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HOW YOUR BRAIN KNOWS WHERE YOUR HAND IS

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ABSTRACT

Proprioceptors provide the central nervous system (CNS) with the feedback information required to compute body posture and to regulate muscle activation accurately during ongoing movement. A large amount of proprioceptive information arrives at the CNS from diverse receptors distributed among muscles, tendons and joints, raising the question of how such information is encoded, combined and used. We here consider and contrast the two most important proprioceptors, muscle spindles and Golgi tendon organs, from the perspectives of psychophysics, neurophysiology and mathematical modeling. The muscle spindle is a particularly complex transducer of both muscle length and velocity whose properties appear to be dynamically optimized via its fusimotor innervation; its sensorimotor role and signal encoding are starting to be well-understood through mathematical modeling but decoding in the CNS appears to be a very difficult computational problem. The Golgi tendon organ is a much simpler transducer whose ensemble properties may provide a linear indication of muscle force; paradoxically, its role in proprioception and sensorimotor regulation remains enigmatic.

INTRODUCTION

The somatic senses provide sensory information to the central nervous system (CNS) but are considered as distinct from the special senses, such as sight, hearing, touch, smell, taste and balance. Three somatic senses include pain, temperature and mechanics. Proprioception refers to a type of mechanical sense and is commonly termed the position or "body sense". It provides the CNS with sensory feedback signals that play important roles in monitoring and controlling body posture and reflex pathways, but activation of its receptors generally does not produce direct conscious sensation.

Early experiments to understand the role of proprioception examined the sensorimotor performance of deafferented subjects lacking proprioceptive feedback. They found that such subjects were able to perform rhythmic tasks such as chewing, swimming, walking, breathing etc. by means of neuronal assemblies in the CNS that are able to generate detailed patterns of motor activity autonomously. However, the performed movements were poorly uncoordinated and inaccurate, especially when visual guidance was not present.

The proprioceptive information available to the CNS originates from receptors located in the muscles, tendons and joints. These receptors are responsible for awareness of position and movement of limbs and trunk, muscle force (effort, tension, heaviness and stiffness) and timing of muscle contraction. While receptor outputs might be theoretically sufficient to provide all the mentioned sensations, psychophysical experiments indicate that many of these sensations are rarely present in the absence of muscle activation, suggesting that centrally generated motor command signals are essential to activate and perhaps to inform the sensory signal processing circuits as to when and how to decode the afferent information (Gandevia et al., 1992).

MUSCLE SPINDLE

Sensory Role

The muscle spindle is the most important proprioceptor, playing a dominant role in kinesthesia and in reflexive adjustments to perturbations. The combined signals from many spindles in each muscle provide the CNS with length and velocity information from that muscle and generate the strongest and fastest adjustments of muscle activation as a form of servocontrol.

Receptor Encoding

At the same time that the spindle supplies the CNS with afferent information, it also receives continuous control through specialized fusimotor efferents (gamma motoneurons) that the CNS controls separately from the alpha motoneurons controlling the bulk of the muscle (Banks and Stacey, 1988; Boyd and Smith 1984). The fusimotor system improves the spindle's ability to encode accurately wide ranges of velocity and length that occur in various natural tasks by shifting its relative importance and sensitivity to the range of length and velocity that the CNS expects to occur during voluntary motor behavior. A typical spindle contains three types of intrafusal muscle fibers: bag$_1$, bag$_2$ and chain (Figure 1). The bag$_1$ fiber is the only fiber that receives dynamic fusimotor control; it is primarily responsible for velocity sensitivity of the spindle. The bag$_2$ and chain fibers receive static fusimotor control and contribute mainly to length sensitivity. All three fiber types are innervated by a primary afferent, while only bag_2 and chain have one or two secondary afferents located on them.

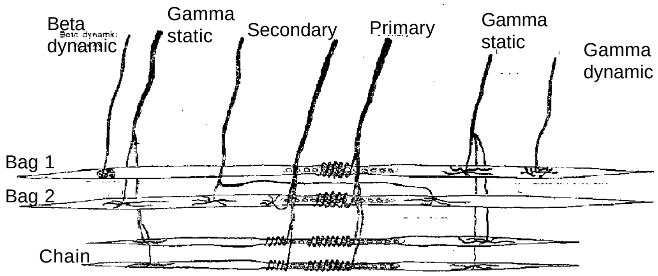

Figure 1. A muscle spindle. Spindle consists of three types of intrafusal fibers which receive several fusimotor inputs (gamma static and dynamic) while giving rise to primary (Ia) and secondary (II) afferent. Figure is modified from Bakker 1980.

The exact pattern and purpose of fusimotor activity during natural motor behavior remain controversial due to the difficulty of accurately recording afferent and especially fusimotor activity during motor behavior. Therefore, theories of motor control usually rely on assumptions about fusimotor activity. One general proposal is that the spindle is thereby programmed by the CNS so as to behave as an optimal transducer (Loeb, 1984; Loeb and Marks, 1985; Scott and Loeb, 1994). The information transmitting capability of a given spindle afferent is limited by the physiological range of firing rates and noisiness in the intervals between successive action potentials. If the spindle had a fixed sensitivity to length and velocity, it would be incapable of distinguishing fine gradations of the wide range of lengths and velocities over which muscles can operate. The CNS can improve utility of the spindle afferent signal by adjusting its sensitivity in consideration of the relatively limited range of lengths and velocities that it expects to encounter during a self-generated behavior such as locomotion.

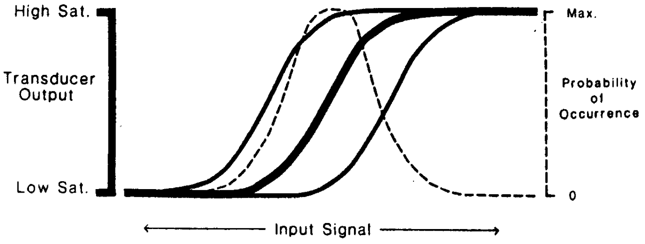

Figure 2. Optimal transducer function (bold line) is the integral of the probability distribution of inputs (dashed line), but performance degrades rapidly for shirts of operating point (thinner sigmoidal curves). Modified from Loeb and Marks, 1985.

Optimal transducer theory is based on information theory, by which it can be shown that the optimal shape for the input/output function of a noisy transducer is the integral of the probability distribution of input states (appendix by Loeb, 1984). The range of states likely to occur in a muscle during a self-generated behavior is best described by a bell-shaped probability distribution around the desired operating point, making the optimal transducer curve sigmoidal in shape (Figure 2). Such a sigmoidal curve can be fully described by two independent variables, the mean and width of the underlying bell-shaped probability distribution. The two types of fusimotor innervation are not isorepresentational with these two independent variables, but they can be combined to position the gain of the transducer optimally in the state space. Such a system involving sensitivity control is not unique to muscle spindles, but 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 under efferent control by the brain (e.g. iris of the eye, stapedius and tensor tympani muscles of the middle ear).

Recordings of fusimotor activity during natural motor behavior are scarce due to the difficulty of the experiment. Many scientists have attempted to infer fusimotor pattern by comparing more easily recorded afferent activity during cyclical activities such as locomotion to activity recorded when the same kinematics were imposed on the passive animal in the absence of fusimotor activity (called a difference signal). The observations of such experiments are valuable but must be interpreted cautiously. This is particularly true regarding dynamic fusimotor control, which affects only the primary afferents but whose effects interact nonlinearly with the effects of static fusimotor control on other endings of the same afferents.

Recently, the records of both spindle afferent and fusimotor efferent firing in medial gastrocnemius muscle (MG) were successfully captured during decerebrate locomotion of the cat, providing more direct insight into fusimotor function (Taylor et al., 2000). However, the kinematics of the joints and muscles in the unloaded decerebrate preparation are quite unlike those of normal locomotion. The residual CNS presumably has no way of adapting fusimotor control for such pathological and unexpected conditions, so the effects of this fusimotor activity on spindle afferent activity during normal locomotion must be inferred by considering the effects of such kinematic differences. The most important deviation between unloaded decerebrate locomotion and natural locomotion occurs during the activity of extensor muscles (such as MG) that normally occurs during the stance phase; in the unloaded decerebrate preparation, the foot never touches the ground. During normal locomotion, the active MG muscle operates close to isometric as it opposes gravity during most of the stance phase, whereas in the unloaded decerebrate preparation, it shortens rapidly. In the decerebrate preparation of Taylor et al. the dynamic fusimotor efferent increased its activity abruptly at the beginning of active shortening of MG, stayed constant during that phase and became silent at the beginning of passive stretch by the antagonist dorsiflexors of the ankle (Figure 3). The authors hypothesized that the increased dynamic fusimotor stimulation during the shortening phase would enhance detection and reflex effects of any unexpected lengthening that might result from obstruction of the limb's trajectory. Furthermore, the residual dynamic fusimotor effects during the initial moments of lengthening resulted in a large burst in primary afferent firing which was hypothesized to represent a cue to the CNS indicating the beginning of the swing phase.

In addition to capturing the dynamic fusimotor pattern during natural locomotor step, Taylor et al. recorded static fusimotor activity as well (Figure 4). They suggested that the reason for the presence of strong static fusimotor activity during the stance phase is related to preventing the afferent from becoming silent during shortening, but the kinematics of normal locomotion (little shortening) seems to require a different interpretation.

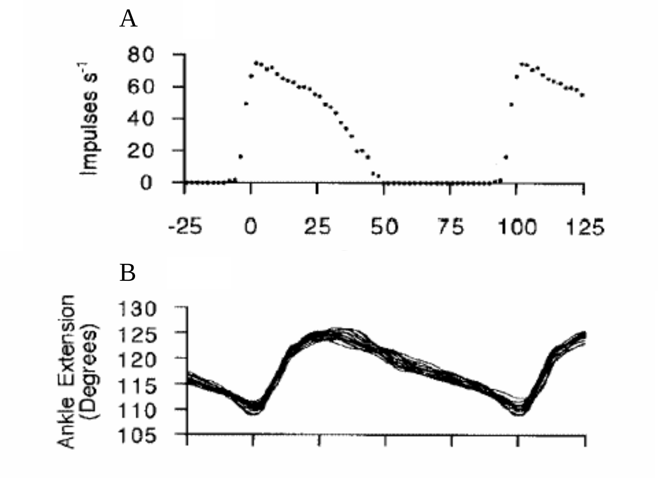

Figure 3. Timing of dynamic fusimotor activity. A. The ensemble mean firing of two dynamic fusimotor units. B. Superimposed are 15 ankle movement records, time-normalized with respect to cycle length. The mean cycle period is 0.96s. Modified from Taylor et al., 2000.

A physiologically realistic model of the spindle (Mileusnic et al., 2002) can be used to provide an objective basis for understanding this and other fusimotor functions. The model demonstrates high accuracy in capturing the spindle's behavior during a variety of ramp, triangular and sinusoidal stretches, and during different fusimotor conditions. In addition, it incorporates the partial occlusion effect that takes place during simultaneous static and dynamic fusimotor activity (which is the case during the natural tasks), as well as appropriate temporal properties of the three types of intrafusal fibers during fusimotor stimulation (see below). The model was inverted in order to use it as a tool to understand the fusimotor role during natural locomotion. In other words, by supplying the inverted model with the records of afferent activity and kinematics during natural locomotion, the inverted model can be used to infer the underlying fusimotor drive. The preliminary results of applying our inverted model to spindle afferent records from intact walking cats (Loeb and Duysens, 1979; Loeb and Hoffer, 1985) agree with the direct recordings of fusimotor activity in the decerebrate cat obtained by Taylor et al. For example, the existence of strong static fusimotor activity during muscle shortening (and almost negligible activity during lengthening) accounts for the preservation of afferent firing under those abnormal kinematic conditions. The dynamic fusimotor effect on the bag$_1$ fiber (the only fiber receiving dynamic innervation) is somewhat different due to the very slow time constants for activation and deactivation of the bag$_1$ fiber, which actually builds up during the shortening, reaches a maximum at the onset of lengthening, and then slowly decreases throughout most of the lengthening phase. This observation seems to agree with decerebrate experimental data except that it suggests the presence of dynamic effect during most of the lengthening rather than just the first part.

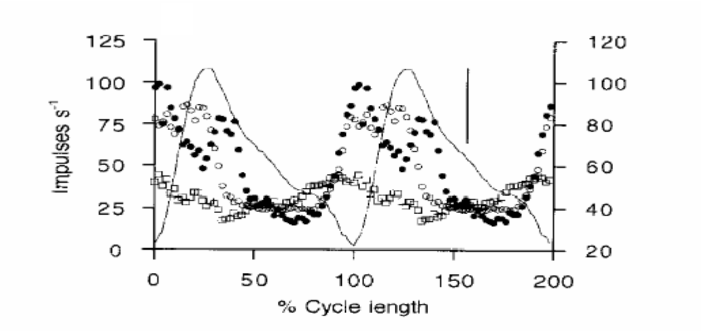

Figure 4. Two types of static fusimotor afferent activity. Type-1 (o, right frequency scale) and type-2 (□ , right frequency scale) static fusimotor activities were recorded during cat's decerebrate locomotion together with secondary afferent difference signal (difference between afferent activity during intact fusimotor activity and afferent activity during same kinematics (ankle angle-thin line) but in the absence of fusimotor activation; △ , left frequency scale). The mean cycle period was 0.65s. Modified from Taylor et al., 2000.

The direct fusimotor recordings by Taylor et al. provided convincing new evidence that the two types of static intrafusal fibers (bag$_2$ and chain) have significantly different properties and that the CNS takes this into account when activating them via separate types of fusimotor static innervation. During the locomotor step the two efferent firing profiles were somewhat out of phase; type-2 drive (presumed to be innervating bag$_2$ fiber) leads the type-1 drive (innervating chain fibers) by 0.17s. Our spindle model indicates that the time advance of type-2 static drive exactly compensates for the extra time it takes the slower bag$_2$ fibers to contract, resulting in the same fusimotor effect simultaneously in bag$_2$ and chain fibers. It remains to be seen whether there are tasks and conditions for which the bag$_2$ and chain effects are modulated separately. Optimal fusimotor control theory does not predict that this would be useful, at least as applied to the current spindle model.

Ensemble Information

The process of converting continuous generator potentials from several, separate transduction sites in each afferent ending into a train of all-or-none action potentials causes the transmitted information to be quite noisy (Stein, 1967). Noise will also be introduced from fluctuations in the response of the intrafusal fibers to similar trains of action potentials in the efferents. The numbers and complexity of muscle spindles suggest that the CNS has a considerable interest in optimizing the available information about muscle length changes, so it is important to understand the nature of the noise and signal processing strategies that might be used to improve the overall signal to noise ratio.

Afferent noise might be reduced by averaging together the signals from many spindle afferents. Psychophysical studies of the perceptual effects of electrical microstimulation of single spindle afferents supports this notion (Macefield et al., 1990). Activation of ensembles of spindles in the muscle elicits strong illusions of joint motion, but activation of single afferent is perceptually undetectable. The activities of two spindles embedded in the same muscle might be quite different, however, due to compartmentalization of motor units and nonhomogeneities in extrafusal fiber lengths during gradual recruitment of motor units. It has been suggested that the population of spindle afferents and their reflex projections onto the motoneurons are similarly compartmentalized so as to permit highly local servocontrol (reviewed in Windhorst et al., 1989). However, the relatively weak gradients observed in the distribution of feedback in muscles with different types of peripheral neuromuscular compartmentalization are inconsistent with this notion (Loeb and Richmond, 1989).

Averaging asynchronous action potentials over time improves the signal-to-noise ratio (and hence the number of bits of information per sample), but it incurs a cost in the data rate. The cat responds to perturbations with a latency of about 20-50ms (including activation delays in the muscle), suggesting that sensory feedback has to be updated at least 20-50 times per second in order not to become the limiting factor. The central rate extracting process is probably the postsynaptic integration of EPSPs; motoneurons that receive monosynaptic projections from spindle afferents have time constants of ~10ms, consistent with this update rate for sensory information. If such a system relied on single spindle afferent activity, each spindle would have to fire at very high rates in order for its information to be reliably decoded and useful. Instead, it is more probable that the system combines the activities of the numerous spindle afferents from the muscle, each firing at lower rates (Stein, 1967; Loeb and Marks, 1985). The question is how many spindle afferents firing at such low rates are necessary to smooth out the central integration. The inputs from independent spindle afferents are highly asynchronous, making the variance of the central integrator output much greater for 10 such afferents firing at 10pps than for a single afferent firing at 100pps. It was calculated that for a 10 msec central integration process, a mean Poisson rate of 600pps (or 60 parallel inputs with 10pps each) was required to achieve a signal to noise ratio equal to that of a single afferent firing at a regular rate of 100pps (Loeb and Marks, 1985).

The relatively large number of afferents needed to supply a rate decoder for asynchronous activity raises the question of how many afferents actually arise from each muscle. The number of spindles varies enormously among different muscles, both in absolute numbers and in spindles per gram of muscle tissue (Banks and Stacey, 1988). For example, the spindle density in neck muscles is ~100 spindles/gram, in digit muscles ~10 spindles/gram, while proximal limb muscles have only ~1 spindle/gram. Such “muscle-centric” views of the spindle may be misleading, however, because the spindles provide information about the position and velocity of joints and their feedback contributes to the regulation of many muscles, not just one muscle in which they are residing. Psychophysical studies suggest that the overall distribution of spindles in the muscles spanning a given degree of freedom of a given joint accounts well for the resolution of position and motion perception in that joint. In fact, such joint-based spindle counts agree with the psychophysical data demonstrating a proximodistal gradient of angular resolution in both the upper and lower limbs. This gradient compensates in part for the simple mechanical fact that angular errors in proximal joints have larger consequences on perceived position of the end-point of the limb than similar errors in distal joints (Hall and McCloskey, 1983; Clark, 1992).

Decoding Problem

The operations of the fusimotor system and the distribution and integration of spindle afferents appear to be consistent with a highly optimized sensory system, but they substantially complicate the task of decoding such information into an integrated sense of posture and kinesthesia, particularly if that task must also be done optimally. One question is whether fusimotor activity can be continuously and freely modulated by the CNS or whether the CNS learns a few, specific fusimotor programs. The complexity of fusimotor effects on our spindle model suggests that the CNS may not have a general purpose module to compute arbitrary fusimotor programs or to deconvolve joint kinematics from the effects of such fusimotor programs on the fly. Instead, it seems more likely that in the course of learning a specific task, the CNS also learns both a specific fusimotor program and a specific deconvolution network to associate afferent activity with absolute states of body posture and motion. In other words, for a specific kinematic task, there exists a learned alpha activation pattern, as well as a learned fusimotor pattern that will keep the spindle in optimal range for those particular kinematics (Schieber and Thach, 1980; Loeb, 1984; Loeb and Marks, 1985; Prochazka et al., 1988). The feasibility of such learning was demonstrated in a very simple model system, but only if the model and the learning conditions included realistic features such as noise and limited dynamic range in the receptors and external perturbations to the system (Loeb et al., 1999).

The location of the spindles in individual muscles introduces another complication in the conversion of their afferent information into a sense of body posture. Most muscles do not act on a single axis of a single joint. Many individual joints have more than one degree of freedom (e.g. shoulder and hip) and over half the muscles cross more than one joint (e.g. long neck and hamstring muscles). In such systems, it turns out that the optimal distribution of a given number of spindles among the various monoarticular and multiarticular muscles depends on the coordinate frame in which body posture is actually computed (Scott and Loeb, 1994). For the purpose of this study, a very simple system consisting of two uniaxial joints and three muscles (two monoarticular and one biarticular) was designed. The sensors were all pure length sensors with no fusimotor variability. If posture was computed in joint angle coordinates, the optimal distribution of receptors places all of them in only the monoarticular muscles. If posture was computed in the Cartesian coordinates of the end-point of the limb, the optimal distribution changed systematically with the orientation of the limb (when the arm is nearly fully extended, the optimal solution biases toward spindles located within the proximal monoarticular and the biarticular muscles, while as the limb end-point approaches the body, the optimal distribution is when more spindles are in the distal monoarticular muscle). For the coordinate frame of segmental angle in an external reference frame, yet another distribution is optimal. The actual distribution of spindles in analogous muscles of the elbow and shoulder appears to be intermediate among these different “optimal” distributions. When the distribution of spindles across virtually all of the muscles of the body was considered, an optimal information extractor operating in joint angle space predicted a proximodistal gradient of angular resolution that was strikingly similar to that measured psychophysically (Hall and McCloskey, 1983; Clark, 1992). All of this is consistent with the notion that the contribution of the spindles to proprioception has been carefully optimized as a result of both phylogenetic development of the species and sensorimotor learning in the individual.

GOLGI TENDON ORGAN

Sensory Role

The Golgi tendon organs (GTOs) represent the second most prominent source of proprioceptive information. They are mechanoreceptors found in mammalian skeletal muscles that were traditionally viewed as providing the CNS with a sense of muscle force via their Ib afferents. More recent psychophysical experiments argue against those early views, however, suggesting instead that we actually perceive motor "effort" via centrally generated motor commands rather than actual force from GTO feedback (Jones, 1986). There are many sources of such recursive "efference copy" signals, including the Renshaw cells of the spinal cord, which receive recurrent collaterals from the alpha motoneurons that provide the final common pathway in the activation of the muscles themselves (Windhorst, 1990). Therefore, while GTO is a much simpler proprioceptor than spindle, the role of its feedback in proprioception is still very unclear.

Receptor Encoding

The number of GTOs varies widely among muscles (5-50) but in most cases is somewhat smaller than the number of muscle spindles in the same muscle (Jami, 1992). The GTO receptor consists of bundles of collagen fibers that connect small fascicles of muscle to the whole muscle tendon or aponeurosis. In other words, GTO is placed in series between muscle fibers ("muscle end") and tendon and aponeurosis ("tendon end"). Between the two ends, the collagen fibrils that are attached to various muscle fibers divide, mix and fuse in a complex network. The number of muscle fibers that insert into a single GTO varies, but in most cases is between 3-50. They are usually all from different motor units.

Each GTO receptor responds nonlinearly to the active tension produced by muscle fibers inserting into it, each from a separate motor unit (MU) whose muscle fiber type (e.g. slow, fast-twitch fatigable or fast-twitch nonfatigable), relative activation and tension-producing capabilities may be quite different from adjacent fibers. Based on the arrangement of collagen fibers within the GTO capsule, a single GTO receptor can be expected to produce activity that is monotonically but nonlinearly related to the tension of the inserting muscle fibers. The activity appears to depend on the order in which inserting muscle fibers are recruited as well as on the types of muscle fibers that are exerting tension onto GTO. For example, MUs with small (slow MUs) as well as large forces (fast fatigable MUs) produce comparably high discharge frequencies in tendon organs when activated. For many years, researchers have argued about the existence of different gradient tensions that need to be reached for different GTOs to begin firing. Later, it was shown that existence of such gradients is to be expected because not all the motor units being activated will have fibers inserting into individual GTOs. The limited and essentially random sampling of motor units by each individual GTO makes it an unreliable indicator of total muscle tension.

Ensemble Information

Unsurprisingly, researchers turned to studying the ensemble GTO activity to see if it would be a better measure of active force in the muscle than the individual sensors. In experiments by Jami et al. (1992), simultaneous recordings were obtained from ten tendon organs innervating the cat peroneus tertius muscle (an unusually small limb muscle) while its motor units were stimulated individually (Figure 5). While electrical stimulation of two motor units almost doubled the muscle force, the average response of all GTOs was approximately equal to the average discharge when only a

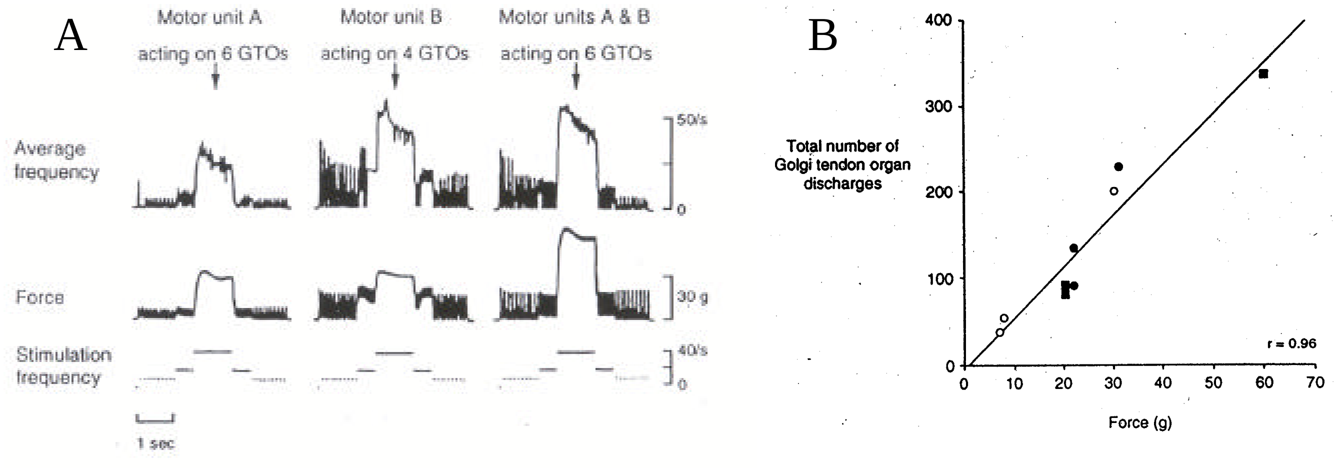

Figure 5. Responses of ten tendon organ afferents innervating peroneus tertius muscle in the cat to motor unit forces produced by stimulation of one or two motor units. A. Average tendon organ responses to the forces from motor unit A (left panel), motor unit B (middle panel), and both motor units (right panel). Stimuli given at 10, 20 and 40 Hz. Motor unit A activated six tendon organs and motor unit B activated four tendon organs (shared with motor unit A). Average tendon organ response calculated from the responses of the activated tendon organs. When both motor units contracted to 40 Hz stimulation, force at the tendon adds as expected from the algebraic sum of the force to each motor unit, but the average discharge frequency does not exceed that when 2 contracts alone. B.Predicted ensemble response for the data in part A of the figure when the total number of tendon organ discharges is calculated (from their average discharge and the number activated). Total tendon organ input increases very well with tendon force. Modified from Jami, 1992.

single motor unit having stronger influence on average GTO response was stimulated. On the other hand, the ensemble firing of all the GTOs in the muscle during activation of multiple motor units was found to increase linearly with the increase in force. These observations suggest that the ensemble of GTOs *could* be used to compute muscle force accurately from the *sum* of all GTO afferent activity in the muscle. By contrast, the computation of length from spindle afferents appears to be based on the *mean* of the activity from all of the sensors.

Even for the extremely small and simple muscle studied by Jami et al., only a fraction of the motor units could be controlled due to the complexity of the experimental set-up. Many questions remain about the precision and accuracy of force information available to the CNS from larger muscles with more complex arrangements of motor units and muscle fiber types. We hope to address these questions by mathematical models of these complex systems. We have completed a model of transduction in individual GTOs that accounts well for the temporal dynamics and spatial summation seen in records from Jami et al. and others. We have developed a biologically realistic statistical model of GTO distributions across the muscle-tendon junction where individual receptors receive a realistic sample of muscle fibers belonging to different motor units. In a heterogeneous muscle, such as medial gastrocnemius, the types of fibers inserting into a GTO capsule depend statistically on its relative location in the muscle-tendon junction due to the nonhomogeneous distribution of different fiber types across the muscle. In MG and most muscles, the GTOs are preferentially distributed in the deep ("core") region of the muscle, which usually has a high density of slow muscle fiber types. A realistic muscle model (Virtual Muscle, Cheng et al., 2000) is available to compute the relative recruitment and force levels of individual motor units according to different conditions of use that affect recruitment order and frequency modulation of motor units as well as length and velocity of muscle motion. We believe that such a detailed model will be a useful tool in testing the ensemble hypothesis in models of various normal and pathological muscles.

Decoding Problem

Our knowledge of how the CNS actually decodes GTO information is very limited because its obvious role as a transducer of individual muscle force does not correspond either to psychophysical performance or to the known pattern of projections from these afferents. Traditionally, GTO force feedback was believed to be involved in reflex inhibition of the receptor-bearing muscles because of the discovery of a class of spinal inhibitory interneuron (IbIn) that received input from GTOs and sent outputs to alpha motoneurons of the same muscle. However, the actual projections of GTOs are much more diffuse and the IbIn actually receives input from many different sensory receptors in skin and muscle as well as descending pathways from the brain (reviewed by McCrea, 1986).

In the spinocerebellar pathways thought to provide kinesthetic information for postural coordination, the signals from spindle and GTO afferents tend to converge on individual projection interneurons. Many muscles have substantial elasticity of the tendons and other connective tissue between the muscle fibers and their skeletal attachments, so the length of the muscle spindles is determined not only by the joint angles but also by the stretch of this series elasticity depending on muscle force. Thus, information from the GTOs could be a necessary part of the deconvolution problem to convert spindle afferent activity to an unambiguous indicator of posture regardless of the motor task underway (Loeb, 1986).

The net effect of force feedback from GTOs is actually positive rather than negative under some conditions of use. During the stance phase of locomotion in cats, positive GTO feedback was found to play a crucial role in reinforcement of muscle force (Duysens and Pearson, 1980). These observations prompted additional human studies where muscles acting about the wrist and ankle were activated by feedback-controlled electrical stimulation, mimicking tendon organ signals (Prochazka et al., 1997). The study concluded that positive force feedback is very effective and surprisingly stable way of controlling the muscles, in contrast to the classical teachings of industrial servocontrol for motors. The inclusion of realistic delays associated with tendon organ reflexes actually provided an additional stabilizing effect from the positive force feedback.

CONCLUSION

Our body is faced with an enormous problem: to monitor and control hundreds of muscles to perform a wide variety of motor tasks. Feedback of state information from those muscles is essential to achieve on-line control and to inform the higher planning centers about the outcomes of their strategies. We are close to being able to account for kinesthesia from the transducer mechanisms of individual receptors and the information content of ensembles of such sensors. We are close to understanding what information is available about muscle force, although we lack a clear picture of how such information is actually used either for perception or control. This type of model-based "vertical" analysis enables testing of the underlying hypothesis of this review - that the CNS optimizes and combines activities of numerous spindles and GTOs in the muscle to obtain the most accurate and useful information.

Theories of motor control are necessarily theories of sensorimotor coordination. The sensory feedback described here is integrated continuously with feedforward control signals at every stage of the neuraxis. A hypothesis about the role of a higher center is not meaningful without at least an implicit model of all of the signals and computations in the lower centers. Such models collectively represent what David Marr (1982) called a "theory of computation" in reference to visual information processing. If the system under study encompasses many such levels, it becomes increasingly important to provide quantitative models of the hypothesized or postulated processes. This is particularly true if the processes are nonlinear because the behavior of such systems is often difficult to intuit.

The models and hypotheses presented here concern the lowest levels of the sensorimotor system, but they are already complex. At least in part, this is because the lower levels are highly evolved to have intrinsic properties and behaviors that were useful in primitive organisms lacking higher control centers and because those properties and behaviors remained useful as higher centers evolved to extend the behavioral repertoire of the organisms (Partridge, 1982; Loeb, 1989). In this way, biological organisms are strikingly different from most engineered systems. Theories of control have been largely derived from and for engineered systems, but biological systems continue to have many advantages in their efficiency, adaptability, fault-tolerance, stability and generally graceful performance. This motivates attempts to mimic the biological strategies in engineered systems. We would suggest that biomimetic strategies may need to start with a consideration of the special properties of biological proprioceptors and their distributed deployment in the musculoskeletal system.

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