

12

Neuromechanical Interaction in Cyclic Movements

James J. Abbas and Robert J. Full

1 Introduction

Cyclic behaviors, such as breathing, chewing, and locomotion, serve our basic needs for respiration, nutrition, and transportation. They are performed on a daily basis in a wide variety of situations and often for extended periods of time. Therefore, the mechanisms by which they are generated must be reliable, versatile, durable, and efficient. In some cases, these specific needs have resulted in the evolutionary development of specialized neural, muscular, and/or skeletal structures.

This chapter describes some of these structures that are specialized for cyclic movements and explain (or speculate on) how they fit the needs of the overall system. The focus is on locomotor systems, with a particular emphasis on the interaction between the neural and mechanical (muscular and skeletal) systems. The approach is decidedly integrative, drawing from studies on a wide variety of locomotor behaviors (walking, crawling, swimming, flying) in a wide variety of animals (bipedal, polypodal, aquatic, winged).

Locomotion can be viewed as a multiobjective control problem. While the primary concern is “get me over there,” several other objectives might come into play. First, the animal might try to avoid any physical harm that might occur during the process of moving. This could include escaping from a predator (which would put severe time constraints on “get me over there”), avoiding obstacles, and maintaining balance. Second, the animal might try to keep energy expenditure low during locomotion. Achieving an absolute minimum of energy expenditure may not be a primary concern,

but keeping expenditures low is definitely advantageous. Finally, the animal might also be concerned about conveying a specific appearance during locomotion such as authority, ferocity or attractiveness.

1.1 Interactions Determine Movement Pattern

The neural control system that achieves these multiple, complex objectives has often been viewed as having a hierarchical structure (Ghez 1985). A purely hierarchical system would be organized in such a way that the high level goal of “get me over there” is systematically broken down to subtasks and parceled out to lower and lower levels of the organizational structure. For example, the high level command for locomotion would result in the coordinated activity of neural subsystems for controlling posture, balance, forward progression, and so on. Each subsystem would further parcel out its task to lower-level subsystems; one such low-level subsystem may be charged with the task of controlling hip flexion toward the end of swing phase. Although this view may at times be convenient, it is clear that it does not adequately describe the structure of neural control systems. In a modified version of the hierarchical structure, the chain of command would be less clearly defined and specific goals of each subsystem may be more global in nature. Here, coordination is achieved through the interaction of various components, rather than through the successive delegation of tasks from higher to lower level structures. Ghez (1985) describes this as a parallel structure that complements

the hierarchy; Cohen (1992) goes further to describe the overall structure as a "heterarchy." Thus, even at a general block diagram level of description, there is ambiguity and limitations to our understanding of the organization of neural control systems for locomotion.

This issue of hierarchy in the nervous system can also be used as a framework in which to view the neuromechanical system. Muscles, skeleton, and environment are often studied separately from the nervous system and are viewed as mechanical components that constitute the system to be controlled. Motor commands from the lowest level in the hierarchy of the nervous system (motoneurons) are specified in such a way that the resulting movement/posture of the skeletal system meets the higher level objectives (i.e., the movement pattern is directed from above). In a more integrated view, the movement pattern is a result of the interactions among the neural and mechanical components (Chapter 14; see Raibert and Hodgins 1992; Chiel and Beer 1993; McGeer 1993; Chapter 13). Here, the mechanical system is no longer just an object with properties to be reckoned with, it is one of many system components whose properties influence the overall system behavior. This complex interaction of the neural and mechanical dynamic systems has been described as a "self-organizing" process that results in the formation of movement patterns (Schoner and Kelso 1988).

These concepts regarding neural organization and neuromechanical interactions are by no means new ideas. It has long been accepted that neural control systems are not entirely hierarchical and that movement patterns are the result of interaction between neural and biomechanical systems. However, motor control studies have primarily focused on a specific neural or biomechanical component for two reasons: (1) there is still a lack of detailed understanding of the various components and (2) many of the experimental techniques that are available necessitate the use of reduced preparations of neural system components or musculo-skeletal system components in which the interactions are removed. Note that there are exceptions in which clever experimental techniques have been used to study the interactions in an intact or semi-intact preparation, but these are the exceptions. In many cases, this lack of suitable experimental techniques has often been successfully overcome through the use of mathematical mod-

els and computer simulations (e.g., Loeb and Levine 1990; Chapter 15).

This chapter briefly describes the neural and biomechanical components and then focuses on the interactions among the components, as revealed by both experimental and modeling studies. Throughout this chapter, and more generally in the study of neural control of locomotion, there are several concepts that recur. One is the notion that the neural and biomechanical components have evolved together and that they develop and adapt together in a given individual animal. A second is that there is conservation across species (i.e., over a wide range of sizes, body structures, and modes of locomotion we see similarities in the neural and biomechanical components as well as in the manner in which the components are organized). A third is that an approach to studying motor control that utilizes a combination of biological and engineering techniques will lead to greater insight than a less integrated approach.

2 Features of Biomechanical Systems for Locomotion

Many chapters in this book include material on muscle biomechanics, soft tissue biomechanics, and skeletal biomechanics, especially in Sections II, III, and VII). This section focuses on specific issues that are important for understanding cyclic movements in general, and locomotion in particular.

Biological systems use a variety of modes of locomotion, including bipedal locomotion, polypodal locomotion, flying, and swimming. Many animals are capable of utilizing several modes of locomotion, such as birds that can fly, walk, and even swim. Obviously, in a given animal, certain biomechanical constraints must be met in order to utilize a given form of locomotion. For example, appendages capable of providing lift are required for flight; appendages capable of supporting body weight are required for legged locomotion; and some means of propulsion in water is required for swimming. The mechanical structures used for the various forms of locomotion include endoskeletons, exoskeletons, and hydrostatic skeletons (a fluid-filled tube surrounded by muscle).

Chapters in this section include descriptions of studies on locomotion of the leech (hydrostatic

skeleton) (Chapter 14), legged locomotion of the stick insect (exoskeleton) (Chapter 16), swimming of the lamprey (aquatic vertebrate) (Chapter 15), walking in humans and cats (legged vertebrates) (Chapter 18; Chapter 17), as well as studies on a wide variety of legged animals (Chapter 13).

2.1 Muscle and Skeletal Dynamics

In segmented skeletal systems, movements that involve just a single segment can exhibit complex dynamic properties because of passive joint stiffness and damping as well as the inertial properties of the limb (Audu and Davy 1985). Over limited ranges of movements, passive joint properties are often assumed to be linear, but characterization over the normal range of movement has often demonstrated that nonlinear properties can be functionally significant (Chapter 7). Musculotendon actuators exhibit complex length-, velocity-, and activity-dependent behavior (Chapter 2; McMahon 1984; Zajac 1989; Ettema and Huijing 1990; Hof 1990; Mungole and Winters 1990; Zajac and Winters 1990) that are functionally significant. The physical properties of tendons vary widely for different muscles within or across animals and are clearly specialized for critical tasks. A good example of the important role of tendon properties is the ability of the plantar flexor tendon to store elastic energy (Alexander and Vernon 1975; Biewener and Baudinette 1995).

Locomotion, however, typically involves movements of several segments of two or more limbs and therefore the situation is much more complex than the mechanics of single segment movements (Winter 1987, 1990; Hinrichs 1990; Yamaguchi 1990; Zernicke et al. 1991). Here, one must also consider the effects of intersegmental coupling (e.g., a swinging thigh exerts forces and moments that tend to accelerate the shank) as well as inter-limb coupling (e.g., a swinging right leg exerts forces and moments that tend to accelerate the left leg). Thus, in systems with segmented skeletons, it is clear that movements such as locomotion must involve the coordinated activity of a set of muscles and that the mechanics of the musculoskeletal system will greatly influence the pattern of neural activity that drives the movement.

A remarkable feature of locomotor systems, however, is the degree to which running, hopping and trotting of complex multi-segment mechanical

systems can be explained by relatively simple spring-mass type models (Chapter 13). For legged locomotor systems, it appears as though the complex details of the various system components are integrated in order to result in an overall spring-mass type behavior while simultaneously providing the ability to perform a range of locomotor and nonlocomotor activities.

2.2 Locomotion as a Multistate Process

The locomotor cycle has often been described as having multiple phases, or ‘states’ (Winter 1987; Inman et al. 1994). That is, at any point in time the body may be in one of several states and the process of locomotion involves a repeated set of transitions among these states. For example, we can use a very broadly defined set of states (see Figure 12.1) to define bipedal locomotion: right double-support (both feet on ground with right leg forward), left swing, left double-support, right swing. A more detailed description might include such states as midstance, initial contact, terminal swing, and so on. A full description of behavior would include some nonlocomotor states (standing, sitting, falling, etc.) as well as states for different forms of locomotion (walking, running, hopping, crawling, etc.). Note that as speed gradually increases from a slow walk

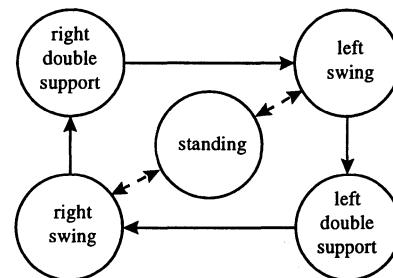


FIGURE 12.1. Simple multistate model of biped locomotion. Each circle represents a possible state in the system. Individual states may be differentiated by different biomechanical configurations or by different control goals. In this diagram, normal gait would involve a clockwise progression of the system from one state to another around the perimeter following the solid lines. Cyclic activity may be interrupted by entering the “standing” state in the center of the diagram. A more complete multistate model of this sort may include a further breakdown of the locomotor states listed here, as well as additional states for other cyclic and noncyclic tasks.

to a fast run one would see changes in the state sequence, changes in the time between state transitions as well as modifications within a given state (e.g., double-support during a fast walk would not just be a fast version of the kinetic and kinematic trajectories of double-support during a slow walk (Winter 1987)).

One important feature of the mechanics of locomotor systems is that there are state-dependent effects that are often significant. That is, in many instances, the result of a neural action may strongly depend on the biomechanical configuration of the body. For example, activation of the gastrocnemius muscle towards the end of stance phase will result in forward propulsion of the body (and knee extension) while activation of the same muscle at the beginning of stance phase will result in backward propulsion of the body (and knee flexion).

A second important feature of the mechanics of locomotor systems is that although movement patterns are stereotyped, there is a wide range of variability within a given movement pattern for a given individual. That is, the kinematic and kinetic trajectories for a given state may vary widely from one cycle to another—there is not a unique solution to the problem of getting from one state to another. The sources of this variability may be environmental (e.g., obstacles, interactions with other movement patterns such as lifting an arm), mechanical (e.g., muscle fatigue or response variability) or neural (intrinsic variability in motor pattern output).

In summary then, locomotor systems include a wide range of biomechanical structures that can utilize different modes of locomotion in a variety of movement patterns. The range of possible configurations for a biomechanical system can be viewed as having a finite number of possibilities, called “states.” Locomotion can be represented as a cyclic movement of the biomechanical system through a subset of all possible states and the details of movement within a given state may vary from one locomotor cycle to another.

3 Neural Systems

Experimental evidence in a wide variety of animals has indicated the presence of pattern generating neural circuits that drive cyclic movements (Grillner 1981; Cohen et al. 1988). The general structure

of the neural system is shown in Figure 12.2. Typically, the “pattern generator” receives inputs from other neural centers and from the periphery that modulate its outputs. The neural mechanisms used to generate the oscillatory patterns may include cellular properties of specific neurons (voltage and time-dependent membrane channels) as well as network properties (patterns of interconnections among neurons in the pattern generator circuit). The general structure shown in Figure 12.2 as well as the neural mechanisms used to generate oscillatory patterns are similar in a wide variety of animals; the variety appears to be in the details of how

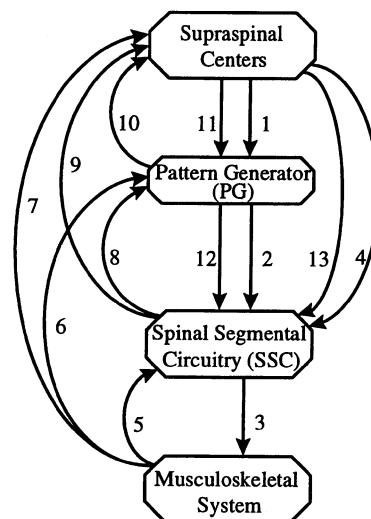


FIGURE 12.2. Interactions among components of the neural system and the musculoskeletal system. Numbered pathways are described as follows:

Motor commands:

1. descending inputs to PG
2. PG motor commands
3. motoneuron outputs
4. descending supraspinal motor commands

Feedback pathways:

5. local spinal reflex pathways
6. reflex pathways to PG
7. supraspinal reflex pathways
8. ascending signals from SSC to PG
9. ascending signals from SSC to supraspinal centers
10. ascending PG outputs

Modulatory pathways:

11. supraspinal modulation of PG reflexes
12. PG modulation of spinal reflexes
13. supraspinal modulation of spinal reflexes

the basic elements are utilized to achieve specific motor output patterns. The following sections describe the organization of pattern generating circuits and how their behavior is influenced by modulatory inputs from other neural centers and from the periphery.

3.1 Pattern Generator

A “pattern generator” (or “central pattern generator”) is a group of neurons that is capable of generating oscillatory outputs in the absence of phasic inputs. A classic and well-studied example of a vertebrate pattern generator is the spinal circuitry of the lamprey (Chapter 15; Cohen and Wallen 1980; Grillner et al. 1991). In this eel-like vertebrate, an *isolated* piece of the spinal cord (consisting of as little as a few spinal segments) can generate stereotyped patterns of activity that are similar to the motor patterns exhibited during locomotion in the intact animal (Cohen and Wallen 1980). This “fictive locomotion” preparation clearly demonstrates existence of pattern generating circuitry in the spinal cord and has been an important tool in characterizing the neural mechanisms that generate the oscillatory behavior. Similar pattern generator circuits have been studied in several invertebrate [e.g., Tritonia (Getting and Dekin 1985), Lymnaea stagnalis (Elliot and Benjamin 1985), crayfish (Mulloney et al. 1993)] and vertebrate preparations [e.g., rat (Cazalets et al. 1995; Smith et al. 1988), cat (Pearson and Rossignol 1991)]. In many of these animals, there may not be conclusive evidence of a pattern generator in the truest sense (i.e., “in the absence of any phasic inputs”), but many pattern generator properties, structures and mechanisms have been identified. Several recent studies in humans have suggested the existence of a spinal pattern generator for locomotion (Calancie et al. 1994; Illis 1995; Gerasimenko et al. 1996), although its properties have not yet been characterized.

Neural circuits utilize a variety of mechanisms in order to generate oscillatory output patterns. The oscillatory behavior of some neural circuits is driven by the intrinsic oscillatory membrane properties of an individual neuron in the circuit. These cells, often called “pacemaker” neurons, are sometimes capable of generating oscillatory outputs when isolated from all other cells in the network. Pacemaker properties of isolated neurons are the

result of membrane channels with voltage- and time-dependent ionic conductances (Epstein and Marder 1990). The oscillatory behavior of other neural circuits is driven by the pattern of synaptic connections among the various neurons in the network, none of which has specialized membrane pacemaker properties. This type of circuit is termed a “network oscillator.” Examples of synaptic connectivity that are often components of a network oscillator are mutual inhibition and recurrent inhibition (see Figure 12.3). Several computer modeling studies have clearly demonstrated that pure forms of pacemakers and network oscillators are capable of generating oscillatory patterns (Brodin et al. 1991; Ekeberg et al. 1991; Buchanan 1992; Jung et al. 1996). However, most neural circuits appear to utilize a combination of pacemaker and network properties to generate oscillatory patterns (Getting and Dekin 1985; Grillner et al. 1991; Pearson 1993; Rossignol and Dubuc 1994).

3.2 Modulatory Inputs to the Pattern Generator

The pattern generator produces a cyclic set of neural trajectories, but often it is capable of generating many different patterns (Harris-Warrick and Marder 1991; Katz and Frost 1996). The variety in such patterns may be in such characteristics as the relative timing, frequency, duty cycle, and/or amplitude or it may be that the PG circuit is capable of generating patterns that are qualitatively very different (e.g., switching from a pattern suitable for running to one suitable for hopping.) This variety in output patterns can be generated by one or more of several different mechanisms. Although there may be mechanisms that are entirely internal to the pattern generator, we will focus on mechanisms that involve modulatory inputs from neurons other than the core pattern generating circuitry.

One of the more important mechanisms for modulating pattern generator activity is that of “tonic drive” (i.e., a steady nonphasic input that results in modifications to the output pattern). An example of this type of modulatory tonic drive is the excitation of spinal PG circuit from supraspinal centers in the reticular formation of the brainstem, as shown in pathway #11 in Figure 12.2. In several animals, it has been shown that increased levels of tonic activity in the reticular formation leads to in-

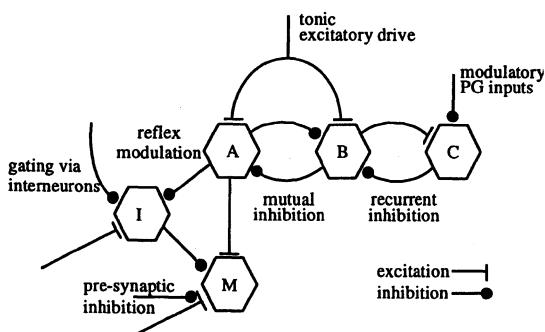


FIGURE 12.3. Neural connectivity for pattern generation and reflex integration. This simplified schematic illustrates several types of connections that may be used by neural circuits to generate oscillatory patterns and to incorporate afferent information. In this schematic, neurons A, B, and C belong to the pattern generator, while neurons I and M are part of the spinal segmental circuitry. The primary oscillatory circuit is formed by neurons A and B, which are in *mutual inhibition* and therefore will oscillate out-of-phase with each other. *Tonic excitatory drive* to PG neurons A and B may be required for oscillation and may be used to modulate frequency. Neuron B excites C which in turn inhibits B, thus demonstrating *recurrent inhibition*. This mechanism may be used in pattern generating circuitry to influence duty cycle as well as frequency. *Modulatory PG inputs*, possibly from supraspinal centers or reflex pathways, may alter the PG output via inhibition (or excitation). In the simplified schematic, they are shown as acting on neuron C, but they may act on any or all of the PG neurons. Motoneurons (M) receive motor commands from the PG and supraspinal centers as well as from afferents. The reflex actions may be directly onto the motoneurons and may be mediated by interneurons (I). The input labeled “*gating via interneurons*” demonstrates an inhibitory input that could act to shut down the reflex pathways by preventing neuron I from firing. The source of the gating signal may be from afferents, supraspinal centers or the PG. *Reflex modulation* is similar to gating, except that the effect may be graded, rather than on or off. In the schematic, reflex modulation is indicated as a cyclic modulation of interneuron mediated reflexes. *Pre-synaptic inhibition* is a mechanism where the inhibitory effect is on the pre-synaptic terminal, rather than the dendrite or cell body. This mechanism may provide a way to selectively deactivating specific inputs to the post-synaptic neuron.

creased frequency of oscillation of the spinal pattern generator (Armstrong 1988). The tonic drive signals may influence PG activity by directly depolarizing the membrane of PG neurons, thereby

bringing them closer to threshold and reducing the time required for the pacemaker or network properties to drive them above threshold. Another possible scenario is that the tonic drive may influence the PG indirectly through the action of neuromodulators. Here, the tonic drive signals may cause the release of neuromodulators (e.g., neuropeptides, calcium ions) which in turn modify the membrane properties of some or all of the PG neurons. These types of changes in membrane properties can produce subtle changes in the PG output pattern such as modulation of frequency, or they can produce drastic changes in the configuration of the network that would result in a functionally distinct output pattern (Harris-Warrick 1988; Harris-Warrick and Marder 1991; Skinner et al. 1994; Brodfuehrer et al. 1995; Katz and Frost 1996).

Another important mechanism for modulating PG activity is via phasic inputs that may produce transient or long-lasting effects. These phasic inputs to the PG are often derived from afferent signals (as described in the next section and illustrated as pathway #6 in Figure 12.2), but they also may originate from within the nervous system. For example, descending phasic inputs (Barnes 1984; Armstrong 1988) may be responsible for initiating or terminating oscillatory activity (via pathway #11 in Figure 12.2). Inputs from supraspinal centers also play an important role in interlimb and inter-segmental coordination (Armstrong 1986; Drew 1991; Rossignol et al. 1993). Studies in humans have shown that voluntary noncyclic motor actions performed during locomotion, such as raising an arm or stepping over an obstacle, may result in modifications to motor pattern output that may last for one or more cycles. (Hirschfeld and Forssberg 1991; Patla et al. 1991). While these specific studies could not distinguish between effects on the pattern generator and effects that bypassed the pattern generator, the extensive coordination that was exhibited suggest a pattern generator-mediated mechanism.

4 Interactions in Neuromechanical Systems

Neural signals from motoneurons cause muscle fibers to contract; as muscle fibers contract they generate forces that act on the skeletal structure to

result in posture and movement. This “forward” path, although fairly straightforward at a general level of description, is exquisitely complex at a detailed level of analysis. Ionic concentrations in the sarcoplasmic reticulum, heterogeneity in sarcomere lengths (Chapter 3; Morgan 1990), distribution of fibers of a given motor unit, muscle length-tension and force-velocity properties, muscle moment arm dependence on joint angle (Zajac 1989), and the passive mechanics of tendons, ligaments, joint capsule, and skeletal segments (Aduu and Davy 1986; Alexander and Ker 1990; Alexander 1993) can all have profound effects on the resulting posture and movement. Several chapters in this book describe many of the more important features of this “forward” path, from neural outputs to movement. This section focuses primarily on the feedback pathway (i.e., how do the mechanical components of the system influence the pattern of signals generated by the neural control system?). Inputs from the mechanical system (periphery) are transmitted to the neural control system via proprioceptive and exteroceptive afferent pathways. Note that these pathways may involve direct transduction of mechanical quantities (e.g., touch sensors in the feet) or may follow a less direct pathway (e.g., visual feedback of limb position).

4.1 Influence on Multiple Time Scales

Signals from the periphery can influence neural output patterns on several different time scales. First, the two systems have coevolved to meet the demands of various environments. Skeletal structure, passive musculotendon properties, active muscle contractile properties, motoneuron structure, pattern generator network architecture, neuromodulator properties, and so on, have simultaneously evolved to result in locomotion that is adequate for a given animal. Obviously, the mechanical properties of the body have influenced the evolution of the neural control system.

Over the course of an animal’s life, the neural and mechanical systems codevelop. The neural control system in a given individual develops to meet the requirements of the mechanical system as it develops (and vice versa, but probably to a lesser extent). The combined processes of evolution and development result in the detailed structure of the neural control system.

Throughout the duration of a cyclic activity, such as locomotion, signals from the mechanical system are used to adapt motor patterns. For example, neural activity patterns may be adapted during the course of a walk to account for changing loads, changing slopes or muscle fatigue.

Within the locomotor cycle, sensory inputs are used to detect discrete events that may trigger a transition from one state to another. For example, activation of flexor muscle spindle afferents can facilitate the initiation of swing phase. These inputs may be used to detect “ordinary” events that would be a part of the normal cycle, to detect “extraordinary” events, such as a stumble or slip, or to initiate or terminate locomotion. These inputs affect the PG activity patterns and may, in some cases, be an essential component of pattern generator function.

Finally, sensory inputs are used within specific phases, or states, of the locomotor cycle to influence the form of the pattern being generated. For example, stretch reflex inputs may influence the activity of agonist and antagonist muscles during one phase of the gait cycle, but may not have any effect during other phases. These modulated reflexes, which appear to be widely used in neural control systems, can be described in terms of multi-state models as state-dependent reflexes. The mechanism for such modulation may involve inputs to the pattern generator or may only involve inputs to the local spinal circuits that process pattern generator signals.

The sections that follow describe some specific examples of interactions between neural and mechanical systems.

4.2 Modulation of PG Activity via Afferent Pathways

In normal operation, the pattern generator activity is continuously modulated (Katz and Harris-Warrick 1990; Baev et al. 1991) by input signals from afferents that may be either periodic or non-periodic (see pathway #6 in Figure 12.2). Periodic inputs to the PG can result in *entrainment* of the PG oscillator by the periodic stimulus. An oscillator is said to be entrained by a stimulus when the frequency of the oscillator adjusts to match that of the stimulus. A good example of entrainment of the PG oscillator is demonstrated with the semi-intact

preparation of the lamprey where an imposed mechanical oscillation of the tail entrains the spinal oscillator (McClellan and Sigvardt 1988; McClelland and Jang 1993). A similar, but more complicated example, is demonstrated by the spinal cat walking on a treadmill (Forsberg and Grillner 1973). Here, the movement of the treadmill provides a mechanical stimulus by passively moving the limbs into extension. This mechanical stimulus generates neural activity to generate active flexion and therefore results in stepping movements. The speed of the treadmill influences the frequency of passive limb movement, which entrains the neural oscillator. A third example of entrainment is that of a human walking to the beat of a metronome (Chapter 18).

Phasic inputs to the PG that are nonperiodic may also result in modifications to the pattern of PG activity. For example, a bump on the leg may result in modifications the PG pattern for the present cycle, but have no effect on subsequent cycles. It is also possible, however, for a phasic input to trigger a transition from one oscillatory pattern to another oscillatory pattern (e.g., walk to run) or it may result in cessation of all oscillatory activity (e.g., walk to stand). A third possibility is that the effect of the input may be transient in that the system rapidly returns to its original pattern, but that the pattern is phase-shifted with respect to where it would have been without the stimulus (see Figure 12.4). This type response is termed a *phase-resetting* reflex, and appears to be used often in locomotor (Hiebert et al. 1996) and other cyclic activities.

Another important issue to consider regarding transient inputs to the PG is that of *phase-dependence*. That is, the response of the PG to an input may depend upon the phase at which the signal arrives. For example, activation of the flexor muscle afferents during stance phase results in a shortened stance phase and a resetting of the locomotor rhythm, but activation during swing phase does not (Hiebert et al. 1996). In the multistate model of locomotion described above, this phase-dependent reflex would be described as a state-dependent effect, but phase-dependence may also be used to describe changes in the response within a specified state.

It should be noted that the mechanisms that re-

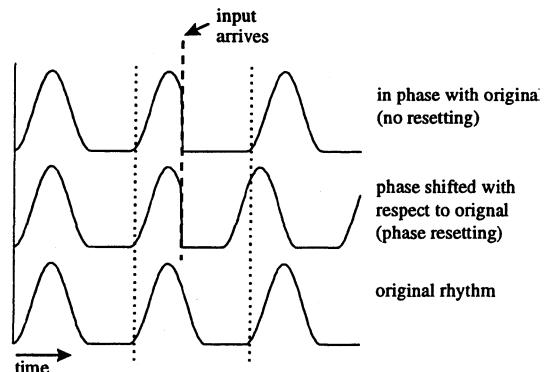


FIGURE 12.4. Effects of phasic inputs to the pattern generator. The traces above illustrate two possible effects of perturbations on the pattern generator output. The bottom trace is the “unperturbed” rhythm. The middle trace demonstrates a reflex in which the phase has been “reset” (i.e., after one short cycle, the phase is shifted with respect to its original rhythm). The top trace demonstrates a reflex without resetting (i.e., the oscillator returns to its original pattern and phase after the perturbation).

sult in entrainment, phase-resetting, and phase dependence are most likely related to the cellular and network properties that are responsible for the dynamic oscillatory behavior of the PG. Voltage-dependent and time-dependent membrane channels and network configurations have all been demonstrated to be capable of altering the effect of inputs on PG activity (Brodin et al. 1991; Traven et al. 1993; Rossignol and Dubuc 1994; Abbas 1996).

4.3 Processing PG Outputs with Afferent Signals

Signals from the pattern generator must eventually reach motoneurons, but in many animals these signals are substantially processed along the way. In more complex vertebrates, for example, the signals pass through the complex network of motoneurons, primary afferent neurons, Renshaw cells and other interneurons, and so on. (Baldissera et al. 1981; Burke 1990). There is considerable evidence to demonstrate that these cells do not belong to the core pattern generating circuitry and that they receive oscillatory inputs during locomotion (Pratt and Jordan 1987), presumably emanating from the pattern gen-

erator. The local circuits formed by these spinal neurons are some of the earliest identified components of neuromotor control systems and are probably the most well understood components of the mammalian central nervous system. The monosynaptic, disynaptic and polysynaptic reflex pathways mediated by these neurons (pathway #5 in Figure 12.2) have been very well studied because they are relatively accessible: a quantifiable motor response can be readily evoked by a repeatable stimulus.

The most widely studied reflex pathway is the muscle stretch reflex in which signals from muscle spindles travel via the Ia-afferent pathway to cause monosynaptic activation of the homonymous alpha motoneurons and disynaptic inhibition of the antagonist motoneurons (Carew 1985). An interesting aspect of this reflex loop is that the muscle spindles are innervated by gamma motoneurons. An early view of role of gamma system (the gamma-loop length-servo hypothesis) stated that movement is generated by activation of gamma motoneurons, thus reflexly activating the alpha motoneurons, resulting muscle contraction (Carew 1985). According to this view, the motor control system works much like a classic feedback control system with specification of a setpoint that is achieved via a feedback loop. While it is now appears that this mode of operation is not as dominant as was once believed, it clear that these reflex pathways exist and that they are active during goal-directed movements as well as during locomotion. Therefore, the signal that is sent to a given muscle during the locomotor cycle includes a component from the local afferent pathways as well as a component from the pattern generator.

One issue that arises, then, is to determine the manner in which the two signals are combined—is it just simple addition of the feedforward component from the PG to the feedback component from afferents? Experimental and computer simulation studies have indicated that motoneurons alone are capable of performing complex integration of signals from multiple sources (Burke 1990; Segev et al. 1990). The mechanisms that mediate the interactions between the two components may be at the network level [e.g., presynaptic inhibition (Segev 1990) as shown in Figure 12.3.] or at the cellular level (e.g., involving second messenger systems).

An important aspect of this afferent component

is that the feedback gains can be highly modulated depending upon several factors such as attention, movement pattern selection, movement speed and phase within the movement cycle (see pathway #12 in Figure 12.2). This concept of “sensorimotor gain control” (Prochazka 1989) appears to be widely used in the nervous system for a variety of movements, and it has been widely observed during locomotion as well as other cyclic activities (Sillar and Roberts 1988; Koerber and Mendell 1991; Murphy and Martin 1993). First, the reflex gain can be increased at times when feedback might be particularly useful and it can be learned (Evatt et al. 1989; Wolpaw and Lee 1989; Abbruzzese et al. 1991). This type of modulation, which is linked to such higher cortical functions as anticipation, is an example of reflex modulation mediated by higher centers in the nervous system. Second, the reflex gain can be modulated depending upon the type of activity. It has been shown that the human soleus H-reflex gains are lower during running than during walking (Capaday and Stein 1987), while gains during walking are lower than stance (Capaday and Stein 1986). Third, studies on walking at different speeds have demonstrated that lower reflex gains are utilized at higher movement speeds (Zill and Moran 1981). Animals with a slower locomotor cycle appear to utilize higher reflex gains than animals with faster locomotor cycles to the extent to which the reflex mechanisms may dominate and actually be a critical component of the pattern generating circuitry (Chapter 16; Nothof and Bassler 1990). Lastly, studies on cats (Duenas et al. 1990) and humans (Stein and Capaday, 1988; Edamura et al. 1991) have demonstrated that reflex gains are actively modulated throughout the gait cycle. This modulation has been observed in reflex gains from muscle afferents (Dietz et al. 1985), cutaneous afferents (Forssberg et al. 1975; Yang and Stein 1990) and proprioceptors (Hasan and Stuart 1988). The source of the modulatory inputs to the spinal reflex circuits may be directly from the pattern generator, from cyclic afferent inputs, or from oscillatory supraspinal centers. Many aspects of reflex modulation are thoroughly reviewed in (Prochazka 1989); activity-dependent and phase-dependent modulation are discussed in Chapter 17.

Thus, to summarize the most important aspects of these spinal reflex pathways: (1) they are often

active during locomotion, (2) they operate to supplement and interact with the signals from the pattern generator, (3) their strength can be modulated through the course of the locomotor cycle, and (4) the relative importance of the feedforward path (from the pattern generator) and the feedback path (via local afferent pathways) may depend upon the speed of the movement being generated as well as other factors.

5 Implications for Biology and Engineering

5.1 Understanding Cyclic Movement Generation

This view of the locomotor control system is centered around a pattern generator and includes supraspinal centers, spinal segmental circuitry, and musculoskeletal mechanical components. The motor pattern results from the interaction of the dynamics of the neural system components with the dynamics of the mechanical system components. Several examples of different forms of interactions amongst the various neural and mechanical components are described.

In its purest form, a pattern generator can produce oscillatory signals in the absence of phasic inputs. On the other hand, in the absence of pure pattern generator circuitry, oscillatory patterns may result from a repeating sequence of reflex-driven movements. Although biological examples of each of these extremes may exist, it may be best to view these as two ends of a spectrum, with most animals using a combination of intrinsic pattern generator and reflex mechanisms. The pattern generator mechanism may be more prominent in animals with fast locomotor cycles, while the reflex mechanisms may be more prominent in animals with slower locomotor cycles. Similarly, in a given animal, the relative importance of the two mechanisms may depend upon walking speed and/or environmental conditions.

The examples in this chapter and the perspectives that follow have drawn from a wide variety of studies on a wide variety of animals. The work cited ranges from studies that utilized intracellular recordings in isolated invertebrate ganglia to studies that utilized kinematic and kinetic analysis of

humans. The future of the study of locomotor control systems will undoubtedly include many studies on isolated cells to characterize cellular mechanisms as well as studies on behaving humans to characterize various movement patterns and these studies will continue to provide important contributions to our understanding of the various aspects of the motor control system. The challenge is, as it has always been, to explain the behavioral data in terms of the mechanisms identified in the reduced preparations. An understanding of the interactions between the neural and mechanical systems is an integral part of this challenge.

To understand the neuromechanical interactions in locomotor systems, two approaches may prove to be particularly useful. First, there is a need to develop and exploit experimental paradigms to investigate the interactions between the various components. Isolated muscle preparations and fictive locomotor preparations, while extremely useful for understanding components of the motor control system, can provide only limited information regarding the interactions amongst the components. Technological innovations such as those that allow for neural recordings, muscle length changes and muscle force measurements in behaving animals and experimental paradigms, such as those that use behaving animals to investigate neural connectivity patterns, may provide even more important contributions to the field in the future. These data can also provide the neural activation and muscle strain conditions actually seen by the musculotendon system during rhythmic behavior. More controlled experimental paradigms, such as musculo-tendon work-loop analysis (Josephson 1985), which take advantage of these relevant conditions, providing an avenue for integration of isolated preparations with whole animal behavior. The second approach that may be critical is to utilize mathematical models of combined neural and mechanical systems (Loeb and Levine 1990). This approach draws from a long history of development of neural (Koch and Segev 1989; Schwartz 1990; Calabrese and De-Schutter 1992; Cohen et al. 1992; Selverston 1993; Bower 1996) and musculoskeletal models (Zajac 1989; Zajac and Winters 1990) and exploits recent advances in computing technology. Here, the use of mathematical models may be particularly useful because experimental analysis and modeling efforts have led to the development of (arguably limited)

models of neural and mechanical components, but detailed experimental investigations of the interactions are not currently possible. Several recent examples of studies that have utilized models of combined neural and mechanical systems can be found in this book. (Chapter 15) as well as in the literature (Beer and Chiel 1993; Ekeberg 1993; McFadyen et al. 1994; Taga 1995; Winters 1995; Blum and Leung 1996; Hatsopoulos 1996).

5.2 Designing Improved Movement Control Systems

In many fields of engineering there is a growing interest in the area of biomimicry; that is, how can the principles derived from our understanding of biological systems be utilized to design better engineering systems. Advanced engineering designs of novel materials, lubricants, and image processing systems have successfully incorporated ideas inspired by biological systems into artificial systems. Several research groups involved in the development of locomotion systems have borrowed from biological systems in the design of either the mechanical or control systems component.

Perhaps the most active area in this regard is the development of robots that locomote and perform useful functions. For example, biological foundations have been used to design intelligent systems for motor control that achieve a degree of autonomy (Brooks 1989; Beer et al. 1992). Many of these new engineering systems are targeted at replacing and/or supplementing human operators with the development of robot systems that can move, manipulate objects, gather information, make decisions, and act on them. These systems will require that the robots have intelligence and motor control capabilities that approach those of animal cognitive and motor control systems.

A second important engineering application is the design of controllers for use in systems that electrically stimulate paralyzed muscles to restore function to people with neurological disorders (see Section IX, for descriptions of Functional Neuromuscular Stimulation (FNS) systems). Biologically inspired systems for controlling cyclic movements have been developed for intended use in restoring locomotor function (Abbas and Chizeck 1995; Abbas 1996; Chapter 46). In addition, effective utilization of the ability of the

spinal cord to modulate reflexes has been proposed as a means of enhancing FES system function (Fung and Barbeau 1994).

The view of locomotor systems presented in this chapter includes several key features that may be important in the design of engineering systems for cyclic movement. To design a system that will generate cyclic movements such as locomotion, the mechanical properties of the system should be well suited for the "regular" movement pattern(s) and the controller should be capable of exploiting those properties. A control system that utilizes such ideas as a pattern generator, phase-resetting reflexes, reflex modulation, and so on, may provide advantages in terms of mechanical and/or computational efficiency and the capability of generating a variety of movement patterns at different speeds. While it may be possible to incorporate these features using standard control system structures, mathematical models of neural processing systems may be an effective and efficient way to achieve these objectives (Beer 1990; Abbas 1996).

References

- Abbas, J.J. (1996). Using neural models in the design of a movement control system. *Computational Neurosci.*, Bower, J.M. (ed.), pp. 305–310, Academic Press, New York.
- Abbas, J.J. and Chizeck, H.J. (1995). Neural network control of functional neuromuscular stimulation systems. *IEEE Trans. BME*, 42:1117–1127.
- Abbruzzese, M., Reni, L., and Favale, E. (1991). Changes in central delay of soleus H-reflex after facilitatory or inhibitory conditioning in humans. *J. Neurophys.*, 65:1598–1605.
- Alexander, R.M. (1993). Optimization of structure and movement of the legs of animals. *J. Biomech.*, 26:1–6.
- Alexander, R.M. and Ker, R.F. (1990). The architecture of leg muscles. *Multiple Muscle Systems: Biomechanics and Movement Organization*. Winters, J.M. and Woo, S.L.-Y. (eds.), pp. 568–577, Springer-Verlag, New York.
- Alexander, R.M. and Vernon, A. (1975). Mechanics of hopping by kangaroos (Macropodidae). *J. Zool. Lond.*, 177:265–303.
- Armstrong, D.M. (1986). Supraspinal contributions to the initiation and control of locomotion in the cat. *Prog. Neurobiol.*, 26:273–361.
- Armstrong, D.M. (1988). The supraspinal control of mammalian locomotion. *J. Physiol.*, 405:1–37.
- Audu, M.L. and Davy, D.T. (1985). The influence of

- muscle model complexity in musculoskeletal motion modeling. *J. Biomech. Eng.*, 107:147–157.
- Baev, K.V., Esipenko, V.B., and Shimansky, Y.P. (1991). Afferent control of central pattern generators: experimental analysis of locomotion in the decerebrate cat. *Neuroscience*, 43:237–247.
- Baldissera, F., Hultborn, H., and Illert, M. (1981). Integration in spinal neuronal systems. *Handbook of Physiology, Sect. 1: The Nervous System II, Motor Control*. Brooks, V.B. (ed.), pp. 509–595, American Physiological Society. Waverly Press, Bethesda, Maryland.
- Barnes, C.D. (1984). *Brainstem Control of Spinal Cord Function*. Academic Press, New York.
- Beer, R.D. (1990). *Intelligence as Adaptive Behavior: An Experiment in Computational Neuroethology*. Academic Press, Boston.
- Beer, R.D. and Chiel, H.C. (1993). Simulations of cockroach locomotion and escape. *Biological Neural Networks in Invertebrate Neuroethology and Robotics*.
- Beer, R.D., Ritzmann, R.E., and McKenna, T. (eds.), pp. 267–286, Academic Press, New York.
- Beer, R.D., Chiel, H.J., Quinn, R.D., Espenschied, K.S., and Larsson, P. (1992). A distributed neural network architecture for hexapod robot locomotion. *Neural Computation*, 4:356–365.
- Biewener, A.A. and Baudinette, R.V. (1995). In vivo muscle force and elastic energy storage during steady-speed hopping of tamar wallabies (*Macropus eugenii*). *J. Exp. Biol.*, 198:1829–1841.
- Blum, E.K. and Leung, P.K. (1996). Modeling and simulation of human walking: a neuro-musculo-skeletal model. *Computational Neurosci.* Bower, J.M. (ed.), pp. 323–327. Academic Press, New York.
- Bower, J.M. (ed.). (1996). *Computational Neurosci.*, Academic Press, New York.
- Brodfuehrer, P.D., Debski, E.A., O'Gara, B.A., and Friesen, W.O. (1995). Neuronal control of leech swimming. *J. Neurobiol.*, 27:403–418.
- Brodin, L., Traven, H., Lansner, A., Wallen, P., and Grillner, S. (1991). Computer simulations of N-methyl-D-aspartate receptor-induced membrane properties in a neuron model. *J. Neurophys.*, 66:473–484.
- Brooks, R.A. (1989). A robot that walks: emergent behaviors from a carefully evolved network. *Biological Neural Networks in Invertebrate Neuroethology and Robotics*. Brooks, R.A. (ed.), pp. 355–363, The MIT Press, Cambridge, Massachusetts.
- Buchanan, J.T. (1992). Neural network simulations of coupled locomotor oscillators in the lamprey spinal cord. *Biol. Cybern.*, 66:367–374.
- Burke, R.E. (1990). Spinal cord: ventral horn. *The Synaptic Organization of the Brain*. Shepherd, G.M. (ed.), pp. 88–132, 3rd edn. Oxford University Press, New York.
- Calabrese, R. and DeSchutter, E. (1992). Motor-pattern-generating networks in invertebrates: modeling our way toward understanding. *TINS*, 15:439–444.
- Calancie, B., Needham-Shropshire, B., Jacobs, P., Willer, K., Zych, G., and Green, B.A. (1994). Involuntary stepping after chronic spinal cord injury. Evidence for a central rhythm generator for locomotion in man. *Brain*, 117:1143–1159.
- Capaday, C. and Stein, R.B. (1986). Amplitude modulation of the soleus H-reflex in the human during walking and standing. *J. Neurosci.*, 6:1308–1313.
- Capaday, C. and Stein, R.B. (1987). Difference in the amplitude of the human soleus H-reflex during walking and running. *J. Physiol.*, 392:513–522.
- Carew, T.J. (1985). The control of reflex action. *Principles of Neural Science*. Kandel, E.R. and Schwartz, J.H. (eds.), pp. 457–468, Elsevier Publishers, New York.
- Cazalets, Jean-R., Borde, M., and Clarac, F. (1995). Localization and organization of the central pattern generator for hindlimb locomotion in newborn rat. *Neuroscience*, 15:4943–4951.
- Chiel, H.J. and Beer, R.D. (1993). Neural and peripheral dynamics as determinants of patterned motor behavior. *The Neurobiology of Neural Networks*. Gardner, D. (ed.), pp. 137–164, The MIT Press, Cambridge, Massachusetts.
- Cohen, A., Ermentrout, B., Kiemel, T., Kopell, N., Sigvardt, K., and Williams, T. (1992). Modelling of intersegmental coordination in the lamprey central pattern generator for locomotion. *TINS*, 15:434–438.
- Cohen, A.H. (1992). The role of heterarchical control in the evolution of central pattern generators. *Brain, Behav. Evol.*, 40:112–124.
- Cohen, A.H. and Wallen, P. (1980). The neuronal correlate of locomotion in fish. ‘fictive swimming’ induced in an in vitro preparation of the lamprey spinal cord. *Exp. Brain Res.*, 41:11–18.
- Cohen, A.H., Rossignol, S., and Grillner, S. (eds.). (1988). *Neural Control of Rhythmic Movements in Vertebrates*. John Wiley & Sons, New York.
- Dietz, B., Quintern, J., and Berger, W. (1985). Afferent control of human stance and gait: evidence for blocking of group I afferents during gait. *Exp. Brain Res.*, 61:153–163.
- Drew, T. (1991). Functional organization within the medullary reticular formation of the intact unanesthetized cat III. Microstimulation during locomotion. *J. Neurophys.*, 66:919–938.
- Duenas, S.H., Loeb, G.E., and Marks, W.B. (1990). Monosynaptic and dorsal root reflexes during loco-

- motion in normal and thalamic cats. *J. Neurophys.*, 63:1467–1476.
- Edamura, M., Yang, J.F., and Stein, R.B. (1991). Factors that determine the magnitude and time course of human H-reflexes in locomotion. *J. Neurosci.*, 11: 420–427.
- Ekeberg, O. (1993). A combined neuronal and mechanical model of fish swimming. *Biol. Cybern.*, 69:363–374.
- Ekeberg, O., Wallen, P., Lansner, A., Traven, H., Brodin, L., and Grillner, S. (1991). A computer based model for realistic simulations of neural networks. *Biol. Cybern.*, 65:81–90.
- Elliot, C.J.H. and Benjamin, P.R. (1985). Interactions of pattern-generating interneurons controlling feeding in lymnaea stagnalis. *J. Neurophys.*, 54:1396–1421.
- Epstein, I.R. and Marder, E. (1990). Multiple modes of a conditional neural oscillator. *Biol. Cybern.*, 63:25–34.
- Ettema, G.J.C. and Huijing, P.A. (1990). Architecture and elastic properties of the series elastic element of muscle-tendon complex. *Multiple Muscle Systems: Biomechanics and Movement Organization*. Winters, J.M. and Woo, S.L.-Y. (eds.), pp. 57–68, Springer-Verlag, New York.
- Evatt, M.L., Wolf, S.L., and Segal, R.L. (1989). Modification of human spinal stretch reflexes: preliminary studies. *Neur. Lett.*, 105:350–355.
- Forssberg, H. and Grillner, S. (1973). The locomotion of the acute spinal cat injected with clonidine i.v. *Brain Res. Bull.*, 50:184–186.
- Forssberg, H., Grillner, S., and Rossignol, S. (1975). Phase dependent reflex reversal during walking in chronic spinal cats. *Brain Res.*, 85:103–107.
- Fung, J. and Barbeau, H. (1994). Effects of conditioning cutaneomuscular stimulation on the soleus H-reflex in normal and spastic paretic subjects during walking and standing. *J. Neurophys.*, 72:2090–2104.
- Gerasimenko, Y., McKay, W.B., Pollo, F.E., and Dimitrijevic, M.R. (1996). Stepping movements in paraplegic patients induced by epidural spinal cord stimulation. *Soc. Neurosci. Abstracts*, 22:1372.
- Getting, P.A. and Dekin, M.S. (1985). Tritonia swimming: a model system for integration within rhythmic motor systems. *Model Neural Networks and Behavior*. Selverston, A.I. (ed.), pp. 3–20, Plenum Press.
- Ghez, C. (1985). Introduction to the motor systems. *Principles of Neural Science*. Kandel, E.R. and Schwartz, J.H. (eds.), pp. 427–442, 2nd edn. Elsevier, New York.
- Grillner, S. (1981). Control of locomotion in bipeds, tetrapods and fish. *Handbook of Physiology, Sect. 1: The Nervous System II, Motor Control*. Brooks, V.B. (ed.), pp. 1179–1236, American Physiological Society, Waverly Press, Bethesda, Maryland.
- Grillner, S., Wallen, P., Brodin, L., and Lansner, A. (1991). Neuronal network generating locomotor behavior in Lamprey: circuitry, transmitters, membrane properties, and simulation. *Annu. Rev. Neurosci.*, 14:169–199.
- Harris-Warrick, R.M. (1988). Chemical Modulation of Central Pattern Generators. *Neural Control of Rhythmic Movements in Vertebrates*. Cohen, A.H., Rossignol, S., and Grillner, S. (eds.), pp. 285–331, John Wiley & Sons, New York.
- Harris-Warrick, R.M. and Marder, E. (1991). Modulation of Neural Networks for Behavior. *Annu. Rev. Neurosci.*, 14:39–57.
- Hasan, Z. and Stuart, D.G. (1988). Animal solutions to problems of movement control: the role of proprioceptors. *Annu. Rev. Neurosci.*, 11:199–223.
- Hatsopoulos, N.G. (1996). Coupling the neural and physical dynamics in rhythmic movements. *Neural Computation* 8:567–581.
- Hiebert, G.W., Whelan, P.J., Prochazka, A., and Persons, K.G. (1996). Contribution of hind limb flexor muscle afferents to the timing of phase transitions in the cat step cycle. *J. Neurophys.*, 75:1126–1137.
- Hinrichs, R. (1990). Whole body movement: coordination of arms and legs in walking and running. *Multiple Muscle Systems: Biomechanics and Movement Organization*. Winters, J.M. and Woo, S.L.-Y. (eds.), pp. 694–716, Springer-Verlag, New York.
- Hirschfeld, H. and Forssberg, H. (1991). Phase-dependent modulations of anticipatory postural activity during human locomotion. *J. Neurophys.*, 66:12–18.
- Hof, A.L. (1990). Effects of muscle elasticity in walking and running. *Multiple Muscle Systems: Biomechanics and Movement Organization*. Winters, J.M. and Woo, S.L.-Y. (eds.), pp. 591–607, Springer-Verlag, New York.
- Illis, L.S. (1995). Is there a central pattern generator in man? *Paraplegia*, 33:239–240.
- Inman, V.T., Ralston, H.J., and Todd, F. (1994). Human locomotion. *Human Walking*. Rose, J. and Gamble, J.G. (eds.), pp. 1–22, 2nd ed. Williams & Wilkins, Baltimore.
- Josephson, R.K. (1985). Mechanical power output from striated muscle during cyclic contraction. *J. Exp. Biol.*, 114:493–512.
- Jung, R., Kiemel, T., and Cohen, A.H. (1996). Dynamic behavior of a neural network model of locomotor control in the lamprey. *J. Neurophys.*, 75:1074–1086.
- Katz, P.S. and Forst, W.N. (1996). Intrinsic neuromodulation: altering neuronal circuits from within. *TINS*, 19:54–61.
- Katz, P.S. and Harris-Warrick, R.M. (1990). Neuromodulation of the crab ploric central pattern generator by serotonergic/cholinergic proprioceptive afferents. *J. Neurosci.*, 10:1495–1512.

- Koch, C. and Segev, I., Editors, (1989). *Methods in Neuronal Modeling: From Synapses to Networks*. The MIT Press, Cambridge, Massachusetts.
- Koerber, J.R. and Mendell, L.M. (1991). Modulation of synaptic transmission as Ia-afferent connections on motoneurons during high-frequency afferent stimulation: dependence on motor task. *J. Neurophys.*, 65:1313–1320.
- Loeb, G. and Levine, W. (1990). Linking musculoskeletal mechanics to sensorimotor neurophysiology. *Multiple Muscle Systems: Biomechanics and Movement Organization*. Winters, J.M. and Woo, S.L.-Y. (eds.), pp. 165–181, Springer-Verlag, New York.
- McClellan, A.D. and Jang, W. (1993). Mechanosensory inputs to the central pattern generators for locomotion in the lamprey spinal cord: resetting, entrainment and computer modeling. *J. Neurophys.*, 70:2442–2454.
- McClellan, A.D. and Sigvardt, K.A. (1988). Features of entrainment of spinal pattern generators for locomotor activity in the lamprey spinal cord. *J. Neurosci.*, 8:133–145.
- McFadyen, B.J., Winter, D.A., and Allard, F. (1994). Simulated control of unilateral, anticipatory locomotor adjustments during obstructed gait. *Biol. Cybern.*, 72:151–160.
- McGeer, T. (1993). Dynamics and control of bipedal locomotion. *J. Theor. Biol.*, 163:277–314.
- McMahon, T.A. (1984). *Muscles, Reflexes, and Locomotion*. Princeton University Press, Princeton, New Jersey.
- Morgan, D. (1990). Modeling of lengthening muscle: the role of inter-sarcomere dynamics. *Multiple Muscle Systems: Biomechanics and Movement Organization*. Winter, J.M. and Woo, S.L.-Y. (eds.), pp. 45–56, Springer-Verlag, New York.
- Mulloney, B., Murchison, D., and Chrachri, A. (1993). Modular organization of pattern-generating circuits in a segmental motor system: the swimmerets of crayfish. *Sem. Neurosci.*, 5:49–57.
- Mungiole, M. and Winters, J.M. (1990). Overview: influence of muscle on cyclic and propulsive movements involving the lower limb. *Multiple Muscle Systems: Biomechanics and Movement Organization*. Winters, J.M. and Woo, S.L.-Y. (eds.), pp. 550–567, Springer-Verlag, New York.
- Murphy, P.R. and Martin, H.A. (1993). Fusimotor discharge patterns during rhythmic movements. *TINS*, 16:273–278.
- Nothof, U. and Bassler, U. (1990). The network producing the “active reaction” of stick insects is a functional element of different pattern generating systems. *Biol. Cybern.*, 62:453–462.
- Patla, A.E., Prentice, S.D., Robinson, C., and Neufeld, J. (1991). Visual control of locomotion: strategies for changing direction and for going over obstacles. *J. Exp. Psych.*, 17:603–634.
- Pearson, K.G. (1993). Common principles of motor control in vertebrates and invertebrates. *Annu. Rev. Neurosci.*, 16:265–297.
- Pearson, K.G. and Rossignol (1991). Fictive motor patterns in chronic spinal cats. *J. Neurophys.*, 66:1–14.
- Pratt, C.A. and Jordan, L.M. (1987). Ia inhibitory interneurons and renshaw cells as contributors to the spinal mechanisms of fictive locomotion. *J. Neurophys.*, 57:56–71.
- Prochazka, A. (1989). Sensorimotor gain control: a basic strategy of motor systems? *Prog. Neurobiol.*, 33:287–307.
- Raibert, M.H. and Hodgkins, J.K. (1993). Legged robots. *Biological Neural Networks in Invertebrate Neuroethology and Robotics*. Beer, R.D., Ritzmann, R.E., and McKenna, T. (eds.), pp. 319–353, Academic Press, New York.
- Rossignol, S. and Dubuc, R. (1994). Spinal pattern generation. *Curr. Opin. Neurobiol.*, 4:894–902.
- Rossignol, S., Saltiel, P., Perreault, M.C., Drew, T., Pearson, K., and Belanger, M. (1993). Intralimb and interlimb coordination in the cat during real and fictive rhythmic motor programs. *Sem. Neurosci.*, 5:67–75.
- Schoner, G. and Kelso, J.A.S. (1988). Dynamic pattern generation in behavioral and neural systems. *Science*, 239:1513–1520.
- Schwartz, E.L. (ed.). (1990). *Computational Neuroscience*. The MIT Press, Cambridge, Massachusetts.
- Segev, I. (1990). Computer study of presynaptic inhibition controlling the spread of action potentials into axonal terminals. *J. Neurophys.*, 63:987–998.
- Segev, I., Fleshman, J.W., and Burke, R.E. (1990). Computer simulation of group Ia EPSPs using morphologically realistic models of cat alpha-motoneurons. *J. Neurophys.*, 64:648–660.
- Selverston, A. (1993). Modeling of neural circuits: what have we learned? *Annu. Rev. Neurosci.*, 16:531–546.
- Sillar, K.T. and Roberts, A. (1988). A neuronal mechanism for sensory gating during locomotion in a vertebrate. *Nature*, 331:262–265.
- Skinner, F., Kopell, N., and Mardner, E. (1994). Mechanics for oscillation and frequency control in reciprocally inhibitory model neural networks. *J. Comp. Neurosci.*, 1:69–87.
- Smith, J.C., Feldman, J.L., and Schmidt, B.J. (1988). Neural mechanisms generating locomotion studied in mammalian brain stem-spinal cord in-vitro. *FASEB J.*, 2:2283–2288.
- Stein, R.B. and Capaday, C. (1988). The modulation of human reflexes during functional motor tasks. *TINS*, 11:328–332.
- Taga, G. (1995). A model of the neuro-musculo-skeletal

- system for human locomotion I: emergence of basic gait. *Biol. Cybern.*, 73:97–111.
- Traven, H.G.C., Brodin, L., Lansner, A., Ekeberg, O., Wallen, P., and Grillner, S. (1993). Computer simulations of NMDA and non-NMDA receptor-mediated synaptic drive: sensory and supraspinal modulation of neurons and small networks. *J. Neurophys.*, 70:695–709.
- Winter, D.A. (1987). *The Biomechanics and Motor Control of Human Gait*. University of Waterloo Press, Waterloo, Canada.
- Winter, D.A. (1990). *Biomechanics and Motor Control of Human Movement*. John Wiley & Sons, New York.
- Winters, J.M. (1995). An improved muscle-reflex actuator for use in large-scale neuromusculoskeletal models. *Ann. Biomed. Eng.*, 23:359–374.
- Wolf, H. and Laurent, G. (1994). Rhythmic modulation of the responsiveness of locust sensory local interneurons by walking pattern generating networks. *J. Neurophys.*, 71:111–118.
- Wolpaw, J.R. and Lee, R.L. (1989). Memory traces in primate spinal cord produced by operant conditioning of H-reflex. *J. Neurophys.*, 61:563–572.
- Yamaguchi, G.T. (1990). Performing whole-body simulations of gait with 3-D, dynamic musculoskeletal models. *Multiple Muscle Systems: Biomechanics and Movement Organization*. Winters, J.M. and Woo, S.L.-Y. (eds.), pp. 663–679, Springer-Verlag, New York.
- Yang, J.F. and Stein, R.B. (1990). Phase-dependent reflex reversal in human leg muscles during walking. *J. Neurophys.*, 63:1109–1117.
- Zajac, F. and Winters, J. (1990). Modeling musculoskeletal movement systems: joint and body segmental dynamics, musculoskeletal actuation, and neuromuscular control. *Multiple Muscle Systems: Biomechanics and Movement Organization*. Winters, J.M. and Woo, S.L.-Y. (eds.), pp. 121–148, Springer-Verlag, New York.
- Zajac, F.E. (1989). Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. *CRC Crit. Rev. Biomed. Eng.*, 17:359–411.
- Zernicke, R.F., Schneider, K., and Buford, J.A. (1991). Intersegmental dynamics during gait. Patla, A.E. (eds.), pp. 187–202, Elsevier Science Publishers, New York.
- Zill, S.N. and Moran, D.T. (1981). The exoskeleton and insect proprioception: III Activity of tibial campaniform sensilla during walking in the american cockroach. *Periplaneta americana. J. Exp. Biol.*, 94:57–75.