

# Muscle spindles, Golgi tendon organs, and the neural control of skeletal muscle

JOHN N. HOWELL, Ph.D.

Ohio University  
College of Osteopathic Medicine  
Athens, Ohio

MARC D. BINDER, Ph.D.

University of Washington  
School of Medicine  
Seattle, Washington

T. RICHARD NICHOLS, Ph.D.

Emory University  
Atlanta, Georgia

GERALD E. LOEB, M.D.

National Institutes of Health  
Bethesda, Maryland

The purpose of this report is to share with the readership of JAOA, highlights of a symposium held at the 30th Annual Research Conference of the AOA in March 1986. The invited speakers in the symposium were Dr. Gerald E. Loeb of the National Institutes of Health, who also delivered the keynote address, Dr. Marc D. Binder of the University of Washington, and Dr. T. Richard Nichols of Emory University. Dr. John N. Howell of the Ohio University College of Osteopathic Medicine, program chairman for the 1986 conference, acted as moderator for the symposium.

In introducing the symposium, Dr. Howell pointed out that the traditional importance of somatic dysfunction and its treatment in osteopathic practice has led to a natural interest within osteopathic medicine in the problem of control of skeletal muscle function. In 1974, Korr published an important article entitled, "Proprioceptors and somatic dysfunction."<sup>1</sup> In it he related the clinical findings of osteopathic practitioners to what was then known about the physiology of the proprioceptive organs within skeletal muscle. Specifically, he postulated that alterations of the gain of the stretch receptor system might contribute to the etiology of somatic dysfunction and to its treatment through osteopathic manipulative treatment. Korr's hypothesis has been widely accepted within osteopathic medicine because it provided a mechanism that appeared to be consistent with a good deal of clinical experience. However, as Korr pointed out in a recent article,<sup>2</sup> his hypothesis still awaits testing in the laboratory. Since the publication of Korr's hypothesis, additional information has come to light about the function of muscle proprioceptors. The goal of the symposium was to summarize this newer information so that it might be available for integration into thinking about the pathophysiology and treatment of somatic dysfunction.

Dr. Binder led off with a summary of the traditional ideas about how muscle spindles and Golgi tendon organs function and then focused on newer information about the tendon organs. On

anatomical grounds, it is clear that the spindles are arranged parallel to the extrafusal muscle fibers and are thus suited to sensing length changes of the muscle. The tendon organs, on the other hand, are located in series with the muscle fibers and are thus suited to detecting force generated by the muscle fibers. Spindles have been known for some time to be sensitive to very small perturbations in muscle length, producing a reflex activation, or shortening, of the muscle being stretched. In contrast, tendon organs were thought to respond only to high levels of force and to provide protection against the development of too much force by inhibiting the homonymous muscle (i.e., muscle of origin of the reflex).

Recent work has shown this idea about tendon organ function to be unlikely.<sup>3,4</sup> Each tendon organ provides a point of insertion for 3 to 25 muscle fibers.<sup>5</sup> Experimental stimulation of a single motor unit, one or more fibers of which insert on a given tendon organ, will stimulate that organ, producing a train of spikes in Ib afferent neurons to the spinal cord. Stimulation of a motor unit which has no fibers inserting on a particular tendon organ sometimes silences that tendon organ if it has been previously activated by sustained stretch of the muscle. This presumably results from unloading of the tendon organ by virtue of contraction of adjacent muscle fibers. Each tendon organ appears to provide insertion for fibers from motor units producing a wide range of forces. Thus, each organ may sample muscle activity over the full range of force development, from the small motor units that are the first to be recruited to the large units that are recruited only during maximal contractions. This means that the tendon organ input to the cord is not restricted to conditions of high force development but can be graded over the entire range of muscle force.

Determination of the effect of Golgi tendon activity on neurons within the spinal cord has been difficult because it has not been possible to selectively stimulate the tendon organs or their Ib afferent fibers without at the same time stimulating the muscle spindles or their Ia sensory fibers. Recently it has been shown that application of prolonged, high-frequency, low-amplitude vibration to muscles, which is an effective stimulus to the muscle spindles,<sup>6</sup> can cause a transient elevation of the electrical thresholds of the Ia fibers.<sup>7</sup> Under these conditions the Ib fibers can be selectively stimulated and their cen-

tral connections studied.<sup>8</sup> Available evidence indicates that activation of the Ib sensory fibers, like the activation of cutaneous afferents, can cause either excitatory or inhibitory postsynaptic potentials to occur in motoneurons.<sup>9</sup> The site of integration involving the Ib input as well as inputs from other areas within the central nervous system appears not to be the motoneurons, but rather interneurons in laminae V and VI.

Dr. Nichols traced the development of theories concerning the mechanical aspects of the spindle-mediated stretch reflex and went on to point out that most of our knowledge has been based on the study of single muscles. He stressed the need for extending the analysis of stretch reflexes to groups of synergistic muscles acting together upon a joint. A rather extreme view of the role of the stretch reflex system was proposed in 1953 by Merton<sup>10</sup> who hypothesized that normal activation of muscle might always be preceded by gamma activation of the muscle spindles, and the resultant stimulation of Ia afferents would in turn provide the excitatory input to the alpha motor neurons and cause muscle contraction. This theory was referred to as the "follow-up length servo hypothesis." It stressed the feedback control of muscle length and the primacy of gamma activation for muscle contraction. It is now known, however, for many movements, including ballistic types and patterned activities of a repetitive nature, simultaneous activation of both gamma and alpha motor neurons occurs, generally referred to as coactivation.<sup>11</sup> Because the larger alpha motor neurons conduct action potentials faster than the smaller gamma fibers, coactivation implies that extrafusal muscle fibers must be activated before intrafusal fibers. Thus the initial phase of contraction occurs independently of any feedback contribution from the muscle spindle system. Furthermore, it was pointed out that the Golgi tendon organs might also play an important role in feedback control, so that not only muscle length, but some function of both force and length would be controlled.<sup>12</sup>

The latter idea was extended further by Houk,<sup>13</sup> who suggested that the parameter controlled by stretch reflex might be stiffness, defined as the ratio of force change to length change. Nichols and Houk<sup>14</sup> demonstrated that the linearity of the spring-like behavior of muscles in the decerebrate cat preparation was lost when the proprioceptive feedback loop was interrupted, i.e. when the dorsal

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roots were cut. In the absence of reflex control, muscles demonstrated highly nonlinear properties which included a brief failure, or yield, of force generation when the active muscle was stretched.

The linearization and maintenance of the spring-like properties of muscle and the enhancement of stiffness by the stretch receptors occurs in both the extensors and flexors of the feline ankle, but not equally so. Reflex action is weaker in the flexors than in the anti-gravity extensors. However, this inequality is not intrinsic to the muscles; it is a function of the organization of the neural control system. Certain brain stem lesions can alter relative reflex strength, and it has now been shown that monosynaptic reflex strength can be changed through operant conditioning.<sup>15</sup> These experimental observations emphasize the degree of control exerted by the descending influences within the central nervous system over the reflex activity that occurs in the cord. This comes as no surprise to clinicians accustomed to taking advantage of the Jendrassik maneuver to enhance reflex activity in patients.

Dr. Nichols went on to present the results of recent studies from his laboratory that demonstrated interactions between the flexors and extensors at the feline ankle joint, muscles that function together at a joint and can thus be regarded as a myotatic unit. Although the extensors exhibit greater stretch reflex activity than the flexors, they do not have a correspondingly powerful inhibitory effect on flexor activity. Stretch of the flexors, on the other hand, produces a strong inhibitory effect on the extensors. This may relate to the greater force capability and reflex gain of the anti-gravity extensors in the cat, making it necessary for these muscles to be inhibited in order for their weaker antagonists to shorten during a flexion movement. These observations illustrate how the action of two muscles acting on the same joint is coordinated, allowing them to act together as a unit. Such interaction undoubtedly occurs not only between antagonists about a single joint but also between synergists and between muscles acting on different joints within the same or even different limbs, as, for instance, in the crossed extensor reflex.

The final speaker of the symposium was Dr. Loeb. He too emphasized the need to consider the integrative aspects of proprioceptor function, reminding us that the stretch receptors are not "wholly owned subsidiaries" of the muscles in which they reside. On the contrary, their signals go many places in the central nervous system and they are in turn influenced by signals originating in many loci. One experimental approach to these issues is to make measurements in intact, conscious animals, rather than in the reduced preparations (i.e., anesthetized or decerebrate) that are useful for the elucidation of the receptor mechanisms themselves. One important question is whether or not the signals sent to the

spinal cord from the muscle spindles in behaving animals correlate with length or velocity or any other identifiable variable.

Dr. Loeb described experiments carried out in his laboratory at NIH on conscious animals carrying surgically implanted muscle length and force transducers, EMG electrodes, electrodes for recording Ia units from a lumbar dorsal root ganglion, an electrode cuff around the femoral nerve for recording nerve activity and for irrigation of the nerve with local anesthetic from an external syringe, and electrodes for stimulating the saphenous nerve and the nerve to the hamstrings.<sup>16-18</sup> The results showed that no simple correlation between Ia firing and length or velocity exists. Spindles generate signals over a variety of lengths whether the muscles are shortening or lengthening. As has been recognized for some time, there must be a fusimotor program causing contraction of the intrafusal fibers in order to maintain spindle sensitivity and thus to keep information coming in to the central nervous system at all times.

In recent years it has been shown that there are at least two identifiable types of gamma innervation to the intrafusal fibers, a gamma dynamic system largely associated with one type of nuclear bag fiber and a gamma static system associated with a different type of nuclear bag fiber and with nuclear chain fibers.<sup>19</sup> The nuclear bag fibers under gamma dynamic control appear to be responsible for the sensitivity of the primary afferent endings to velocity and acceleration, whereas the nuclear chain fibers are responsible primarily for the static length sensitivity of both primary and secondary endings. Activity in the gamma system, both dynamic and static, is such that afferent information from the stretch receptors continues to flow into the central nervous system during patterned activity involving any combination of muscle shortening and lengthening. In order for this to occur, the activation patterns of the gamma fibers must be driven independently of alpha motor neurons.

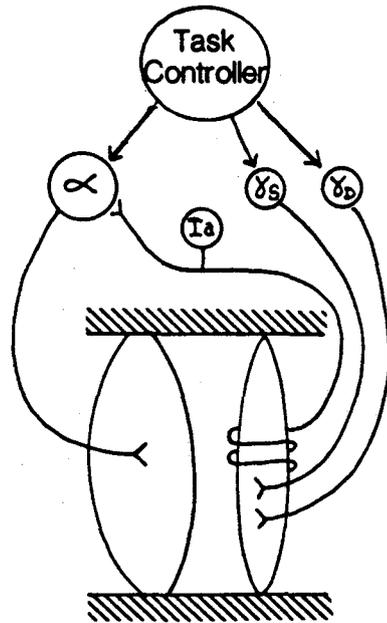
The frequency of firing of Ia afferents from the spindles during voluntary motor behavior tend to be restricted to the range of 50 to 200 pulses per second regardless of the muscle activity occurring. Theoretical considerations<sup>20</sup> suggest that firing rates below this range do not occur because the rate of information transfer from spindles would become limiting, i.e., would be too low to provide useful information during continuing motor function. At frequencies above 200 pulses per second, the signal to noise ratio becomes severely eroded, possibly because of the existence of multiple transduction zones within the Ia neuron innervating the intrafusal fiber. Normally the two transduction zones are electrically coupled, somewhat like the S-A and A-V nodes of the heart, so that the faster zone locks the other zone to its pace. Under conditions of intense activation, however, these zones

may become uncoupled so that each zone generates signals independently, producing irregular interspike intervals and a noisy signal. Thus, the job of the gamma program appears to keep the spindle adjusted so that the firing rate in the sensory Ia fibers is kept within the appropriate range for optimal signaling. This appears to occur in the cat during pre-programmed motor patterns such as locomotion and even paw-shaking, but does not occur in response to single unexpected perturbations.<sup>18</sup>

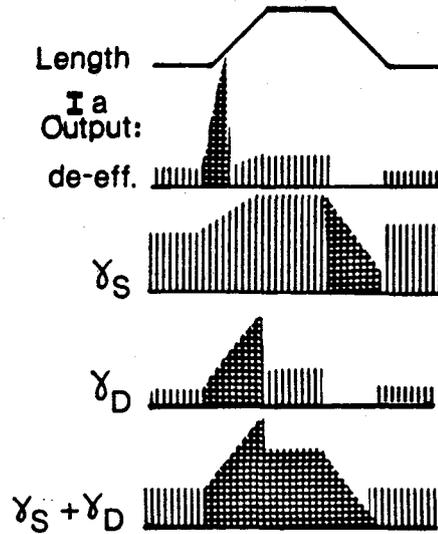
The question remains as to just what is being sensed and regulated by the spindle system. The possibilities provided by the gamma system suggest that different parameters can be regulated depending on the type of activity occurring in the gamma efferent system. In muscles whose length is being changed passively by the action of gravity or of other muscles, the gamma motoneurons may act alone to establish the mixture of static (length) and dynamic (velocity) influences on spindle afferent sensitivity that is appropriate for the anticipated muscle length changes. In active muscles, similar fusimotor control may be viewed as part of the servocontrol loops involving active alpha motoneurons that regulate length, stiffness, or other features of motor output, depending on the motor task being performed. These variations are represented schematically in Figure 1.

Several interesting points arose during the discussion that followed the presentations summarized above. Although we tend to focus on the well-defined proprioceptive sense organs in muscle, namely the spindles and the tendon organs, free nerve endings are also found in muscles. Much of their function is not known but it is conceivable that they too are important in proprioception, and they may be particularly important in the response to direct therapeutic manipulation of muscle, perhaps acting through interneurons that carry oligosynaptic reflexes and/or establish baseline levels of alpha motoneuron polarization. The idea that altered output of the gamma system plays a role in altering the sensitivity of the myotatic reflex has not yet found support experimentally. For instance, the Jendrassik maneuver, which is employed clinically in order to enhance the stretch reflex response, is not mediated by alterations in gamma output.<sup>21</sup> It appears to result from changes in the excitability of the motor neurons themselves in a way that is not related to activity in the gamma loop. However, this observation does not appear to exclude the possibility, suggested by Korr, that gamma loop changes occur in the kind of pathologic dysfunction that is seen clinically. Given the importance of the gamma loop output in maintaining sensory information flow from the spindles during muscle activity, any inappropriate changes would certainly be expected to have serious pathologic consequences. It is clear that direct measurements are needed to resolve this question.

### A. Basic Control Circuit



### B. Transducer Sensitivity Control



### C. Motor Tasks and Control Modes

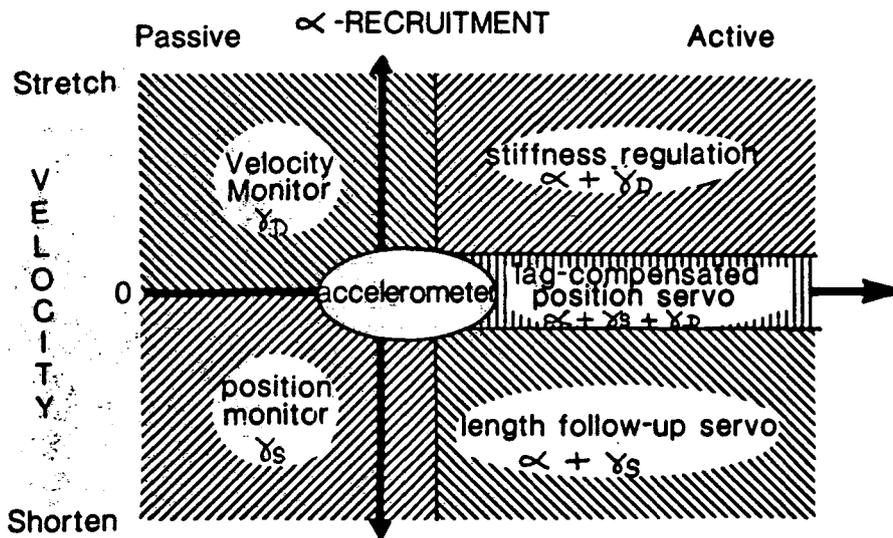


Fig. 1. (A) Archetypical servocontrol circuit employing excitatory feedback from muscle spindle primary afferents ( $I_a$ ) onto alpha motoneurons ( $\alpha$ ). The absolute and relative sensitivity of the afferent to length and velocity perturbations is under the control of at least two types of fusimotor neurones, gamma static ( $\gamma_s$ ) and gamma dynamic ( $\gamma_D$ ). (B) Various states of the spindle  $I_a$  output in response to a ramp perturbation of length, shown with cross-hatched areas of maximal sensitivity (defined as largest change in output without saturating). In the de-efferented state (de-eff), the afferent is hypersensitive to the onset of a lengthening perturbation; under gamma static influence, activity is generally high except during muscle shortening which exceeds the rate of intrafusal muscle contraction; under gamma dynamic influence, activity is strongly dependent on velocity of stretch, with no activity during shortening; under combined static and dynamic influence, spindle afferent discharge can follow at least modest rates of lengthening and shortening. (C) The work of the muscles is divided into a two dimensional space whose axes are velocity (ordinate) and degree of recruitment (abscissa). Several different functions for spindle afferent feedback are indicated in the various domains of this space for which they are best suited, together with the general pattern of extrafussal ( $\alpha$ ) and intrafusal ( $\gamma_s$  and  $\gamma_D$ ) recruitment needed to function optimally in these domains. During active lengthening (upper right), the enhanced stretch sensitivity provided by gamma dynamic activity would be used to improve the stiffness of the muscle when it is used as a spring; during active shortening (lower right), gamma static activity is needed to maintain spindle activity above zero to provide an error signal for a length follow-up servo. In the near-isometric active state between them, the modest velocity-dependency of the afferent provides a phase leading detector of small stretches which might help to compensate for the motor lag time; in the low recruitment, near isometric state at the centre, the hypersensitivity of the de-efferented spindle to small stretches provides the earliest indication of a small stretch of the resting muscle; in the passive (inactive) muscle at left, fusimotor activity could be used to optimize the spindle afferent signal during lengthening (upper left) and shortening (lower left), presumably for use in the control of active antagonist muscles or to provide general kinesthetic information to higher centres. (Reprinted with permission from Loeb, G.E., J Exp Biol 115:137-46, 1985.)

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