nuclei. These variations prompted the following hypothesis: a partitioning of monosynaptic Ia EPSPs will be present in motor nuclei supplying muscles with regions capable of independent and different actions.

Two motor nuclei (Fig. 1) supplying hindlimb muscles of the adult cat were selected as candidates to test this hypothesis—the semimembranosus (SM) in which partitioning was previously reported as absent (Eccles & Lundberg, 1958) and the lateral gastrocnemius (LG) in which anatomical (English & Letbetter, 1982a,b; English & Weeks, 1984; Weeks & English, 1982) and kinesiological (Russell, Dunbar, Rushmer, McPherson & Phillips, 1982; English, 1984) evidence suggest that partitioning should be present.

A secondary aim, in the event of encountering partitioning, was to determine the relative contributions of topographic and species specificity to its presence.

The model was the anesthetized, spinalized (T12-L1 level) adult cat (2-3 kg). Hereafter, unless otherwise stated, the animal model under consideration the adult cat. For ease of reading, relevant terminology has been summarized in the glossary.
Fig. 1. Anatomical aspects of the project. Left: Schematic of the left hindlimb of the cat showing the two test muscles, semimembranosus (SM) in the thigh and lateral gastrocnemius (LG) in the leg. Right: Enlargement of the hindlimb to illustrate the innervation pattern of the two muscles. The SM nerve, from the sciatic nerve (in black), divides into two major branches which supply the two muscle heads. The LG nerve, from the tibial component of the sciatic nerve, shows four primary nerve branches. Top: Enlargement of the L6-S1 segments of the spinal cord to show the relative locations of the two test (SM, LG) motor nuclei. Each neuron pair represents the connections between the total Ia afferent population and single alpha motoneurons.
Anatomical Considerations

Four structural arrangements are discussed which offer a possible anatomical basis for partitioned effects. They include the branching and innervation patterns of intramuscular nerves, the projection of spindle afferents within the spinal cord, the topographic organization of motor nuclei within the spinal cord and the somatotopic relations between spinal motor nuclei and their target muscles.

Intramuscular Nerve Branching

A muscle nerve undergoes a natural and progressive branching process immediately before and after entering the muscle. The first of these branches are defined as primary muscle-nerve branches. The neuromuscular innervation patterns they produce have both predictable and variable components which vary in different muscles. In recent years, attention has been directed to this feature of peripheral neuromuscular organization because it may represent a principle of neuromuscular development with functional implications.

Motor Innervation Patterns. Letbetter (1974) was the first to demonstrate with the technique of glycogen depletion, that the territory of muscle fibers innervated by a primary muscle nerve branch occupied a distinct region or "compartment" of the muscle. His test muscle was medial gastrocnemius (MG). Subsequently, it was shown in his laboratory that little overlap of muscle fibers occurred between these MG compartments (Farina, 1978), now referred to as "neuromuscular compartments" (English, 1984; English & Weeks, 1984).
Further studies, using a similar glycogen depletion of muscle fibers innervated by primary muscle nerve branches, have identified a number of muscles which show neuromuscular compartments. The biceps femoris (BF) muscle showed three neuromuscular compartments, an anterior (BFa), a middle (BFm) and a posterior (BFp) one (English & Letbetter, 1981). The authors noted that BFm may well show a more complex organization which was brought out upon further investigation (Botterman et al., 1983a). Semitendinosus (ST), a muscle consisting of two parts (i.e., proximal, STp; and distal, STd) receiving separate primary nerve branches (Chin, Cope and Pang, 1962), showed two corresponding compartments (English & Letbetter, 1981; Bodine, Roy, Meadows, Zernicke, Sacks, Fournier & English, 1982). Iliya & Dum (1984) showed that the primary nerve branches to the tibialis anterior (TA) muscle innervated two separate neuromuscular compartments, an anterior and a posterior one.

The innervation pattern of the LG muscle nerve involves four primary branches. Glycogen depletion of the muscle fibers innervated by these branches showed that three of the four observed muscle compartments corresponded roughly to the three unipennate heads of the muscle (English & Letbetter, 1982a). A medial compartment (LGm) coincided with the medial head; a lateral compartment (LG1) with the distal part of the lateral head; an intermediate compartment (LG3) with the distal part of the intermediate head and a proximal compartment (LG2) which incorporated the proximal parts of both the lateral and intermediate heads.
Despite differences in whole muscle architecture, the above-cited muscles were subdivided into neuromuscular compartments by their primary nerve branches. In all cases studied, the primary branching of the muscle nerve appeared to govern the distribution pattern of motor unit territories throughout the muscle. Although the sample must be increased, this organization may well represent a general principle of design in vertebrate muscles (English, 1984).

Spindle Innervation Patterns. A subsequent study from Letbetter's laboratory (Farina, 1978) showed that, with few exceptions, spindles located within a single neuromuscular compartment of MG also received their sensory Ia innervation via the same primary nerve branch which supplied that compartment's muscle fibers. A functional correlate to this structural arrangement was provided by Cameron et al. (1981), who demonstrated that muscle receptors were more sensitive to contractions of their own neuromuscular compartment (sensory partitioning) than to contraction of adjacent and more distant regions of the muscle.

Intraspinal Projection of Ia Afferents

Direct study of the intraspinal projection of individual Ia afferents which are electrophysiologically identified has been achieved with intra-axonal staining methods (e.g., horseradish peroxidase, HRP). Consistent with previous work on Golgi-stained material (Scheibel & Scheibel, 1969), the Ia axon has been shown to enter the spinal cord and bifurcate into ascending and descending branches in the dorsal funiculus. Main collateral branches divide from the ascending and descending
branches to project ventrally toward the ventral horn. The recent HRP work on individual Ia afferents has extended the description of their main Ia collaterals, as well as added direct information concerning the number of terminals distributed by single Ia afferents in motor nuclei.

The overall anatomy of the filled Ia afferents has been described similarly by researchers from several laboratories (Brown & Fyffe, 1978, 1981; Ishizuka, Mannen, Hongo & Sasaki, 1979; Burke, Walmsley & Hodgson, 1979). The main collaterals divide from the ascending and descending branches at approximately 1 mm intervals. Terminal arborizations from these collaterals in the spinal gray are characteristically noted in Rexed’s (1952, 1954) Lamina V-VI, the intermediate zone and in Laminae VII (the zone containing Ia inhibitory interneurons; Jankowska & Lindstrom, 1972). However, the major terminal field of the main Ia axon collaterals was noted consistently in Lamina IX (the motor nuclei).

Examination of the distribution of terminal arborizations of individual Ia fibers among motoneuronal cell columns (Romanes, 1951) in Lamina IX showed arborizations within several motor nuclei; the greatest density of terminals, however, was in the cell column containing the homonymous motoneurons. Such anatomical data are consistent with the physiological data on the higher percentage of Ia afferents that make monosynaptic connections with homonymous motoneurons as compared to heteronymous cells (Mendell & Henneman, 1971).

No significant grouping of collaterals about the dorsal root entry zone (usually viewed in sagittal sections) has been reported
(Brown & Fyffe, 1978; Ishizuka et al., 1979). Such a finding would support the importance of topography in the distribution of Ia connections. The HRP work has not demonstrated a clear topographic substrate for central partitioning. But it is premature to preclude the existence of such a topographic substrate, since there is some question as to the ability of the HRP to fill all the collaterals of a single Ia (or any other) axon (for review: Ishizuka et al., 1979; Brown, 1981).

Work on the projection of spindle afferents within the spinal cord has not progressed far enough to provide categorical evidence on the number of terminals distributed by individual Ia afferents to different motor nuclei or on the number of terminals contacting a homonymous motoneuron as compared to a heteronymous cell. Such data could provide further evidence for a structural basis for a central partitioning of Ia effects.

Organization of Spinal Motor Nuclei

The most detailed and influential work on the location of motoneuronal pools innervating single hindlimb muscles was performed by Romanes (1951). Using chromatolysis as a cell marker, Romanes demonstrated that motoneurons innervating a particular muscle are located in relatively discrete cigar-shaped longitudinal columns, termed the spinal motor nuclei. These nuclei occupy discrete regions within ventral portions of the spinal-cord gray matter, subsequently termed Lamina IX (Rexed, 1952, 1954). The motor-nuclei locations were reconstructed by Romanes (1951) from serial transverse sections, as well as in accord with segmental levels.
An important feature of Romanes' classic work was that the position of any given cell column was not highly correlated with the segments of the spinal cord. Nevertheless, the length of an individual column and its position relative to other cell columns remained quite constant. In addition, the motor cell groups did not have sharply defined boundaries. Indeed, at certain segmental levels, the transverse sections showed cell bodies which innervated different muscles co-extensive within the column. For example, MG, soleus (SOL), popliteus and tibialis posterior motoneurons were found in column 5 at the L7 level and sartorius (SART) and rectus femoris (RF) cell bodies were in column 1 at the rostral L5 level. Such a finding supports a major role for species specificity in the establishment of Ia-motoneuronal connections.

Several subsequent studies have used improved techniques to delineate the location of spinal motor nuclei (e.g., Burke, Strick, Kanda, Kim & Walmsley, 1977), but not to the detriment of Romanes' original (1951) work, which continues to be a valuable reference for intracellular studies on motoneurons supplying hindlimb muscles.

Somatotopic Considerations

Certain somatotopic relations are known to exist between peripheral and central structures. For example, the afferents and efferents of muscle groups are arranged somatotopically at the spinal cord level, following the same craniocaudal sequence as the dermatomes (Sherrington, 1892; Kuhn, 1953). However, the extent of cord-to-muscle
(displayed by alpha axons) or muscle-to-cord (displayed by muscle receptor afferents) somatotopy is uncertain.

**Cord-to-Muscle Topography.** Somatotopy in the motor outflow to a muscle was reported by Swett, Eldred & Buchwald (1970). By stimulating teased "naturally-occurring" ventral rootlets in a rostrocaudal sequence, these investigators demonstrated a pattern of progressively overlapping zones of contraction in the MG muscle. The most rostral filaments contained axons that innervated muscle units located along the dorsal margin of the muscle and the most caudal filaments innervated units in the ventral region.

A subsequent HRP study by Burke et al. (1977) reported a greater percentage of large motoneurons in the dorsal margin of the MG nucleus, a finding which corresponded to an earlier one that the dorsal part of the muscle contained a greater percentage of fast-contracting, fatigue-sensitive type FF motor units (nomenclature of Burke, Levine, Tsairis & Zajac, 1973) which are known to have the largest cell bodies (for review: Burke, 1981; Henneman & Mendell, 1981; Stuart & Enoka, 1983). This relationship, however, was significant in only one animal in the Burke et al. (1977) study. Furthermore, their finding is in conflict with an electrophysiological study (Clamann & Kukulka, 1977) which reported no correlation between a motoneuron's axonal conduction velocity, an approximate indicator of cell size (Burke, 1981; Henneman & Mendell, 1981; Stuart & Enoka, 1983) and the axon's position of exit from the spinal cord. However, Burke et al. (1977) reported that this cord-to-muscle topography (judged from noting the location of muscle
unit contraction upon intracellular stimulation of MG motoneurons) held up throughout their earlier studies of the MG muscle (Burke, 1967; Burke et al., 1973; Burke & Tsairis, 1973).

Afore-mentioned studies on the organization of primary muscle nerve branches have provided evidence for "a topographic relation between the location of a motoneuron within its motor nucleus and the position of its innervated muscle fibers within the muscle" (Iliya & Dum, 1984). Motoneurons in the cord were classified as belonging to a given primary nerve branch by retrograde labeling with HRP. Within the muscle, glycogen depletion of the muscle fibers supplied by a given nerve branch showed that the territories were quite segregated. Overall, motoneurons innervating the primary nerve branches were reported to show an organization within the motor nucleus which related to the position (e.g., muscle head or neuromuscular compartment) of its fibers in the muscle.

Currently, cord-to-muscle topography has been reported for the following muscles: biventer cervicis (BC) and splenius (SP; Brink, Jinnai & Wilson, 1981); BF (Letbetter & English, 1981); ST (Letbetter & English, 1981); SART (Pratt, Yee, Chanaud & Loeb, 1984); MG (Weeks & English, 1983); LG (English & Letbetter, 1982, Weeks & English, 1982, English & Weeks, 1984); and TA (Iliya & Dum, 1984). Of these, the ST muscle displays the weakest cord-to-muscle organization.

Muscle-to-Cord Topography. There have been far fewer studies on muscle-to-cord topography. In 1959, Swett & Eldred reported that the location of muscle receptor endings (including those with Ia axons) in
the MG and SOL muscles (studied by noting afferent responses to gentle punctate stimulation of the muscle with a fine probe) showed no strong relation to the segmental level of their afferents' entry into the spinal cord. Nevertheless, a subtle progression was noted in which the sensitive region for receptor activation in both muscles moved medially (i.e., away from LG) as more caudal roots were examined.

Farina (1978) reported that muscle spindles confined to a single neuromuscular compartment of MG received their Ia sensory innervation via the same nerve branch which supplied the surrounding skeletomotor muscle fibers. This finding deserves consideration in regards to a subsequent electrophysiological study in which the majority of muscle-receptor afferents from a single neuromuscular compartment were found to cluster into contiguous (2-4) subdivisions of the dorsal roots (Cameron et al., 1981). However, these two sets of observations do not, in themselves, prove that the MG muscle exhibits strong muscle-to-cord topography.

**Summary.** Some progress has been made in the examination of cord-to-muscle topography. It is evident to varying extents in some but not all motor nuclei-muscle complexes. However, little information is available concerning muscle-to-cord topography. Further work is clearly needed to clarify the extent to which topographic relations exist between the spinal cord and muscles and vice-versa.

**Physiological Issues**

Physiological issues concerning muscle structure and function are discussed which have relevance to testing for partitioned effects.
within the motor nucleus-muscle complex. In addition, the question is raised as to whether central partitioning is a principle of neural design and function or a specialization in selected input systems to motoneurons and selected motor nucleus-muscle complexes.

Intramuscular Localization of Proprioceptive Reflexes

There is no general agreement on usage of the term "proprioceptive reflex". In this report, the definition favored is one which accommodates Evarts (1981) emphasis that Sherrington's original (1906) position was that proprioceptors should be defined as deep receptors activated by "the organism's own acts". As such, the spindles are certainly proprioceptors and their segmental reflex actions should be considered as proprioceptive reflexes, particularly, as emphasized by Sherrington (1906), when they are activated by small disturbances brought about by internal factors within the neuromuscular system itself (for further review: Binder & Stuart, 1980).

Two such reflexes are the stretch and the muscle-tap reflex. The stretch reflex involves a rapid (phasic or dynamic) and a sustained (tonic or static) excitatory response of a muscle to a stretch stimulus that also has rapid and sustained characteristics (Matthews, 1972; Lance & McLeod, 1981). Several types of muscle receptor and their afferents are activated by this stimulus (Rymer, Houk & Hasan, 1979; Houk & Rymer, 1981) including in particular, the muscle spindles and their Ia afferent axons. The reflex response in the stretch reflex is attributed to both monosynaptic and polysynaptic muscle-afferent actions on motoneurons including, the monosynaptic action of Ia afferents (Matthews, 1972).
The muscle-tap reflex involves a rapid and short-lived excitatory response of a muscle to brief and gentle tap applied to the muscle's surface or to its tendon. This reflex is similar in most respects to the tendon-jerk reflex (McKeon & Burke, 1983) and, again, several types of muscle receptors are activated (Burke, Gandevia & McKeon, 1983, 1984), among which the spindles and their Ia afferent axons are most noticeable. The reflex response is more dominated by monosynaptic afferent actions than in the stretch reflex, including in particular the action attributable to Ia afferents.

In the laboratory, both the stretch and muscle-tap reflexes usually are brought about by use of external stimuli (i.e., stretch and tap, respectively) but these disturbances simulate naturally occurring ones which could be generated within the neuromuscular system itself (i.e., external stretch simulates stretch evoked by action of antagonist muscles and the tap simulates internal "errors" in motoneuronal drive to either the test muscle or its antagonists).

In summary, an association should exist between the presence or absence of partitioned Ia EPSPs in a spinal motor nucleus and the presence or absence of localized proprioceptive-reflex effects within the muscle supplied by that nucleus, including the presence or absence of a localization of the stretch and muscle-tap reflexes. However, the available evidence is too scanty to allow a position on this possibility.

The stretch reflex. Localization of the stretch reflex to a small portion of a single muscle was first reported by Cohen (1953,
1954). First (1953), he showed in the unanesthetized decerebrate cat that the reflex response of an isolated muscle strip (i.e., a few fascicles) in rectus femoris (RF) to small stretches was usually confined to the strip. The remainder of the muscle showed no response. Subsequently (1954), he found that reflexes which increased the generalized excitability levels of the relevant motoneurons (i.e., neck and crossed extension reflexes) reduced the degree of stretch reflex localization in both the RF and vastus intermedius (VI) muscles while increasing the force output of these muscles and other components of the quadriceps femoris muscle group.

The importance of these findings would warrant repeating the experiments, especially with the advent of more rigorous techniques for analysis of the stretch reflex (e.g. McGrath & Matthews, 1973). It would also be helpful if a study was undertaken that tested for the partitioning of Ia EPSPs in the motor nuclei supplying the RF and VI muscles. However, a similar localization of the stretch reflex has recently been reported (Bilotto, Schor, Uchino & Wilson, 1982; Ezure, Fukushima, Schor & Wilson, 1983) in a neck muscle, splenius (SP), as has the partitioning of Ia EPSPs in its motor nucleus (Brink et al., 1981).

The muscle-tap reflex. There was no evidence of intramuscular reflex localization in two recent studies on the muscle-tap reflex in human jaw-closing (Smith, Pratt and Moore, 1983) and the TA (McKeon, Gandevia & Burke, 1983) muscles. The report on the jaw-closers is still in abstract form and, for the moment, it seems best to take on face value its authors' claim that the stimulus provided a "restricted
activation of spindles" in both the masseter (MA) and temporalis (TE) muscles. (Muscle identification was provided by Moore in a personal communication).

The distribution of muscle spindles throughout these two muscles is not known. In the cat, these receptors are limited to a small portion of each muscle (Lund, Richmond, Toulomis, Patry & Lamarre, 1978) but there is no a priori reason to believe the distribution need be similar in the human. Certainly, the results seem at odds with the hypothesis under consideration in this project, because jaw closing muscles exemplify the capability of selected muscle to contribute force in a variety of directions, thereby suggesting that components of these muscles should be capable of somewhat independent action.

The second muscle-tap study (McKeon et al., 1983) was preceded by one (McKeon & Burke, 1983) showing that the mechanical stimulus to TA did indeed activate a limited number of spindle afferents. Thus, the results demonstrating a lack of intramuscular reflex localization seemed quite convincing. The authors' viewpoint, like the hypothesis to be tested, was that such localization should only be anticipated in multifunctional muscles. In their opinion, TA does not meet this criterion; a puzzling argument in view of the fact that TA contributes in the human to both ankle dorsi-flexion and inversion (Kendall & McCreary, 1983) of the foot.

Summary. To this point, there is evidence both for and against an intramuscular localization of proprioceptive reflexes. Rectification of this dilemma will require repetition of some of the existing data
base and its expansion to include analysis of a wider variety of muscles throughout the body.

In-Series vs. In-Parallel Muscle Structure

Force developed by single contractile elements sum in-parallel, not in-series. Probably for this reason, most striated muscles exhibit an in-parallel arrangement between their fibers. In the cat hindlimb, at least one muscle, ST, violates this principle.

The ST muscle is completely subdivided by a tendinous inscription into two in-series compartments, STp and STd (Chin et al., 1962; Bodine et al., 1982). Muscle units in one compartment have been shown to exert an in-series influence over spindles located in the other compartment (Botterman et al., 1983b). Consistent with basic mechanics, intramuscular reflex localization would be inefficient in ST (Bodine et al., 1982) because force generated by activation of a single compartment would be attenuated by the visco-elastic properties of the other passive in-series compartment. This argument suggests that the lack of partitioning of Ia EPSPs in the ST motor nucleus (Botterman et al., 1983b) may be related to its atypical structure.

Two cat neck muscles, SP and BC also have in-series fiber components but they are alongside in-parallel components (Richmond and Abrahams, 1975). Intramuscular localization of the stretch reflex has been reported in SP (Bilotto et al., 1982; Ezure et al., 1983) as has a partitioning of Ia EPSPs (Brink et al., 1981). Such reports do not weaken the argument that an intramuscular reflex localization would be inappropriate for ST, since SP has fibers arranged both in-series and
in-parallel. Further speculation on force development in SP and BC must
await a more detailed analysis of the actions and biomechanics of these
unusual muscles.

Muscle Function vs. Structure

Sherrington (1910) noted that reflex responses did not always
produce the same response throughout a two-headed muscle regarded (by
anatomical nomenclature) as one muscle. The nerve supply sometimes
included two or more divisions, possibly in accord with the complex
actions. For example, the BF muscle which takes origin from the
tuberosity of the ischium, consists of an anterior part (BFa) which
crosses one joint and a posterior part (BFp) crossing two joints. BFp
inserts onto the tibia, receives at least one separate division of the
nerve, produces flexion at the knee joint and extension at the hip joint
and is the only part of the BF muscle found by Sherrington (1910) to
contract in the flexion reflex. In contrast, BFa inserts onto the
femur, produces extension at the hip joint, also receives its "own"
nerve branches and is, according to Sherrington (1910), relaxed in the
flexion reflex, but contracted in the crossed extension reflex.

Quite recently, Zajac (1984) has studied the behavior of the BF
muscle and other two-joint posterior thigh muscles during jumping.
Adductor femoris, SMA and BFa were shown to be "activated
synergistically as one group yet differently from the synergistic
activation" of gracilis, ST and BFp.

These reflex and "voluntary" (jumping) responses of muscle show
that a muscle or part of a muscle, or, as discussed below, even specific
muscle units (Loeb, 1984) within a part of a muscle, may belong to a distinct functional group (e.g., flexors or extensors). As a result, motor-control studies should consider the functional entity if it differs from the anatomical entity (for review: Loeb, 1984).

Design vs. Functional Aspects of Partitioning

In this project, central partitioning was considered from a design point of view, i.e., as to how the alpha motoneuron pool and spindle afferents are organized to produce this phenomenon. Inherent in this view is the assumption that these partitioned spinal connections have a role in movement. However, the specific role partitioning plays in motor control is beyond the scope of this study, except to point out that such an arrangement would provide the CNS with a rapidly conducting reflex pathway for compensating for small intramuscular disturbances ("errors") which are known to generate positional errors even in the presence of fixed external loads (for review: Botterman, Binder & Stuart, 1978; Binder & Stuart, 1980).

The "law of Ia receptivity". The partitioning of Ia projections within motor nuclei may be viewed as an extension and a refinement of the "law of Ia receptivity" (Eccles, Eccles & Lundberg, 1957; Eccles & Lundberg, 1958) which suggests that the Ia connectivity patterns of motoneurons are related to muscle synergies and evolved, presumably in a developmental and even evolutionary sense, to assist in the motor act of stepping. Work on the partitioning hypothesis has suggested a refinement of this law in the sense that the focus is shifted from "whole" muscle, as defined anatomically, to neuromuscular compartments
which may occupy different heads of muscle or different volumes within a single-headed muscle.

The suggestion (Eccles et al, 1957) that heteronymous Ia connectivity patterns evolved to assist in locomotion requires modification in light of recent work (O'Donovan, Pinter, Dum & Burke, 1982) on two muscle synergists, flexor digitorum longus (FDL) and flexor hallucis longus (FHL). These two muscles are anatomical synergists, with similar origins and a common tendon. They exert the same mechanical action and are interconnected by strong monosynaptic group Ia excitation yet they are activated in different phases of the step cycle. The most stereotyped activation of FDL during locomotion was at the onset of the swing phase of the step; whereas, that of FHL was during the stance phase. The muscle synergy of FDL and FHL seems not to be expressed during locomotion. However, the strong Ia connections between these two muscle may well subserve a different motor act (e.g., claw protrusion; Goslow, Stauffer, Nemeth & Stuart, 1972). Certainly, strong Ia connectivity between two muscles does suggest a functional synergism, but this synergism may or may not relate to locomotion.

Loeb's "Task-Group" Hypothesis. Recently, Loeb (1984) has proposed a "task-group" hypothesis which states that differing combinations of activity in alpha, beta and gamma motoneurons and of muscle spindles can be effected in the production of different motor acts. This hypothesis was stimulated by recent work undertaken in Loeb's laboratory on motor-unit behavior during natural movements of conscious cats (Hoffer, Loeb, O'Donovan & Pratt, 1980; Hoffer, Sugano,
Marks & Loeb, 1982) as well as on the powerful modulation of muscle spindles during such movements (Loeb & Duysens, 1979; Loeb & Hoffer, 1981; Hoffer & Loeb, 1981) by a variety of fusimotor effects (i.e., action on spindle intrafusal fibers by static and/or dynamic beta and gamma motoneurons). Loeb's recent review (1984) emphasizes that the task-group hypothesis is also consistent with work from several other laboratories on the firing patterns of spindle afferents during the natural movements of cats, other animals and the human (for review, see also Prochazka & Hulliger, 1983).

If monosynaptic spindle Ia reflex actions participate in the control of such natural movements, then the organization of task groups must parallel that of partitioned reflex connections. This point cannot be addressed at this time because technical limitations dictate that work on the task group hypothesis must proceed in parallel with work on the partitioning hypothesis.

Establishment of a Principle vs. a Specialization

The question may be raised: Is central partitioning of Ia EPSPs a general principle in the organization and function of each motor nucleus-muscle complex, or a specialization only relevant in selected complexes? Due to sampling limitations, this question cannot be answered in any single study addressing the partitioning hypothesis. However, as discussed below, there are compelling reasons to undertake more studies, like the present one on a wide variety of motor nuclei-muscle complexes throughout the body.
An allied issue is whether central partitioning is a general principle of neuromuscular design and function or limited to the Ia afferent-motoneuronal connection. This question involves three interlocking issues.

1) The only experimental evidence available on this question is from the SP motor nucleus-muscle complex. The SP muscle exhibits an intramuscular localization of the stretch reflex (Bilotto et al., 1982; Ezure et al., 1983) which has a close association with the partitioning of Ia EPSPs observed in this muscle's motor nucleus (Brink et al., 1981). However, there is no analogous localization during reflex responses to optokinetic stimuli (Wilson, Precht & Dieringer, 1983). This set of studies should be extended to test for partitioned responses to motoneuronal input from other species of primary afferents and from descending tracts. Of these, the most promising candidate for partitioned effects is the corticospinal tract which has recently been shown (albeit indirectly) to produce such effects in human facial muscles during speech (Abbs, Gracco & Blair, 1984). However, facial muscles lack muscle spindles (Barker, 1974). For this reason, a more relevant study is that of Clough, Kernell & Phillips (1968) in the baboon. It revealed a close association between the relative strength of corticospinal EPSPs in various motor nuclei supplying the forelimb and the relative strength of homonymous Ia input to their nuclei.

2) In SP, the neuromuscular compartments exhibiting stretch-reflex localization are the same ones that receive partitioned Ia EPSP effects by way of their innervating motoneurons. If other input
systems to the SP motor nucleus can indeed evoke partitioned effects, it would be of great interest to determine if these effects were qualitatively similar to those observed in the stretch reflex. In other words, can partitioned effects occur across motor units within different neuromuscular compartments or are the effects only between compartments?

3) Motoneurons can readily be divided into FF, FR and S categories on the basis of the mechanical properties of their muscle units they supply (Burke, 1981; Stuart & Enoka, 1983). The relative effects of primary afferent systems and descending tracts on their different motoneuron types are not necessarily similar. As reviewed by Stuart & Enoka (1983), the relative strength of effects are qualitatively similar (i.e., FF<FR<S) for monosynaptic Ia EPSPs, recurrent inhibitory postsynaptic potentials (recurrent IPSPs) and disynaptic IPSPs from Ia afferents supplying antagonist muscles. Conversely, inputs that do not distinguish between the different motoneuron types (i.e., FF-FR=S) include those from spindle group II afferents, the vestibulospinal tract and a more complex pathway which provides presynaptic inhibition to MG motoneurons from group I afferents supplying the BFa and ST muscles. By analogy, these various results suggest that in motor nuclei receiving partitioned Ia EPSPs, partitioned PSP effects should be anticipated from some of the other input systems to the motoneurons.

In summary, the issue of how partitioned Ia EPSPs in selected motor nuclei will generalize to other input systems is a complex one
that will take substantial time to resolve, due to the painstaking nature of the necessary data collection.

**Developmental Considerations**

An underlying assumption of the present project and its precedents is that study of the adult nervous system can provide insight into developmental factors (e.g., topographic and species specificity: Lichtman & Frank, 1984; Lichtman, Jhaveri & Frank, 1984) that come into play during the development of Ia afferent-motoneuronal connections. At this stage, no definitive developmental research has been undertaken on the Ia afferent-motoneuronal connection (Landmesser, personal communication). However, recent progress has been made in our understanding of the development of the mammalian spinal cord and its connections with muscle.

The advent of the electron microscope (Bodian, 1970) promoted the concurrent study of "progressive development of motor behavior and progressive development of circuitry and synaptic structure" in subsystems (e.g., spinal cord segments) of the vertebrate nervous system. A good example of the information obtainable with such a combined approach is found in the series of studies on the development of functional circuits in the spinal cord of macaque embryos (Bodian, 1966b, 1968). This initial information on the development of spinal cord circuitry has since been verified in other animal models as summarized below.

Currently, much of what is known about motoneuronal development (Landmesser, 1980) comes from studies on segments of the amphibian and
avian spinal cords that supply limbs. Two particularly influential reports of this information appeared in a 1976 summary of a symposium on the control of locomotion (Herman, Grillner, Stein & Stuart, 1976). First, Landmesser summarized research which addressed the problem of how motoneurons in the limb-moving segments of the vertebrate spinal cord established appropriate peripheral and central connections. The major questions raised in this review included: 1) how motoneurons are specified—by their peripheral targets, their position in the cord or some combination of mechanisms; 2) how axons from motoneurons are selectively guided to the proper cells and 3) how appropriate synapses onto motoneurons are formed.

Landmesser's (1976) review emphasized that studies of manipulated development of the chick embryo have begun to provide answers to the above questions. Motoneurons in the chick have been found to be specified early with respect to their peripheral terminations and selectively grow to certain positions in the limb. The orderly pattern of peripheral innervation observed cannot be accounted for by a random outgrowth of axons followed by cell death of the improperly connected motoneurons nor by a timed sequence of innervation. Coordinated muscle activity is observed early in the chick in the absence of descending and sensory input, when motoneurons are connected to their muscles and spinal interneurons to motoneurons. This early coordination of muscle activity suggests that the responsible neural circuits also develop rather selectively within the spinal cord.
The second review was that of Szekely (1976) who discussed experiments on the development of spinal cord segments in amphibians (e.g., Xenopus, newt, urodela). Results suggest that coordinated muscle activity is observed early in development. In addition, the movement patterns (forelimb-like vs. hindlimb-like) as well as the rhythm of the limb movements appear to be predetermined in the segments of the spinal cord that supply the respective limb. Such results suggest that different segments of the spinal cord innervating forelimb vs. hindlimb are capable of generating different output patterns for the movement of the forelimbs vs. hindlimbs.

The neural networks necessary for these coordinated patterns of movements were the motoneurons and their neighboring spinal interneurons. Later-developing descending and sensory input to the spinal cord was postulated to modify rather than substantially alter the spinally-generated movement patterns. However, far more work is required on this fundamental issue.

Szekely (1976) also summarized beginning studies on the time course of these functional movement patterns which indicate that very early transplants of thoracic cord segments into the brachial region of the spinal cord are capable of replacing the function (wing-type) of the brachial segments. Such timing studies suggest that spinal cord segments are "neutral" in their function early in development. In the future, transplants of thoracic segments to limb-moving segments of the spinal cord will permit examination of the adaptations required of
spinal neurons (i.e., interneurons and motoneurons) for their output (i.e., motoneurons) to move a limb.

Subsequent to these reviews, numerous studies in developmental neurobiology have been added in support of early work (Hughes, 1968) that the development of the spinal cord is essentially similar in frogs, birds and mammals (rat: Altman & Bayer, 1984; mouse: Lance-Jones, 1984; monkey: Gribnau & Geijsberts, 1984; cat: Windle et al., 1933; and, human: Windle & Fitzgerald, 1937).

A recent combination of techniques (electrophysiological, anatomical and various embryonic manipulations: Landmesser & O'Donovan, 1984; Landmesser, 1984; Lance-Jones, 1984a,b) permit examination of the overall mechanisms responsible for the interface between the developing nervous system and the limb bud. Labelling small numbers of identified motoneurons with HRP and charting the trajectories made by their axons as they grow into the limb during both normal and manipulated development have permitted insights into the possible developmental mechanisms involved.

In observing the development of the innervation pattern of the chick hindlimb, the plexus formation and the muscle nerves entering the limb were reported to show very consistent patterns. Tracing HRP-labelled axons has revealed that motoneurons are rather precisely guided into the limb. Neither cell death of wrongly-projecting motoneurons, retraction of their axons nor patterning of neural activity could account for these basic innervation patterns.
Tosney & Landmesser (1984) examined passive and active mechanisms reported to play a role in neuronal pathfinding in vertebrate limbs. The passive elements consisted of "limb-imposed or permissive" pathways for axon growth. An orderly outgrowth of these axons in space and time (Summerbell & Stirling, 1981) has been proposed as responsible for the specific nerve plexus pattern. The active elements included any specific environmental cues to which the growth cones respond.

One observation of a passive element is the nerve plexus pattern at the limb base which is constant in the absence of peripheral targets for the axons. In addition, the gross anatomical formation is constant despite whether the axons traversing it are appropriate or foreign. This suggests that certain non-specific permissive pathways are present in the embryonic environment. However, the local environment of the growth cones appears to be critical in providing permissive pathways, as well as in specifying which populations of growth cones are located at specific positions within the pathways.

In experiments upon double-dorsal limbs (Lance-Jones, 1982) and muscle remnants (Tosney & Landmesser, 1984), axons which had been manipulated to grow down incorrect permissive pathways could still in the presence of their normal targets respond to cues from these structures. These local cues would result in the axons leaving the incorrect pathways to make connections with their normal targets. In order to reach their correct targets, these axons had to traverse normally less permissive mesenchyme. These results suggest that specific environmental cues (e.g., specific chemical cues) of some sort
are required to explain axon behavior during both normal and manipulated development.

The results on how developing axons find their targets from a variety of experimental manipulations on the chick embryo have been interpreted as "indicating that classes of motoneurons exist possessing distinct biochemical identities prior to axon outgrowth, and that they are capable of navigating within the limb by responding to environmental cues" (Landmesser, 1984; p. 337).

In summary, sufficient progress has been made on developmental aspects of cord-to-muscle connectivity to facilitate future study on the developmental aspects of muscle-to-cord connectivity. A continuing stimulus for such research, is the potential role of topographic and species specificity in the development of Ia afferent-motoneuronal connections, as observed in the adult animal.

Topographic and Species Specificity

The efficacy of excitatory monosynaptic connections between spindle Ia afferents and their target motoneurons may in part be attributable to either topographic or species specificity, or more likely, to some combination of the two factors.

If topographic specificity governed the establishment of Ia-motoneuronal connections then there would be a need for pronounced cord-to-muscle and muscle-to-cord topography. In addition, all Ia afferents would have to make stronger connections with motoneurons in close proximity to their spinal-cord entry point. Consequently, the
entry point of the Ia afferents in the spinal cord would dictate which motoneurons received the most effective synaptic connections.

Alternatively, if species specificity dictated the development of Ia-motoneuronal connections, the test afferent would show a preferential connectivity with its own homonymous-branch motoneurons (> own-branch EPSPs) and a reduced connectivity with other homonymous-branch motoneurons (< other-branch EPSPs), regardless of where the afferent entered in relation to the motor nucleus.

The present study and others like it may well provide a stimulus for further work on developmental neurobiology (for review: Lund, 1978; and Barondes, 1976) as it relates to these connections. One such example is found in the recent work of Iliya & Dum (1984). They examined cord-to-muscle topographic relationships in 1, 6 and 12 week old kittens as well as in adult cats. Neuromuscular compartments were present and topographically organized for all age groups studied. The authors concluded that neuromuscular compartments represent "a reproducible developmental unit with distinct anatomical, physiological and possibly functional properties".

**Intracellular Recording of EPSPs in Motoneurons Supplying Hindlimb Muscles**

Studies prior to the advent of the intracellular (IC) recording technique for measurement of postsynaptic potentials (PSPs) (Brock, Coombs & Eccles, 1951; Alanis & Matthews, 1952; Woodbury & Patton, 1952) are excluded from this review. Clearly, the origins of the partitioning hypothesis are found in the work of Camis (1910) and Sherrington (e.g.,
1910; see also Cooper, Denny-Brown & Sherrington, 1926) on overall spinal reflex organization and Lloyd (e.g., 1946a,b; see also Lloyd, Hunt & McIntyre, 1955) on monosynaptic reflex testing. However, these studies provided largely, but not completely (e.g., Binder, 1980), indirect evidence which has been superseded by more direct information on Ia-alpha motoneuron connectivity as revealed by the IC recording technique.

IC recording of PSPs permits a quantitative examination of EPSPs and inhibitory postsynaptic potentials (IPSPs) recorded from single motoneurons. According to Burke & Rudomin (1977), information gained from the study of Ia EPSPs includes: 1) knowledge of synaptic connections between afferents and motoneurons based on EPSP presence, 2) a quantitative estimate of the number of terminals per afferent per motoneuron based on EPSP amplitude, 3) an indication of the location of the afferents' terminals on the motoneuron (i.e., soma, proximal dendrites, distal dendrites) based on EPSP waveform characteristics (e.g., rate of rise).

EPSPs may be evoked by the synchronous electrical activation of all or some of the Ia axons in a given nerve or nerve branch (i.e., composite EPSPs). A more precise technique involves use of spike-triggered averaging (STA, for review: Kirkwood & Sears, 1980), which provides measurements of EPSPs produced by a single impulse from a single Ia afferent onto its target motoneurons (i.e., single-axon EPSPs).
Studies of composite Ia EPSPs evoked by stimulation of muscle nerves characteristically show that EPSP amplitudes in motoneurons supplying cat hindlimb muscles are greater in homonymous than heteronymous cells. Studies of single-axon EPSPs have provided an explanation for this difference, namely, that motoneurons to a given muscle receive Ia input from most spindle afferents in that muscle and from fewer afferents in synergistic muscles (for review: Burke, 1981; Henneman & Mendell, 1981).

EPSPs may be compared between motoneurons which innervate the same muscle supplied by the stimulated afferents (i.e., homonymous EPSPs), as well as between motoneurons which innervate different muscles with similar actions (i.e., the synergic class of heteronymous EPSPs). Furthermore, within the homonymous motor nucleus, EPSPs produced in motoneurons supplying the nerve branch being stimulated (own-branch EPSPs) can be compared to those from motoneurons supplying other branches (other-branch EPSPs).

Use of these various techniques in studies of direct relevance to this project has largely been undertaken on motoneurons supplying hindlimb muscles. This work is reviewed first. However, work on motoneurons supplying other muscle-control systems is also important, particularly because of the increasing awareness that subtle and sometimes striking differences exist between the different muscle-control systems (e.g., hindlimb vs. forelimb vs. respiratory vs. head & neck) in the design and function of their segmental motor-control systems (e.g., Abrahams, 1977; Jankowska & Odutola, 1980).
Intersynergic Ia Connections

Composite Ia EPSPs

Early work on "hindlimb" motoneurons. Eccles, Eccles & Lundberg, (1957) and Eccles & Lundberg's (1958) classic work on Ia-motoneuronal connectivity patterns for hindlimb muscles emphasized that, with few exceptions, EPSPs evoked by stimulation of a variety of peripheral nerves to single muscles were greater in homonymous than heteronymous cells. In addition, some seemingly specific and perhaps specialized connections were noted between Ia afferents supplying selected muscles and their heteronymous motoneurons.

The specificity of heteronymous connections was exemplified by the two-joint muscles: gracilis (GR), ST and SM. GR afferents produced larger composite Ia EPSPs in ST motoneurons, despite the nearer location of SM cells to GR motoneurons in the spinal cord. In addition, GR afferents gave no measurable Ia input to BFp and BFa motoneurons which were located at the same relative rostrocaudal position in the cord as ST cells. The ST afferents produced larger composite Ia EPSPs in GR cells than in SM cells. However, stimulation of the nerve to ST also gave a strong Ia input to BFp cells and much smaller input to BFa cells.

Eccles et al. (1957) also reported that stimulation of the plantaris nerve produced the largest EPSPs in its homonymous motoneurons and significantly larger EPSPs in heteronymous motoneurons innervating SOL as compared to MG cells, despite the similar actions of the SOL and
MG muscles and similar locations of their motoneuronal cell bodies in the spinal cord.

In view of the cell locations of LG, SOL and MG motoneurons (LG cells being somewhat more rostral), the specificity of their Ia afferent-motoneuronal connections is striking. In the Eccles et al. (1957) study, stimulation of each of the three muscle nerves always produced larger composite Ia EPSPs in the homonymous motoneurons. Again, despite MG cells being adjacent to SOL cells, SOL Ia input was stronger to LG than to MG cells. Likewise, LG Ia input was stronger to SOL than to MG cells. The patterns of other heteronymous Ia inputs also suggested that LG cells were more similar to SOL than to MG cells in their Ia afferent-motoneuronal connections. MG Ia input was stronger to LG than with SOL motoneurons. In addition, the MG Ia input to LG cells was as strong as to its own homonymous cells. These findings have withstood the test of time (Baldissera, Hultborn & Illert, 1981) except for the last one. It is now well accepted that MG Ia input is indeed stronger to homonymous MG cells than to heteronymous LG cells.

Based on the Eccles et al. (1957) and Eccles & Lundberg (1958) data, and information on cell body location relative to the different motor nuclei, Eccles (1964) suggested species specificity (his "species recognition") as a major factor governing the development of Ia-motoneuronal connections—in accord with functional relationships, rather than anatomic proximity (topographic specificity). The key argument against topographical factors rested on examples in which afferents made stronger connections with heteronymous cells in nuclei
some distance from its own and, more importantly, often bypassing motoneurons innervating other synergists.

Single-Axon Ia EPSPs

A Recent Report on MG and LG. Henneman's laboratory used the more precise technique of STA to examine single-axon EPSPs in MG and LG motoneurons evoked by impulses from single MG Ia afferents (Mendell & Henneman, 1971). These afferents were found to project to greater than 90% of their homonymous motoneurons, as compared to only 65% of their heteronymous cells. In addition, individual EPSPs were of larger amplitude in homonymous motoneurons than heteronymous cells.

Their evidence (further analyzed in Luscher, Ruenzel & Henneman, 1980) concerning homonymous and heteronymous motoneuron responses with respect to the spinal-cord location of their cell bodies supports the contribution of topographic factors to the organization of these monosynaptic connections. Since the LG motor nucleus is more rostral than that of MG, two cell regions were identified: one consisting of LG motoneurons rostral to the MG cells studied; and, the second involving a region in which LG and MG cell bodies were co-extensive. In the co-extensive region, the ratio between the number of cells receiving an EPSP from the MG-Ia afferent studied to the total number of similar cells was not significantly different between MG and LG motoneurons. In a comparison of cells in the two regions, it was noted that MG afferents tended to make more synaptic contacts with heteronymous cells at the same level as homonymous motoneurons than with more distant heteronymous cells. Further inferences from this study on the role of topographic
factors in establishing monosynaptic connections are not possible, since
the entry points of the afferents into the spinal cord were not
reported.

Another Report on MG and LG, together with SOL. In 1976, Scott
& Mendell reported a significant difference in the projection frequency
and mean EPSP amplitude of individual Ia afferents from the MG muscle
onto MG cells as compared to synergistic LG and SOL motoneurons. For
all three sets of motoneurons, their data supported an increased
projection frequency and greater mean EPSP amplitude for homonymous as
compared to heteronymous motoneurons. Both topographic specificity
(their "location-specificity") and species specificity were proposed to
contribute to the organization of monosynaptic Ia connections with
motoneurons. Species specificity was supported by the difference in the
projection frequency of SOL Ia afferents to MG and SOL motoneurons, the
cell bodies of which are co-extensively distributed in the spinal cord.
Topographic specificity gained support from the observation that Ia
afferents from LG produced larger EPSPs in rostral than in caudal LG
motoneurons, whereas MG Ia afferents produced larger EPSPs in caudal
than in rostral MG motoneurons (see also Munson & Sypert, 1979a,b).
Both findings are consistent with the observed topography of LG
afferents, which enter the cord rostral to MG afferents. Since cell-
body location was reported and afferent entry point was not, the
observed topographic effects were simply stated to be consistent with
the more rostral entry of LG afferents into the spinal cord.
Summary. For heteronymous Ia connections to motoneurons supplying synergists, there are examples where species specificity seems more important than topographic specificity, examples of the reverse and even further examples where both mechanisms may be of near-similar significance. The "rules" governing these differences are far from obvious and it may well be that further studies on the adult animal will shed no further light on this fundamentally developmental issue.

Homonymous-Branch Ia Connections

Composite EPSPs

Recent full-length reports on composite own- and other-branch Ia EPSP studies provide evidence for central partitioning in two motor nuclei supplying hindlimb muscles (BF: Botterman et al., 1983a; MG: Lucas & Binder, 1984) and no partitioning in another (ST: Botterman et al., 1983b). In addition, these recent reports were preceded by the influential work of Eccles & Lundberg (1958) which demonstrated partitioned Ia effects in the BF and SART nuclei but not in the SM nucleus.

Before reviewing specific studies, two main points should be kept in mind concerning the relative strength of homonymous Ia EPSPs.

1) Information is needed on more motor nuclei to find out if central partitioning is a developmental principle or a specialization in the organization of each motor nucleus. A plausible prediction (particularly for hindlimb muscles) is that whenever a muscle a) exhibits a pronounced nerve-branching pattern, b) is biarticular and
complexly structured and, c) has an in-parallel arrangement of its muscle fibers, there will be strong evidence for central partitioning.

Conversely, for one-joint muscles of simple structure and extensive motor-unit territories (e.g., SOL; Burke, Levine, Salcman & Tsairis, 1974), a lack of central partitioning would be predicted. Since the former situation is far more typical in mammals, central partitioning of afferent effects may well be a principle of development. Similarly, in motor nuclei supplying hind-limb muscles exhibiting an atypical in-series relationship between its neuromuscular compartments (e.g., ST), partitioned Ia effects would not be predicted because the separate activation of these compartments would lead to an inefficient development of muscle force (Botterman et al., 1983b; Bodine et al., 1982).

Further resolution of these issues will require detailed consideration of each test muscle's development, design, actions and afferent connections within the CNS.

2) Further examination is needed of motor nuclei in which there is clear evidence for (or against) central partitioning--to test for the presence (or absence) of causative factors. This examination should bring out the reason(s) why partitioning is present in one nucleus and absent in another. Currently, topographic specificity and species specificity are viable candidates for causative factors, although other candidates may, in time, be recognized.

Early work on BF, SART and SM. Eccles & Lundberg (1958) were the first to show that motoneurons supplying a two-joint muscle
exhibited a characteristic Ia receptivity pattern to input from the unifunctional components. For example, BF motoneurons were Ia receptive to input from both hip extensors and knee flexors. However, motoneurons supplying BFa received a stronger Ia projection from that compartment of the muscle than from the BFP compartment. Likewise, BFP motoneurons received greater Ia input from the BFP compartment and very little from the BFa one.

In two of Eccles & Lundberg's (1958) experiments, motoneurons supplying the SART muscle were separated into two populations: SARTa cells innervating the lateral (anterior) head of the muscle, which inserts onto the patella, with innervation directly from the femoral nerve; and, SARTm cells supplying the medial head, which inserts onto the tibia with innervation indirectly from the femoral nerve via the saphenous nerve. At that time, the SARTa head was thought to have had a predominately knee extensor action and the SARTm head a flexor action (Sherrington, 1910; cf. Loeb, 1984).

Surprisingly, Eccles & Lundberg's (1958) description of these two SART experiments was incomplete. It can only be inferred that, for homonymous EPSPs (their Table 2A), they stimulated both nerve branches simultaneously, and did not compare the amplitude of the homonymous-branch EPSPs as evoked by the separate stimulation of each nerve branch. Nonetheless, their data clearly showed that SARTa cells were most Ia receptive to homonymous input, as well as to two other hip flexor-knee extensor muscles, RF and tensor fascia latae (TFL). In contrast, SARTm cells, which also received their strongest Ia input from
the homonymous nerve branches, received virtually no Ia input from RF and TFL. This arrangement is yet another example of separate components of a muscle, each with a different function, being distinguishable by their distinct and different patterns of heteronymous Ia input.

Interestingly, in SM, another muscle with two heads, Eccles & Lundberg (1958) reported no significant difference in the strength of Ia input to the motoneurons supplying the two parts. Since these parts receive separate nerve branches and have different attachments, one onto the femur (SMA) and one onto the tibia (SMp), motoneurons supplying each part would be expected to show a distinct Ia-receptivity pattern (consistent with BF, SART and possibly other motor nuclei). However, no data were provided in the Eccles & Lundberg (1958) report on SM motoneurons to support their influential statement of no partitioned Ia effects. The present project further examines this issue.

A recent report on BF. Recently, Botterman et al. (1983a) extended the work on Ia connectivity in the BF motor nucleus to demonstrate the partitioning of monosynaptic Ia effects to motoneurons classified as either hip extensors and supplying two different parts of the muscle (BFa and BFm) or as knee flexors also supplying two different muscle parts (BFm and BFp). The approach involved analysis of composite Ia EPSPs evoked by the synchronous electrical activation of all the Ia axons in a given BF muscle nerve branch, BFa and BFp, as studied far earlier by Eccles & Lundberg (1958), and in addition, the BFm branch to the middle part of the muscle.
BFm cells were classified as flexors (flex) or extensors (ext) on the basis of their Ia receptiveness to input from nerves to the SM and ST muscles. This division was justified on the basis that SM, although a two-joint muscle, was thought at that time to act as a pure hip extensor (Sherrington, 1910; cf. however, Engberg & Lundberg, 1969) and that ST, although also biarticular, was classically thought to act as a pure knee flexor during the flexion reflex and locomotion (Sherrington, 1910; cf. however, Perret & Cabelguen, 1976).

A partitioning of the monosynaptic Ia reflex effects was demonstrated by comparing the Ia-EPSPs of BFa and BFm (ext) cells to input from BFa and BFm nerve branches and by comparing the BFp and BFm (flex) cells to input from BFp and BFm nerve branches. In all instances, own-branch EPSPs were of greater amplitude than other-branch EPSPs. There was also an indication that both topographic specificity and species specificity contributed to the observed partitioned effects.

Report on ST. Central partitioning was not found in the ST motor nucleus (Botterman et al., 1983b). Upon stimulation of the STp nerve branch supplying the proximal neuromuscular compartment, the mean amplitudes of composite EPSPs recorded from STp cells were not significantly different from those recorded from STd cells which supply the distal compartment. Likewise, stimulation of the STd nerve branch produced EPSPs of similar amplitude in STp and STd motoneurons.

Examination of cell-body locations in the spinal cord showed that the tested STp and STd cells were co-extensive, with the exception of the extremes of the motor nucleus, where STp cells were most rostral and
STD more distal, a finding which was in keeping with the results of a previous HRP study from Letbetter's laboratory (Letbetter & English, 1981). Analysis of volleys recorded from the muscle nerve elicited by stimulation of different divisions of the dorsal roots showed only a slight tendency for the afferents to enter the spinal cord in a somewhat more rostral location than the STD afferents (Botterman et al., 1983b). These results suggested that topographic factors are less pronounced in ST than in BF, particularly for cord-to-muscle relationships. Whether this difference is sufficient to explain the lack of Ia EPSP partitioning in the ST nucleus will require further study.

A recent report on MG. A recent composite EPSP study has provided strong evidence of Ia EPSP partitioning in the MG motor nucleus (Lucas & Binder, 1984). This muscle is supplied with 4-7 primary nerve branches (Farina, 1978). The result of Lucas & Binder (1984) showed that Ia input from groups of branches to their own motoneurons was significantly greater than input to motoneurons contributing axons to other branches. Since afferent entry points and cell body locations were not reported, the relative contributions of topographic versus species specificity to the partitioned Ia effects remained unknown.

Single-axon EPSPs

Divergent reports on MG. A subsequent single-axon EPSP study in the MG motor nucleus by Lucas, Cope & Binder (1984) provided results essentially similar to their composite EPSP study (Lucas & Binder, 1984). In addition, the STA approach permitted the conclusion that partitioned Ia effects were attributable to single Ia axons providing larger EPSPs.
to own-branch motoneurons than to other-branch motoneurons rather than the alternative possibility that they projected to a greater number of own- than other-branch cells.

Another STA study on the MG motor nucleus-muscle complex involved use of a different and technically virtuosic experimental approach (Munson, Fleshman, Zengel & Sypert, 1984). Measurements were made of the amplitude of single-axon Ia EPSPs in motoneurons and the strength of mechanical coupling between contractions of the muscle units supplied by the motoneurons and the spindles supplied by the Ia afferents. The results suggested that the association between these two strengths (one central and one peripheral) was limited at best and restricted to a quite limited number of MG motoneurons. This result argues against the overall validity of the partitioning hypothesis as applied to the MG-motor nucleus complex. However, the findings (particularly on the peripheral association between motor units and muscle receptors) are somewhat indirect and they certainly cannot be used to downgrade the significance of the composite and single-axon Ia EPSP studies from Binder's laboratory (Lucas & Binder, 1984; Lucas et al., 1984) which have provided such strong evidence for Ia EPSP partitioning in the MG motor nucleus.

Uniformity of ST findings. In 1978, Nelson & Mendell provided evidence that the projection frequency of single Ia afferents from either the proximal or distal neuromuscular compartments of the ST muscle were identical to motoneurons supplying one or the other of these two compartments. In addition, no differences in single-axon Ia EPSP
amplitudes were observed in these various comparisons. The authors did not comment upon the relevance of these findings to the partitioning hypothesis, as occurred several years later when Botterman et al. (1983b) undertook a composite Ia EPSP study which confirmed the earlier Nelson & Mendell (1978) findings and extended them by providing evidence as to why the ST muscle should be considered atypical for a hindlimb muscle.

The Issue of Motoneuron Type

In the two recent MG studies from Binder's laboratory (Lucas & Binder, 1984; Lucas et al., 1984), motoneuron type (FF, FR or S; nomenclature of Burke et al., 1973) was adjudged indirectly by measurement of rheobase (lowest for type S cells) and input resistance (lowest for type FF and FR cells). It was shown that partitioned Ia EPSPs were far more pronounced for putative type F (FF and FR) than putative type S motoneurons. Similarly, in the recent Munson et al. (1984) study, motoneurons were classified as FF, FR or S on the basis of the mechanical properties of the muscle units supplied by the motoneurons. In this study, evidence for partitioned Ia EPSP effects was far weaker, and only evident for type FF motoneurons.

Findings from these two studies cannot be compared to the recent BF study from this laboratory (Botterman et al., 1983a) in which partitioned Ia EPSP effects were demonstrated. In the BF study, only a few type S cells were studied as adjudged indirectly by the input resistance values which suggested that the tested motoneuron population was largely type F cells.
The issue of motoneuron type is clearly an important one but it was not addressed in the present project for four reasons.

1) The two test motor nuclei, SM and LG, probably contain a relatively small percentage of type S motoneurons as adjudged indirectly by the percentage of SO fibers (nomenclature of Peter, Barnard, Edgerton, Gillespie & Stemple, 1972) in the two muscles (approximately 10% and 18% as compared to 25% in the MG muscle; values of Ariano, Armstrong & Edgerton, 1973).

2) The experimental protocol required the preparation to be paralyzed. (This facilitates the search for relevant motoneurons during microelectrode tracking in the spinal cord). Consequently, direct motoneuron typing (i.e., on basis of mechanical properties of the supplied muscle units) could not be undertaken. Putative classification (i.e., by cell input resistance and rheobase) was still feasible but complicated by the use of chloralose anesthesia (Powers, 1982), which was preferred over barbiturate anesthesia (used in the above-cited MG studies) in order to provide long periods of stable excitability levels of the spinal cord (undocumented experience of this laboratory).

3) The finding that partitioned Ia EPSP effects were largely limited to type F motoneurons of the MG motor nucleus (Lucas & Binder, 1984; Lucas et al., 1984; Munson et al., 1984) does not necessarily generalize to motoneurons in other nuclei. The stretch reflex of the decerebrate cat is thought to engage primarily type S motoneurons (Burke, 1981; Henneman & Mendell, 1981). In this preparation, an intramuscular localization of this reflex has been demonstrated in the
RF and VI muscles of the hindlimb (Cohen, 1953, 1954) and the SP muscle of the neck (Bilotto et al., 1982; Ezure et al., 1983). At this time, these results are at least as compelling as the above-cited EPSP studies on the MG motor nucleus.

4) If the finding that partitioned Ia effects are insignificant for type S motoneurons (Lucas & Binder, 1984; Lucas et al., 1984; Munson et al., 1984) generalizes to other motor nuclei, the functional significance of the partitioning hypothesis could be questioned. Since the viewpoint has been advanced that sensory and central partitioning could contribute most effectively to the control of low-force and finely graded contractions (Botterman, Binder & Stuart, 1978; Binder & Stuart, 1980). The orderly recruitment phenomenon generally prevails during such contractions (Burke, 1981; Henneman & Mendell, 1981), which limits motoneuron engagement largely to type S and possible type FR motoneurons (Stuart & Enoka, 1983). However, a violation of orderly recruitment often occurs when a multifunctional muscle contributes its force to different actions (e.g., flexion vs. abduction).

The thrust of the hypothesis under consideration in this project is that partitioned Ia EPSPs should be more evident in motor nuclei supplying multifunctional muscles. To test this hypothesis, two muscles were chosen (SM and LG) in which such multifunctional activity has been observed. Most interestingly, in one of these muscles (LG), a motor-unit recruitment pattern has been observed that would bring into play type F motor units during relatively low-force contractions (English, 1984).
In summary, the relation between motoneuron type and the potential functional efficacy of the partitioning hypothesis is an important and timely issue. However, not one that demanded priority over the hypothesis adddressed in this project.

An Issue of Nomenclature

An expanded classification scheme for motoneurons is now necessary to distinguish between the various subdivisions found in any motor nucleus. For example, it is useful, as in this and other recent reports from this laboratory (Botterman et al., 1983a,b), to refer to the motoneurons by the nerve branch to which they contribute their axons, reflecting the differences in monosynaptic Ia connectivity and motor nucleus-muscle organization between motoneurons innervating different muscle regions (see also Letbetter & English, 1981; Fritz, Illert & Saggau, 1981; Weeks & English, 1982, 1983; Fullerton, Joseph, Guian & Norris, 1983).

An additional reference is required for motoneurons as to the muscle units that they supply, i.e., "type-identified" as FF, FR or S (Burke et al., 1981; see also Sickles & Oblack, 1984). For one of the present test muscles, "semimembranosus-anterior (FF)" would stand for a motoneuron which supplied an FF unit whose muscle fibers are located in the anterior part of SM.

Finally, a functional classification of motoneurons may be needed to delineate certain functional groups (e.g., based on the projection pattern of Ia afferents, Eccles & Lundberg, 1958; cf. O'Donovan, Pinter, Dum & Burke, 1982; or "task groups", Loeb, 1984).
Such functional groups may not necessarily correspond to distinct anatomical subdivisions of a muscle-motor nucleus complex (see also Hoffer et al., 1980). For SM, reference to a motoneuron supplying a FF unit in the anterior part of the muscle whose Ia receptivity pattern is consistent with the "extensor" group could be referred to as "semimembranosus-anterior (FF extensor)" and abbreviated as "SMa (FF ext)".

**Extracellular Recording of PSPPs in Motoneurons**

The postsynaptic population potential (PSPP) technique was developed in Henneman's laboratory. The first report established the validity and suggested the potential importance of measuring single-axon PSPPs (Luscher, Ruenzel, Fetz & Henneman, 1979). In the second report (Luscher et al., 1980), a strong topographic influence was demonstrated in the monosynaptic Ia connections of the MG muscle. Single MG Ia axons entering the cord from a select dorsal root (L7 or S1) evoked larger PSPPs in motoneurons contributing axons to the corresponding ventral root than to motoneurons supplying an adjacent ventral root (for an interesting precedent, see Binder, 1980). The amplitude of the PSPPs correlated with the exact entry level of the afferent fibers, suggesting that Ia axon collaterals give off more terminals to motoneurons located near the spinal-cord entry point of their parent axon. Interestingly, this possibility could be proven by use of the HRP staining technique, but technical difficulties preclude a definitive answer for several more years.
A PSPP elicited by the impulses of a single afferent axon involves the response of an unidentifiable population of cells. More specifically, the net response of the afferent's input, including homonymous and heteronymous EPSPs and heteronymous IPSPs. Since several cell species are represented, this technique, in effect, factors out the contribution of species specificity to the establishment of afferent-motoneuronal connections. In the absence of a test for such specificity, the PSPP approach shows that the central connections of single Ia afferents from at least the MG muscle are topographically organized.

**Intracellular Recording in Motoneurons Other Than Those Supplying Hindlimb Muscles**

The partitioning hypothesis may not generalize to muscle-control systems other than those for hindlimb muscles. For instance, even the monosynaptic Ia-motoneuronal connection is absent in some motor nuclei, including those supplying the diaphragm (Gill & Kuno, 1963) and selected jaw-opening muscles (Kidokoro, Kubota, Shuto & Sumino, 1968) and in many motoneurons within motor nuclei supplying the perianal sphincters (Mackel, 1979). Similarly, as reviewed by Jankowska & Odutola (1980), disynaptic inhibition of motoneurons by Ia input from antagonist muscles (reciprocal Ia inhibition) is only a feature of reflex organization between flexor and extensor muscles of the limbs, being absent in connections between adductors and abductors of the limbs as well as in motor nuclei supplying jaw, neck, respiratory and perianal-sphincter muscles.
Despite these considerations and several others summarized by Jankowska & Odutola (1980), a number of muscles in different muscle-control systems appear to be good candidates for partitioned effects. As summarized below, the partitioning hypothesis may well generalize to several muscle-control systems.

Jaw-Closing Muscles

In the cat jaw-closing muscles, masseter (MA) and temporalis (TE), the spindles, tendon organs and type SO muscle fibers (supplied by low-threshold type S motoneurons) are restricted to a small portion of each muscle (Lund et al., 1978). In addition, few of the MA and TE motoneurons receive monosynaptic Ia connections, a finding which suggests that such connections might be limited to motoneurons supplying the SO-rich portion of each muscle (Appenteng, O'Donovan, Somjen, Stephens & Taylor, 1978). Taken together, these two studies suggest that the partitioning hypothesis might have a special relevance for the cat MA and TE muscle, even though, as discussed above, such relevance might not extend across species to the human.

Neck Muscles

Partitioning has been reported by Wilson's laboratory (Brink et al., 1981) in two neck muscles, SP and BC. These muscles are partially subdivided by tendinous inscriptions (Richmond & Abrahams, 1975), and receive innervation from three to four spinal segments. Each subdivided neuromuscular compartment is innervated by a selected group of motoneurons from within the entire population of SP motoneurons.
Composite EPSP studies have shown that the monosynaptic EPSPs evoked by stimulation of the segmental muscle nerve which contained the motoneuron's axon were greater in mean amplitude and frequency of occurrence than those produced by stimulation of other segments (Brink et al., 1981). There was strong evidence that topographic factors contributed to the observed partitioning, but the issue of species specificity was not addressed. As described earlier, the same laboratory subsequently demonstrated an intramuscular localization of the stretch reflex in SP (Bilotto et al., 1982; Ezure et al., 1983)—an important finding, preceded only by Cohen's (1953, 1954) classic observations on the RF muscle. At this stage, the strongest evidence for the validity and importance of the partitioning hypothesis is this SP data, which should now be extended to address the issues of motoneuron type and species specificity.

Forelimb Muscles

The flexor carpi radialis muscle of the cat forelimb (a wrist flexor) would be an interesting candidate to test for partitioned effects. Like MA and TE, this muscle's spindles, tendon organs and SO fibers are restricted to a small portion of the muscle (Richmond & Stuart, 1984). There are several other muscles of interest in the cat forelimb which should be analyzed for partitioned effects. The five-headed cat flexor digitorum profundus is one example because the relative proportion of fibers supplied by the FF, FR and S motoneurons differs so remarkably from one head to the other (Gonyea, Marushia & Dixon, 1981).
Of equal interest are muscles in the human forelimb, some of which show different patterns of motor-unit recruitment when used in different types of movement. This group includes three emphasized in Denny-Brown's classic 1949 report on the electromyogram (EMG); flexor digitorum profundus, flexor carpi ulnaris and palmaris longus. In addition, three other human forelimb muscles have been reported to show motor-unit recruitment reversals. They include abductor pollicis brevis and extensor digitorum communis (Thomas, Schmidt & Hambrecht, 1978) and the first dorsal interosseus (Desmedt & Godaux, 1981). Clearly, the forelimb is a muscle-control system worthy of examination by the partitioning hypothesis.

Respiratory Muscles

The diaphragm has been reported to be supplied by no motoneurons receiving monosynaptic homonymous Ia connections (Gill & Kuno, 1963). Yet interestingly, the few spindles in this muscle are localized to a small part of the muscle, in the crural region (Duron, 1981). As in the Appenteng et al. (1978) study on MA and TE motoneurons, the possibility exists that a few phrenic motoneurons, which supply this crural region, do indeed receive monosynaptic Ia projections from the same part of the muscle. Alternatively, there is a recent demonstration that a short-duration "stretch" of the crural part of the muscle evokes a short-latency, but not monosynaptic, reflex EMG response (Frazier, 1985). Yet to be determined is if this response is limited to or extends beyond the crural region of the diaphragm.
The intercostal motoneurons and musculature are of great interest in relation to the partitioning hypothesis. Again, there are spindle-rich and spindle-poor regions of this musculature (Duron, 1981). A possible association between this observation and the relative amplitude of monosynaptic composite and single-axon Ia EPSPs in motoneurons supplying the spindle-rich and spindle-poor regions of this musculature needs to be examined. A pronounced cord-to-muscle and muscle-to-cord somatotopicity has been shown in the strength of monosynaptic and possibly polysynaptic connections between spindle afferents and motoneurons supplying the external intercostal musculature (Kirkwood & Sears, 1982a,b). Although technically difficult experiments, the motoneuronal sample sizes need to be increased and tests added to address the spindle-density issue and the possibility that species specificity contributes to the observed afferent-motoneuronal connections.

In summary, evidence is compelling that the partitioning hypothesis should be relevant to a variety of muscle-control systems. This viewpoint is consistent with the need to establish if partitioning is a principle or a specialization of segmental reflex organization and function.

**Summary and Rationale for Present Study**

**Summary**

This and many other studies reviewed in this chapter, have evolved from a renewed interest in the possibility that the CNS can
control separate parts of a single muscle. This renewed interest relates to the promulgation by this laboratory (Binder et al., 1977; Stuart & Binder, 1977) of the partitioning hypothesis. This hypothesis included the concept of peripheral sensory partitioning for mammalian muscle receptors and a spinal-cord correlate, central partitioning. The muscle receptors were proposed to monitor the activity of a select number of muscle units in the parent muscle, in addition to responding to more global changes in length and tension. Subsequently, each receptor afferent was proposed to provide stronger synaptic input to motoneurons innervating the muscle units to which it was responsive than to other motoneurons within the homonymous and functionally related pools.

The existence of central partitioning was required to ensure a functional significance to the sensory-partitioned input. Both components, peripheral and central, would be required for an intramuscular localization of proprioceptive reflexes, including the stretch reflex which has been demonstrated to exhibit behavior in keeping with the partitioning hypothesis (e.g., Cohen 1953, 1954; Ezure et al., 1983). However, other proprioceptive reflex studies in humans have not supported the partitioning hypothesis (e.g., Smith et al., 1983; McKeon et al., 1984) thereby stimulating the need for further work and further refinement of the hypothesis.

The homonymous monosynaptic Ia pathway to motoneurons is presumably critical to the operation of low-threshold segmental proprioceptive reflexes (Matthews, 1972; Binder & Stuart, 1980; Evarts,
1981; Houk & Rymer, 1981). In addition, it has been a high priority for the testing of central aspects of the partitioning hypothesis. Studies prior to the present one have shown that this pathway has partitioned effects to some (Brink et al., 1981; Botterman et al., 1983; Lucas & Binder, 1984) but not all (e.g., Botterman et al., 1983b) motor nuclei. These results required revision of the hypothesis to restrict its applicability to motor nucleus-muscle complexes which were involved in multifunctional motor tasks. Then, as in this project, appropriate motor nuclei and muscles were selected to test the revised hypothesis.

Rationale

The strategy for the present study was to use the composite EPSP technique to test for partitioning of monosynaptic Ia reflex effects in the motor nuclei supplying the SM and LG muscles. The composite EPSP technique seemed best suited for a relatively quick determination (albeit in demanding experiments) of the partitioning of Ia EPSP effects in either motor nucleus and, if present, whether the factors of topographic specificity and species specificity may have contributed to the development of these afferent-motoneuronal connections.

The selection of the SM and LG motor nuclei was based on, for the most part, similar considerations. In the case of the SM, partitioning was once reported absent in this nucleus (comparing SMa and SMp, Eccles & Lundberg, 1958). However, the experiment was inadequately described, which has made it difficult to accept the conclusion outright, even though it appeared in a particularly influential report. Furthermore, kinesiological evidence (Engberg & Lundberg, 1969)
suggested that partitioned Ia EPSP effects should indeed be evident in this nucleus.

The selection of the LG motor nucleus was not prompted by any previous Ia EPSP studies. Rather, its selection was based on recent studies which have suggested that its structure is quite complex (English & Letbetter, 1982a). In addition, there is intriguing evidence that its four neuromuscular compartments can indeed be activated somewhat independently during natural movements (Russell et al., 1982; English, 1984).
PARTITIONING OF MONOSYNAPTIC IA EXCITATORY POSTSYNAPTIC POTENTIALS IN THE MOTOR NUCLEUS OF THE CAT SEMIMEMBRANOSUS MUSCLE

Summary

1. A partitioning of monosynaptic Ia excitatory postsynaptic potentials (EPSPs) has been demonstrated in the semimembranosus (SM) motor nucleus of the cat.

2. In anesthetized low-spinal cats, intracellular recordings were made of the Ia EPSP responses from SM motoneurons to electrical stimulation (Group I range) of nerve branches supplying the anterior (SMA) and posterior (SMP) heads of semimembranosus, the anterior (BFA) and posterior (BFp) parts of biceps femoris, and the distal part of semitendinosus (STD). Recordings were also made during stimulation of nerves to the gracilis (GR) muscle and to the vasti (V) muscle group.

3. Stimulation of the SMA nerve branch produced Ia EPSPs of greater amplitude in SMA motoneurons than in SMP cells; likewise, stimulation of the SMP nerve branch produced larger EPSPs in cells which supplied the posterior head rather than those supplying the anterior head.

4. The distribution of heteronymous inputs provided clear-cut evidence of partitioning of Ia EPSPs in two of the five pathways studied. Evidence was suggestive of localization in a third pathway. Stimulation of the nerve branches to components of two "flexor" muscles
(Sherrington, 1910), BFp and STD, produced larger EPSPs in SMp cells than in SMa motoneurons. A tendency was found for stimulation of the nerve to BFa (an "extensor") to produce larger EPSPs in SMa than in SMp motoneurons. However, this effect was of borderline (p>0.05) significance. The limited monosynaptic input produced by stimulation of the nerves to the GR and V muscles showed that their Ia axons do not distinguish between the two SM cell groups.

5. A slight topographic organization of motoneurons within the SM motor nucleus was found, with SMa cells encountered, on average, at a more rostral level of the spinal cord than SMp cells. A similar topographic arrangement was observed in the rostrocaudal distribution of Group I afferent fibers in the dorsal roots and motor axons from the two sets of motoneurons in the ventral roots. Again, SMa fibers were represented in root segments more rostral than those of SMp. These findings are consistent with "topographic specificity" (Scott & Mendell, 1976) contributing to the observed pattern of homonymous Ia connections.

6. A role for "species specificity" (Scott & Mendell, 1976) in determining the observed pattern of homonymous Ia connections was indicated by species-dependent differences in EPSP amplitude in pairs of SMa and SMp motoneurons at similar rostrocaudal locations in the spinal cord.

7. The pattern of heteronymous connections to the SM motor nucleus also showed evidence for species specificity. However, no clear topographic pattern was evident in these connections.
Introduction

Recently, "partitioning" of Ia EPSPs has been demonstrated in five motor nuclei of the cat spinal cord (splenius, SP, and biventer cervicis, BC: Brink, Jinnai & Wilson, 1981; biceps femoris, BF: Botterman, Hamm, Reinking & Stuart, 1983a; medial gastrocnemius, MG: Lucas & Binder, 1984; Lucas, Cope & Binder, 1984; lateral gastrocnemius, LG: Vanden Noven, Hamm & Stuart, 1983b, 1984). In these nuclei, it has been shown that spindle Ia afferents from the homonymous muscle make more effective (i.e., as determined by differing amplitudes of EPSPs) connections with their "own" motoneurons (i.e., those that supply the same region of the muscle in which the afferents' receptors are located), than with motoneurons supplying other regions of the muscle (see also, Munson, Fleshman, Zengel & Sypert, 1984). These findings are consistent with others on the presence of an intramuscular localization of the stretch reflex in three cat muscles (rectus femoris, RF, and vastus intermedius, VI: Cohen, 1953, 1954; SP: Bilotto, Schor, Uchino & Wilson, 1982; Ezure, Fukushima, Schor & Wilson, 1983).

However, at least one spinal motor nucleus of the cat does not exhibit a partitioning of Ia EPSPs (semitendinosus, ST: Nelson & Mendell, 1978; Botterman, Hamm, Reinking & Stuart, 1983b). In addition, there may be no intramuscular localization of short-latency (including the Ia pathway) proprioceptive reflex effects in two human muscles, masseter (Smith, Pratt & Moore, 1983) and tibialis anterior (McKeon, Gandevia & Burke, 1984). This potential variability has prompted us to consider the possibility that a partitioning of Ia EPSPs is present in
motor nuclei supplying muscles with regions capable of independent and different actions (viz. BF: Botterman et al., 1983a). This laboratory has already shown that the partitioning is absent in one motor nucleus that supplies a muscle in which a functional disadvantage would occur if a dissociation of intramuscular actions were to occur (viz. ST: Botterman et al., 1983b; see also, McKeon et al., 1983).

For a candidate to test this possibility, we chose the cat semimembranosus (SM) muscle, a hindlimb muscle which takes origin from the tuberosity of the ischium. This muscle has two heads (Peters & Rick, 1977); an anterior (SMa) one which attaches to the distal femur and a posterior (SMP) one connecting to the proximal tibia. Each head has been shown to have somewhat different actions during stepping (Engberg & Lundberg, 1969). However, in contrast to the prediction according to our hypothesis, Eccles & Lundberg (1958) reported no significant differences in the Ia distribution (i.e., amplitudes of Ia EPSPs in motoneurons when stimulating homonymous and heteronymous nerve branches) between the two heads.

As presented in a preliminary account (Vanden Noven, Koehler, Hamm & Stuart, 1983a), evidence has been found for partitioning of Ia projections between the anterior and posterior cell groups within the SM motor nucleus. In addition, this composite Ia EPSP study provides data on the relative contributions of "location specificity" (hereafter topographic specificity) and "species specificity" to these partitioned effects (Scott & Mendell, 1976; Lusher, Ruenzel & Henneman, 1980). For the present purposes, topographic specificity suggests that the efficacy
of excitatory monosynaptic connections between spindle Ia afferents and their target motoneurons is attributable to their anatomical proximity within the spinal cord. Whereas, species specificity suggests that this efficacy is independent of topographic relationships within the spinal cord and rather, dependent on the site of the peripheral terminations of the axons.

Methods

Preparation

Adult cats (2.5-4.0 kg) were anesthetized for initial surgical procedures with halothane, nitrous oxide and oxygen. A mixture of alpha-chloralose (60 mg/kg) and urethane (600 mg/kg) was given intravenously during preparation of the hindlimb and subsequent recording. Additional doses of choralose-urethane mixture were given, as needed, throughout the experiment. For recording, the animal was mounted in a Goteborg-type frame, paralyzed by the intravenous administration of gallamine triethiodide and artificially respired.

Selected muscle nerves were cut and subsequently mounted on bipolar stimulating electrodes. For the test muscle, SM, the dissection involved the detachment and reflection of the BF from its insertion to expose the nerve branches to SM, ST and SF (Fig. 2). The SM nerve was separated into its two primary nerve branches: SMa which innervates the anterior (femoral) head and SMP supplying the posterior (tibial) head.

Heteronymous nerve branches prepared for stimulation included those supplying the anterior and posterior parts of BF and the distal
Fig. 2. Hamstring innervation. A schematic view of the innervation of the hamstring muscles, as viewed by reflecting the anterolateral border of biceps femoris to expose its innermost surface and the dorsal surfaces of semimembranosus and semitendinosus. Common features of hamstring innervation include: nerve branches to the anterior (BFa) and posterior (BFp) parts of biceps femoris; a nerve to semimembranosus which divides to innervate its anterior (SMa) and posterior (SMp) parts; and nerve branches to the proximal (STp) and distal (STD) compartments of semitendinosus (Chin, Cope, & Pang, 1962). The innervation of the middle (BFm) part of biceps femoris (indicated by dashed lines) may be innervated by a deep nerve branch that divides from the branch to BFa or by a separate branch that divides from a more distal level of the hamstring nerve trunk.
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Recording Procedures

Dorsal root volleys produced by stimulation of the test nerves/branches were recorded with a monopolar stainless steel electrode, placed under the L6-S1 dorsal roots. An indifferent electrode was placed in the back musculature.

Intracellular potentials were recorded from motoneurons using glass microelectrodes filled with 2M-potassium citrate. The tips of these electrodes were broken to 1-1.5 μm and bevelled (Botterman et al., 1983a) to a final impedance of 3-5 MΩ.

Motoneurons were identified as supplying the SMA or SMp muscle head on the basis of their antidromic invasion from stimulation of one or the other of the two SM nerve branches. Motoneurons were accepted for study if their "resting" potentials were at least 50 mV. Once impalement was secure, EPSPs were elicited by stimulation of the test muscle nerve branches using 0.1 ms stimulus pulses at a rate of 2 Hz. Stimulus strengths were graded to achieve the maximum Ia EPSP (approximately 2X threshold). If a cell was activated antidromically before the attainment of a maximum Ia EPSP, 50 ms pulses of hyperpolarizing current were injected through the electrode at sufficient intensity to block the antidromic action potential, leaving the EPSP superimposed on an M spike (Hamm, Botterman, Reinking & Stuart, 1983). Measurements were also made of rheobase (technique of Fleshman, Munson, Sypert & Friedman, 1981) and input resistance (Barrett & Crill, 1974). These measurements were accepted as indicators of the cell's
intrinsic properties in the absence of severe electrode polarization and if the resting potential remained at least 50 mV during the tests.

The locations of the test motoneurons within the spinal cord were plotted as well as the distribution of volleys produced in each nerve branch by stimulation of the dorsal and ventral roots. Motoneuron positions along the rostrocaudal axis of the spinal cord were noted relative to a reference point at the L6-L7 dorsal-root junction (Stauffer & Watt, 1976). At the end of each experiment, the L5-S1 dorsal and ventral roots were sectioned and individually put up on a stimulating electrode. Each root was stimulated to produce a maximal Group I volley while recording sequentially from the two nerve branches to SM. This procedure provided information on the distribution of Group I afferents and efferents in each nerve branch to the various dorsal and ventral roots, respectively.

Data Analysis

Several waveforms were stored concurrently on FM tape for off-line analysis using a signal averager and small laboratory computer. They included: high-gain EPSPs (16 samples), dorsal root volleys, low-gain motoneuron potentials and the amount of current passed into the cell for various tests.

To correct an EPSP record containing an M spike so as to account for the contribution of the spike, an "average" M spike was subtracted from each homonymous "M + EPSP" record (Hamm et al., 1983). The average M spike was obtained from 52 SM motoneurons in control preparations with sectioned dorsal roots.
Intrinsic Properties of SM Motoneurons

Ia EPSP amplitude has been shown to be dependent, to some extent, on motoneuron "type", increasing in the order FF, FR, S (nomenclature of Burke, Levine, Tsairis & Zajac, 1973; see also Burke, 1981). Therefore, any difference in mean EPSP amplitude between the two SM motoneuron groups could be attributed to significant differences in the numbers of type FF, FR and S cells within each group. Consequently, it was necessary to estimate if the two SM cell groups were similar with respect to the different motoneuron types.

In Munson's laboratory, rheobase and input resistance values have been found to provide an indirect estimate of the different motoneuron types in barbituate-anesthetized cats (Fleshman et al., 1981). Rheobase values >10 nA were found predominately in type F cells, whereas those <5 nA were from type S. In addition, the division of rheobase by input resistance (nA/MΩ; Munson, 1983) provided an index for separation of the different motoneuron types with FF>18>FR>7>S.

For our present sample of SM motoneurons, measurements were made of rheobase and input resistance and the ratio calculated of rheobase/input resistance in order to compare the distribution of these values for the SMA and Smp cell groups. As shown in Table 1, the mean values of these variables were not found to be significantly different between the two SM populations.
Table 1. Intrinsic characteristics of SM motoneurons.

<table>
<thead>
<tr>
<th>Cell Group</th>
<th>SMa Motoneurons</th>
<th>SMP Motoneurons</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resting potential (mV)</td>
<td>62.5 ± 1.0 (86)</td>
<td>62.0 ± 0.83 (40)</td>
</tr>
<tr>
<td>Input resistance (MΩ)</td>
<td>0.59 ± 0.05 (40)</td>
<td>0.57 ± 0.05 (40)</td>
</tr>
<tr>
<td>Rheobase (nA)</td>
<td>15.09 ± 1.33 (40)</td>
<td>13.51 ± 1.21 (40)</td>
</tr>
<tr>
<td>Rheobase/Input Resistance (nA/MΩ)</td>
<td>33.01 ± 3.69 (40)</td>
<td>47.69 ± 10.34 (40)</td>
</tr>
</tbody>
</table>

Values expressed as mean ± S.E. of mean (with number of cells in parentheses).
In Fig. 3A, the distributions of rheobase and input resistance values are plotted for the two SM cell groups. The similarity of the two distributions suggests that the two cell populations had similar compositions with respect to motor-unit type. The values of rheobase suggest that the majority of motoneurons in both groups were type F (FF+FR), with type S motoneurons being represented minimally (ca. 12.5%). Likewise in Fig. 3B, the distribution of rheobase/input resistance ratios is plotted. Again, the two distributions are similar (Table 1) and suggest a predominance of type F motoneurons.

This separation of SM motoneurons into the different motoneuron types by rheobase is only a rough estimate since the SM values in chloralose-anesthetized cats may not be comparable (Powers, 1982) to the MG values of Fleshman et al. (1981) and Munson (1983). However, the estimated separation is in keeping with the histochemical study of Ariano, Armstrong & Edgerton (1973) of fiber-type distributions within the two heads of the SM muscle. SMa was reported to show only 10% SO fibers; likewise, SMP had 9% SO fibers. Such a small percentage of SO fibers suggests far fewer type S than type F motoneurons, since the innervation ratio of type S motor units in cat hindlimb muscles can be anticipated to be similar to that of type FR units and somewhat smaller than that of type FF units (for review: McDonagh, Binder, Reinking and Stuart, 1980; Burke, 1981).

Alternatively, Hultborn & Katz (1983) have used the product of rheobase and input resistance of MG motoneurons (also barbiturate anesthesia) as an indirect measure of firing threshold (i.e., $nA \times \Omega =$
Fig. 3. Distribution of input resistance and rheobase values for SM motoneurons. A: Scatter plot of rheobase versus input resistance for the present sample of SM motoneurons (N=82). Below the lower dotted line represent presumed type S motoneurons (cf. Fleshman et al., 1981), whereas those above the upper line represent type F cells. B: Distribution of rheobase/input resistance ratios for SM motoneurons. Data plotted on a log2 scale to provide suitable display for this multiplicative relationship. Arrows denote approximate divisions between type S (0-7); type FR (7-18) and type FF (18) motoneurons (cf. Munson, 1983). Both plots suggest that the present SM cell population consists of primarily type F (large) motoneurons.
mV) and showed that, in their sample, it increased in the order of S, FR, FF with mean values of 4.6, 8.9 and 13.4 mV, respectively. However, this second procedure led to ambiguous results (Munson, 1984, personal communication) when applied to the type-identified population of MG motoneurons from the studies of Fleshman et al. (1981) and Munson (1983).

Homonymous Ia EPSPs

Fig. 4 gives examples of Ia EPSPs in an individual SMA as well as a SMP motoneuron due to stimulation of the nerve branches supplying the two heads of the SM muscle. The "own-branch" EPSPs have been corrected for the presence of an M spike. As shown here, the own-branch EPSPs were often larger than the "other-branch" ones, in contrast to the earlier findings of Eccles & Lundberg (1958). These differences were significant when the full sample was compared (Table 2). Each cell exhibited an EPSP from stimulation of its own nerve branch and most cells (94%) responded with an EPSP to stimulation of the other branch. The degree of partitioning was similar for the input from both nerve branches as judged by the similar magnitudes of the differences between own-branch and other-branch EPSP values in the two cell groups (0.34 and 0.30 mV for stimulation of SMA and SMP nerve branches, respectively). Likewise, the sums of own-branch and other-branch EPSPs were quite similar (1.30 and 1.26 mV, respectively). The two comparisons suggest no asymmetries in the synaptic input received by each cell group, a feature consistent with a similar distribution of motoneuron types in
Fig. 4. Composite homonymous EPSPs recorded in SMa and SMp motoneurons. EPSPs produced by stimulation of the SMa and SMp nerve branches are displayed in an individual SMa cell (left) and SMp cell (right). Below each intracellular trace is the dorsal-root recording. For own-branch EPSPs, hyperpolarizing current was injected, as necessary, into the cells to block the response to the "M spike + EPSP". The original records are indicated by continuous lines, while the records which have been corrected for the M spike are shown by dotted lines. A tendency can be seen for the own-branch EPSPs to be the largest.
Table 2. Amplitudes of mean composite monosynaptic Ia EPSPs evoked by stimulation of homonymous nerve branches from SM.

<table>
<thead>
<tr>
<th>Nerve branch stimulated</th>
<th>SMa Motoneurons</th>
<th>SMP Motoneurons</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMa</td>
<td>0.79 ± 0.07 **</td>
<td>0.45 ± 0.05</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>(86/86)</td>
<td>(76/76)</td>
<td></td>
</tr>
<tr>
<td>SMP</td>
<td>0.51 ± 0.04 **</td>
<td>0.81 ± 0.05</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td>(82/86)</td>
<td>(76/76)</td>
<td></td>
</tr>
<tr>
<td>Sum</td>
<td>1.30</td>
<td>1.26</td>
<td></td>
</tr>
</tbody>
</table>

EPSP values (in mV) expressed as mean ± S.E. of mean (with number of observed EPSPs / total number of cells examined in parentheses). Comparisons should be limited to the effects of a given nerve branch on the two cell groups to avoid any differences in amplitude due to a variable number of afferents between the nerve branches. Asterisks indicate significant differences between adjacent EPSP averages in each row (** p < 0.001; two-tailed Student's t test).
the two cell groups. Consequently, the normalization used by Botterman et al. (1983a) was not employed in this study.

Heteronymous Ia EPSPs

Table 3 shows evidence for a partitioning of heteronymous Ia EPSPs in at least two of the five tested pathways. The majority of SM motoneurons received inputs from the heteronymous hamstring-nerve branches. Stimulation of the nerve branches to BFp and STd produced significantly larger EPSPs in SMP motoneurons than in SMA cells. In addition, stimulation of the nerve branch to BFa produced larger EPSPs in SMA than SMP motoneurons. However, this effect proved to be of borderline significance (0.05<p<0.06; two-tailed Student's t test). The limited number of monosynaptic EPSP responses observed upon stimulation of the nerves to GR and V showed no significant partitioning of input to the two cell groups in the SM motor nucleus.

Topographic and Species Specificity in the SM motor nucleus

Evidence for the contributions of topography and species specificity to the observed partitioning of Ia EPSPs was sought in the topographic organization of SM motoneurons and Group I afferents as well as in the dependence of EPSP amplitude on motoneuron location and species. If topographic specificity governed the establishment of Ia-motoneuronal connections, then motoneurons in close proximity to the afferents' entry points would receive the strongest connections. (Luscher, Ruenzel & Henneman, 1980). In the present case, a partitioning of Ia EPSPs would result if SMA and SMP motoneurons had
Table 3. Amplitudes of mean composite monosynaptic Ia EPSPs evoked by stimulation of heteronymous inputs to SM motoneurons.

<table>
<thead>
<tr>
<th>Nerve/branch stimulated</th>
<th>SMa Motoneurons</th>
<th>SMp Motoneurons</th>
</tr>
</thead>
<tbody>
<tr>
<td>BFa</td>
<td>0.27 ± 0.02</td>
<td>0.21 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>(70/73)</td>
<td>(65/72)</td>
</tr>
<tr>
<td>BFp</td>
<td>0.25 ± 0.03 *</td>
<td>0.38 ± 0.04</td>
</tr>
<tr>
<td></td>
<td>(65/72)</td>
<td>(59/69)</td>
</tr>
<tr>
<td>STD</td>
<td>0.28 ± 0.04 **</td>
<td>0.74 ± 0.07</td>
</tr>
<tr>
<td></td>
<td>(60/74)</td>
<td>(66/73)</td>
</tr>
<tr>
<td>GR</td>
<td>0.08 ± 0.03</td>
<td>0.12 ± 0.04</td>
</tr>
<tr>
<td></td>
<td>(10/29)</td>
<td>(8/19)</td>
</tr>
<tr>
<td>V</td>
<td>0.17 ± 0.04</td>
<td>0.10 ± 0.05</td>
</tr>
<tr>
<td></td>
<td>(19/42)</td>
<td>(5/34)</td>
</tr>
</tbody>
</table>

EPSPs (in mV) expressed as mean ± S.E. of mean (with number of observed EPSPs / total number of cells examined in parentheses). Comparisons are limited to the effects of each nerve branch on the two cell groups to avoid differences in the number of afferents between nerve branches. Asterisks indicate significant differences between adjacent EPSP averages in each row (* p < 0.02; ** p < 0.001; two-tailed Students's t test).
different mean locations corresponding to different mean afferent entry points of their respective Ia afferents. However, EPSP amplitude could conceivably be independent of the relative topography between afferents and motoneurons. Therefore, a topographic organization is a necessary but not sufficient condition for topographic specificity. In contrast, if species specificity dictated the development of Ia-motoneuronal connections, the test afferents would show preferential connectivity (i.e., greater amplitude of EPSPs) with their own homonymous-branch motoneurons in comparison to connectivity with other homonymous-branch motoneurons, regardless of the relative locations of motoneurons and afferents.

Homonymous connections. A topographic organization was observed in the SM motor nucleus and corresponding dorsal and ventral roots. Fig. 5 shows the locations of SMA and SMp motoneurons relative to the junction of the L6-L7 dorsal roots. Despite extensive overlap of these two cell groups, the mean locations (arrows) were significantly different (p<0.02; Student's t test) with the SMA mean slightly more rostral than the SMp mean.

Evidence for a topographic organization of Group I and alpha-motor fibers is demonstrated in Fig. 6, which shows the points of entry or exit of these fibers within the dorsal and ventral roots, respectively. In Fig. 6 (left-side), a distinct topographic organization is evident in the ventral roots. A larger percentage of the SMA motor axons were found in the more rostral roots (primarily, L6), whereas, a greater percentage of SMp axons were found in the more
Fig. 5. Spinal-cord location of SM motoneurons. Graphs show rostro-caudal locations relative to the L6-L7 dorsal root junction (with arrows at mean location of the SMa and SMp cell groups). The population totaled 162 cells from 9 experiments (86 SMa and 76 SMp cells). On average, the SMa cells were slightly more rostral than the SMp cells (statistics in text).
Fig. 6. Topography of axonal connections between the spinal cord and the SM muscle. Maximum Group I (afferent) and alpha axon (efferent) volleys were recorded in SMa and SMp nerve branches in response to stimulation of sectioned L5, L6, L7 and S1 dorsal and ventral roots, respectively. The volley for each branch was expressed as a percentage of the total for that nerve branch (i.e. percent of L5+L6+L7+S1 volleys). On the left, the average values (+ S.E. of mean) of the percent volleys produced in the SMa and SMp nerve branches by stimulation of each root are shown. These data show that SMa had a stronger representation than SMp, in the L6 dorsal and ventral roots, the reverse occurring in the L7 roots. This topographic organization is confirmed in the right part of the Figure. Plotted here are the averages (+ S.E. of mean) of the differences between the percent volleys recorded in the anterior and posterior SM nerve branches in each experiment due to stimulation of each dorsal and ventral root division (* p<0.05).
caudal roots (primarily, L7). This finding is consistent with the more rostral location of SMa cells in the SM motor nucleus. A similar, though less distinct, topographic organization was found in the dorsal roots.

Differences in the distribution of the afferents and efferents were tested for statistical significance by taking pairwise differences in the amplitudes of the volleys produced in the SMa and SMP nerve branches by stimulation of each dorsal or ventral root segment in each experiment. In both dorsal and ventral roots (right-side Fig. 6), the SMa nerve branch received a larger percentage of its volley from the L6 root than SMP did, while SMP's L7 volley was a greater part of its total than was SMa's L7 volley. In averaging these pairwise differences, data were excluded from two cats: one whose lumbosacral cord was markedly pre-fixed and one with a post-fixed cord (Romanes, 1951); however the trend was the same in these two as in the larger sample.

The preceding results demonstrate the existence of a slight topographic organization in the SM motor nucleus. However, our data indicate that species specificity contributes prominently to this partitioning of Ia projections.

Fig. 7 shows that along the length of the motor nucleus the SMa nerve branch (top) produced larger EPSPs in the SMa cells as compared with those from SMP cells. Likewise, the SMP nerve branch (bottom) produced larger EPSPs in the SMP cells throughout most of the nucleus.
Stimulation of SMa Nerve Branch

Stimulation of SMp Nerve Branch

Fig. 7. Relationship between EPSP amplitude and spinal cord location of the tested SM cells. Graphs show rostrocaudal distributions of homonymous EPSP amplitudes for SMa and SMp motoneurons. SMa and SMp cells were grouped in 1 mm bins according to their rostrocaudal distance from the L6-L7 junction. Within each bin, average EPSP amplitudes due to stimulation of the SMa nerve branch (top) and the SMp branch (bottom) are plotted against location. The number of cells contributing to the average within each bin is indicated just above the axis-marking location. Partitioning of Ia EPSPs due to stimulation of each nerve branch is evident throughout the length of the motor nucleus. This arrangement suggests a role for species specificity in the observed partitioned Ia effects.
As shown in Fig. 8A, potential effects due to topographic specificity were minimized by examining the difference between the EPSPs produced upon stimulation of the SMa (or SMp) nerve branch in pairs of motoneurons (SMa and SMp) located within 0.5 mm of each other. Each SM nerve branch appeared to "recognize" its own cell over the other-branch cell, which supports a role for species specificity in determining the pattern of homonymous Ia projections.

In making these comparisons, the pairs were selected with certain restrictions: 1) no single cell was included in more than three pairs and 2) a cell pair was not accepted if the difference in input resistance of the cells was greater than 0.3 MΩ (the average difference between type FF and FR motoneurons, at least for cells supplying the MG muscle; Fleshman et al., 1981).

Results in Fig. 8A are consistent with the differences found in Table 2. Although the difference in the effects of the SMa nerve branch on SMa and SMp cells was not significant, the EPSP amplitudes still tended to be larger in the SMa cells (0.05 < p < 0.1). According to Figs. 7 and 8A, species specificity in the SM motor nucleus accounted for at least some of the observed partitioning of its Ia projections.

**Heteronymous connections.** Fig. 9 shows the distribution of EPSP amplitudes throughout the SM motor nucleus upon stimulation of three heteronymous nerve branches (BFa, BFP and STd). In previous work (Botterman et al., 1983a,b); Ia afferents from BFa, BFP and STd were shown to enter the cord at a more caudal level than that found in the present work for afferents from the SM muscle. If topographic
Fig. 8. Pairwise comparison of EPSP amplitudes in adjacent SM motoneurons. To minimize the effects of topographic specificity 51 pairs of SMa and SMp motoneurons were formed from cells in each experiment which were located within 0.5 mm of one another. Differences in EPSP amplitudes between the cells of each pair (SMa-SMp) in response to stimulation of a particular homonymous (A) or heteronymous (B) nerve branch were averaged for each set of pairs. The means (+ S.E. of mean) of these differences are displayed here for each group of cell pairs. A shows the responses to stimulation of the homonymous nerve branches. The differences observed in cell pairs upon stimulation of SMa are not significant; yet the EPSP amplitudes still tend to be larger in the own-branch (SMa) cells. B illustrates significant differences in each group of cell pairs upon stimulation of the heteronymous nerve branches (0.05 < p < 0.10). * p < 0.025, ** p < 0.0005. These various differences in EPSP amplitudes also support a role for species specificity in determining the strength of both homonymous and heteronymous Ia projections.
specificity were to be a factor in establishing partitioned Ia effects in this case, larger EPSPs produced by a heteronymous nerve branch should be found for both cell groups in the caudal part of the motor nucleus. Fig. 9 shows that a contribution of topographic specificity was not evident in these heteronymous inputs to the SM motor nucleus.

Alternatively, the pattern of distribution of EPSP amplitudes due to stimulation of heteronymous nerve branches to the two SM cell groups indicated some form of species specificity. Stimulation of either the BFa or STd nerve branch produced larger EPSPs in one cell species throughout the length of the SM motor nucleus, the effect being most pronounced with the STd nerve branch. However, a similar effect was not clearly distinguishable with the BFp nerve branch.

The significant differences found in Table 3 were also present in the pairwise comparisons (Fig. 8B), suggesting a role for species specificity in determining the distribution of EPSPs for inputs from BFp and STd. Given two SM cells, an anterior and a posterior one in the same relative location, stimulation of the two "flexor" nerves, BFp and STd, produced larger EPSPs in the SMp (hip extension-knee flexion) motoneurons than SMa (hip extension) cells. In addition, the ability of BFa ("extensor") input to "recognize" SMa over SMp cells was significant in the pairwise comparisons (Fig. 8B; cf., Fig. 9), supporting the evidence in Table 3 of a difference in EPSP amplitudes due to stimulation of BFa.
Fig. 9. Rostrocaudal distribution of heteronymous EPSP amplitudes for SMa and SMP motoneurons. As in Fig. 6, average EPSP amplitudes due to stimulation of heteronymous (i.e., BFa, BFp, STd) nerve branches are plotted against location. Partitioned Ia effects are evident throughout the length of the SM motor nucleus upon stimulation of the nerve branches supplying BFa and STd, but not BFp.
Fig. 9. Rostrocaudal distribution of heteronymous EPSP amplitudes for SMa and SMp motoneurons.
Discussion

Partitioning of Ia EPSPs

The present results complete a sequence of studies that tested for the presence and extent of partitioning of monosynaptic Ia EPSPs in motor nuclei supplying cat hamstring muscles (i.e., BF: Botterman et al. 1983a; ST: Botterman et al. 1983b; and SM: present paper). As hypothesized, both BF and SM, which have regions capable of independent and different actions, show a partitioning of Ia EPSPs within their motor nuclei.

In both studies, the motoneuron sample was limited to largely putative type F cells. As a result, it is not known if the type S cells would receive similar partitioned effects (cf. Lucas & Binder, 1984; Lucas et al., 1984; Munson et al., 1984). At present, this issue remains open for further investigation (see Discussion section in Chapter 3).

Results on ST (Botterman et al., 1983b), which does not show partitioning, are also consistent with the hypothesis since this muscle would be at a functional disadvantage if its intramuscular actions were dissociated between its two in-series compartments (Bodine, Roy, Meadows, Zernicke, Sacks, Fournier & Edgerton, 1982).

Homonymous Ia EPSPs. In view of earlier statements in the influential report of Eccles & Lundberg (1958), it was necessary to test SM for a partitioning of Ia EPSPs. Although no data were presented,
they reported no differences in monosynaptic Ia projections to the SM motoneurons supplying the anterior and posterior heads of the muscle.

Contrary to this earlier report, we have found evidence for a partitioning of Ia EPSPs when comparing responses of motoneurons supplying the anterior and posterior heads of SM. However, having established partitioning, the question remains as to whether it is really an "intrahomonymous" effect or more analogous to the heteronymous connections between soleus (SOL), MG and LG (i.e., the three heads of the triceps surae muscle).

The extent of Ia partitioning between SOL, MG and LG motor nuclei was compared by Lucas & Binder (1984) to that within the MG motor nucleus. This comparison was accomplished by use of a "weighting factor" which expressed the strength of Ia connections from a given MG nerve branch to its "own" motoneurons relative to that of "other" motoneurons. (The weighting factor for each nerve branch was obtained by expressing the EPSP produced by the nerve branch being considered as a fraction of the EPSP produced by all branches. The weighting factor was then calculated as the ratio of the average fractional EPSP in the nerve branch's own motoneurons to that in its other motoneurons). The mean value of the index for nerve branches in MG was 1.8. Using the data of Eccles, Eccles & Lundberg (1957), weighting factors of 2.3, 2.7 and 3.1 were calculated for the nerves to MG, LG and SOL, respectively. Thus, Ia input was shown to distinguish to a greater degree between the motoneurons innervating the three heads of triceps surae than within the motoneuron pool innervating the single head of MG.
In the case of SM, our data do not permit an examination of the strength of Ia connections within the motor nucleus innervating only one head, but the average weighting factor between heads is 1.7. Therefore in terms of Ia projection patterns, the strength of partitioning between the two heads of SM is more similar to that seen within a single head (i.e., MG) of the triceps surae muscle (likewise our data on LG, Chapter 3, provide a weighting factor of approximately 1.8).

**Heteronymous Ia EPSPs.** The results of Table 3 indicate that partitioning of heteronymous Ia projections exists within the SM motor nucleus for the hamstring inputs. The partitioned effects from BFa were not as strong as those observed from BFP and STd. The other heteronymous inputs, GR and V, did not show localized Ia effects in the SM motor nucleus.

The lesser degree of partitioning that BFa produced suggests that both SM cell groups can be activated concomitantly with the extensors while SMP cells are engaged preferentially during knee flexion activity. The strong Ia partitioning effect produced by STd in SMP cells is consistent with the finding (Engberg & Lundberg, 1969) that the electromyographic (EMG) activity produced in SMP during locomotion mimics that of ST with predominate activity during knee flexion until higher speeds are reached (e.g., trot) at which time the EMG activity pattern becomes more similar to that seen in hip extensors (i.e., SMA, BFA, adductor femoris).

Neither GR nor Vasti Ia input showed a significant ability, based on the distribution and amplitude of monosynaptic EPSPs, to
distinguish between the two groups of SM motoneurons. According to Sherrington (1910) and Eccles & Lundberg (1958), GR would be considered predominately a knee flexor while the V would be knee extensors. Functional considerations would predict a stronger Ia connectivity pattern between GR and SMp, whose actions are hip extension and knee flexion. The vasti (knee extensors) would not be expected to give excitatory input to SMp cells due to their antagonistic knee flexor action. The absence of partitioned Ia inputs to support these functional trends within the SM motor nucleus may reflect inadequate sample sizes (48 and 76 cells, respectively) or the lack of major synergies between these muscles (cf. however, Zajac, 1984).

Topographic and Species Specificity

The extent to which topographic and species specificity are present in the motor nuclei of the hamstring muscle group varies as does the extent of partitioning of Ia EPSPs. Both may well contribute to the observed partitioning in BF (Botterman et al., 1983a). The absence of a significant topographic organization of ST motoneurons (Botterman et al., 1983b) was accompanied by a lack of partitioning of Ia EPSPs and a weak topographic pattern of Ia connections in the motor nucleus. In the SM motor nucleus, both topographic and species specificity may contribute to the partitioning of Ia EPSPs. Sufficient cord-to-muscle and muscle-to-cord somatotopicity exists for topographic specificity to play a role in establishing the partitioned effects. That species specificity plays a role in establishing partitioning is supported in the pairwise comparisons (a test for species specificity which is not
influenced by topographic specificity; Fig. 8). However, the magnitude of "recognition" by the SM nerve branches of their own cells in pairwise comparisons does not account for all of the observed partitioning of Ia EPSPs (cf. Table 2 and Fig. 8).
PARTITIONING OF MONOSYNAPTIC IA EXCITATORY POSTSYNAPTIC POTENTIALS IN THE MOTOR NUCLEUS OF THE CAT LATERAL GASTROCNEMIUS

Summary

1. Experiments were conducted to test the hypothesis that a partitioning of monosynaptic excitatory postsynaptic potentials (EPSPs) is present in motor nuclei supplying muscles with regions capable of different actions.

2. Intracellular recordings of synaptic potentials were made in lateral gastrocnemius (LG) motoneurons in anesthetized low-spinal cats. The effects were tested of stimuli (Group I range) to the four primary nerve branches of the LG nerve supplying muscle compartments LGm, LG1, LG2 and LG3 (terminology of English, 1984) and the nerve to a heteronymous muscle, soleus.

3. Stimulation of a given LG nerve branch produced monosynaptic Ia EPSPs of greater amplitude in "own-branch" motoneurons than "other-branch" cells. A significant partitioning of mean Ia EPSPs was found in three (LG1, LG2, LG3) out of the four homonymous pathways studied.

4. A double-normalization was performed to eliminate the contributions of differences in the number of Ia afferents in each nerve branch and for differences in cell type which might affect the amplitudes of the EPSPs between these four cell groups (e.g., differences in the number of cells supplying FF, FR and S muscle units).
This double-normalization confirmed that the partitioning of monosynaptic Ia inputs upon stimulation of LG2 and LG3 could not be attributed to these potential differences. In addition, the effects of LGm stimulation were found to be significantly greater in the LGm motoneurons as compared to the other cell groups.

5. Heteronymous input (from soleus) to the LG motor nucleus showed some partitioned effects. Motoneurons innervating compartment LG2 received larger EPSPs from soleus than did the cells supplying compartments LG1, LG3 and LGm.

6. The contributions of topographic specificity and species specificity in the establishment of these Ia afferent-motoneuronal connections were examined. Cell location sites within the spinal cord were consistent with topographic specificity making some contribution to the observed pattern of homonymous Ia connections. A more prominent role for species specificity was indicated by species-dependent differences in EPSP amplitude in pairs of LG motoneurons (e.g., LGm vs LG2) at similar rostrocaudal locations upon stimulation of a given homonymous or heteronymous nerve/branch.

Introduction

A partitioning of monosynaptic Ia EPSPs has been shown in motor nuclei supplying several cat muscles including two in the neck, biventer cervicis and splenius (BC and SP, respectively; Brink, Jinnai & Wilson, 1981) and three in the hindlimb, biceps femoris (BF; Botterman, Hamm, Reinking & Stuart, 1983a), medial gastrocnemius (MG; Lucas & Binder, 1984; Lucas, Cope & Binder, 1984; cf. also, Munson, Fleshman, Zengel &
Sypert, 1984) and semimembranosus (SM; Vanden Noven, Hamm & Stuart, 1983b). The muscle nerves supplying these muscles divide into primary muscle nerve branches which innervate discrete sub-volumes of muscle (i.e., neuromuscular compartments in BC, SP, BF and MG and separate muscle heads in SM). These neuromuscular compartments either are (SP: Bilotto, Schor, Uchino & Wilson, 1982; BF: Sherrington, 1910; SM: Engberg & Lundberg, 1969) or may be (BC, MG) capable of both combined and somewhat separate action.

Similar partitioning has not been observed in the motor nucleus of another cat hindlimb muscle, semitendinosus (ST; Nelson & Mendell, 1978; Botterman, Hamm, Reinking & Stuart, 1983b), in which its two muscle compartments are combined in an atypical in-series arrangement. Neither compartment of ST seems capable of independent activity (Murphy, Roy & Bodine, 1981), the presence of which might reduce the mechanical efficiency of the whole muscle (Botterman et al., 1983b; Bodine, Roy, Meadows, Zernicke, Sacks, Fournier & Edgerton, 1982).

The motor nucleus supplying the cat hindlimb muscle, lateral gastrocnemius (LG) was selected as the candidate to test the hypothesis that a partitioning of Ia EPSPs is present in motor nuclei supplying muscles with regions capable of different actions. Its muscle nerve has been shown to divide into four primary nerve branches which are supplied by four separate groups of LG motoneurons (Weeks & English, 1982). Each branch innervates an identified neuromuscular compartment (English & Letbetter, 1982a). In addition, the compartments have been shown to
exhibit varying patterns of activation during locomotion (English, 1984) and during natural postural movements with imposed perturbations (Russell, Dunbar, Rushmer, McPherson & Phillips, 1982).

It will be shown that partitioned Ia EPSPs are a prominent feature within the LG motor nucleus. This finding is discussed in relation to the ever-expanding literature on the partitioning hypothesis. Some preliminary data have been presented in abstract form (Vanden Noven, Hamm & Stuart, 1983b, 1984).

Methods

A complete account of the methods has been provided in the previous chapter. This account will highlight key features of the 18 LG experiments analyzed for this study.

The test muscle nerve (Fig. 10) and those used to assist the microelectrode search for motoneurons were cut and mounted on bipolar stimulating electrodes. To provide space in the leg bath for the stimulating electrodes, the BF, ST and SM-posterior (tibial head) muscles were removed in the thigh; as were the plantaris, medial and lateral gastrocnemius muscles in the leg.

The dissection of the LG-soleus nerve branches (English & Letbetter, 1982a) involved the detachment of the tendo calcaneus and reflection of three calf muscles (plantaris, medial and lateral gastrocnemius). The heteronymous nerve to soleus (SOL) was separated out of the nerve bundle leaving the four primary branches to LG (LGm, LG2, LG1 and LG3; terminology of English, 1984).
Primary Nerve Branch innervation Pattern

Muscle Compartment:     Muscle Head:
LGm         medial
LG2         prox. parts of lateral and intermediate
LG1         distal part of lateral
LG3         distal part of intermediate

Fig. 10. Innervation of the LG muscle. The schematic shows the innermost surface of the muscle and the four primary nerve branches which supply four discrete neuromuscular compartments within the three muscle heads (terminology of English, 1984).
A test for current spread (Fig. 11) of the stimulating pulses between the small LG nerve branches was used to verify that the current was activating afferents exclusive to the stimulated nerve branch. Adjacent branches were stimulated separately and then in pairs with a 0.5 ms delay. A delay of 0.5 ms (or 1.0 ms in some cases) was selected to ensure that any axons in the second branch which were stimulated by current spread from stimulation of the first branch would be refractory upon subsequent stimulation of their parent nerve branch. An average (256 sweeps) of the dorsal root volleys was made for each stimulation run. The average of the first dorsal root volley was subtracted from the average of the pair of dorsal root volleys. The subtracted dorsal root volley was compared to the volley produced by stimulation of the second nerve branch alone. Any differences, greater than the background noise of the volley, between these two waveforms was taken to indicate current spread. All EPSP data reported in the Results section were produced by stimulation of nerve branches in which no current spread was evident.

Own-branch EPSP records containing M spikes were corrected to the EPSP (see Fig. 12) by subtracting an "average" LG M-spike from each "M + EPSP" record (N=47, control preparations with sectioned dorsal roots; Hamm, Botterman, Reinking & Stuart, 1983).

In previous reports from this laboratory (Botterman et al., 1983a,b; Chapter 2 in present report) evidence for the potential contributions of topographic specificity and species specificity to the observed partitioning of Ia EPSPs was obtained by knowledge of the
Fig. 11. Test for spread of stimulation current between LG nerve branches. Adjacent nerve branches were examined for current spread by stimulating the branches separately or in pairs and averaging (256 sweeps) their dorsal root volleys. The average shown in A was produced by stimulation of the LG1 nerve branch. The B average (continuous line) was due to stimulation of the LG3 branch. The average displayed in C was produced by stimulation of LG1 followed 0.5 ms later by stimulation of LG3. At this interval, any axons in the LG3 nerve branch which were activated by current spread in the stimulation of LG1 would be refractory. The dashed line average in B shows the difference between the A and C averages. Any differences between this subtracted waveform and the continuous-line average in B was viewed as an indication of current spread.
peripheral intramuscular terminations of the test nerve branches and by measurements of the spinal-cord locations of both the tested motoneuronal cell bodies (assuming the microelectrode is in the cell's somata; see Burke & Rudomin, 1977) and the afferent entry zone of the stimulated nerve branches. The latter measurement (achieved at the conclusion of the experiment by stimulating the peripheral end of the cut dorsal roots) was not possible in this instance, because of electrotonic conduction of the volleys between the small LG nerve branches. However, some inferences on topographic specificity could be made despite the lack of this measurement.

Statistical analyses, including analysis of variance and post-hoc multiple range tests were performed using commercial statistical packages. Where appropriate, the Student's t and Student Newman-Keul (post hoc) tests were used to examine potential differences.

Results

Classification of LG motoneurons

Differences in the mean Ia EPSP amplitudes among the four LG cell groups (supplying separate neuromuscular compartments) might well be accounted for by significant differences in the numbers of type FF, FR and S (nomenclature of Burke, Levine, Tsairis & Zajac, 1973) motoneurons within each group, since Ia EPSP amplitude has been shown to increase in the order: FF<FR<S (Burke, 1981). An indirect estimate of the different motoneuron types was obtained by using rheobase and input resistance values to ascertain if the four LG groups were similar. In
barbiturate-anesthetized cats, Munson and his colleagues have shown for MG motoneurons that rheobase values >10 nA were found predominately in type F cells, whereas those <5 nA were from type S (Fleshman, Munson, Sypert & Friedman, 1981). Similarly, the division of rheobase by input resistance (nA/MΩ) provided an index for separation of the different motoneurons with FF>18>FR>7>S (Zengel, Reid, Sypert & Munson, 1985).

The present population of cells on which reliable measurements were made showed predominately low values for input resistance (89.5% <1.0 MΩ; 2% >1.5 MΩ). Rheobase values were distributed over a relatively wide range, 64% with values >10 nA and only 11.3% with values <5 nA. As shown in Table 4, the mean values of input resistance, rheobase and rheobase/input resistance were not significantly different among the four LG cell groups. These values also suggested that the sampled cells included only 10-12% type S motoneurons. This percentage is somewhat lower than the 17% SO fibers (supplied by type S motoneurons) reported for the fiber-type distribution of LG in the histochemical study of Ariano, Armstrong & Edgerton (1973). In general, it can be anticipated that the innervation ratio of type S motor units in cat hindlimb muscles will be similar to that of type FR units and somewhat smaller than that of type FF units (for review: McDonagh, Binder, Reinking & Stuart, 1980; Burke, 1981). Consequently, the percentage of type S motoneurons should be somewhat greater than 17%, according to Ariano et. al. (1973).

English & Letbetter (1982b) examined the fiber-type distributions in the four muscle compartments of LG. Type SO fibers
Table 4. Intrinsic characteristics of LG motoneurons.

<table>
<thead>
<tr>
<th></th>
<th>LGm</th>
<th>LG2</th>
<th>LG1</th>
<th>LG3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Resting potential</strong></td>
<td>65.4 ±1.5</td>
<td>64.8 ±0.89</td>
<td>63.6 ±1.0</td>
<td>65.5 ±0.94</td>
</tr>
<tr>
<td>(mV) 50-80</td>
<td>(24)</td>
<td>(66)</td>
<td>(56)</td>
<td>(56)</td>
</tr>
<tr>
<td><strong>Input resistance</strong></td>
<td>0.48 ±0.06</td>
<td>0.59 ±0.07</td>
<td>0.50 ±0.05</td>
<td>0.47 ±0.04</td>
</tr>
<tr>
<td>(MΩ) 0.16-2.0</td>
<td>(20)</td>
<td>(38)</td>
<td>(36)</td>
<td>(39)</td>
</tr>
<tr>
<td><strong>Rheobase</strong></td>
<td>15.3 ±1.55</td>
<td>13.9 ±1.57</td>
<td>16.2 ±1.44</td>
<td>15.4 ±1.43</td>
</tr>
<tr>
<td>(nA) 2.9-29</td>
<td>(20)</td>
<td>(38)</td>
<td>(37)</td>
<td>(40)</td>
</tr>
<tr>
<td><strong>Rheobase/Input</strong></td>
<td>54.3 ±11.4</td>
<td>41.1 ±6.1</td>
<td>52.8 ±9.5</td>
<td>51.2 ±7.6</td>
</tr>
<tr>
<td>resistance (nA/MΩ)</td>
<td>6.5-198</td>
<td>2.2-178</td>
<td>4.2-300</td>
<td>4.3-172</td>
</tr>
</tbody>
</table>

Values expressed as mean ± S.E. of mean followed by the range of values and number of cells (in parentheses).
accounted for 2% of the fibers in LGm, 17% in LG2, 12% in LG1 and 24% in LG3. Comparing our cells with rheobase values <5 nA (presumably type S), we found 5%, 18%, 5% and 10% respectively. This mismatch in percentage values suggests that the number of motoneurons making up our LG1 and LG3 cell groups is biased towards the large (type F) cells.

According to the histochemical data of English & Letbetter (1982b), we had expected to see some differences in the intrinsic properties of the LG motoneurons which reflected their observed differences in fiber-type distributions. However, our population of LG motoneurons appears to be dominated by type F cells overall as well as within the individual cell groups.

The Test for Partitioning of Ia EPSPs

Figs. 12 and 13 provide examples of Ia EPSPs in individual LG motoneurons due to stimulation of LG nerve branches supplying one of the neuromuscular compartments. As shown here, the pattern of EPSP amplitudes was found to vary upon stimulation of the different nerve branches; own-branch EPSPs were usually larger than the other-branch EPSPs.

The test for partitioning of Ia EPSPs was made by comparing the monosynaptic Ia EPSPs in the four LG cell groups produced by stimulation of the nerve inputs. As shown in Table 5, mean EPSP amplitudes varied among the four LG cell groups upon stimulation of the five inputs. The differences in mean EPSP amplitude among the four cell groups were significant upon stimulation of the LG2, LG1 and LG3 branches.
Fig. 12. Composite homonymous EPSPs recorded in LGm and LG2 motoneurons. EPSPs produced by stimulation of the four LG nerve branches are displayed in a single LGm cell (left) and a LG2 cell (right). Below each intracellular trace is the corresponding dorsal-root recording. For some own-branch EPSPs, hyperpolarizing current was injected, as necessary, into the cells to block the antidromic response to the "M spike + EPSP". The original records are indicated by continuous lines, while the record which has been corrected for the M spike is shown by dotted lines. A tendency can be seen in this and Fig. 13 for own-branch EPSPs to be the largest.
Fig. 13. Composite homonymous EPSPs recorded in LG1 and LG3 motoneurons. For description, see legend to Fig. 12.
Table 5. Amplitudes of mean composite monosynaptic Ia EPSPs evoked by stimulation of LG muscle nerve branches and SOL nerve.

<table>
<thead>
<tr>
<th>Branch stimulated</th>
<th>LGm</th>
<th>LG2</th>
<th>LG1</th>
<th>LG3</th>
<th>SUMMARY</th>
</tr>
</thead>
<tbody>
<tr>
<td>LGm</td>
<td>0.31 ±0.06</td>
<td>0.18 ±0.03</td>
<td>0.24 ±0.05</td>
<td>0.29 ±0.05</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(24)</td>
<td>(54)</td>
<td>(51)</td>
<td>(52)</td>
<td></td>
</tr>
<tr>
<td>LG2</td>
<td>0.41 ±0.08</td>
<td>1.05 ±0.13</td>
<td>0.66 ±0.06</td>
<td>0.65 ±0.07</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(24)</td>
<td>(66)</td>
<td>(55)</td>
<td>(55)</td>
<td></td>
</tr>
<tr>
<td>LG1</td>
<td>0.30 ±0.05</td>
<td>0.42 ±0.04</td>
<td>0.69 ±0.07</td>
<td>0.54 ±0.07</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(24)</td>
<td>(62)</td>
<td>(56)</td>
<td>(55)</td>
<td></td>
</tr>
<tr>
<td>LG3</td>
<td>0.26 ±0.05</td>
<td>0.49 ±0.07</td>
<td>0.59 ±0.07</td>
<td>0.76 ±0.07</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(24)</td>
<td>(66)</td>
<td>(56)</td>
<td>(56)</td>
<td></td>
</tr>
<tr>
<td>Nerve stimulated</td>
<td>SOL</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.43 ±0.07</td>
<td>1.69 ±0.20</td>
<td>1.02 ±0.11</td>
<td>0.92 ±0.09</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(19)</td>
<td>(53)</td>
<td>(53)</td>
<td>(54)</td>
<td></td>
</tr>
</tbody>
</table>

EPSP values (in mV) expressed as mean ± S.E. of mean (with number of cells examined in parentheses). Comparisons should be limited to the effects of a given nerve branch on the four cell groups to avoid any differences in amplitude due to a variable number of afferents between the nerve branches. Analysis of variance showed significant differences between mean EPSPs upon stimulation of the LG2, LG1 and LG3 (not LGm) nerve branches and the SOL nerve. Significant differences (* p<0.05; ** p<0.001) between own-branch motoneurons versus other-branch cells based on post-hoc test (Student Newman-Keuls) are reported in summary column. Significant differences due to stimulation of the SOL nerve are also shown.
Stimulation of the LGm branch produced EPSPs of similar amplitude in the four cell groups.

The mean amplitudes of own-branch EPSPs were greater in the above three cases as compared to those of other-branch EPSPs. Afferent input from the LG2 branch produced larger EPSPs in LG2 cells as compared to LGm, LG3 and LG1 cells. EPSPs produced in LG1 cells upon stimulation of the LG1 branch were significantly greater from those in LGm and LG2 cells, but not in LG3 cells. Similarly, stimulation of the LG3 branch produced significantly larger EPSPs in LG3 cells as compared to LGm and LG2 cells, but not to LG1 cells.

In addition, Table 5 shows evidence for a partitioning of heteronymous Ia EPSPs. Stimulation of the SOL nerve produced significantly larger EPSPs in LG2 motoneurons as compared to the LGm, LG1 and LG3 cells. The effect of SOL stimulation onto LG1 cells also was greater than that to LGm cells.

Comparisons limited to the effects of a given nerve branch onto the four cell groups avoids differences due to variations in the number of afferents for a given nerve branch. However, the mean EPSP differences observed may also have been due to variations in cell type (i.e., innervating FF, FR and S) between the cell groups, which were possibly too subtle to be brought out by measurements of the cells' intrinsic characteristics (Stuart & Enoka, 1983; see their Table 17-2).

A normalization procedure (Botterman et al., 1983a) was used to factor out possible variations in cell type. Each cell's EPSP produced by stimulation of a single branch was divided by the sum of the EPSPs.
contributed by the four LG branches which supplied that cell. The division of these quantities, both of which depend on motor unit type, should therefore provide a normalized EPSP which is independent of cell type. The procedure was based on the fact that motor unit type should be reflected by the EPSP amplitude contributed to a given motoneuron by the total Ia afferentation of the test nerve branches. The results of this normalization suggested that partitioning may exist in all four homonymous cases. The significant differences found in Table 5 were maintained. In addition, stimulation of the LGm nerve branch was found to produce significantly larger EPSPs in LGm cells as compared to LG2, LG1 and LG3 (p<0.001).

A further concern was over the variable sizes of nerve branches between experiments and the sampling bias that this variation could produce due to the tendency to sample motoneurons from the nerve branch with the greatest number of Ia afferents in any one experiment. This concern prompted us to use a double-normalization procedure (Vanden Noven, Hamm & Stuart, 1983b). The goal of this procedure was to eliminate the effects on EPSP amplitude of variations in cell properties (e.g., cell type) and of variations in afferent content between the LG nerve branches. The EPSPs for a given nerve branch-cell group combination were normalized as follows

\[
\text{nEPSP} = \frac{\text{EPSP}}{\text{EEPSP}} \cdot \frac{\text{DRV}}{\text{EDRV}}
\]

The sums were taken for the EPSPs and dorsal-root volleys (DRVs) over all nerve branches (i.e., LGm, LG2, LG1, LG3). In addition to the
previous assumption stated for the EPSP-normalization, this procedure involved two assumptions. 1) Each DRV amplitude was considered proportional to the number of Ia afferents in that nerve branch. 2) Each EPSP amplitude would equal the product of the number of Ia afferents and the mean single-fiber EPSP amplitude for a given nerve branch-single cell combination.

The natural log of these values was calculated in order to normalize this distribution of ratios. The averages of the transformed values are presented in Table 6. The significant differences found in Table 5 are present with the exception of LG1 effects, although a tendency still exists for own-branch EPSPs to be largest. In addition, this double-normalization showed LGm to produce significantly larger EPSPs in LGm cells as compared to the other LG cell groups. This effect had been brought out previously by the EPSP-normalization procedure.

The normalization procedures were useful in these experiments as controls to verify to what extent the differences observed could be accounted for by differences in cell type and/or afferent number. These procedures brought out the significant effects upon stimulating LGm, a very small nerve branch, onto its own cells which are reported to be primarily type FF (English & Letbetter, 1982b). Both the smaller number of afferents in the LGm branch and predominance of type FF cells in the LGm group would result in smaller EPSPs as compared to effects from larger nerve branches (greater number of Ia afferents) onto cells of mixed type.
Table 6. Mean double-normalized composite monosynaptic Ia EPSPs evoked by stimulation of LG nerve branches displayed as Ln values.

<table>
<thead>
<tr>
<th>Branch stimulated</th>
<th>LGm</th>
<th>LG2</th>
<th>LG1</th>
<th>LG3</th>
<th>SUMMARY</th>
</tr>
</thead>
<tbody>
<tr>
<td>LGm</td>
<td>+0.47 ±0.17</td>
<td>-0.45 ±0.12</td>
<td>-0.15 ±0.11</td>
<td>-0.13 ±0.11</td>
<td>LGm&gt;LG2**</td>
</tr>
<tr>
<td></td>
<td>(20)</td>
<td>(40)</td>
<td>(36)</td>
<td>(40)</td>
<td>LGm&gt;LG1**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>LGm&gt;LG3**</td>
</tr>
<tr>
<td>LG2</td>
<td>-0.11 ±0.08</td>
<td>+0.34 ±0.07</td>
<td>+0.06 ±0.07</td>
<td>+0.04 ±0.07</td>
<td>LG2&gt;LGm**</td>
</tr>
<tr>
<td></td>
<td>(22)</td>
<td>(64)</td>
<td>(55)</td>
<td>(54)</td>
<td>LG2&gt;LG1**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>LG2&gt;LG3**</td>
</tr>
<tr>
<td>LG1</td>
<td>-0.11 ±0.16</td>
<td>-0.30 ±0.10</td>
<td>-0.01 ±0.08</td>
<td>-0.12 ±0.11</td>
<td>LG3&gt;LGm**</td>
</tr>
<tr>
<td></td>
<td>(23)</td>
<td>(62)</td>
<td>(55)</td>
<td>(52)</td>
<td>LG3&gt;LG2**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>LG3&gt;LG1**</td>
</tr>
<tr>
<td>LG3</td>
<td>-0.50 ±0.20</td>
<td>-0.37 ±0.09</td>
<td>-0.36 ±0.08</td>
<td>-0.09 ±0.09</td>
<td>LG3&gt;LGm**</td>
</tr>
<tr>
<td></td>
<td>(21)</td>
<td>(55)</td>
<td>(52)</td>
<td>(55)</td>
<td>LG3&gt;LG2**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>LG3&gt;LG1**</td>
</tr>
</tbody>
</table>

Mean natural log values of double-normalized EPSPs + S.E. of mean are presented (with number of cells examined in parentheses). Double-normalization procedure explained in the text. Statistical analysis performed as in Table 2 (comparison again limited to effects of a given nerve branch onto the four cell groups). Analysis of variance showed significant differences upon stimulation of LGm, LG2 and LG3, but not LG1. Significant differences (post-hoc test) between own-branch motoneurons versus other-branch cells are summarized in the right column (** p<0.001). The appropriateness of these analyses were checked by examining the final distribution of values and by performing a propagation of errors analysis. The distribution was a reasonable approximation of a Gaussian distribution and the propagation of errors analysis showed that measurement error made only a minor (<10%) contribution to the variability of these values.
In addition, the differences observed upon stimulation of LG1 in the "raw" data and with the EPSP-normalization procedure were not present following the double-normalization procedure. This discrepancy suggests that the sample of LG1 cells contains a number of cells from experiments in which the nerve branch was quite large. In this case, the own-branch nerve size would account partially for the greater EPSP amplitudes in the LG1 cells by virtue of the increased number of Ia afferents. The effect of LG1 stimulation onto its own cells may still be larger as compared to the other LG cell categories, but our present sample does not permit a conclusive statement.

Topographic and Species Specificity in the LG Motor Nucleus

Histograms giving the spinal-cord locations of the four categories of tested cells (i.e., LGm, LG1, LG3 and LG2) are shown in Fig. 14. An analysis of variance revealed that their mean locations were different (p<0.001). This difference was based on the mean location of LGm cells being more rostral than both that of the LG2 cells (post-hoc multiple range test; p<0.001) and that of the LG3 cells (same post-hoc test; p<0.05).

These differences in mean cell location share some similarities with the findings of Weeks & English (1982). Despite extensive overlap, they found a significant topographic-like organization in the order LGm, LG2, LG1, LG3, from rostral to caudal. The more caudal position of the presently studied LG2 cells may reflect a greater sampling of LG2 cells from the caudal part of its pool. Conceding this difference, the present population of LG motoneurons revealed a topographic organization.
Fig. 14. Spinal-cord location of LG motoneurons. Rostrocaudal locations (with arrows at means) for LGm, LG2, LG1 and LG3 cell groups are presented relative to the L6-L7 dorsal-root junction. The sample included 202 cells from 18 experiments. Mean location of LGm cells was significantly more rostral than the LG2 and LG3 means (statistics in text).
Fig. 14. Spinal-cord location of LG motoneurons.
which is consistent with a possible contribution from topographic specificity in the establishment of the partitioned Ia EPSP effects.

Fig. 15 shows the relationship between EPSP amplitude and rostrocaudal location of motoneurons in the four LG cell groups upon stimulation of the homonymous nerve branch, LG2, and the heteronymous nerve, SOL. A similar analysis was performed for the other homonymous nerve branches, but with equivocal results.

The LG2 graphs in Fig. 15 show no clear pattern between EPSP amplitude and cell location. However, the amplitudes are greater in LG2 cells throughout the length of the nucleus, indicating that species specificity (LG2 Ia-afferents onto LG2 motoneurons) plays an important role in determining these EPSP amplitudes.

The SOL graphs are suggestive of a rostrocaudal EPSP dependence for LG2 and possibly LG1 cells, but the results are far from conclusive. Interestingly, the LG2 nerve branch and the SOL nerve share a topographic relationship by dividing from a common nerve trunk following its separation from the whole LG-SOL nerve bundle. If topographic specificity were to be a factor, i.e., the distribution of EPSPs were determined by entry point of the afferents, larger EPSPs should be found for all cell groups in the same part of the motor nucleus. Although such topographic effects were absent, the SOL effect on LG2 cells suggests a contribution of species specificity (see also Table 5).

The pairwise comparisons in Fig. 16 provides an analysis in which potential effects due to topographic specificity are eliminated. The difference between the EPSP amplitudes upon stimulation of a given
Fig. 15. Relationship between EPSP amplitude and spinal-cord location of the tested LG cells. Graphs show rostrocaudal distributions of homonymous EPSP amplitudes due to stimulation of a homonymous nerve branch, LG2, and the heteronomous nerve, SOL. LG cells were grouped in 1 mm bins according to their rostrocaudal distance from the L6-L7 junction. Within each bin, average EPSP amplitudes due to stimulation of the LG2 nerve branch (left) and the SOL nerve (right) are plotted against location. The number of cells contributing to the averages is indicated below each bin. See text for explanation of how this analysis revealed a prominent role for species specificity in the partitioning of LG2 and SOL EPSPs in the LG motor nucleus.
Fig. 16. Pairwise comparisons of EPSP amplitudes in adjacent LG motoneurons. To minimize the effects of topographic specificity, 74 pairs of LG motoneurons from the same experiment were formed, with each pair located within 0.5 mm of one another. Differences in EPSP amplitudes between the cells of each pair in response to stimulation of a particular homonymous nerve branch or the heteronymous (SOL) nerve were averaged for each set of pairs. The means (± S.E. of mean) of these differences (*, p[0.05) are displayed here for each group of cell pairs. Similar analysis of the normalized EPSP data showed an additional pair (+, p[0.05) to be significant and others to be borderline (? , 0.05|p[0.10). This analysis also revealed a prominent role for species specificity in the partitioning of Ia EPSPs in the LG motor nucleus.
Fig. 16. Pairwise comparison of EPSP amplitudes in adjacent LG motoneurons.
nerve branch was examined in pairs of LG motoneurons located within 0.5 mm of each other. A tendency was observed for a given nerve branch to provide a larger EPSP to its own cell over the other-branch cell. This tendency was significant (p<0.05; Student's t test) in 6 of 12 cases. A similar analysis of these cell pairs was performed in the EPSP-normalized and double-normalized data to ensure that the differences observed were not due to differences in cell type or variations in the number of Ia afferents in each nerve branch. The significant effects observed in the pairwise mean EPSP data were maintained in both normalization data sets. In addition, the differences between five other pairs were brought out as significant (p<0.05; 2 pairs) or of borderline (0.05>p<0.10; 3 pairs) significance. The ability of a given nerve branch to "recognize" its own cell over the other-branch cell at the same rostrocaudal location supports a prominent role for species specificity in determining the efficacy of the observed Ia projections.

Discussion

This and some other recent studies have resulted from a renewed interest in the possibility that the nervous system can control separate regions of a single muscle. To stimulate such effort, this laboratory proposed in 1977 the "partitioning" hypothesis (Binder, Smith, Reinking & Stuart, 1977; Stuart & Binder, 1977). It suggested an association between the interactions of motor units and selected muscle receptors within the muscle (sensory partitioning; Binder et al., 1976) and interactions between muscle-receptor afferents and motoneurons within
the spinal cord (central partitioning). At the same time, similar hypotheses from a more theoretical approach were proposed by Windhorst (1978a,b).

Interestingly, precedents to these hypotheses may date back to the early 1900's. Sybil Cooper was reported to have shown a long-sustained interest in partitioned effects (Porter, personal communication). However, no published accounts are available of her findings and viewpoints. Her early work with Denny-Brown and Sherrington (1926) on fractionated reflex responses of single muscles (see also Camis, 1910) may well have provided the stimulus for this reported interest.

The first demonstration of an intramuscular localization of the stretch reflex was the Ph.D. research work of Cohen (1953). In his literature review, Cohen cited his professor's view (Fulton, 1949) that the stretch reflex might be so finely localized as to serve a single muscle fascicle. Although erroneous, since a motor unit's territory was subsequently shown to be more dispersed than a single fascicle (Burke, 1981), this view apparently motivated Cohen's classic (1953, 1954) work on the stretch reflex. In 1955, Lloyd, Hunt & McIntyre described an electrophysiological attempt to test the possibility that "the transmitter potentiality of a given monosynaptic reflex afferent fiber with respect to the motoneurons supplied is related in some way to anatomical propinquity of receptor origin and effector termination within the muscle of the synergic unit." However, apparently for technical reasons, the results were confined to heteronymous
comparisons, and research on this topic appears to have been abandoned until its revival by this laboratory and Windhorst in the late 1970's (for review: Binder & Stuart, 1980).

Topographic and Species Specificity

Findings such as the present ones on partitioned Ia effects within a spinal motor nucleus promote consideration of the underlying mechanisms which determine these Ia afferent-motoneuronal connections (Lichtman, Jhaveri & Frank, 1984). If the dendrites and cell bodies of motoneurons are spatially segregated in the spinal cord and if the afferent fibers only project to certain locations in the cord then a proper matching (topographic specificity) would occur between own-branch afferents and motoneurons. Alternatively, if the own-branch motoneurons intermingle with those of other-branch cells then a partitioned distribution of EPSPs would have to result from some species-specific effect which may have occurred during development (Lichtman et al., 1984) or possibly come about during post-natal usage.

In the LG motor nucleus, our cell-location data are consistent with a contribution from topographic specificity to the observed partitioned Ia effects. However, other evidence (particularly that in Figs. 15-16) supports a major role for species specificity.

These findings compliment those from a variety of studies that have tested, in adult animals, for the relative importance of topographic specificity and/or species specificity in the establishment of monosynaptic Ia connections with motoneurons. Initially these factors were examined within motor nuclei supplying different muscles
Encapsulation of this work for the different motor nuclei suggests that the dominance of one factor over the other can vary or even reverse. However, none of these studies on the adult animal have provided information on why one or the other of these mechanisms should predominate in a given motor nucleus. Since the issue appears to be a developmental one, further studies on the adult animal may be of limited usefulness (cf. however, Lichtman et al., 1984; Lichtman & Frank, 1984).

Current Status of the Partitioning Hypothesis

Table 7 summarizes the current evidence for a partitioning of monosynaptic Ia EPSPs and an intramuscular localization of two proprioceptive reflexes, the stretch reflex and a "muscle-tap" reflex. A partitioning of Ia EPSPs has been found in motor nuclei supplying six muscles, an exception being ST, which is structurally atypical for a hindlimb muscle. Intramuscular localization of the stretch reflex has been shown in three muscles, but, in another muscle no localization was reported for the tap reflex (similarly, an abstract has reported no localization of this reflex in two other muscles). Evaluation of these various results involves consideration of motoneuron type and activity. In addition, testable models of the partitioning hypothesis are considered, as well as their relation to the "task group" hypothesis of Loeb and his colleagues (Loeb, 1984).
Table 7 presents results from studies which employed different experimental paradigms to test somewhat different versions of the partitioning hypothesis. The results of the present study are directly comparable to the other Ia-EPSP studies in Table 7 in which Ia input was characterized in relation to primary branches of the muscles' nerve (i.e., Brink et al., 1981; Botterman et al., 1983a,b; Lucas & Binder, 1984; Lucas et al., 1984). Less direct is the comparison of these various results to the Ia-EPSP study from Munson's laboratory, in which Ia input was characterized by a physiological test of the extent to which Ia afferent discharge was influenced by contraction of single motor units (Munson et al., 1984). In general, the strength of this type of mechanical coupling is strongest when the motoneurons and the receptors occupy the same neuromuscular compartment, but exceptions have also been noted (Cameron et al., 1981; Osborn & Binder, 1981). Perhaps these exceptions are sufficient to explain why the Table 7 results from Munson's laboratory differ from those obtained in Binder's laboratory (Lucas & Binder, 1984; Lucas et al., 1984), even though the same test muscle (cat MG) was used.

A second caveat concerning Table 7 is that only its Ia-EPSP studies involve exclusive consideration of the monosynaptic Ia pathway to motoneurons. The stretch reflex and the muscle-tap reflex are mediated only in part (and to differing degrees) by this pathway. In addition, the polysynaptic contributions to these two reflexes also differ from one another, in relation to the relative contribution of Ia and other species of afferent input (Matthews, 1984; Burke et al., 1983,
Despite these cautions, all of the studies summarized in Table 7 test hypotheses that fall under the rubric of "partitioning" to the extent that they seek a spinal correlate to peripheral relationships (anatomical and/or physiological) between motor units and muscle receptors.

**Motoneuron Type**

Table 7 shows that this laboratory has demonstrated the presence of partitioned Ia effects in motor nuclei supplying the BF, SM and LG muscles. In all three cases, the studied motoneurons were limited largely to the putative type F (FF+FR) population. Binder's laboratory has recently provided evidence of a similar result for the putative type F population of the MG nucleus (Lucas & Binder, 1984; Lucas et al., 1984). However, in addition, their work provided clear evidence that partitioned Ia effects were less obvious in the putative type S motoneuron population, which is more prevalent in the MG than in the BF, SM and LG motor nuclei.

The findings of Lucas & Binder (1984) and Lucas et al., (1984) have been supported, in part, by a recent study from Munson's laboratory on type-identified motoneurons in the same motor nucleus. Another version of the partitioning hypothesis was tested, that "motor unit-muscle spindle pairs that are coupled strongly mechanically will also be coupled strongly synaptically" (Munson, Fleshman, Zengel & Sypert, 1984; cf. Binder & Stuart, 1980). This hypothesis was supported for the FF population of motoneurons (albeit weakly) and refuted for the FR and S populations.
Table 7. Current evidence concerning partitioning of Ia EPSPs and intramuscular localization of proprioceptive reflexes.  

<table>
<thead>
<tr>
<th>Test</th>
<th>Species</th>
<th>Motor Nucleus/Muscle</th>
<th>Partitioning/ Localization</th>
<th>Reference(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(state)</td>
<td>(+ or -)</td>
<td></td>
</tr>
<tr>
<td><strong>Ia EPSP</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cat</td>
<td>Spinalum</td>
<td>(intact, brain, unanesthetized)</td>
<td>Mediator cerevisae (991)</td>
<td>Brink et al., 1981</td>
</tr>
<tr>
<td></td>
<td>Biceps femoris</td>
<td>(low-spinal, unanesthetized)</td>
<td>Semimembranosus (711)</td>
<td>Botterman et al., 1983a</td>
</tr>
<tr>
<td>cat</td>
<td>Medial gastrocnemius</td>
<td>(intact, brain, unanesthetized)</td>
<td>☐</td>
<td>Lucas &amp; Rinder, 1994</td>
</tr>
<tr>
<td></td>
<td>Semimembranosus</td>
<td>(low-spinal, unanesthetized)</td>
<td>☐</td>
<td>Lucas et al., 1994</td>
</tr>
<tr>
<td></td>
<td>Lateral gastrocnemius</td>
<td>(high-spinal, unanesthetized)</td>
<td>☐</td>
<td>Munson et al., 1994</td>
</tr>
<tr>
<td><strong>Proprioceptive Reflexes</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cat</td>
<td>Rectus femoris</td>
<td>(decererate, unanesthetized)</td>
<td>☐</td>
<td>Cohen 1953, 1954</td>
</tr>
<tr>
<td></td>
<td>Vastus intermedius</td>
<td>(decererate, unanesthetized)</td>
<td>☐</td>
<td>Cohen 1954</td>
</tr>
<tr>
<td>cat</td>
<td>Spinalum</td>
<td>(decererate, unanesthetized)</td>
<td>☐</td>
<td>Blott et al., 1982</td>
</tr>
<tr>
<td></td>
<td>Vastus intermedius</td>
<td>(decererate, unanesthetized)</td>
<td>☐</td>
<td>Hore et al., 1983</td>
</tr>
<tr>
<td>human</td>
<td>Tibialis anterior</td>
<td>(intact, brain, unconscious)</td>
<td>☐</td>
<td>Nelson et al., 1984</td>
</tr>
</tbody>
</table>

1 Studies presented in order of their publication. Reflex groups includes four on the stretch reflex (Cohen, 1953, 1954; Blott et al., 1982; Hore et al., 1983) and one on the muscle-tap reflex (McKernan et al., 1963).

2 50 fiber-type percentages taken from: Ariano et al. (1993); cat biceps femoris, medial and lateral gastrocnemius, rectus femoris, semimembranosus, semitendinosus, rectus intermedius, Johnson et al. (1992); human tibialis anterior; McKernan & Stromberg (1992); cat biventer cervicis and splenius.

3 (+) = present; (-) = absent.

4 ☐ = is for putative F (Lucas & Binder, 1998; Lucas et al., 1994) or weakly a for type-identified FF population (McKernan et al., 1994). The same studies indicated for putative S and type-identified F and S electromyograms, respectively.

5 An abstract is available (Smith et al., 1981) which suggests a lack of intramuscular localization of the muscle-tap reflex in two human jaw-clenching muscles, masseter (25% 50 fibers, Hensel et al., 1972) and temporalis (1921, Hensel et al., 1972).
If the finding of a lack of partitioned effects in a selected population of motoneurons of the cat MG nucleus generalize to the low threshold motoneurons of other motor nuclei, then the original focus of the partitioning hypothesis is called into question. Originally, the emphasis was on how partitioning might contribute to the control of low-force and finely-graded contractions (Botterman, Binder & Stuart, 1978; Binder & Stuart, 1980) which, for many movements, appear to involve usage of type S motoneurons (Burke, 1981; Henneman & Mendell, 1981; Stuart & Enoka, 1983).

The five published studies that have tested for an intramuscular localization of proprioceptive reflexes (Table 7) have not resolved the issue of the relationship between partitioning and motoneuron type. In all five cases, the low forces developed by the test muscles suggest that tested reflex outputs were brought about by the engagement of type S motoneurons (Stuart & Enoka, 1983). However, in four of the studies, an intramuscular localization of the reflex was observed (cat RF, VI and SP muscles), while in the fifth study, an analogous localization was absent (tibialis anterior, TA; see also Table 7 footnote abstract on human masseter, MA and temporalis, TE).

Further complicating this motoneuron type issue is the inability to account for the differences in Table 7 on the basis of the relative number of type S0 fibers in the test muscle. This expectation is prompted by the correlation between the relative number of type S0 fibers in a muscle with the number of type S motoneurons in the motor nucleus (Burke, 1981). For example, Table 7 shows that partitioned
effects were absent in the study on the human TA muscle, which has a high (73%) percentage of SO fibers, but present in the cat VI muscle which has an even higher representation (98%) of these fibers. Similarly, partitioned effects were shown in published studies on the cat BF and SM muscles which have low percentages of type SO fibers (12 and 10%, respectively), but described as absent in the abstract of the study on the human MA muscle (Smith et al., 1983), which is composed of 26% type SO fibers, a relatively low value for a human muscle (see Table 4 in Johnson, Polgar, Weightman & Appleton, 1973).

In summary, the issue of partitioning in relation to motoneuron type is still an open one. However, the existing data base suggests that motoneuron type alone can not explain why partitioning is present in some motor nuclei and absent in others.

Motoneuron Activity

The presented results are in keeping with the EMG evidence from two laboratories that motoneurons supplying different parts of the LG muscle can exhibit somewhat different activity patterns. First, Rushmer's laboratory (Russell et al., 1982) has reported that when the conscious cat is subjected to postural perturbations (e.g., horizontal translations of the body, unloading of the hindlimb), the three tested LG neuromuscular compartments (LGm, LG1 and LG3) could be activated independently, and, in a manner which seemed appropriate for the postural task.

In a second study by English (1984) on the treadmill locomotion of conscious cats, there was evidence that the four neuromuscular
compartments in LG exhibited subtly different activation patterns. These patterns were often consistent with the orderly recruitment phenomenon (Stuart & Enoka, 1983). For example, the LG3 compartment, which is composed of the highest percentage of type SO fibers (23%) in the LG muscle, showed the greatest amount of activity at slow stepping speeds which are associated with small ankle-extensor forces (Walmsley, Hodgson & Burke, 1978). Conversely, the LGm compartment, which is composed predominately of type FG fibers (82%) displayed relatively greater activity at higher stepping speeds associated with higher muscle forces.

Upon occasion in this second study (English, 1984), the activation pattern of the LG compartments was not consistent with the orderly recruitment phenomenon. For example, the LGm compartment sometimes displayed substantial EMG activity at slow stepping speeds. In these instances, it is conceivable that the plane of force development by the LG muscle differed subtly, a change that has been shown to alter motor-unit recruitment order (e.g., Denny-Brown, 1949; Thomas, Schmidt & Hambrecht, 1978; Desmedt & Godaux, 1981). If the finding of recruitment reversals by English (1984) on the LG muscle can be shown to generalize to other muscles, such as BF and SM, then it might suggest a functional significance to the partitioned Ia effects even if their distribution is restricted largely to type F motoneurons.

Even though English (1984) studied the same four neuromuscular compartments whose motoneurons were tested in this study, the different activation patterns he observed can not be assumed to have
been brought about by partitioned Ia effects in the motor nucleus. Similarly, demonstration of partitioned effects attributable to a primary afferent system need not generalize to other afferent systems (viz., Stuart & Enoka, 1983), nor to descending systems controlling motoneuronal discharge. For example, the SP muscle exhibits an intramuscular localization of the stretch (cervicocollic) reflex (Bilotto, Schor, Uchino & Wilson, 1982; Ezure, Fukushima, Schor & Wilson, 1983) and a partitioning of Ia effects in its motor nucleus (Brink et al, 1981). However, it exhibits no analogous intramuscular localization during its reflex activation by optokinetic stimuli (Wilson, Precht & Dieringer, 1983). It would be of interest to test the SP motor nucleus for partitioned EPSP effects from the corticospinal tract, since it appears to control partitioning of facial muscle activity during speech (Abbs, Gracco & Blair, 1984) and, of more direct relevance, since the relative strength of monosynaptic corticospinal EPSP effects on motor nuclei supplying various forelimb muscles in the baboon have been shown to be paralleled by the relative strength of homonymous Ia input to the same nuclei (Clough, Kernell & Phillips, 1968).

Testable Models of the Partitioning Hypothesis

Fig. 17A-B provides models of the two anatomical (and developmental) extremes of the central partitioning hypothesis that were tested in the present and this laboratory's previous (Botterman et al., 1983a,b; Chapter 2) studies. In both models, the peripheral neuromuscular arrangement is identical, with two motoneurons
Fig. 17. Models of the partitioning hypothesis. A-B: The hypothesis in its present testable form. Shown is a motor nucleus in the brainstem or spinal cord and the muscle it innervates. Two motoneurons are shown (MN1 and MN2) supplying muscle units which occupy territories in two separate neuromuscular compartments (NMC1 and NMC2; shaded areas). While these two motor units can act in concert, they also have the capacity for separate or somewhat separate actions (e.g., contribution to flexion during stepping). Associated with these differences are differences in the relative strength of monosynaptic input that the motoneurons receive from Ia afferents supplying the same two compartments. The present version of the hypothesis accommodates extreme topographic specificity (A) or species specificity (B) in the motor nucleus and any gradation between them. C: A possible variation of the hypothesis. In this instance, the two motor units still have the capacity for independent action but their muscle fibers occupy the same neuromuscular compartment as do the Ia afferents providing the partitioned effects. This version of the hypothesis can accommodate present (e.g., Loeb, 1984) and future studies on the behavior of single motor units, fusimotor neurons and spindle afferents during natural movements. However, this model cannot be tested with present-day techniques.
Fig. 17. *Models of the partitioning hypothesis.*
(representing groups of cells) supplying different heads or compartments of the muscle. At the central level, the motoneurons receive partitioned Ia effects from two afferents (also representing groups of cells supplying different compartments); either with (Fig. 17A, topographic specificity); or without (Fig. 17B, species specificity) an anatomical separation of their cell bodies in the motor nucleus. The hypothesis can accommodate either extreme or any gradation between them as was actually observed in all four studies.

Relation Between the Partitioning and the Task-Group Hypotheses

At least in some muscles, motor units occupying the same neuromuscular compartment may have the capability for independent action. No kinesiological evidence is available on this point, but the possibility cannot be excluded on the basis of recent work undertaken in Loeb's laboratory (Hoffer, Loeb, O'Donovan & Pratt, 1980; Hoffer, Sugano, Marks & Loeb, 1982; Loeb, Pratt & Marks, 1984). Motoneurons supplying the anterior part of the cat sartorius (SARTa) muscle were found to become active during either the swing (flexor) or stance (extensor) phase of the step, but not in both phases. As yet, it is not known if these flexor and extensor motoneurons supply different parts of SARTa. In addition, this result may not generalize to all other muscles (viz., the opposite results obtained by Perret & Cabelguen, 1980, for ST motoneurons). Nonetheless, the SARTa results are sufficiently compelling to suggest the need to evaluate the model proposed in Fig. 17C. It shows motoneurons supplying the same neuromuscular compartment that have the capability for different actions.
and which receive partitioned Ia effects. For this to occur, the Ia afferents from the same compartment must also be divisible into two groups on the basis of their differential (e.g., flexor vs. extensor) responses during movement. This possibility is easy to envision for muscle spindles whose discharge can be modulated so powerfully by a variety of fusimotor effects (i.e., action on their intrafusal fibers by static and/or dynamic beta and gamma motoneurons). Evidence of this type is beginning to emerge from the laboratories of Loeb and Prochazka with demonstrations of spindles exhibiting different behaviors in different types (strategies) of movement (for review: Prochazka & Hulliger, 1983; Loeb, 1984).

The task group hypothesis can accommodate the model of Fig. 17C since it proposes that differing combinations of alpha, beta and gamma motoneurons and of muscle spindles and their central actions combine for the elaboration of different motor actions (for an ad seriatim review: Loeb, 1982; Loeb, Marks, Rindos, O'Malley, Chapelier & Levine, 1983; Marks, Loeb & Hoffer, 1983; Loeb, 1984). This hypothesis (Loeb, 1984) may be unique in that it was formulated to account for the "kinematics of the tasks actually performed by muscles under natural conditions" and it can address the "diversity observed in mammalian motor function". Loeb (1984) has emphasized that "the task group is a functional organization that is independent of and probably subsumes microanatomical organizations such as mechanical compartmentalization" (citing the previous studies on sensory partitioning of: Binder, Kroin, Moore, Stauffer and Stuart, 1976; Cameron, Binder, Botterman, Reinking &
Stuart, 1981; Windhorst and Schwestka, 1982). This viewpoint is based on the results of virtuosic experiments. However, like the model proposed in Fig. 17C, technical limitations will impede its full exploration.

The Fig. 17C version of partitioning is broader than the Fig. 17A-B models in that it associates the partitioning of monosynaptic Ia input with the action and usage of motoneurons (alpha, beta and gamma) in addition to the mechanical consequences of their activation. However, despite its intuitive attractiveness, the Fig. 17C model cannot be tested at present since the techniques are not yet available which can combine a functional means of classifying motoneurons and Ia afferents with the intracellular recording techniques required for the study of postsynaptic effects in the same motoneurons. Furthermore, the incidence with which a functional partitioning of the motor nucleus-muscle complex occurs independent of compartmentalization remains to be established.

Fortunately, much remains to be gained by the continued testing of the partitioning hypothesis in its present (Fig. 17A-B) form. For example, it is still not known if the partitioning hypothesis addresses a principle of motor design and control or if it is only relevant in specialized instances. This issue requires the testing of further spinal and brainstem motor nuclei contributing to a variety of muscle control systems (e.g., hindlimb, respiratory system, forelimb, head-neck). Furthermore, it is still not known if the hypothesis is of special relevance for muscles in which the spindles, tendon organs and
oxidative muscle fibers are restricted to a limited volume of the muscle (Botterman et al., 1978; Appenteng, O'Donovan, Somjen, Stephens & Taylor, 1978; Richmond & Stuart, 1984). Even in those instances in which partitioned Ia effects have been observed in a motor nucleus, it is not known if other primary afferents and descending control systems evoke similar (or different) partitioned effects (cf., Wilson et al., 1983). Until these various issues are addressed, it would seem that work on the partitioning hypothesis should proceed in parallel with that on the task group hypothesis; the former emphasizing the design and the latter the function of various components of the segmental motor control system.
OVERALL SIGNIFICANCE OF THE PRESENT PROJECT TO THE FIELD OF MOTOR-CONTROL NEUROBIOLOGY

Some influential findings from the laboratories of Sherrington (1910) and Eccles (Eccles, Eccles & Lundberg, 1957; Eccles & Lundberg, 1958) were reassessed in this project. Interestingly, these findings contributed to the award of their respective 1932 and 1963 Nobel Prizes. Our subsequent revision serves as a reminder of the ephemeral nature of even the most influential of twentieth-century findings in the field of CNS electrophysiology. The process of reassessing previous data and conclusions by new hypotheses serves as an important stimulus for growth to the overall field of neurobiology.

A key central component of the partitioning hypothesis was addressed in this study by examining the monosynaptic Ia connections between muscle spindles and their homonymous motoneurons in motor nuclei supplying the semimembranosus and the lateral gastrocnemius muscles. Both muscles are composed of subvolumes that have been shown to exhibit somewhat separate actions during natural movements.

The results support the central partitioning component of the partitioning hypothesis with evidence for a partitioning of monosynaptic Ia EPSP effects to the motoneurons of both nuclei. The central partitioning hypothesis has been useful in ferreting out further information on the design of the homonymous Ia pathway, particularly in the hindlimb motor-control system. Yet findings from this and other
laboratories, suggest that the partitioning of monosynaptic Ia reflex effects may generalize to other motor nuclei. To test such an idea will require the examination of many more nuclei which supply muscles subserving a variety of motor-control functions (e.g., head-neck, forelimb, respiratory, hindlimb).

Continued testing of the partitioning hypothesis in other motor-control systems raises an issue common to neurobiology. Namely, when does a hypothesis begin to address a principle of neural design and function and rather than a specialization or set of specializations that are only pertinent to the experimental paradigm being employed? This issue has not yet been resolved for the hypothesis under consideration even though its testing continues to contribute substantially to the furthering of our understanding of the segmental motor-control system.

The present results invite further consideration of their potential association with the kinesiological capabilities of the two test muscles. As yet, this analysis cannot be undertaken due to present-day techniques. In the future, such an analysis will be required if design features of the segmental motor-control system (exemplified by the present study) are ever to be correlated with its functional features (exemplified by studies showing motoneuron activity patterns during movement).

Other issues of broad significance to motor-control neurobiology can be considered in the context of this project. For example, what is a muscle? This question is far from esoteric because it emphasizes a
current dilemma in motor control when discussing structural or functional subdivisions of an anatomically-defined muscle. Different parts of a muscle may show varying characteristics in regards to anatomy (e.g., muscle heads, neuromuscular compartments), biomechanics and/or kinesiology. Likewise, can electrophysiological analysis of the adult nervous system provide indications of its developmental sequence? This, too, is an open question which bring out the need for further studies along the lines of the present work.

It is both intriguing and sobering that so much has yet to be learned about the monosynaptic Ia-motoneuronal connection within the mammalian CNS. The current project contributed to our knowledge of this much-studied connection, and brought out the need for still further studies, to be undertaken under the rubric of the partitioning hypothesis.
GLOSSARY

Partitioning Hypothesis: An evolving hypothesis concerned with the interactions between motor units and muscle receptors at both the muscle and spinal cord levels of the segmental motor-control system. It encompasses two major concepts, sensory partitioning and central partitioning.

Sensory Partitioning: The concept that muscle receptors are particularly sensitive to the activity of adjacent muscle units in the parent muscle, in addition to being responsive to more global changes in whole-muscle length and force.

Central Partitioning: The concept that each muscle-receptor afferent provides its most effective synaptic input to motoneurons supplying the neuromuscular compartment in which the receptor is located than to other motoneurons supplying other neuromuscular compartments in the homonymous and functionally related muscles.

Recent reports from this laboratory used the term "localization" as a synonym for "central partitioning". However, in the present report, localization is discarded because it implies a mechanism (i.e., topographic specificity) which may or may not contribute to the presence of central partitioning.

The present definition of central partitioning should be separated from the concept that the motor nucleus-muscle complex is
organized to maximize the participation of "oxidative" muscle fibers (i.e., those belonging to type S and FR motor units; nomenclature of Burke et al., 1973) in finely graded contractions (cf. Cameron et al., 1981; Munson et al., 1984). This concept is an extension of the orderly-recruitment phenomenon, a particularly robust one if limited to consideration of contractions along the muscles' optimal plane for force development (Stuart & Enoka, 1983; Enoka & Stuart, 1984). Even though oxidative muscle fibers are often found to be concentrated within a subvolume of a muscle which is usually along a muscle's line of pull (Botterman et al., 1978), the orderly recruitment phenomenon does not concern central partitioning in the sense tested in this study.

**Intramuscular Localization of the Stretch Reflex:** The proposition that the reflex response (involving, in particular, monosynaptic and polysynaptic spindle afferent inputs to motoneurons) to stretch of a part of a muscle can be directed back to the same part of the muscle. When present, this phenomenon must be attributable, in part, to both sensory and central partitioning.

**Topographic Specificity** (also location specificity, topographic weighting, somatotopy, topography): The tendency for the central nervous system to preserve, to a greater or lesser degree, in its various pathways and nuclei, an orderly layout or "map" of a body area such as the retina, cochlea, cutaneous surface or muscle mass of the body (Angevine and Cotman, 1981).
For the present purposes, topographic specificity refers to a situation in which the efficacy of excitatory monosynaptic connections between spindle Ia afferents and their target motoneurons is attributable in part to their anatomical relationships within the spinal cord.

Species Specificity: For the present purposes, this term is used to explain a situation in which differences in connectivity between muscle afferents and motoneurons are shown to involve factors other than the presence of topographic specificity.

The species of motoneurons under consideration are those of one muscle whose cell bodies are at the same location within the spinal cord but whose peripheral axonal terminations are in different parts of that muscle. Species specificity is claimed when an afferent provides a stronger synaptic input to the motoneuron supplying the same part of the muscle as the afferent.

Motoneuron Activity vs. Muscle Action: In the motor-control literature, the terms "motoneuron action" and "muscle action" are often used interchangeably. This practice is inappropriate and avoided in this report because muscle action is dictated by the anatomical connections of muscles, whereas motoneuron action (hereafter, motoneuron activity) is a manifestation of CNS activity.

Specifically, in this report, motoneuron activity is described in relation to a phase of movement in which a selected set of
motoneurons has been activated, whereas muscle action refers to the movements to which a muscle can contribute force by virtue of its anatomical attachments.

**Synergists:** Muscles which show a similar mechanical action (i.e., common degree of freedom) at the same joint, as suggested by their attachments.

**Neuromuscular Compartment:** An anatomical term describing a distinct sub-volume of muscle in which the muscle fibers and its receptors are innervated exclusively by a primary branch of the whole-muscle nerve.

Recently, this and other laboratories have used the terms "intramuscular" and/or "muscle" compartment as synonyms for neuromuscular compartment. In this report, the latter term is favored because it provides the rationale for the division of the muscle into sub-components.

**Motor Nucleus** (also motoneuronal pool): A cigar-shaped constellation of motoneuronal cell bodies within the spinal cord. These motoneurons innervate the skeletomotor and fusimotor fibers of a single muscle. Motor nuclei may overlap, in which case adjacent cell bodies may innervate different muscles.
Homonymous Motoneurons: Motoneurons which innervate muscle units within the same "parent" muscle or neuromuscular compartment as the test afferent.

Heteronymous Motoneurons: Motoneurons which innervate muscle units within muscles other than the test afferent's parent muscle.

Motoneuron Type: For motoneurons supplying skeletomotor fibers, the convention of this laboratory (Stuart & Enoka, 1983) is to use the same nomenclature system for motoneurons as for the muscle units they supply (cf. Sickles & Oblack, 1984). Thus, FF, FR and S motoneurons refer to those supplying FF, FR and S muscle units (nomenclature of Burke et al., 1973).

Composite Monosynaptic Ia Excitatory Postsynaptic Potential (hereafter composite Ia EPSP): As recorded with an intracellular (IC) electrode, the excitatory (depolarizing) synaptic potential produced in a motoneuron by the monosynaptic action of single impulses "arriving more or less synchronously in two or more afferent fibers" (usually a large number; Burke & Rudomin, 1977). They can be produced by a brief (0.1ms) shock to a muscle nerve or by a quick (5-20 ms) muscle stretch.

Homonymous-Branch EPSP: A composite Ia EPSP produced by stimulation of a branch of the homonymous muscle nerve.
Own-Branch EPSP: A composite Ia EPSP produced by stimulation of that branch of the homonymous muscle nerve to which the test cell contributes its axon.

Other-Branch EPSP: A composite Ia EPSP produced by stimulation of a branch of the homonymous muscle nerve other than the test cell's own branch.

Ia-Receptiveness of a Motoneuron: Eccles, Eccles & Lundberg (1957) introduced this term to indicate the strength of composite Ia input from various muscles to a single motoneuron, relative to the strength of its homonymous input.

The term "Ia receptive" also has been used recently to indicate from which muscles a motoneuron receives Ia input. In general, motoneurons receive Ia input from their homonymous muscle, and, usually to a lesser degree, Ia input from other muscles with actions synergistic to those of the homonymous one.
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