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Corresponding Author	Family Name	**Loeb**
	Particle	
	Given Name	**Gerald E.**
	Suffix	
	Division	Department of Biomedical Engineering
	Organization	University of Southern California
	Address	Los Angeles, CA, USA
	Email	gloeb@usc.edu

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Spinal Cord, Integrated (Non CPG) Models of

Gerald E. Loeb*
Q1 Department of Biomedical Engineering, University of Southern California, Los Angeles, CA, USA

Synonyms

Adaptive control; Motor control; Motor learning; Reflex; Regulator; Segmental control; Servo control; Voluntary behavior

Definition

Spinal cord refers to the central nervous system (CNS) in vertebrates below the foramen magnum, between the brainstem and the peripheral nervous system, not including the autonomic ganglia.

Learned sensorimotor behavior refers to all types of voluntary musculoskeletal activation that accomplish a behavioral goal and that utilize sensory feedback during execution, but here excluding cyclical locomotor behaviors known to be generated and controlled autonomously by central pattern generators residing within the spinal cord itself (see "Cross-References"). Q2

Detailed Description

The spinal cord is not part of the brain; together they constitute the central nervous system of vertebrates. The spinal cord alone is capable of controlling complete motor behaviors such as locomotion. It can generate complex sequences of muscle activation and alter them to ambient conditions detected by somatosensory afferents. The well-studied role of the spinal cord in locomotion is covered in other entries ("▶ Vertebrate Pattern Generation: Overview"); this article considers whether and how the same spinal circuits contribute to voluntary motor behavior that is ultimately controlled by the brain.

Historical and Methodological Perspective

Several anatomical features of the spinal cord made it an attractive target for the earliest neurophysiological investigations. Its connections to and from the peripheral nervous system of the body are arranged in four laterally and dorsoventrally segregated and highly elongated rows of roots. These are divided and gathered into spinal nerves based on the openings between adjacent vertebrae. These roots and their associated peripheral nerves are readily traced by gross anatomical dissection to various target structures (individual muscles and regions of skin) whose function can be easily observed and manipulated. About 200 years ago, the anatomist Charles Bell and, separately, the physiologist Francois Magendie discovered that the ventral roots conveyed the motor commands to the muscles (Bell 1811) while the dorsal roots conveyed only sensory information (Magendie 1822), respectively. This laid a foundation for the interpretation of clinical phenomena such as the knee-jerk reflex, well known to nineteenth-century neurology. At the turn of the twentieth century, Sir Charles

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*Email: gloeb@usc.edu

Sherrington systematically extended the set of spinal reflexes to include both excitatory and inhibitory responses as well as interlimb effects and suggested that such reflexes constituted the building blocks of spinally mediated behaviors such as locomotion (Sherrington 1910).

As electrophysiological methodology developed during the middle of the twentieth century, it became possible to identify the individual neurons and circuits responsible for behavioral phenomena. The spinal interneurons came to be divided and identified by the nature of the input and output connections by which they were first identified. The newly discovered proprioceptors and spinal interneurons appeared to correspond to the feedback circuits utilized by the emerging field of servo control engineering to stabilize electrical and mechanical systems (including the instrumentation that those electrophysiologists generally had to build for themselves). This suggested that the reflexes might be just the most visible manifestations of continuous servo control, in which the spinal circuitry could simplify the problem of motor control by linearizing the complex mechanical properties of the musculoskeletal system (Houk 1979). It gradually became clear, however, that the actual input and output connections to spinal interneurons and motoneurons were far broader than predicted by servo control. The most local circuits were the easiest to find but the cumulative effects of the more widespread circuits are probably much larger. Furthermore, the strength and even the sign of many spinal reflexes were found to be modulated during both locomotor and voluntary motor behaviors (Burke 1999).

Neurophysiological studies of voluntary behaviors have focused mostly on the cerebral cortex of the brain, correlating neural activity recorded by chronically implanted microelectrodes with observable kinematics and/or muscle activity in the limb. However, the vast majority of corticospinal projections end on spinal interneurons rather than the motoneurons that activate muscles directly (Rathelot and Strick 2009). These interneurons are vigorously active during learned, voluntary limb movements (see Fig. 1 below from Perlmutter et al. 1998). The threshold nonlinearity of spiking neurons implies that the cortical commands can be seen as enabling reflexive

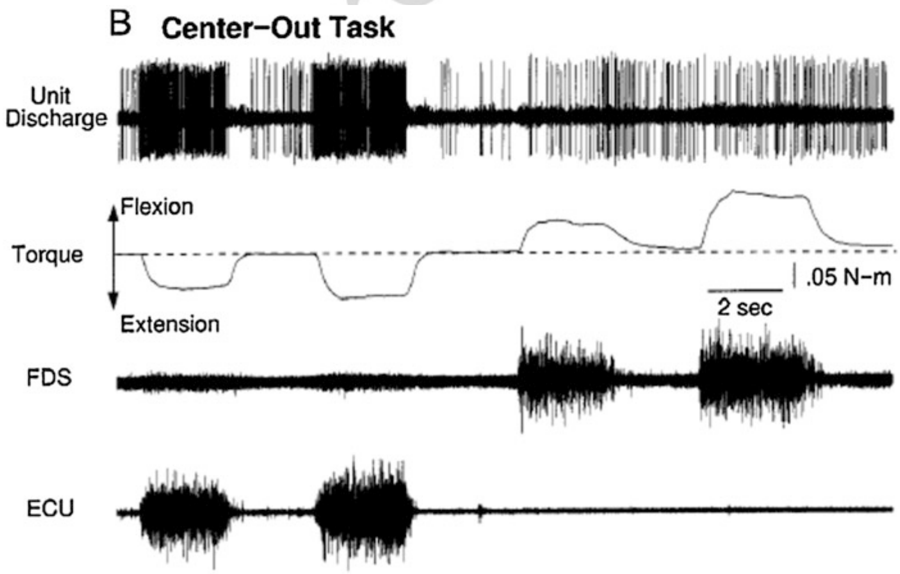

Fig. 1 Extracellularly recorded spikes from a spinal premotor interneuron recorded as monkey-generated isometric ramp-and-hold torques in flexion and extension at the wrist in order to match a visual cue; *FDS* = *EMG* from flexor digitorum superficialis, *ECU* = *EMG* from extensor carpi ulnaris. Note strong correlation with ECU during extension torques but substantial activity during flexion torques that was not correlated with FDS modulation (From Perlmutter et al. 1998)

adjustments or, equally, that the ongoing somatosensory feedback enables the commanded behavior. Early attempts to tease this apart relied on the latencies of various responses to strong electrical stimuli, which depend on the physical lengths of the circuits and the conduction velocities of the axons. This can be used to compute the minimal latency of the fastest possible responses such as the monosynaptic stretch reflex, but it does not help with mechanical stimuli whose asynchronous afferent signals may undergo substantial temporospatial integration in the interneurons at every level before any response is seen.

This entry summarizes what is now known about the connectivity of the spinal circuits (for a detailed review, see Pierrot-Deseilligny and Burke 2005). Much of that information comes from histological tracing and electrophysiological studies of the spinal cord of the cat, supplemented by clinical studies of human limb reflexes. There are substantial specializations in other species and other parts of the body such as the axial muscles of the neck and trunk (Richmond and Loeb 1992). This review also considers theories and models regarding how these spinal circuits could contribute to control of learned, voluntary limb movements. Other parts of the brain such as the cerebellum have equally well-developed connections to and from spinal cord (Spanne and Jörntell 2013) compared to the cerebral cortex. Damage to the cerebellum produces different but equally profound sensorimotor disorders, but its role in voluntary behavior is even less well understood. The actual functional relationships between the brain and the spinal cord remain contentious.

Basic Components

Somatosensory Afferents

A general review of somatosensation can be found elsewhere; this is a brief summary of the afferents whose modalities and conduction velocities resulted in the naming conventions for the interneurons described below.

- **Spindle Primary Afferents (Ia)**: Most muscles contain 20–500 elaborate sense organs attached in parallel with their muscle fibers. These muscle spindles each contain several specialized and separately innervated intrafusal muscle fibers. Each spindle is innervated by one rapidly conducting, primary afferent axon (Aα) whose local sensory endings consist of spirals wrapped around the middle of each of the intrafusal muscle fibers. These Ia afferents are exquisitely sensitive to stretch of the muscle (and hence of the spindle and its intrafusal muscle fibers). The absolute and relative sensitivities of the Ia afferents to length versus velocity are modulated over a wide dynamic range by centrally controlled activation of their various types of intrafusal muscle fibers (Loeb 1984).
- **Golgi Tendon Organ (GTO) Afferents (Ib)**: Most muscles contain 20–200 simple sense organs attached in series with various subsets of their muscle fibers, making them sensitive to active muscle force. Each GTO is innervated by one rapidly conducting primary afferent axon (Aα). The random sampling of muscle fibers makes the response of a given GTO somewhat idiosyncratic, but the generally orderly recruitment of motor units results in ensemble activity of the Ib afferents that accurately reflects total muscle force (Mileusnic and Loeb 2009).
- **Group II Afferents**: The smaller and slower conducting myelinated axons (Aβ) in peripheral nerves are designated as Group II. They include both cutaneous mechanoreceptors with a wide range of sensitivities in both glabrous and hairy skin plus secondary spindle afferents attached to a subset of the intrafusal muscle fibers and sensitive mostly to absolute length. Some cutaneous stretch sensors contribute to the sense of body posture and motion in combination with the spindle afferents (Gandevia 1996); others are better suited to detecting intermittent contact with external objects.

- **Group III and IV Afferents**: The smallest myelinated (Aδ) and unmyelinated (C) sensory nerve fibers innervate a wide range of specialized receptors for strain, temperature, pain, and metabolic products. Their signals are processed locally by dorsal horn interneurons, many of which project to some of the spinal interneurons or their presynaptic inputs. Their slow conduction velocities lead to the presumption that they do not contribute importantly to moment-to-moment coordination but they probably modulate the state of the system in response to fatigue and injury (Martin et al. 2006).
- **Recurrent Motoneuron Collaterals**: Most alpha motoneurons give off collateral branches before leaving the spinal cord en route to the muscles. While not truly sensory, these efference copy signals provide feedback regarding important state variables of the system, contributing to both the reflexive behavior of the spinal cord itself and the ascending information that is conveyed to the brain (Windhorst 1990).

Presynaptic Modulation

An important feature of many spinal circuits is the presence of synaptic triads, in which the synaptic boutons of one neuron (modulator) end on the boutons of another neuron (transmitter) rather than on the cell body or dendrites of the receiver neuron. These presynaptic pathways may exert either depolarizing or hyperpolarizing effects on the resting membrane potential of the transmitter boutons. When a spike arrives at the transmitter bouton, the amplitude of the voltage excursion depends on this resting potential; the amount of transmitter that is released depends strongly on the voltage excursion. A depolarizing presynaptic modulation thus has the effect of inhibiting the efficacy of the transmitter; a hyperpolarizing modulation facilitates the transmitter. The presynaptic inhibitory effects of many cutaneous afferents have been particularly well described (Rudomin and Schmidt 1999). The monosynaptic stretch reflex is also presynaptically inhibited by descending cortical pathways (Meunier and Pierrot-Deseilligny 1998) and in fatigued muscles (Baudry et al. 2010). The full extent of sources and recipients of presynaptic inhibition and facilitation is not known.

Limb Dynamics

Physiologists look for ways to simplify complex musculoskeletal anatomy and mechanics in order to identify organizing principles of control. By focusing on one axis of motion of one joint (e.g., dorsiflexion/extension of the ankle joint), it is possible to describe all the muscles that create a positive moment as synergists and all that create a negative moment as antagonists. Activation of the muscles in each group will have opposite effects on the joint torque, and motion of the joint in this axis will have opposite effects on the stretch receptors in these two groups of muscles. Unsurprisingly, the reflexes elicited by afferents from synergistic muscles are substantially different and often opposite in sign from those elicited by the same types of afferents from the antagonist muscles (Sherrington 1908). Much of the terminology below reflects this natural reciprocity of function and connectivity.

Unfortunately, most musculoskeletal anatomy and dynamics are not well described by simple reciprocity. Most joints have more than one axis of motion (see also degree of freedom; DOF Degrees of freedom http://www.springerreference.com/docs/html/chapterdbid/114965.html) and the majority of mammalian muscles cross more than one joint. The lengths of the muscles and their moment arms on each axis of motion depend on the posture and motion of all the axes of all the joints that they cross. Muscles that are synergists for the restricted motion described above may be undergoing length changes that are opposite in sign and generating torques in other axes that are opposite in sign. Furthermore, a skeleton consisting of a series of linked inertial masses is subject to intersegmental dynamics, sometimes summarized as Coriolis effects. Acceleration induced by a muscle crossing one joint results in angular accelerations at distant joints, similar to the complex sequence of motion induced by cracking a whip from its proximal end (Zajac and Gordon 1989). The idealized classical circuits described below use the terminology of synergist and antagonist, but most muscles relate to most other muscles via combinations of both types of circuitry (designated as a "partial synergist" relationship). The net effects depend on the gains in the competing pathways, which are strongly modulated by both descending and local pathways, as discussed in Coordination and Regulation.

Spinal Circuits

Ia Monosynaptic Stretch Reflex

The tendon jerk reflexes (e.g., knee, ankle) are the fastest and most reliable responses because they involve only one synapse between a rapidly conducting Ia spindle afferent and an alpha motoneuron. The Ia afferents from a given muscle project to most or all of the motoneurons that control that muscle (homonymous projection; HOM in Fig. 2) and to many of the motoneurons of synergist (SYN) muscles (Eccles et al. 1957a). Nevertheless, the strength of the observable response can be substantially modulated by postsynaptic polarization of the receiving pool of motoneurons via other synaptic inputs and by presynaptic inhibition or facilitation of the Ia synapse itself. The brain can learn to change the gain of even this direct connection (Wolpaw 201

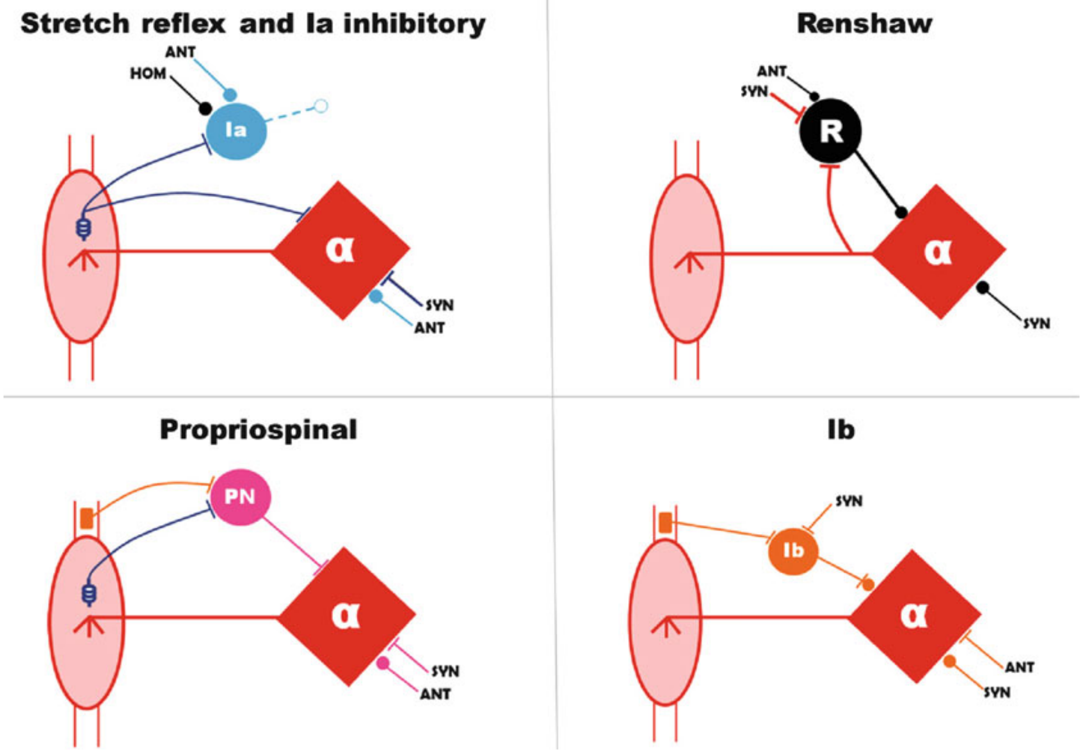

Fig. 2 Five classical interneuronal pathways that comprise the model from the perspective of a single muscle. Projections from neural elements associated with self (*HOM*) as well as synergist (*SYN*) and antagonist (*ANT*) muscles are shown with color codes: Ia inhibitory interneurons are *blue*, Ib inhibitory interneurons are *orange*, and Renshaw inhibitory interneurons are *black* (Illustration from Tsianos et al. 201

Q3

Ia Inhibitory Interneurons

Spindle Ia afferents excite a class of inhibitory interneurons that project to the motoneurons of antagonist muscles (Eccles and Lundberg 1958). Thus, stretching one muscle tends to inhibit activity that may be occurring in the antagonist muscles and that would otherwise oppose the excitatory stretch reflex described above. It is important to remember that the spindle receptors of both the synergist and antagonist muscles are generally biased by their respective fusimotor efferents so that they are generating continuous activity. Sudden perturbations that give rise to excitatory and inhibitory reflexes are just the most obvious manifestation of a continuous push-pull servo control system. These reciprocal circuits work continuously to maintain stable body posture and minimize energetically wasteful cocontraction of mutually antagonistic muscles.

Ib Inhibitory Interneurons

The force-sensitive Golgi tendon organs excite a class of inhibitory interneurons that project to their own and synergist motoneurons (Eccles et al. 1957b). This results in a simple servo controller that tends to stabilize fluctuations in force. The story does not end there, however. The Ib inhibitory interneurons actually receive inputs from a wide range of cutaneous and proprioceptive afferents, and they project widely to both synergistic and antagonistic motoneurons. Furthermore, Ib inhibitory interneurons project to each other, resulting in disinhibition whereby force feedback can actually result in positive, self-reinforcing feedback loops (McCrea 1986). This complexity is summarized in Fig. 2 (Ib, bottom right) and Fig. 3 with a symbol denoting the selectability of both excitatory and inhibitory effects between the Ib inhibitory interneuron and homonymous alpha motoneuron.

Renshaw Inhibitory Interneurons

The recurrent motoneuron collaterals excite an interneuron that inhibits the homonymous motoneurons and their synergists, in the manner of a servo control governor preventing runaway activation of the muscles. These Renshaw inhibitory interneurons also project to the Ia inhibitory neurons of the same muscle, resulting in a disinhibition of the antagonist motoneurons (Windhorst 1990).

Propriospinal Excitatory Interneurons

There are clusters of excitatory spinal interneurons located just rostral to both the cervical and lumbar enlargements wherein the limb motor nuclei are located. These interneurons receive direct excitatory projections from both Ia and Ib afferents as well as strong descending control from the brain (Jankowska et al. 1973). They have been implicated in the initiation of voluntary limb movements via their excitatory and inhibitory effects on synergist and antagonist motoneurons, respectively (Lundberg 1992).

Cutaneous Reflex Interneurons

Activity in cutaneous afferents can produce strong and widely distributed excitation and inhibition of motoneurons. The pathways all go through chains of at least two interneurons, however, each of which is subject to modulation by other afferents, other interneurons, and descending signals from the brain. The functional contribution of cutaneous feedback is obvious from studies of dexterous manipulation of objects (Johansson and Flanagan 2009), but specific circuit models are not available.

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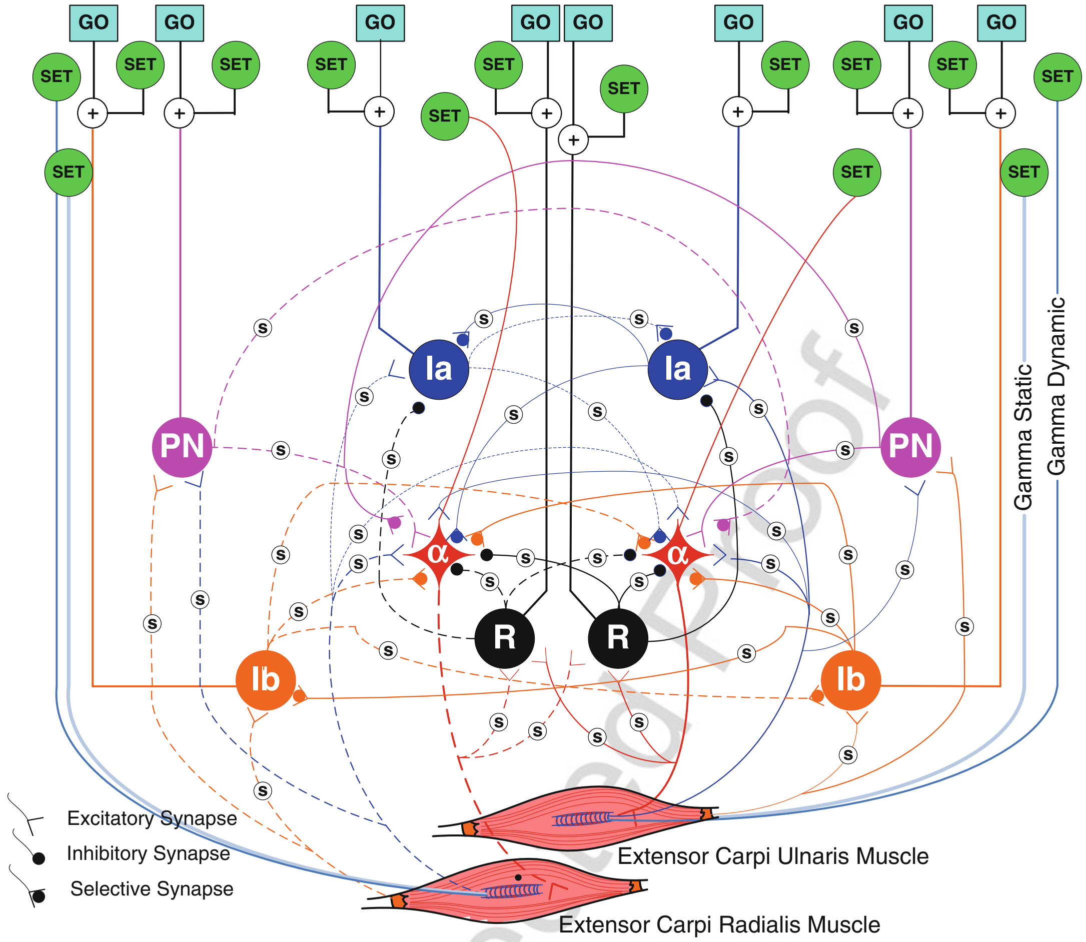

Fig. 3 The major proprioceptive feedback circuits between two wrist muscles that are synergists for some tasks (e.g., extension) and antagonists for others (e.g., radioulnar deviation); color code is the same as in Fig. 1. Tasks were controlled by learning a background pattern of *SET* signals to designated spinal neurons and presynaptic gains (*S* in *circles*) and a *GO* pattern to initiate the task via only the spinal interneurons (Figure from Raphael et al. 2010)

Spindle Secondary Interneurons (Group II)

The tonic stretch reflex and perhaps some of the knee-jerk reflex may be generated by disynaptic excitation arising from Group II muscle afferents. These same interneurons also receive input from Flexor Reflex Afferents (see below). It has been proposed that these Group II interneurons and others resulting in disynaptic inhibition contribute to voluntary behaviors (Lundberg et al. 1987), but there is little direct evidence as yet.

Flexor Reflex Afferents

Nociceptive cutaneous afferents (Group III = Aδ fibers, Group IV = C fibers) give rise to the flexion reflex, consisting of coordinated activation of ipsilateral limb flexors and often accompanied by contralateral limb extension (Anden et al. 1964; Duysens et al. 2013). It is prominent during locomotion, enabling the limb to withdraw from an obstructive or aversive stimulus to get around an obstacle. Specific models of these oligosynaptic circuits are not available.

Commissural Interneurons

Interneurons that project across the midline appear to be useful for interlimb coordination during locomotion (Jankowska 2008). Specific circuit models are not available and their role in learned motor behaviors is unknown.

Central Pattern Generators (CPG)

As discussed elsewhere (McCrea and Rybak 2008), the spinal cord contains reciprocally inhibited groups of interneurons that function as self-sustaining oscillators for cyclical behaviors such as locomotion. Their relatively simple, alternating rhythms are converted into the more subtly phased activation of individual muscles by the interneuronal circuits listed above and perhaps unknown others. Their rhythms can be altered or even reset by somatosensory feedback and descending control. It is unknown whether these CPG circuits are utilized for learned motor behaviors that have similar oscillatory patterns.

Decision and Command Versus Coordination and Regulation

The general notion is that the brain is strategic, deciding what voluntary movement should be executed and when, while the spinal cord is tactical, dealing with the details of apportioning the physical work among various muscles and making reflexive adjustments to cope with local conditions. Most of the theories described below were motivated by the desire to simplify these problems, both so that the process could be understood by researchers and so that the brain could actually solve them. Nevertheless, from the relatively slow rate at which infants develop motor coordination, it is apparent that this is a very hard problem requiring a great deal of adaptive learning by the brain. Simple and intuitive theories may not be consistent with reality.

Fusimotor Servo Control

If the brain plans movements according to the desired trajectory of limb postures, then there has to be a computation to convert that plan into the net drive to each of the muscles required to stay on that trajectory. The complex mechanical dynamics of a multiarticular limb plus the highly nonlinear force-generating properties of muscle make such a calculation difficult, to say the least. Servo control offers a way out of this dilemma. Muscle activation could be commanded (or at least assisted) by first activating fusimotor neurons, thereby turning on muscle spindle afferents, and then allowing the excitatory reflexes from those afferents to turn on the motoneurons until the muscle shortened to the point where the fusimotor effects were negated (Merton 1953).

These ideas have fallen out of favor for two reasons. One is the lack of evidence for sufficiently high gains in these pathways or for fusimotor drive and spindle afferent activity that clearly leads the alpha motoneuron activity. The second is the recognition that the spindle afferents are responsible for much of the senses of posture and kinesthesia (Scott and Loeb 1994), which must be independent of muscle activation. It seems more likely that the fusimotor system is used to optimize the sensitivity of the spindle afferents to the expected range of voluntary movements, thereby improving rather than degrading these critical senses (Loeb and Marks 1985).

Reciprocal and Equilibrium Control

Another way to solve the above-stated problem of getting a complex musculoskeletal system into the desired posture is to take advantage of the springlike properties of mutually antagonistic sets of muscles at each joint. Active muscles themselves tend to behave like springs, increasing their force output when stretched and decreasing it when shortened. Simply coactivating mutually antagonistic muscles at different levels necessarily results in various postures (Bizzi et al. 1993); perturbations away from those postures are automatically resisted by the effective mechanical impedance of the system (which includes springlike terms related to joint angle plus terms related to joint velocity and acceleration (Hogan 1984)). The ability of such a control system to follow dynamic trajectories can be greatly enhanced by including the reciprocal reflexes mediated by spindle afferents, and they can be more subtly modulated by further including fusimotor control. This is the so-called gamma equilibrium-point hypothesis (Feldman 1966; Feldman et al. 1998). A more general model of how the brain could utilize the reciprocally organized spindle feedback was presented by Maier et al. (2005).

While these muscle properties and reflexes certainly affect the properties of the system that the brain must control, they do not by themselves seem to account well for many observed behaviors (Kistemaker et al. 2007). Equilibrium control predicts more inefficient and undesirable cocontraction of muscles than is generally observed. It has difficulty with highly dynamic movements or when the goal is to control force on an object or surface rather than position. Finally, it is difficult to extend these schemes to account for the many multiarticular muscles and for the intersegmental dynamics of limbs.

Inverse Dynamics Models

Presumably the brain generates the command signals to the spinal cord that will result in the desired limb trajectory. If the brain were sending signals directly to the motoneurons, it could learn an inverse model of the musculoskeletal mechanics and then employ an optimization scheme to compute an effective and efficient pattern of commands (Kawato 1999; Scott and Norman 2003). It would also have to monitor the sensory feedback and compute the necessary adjustments (Scott 2004), suppressing or taking into account any reflexes that would be occurring simultaneously in the autonomous circuits of the spinal cord (and probably other lower centers). But the brain is largely sending signals to the spinal interneurons themselves. In order to compute those commands, the brain would require an inverse model that included also the connectivity of the interneurons plus a forward model of the sensory afferents that project to those interneurons. It is unclear how the brain could learn such a complex model.

Regulator Models

Rather than trying to assign specific roles to each individual reflex or circuit, it may be more productive to look at the emergent properties of the complete spinal cord network. One approach is to ask what sorts of connections between afferents and efferents would be useful for solving typical problems in motor control. Given certain constraints, it is possible to apply an engineering tool for designing a linear quadratic regulator (LQR), which is essentially a matrix of excitatory and inhibitory gains between all possible pairs of input and output signals. The solution minimizes a cost function that reflects both the deviations from the desired state of the system and the expense of efforts to correct such deviations. When such a matrix was computed for maintaining stable standing posture in the hindlimb of a cat, the patterns of connections bore a striking resemblance to the patterns of connectivity in the major known interneuronal circuits listed above (Loeb et al. 1990; He et al. 1991). The matrix computed for a different mechanical state such as when freely moving through space would be substantially different, similar to the changes in reflex gains known to occur for such state changes. The methods used by engineers to compute such LQRs are unlikely to be employed by the brain, but it is possible that they could be approximated by trial-and-error iteration over the lifetime of the animal.

While LQR analysis provides some insights into the general utility of the spinal cord for responding to perturbations, it does not provide a way to generate the desired states or trajectories in the first place. The general absence of direct cortical drive to the alpha motoneurons and the targeting of that drive onto the interneurons that mediate the reflexes suggest that the brain must plan simultaneously both the nominal behavior and desirable responses to anticipated perturbations (Loeb et al. 1999). The difficulty of computing such plans from inverse models suggests that they must be learned and stored as lookup tables and then replayed whenever the brain is called on to perform a familiar or at least similar task. Given the very large number of different interneuronal drives and synaptic gains in the spinal circuitry, is it feasible for solutions to be learned by trial-and-error exploration of this huge hyperspace?

Reasonably complete models of the classical spinal circuits that employ proprioceptive feedback (for the first five spinal circuits above, see Figs. 2 and 3) were constructed for an idealized 2DOF, 4-muscle wrist model (Raphael et al. 2010) and for a 2DOF, 6-muscle planar elbow-shoulder system (Tsianos et al. 2011). In both cases, simple trial-and-error adjustment from initially random states of the spinal cord resulted in kinematically successful and energetically efficient performance of a wide range of typical behaviors (resisting perturbations, rapid reaching to precise postures, compensation for viscous curl-fields, generating precise end-point forces). Success was attributed to the large number of "good-enough" solutions offered by the spinal circuitry, which seems to have little tendency to become entrapped in poor local minima. Solutions to one task provided useful starting points to learn new tasks, and sparse sets of such sequentially learned tasks could be interpolated to achieve intermediate behaviors despite the nonlinearity of the underlying neuromusculoskeletal system (Tsianos et al. 2011). Somewhat disconcertingly, this implies that the internal representations of and strategies for a given motor behavior may differ substantially among individuals. That would be consistent with the differences that emerge when physically "normal" individuals try to learn a new and unusual sport, but it makes it difficult to design and interpret experiments that usually require pooling data from many individuals.

Conclusions

The role of the spinal cord in learned sensorimotor behaviors remains contentious and may be shifting as animals evolve toward a wider repertoire of learned rather than instinctive behaviors. The propriospinal interneurons provide a case in point. In cats, these interneurons and their contribution to reaching movements are relatively easily demonstrated. In nonhuman primates, they are difficult to excite and, therefore, to find at all in anesthetized preparations (Alstermark et al. 2007). One possibility is that the resting bias of the spinal interneurons and perhaps other subcortical circuits may become hyperpolarized to suppress their reflexive responses until the cortex decides what combination of those reflexes will generate a more reasoned response. Another possibility is that the cortical systems that presumably subserve learned behaviors may simply overwhelm the other inputs to the spinal circuitry to take fairly direct control of the musculature, including the responses to perturbations (Kurtzer et al. 2008). Ignoring the phylogenetically old but sophisticated coordination provided by spinal interneurons might make sense if the brain needs to develop an internal model of the plant in order to compute motor programs de novo. Conversely, these circuits may be very useful if the brain must learn, store, and recall its repertoire without such online computation. Newly evolved musculoskeletal systems and functions such as dexterous manipulation of objects and vocalized speech may have no choice but to rely on newly evolved direct corticomotoneuronal projections, whether they are computing or recalling motor programs, but even these undergo substantial modulation by spinal circuits (Petersen et al. 2010).

Nevertheless, it is worth remembering that the first problem faced by a newborn brain is system identification. It does not "know" that the external world and its own body exist, much less what effects its various output axons will have on that body. In the process of self-organizing that knowledge, the brain will discover and learn to cope with whatever musculoskeletal apparatus and local neural circuitry exist. Learning a new task must inevitably involve decisions about which components of the apparatus and the circuitry appear to be useful and which need to be ignored or suppressed. The challenge to the developing organism is to learn those tasks as quickly as possible, not to conform to abstract theories of how those tasks might be learned or performed.

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