

*The Control and Responses of Mammalian
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Executed Motor Tasks*

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OVERVIEW

History

The importance and sophistication of muscles as sources of somatosensory information is a relatively recent and ongoing discovery. The presence of large myelinated afferents and their termination in specialized receptor structures in muscles was first identified by Sherrington in 1894 [127]. Following Rossi's prescient arguments in 1927 [120a], systematic research on the separate fusimotor innervation of these receptors essentially began with Leksell's monograph in 1945 [88].

Two factors contributed to a long series of attempts to relate the whole ensemble of muscles, receptors, and controllers to simple, local feedback schemes in the spinal cord. First was the widespread belief that this class of proprioceptors did not project sensory information to the cerebral cortex and did not give rise to conscious sensation. Second was the interest among physiologists in the newly emerging engineering discipline of linear control theory, which dominated the design of much physiological laboratory equipment, from amplifiers to torque motors. All of this fit well with the Sherringtonian notion of strong, simple spinal reflexes, easily studied in reduced preparations, as the basic building blocks of motor control.

Both factors appear to have been misleading. It is now clear that muscle spindle afferents do project strongly to sensorimotor areas of cerebral cortex [1, 107, 129], and that a considerable part of our kinesthetic sense does, in fact, arise from muscle receptors, as well as from joint or skin stretch receptors [50, 56, 120]. It is now also clear that virtually every aspect of skeletal motor control is profoundly nonlinear, from the force output of muscles to the transducer characteristics of the proprioceptors and the integrative properties of synaptic transmission. Natural examples of linear motor control have

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been found (e.g., the vestibulo-ocular system), but they have always proved to be special cases that cannot be generalized to the more highly varied activities of most appendages.

Methodology

A further obstacle to the development of a comprehensive theory of sensorimotor integration has been the historical division of muscle laboratories, into those studying the mechanical output properties of the muscle and those studying the mechanical sensitivity of the proprioceptors.

Students of motor units have tended to view them as machines that work by shortening (sign convention for velocity is negative). Students of muscle spindles have tended to view the receptors as sensors of stretch (sign convention for velocity is positive). When stated that abruptly, the likelihood of satisfactorily explaining how the one controls the other seems low indeed. Yet most of our information about contractile machinery and about the spindle afferents does come from these opposite dynamic states of the structure that they share, the muscle. Extrafusal muscle fibers are usually studied in devices that apply known resistance to shortening, whereas muscle spindles are studied in devices that apply known stretches. Relatively little is known about the tension-generating properties of muscle during active lengthening, a state that occurs regularly in nature and is characterized by large nonlinearities for which, presumably, there must be some suitable control algorithm. Conversely, relatively little is known about the transducer properties of muscle spindle afferents during moderate to rapid shortening, a state that also occurs frequently in nature, but in which spindle afferents produce zero output unless provided with an intense and probably complexly modulated fusimotor drive.

The last 20 years have seen the development of a number of preparations in which researchers have observed, under at least quasi-normal operating conditions, the natural activity of muscle spindle afferents and, almost inadvertently, the work of their extrafusal muscles. These preparations are diverse, and recordings from them represent random samples of the range of normal behavior that owe more to quirks of technical feasibility than to any systematic attempt to survey normal behavior. The data have been highly heterogeneous and confusing, at least in the context of preexisting theories of motor control such as length servos and alpha-gamma coactivation (see pp. 161–163 and Fig. 2). Each such theory sought to provide a single, unifying principle of motor control that would use the transducer characteristics of lengthening muscle spindles to account for the regulation of shortening muscle fibers. The theories neither anticipated nor responded to the conditions actually observed in muscles oper-

ating under normal behavior. In this sense, the diversity of conditions for which data have become available provides a quick and rather negative conclusion about the adequacy of these theories. However, the data are still too sketchy to provide definitive support for new theories.

This review first considers the general scope of the kinematic control problems that emerge during normal skeletal muscle function. Considerable attention is given to structuring existing data on muscle and receptor properties in terms general to both, emphasizing in particular the range of velocities of motion, both positive and negative. A theoretical examination of the problem of optimizing the sensory information obtained under such varied conditions follows, a subject that has been given less attention for proprioception than for other sensory modalities and that suggests a new way of thinking about the fusimotor control of spindles. The existing literature on spindle function during normal movement is then reviewed, with the specific aim of identifying possible optimal control principles for each particular movement. Finally, I propose a new term, *task groups*, to describe patterns of task-dependent sensorimotor recruitment that are consistent with these notions of optimal control.

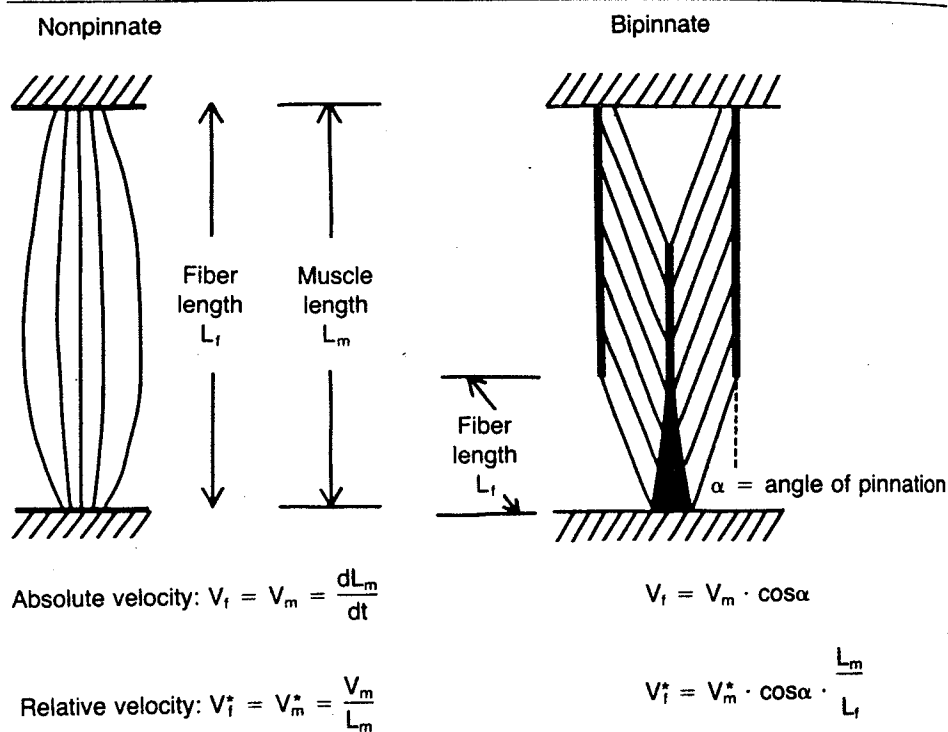
Units of Measure

Before attempting to reconcile the work of the motor units with the activity of the muscle spindles, one must consider the properties of each alone for the range of conditions over which muscles operate. This immediately presents a problem of finding some common measure to relate muscles engaged in activities as diverse as respiration, mastication, locomotion, and fine manual manipulation.

Absolute measures of velocity, such as millimeters per second, do not account for the accommodation of motion by distributing it over a long muscle versus a short muscle. Expressing the motion as a fraction of the rest length of the muscle (or some other standard such as maximal physiological length) is an improvement, but the underlying assumption is that the muscles fibers (to which the spindles are attached in parallel) are experiencing a similar fractional length change. In pinnate muscles, which thereby pack large numbers of obliquely oriented but short muscle fibers into a simple fusiform profile, the relative velocity experienced at each muscle fiber depends more on its individual length than on overall muscle length (Fig. 1). There are also correction factors for the change in pinnation angle caused by "parallelogram" motion of fascial planes, moving parallel to each other because of the need to conserve internal muscle volume [51, 52]. Although pinnation is widespread and considerable in muscles that generate large forces (angles to 21° [122]), this factor is rarely considered when velocities are calculated. The term *velocity* in this

FIGURE 1

Effects of pinnation on velocity. A given velocity of whole muscle stretch or shortening impacts differently on the individual muscle fibers and spindles, depending on the internal fiber architecture of the muscle. The equations appropriate to simple nonpinnate muscles (fibers run parallel to the muscle and end to end) and pinnate muscles (fibers run obliquely between fascial bands) are compared.



review refers to corrected fractional velocity of muscle fibers and spindles, using relationships developed by Gans [51], although this must often represent a very rough estimate based on fragmentary data.

Except where specified, the term *spindle afferents* is used here to refer to only the primary endings, for which there are considerably more data because of their large size and easily recorded signals. By virtue of their speed of conduction and monosynaptic reflexes onto motoneurons, the primaries have been assumed to have a more important role, at least in rapid and fine movement control. Fortunately, these afferents include all of the complexities and nonlinearities of transduction and fusimotor control that must be explained, while the

secondaries may be viewed, with some oversimplification, as providing a subset of the proprioceptive information, lacking for the most part the velocity terms and dynamic fusimotor control (see Fig. 3).

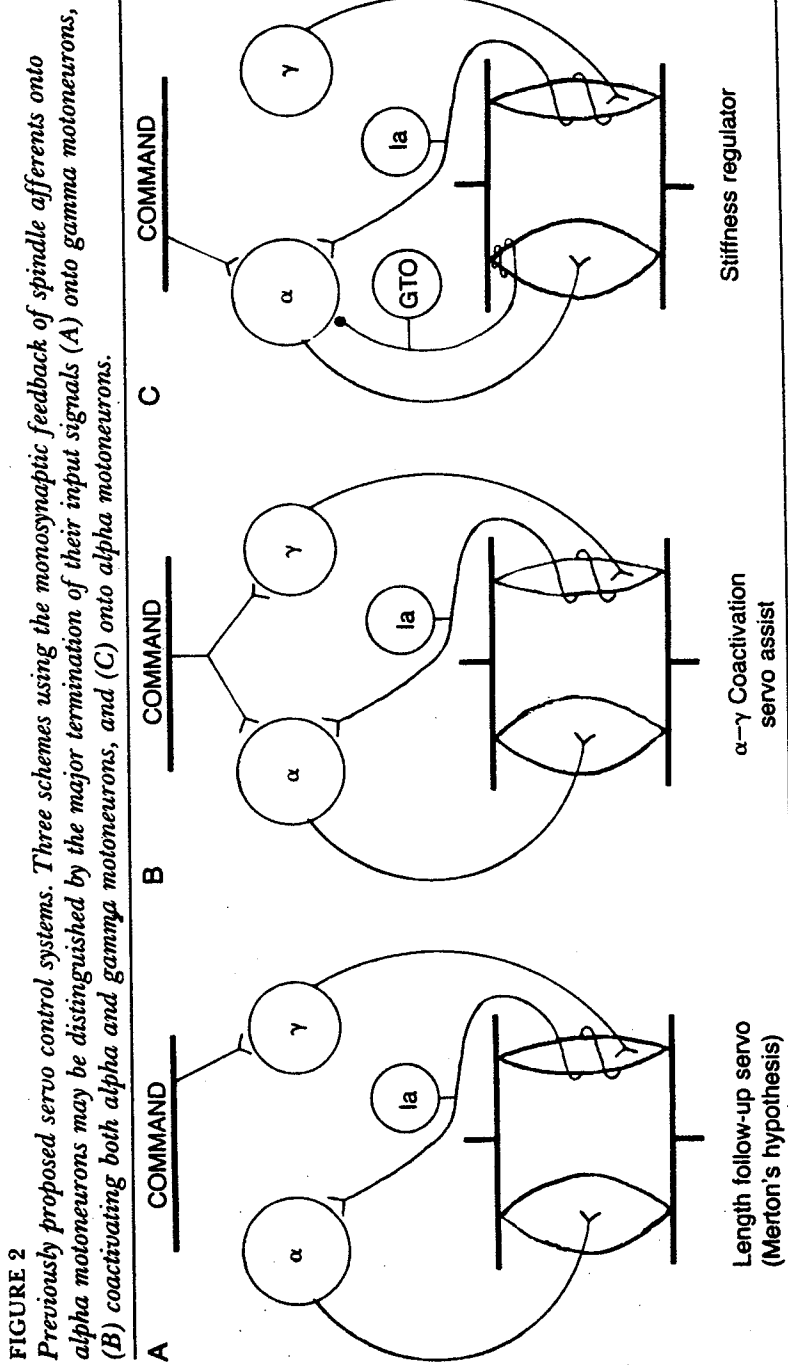
KINEMATICS AND CONTROL

Servo Control Theories

The usual purpose for activating a muscle is to cause some state of motion (or lack of motion) to occur in the limb. Kinematics is the study of motion, and motion per se is quantified by velocity. While other terms such as absolute position have important effects (e.g., changing lever arms or degree of actomyosin overlap in the sarcomeres), these effects tend to be local to the particular mechanical system in question and are often poorly described for biological systems. Velocity (particularly corrected relative velocity of muscle fibers; see later discussion) is a useful comparative descriptor for mechanically diverse systems. As we shall see, it is also an efficient coordinate system for transducers and control loops operating with a limited dynamic range in their signals.

If we imagine the central command to be expressed in terms of a time course of velocity, then it is apparent that the required activation of the muscle can only be calculated by taking into account the current position and motion of the limb. Furthermore, if the limb is subject to external loading or if the muscles behave unpredictably as a result of fatigue or potentiation, the central controller will have to make use of this proprioceptive information during the course of the movement, to appropriately adjust the activation state. If this calculation is made by fixed linear combinations of the command signal and the proprioceptive signal, we have a simple linear servo controller.

Figure 2 shows three variations on this theme. The first historically was Merton's hypothesis regarding the use of the fusimotor neurons as the primary initiator of muscle contraction [105]. In principle, a new position of the muscle can be specified by setting the firing rate of the gamma motoneurons alone. This gives rise to a change in the discharge rate of the spindle afferents. Through their projections onto the alpha motoneurons, this change results in a similar change in extrafusal activity until the muscle arrives at a new equilibrium point. There the spindle and motoneuron firing rates are at equilibrium and the tension output is balanced against the load, resulting in zero motion. Such a system is slow and prone to oscillation in the face of inertial loads [130]. Furthermore, it makes two major predictions that are not supported by more recent data. First, it suggests that the main output of the motor command centers should be to



the gamma rather than the alpha motoneurons. Second, it suggests that movement should always be preceded by a burst of spindle afferent activity as a result of such fusimotor activity.

The next hypothesis was that of length-servo assisted motion [58, 102, 130]. In this scheme, the alpha and gamma motoneurons are activated simultaneously by the same command signal, *alpha-gamma coactivation* in the terminology of Granit [58]. The degree of influence of the spindle afferent feedback on the motoneurons thus varies directly with the degree to which the actual trajectory departs from the desired trajectory. If the intrafusal and extrafusal motions coincide exactly, there will be no change in the state of activity of the spindle afferents and no feedback error. Overlooking for the moment the diverse speeds of contraction and receptor effects of the various intrafusal and extrafusal muscle fibers, this notion has some merit for the control of single muscles shortening against a load. However, coactivation would not necessarily be useful for feedback during the performance of tasks in which the extrafusal muscle is required to act as a stiff spring against a lengthening load. In this and in other circumstances described later, intrafusal activity appears to be modulated in ways that seem somewhat independent of extrafusal recruitment. Furthermore, studies of movements by deafferented animals have suggested that the effective gain of the feedback loop is quite small [13].

More recently, Houk has hypothesized that spindle feedback is used in concert with the negative tension feedback from Golgi tendon organs to stabilize the stiffness of the muscle [74]. Stiffness is defined operationally as responding force output divided by the disturbing length change, a relationship that appears to be linearized by the complex interplay of intrinsic muscle properties and proprioceptive feedback. In this context, motor command signals to the alpha motoneurons can be viewed as supplying a bias upon which a superimposed net excitatory proprioceptive signal will cause their recruitment [7, 74]. This formalizes the relationship between descending control signals and the properties of the final common pathway of output. This notion has merit for tasks in which one needs to maintain a position with a variable degree of compliance. However, it does not account for the actual temporal patterns of recruitment of muscles seen during rapid voluntary movements [53], and it does not explain the ability to make reasonably controlled movements in the face of severe disturbance of the spindle signal by vibration [34].

All of the preceding hypotheses share a common strength and weakness. They all are based on sound concepts of servo control

theory and on circuit elements known to be anatomically present. However, each accounts well for only a highly constrained class of muscle function. Before attempting to reconcile their conflicts or proposing alternatives, let us examine the range of muscle work for which any general theory of motor control must account.

Range of Muscle Kinematics

The muscles engaged in mastication and respiration generally work by shortening at modest velocities against frictional, viscous, and somewhat elastic loads. The total ranges of the movements are usually small, although these muscles may under different circumstances participate in larger and faster shortening movements. Most important, they generally do not generate active tension while being stretched by external forces—so-called active lengthening.

The active lengthening condition arises quite commonly in the antigravity (extensor) muscles of the limbs during locomotion. These muscles act in a spring-like manner to absorb the body weight, at first yielding under the load and then maintaining near isometric or slightly shortening length over the remainder of the stance (load-bearing) phase of gait [45, 57, 106]. In muscles that are principally extensors, the lengthening velocity of the muscle appears to be modest, but many of these muscles are pinnate, implying considerably larger fractional velocities at the muscle fibers and spindles. For example, the correction for fiber architecture in the medial gastrocnemius of the cat [51, 122] (Fig. 1) changes the typical walking velocity (negative or positive, small excursions) of 0.2 rest lengths/s in the muscle to 0.8 rest lengths/s for the individual constituent fibers and, presumably, the spindles in parallel with them.

The anatomically diverse muscles of the cat hindlimb provide examples of an extraordinary range of velocities during just walking and trotting. Even if one supposes that we need consider proprioceptive control only during periods of extrafusal activity (a very unwise supposition), the various muscles generate force while undergoing velocities ranging from -3 to $+3$ rest lengths/s. In some cases, both extremes of this active velocity range occur within a single muscle (e.g., anterior sartorius) [92] (see Fig. 9, p. 190). It is interesting that pinnation is notably absent in muscles that undergo the larger overall muscle velocities (e.g., hamstrings and sartorius); instead, at least some of these muscles employ short muscle fibers in series with each other or with fine connective tissue strands [40] (F.J. Richmond, A.J. Rindos, and G.E. Loeb, unpublished material), configurations that have not been subjected to rigorous mechanical analysis.

At the other extreme, we must consider the fine manipulative motions of the hand and finger muscles, which have provided much of

the data from human subjects. In these tasks the velocity and the range of movement are highly constrained. Control of these movements is of particular interest because they occur over ranges for which deafferented spindles have special high-sensitivity mechanisms not seen in spindles subjected to larger movements or to fusimotor contraction [68, 81].

Tension Output Properties of Muscle

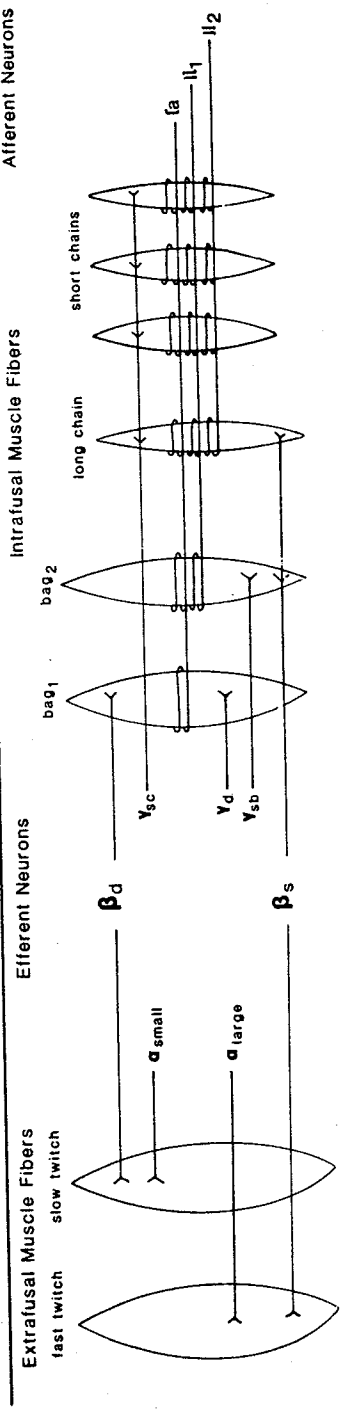
The force-velocity relationships of muscle fibers have been carefully studied in single muscle fibers of frog and in whole muscles of many species, although again there has been little systematic attempt to correct for the angle of pinnation effect on both velocity and the transfer of muscle fiber tension to the tendon. Fairly complete data are available for active shortening, and are generally well summarized by Hill's equation for force as a function of velocity and V_{\max} , the velocity at which the contracting whole muscle can sustain no external load [70].







The force output of active muscle during lengthening has been measured by Joyce, Rack, and Westbury [86, 117], but lengthening has been much less intensively studied than the isometric and shortening conditions. When stretch is first applied to an already tetanically active muscle there is a considerable rise in tension output, an effect related to the absolute amount of stretch rather than to velocity. At some point in the stretch, presumably related to the maximal backward excursion of the cross-bridges, the force drops fairly abruptly. However, it tends to remain relatively high (often greater than tetanic isometric force) and is fairly independent of the lengthening velocity. Because the cross-bridges complete dephosphorylation of ATP only after completing a shortening cycle [141], active lengthening is a highly efficient way of generating large forces (albeit negative work), much like the pulling apart of two parallel strings of permanent magnets. There is kinesiologic evidence that the normal recruitment of muscles includes these high-force, negative-work domains [140].

Receptor Sensitivity of Spindles

The sensitivity of muscle spindles to both positive and negative velocities is well known for deafferented spindles. It consists of a short-range sensitivity to small movements that is very high for both velocity and amplitude of the movement with a sudden drop to a much lower sensitivity once the amplitude exceeds some critical value [65, 67, 68, 89]. This point is presumably related to the excursion of intrafusal cross-bridges, which are likely to be attached in some small numbers, even in the absence of fusimotor activation, and which are broken beyond a certain excursion [68]. If the muscle is allowed to sit un-

FIGURE 3 Muscle spindle control and responses. (Top) Afferent and efferent innervation pattern of the muscle spindle, showing pure fusimotor control from gamma motoneurons (dynamic, static chain, and static bag types) and two known types of combined intrafusal and extrafusal innervation through dynamic and static beta motoneurons. Afferents have been divided into primary endings (located at the midpoint of the spindle and influenced by all intrafusal muscle fibers) and two types of secondary endings (located successively more eccentrically and influenced respectively by bag₂ and chains or by chain fibers alone). Variants and intermediate forms of these afferent, efferent, and intrafusal structures are not uncommon. (Bottom) Spindle afferent sensitivity has been divided into four independent additive terms of bias, length sensitivity, dynamic sensitivity (length \times velocity), and stickiness (dash pot-like asymmetrical acceleration). The effects of increasing the strength of each term alone are shown in the first column (bottom to top); the other columns indicate the relative importance of each fusimotor input states. Output patterns have been simplified for clarity; they normally include more gradual transitions and some hysteresis where abrupt step changes are shown here [10, 17]. Pure γ_c effect shown here includes one-to-one driving of primary ending by each chain fiber twitch, an effect not seen on secondary endings that may be decreased by asynchronous combination of several different kinds of fusimotor input, probably the usual physiologic condition.



Fusimotor Effects on Ia Responses deafferented	Y_d or β_d	Y_{sb}	Y_{sc}	β_s	$Y_s + Y_d$
 stiction increase	+	0	0	0	0
 dynamic sensitivity increase	+++	+	0	+	++
 length sensitivity increase	++	+	0	0	++
 bias increase	+	++	++	++	+
 simple length transducer	0	0	0	0	0
 test stretch					

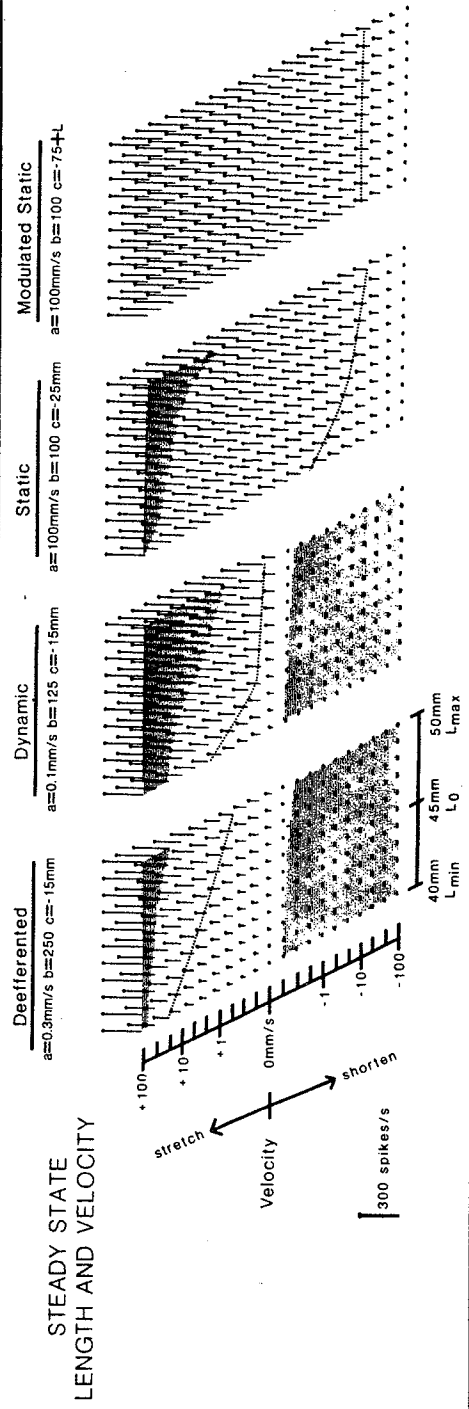
disturbed at a new length, these "sticky" cross-bridges reform and the short-range sensitivity of the afferents returns. The large excursion responses of both primary and secondary endings are a combination of length (independent of velocity) and length \times velocity terms, the latter being much more important in primaries and often near zero in secondaries [102].

The effects of superimposed fusimotor activity are profound, complex, and difficult to anticipate. The magnitude of the effects possible with maximal stimulation of the gamma motoneurons is undeniably large, including the high-frequency activation of afferents during rapid muscle shortening, which normally inactivates deafferented spindles [6]; increases or decreases in the long-range velocity sensitivity [90]; loss of the short-range hypersensitivity noted above [42]; and biasing at constant length [3]. The complexity is because there are at least three functionally different populations of gamma motoneurons innervating at least three or four anatomically and physiologically different intrafusal muscle fiber types [9, 15, 16]. The most common arrangement, as viewed by Boyd and his colleagues [16], is summarized and somewhat simplified in Figure 3, but it should be noted that different and even more complex arrangements have been described in muscles such as the cervical paravertebral system in cats [8, 119].

Muscle spindle afferent sensitivity has been studied under systematic experimental activation of part of the fusimotor innervation of the spindle. These studies have revealed the complex individual and interactive effects outlined in the bottom half of Figure 3 [11, 32, 35, 37, 46, 76, 77, 79, 82, 84]. The natural state of activation of these various fusimotor components during a movement generated by the subject has been observed only rarely (see pp. 177–179, 181) and must usually be inferred indirectly from changes in the activity of the spindle afferents from what has been seen or what was expected in the deafferented state. Given the complexity of the fusimotor system, this is obviously highly problematical for all but the grossest effects.

Hasan has recently put forward a comprehensive model of the spindle transduction process that accounts well for deafferented response data and that enables simulation of many fusimotor effects, represented along a single axis of static to dynamic effects with the deafferented condition at an intermediate point [66]. The model is constructed from terms corresponding to the individual mechanical features of the spindle architecture and its coupling to the muscle, including elastic and viscous properties. This has been used to generate the three-dimensional plots of Figure 4, which schematically survey the ranges of spindle responsiveness for steady-state condi-

FIGURE 4
Spindle Ia activity at steady-state lengths and velocities for various fusimotor states. Vertical "lollipops" indicate firing rate of a spindle primary in response to a given length (horizontal axis; linear) and velocity (diagonal axis; logarithmic) under equilibrated (nontransient) conditions. Each panel simulates a different set of fusimotor conditions, using the indicated coefficient values in Hasan's model (see Appendix). Cross-hatching indicates conditions causing saturated output rates (>300 or <0 spikes/s). Dotted line indicates pairs of input conditions (length and velocity) producing a midrange output of 50 spikes/s.



tions of the usual experimental variables of length and velocity. Regions of high slope signify regions of high sensitivity. Plateaus (cross-hatched) indicate saturation of output (zero or maximum rate of 300 pps), for which conditions the spindle transducer could be considered "out of range"; the dashed line indicates the 50 pps (midrange) iso-output contour.

There are also complex time-dependent responses to length change transients, which are the product of viscoelastic couplings among the sensory transducer, the intrafusal fibers, and the extrafusal muscle. In keeping with this review's emphasis on the velocity over which a muscle must be controlled, it is worth summarizing these effects in terms of velocity. The gamma-dynamic system, innervating bag₁ intrafusal muscle fibers, increases the velocity-dependent response of primary endings relative to the zero-velocity length sensitivity, a difference called the *dynamic index* by Matthews [102]. This effect includes both increases in activity during a given positive velocity (stretch) and decreases in activity (usually to zero) in response to a given negative velocity (shortening). Given the limited total dynamic range of rate encoding of the spindle afferent to the typical 0–300 pps, this has the effect of heightening *relative* sensitivity over a limited dynamic range of velocities (Fig. 4). On the other hand, the gamma-static system, which innervates bag₂ and chain intrafusal muscle fibers, has several effects, all of which tend to increase the *dynamic range* of velocity sensitivity:

1. Gamma-static activation greatly reduces the short-range hypersensitivity of the spindle [35].
2. Gamma-static activation added to gamma-dynamic activity tends to reduce the latter's velocity-dependent effects, particularly for small movements [79].
3. Gamma-static activity, if appropriately modulated, can maintain spindle activity even during rapid shortening of the parent muscle, presumably by preventing the bag₂ and chain fibers from becoming slack [6] (Fig. 4, far right). This effect is more commonly described in terms of a change in firing at a given length, but this obscures the functional significance during negative-velocity excursions. There is both direct and indirect evidence of rapid modulation of gamma-static activity during naturally occurring muscle shortening (see pp. 179, 182, 184, and Figs. 7 and 8).

Transducer Theory: Optimal Design Concepts

Before actually considering the signals generated by spindles during normal movement, it is worth examining some theoretical considerations about the relationships between transducers and the physical events they are designed to encode. It is a truism that the muscle spindle is, in the first place, a sense organ; presumably it contributes

information for a variety of purposes. These may include but are not limited to closed-loop feedback servo control, feed-forward compensation for muscle response time, pure kinesthetic perception, regulation and cuing of program generators, and remote reflex excitation and inhibition of antagonists, contralateral muscles, and distant intersegmental structures (e.g., postural stabilization). Focusing attention on one of these mechanisms and calculating some hypothetically optimal spindle signal for driving such a mechanism has been a frequently employed but not very revealing strategy for understanding the fusimotor control of muscle spindles.

A transducer is a device that converts one form of energy into another. If this is done in some orderly manner, then information (entropy) implicit in the temporal variations of the input energy will be preserved in the output signal. Note that the preservation of information does not require linearity, only predictability. The operating range of a sensory transducer can be characterized by the range of inputs and outputs for which some monotonic, nonzero-slope relationship exists. For general purpose industrial transducers, these ranges are usually fixed by the design of the device, and within these ranges the input-output relationship is linear—they yield proportional changes in output for incremental changes in input anywhere over the operating range (see Fig. 5A).

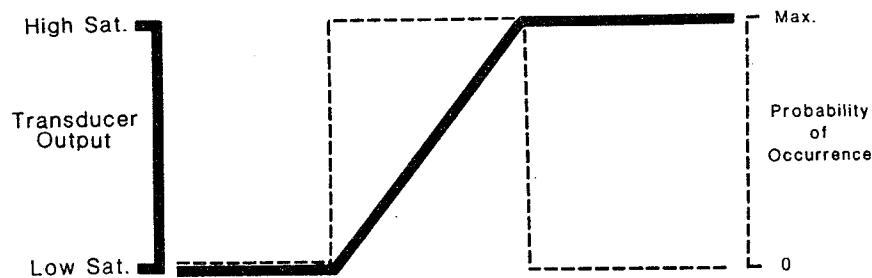
Because of the inevitable presence of noise, the output signals obtained from multiple presentations of the same input will display some range, which we describe by the standard deviation. It is convenient to think of the noise as random fluctuations added to the signal after an ideal, perfect transduction has occurred, but at least some of this noise is intrinsic to the transducer or its encoding scheme (e.g., thermal noise, digital resolution, pulse rate quantization). These errors are distributed more or less equally over the operating range of the transducer, but they are proportionally larger for conditions when the output signal is small. This places a premium on selecting a transducer with an operating range that is well matched to the operating range of the input signal, so that the effects of noise are minimized (signal-noise ratio maximized). However, input signals that exceed the transducer range produce catastrophic failures of the output signal, with saturation and complete loss of incremental information.

The general approach of using well-matched linear transducers is a good signal-noise compromise when the distribution of input signals over time is fairly uniform over most of the transducer operating range, and zero outside it. Furthermore, linear relationships are simple to encode and decode. However, the input signals received by many biological transducers do not usually have such a flat probability distribution, but rather tend toward bell-shaped distributions cen-

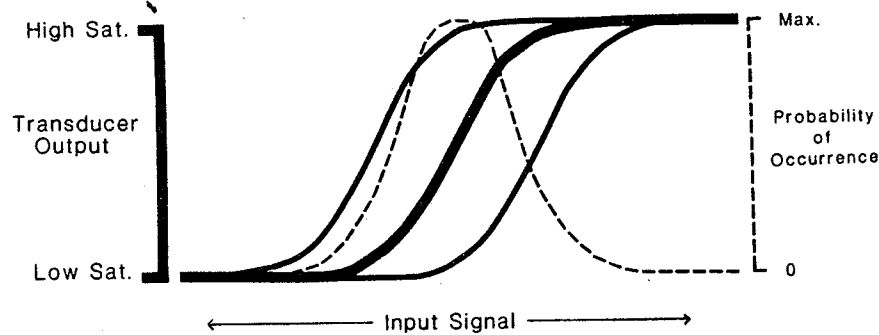
FIGURE 5

Transducer sensitivity curves. (A) Linear. If the probability of occurrence (dotted line) of a given input signal is flat over some defined region, the optimal transducer has a linear output relationship over this region (heavy solid line), with saturation occurring outside the region in either direction. (B) Sigmoidal. If the probability of occurrence is bell-shaped, the optimal transducer curve is a sigmoid, with maximum slope centered at the peak of the bell. Slight shifts between these two curves (light solid lines) seriously degrade the effectiveness of such a transducer. In all cases, the optimal transducer curve is found by taking the integral of the probability distribution curve (see Appendix).

A. LINEAR:



B. SIGMOIDAL:



tered on some favored operating point for the organism (Fig. 5B). The operating point and the width of the distribution around it may change abruptly for different tasks, and may shift gradually for a given task as the organism matures and develops its behavioral strategies and motor capabilities. That the distribution of input signals

for any one activity is not flat suggests certain transducer design strategies that should improve the average signal–noise ratio over time. First, the transducer is best used to signal deviations from the desired operating point of the process, rather than absolute values (e.g., the velocity-dependent signal from the spindle primaries could be centrally integrated to reconstruct limb position rather than relying on an absolute transducer of muscle length or joint angle. Second, the transducer should be maximally sensitive to the changes that occur most often, at the expense of changes that occur rarely. In the bell-shaped distribution of input signals it is apparent that small deviations from the mean operating point occur most frequently, so the largest part of the limited dynamic range of the transducer should be used to encode those signals, to minimize the effects of noise. Although this leaves little dynamic range into which the larger excursions of the input signal must be encoded, limiting their resolution in the face of noise, these signals occur rarely and there will be only a slight decrease in the overall resolution over time.

While this nonlinear transducer sounds complicated, it is in fact simple to find the optimal input–output relationship curve for any probability distribution of behavioral states. It is simply the integral of the probability distribution, turning a bell-shaped curve into the familiar sigmoidal curve of many biological processes (see Fig. 5B and Appendix). A fringe benefit of using such a distribution to arrive at a sigmoidal transducer curve is that the saturation catastrophe, which occurs when the design input range is exceeded, tends to be a continuous rather than a discontinuous change in the slope of the transducer response at this point. However, as Figure 5B indicates, relatively small shifts in the operating point can cause drastic degradation of the transducer sensitivity if they are not properly compensated by shifts in the transducer operating point.

The Spindle as a Transducer with Controlled Nonlinearity

It is useful to think of the muscle spindle as a mechanical transducer of position that is responsive to some combination of absolute length and velocity during the performance of a task. This combination tends to cover a limited, bell-shaped distribution of the physiological range of the muscle motion. Note that there is no reason why the transducer should produce a linear output, or even one well segregated along the dimensions of pure length or pure velocity. Such simple outputs are handy for the design of linear controllers for linear motors, but there is little that is linear about the performance of the muscle as a motor or about the interneuronal integration and transmission of control signals. As we shall see, the changes in slope of the input–output relationships described above have implications beyond a simple change of “gain” or “sensitivity” in a linear device.

The fusimotor system is well suited to set the midpoint of the dynamic range of the spindle afferents at any desired point in the length-velocity plane (Fig. 4). (From considerations of signal theory, I have estimated the midpoint at 50 pulses per second (pps), the center of a log scale from 10 to 300 pps. Saturation at the high end of this range is actually characterized more by noisiness of the spike generation mechanism than by smooth plateauing of output rate, but the effect on information content is the same.) It is also apparent that the fusimotor system can expand or contract the spindle's dynamic range to cover any distribution of inputs that tends to be encountered. Such a system of sensitivity control is by no means unique to the muscle spindle. In fact it is present in many biological sense organs, most of which are equipped with both intrinsically accommodating processes (e.g., light adaptation in the retina, phase locking in cochlear hair cells) and external gain controls (e.g., iris of the eye, stapedius and tensor tympani muscles of the middle ear). All of these features can be viewed as solutions to the problem of optimizing signal-noise ratio for the probability density function of situations likely to be encountered, at the expense of nonlinearity and at the risk of occasional saturation. We shall deal later with the problem of the neural deconvolution of the input signal (motion) from the transducer output (groups Ia and II afferents) and the transducer sensitivity control signal (static and dynamic fusimotoneurons). (Deconvolution is the mathematical term for the process of extricating one or more of several source signals from a composite signal.)

Signal Processing to Optimize Resolution

Another technique to optimize signal-noise ratio is signal averaging. Two forms of averaging that are probably used in the nervous system are averaging over populations of similar receptors (spatial integration) and averaging over time (temporal integration). The latter is particularly appropriate when dealing with the digital pulse rate codes of neurons, in which the amplitude of the signal is given by the instantaneous frequency of discrete events. However, the applicability of this technique to the muscle spindle is questionable. The spindle afferents appear to have been optimized for speed, with the fastest axonal conduction velocities of any neurons in the nervous system delivering signals to the spinal cord within 1 to 10 ms of events in the muscle. However, 100 pps is a fairly brisk firing rate for them, and an accurate assessment of mean rate by temporal integration would require many interpulse intervals, occupying perhaps 100 msec or more. One can imagine a very precise instantaneous interpulse interval analyzer (although not easily in neuronal circuitry). However,

as Matthews has noted, the fusimotor effects on spindles are distinguished by an irregular afferent spike pattern [104] that appears to be ignored as noise by the spinal cord [103].

Furthermore, the deconvolution mentioned above may require an accurate comparison of several asynchronous trains: the afferent and its fusimotor drives. This problem is common to sensory modalities that change receptor characteristics as fast as the input events themselves. Extracting visual object velocity from the combination of the foveally distorted retinal map and the oculomotor and vestibular signals is an analogous problem. Note that we are not supposing any particular coordinates or linearity of the result of this calculation; any meaningful use of the spindle signal to provide an absolute measure of length, velocity, acceleration, or any combination of them requires some such deconvolution. All these considerations argue against temporal averaging to improve the precision of any single spindle's signal.

If we can infer from conduction velocity that speed is of the essence, then we are left with averaging over ensembles of spindle afferents and gamma efferents, all of which must be generating similar spike trains. The great proliferation of spindle endings in small muscles [119], in which one might suppose that fine control was a goal, is consistent with such a mechanism. However, we have already noted that spindles, by virtue of their fusimotor program, can be tailored to a wide range of sensitivities. If this cannot be usefully accomplished on a spindle-by-spindle basis, but only by pooling ensembles, we might expect to find large convergent circuits in which the various afferents and fusimotor efferent signals (or suitable efference copies) are carefully weighted to produce a fast, accurate result. However, such circuits would not need to perform a general deconvolution (probably an impossibility given the nonlinearity); rather, they could efficiently process signals for only very specific fusimotor programs in the context of well-defined ranges of motion.

The successful operation of the same spindles in another very different range with a different sensitivity optimization program would presumably require both an independent source of the fusimotor program and independent summing networks. Because of the close interrelationships among the gamma and alpha motoneurons and their spindle afferent feedback, such dynamic switching could be difficult, if not impossible. Later we examine the concept of task groups, in which independent groups of motoneurons (alpha, gamma, and beta) and their spindles are assumed to be programmed to operate optimally for only restricted kinematic ranges of active length and velocity, enabling fast, simple, and accurate deconvolution and ready application of the proprioceptive signal to motor control. The

great proliferation of spinal interneuron types with diverse and widespread patterns of multimodal convergence [85] is consistent with this oligosynaptic deconvolution.

The sources of the information on fusimotor state required by such a deconvolution network remain unclear. Candidates include efference copy (motoneuron or premotoneuron collaterals) and any correlated sensory signals. There is some evidence from psychophysical experiments on the sense of joint angle to suggest that the Golgi tendon organ (GTO) contributes at least some of this information [121]. Such use of this extrafusal sensor would require that the fusimotor activity be reliably correlated with the extrafusal activity, although not necessarily coactivated or otherwise directly or inversely related. The variability of GTO response to different motor units and nonlinear response to various combinations [59, 83, 118] further suggests that the intrafusal and extrafusal output should follow a strict recruitment order. The task group notion is specifically intended to account for such local temporal invariances of alpha-gamma patterning, while permitting a wide variety of task-specific patterns.

NATURAL ACTIVITY PATTERNS

Armed with some theoretical notion of the scope of the proprioceptive problem, we can now examine the available examples of spindle afferent and efferent activity, in the light of the motor task being performed by the muscles that are host to this activity.

Respiration

The first motor control system that could be studied in any detail during self-generated movements was respiration, which is uniquely independent of consciousness in most aspects of its generation and regulation. Both spindle afferents and fusimotor efferents of the intercostal muscles were adopted as a model system after it became apparent that the diaphragmatic muscles were notably deficient in proprioceptors.

Critchlow and von Euler's technique of low-concentration lidocaine block of the relatively small-caliber gamma motoneuron axons [41] allowed the activity of single spindle afferents to be monitored with and without all or part of their fusimotor influences. This revealed that the strength of the natural fusimotor influence is sufficient to reverse the normal cessation of discharge of the deafferented spindle afferents during muscle shortening, in fact causing increased discharge during active shortening of spindles in both external (inspiratory) and internal (expiratory) intercostal muscles [2, 41]. The

gradual onset of selective fusimotor block and the subsequent return of normal function revealed multiple effects on some spindle afferents, which suggested both tonic and phasic patterns of fusimotor discharge. This has been confirmed by Sears and others using direct gamma motoneuron recordings [44, 48, 124].

The observed activation of the gamma and alpha motoneurons to a given muscle during the same phase of the movement was a strong encouragement to the notion of alpha-gamma coactivation as a principle of motor control [58]. However, the original reports were careful to point out that the alpha-gamma relationships were not strict either in time or amplitude and included anomalies peculiar to the respiratory system, such as activation of gamma motoneurons to inspiratory muscles during passive inflation of the lungs by a respirator [41]. While fusimotor neurons with dynamic and static effects on spindles could be discerned, the identification of the former with the tonically active gamma motoneurons and the latter with the phasically active gammas (as is found in mastication) was never clear. Indeed, in retrospect the spindle afferent patterns are striking in their general lack of dynamic response to velocity under all conditions, in contrast to the high dynamic index often seen in spindles located in muscles that are normally restricted to small excursions. One might speculate that velocity sensitivity would be particularly useful in predicting the trajectory of an inertial mass being moved by a muscle acting through a lever arm, a situation typical of limb and jaw muscles but clearly absent in respiratory muscles.

It is now apparent that the motor control of the respiratory muscles is a specialized system with strong regulatory input from the specialized pulmonary stretch receptors [38]. The activity of the muscle spindles was seen to be highly variable among the various intercostal muscles, and even within apparently homogeneous anatomical units. The complex lever system of the ribs makes muscle fiber length determinations almost impossible from the rib spacings given in the records. A typical inspiratory increase of 2 mm in a 15-mm intercostal space is probably accomplished by a very slight active shortening of external intercostals and a similar passive lengthening of the internal intercostal muscles. Peak inspiratory velocities (probably less than 0.1 rest lengths/s) cause silencing of some external intercostal spindle afferents, while others generate 40 to 60 impulses per second, presumably in response to gamma static biasing. It is not clear whether this variability relates to the presence of different task groups. These muscles are involved in many other tasks (e.g., posture control, vocalization, sneezes and coughs), and these could well involve alternative task group organizations.

During regular breathing in an anesthetized preparation, most

spindle afferents appear to be modulated over ranges within the limits of about 10–100 pps. Sustained zero discharge appears rare, and faster bursts result primarily from complex fusimotor reflexes mediated by cutaneous and pulmonary stretch receptors. It is likely that these latter effects occur fairly regularly during unrestrained behavior, so that the spindle activity is likely to be generally well modulated over most of its dynamic range. Paradoxically, the respiratory muscle spindles represent one of the strongest examples of “servo assistance,” as loss of this input causes clear decreases in respiratory effort and in ability to compensate for load [38]. However, the operative feedback loop clearly includes more than just spindle afferents and motoneurons.

Mastication

The spindles in the masseter muscle are probably the best understood in terms of control, activity, and feedback during voluntary movement. This is largely the result of ingenious exploitation of the accessibility of afferent and efferent neurons in intracranial brainstem pathways, the existence of a stable platform (the skull) for mounting transducers and electrodes, and the ease with which natural cyclical movements may be elicited [134]. The qualification “probably” stems from the unusually homogeneous fiber diameters for both afferents and efferents, which make impossible the usually clear separation of alpha and gamma motoneurons and of spindle primaries and secondaries on the basis of conduction velocity alone [39]. However, Taylor and colleagues have collected a considerable body of circumstantial evidence supporting their contentions for these identifications [39], which will be accepted here at face value.

During lapping and chewing movements in the cat [39, 133] and monkey [55, 87, 99, 101], the spindle secondaries have been observed to discharge in approximate proportion to the length of the muscle, whereas primaries discharge in proportion to the velocity of the movement. When the velocity is negative (i.e., during active closing movements), the primaries tend to become silent whereas the secondaries continue to fire at a rate appropriate for length at each instant. This dichotomy is somewhat similar to the behavior of the primaries and secondaries in deafferented (passive) responses to applied stretches.

However, it is quite clear that a quantitative explanation of spindle activity during eating requires a fairly sophisticated fusimotor program, since the same movements applied to the jaw of a deeply anesthetized animal (presumably functionally deafferented) evoke afferent activity that is substantially different [39]. Indeed, direct recording from presumed fusimotor efferents during voluntary movements reveals a tonic discharge of the dynamic fusimotor fibers

that heightens the velocity sensitivity of the primary endings, and a phasic discharge of the static fusimotor fibers that compensates for the natural tendency of secondaries to be silenced during the shortening peaks [5]. The lack of modulation noted for the dynamic fusimotor activity is in marked contrast to the strongly modulated static activity. However, as with the intercostal muscles, even the gamma-static activity is not quantitatively proportional to the alpha motoneuron activity manifested by the electromyogram (EMG) from the muscle. Some afferent activity appears to reflect the effects of phasically modulated fusimotor influence, in the absence of overt movement just before voluntary movement is initiated [133]. Also, it should be remembered that the interaction of simultaneously activated gamma-static and gamma-dynamic neurons is rate-sensitive and non-linear, with static effects occluding dynamic effects for small stretches and at length minima in large shortenings, while dynamic effects predominate during large stretches [79].

Figure 6 shows a particularly striking example of variability in the fusimotor program for similar jaw movements made during lip licking versus chewing [134]. While the mechanical excursions are similar, the motor control problem during grooming is probably considerably different than that for eating, where the feedback from tooth afferents is known to be a strong influence on motoneurons [99]. The spindle activity during licking is very low during rapid jaw opening and accelerates during a jaw closure of approximately 200°/s, estimated from gross anatomical considerations to represent 2.0 rest lengths/s shortening for the temporalis muscle fibers. This suggests strong gamma-static and little or no gamma-dynamic action. Yet another fusimotor program has been inferred from isometric biting, where gamma-dynamic coactivation appears to predominate, optimizing sensitivity to small fluctuations in muscle length [87]:

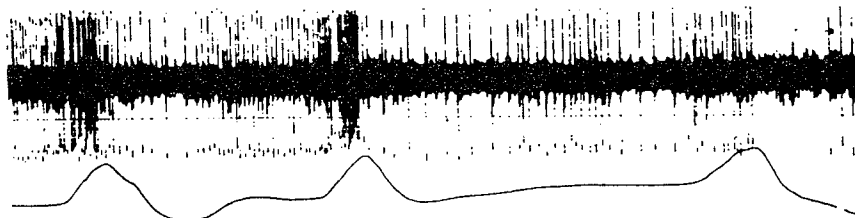
As for all spindle activity, the effect of the afferent activity on the jaw motor program is quite unclear. There is some evidence that the discharge of the spindle afferents during chewing is increased by unexpected resistance to closure [134] but not at normal occlusion [101], consistent with the notion of servo assistance. However, the motor command to the jaw-closer motor pools is robust and substantially independent of this signal [99]. Furthermore, the high rate of discharge in both primaries and secondaries during jaw opening is probably blocked from reflexly activating the closer muscles by a deep hyperpolarization of these motoneurons, as reported by Goldberg and Chandler for guinea pigs during similar movements [54]. The main conclusion is that the fusimotor program has caused the spindle afferents to be modulated over a substantial fraction of their dynamic range of firing rate during the movements generated. This is in agreement with principles of optimal transducer design, but not

FIGURE 6

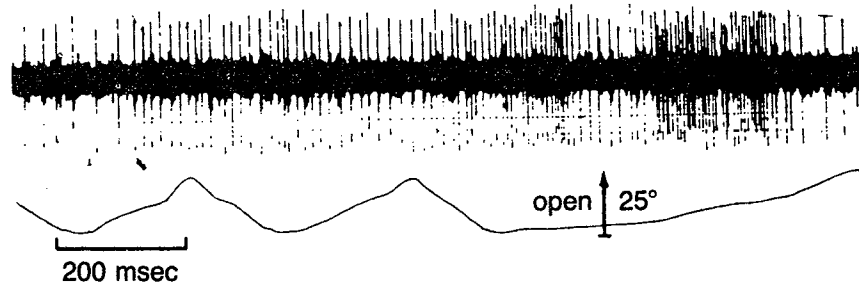
Jaw muscle spindle activity in the cat. Top trace of each pair is the microelectrode record of the activity of a presumed spindle primary afferent from the jaw-closing temporalis muscle; bottom trace is the jaw angle with opening (muscle stretch) upward. Note cessation of neural discharge during muscle shortening while chewing but preservation of activity during similar movements while licking.

SOURCE: Reprinted with permission from Taylor, A., and F.W.J. Cody. Jaw muscle spindle activity in the cat during normal movements of eating and drinking. *Brain Res.* 71:523-530, 1974.

EATING



LICKING LIPS



as predicted by any simple servo control scheme. In fact, for at least some jaw movements, the spindle signal may have little or no direct effect on motoneurons and is perhaps being used to judge the consistency of objects in the mouth to inform higher-level planning of jaw and tongue motion.

Locomotion

Since Sherrington, the cat hindlimb has been an important model system for the study of locomotor control and, indeed, for spinal motor control in general. Most of what is known about the structure and properties of mammalian muscle spindles and their fusimotor control system comes from studies of a few cat hindlimb muscles.

Most, if not all, of the hindlimb myoskeletal specializations are clearly designed to optimize the performance of the major function of this appendage, which produces agile and efficient locomotion at a variety of speeds over a variety of terrains. All of this suggests that data regarding normal spindle function in these muscles might provide excellent tests of general principles of motor control. Three preparations have been studied: (1) decerebrate locomotion, in which spindle afferents were recorded from dissected dorsal root filaments [126]; (2) decerebrate and spinal locomotion with one limb fixed to facilitate alpha and gamma motoneuron recording from dissected muscle nerves [109, 131]; and (3) intact, unanesthetized animals chronically implanted with floating wires in dorsal roots [114] or dorsal root ganglia [94].

To say that the cat hindlimb is largely engaged in the singular task of locomotion is not to say that the individual muscles are all doing the same sort of work. The variety of kinematic behaviors represented covers the complete range of active and passive shortening and lengthening.

The major antigravity extensor muscles of the knee and ankle become active at or just before footfall [47, 60] and generate fairly constant levels of force through much of stance. As the body weight is transferred to the limb (E_2 phase of the Phillipson step cycle; see Fig. 7), extensor muscles yield somewhat in an active lengthening. They are nearly isometric during midstance and begin shortening at an increasing velocity toward the end of stance, even though some extensor muscles decrease or even cease EMG activity considerably before footlift. Prochazka and colleagues have recorded spindle afferents from muscles typical of this group and report that they generate afferent signals that are rather closely related to the actual length of the muscle throughout these active excursions, with additional modest sensitivity to velocity [113, 115] (see Fig. 7). Modulation of firing frequency covers a fairly broad range of about 30–200 pps. Spindle activity in extensors during the passive lengthening and shortening of the swing phase (flexion followed by E_1 extension) is less vigorous than during E_2 stretch, despite larger excursions. Manual replication of the movements during deep barbiturate anesthesia (presumed functional deafferentation) has confirmed the presumption that the spindle activity during the active stance phase is supported by modest fusimotor influences, probably both dynamic and static [115]. This is consistent with the few direct recordings from fusimotor neurons [109, 131] and from stretch sensitivity of spindle afferents [108, 128] in decerebrate walking cats.

There are fewer available spindle records from the ankle dorsi-flexor muscles, which, in contrast to the antigravity extensors, undergo

rapid shortening during their burst of extrafusal activity in the flexion phase. However, in both decerebrate [125] and normal cats [95], these flexor spindle afferents fire during the active shortening (estimated at 1.7 rest lengths/s) with about the same intensity as during the passive lengthening that immediately precedes and follows in late stance and E₁ phases, respectively (Fig. 7). This is strongly indicative of rapidly modulated gamma-static output to flexor muscles. A similar difference between weak static fusimotor effects in extensors and strong effects in flexor muscles has been reported during decerebrate scratching [49] and has been inferred from changes in Ia stretch sensitivity during decerebrate locomotory movement in the contralateral limb [108]. Thus, for both ankle extensors and flexors, spindle afferent activity either is at or passes through the midpoint of the firing rate range during periods of muscle activity, even though the very different kinematics of these muscle groups require quantitatively and qualitatively different fusimotor effects to achieve such activity.

This extensor/flexor dichotomy poses an interesting question for

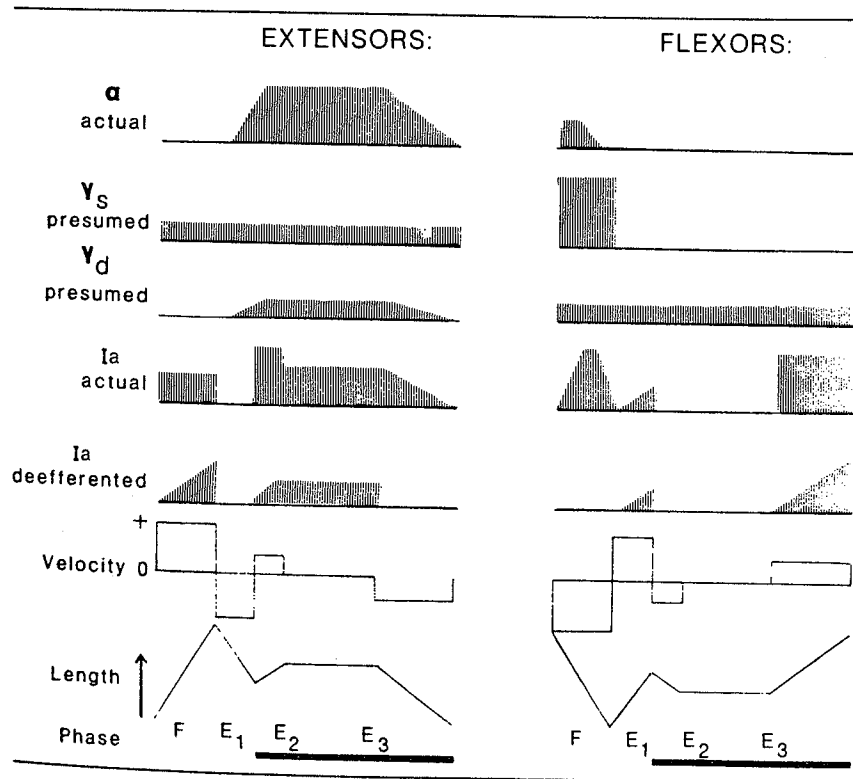
FIGURE 7 (right)

A schematized summary of muscle and spindle activity in cat ankle extensors and flexors during a single step cycle of walking (stance phase indicated by heavy bar at bottom). (Traces from bottom up) Length, shown with stretch of the relevant muscle as an upward deflection; velocity, under a similar convention; Ia activity expected or seen for such movements applied in a functionally deafferented muscle; actual Ia activity usually seen during normal walking; simplest pattern of gamma-dynamic influence consistent with the observed spindle activity; simplest pattern of gamma-static influence; alpha motoneuron activity responsible for active use of the muscle during walking. Note the inverse quantitative differences between alpha activity of the loaded antigravity extensors and the unloaded flexor muscles, and between the weak gamma-static coactivation of the extensors and the strong gamma-static coactivation of the flexors. When combined with the different kinematics of these two muscles during their active periods (mostly isometric in the extensors, rapidly shortening in the flexors), the net results are Ia activity patterns in both muscles that are in the midrange of possible firing rates during the period of use of each group of muscles.

The extensor fusimotor program shown here is based on recent direct recordings from fusimotor axons during decerebrate walking [131] and inferences from stretch sensitivity modulation [108]. Attempts to reproduce normal spindle firing patterns using controlled fusimotor stimulation during replicated locomotor length sequences in anesthetized preparations have suggested less dynamic modulation and more static modulation [4, 75, 80].

spindle function in bifunctional muscles (i.e., muscles used as both extensors and flexors by virtue of biarticular action and two periods of recruitment in each step cycle), which predominate in the proximal hindlimb musculature. There are a few records of spindle afferents from the hamstring muscles [91, 95, 113, 115], which function as hip extensors and knee flexors (see Fig. 10). However, they are difficult to interpret because of the complex excursions of these biarticular muscles, which differ with location within the muscles because of their broad insertions on the tibia.

The bifunctional anterior thigh muscles, including rectus femoris (RF) and sartorius pars anterior (SA), both hip flexors and knee extensors, offer a particularly interesting situation, in which the stance phase excursions are rapidly lengthening and the swing phase excursions are rapidly shortening in a nearly symmetrical, sinusoidal fashion. Both muscles generate two EMG bursts per step cycle, occurring during the maxima of the respective shortening and lengthening velocities (the rectus femoris flexor burst usually appears only during faster walking and trotting) [92] (see Fig. 10, p. 192). Recordings from spindle primary afferents in RF and SA have shown an extraor-



dinary range of behavior [92, 96], in contrast to the much more homogeneous records from unifunctional muscles. In some cases, spindles generate activity in proportion to a combination of length and velocity, with little indication of strong fusimotor modulation during either the flexion or extension EMG burst. This type of behavior is similar to that seen in the ankle extensor muscles, except that the active lengthening during stance is much more pronounced in these combined knee extensors and hip flexors. In other spindles, the group Ia activity during the active shortening in the flexion phase is as high as or higher than that seen during the active lengthening in the stance phase. This is strongly suggestive of rapidly modulated and intense gamma-static activity during active shortening, as also inferred for the pure ankle flexors. Examples of both kinds of spindle afferent behavior are shown in Figure 8.

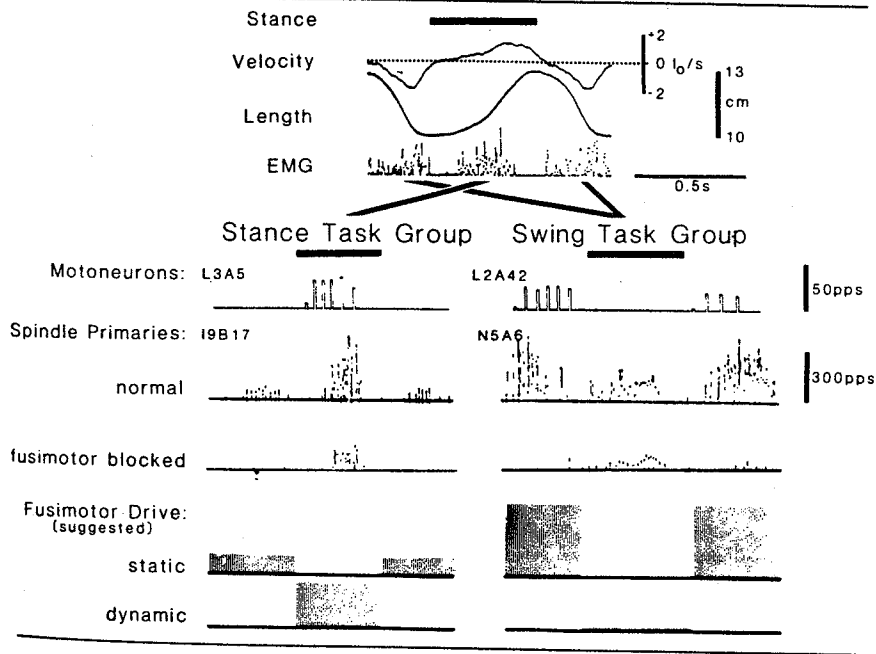
Using partial lidocaine blockade, Hoffer and Loeb [71] have been able to ascribe at least some fraction of the sartorius spindle activity patterns to definite fusimotor drive. In these preparations the femoral nerve innervating these muscles was equipped with a nerve cuff electrode (also used for spike-triggered averaging of unit potentials for conduction velocity determination) that had a percutaneous catheter for drug infusion. The spindle afferent and parent muscle EMG activity were recorded as the animal walked on a treadmill. During walking, a low-concentration lidocaine solution was slowly infused and later flushed away with saline. This drug tends to selectively block conduction in small-diameter fibers (e.g., gamma motoneurons) without affecting larger fibers (e.g., spindle afferents and alpha motoneurons). As in the respiratory muscles [41] (see previous discussion), spindle afferent activity exhibited a progressive stepwise loss during lidocaine infusion. This usually included loss of all or most activity during muscle shortening and up to 70 percent diminution of activity during muscle lengthening. In contrast to the reported effects of such fusimotor blockade on ankle muscles in the decerebrate cat [125], the disruption of the normal pattern of spindle activity caused no noticeable change in the EMG output, patellar force (monitored by an implanted strain gauge), or limb trajectory (unless and until the lidocaine caused direct alpha motoneuron blockade). Afferent activity returned to normal after flushing with saline, again with no change in gait. Figure 8 shows comparative activity traces for spindle afferents before and at the point of maximum fusimotor blockade, from which data inferences have been drawn about the types of fusimotor effects likely to be occurring during normal locomotion.

The diversity of spindle afferent and fusimotor function in a bifunctional muscle like SA is all the more intriguing in view of the

FIGURE 8

Stance and swing task group in sartorius pars anterior muscle. During the two EMG bursts of each step cycle (top center traces, during and between stance period indicated), the SA motoneurons are divided into two independently recruited groups (top trace of groups to left and right). Examples of spindle primary afferent activity shown below, for similar step cycles before and during lidocaine blockade of fusimotor action, suggest a similar division of gamma drive (bottom, shaded traces).

SOURCE: From unpublished records of Loeb, G.E., J.A. Hoffer, M.J. O'Donovan and C.A. Pratt. Methods employed: Muscle length from implanted transducers and velocity from differentiated length; calibrations from measurements of cadaver muscles at limb positions recorded on videotape during walking. EMG records full-wave rectified and integrated into discrete 2-ms duration bins [7a]. Motoneuron activity from chronically implanted ventral root microelectrodes [71a], shown as instantaneous frequency of firing of discriminated single units; similar records for spindle afferents from dorsal root ganglia [71]. Various traces from different animals and different recording sessions all cropped to show one-and-a-half complete step cycles each (swing, stance, and swing phases) for similar walking speeds and gaits, as confirmed by length, force, and multiple EMG records made simultaneously with each.



finding that the SA alpha motoneurons are functionally divided into two groups that are independently recruited during the two phases of EMG activity in stance and swing, respectively [72, 73]. Single SA motoneurons monitored during normal walking (using floating mi-

croelectrodes in the fifth lumbar ventral roots) contribute to either the swing phase or the stance phase burst, but never to both.

Typical afferent and efferent unit activity traces have been organized in Figure 8 into task groups (discussed later) to demonstrate the feasibility of using the fusimotor system to achieve optimized feedback signals in a muscle subject to extreme kinematic heterogeneity. The control of the swing phase SA motoneurons would require selective input from spindles biased to maintain nonzero activity during rapidly shortening flexion. On the other hand, the stance phase SA alpha motoneurons would need to receive their proprioceptive signals mainly from spindles with low activity during the swing phase to avoid an inappropriate stretch reflex recruitment. Such considerations may be even more important in view of the fact that most proprioceptive input to any given muscle (and most terminations of any proprioceptive afferent) involve heteronymous muscles in a complex coordination of synergists, partial synergists, and antagonists. Whatever actual patterns of connectivity are present, it is perhaps most significant that all kinematic conditions of recurring importance to the animal appear to be served by sources of properly biased and well-modulated sensory signals.

Finely Controlled Movements in Humans

Hagbarth and Vallbo's technique of microneurography [62] has been enthusiastically applied by several groups interested in muscle spindle activity in unanesthetized humans. Slender, needle-shaped microelectrodes are percutaneously manipulated by hand into a relatively superficial peripheral nerve known to innervate some group of muscles. Work to date has included recordings from the median nerve near the elbow (wrist pronators and flexors, finger flexors, thumb adductor), the peroneal nerve over the fibular head (ankle dorsiflexors, inverters, and everters; toe extensors) and fascicles of the posterior tibial nerve in the popliteal fossa (ankle plantar flexors).

The limitations of human experimentation and the tenuous stability of the recordings have produced a rather wide range of quality in the records, in terms of both the degree to which records can be ascribed to any particular muscle of origin or receptor modality and the range and documentation of the events purported to cause the activity. However, when viewed as a whole, the data provide clear evidence for surprisingly uniform and consistent patterns of spindle function (for reviews, see [20, 21, 28, 139]). This is all the more surprising because the patterns are quite similar among anatomically diverse muscles, and quite different from patterns reported for what appear to be analogous muscles in animals. The major findings from normal subjects, as organized by Burke [21], are as follows:

1. Muscles at rest have little or no fusimotor activity. This has been surmised from a lack of resting activity in most spindle afferents at neutral muscle lengths [137], the regularity of discharge when present [31], and a lack of change in discharge following complete block of the proximal nerve trunk by lidocaine [61] or pressure [25]. Most cat hindlimb spindles appear under these criteria to have resting fusimotor drive, although this has not been as systematically tested as it has for humans.
2. The level of fusimotor activity cannot be changed voluntarily and independent of alpha motoneuron activity. In particular, after initial disagreement [18, 19], it now appears that clinical techniques for enhancing the stretch and tendon jerk reflexes by "arousal" (e.g., Jendrassik maneuver) act entirely by changing transmission in central pathways [27] rather than by increasing the responsiveness of spindle afferents to the mechanical stimulus [26, 63]. While this method cannot be used in cats, an attempt to cause "arousal" by suddenly turning off all room lights as a cat walked on a treadmill resulted in no change in the gait or unitary spindle afferent activity (unpublished observation).
3. Extrafusil activation of the muscle is always accompanied by, but not preceded by, modest intrafusil activation. For isometric contractions, most spindle afferents increase their activity at the time and to the degree to which force develops in the parent muscle [24, 78, 138], but this may be influenced by many segmental and descending factors [29]. If the muscle is allowed to shorten at anything faster than some small fraction of its rest length per second, the spindle afferents are silenced [23, 64].

The diversity of spindle behavior reported from various animal muscles during various tasks contrasts sharply with the much more consistent findings in voluntarily contracting human muscles. One possible explanation is that there are intrinsic differences between motor control in the segmentally organized behaviors studied in lower mammals (e.g., locomotion, mastication), as opposed to the encephalized behavior studied in humans (e.g., visually guided tracking). This difference may even be reflected neuroanatomically as well as behaviorally; primates are known to have more direct connections between motor cortex and spinal motoneuron pools. However, it may also be that the spindles themselves are different. Human spindle afferents have lower conduction velocity [100], more regular discharge [31], and possibly lower resting length activity than those in cats, in which spontaneous activity usually persists during deep anesthesia. However, the dynamic stretch sensitivities of both primary and secondary endings appear to be virtually identical for human and cat spindles [111]. For smaller primates, conduction is more

similar to that of cats [36], and the various fusimotor effects are also similar [37].

Therefore, before accounting for the spindle activity differences by postulating species differences, it is worth considering the kinematics of the experimental paradigms in which these spindles have been observed. By necessity, the human subjects were limited to relatively slow or small active movements, voluntarily performed *ad libitum* or during a tracking task; programmed movements such as walking and throwing cannot be studied with microneurography. It has been pointed out that the spindle activity observed in human forearm muscles is potentially quite useful for fine manual dexterity tasks in which nearly isometric active movements are controlled [78], and such activity does appear to cause distinctive timing changes in extrafusal activity [30].

While this consideration seems reasonable for forearm muscles, the rationale for such a program in muscles of locomotion such as triceps surae and tibialis anterior is less obvious. However, the human ankle muscles frequently operate passively as detectors of small perturbations caused by swaying during stance, in contrast to the same muscles in the digitigrade quadrupeds. In the absence of fusimotor drive in a quiet muscle, spindles are naturally endowed with a very high sensitivity to small stretches [68]. Very high transducer gain would provide a large, rapidly rising signal to alert the central nervous system (CNS) early in a sway movement. Once the corrective contraction of the parent muscle is initiated, the fusimotor cocontraction can reposition the transducer operating curve to detect the further progress of the sway or its correction [22], both of which will necessarily be at slow velocities, because of the inertial mass of the body.

Still, the notion that the apparent discrepancy between primate (human) and other mammalian spindles would disappear if human spindle activity could be recorded during locomotion is less than satisfying. In that context, one brief but intriguing report by Schieber and Thach of spindle afferent activity from monkey forelimb during a tracking task deserves special mention [123] and, hopefully, attempts at replication in humans. In the behaving monkey, the active and passive lengthening and shortening responses of wrist extensor spindles (recorded at the dorsal root ganglion) was entirely consistent with data from human muscle spindles in similar tasks. However, when the task consisted of a wrist extension superimposed on stabilization against a wrist-extending load to the flexor muscles, the movement was made by simply relaxing the tonically activated wrist flexors. Despite the passive shortening of the extensor muscles, their spindle afferents accelerated their firing, just as if the movement had required active wrist extension. Presumably, the inactive wrist exten-

sors had received static fusimotor input to enable their spindles to provide proprioceptive information about the movement, even though that information could have no effect on the inhibited homonymous motoneurons.

Loeb and Duysens have reported a similar apparent activation of gamma but not alpha motoneurons in two different cat hindlimb muscles that happen to undergo passive shortening during locomotion [95]. Note that such spindle control patterns represent qualitatively different alpha and gamma recruitment, whereas the previously noted extensor–flexor differences might be interpreted as quantitative differences (see Fig. 7).

The apparent homogeneity of spindle function in human studies to date is less mysterious when the muscles are described in terms of their kinematic behavior, instead of their anatomical classification. In this context, the refusal of the fusimotor system to respond to voluntary attempts to change the transducer gain without changing the task is clearly an important attribute. If we assume that this mode of spindle function provides an optimal set of transducer characteristics, and that it is serviced by a deconvolution network that has been fine-tuned to these inputs, the observed stability is clearly desirable.

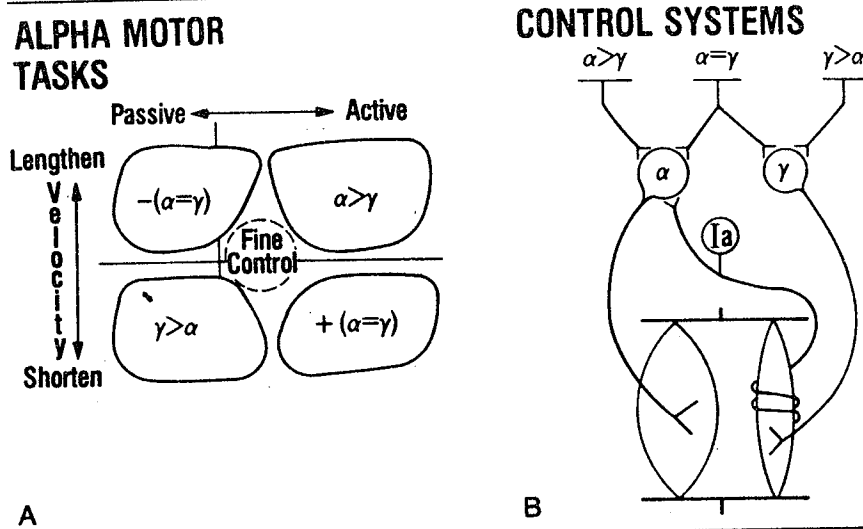
TASK GROUPS: A SYNTHESIS

The activity of spindle afferents from a wide range of muscles performing a wide variety of tasks is consistent with the notion that fusimotor control is normally employed to maintain well-modulated proprioceptive activity for the conditions generally encountered. This implies a role for the fusimotor system that is consistent with the evolutionary appearance in high vertebrates of independent populations of alpha and gamma motoneurons engaged in motor learning and adaptive behavior. This system has largely, but not completely [106a, 106b, 112], supplanted the beta motoneuron system of reptiles and amphibians (see Fig. 3), which can provide only a genetically fixed degree of fusimotor control and no independent timing [116]. The functional equivalent in mammals, alpha–gamma coactivation, has been proposed as a useful principle for the control of actively shortening muscles [58], a mode perhaps seen much more generally in lower vertebrates than in mammals. However, neither this principle nor others [132] that fail to consider the kinematic tasks being performed by the muscles can account for the diversity of mammalian motor function.

The notion of a slowly adaptive proprioceptive program accounts well for the independence of mammalian intrafusal and extrafusal control. At the same time, the short-term stability of the control

FIGURE 9

The task group concept. (A) Muscle activity may be divided into independent axes of motion and recruitment, here vertical and horizontal, respectively. (B) Various patterns of alpha and gamma control that have been described. Actively shortening muscle (lower right quadrant) is best controlled by a pattern of alpha-gamma coactivation that preserves spindle firing during shortening of the muscle. Passively lengthening (upper left quadrant) can be viewed as alpha-gamma coinactivation, where passive spindle properties are appropriate detectors of externally applied lengthening. Muscles that act like springs by actively lengthening (upper right quadrant) require selective recruitment of alpha motoneurons and need to avoid simultaneous recruitment of gamma motoneurons, which would tend to saturate the spindle output when combined with the muscle stretch. Passively shortening muscles (presumably following movements caused by inertia or external forces) need to have selective recruitment of gamma motoneurons to maintain spindle activity at a nonzero level. Note similarities to the three command input strategies for servo mechanisms outlined in Figure 2.



programs and their deconvolution networks explains the general failure to find voluntary or abrupt changes in fusimotor output unless the level of effort or the nature of the motor task is changed.

So far, we have been intentionally vague about the “conditions” that influence the selection of a fusimotor control program for the muscle, other than noting that they concern the length, velocity, and degree of extrafusal output required of the muscle. Figure 9 summarizes one potentially useful way of organizing these conditions,

based on the independent variables of velocity and degree of extrafusal activity (Fig. 9A). The diagram in part B is designed to relate the conditions found in each quadrant of (A) to the relationship between alpha and gamma motoneuron activity most appropriate for those conditions. Interestingly, these three patterns include the same three control systems predicted by the three servo control schemes outlined in Figure 2. In addition to the extremes of the quadrants, it appears likely from human spindle records that there is a specific state associated with fine control of nearly isometric, low-force tasks, which may include the short-range hypersensitivity of quiescent spindles.

This scheme is of particular interest in bifunctional muscles, which in some cases either develop or are designed with apparently independent sets of alpha and gamma control systems, perhaps to cope with extreme heterogeneity of operating conditions. There are several muscles in the cat hindlimb that are bifunctional by virtue of double periods of recruitment in the step cycle and mixed biarticular action (flexing one joint and extending another). We have already noted that the division of the anterior sartorius (SA) alpha motoneuron pool into two independent groups is consonant with the kinematic division of the muscle's work into active shortening during the swing phase and active lengthening during stance. The biarticular hamstring muscles semitendinosus (ST) and posterior biceps (BP) are complete anatomical antagonists to SA, being knee flexors and hip extensors, and they are bifunctional during locomotion, having two periods of recruitment. However, Figure 10 reveals that their two EMG bursts occur when their velocity excursions are virtually identical [98]. It is intriguing, then, that intracellular records from these motoneurons during fictive locomotion indicate that single motoneurons participate in both phases of activation, in contradistinction to the independent populations present in SA motoneurons [110]. The records from muscle spindles in hamstring muscles are still too fragmentary to indicate with certainty whether they are less heterogeneous than SA spindles, as might be expected.

The term *task group* has been suggested by this author to denote an assemblage of alpha and gamma motoneurons, and of spindle and other proprioceptive afferents as well, that is responsible for the performance of a kinematically homogeneous motor task [93] (Figs. 7 and 8). Figure 11 summarizes the main features of the concept:

1. A task group may be a subset or a superset of anatomically defined muscles.
2. Some or all of the afferent and efferent neurons making up the group may participate in other task groups, which are recruited to perform activities that are either kinematically different or have different organizational goals, such as speed for ballistic or reflex move-

FIGURE 10
 (A) Anatomy of hip and knee muscles in the cat. Proximal musculature of the cat hindlimb is divided into examples of monarticular knee extensors (vasti group) (V) and hip extensors (SM and BA) and biarticular antagonistic pairs for hip flexion/knee extension (SA) and hip extension/knee flexion (ST and BP). (B) Work of the hip and knee muscles during walking. The traces show the length excursions of these muscle groups during walking (one-and-a-half step cycles shown, stance phase indicated by heavy bar). The monarticular muscles are extrafusally active once in each step cycle during stance phase indicated by heavy bar. The biarticular muscles are bifunctional in that they are activated twice in each step cycle, in the stance and swing phases. However, note that the velocity profiles (slope of the length trace) for the hamstring muscles ST and BP are quite similar during both periods of muscle activity, whereas such profiles are in opposite directions for the two periods of SA activity. SA motoneurons are divided into two independently recruited task groups for the swing and stance phases, while ST motoneurons appear to be homogeneously recruited twice in each step cycle.

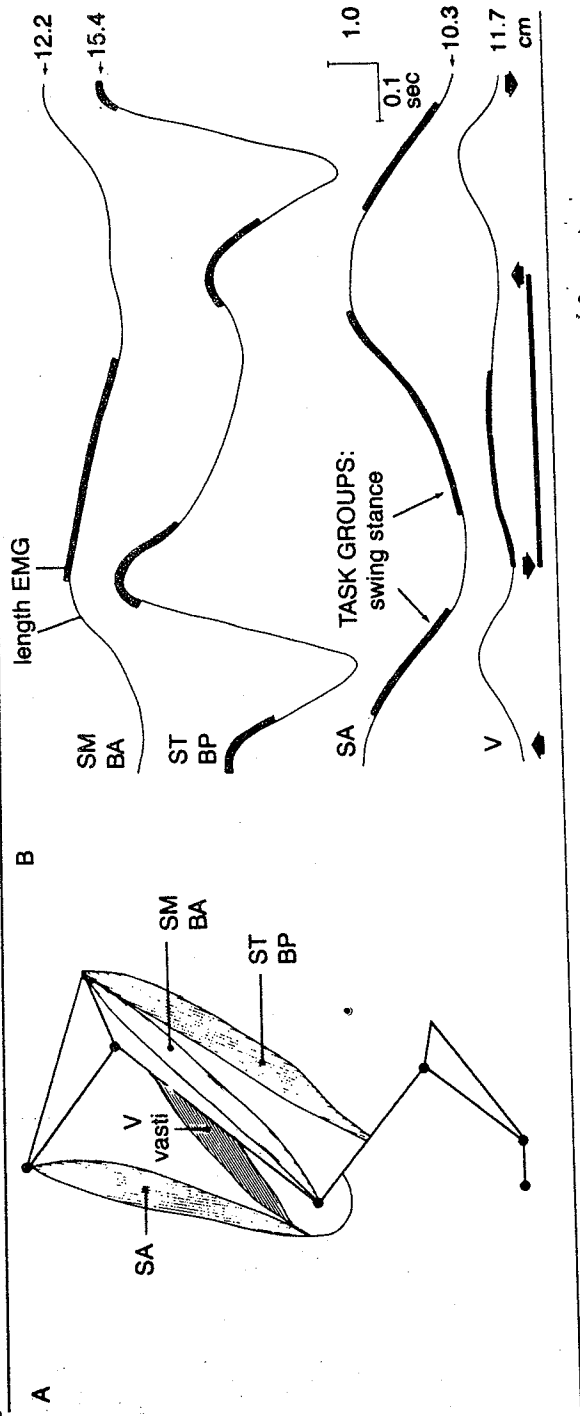
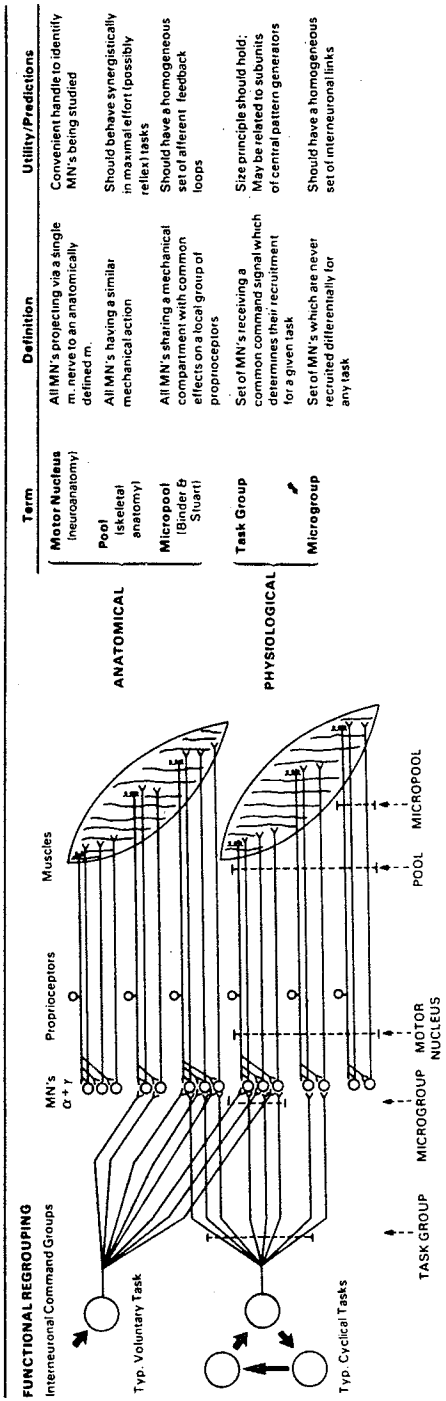


FIGURE 11
Features of task groups. The recruitment of motoneurons to participate in a motor task is proposed to be somewhat independent of the anatomical division of the limb muscle mass into various individual muscles. The neural anatomy gives rise to motor nuclei in the spinal cord, consisting of all the motoneurons projecting to a single muscle nerve, with somata generally clustered into a thin sheet or column in the ventral horn. The mesenchymal anatomy gives rise to motoneuron pools and micropools that are characterized by the homogeneity of their mechanical effects on skeletal movement and on local proprioceptors within the muscles, respectively. During physiological recruitment of at least some muscles, the functional element appears to be a task group of motoneurons, which may be drawn from a subset of one motoneuron pool or a superset of pools from several muscles. It is hypothesized that this task group includes gamma as well as alpha motoneurons, and thus gives rise to a set of proprioceptors whose activity is particularly linked to the performance of the task, by way of fusimotor effects and, possibly, compartmentalized mechanical effects. Other tasks using the same musculature are served by task groups that may or may not overlap, depending on the kinematics of the tasks and the type of feedback control scheme required for each task.



ments [97] or different synergies for joint stabilization [43, 135, 136].

3. The participation of components of the task group is orderly and highly reproducible whenever the task is executed. When the task is performed with varying intensity of effort, there should be strict adherence to some rank-ordered recruitment, such as that suggested by the size principle of motoneurons [69].

4. The task group is a functional organization that is independent of and probably subsumes microanatomical organizations such as mechanical compartmentalization [12, 33, 142]. It is likely to be correlated with anatomical details such as synaptic projections and muscle fiber type distributions [14], but it can only be identified by physiological observation during the behavioral task.

5. A task group represents the identification by the nervous system of a coherent functional state that can be usefully subjected to optimization of sensory information and its motor feedback. It is presumably associated with an ongoing plasticity of neural connectivity which attempts to maintain this optimization in the face of experience and the continuing development of skeletomuscular structures. However, the criticality of this optimization is unlikely to be appreciated unless and until optimal motor performance is required.

CONCLUSIONS

The muscle spindle is beginning to take its place as a full-fledged independent sense organ, whose job is to convey as much information as possible about mechanical events in its environment, the muscle. Just as we are not "prisoners of an invariant length servo," so these sense organs are not prisoners of such single preconceived principles of motor control. The history of sensory neurophysiology is replete with "discoveries" of what appear to be serious design flaws and errors in our sensory transducers but which eventually turn out to be ingenious tricks for optimizing ultimate performance as used by the organism. Many of the inferences that I have drawn from the most recent normal performance data were presaged by P.B.C. Matthews (e.g., [103a]) and others, who studied the spindle as a sense organ rather than as a part of the motor plant. We would do well to consider the contribution of individual elements to the performance of some task only in the context of a thorough understanding of the ways, means, and objectives of the task as a whole, and its relationship to the full spectrum of normal behavior for the organism.

APPENDIX: Spindle Transduction Properties*

Proof of Optimal Transducer Curve Prediction (Fig. 5)

In a long series of signals S , each a single number chosen from a continuous set, the difference between adjacent ordered values of S would be expected to vary inversely with the local probability density of values of S : expectation of $\Delta S \sim 1/P(S)$. Since in the nervous system the transmission of S is contaminated with added noise, it would be useful to expand the sensitivity for values of S where ΔS is small, so that the intervals between adjacent transmitted values would have the same ratio to the added noise. Thus, transmitted value E would be related to S by a transformation T with added noise n ,

$$E = n + T(S),$$

where we have assumed the value of n does not depend on E .

To maintain a constant interval between transmitted signals we would require

$$\Delta E = \frac{dT}{dS} \Delta S = \frac{dT}{dS} \frac{1}{P(S)} = \text{const.}$$

Therefore

$$\frac{dT}{dS} \sim P(S)$$

and

$$T(S) \sim \int_{-\infty}^S P(S) ds.$$

Implementation of Hasan's Spindle Model (Fig. 4)

Hasan [66] has derived a nonlinear differential equation that relates the time-course of firing of a spindle to its length, based mainly on two assumptions: (1) the force required to elongate a *passive* fusimotor sarcomere increases as the product of a spring-like factor and a factor that increases with the cube root of the velocity; (2) an *active* sarcomere behaves merely as a stiffer, shorter spring.

The model has five parameters: a , b , c , h , and p , which Hasan evaluated by finding the best fits of his model's output to data from

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soleus muscle spindle afferents in the deafferented, static, and dynamic conditions. In Figure 4 we have adopted his values for these conditions, except that we have set h to the constant value of 800. This larger value better approximates physiological firing rates for afferents subjected to the full complement of fusimotor influence. The constant c provides static bias to the length L , which enters the equations as $L - c$. Hasan set $L_{\max} = 0$ to avoid the need for another parameter; consequently L and c are negative. Since the parameters were evaluated in part from data on the soleus muscle, we have chosen $L_{\max} = 50$ mm, a typical fiber length for soleus, and have added this to L and to c so that the equations are not changed but the lengths can be compared with the velocities—100 mm/s corresponds to about 2 lengths/s. In the modulated static condition we allowed c to vary with the length, keeping a constant difference of -25 , Hasan's fit for the static condition, while keeping a , b , and h constant. Since the model has only one control parameter, which represents the fraction of sarcomeres in the contractile state, and which controls a , b , c , and h with only one degree of freedom, this uncoupling of c from the other parameters implicitly introduces a second controlling variable into the model.

Hasan gives a simple solution to the equation for the steady state of constant velocity, which we used to generate Figure 4A.

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