

the secondary spindle afferents. It has been shown (Binder et al. 1976; Binder & Stuart 1980a) that not only group Ia afferents but also spindle group II afferents are responsive to a distinctive set of motor units in a muscle. Windhorst and Meyer-Lohmann (1977) suggest that synchrony in neighboring spindles is caused not only by activity in specific motor units, but perhaps also by shared gamma input. It is worth noting that spindle group II afferents seem to have powerful projections, particularly to dynamic  $\gamma$ -motoneurons (see Appelberg et al. 1983; 1986; Johansson 1981; 1985; 1988) and to homonymous as well as heteronymous muscles. It still remains to be investigated whether the central projections of the group II spindle afferents are strongest to the  $\gamma$ -motoneurons that innervate the regions of the muscles accommodating the receptors. The group II projection to  $\gamma$ -motoneurons may constitute a powerful positive feedback circuit with the capacity to enhance the partitioning.

The role of the fusimotor system in the partitioning hypothesis needs to be thoroughly examined, particularly since the control of the fusimotor system can hardly be disregarded in a discussion of the function of the Ia system and of localized stretch reflexes. It seems natural to view the  $\gamma$ -motor spindle system, with its sophisticated descending and reflex control, as a functional unit.

## Central versus peripheral aspects of neuromuscular regionalization

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In their thoughtful and interesting review, Windhorst, Hamm, and Stuart have chosen to discuss the function of partitioning in the neuromuscular system almost exclusively from the point of view of "peripheral requirements." As the authors rightly point out, peripheral factors must often be important. Thus, for instance, in many anatomical "muscles," the various muscle fibers are not all mechanically equivalent with respect to their direction of force (e.g., the deltoid). From a single mechanistic point of view, such muscles are not physiological entities, and in such cases the selective recruitment of different muscle regions is equivalent to the selective recruitment of different anatomical muscles. In a number of known cases of regionalized activation in muscles, however, the relevant muscle portions have all appeared to be mechanically equivalent, that is, the required joint torques could in these instances just as easily have been produced by muscle regions other than those chosen by the central nervous system.

One example of such an *apparently centrally motivated regionalization of intramuscular activity* is the voluntary contraction of the long head of the human biceps brachii: Different intramuscular localization was observed for units used exclusively for flexion and for supination (ter Haar Romeny et al. 1984). Another case is the cat's peroneus longus: Different antero-posterior distribution of activity was observed for contractions caused by a flexion reflex (stimulation of superficial peroneal nerve) and by cortical stimulation (Kandou & Kernell 1989).

Such differences in the *intramuscular* distribution of activation by the central nervous system strongly indicate the presence of corresponding topographical differences in the *intraspinal* distribution of the relevant synaptic effects; there are now many publications demonstrating that there is typically some general relationships between the intraspinal location of motoneurons and the intramuscular location of their muscle fibers (e.g., cat's gastrocnemius medialis, Swett et al. 1970; cat's peroneus longus, Donselaar et al. 1985). Incidentally, it is still

highly uncertain whether these general cord-to-muscle topographical relationships have a specific linkage with peripheral nerve branch compartments, such as those illustrated in Figures 1 and 5 of Windhorst et al.'s target article (data from English & Letbetter 1982b; English & Weeks 1984). In their study of the cat's lateral gastrocnemius, Weeks and English (1985) did observe some correlation between the intraspinal sites of motoneuronal cell bodies and the nerve branch compartments containing their muscle fibers. This relationship was not very precise, however; cells belonging to different neuromuscular compartments were extensively intermingled within the spinal motoneurone pool.

A regionalization of the synaptic distribution in motoneurone pools might in part arise as a side effect of the central nervous system using topographical clues for the organization of different functional sets of spinal interneurons. Motoneurons of different muscles tend to show a different overall localization in the spinal cord. Thus, sets of interneurons that establish different patterns of muscle coordination usually *have* to show topographical differences from each other with respect to their distribution of synapses among different motoneurone pools. Hypothetically, it might not be easy to combine such a necessary "topographical nonhomogeneity" of synaptic distribution *between* pools with a perfect homogeneity of synaptic distribution *within* the various individual pools. For such reasons, different coordinative patterns of muscle use might tend to become associated with quantitatively different distributions of activity in individual motoneurone pools and, consequently, in individual muscles (cf. discussion in ter Haar Romeny et al. 1984). We are at present attempting to test this hypothesis experimentally.

One of the known and obvious ways many muscles are topographically nonhomogeneous is in the distribution of different types of motor units and muscle fibers (e.g., Windhorst et al.'s Figure 5, cited from English & Letbetter 1982b). Windhorst et al. argue that such a regionalization of fiber types would motivate the nervous system to establish a regionalized activation pattern. I suggest that the direction of cause and effect might equally well be reversed. The striking nonhomogeneities in fiber distribution, which are evident in many muscles, might exist mainly as a long-term *result* of centrally motivated nonhomogeneities of muscle activation, as indicated above. We know that the same muscle is often used for a wide variety of motor tasks, some postural and others associated with brief, brisk movements. If such divergent types of motor patterns also tend to differ quantitatively with respect to their topographical distribution of synapses in the motoneurone pool, this may well result in different patterns of long-term activity for different intramuscular regions. We know that the histochemical and physiological properties of muscle fibers may be very markedly altered by changes in their long-term activation patterns (e.g., Kernell & Eerbeek, in press; Pette & Vrbová 1985; Salmons & Henriksson 1981). Thus, the regionalization of fiber types in individual muscles might, in fact, be considered a potentially important clue to the intraspinal topographical organization of different patterns of motor coordination.

## Motor partitioning: Epiphenomena masquerading as control theory

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Departures from a simple "size principle" in the distribution of homonymous proprioceptive feedback in a motor nucleus have heretofore been considered exceptions that draw attention to special problems of motor control in a particular muscle. Wind-

horst, Hamm, and Stuart now propose that such departures are so widespread that they suggest another general principle of motor control termed "partitioning." However, the motley collection of muscles from different appendages in different species that is offered in evidence may speak more to the futility of searching for general principles at all, at least at the level of servo-control of individual muscles.

Some of the examples of partitioning in single muscles are really a belated recognition that the traditional nomenclature of the gross anatomist is somewhat arbitrary. Broad muscles with distributed mechanical actions and multiple, independent muscle nerves such as the sartorius and biceps femoris are clearly divisible using functional and architectural criteria, even if they lack the crude fascial plane that is the sine qua non of gross anatomical dissection.

Many of the remaining examples of partitioned control exhibit distressingly small degrees of localization in muscles with strong reflex control. As the authors note, many of them are consistent with terminal arborizations that have finite extents within the elongated motor nuclei typical of the lumbosacral spinal cord (Lüscher et al. 1980). The rostral-caudal location of motoneurons in these motor nuclei tends to be loosely correlated with the anterior-posterior location of their individual unit territories in the muscles (Pratt et al. 1984; Weeks & English 1985). The correlation is so weak, even across functionally compartmentalized muscles, that it would seem to be an insignificant relic of embryogenesis rather than an important feature of motor control. However, such gradients are probably strong enough to account for most of the Renshaw compartmentalization cited here and for much of the partitioning of spindle feedback. Only one study has tried to correct for this biasing, and the residual partitioning attributable to compartment-specific feedback is not impressive (Vanden Noven et al. 1986).

Muscles with compartments in series instead of in parallel present serious problems for Windhorst et al.'s attempts to concoct a control theory from connectivity. If feedback from spindles is really necessary to correct instabilities inherent in the work of motor units, then it is precisely these in-series muscles that are most in need of such stabilization. The mechanical effect of a motor unit on the spindles of its own compartment (unloading) is exactly the opposite of its effect on spindles in the adjacent compartment (which it stretches). Servo-control predicts not only a particularly strong excitation directed specifically to the homonymous compartment, but inhibition of the heteronymous compartments. Regarding the semitendinosus muscle, which has fairly strong homonymous spindle feedback, Windhorst et al. only make a vague appeal to "very special motor control problems" to account for its completely unpartitioned feedback (Botterman et al. 1983b), but these problems must include those that would appear to mandate partitioning. Regarding the long extensors in the cat neck, Windhorst et al. cite a "strongly partitioned" length feedback but fail to note that the spindle feedback in these muscles is conspicuously sparse and weak (Abrahams et al. 1975), even though they have the highest density of proprioceptors in the body (Richmond & Abrahams 1975a; Richmond & Bakker 1982). Furthermore, the distribution of their spindle projections is not really consistent with compartment-specific partitioning, but rather reflects the tendency of these afferents to project only rostrally from the spinal segment at which they enter, for reasons that remain mysterious (Brink 1988). Both of these examples of in-series motor pools presumably achieve stability through principles of motor control that have yet to be considered. To speak of multiple loops of servo-control in such muscles is to miss the main lesson of these data.

Finally, as Harrison et al. (1983) have pointed out, the real fly in the ointment is the complete absence of central partitioning in proprioceptive pathways that have the strongest mechanical basis for their sensory partitioning. It is arguable that spindle feedback should be incompletely partitioned because the me-

chanical effects of even distant (but parallel) muscle units in the same (and synergist) muscles is only decreased, not negligible. It is now clear, however, that each Golgi tendon organ is exquisitely sensitive to the active mechanical output of only the 10 or so muscle fibers to which it is directly connected (Binder et al. 1977). But the segmental circuits for force feedback seem not even to be selectively partitioned to the homonymous muscle, much less to its compartments or motor units (reviewed in McCrea 1986). This is not consistent with servo-control as we know it.

Windhorst et al. have done a service by reminding us of the complexities and specializations that lurk in individual muscles having singular anatomical names. Yet many of those specializations probably reflect unique motor behaviors that have necessitated control schemes that are just as unique as the muscles. Many of these control schemes may be implemented as distributed circuits for which a decomposition into servoloops for individual muscles or compartments is meaningless.

In control engineering, there is now a well-developed theoretical basis for designing and optimizing such distributed controllers (Athans 1971). Dynamic mechanical analyses of musculoskeletal systems are reinforcing the notion that the work of individual muscles (and hence their control) must be considered at the level of the whole appendage and in the context of the different mechanical constraints imposed by specific behaviors (Zajac & Gordon 1989). We have begun to apply engineering techniques for the design of linear quadratic regulators in which proprioceptive feedback is distributed (without muscle or compartmental prejudice) among the different actuators (motor nuclei) on the basis of the mechanical properties of the whole musculoskeletal system (He et al. 1988; Loeb et al., in press). The patterns of feedback required to optimize performance criteria, which include postural stability and economy, are generally similar to the widely heteronymous projections that have been observed in spinal interneuronal systems to date (reviewed by McCrea 1986).

The notion that the spinal cord functions as a collection of discrete servo-controllers for each muscle has its roots in narrow and outdated views of mechanics and circuitry (Loeb 1987). Rather than propping up such a rickety old theory with dubious refinements such as partitioning, we need to start designing a new edifice.

## Oxidative indexes and muscle spindle densities

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Inspection of available data leaves little doubt that many skeletal muscles can be subdivided morphologically into compartments. Windhorst's target article addresses the question of whether such subdivisions can participate in segmental reflexes independently of the muscle of which they are a part. Overall there should be few objections to the concept of morphological and physiological partitioning; however, some may question the relative importance of the various intramuscular specializations and the relevance of high spindle densities in whole muscles, or in muscle compartments that have high oxidative indexes.

One point that deserves examination is data collection. It is a common practice to describe histochemical fiber-type composition on the basis of single cross sections at the central portion of muscles (e.g., Ariano et al. 1972). Similarly, muscle spindle density is usually expressed as number of spindles/muscle or as number of spindle/g muscle weight. Both measures disregard compartmentalization. Muscles with uniform fiber-type distribution for which average values would be appropriate (such as