Chapter 3
Neural Regulation of Limb Mechanics: Insights from the Organization of Proprioceptive Circuits

T. Richard Nichols, Nathan E. Bunderson and Mark A. Lyle

Abstract Sensory feedback arising from muscle spindle receptors and Golgi tendon organs are known to influence limb mechanics during postural and locomotor tasks. The purpose of this chapter is to synthesize data concerning the organization and actions of these proprioceptive pathways, and then to propose how current models can be used to promote understanding of their functional role in regulating whole limb stiffness. Following a historical introduction, the role of length feedback in transforming the mechanical properties of muscles into more spring-like actuators is reviewed. Next, we describe the organization of intermuscular length and force feedback circuits in the context of the mechanical interrelationships of the muscles involved. Finally, we provide a conceptual framework for understanding the role of proprioceptive feedback in the regulation of limb mechanics across a continuum of behaviors, and show how a developing computational model can be used to understand how these pathways are integrated to regulate limb stiffness. We conclude from a qualitative appraisal of the data that intermuscular length feedback reinforces the mechanical relationships between antagonists and between synergistic muscles that cross the same or different joints. Furthermore, inhibitory force feedback is organized to manage the distribution of stiffness across joints as well as intersegmental dynamics due to the inertial properties of the limb segments.

Keywords Length feedback · Force feedback · Limb stiffness · Neuromechanical integration · Limb mechanics

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B. I. Prilutsky, D. H. Edwards (eds.), *Neuromechanical Modeling of Posture and Locomotion,* Springer Series in Computational Neuroscience,
DOI 10.1007/978-1-4939-3267-2_3

3.1 Introduction

It is generally recognized that sensory feedback arising from muscle receptors and other proprioceptors has a strong influence on muscular activity during postural tasks as well as during locomotion. A definitive understanding of how and to what extent sensory feedback contributes to whole limb coordination has been hampered, however, by several factors, including the complexities of the organization of the neuromechanical system. This complexity arises both from the mechanics of the sensory receptors themselves and from the interactions between neural pathways and the mechanical circuits[1] of the musculoskeletal system. Moreover, systematic experimental testing of the components of the neuromuscular system is challenging. We propose that computational models can help understand these interrelationships. The purpose of this chapter is to synthesize existing experimental data concerning the organization and actions of proprioceptive feedback from muscle spindle receptors and Golgi tendon organs, and then to propose how current models can be used to promote understanding of the manner in which sensory feedback contributes to motor control.

Given the extensive information on feline motor control that is available, this chapter provides a synthesis of data primarily from the feline model concerning the role of proprioceptive feedback on limb mechanics. We first provide some fundamental concepts from the historical literature concerning the interactions between limb mechanics and sensory feedback. The role of length feedback in transforming the mechanical properties of muscles into more spring-like actuators will then be reviewed. Next, we describe the organization of length and force feedback in spinal circuits with reference to the mechanical interrelationships of the muscles involved. Finally, we will synthesize this information to provide a conceptual framework for understanding the role of proprioceptive feedback in the regulation of limb mechanics, and show how a developing computational model can be used to understand how these pathways are integrated to regulate limb stiffness.

Our organizational scheme for length and force feedback is based on two primary sources. First, we utilized data reported by Eccles et al. (1957a, b). These studies have provided an extensive mapping, in anesthetized cats, of proprioceptive pathways arising from group I receptors from most of the major hindlimb muscles by stimulating different peripheral nerves and recording intracellular potentials from motoneurons. The second source is a series of more recent experiments in which the stretch of selected muscles in decerebrate animals was used to probe the sensory network (Nichols and Koffler-Smulevitz 1991; Bonasera and Nichols 1994, 1996; Hyde et al. 1999; Nichols 1999; Wilmink and Nichols 2003; Ross and Nichols 2009). Although there is a substantial literature on connectivity of pathways from group II receptors through a number of interneuronal pathways (Jankowska and Edgley 2010), these pathways have not yet been systematically related to specific

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[1] The musculoskeletal system can be represented as a mechanical network with signals corresponding to the mechanical variables of length and force and their derivatives. These signals become represented in the associated neural circuits of the central nervous system through sensory transduction.

Table 3.1 Abbreviations

ADF	Adductor femoris
ADL	Adductor longus
BFA	Biceps femoris anterior
BFP	Biceps femoris posterior
EDL	Extensor digitorum longus
FDL	Flexor digitorum longus
FHL	Flexor hallucis longus
GMAX	Gluteus maximus
GMED	Gluteus medius
GMIN	Gluteus minimus
GRAC	Gracilis
ILIO	Iliopsoas
LG	Lateral gastrocnemius
MG	Medial gastrocnemius
PB	Peroneus brevis
PEC	Pectineus
PL	Peroneus longus
PLAN	Plantaris
PT	Peroneus tertius
PYR	Pyriformis
QF	Quadratus femoris
RF	Rectus femoris
SART	Sartorius
SOL	Soleus
SM	Semimembranosus
ST	Semitendinosus
TA	Tibialis anterior
TP	Tibialis posterior
VI	Vastus intermedius
VL	Vastus lateralis
VM	Vastus medialis

muscles. Furthermore, we will confine the discussion mainly to pathways that are thought to be located in the spinal cord, given that substantial information about the organization of these pathways is available. Abbreviations for the 31 muscles represented in the model are given in Table 3.1.

3.2 Background: Limb Mechanics and Sensory Feedback

We believe that proprioceptive feedback within a limb is organized to regulate the mechanical properties of the entire limb in addition to the mechanical properties of individual muscles. The limb-centric (as opposed to muscle- or joint- centric) organization of neural feedback reflects our view that limbs, rather than single muscles or joints, are the basic units for producing coordinated movement. This view acknowledges the strong mechanical coupling that exists in a limb due to dynamic properties such as inertial coupling and the multi-joint structure of many muscles. While individual muscles are the output units of the motor system, they are components of an integrated mechanical structure and are seldom activated in isolation. Even if they were activated in isolation, numerous muscles cross more than one joint and/or axes of rotation, and muscles transmit forces through fascia and can be coupled through shared tendons (Carrasco and English 1999; Lawrence and Nichols 1999a; Stahl 2010). Besides the viscoelastic coupling provided by these attachments through tendons and fascia, motions of the limb segments are linked dynamically through inertial interactions as well (Zajac 1993). Because of these physical properties, isolated muscle activation and single joint or limb segment movements are generally not observed in postural and locomotor tasks in nature. It is of course possible to control single joints individually, but this requires integrated action of muscles elsewhere in the limb due to inertial and elastic coupling. Therefore postural and locomotor tasks require organization of muscle activations throughout the entire limb rather than across single joints. Our belief that neural feedback arising from muscles within a limb is organized to regulate both the mechanical properties of muscle as well as intersegmental dynamics is supported by observations of patients with large fiber sensory neuropathy, a global loss of sensation from larger myelinated sensory axons. These patients have great difficulty controlling inertial coupling of limb segments and coordinating motions of the joints (Sainburg et al. 1993, 1995; Gordon et al. 1995).

Initial analyses of proprioceptive circuits focused on the influence of feedback on individual muscles (Liddell and Sherrington 1924; Merton 1953), apparently leaving the more global control of the mechanics of the musculoskeletal system to another level of neural integration. Proprioceptive feedback generally has a profound effect on the mechanical properties of muscles, as reviewed below, but it has become increasingly appreciated that proprioceptive circuits provide neural linkages between muscles and are highly integrated at the level of spinal segments. That is, some proprioceptive pathways project beyond the muscle of origin, indicating that motor control at the spinal level is not based on individual muscles. Given that length feedback from muscle spindle receptors projects to synergists and antagonists, length feedback would appear to provide regulation at the level of joints rather than muscles. However, it has also been shown that the projections of length feedback are not limited by the restrictive definition of the myotatic unit proposed by Lloyd (1946). According to this scheme, Ia connections cannot link muscles crossing different joints, each joint is regulated by one myotatic unit, and any given muscle cannot be a member of more than one myotatic unit. This scheme is an idealized conception and does not accurately reflect the organization of most Ia pathways (Eccles and Lundberg 1958b; Nichols et al. 1999a). For example, the flexor hallucis longus (FHL) and flexor digitorum longus (FDL) muscles in the cat are linked as synergists with respect to toe flexion, and FHL (which has a strong plantarflexion action at the ankle) is linked to the pretibial flexors by reciprocal inhibition (Nichols et al. 1999a). For muscles crossing the hip and knee, the organization of Ia excitation and inhibition is even more complex (Eccles and Lundberg 1958b). That is, a biarticular muscle (for example RF) may have connections through Ia afferents to other muscles that span either or both joints. These observations suggest that joint level control is too restrictive for even the most basic spinal reflex.

Evidence that proprioceptive circuits regulate limb mechanics is to be found in the projections of Ib afferents from Golgi tendon organs. During locomotion, excitatory force feedback is enabled (Pearson 1995; Donelan and Pearson 2004), resulting in an increase in stiffness in the muscles in which it is expressed (Ross 2006) over and above that contributed by length feedback. Excitatory force feedback has been observed mainly in biarticular muscles, so an important action of this feedback is to promote mechanical coupling between the joints that are spanned by the muscles as well as increased stiffness of the joints across which the moment arms of the muscles are greatest. However, a more comprehensive understanding of the actions of the proprioceptive network awaits the construction of suitable computational models.

The distribution of inhibitory force feedback is even wider than the distribution of length and excitatory force feedback. Projections of inhibitory force feedback across joints and axes of rotation are substantially stronger than autogenic (self) projections (Eccles et al. 1957b; Nichols 1994; Nichols et al. 1999a; Nichols and Ross 2009), indicating that the integration of length and force feedback (excitatory and inhibitory) occurs at the level of proprioceptive networks rather than at the level of single muscles. The integration of proprioceptive feedback is more than the superposition of individual ("autogenic") reflex pathways ("composite stretch reflexes" (Liddell and Sherrington 1924), but rather is instantiated by a network of neural circuits that are fully integrated with the mechanical circuits of the musculoskeletal system.

The principle that force feedback is organized to regulate limb mechanics is further illustrated by the absence of Ib projections from muscles that probably do not contribute greatly to intersegmental dynamics, such as FDL (Bonasera and Nichols 1994). This muscle controls the terminal segments of the limb (toes and claws), that have a lesser dynamic influence on the rest of the limb due to their low mass. Muscles that control more proximal joints are generally linked in a variety of combinations by length and force feedback. This observation further supports the hypothesis that proprioceptive pathways contribute to the regulation of whole limb mechanics. The actions of proprioceptive feedback are fully integrated with the intrinsic mechanical properties of muscles and presumably with the more global mechanical properties of the limb.

The organization of the proprioceptive networks combined with a knowledge of the interactions between length and force feedback provides a basis on which to understand their functions. The mechanical properties of limbs can be summarized by the property of impedance that includes components related to elasticity, viscosity and inertia. The terms corresponding to elasticity and viscosity are generally nonlinearly related to position and velocity (Houk et al. 2002), respectively, and frequently lumped together in the motor control literature as "stiffness" despite the fact that the term "stiffness" properly refers to the static mechanical properties of a system (Latash and Zatsiorsky 1993). Houk (1972b, 1979) originally proposed that the combined feedback from muscle spindle receptors and Golgi tendon organs should result in the regulation of muscular stiffness, with the magnitude of stiffness determined by the balance between length feedback and inhibitory force feedback. It was found that stiffness of the soleus muscle is indeed regulated in the decerebrate cat (Nichols and Houk 1976). It was later discovered, however, that this regulation could be attributed to length feedback alone during steady force production (Houk et al. 1981) and measurements of the strength of autogenic, inhibitory force feedback showed it to be quite weak (Rymer and Hasan 1980). Since inhibitory force feedback is mainly heterogenic and widely distributed, the integration of length and force feedback, and therefore the regulation of stiffness, occurs at the level of proprioceptive networks that regulate limb mechanics rather than the level of individual muscles. The loss of proprioceptive feedback from specific muscles results not only in a reduction of stiffness of the corresponding joints, but alterations in interjoint coordination as well (Cope et al. 1994; Abelew et al. 2000; Maas et al. 2007; Chang et al. 2009).

In addition to regulating the mechanical responses of limbs, proprioceptive feedback in conjunction with other sources of sensory information can provoke the expression of new patterns of activity when the motor task is changed. Feedback from sources extrinsic to the limb is generally concerned with influencing the patterns of muscular activity in a task-specific manner, presumably through the pattern formation network in the spinal cord (Lafreniere-Roula and McCrea 2005). For example, integrated sensory information from the otolith organs and from muscle spindle receptors in the muscles of the neck, representing a body-orientation signal (Brink et al. 1985; Marchand et al. 1987), regulates the pattern of muscular activity during ramp walking when compared to that observed during level walking (Smith and Carlson-Kuhta 1995; Gottschall and Nichols 2007; Nichols et al. 2014). The data suggest that, during downslope walking, the body orientation signal results in reduced activity in the gastrocnemius muscles, absence or greatly reduced activity of muscles of propulsion, and activation of hip flexors (Gottschall and Nichols 2007, 2011). These actions contribute to the braking action of the limbs required for controlled downslope locomotion (Nichols et al. 2014).

Besides changes in activation pattern, the body orientation signal has been shown to reduce limb stiffness through enhanced inhibitory force feedback (Nichols et al. 2014). This reduction in limb stiffness complements the braking action provided by distal anti-gravity and hip flexor muscles. The weightings of different inhibitory pathways (Bonasera and Nichols 1994; Wilmink and Nichols 2003; Ross and Nichols 2009) suggest that force feedback can be organized to determine how stiffness is distributed across the joints of the limb. The emergence of excitatory force feedback during locomotion (Pearson 1995) and modulation of inhibitory force feedback under different conditions (Nichols et al. 2014) strongly suggests that force feedback is an important variable for regulating limb stiffness in a task dependent manner. The modulation of muscular activity and proprioceptive pathways is consistent with the task specific use of the limb.

Although the modification of muscular activation patterns can be attributed mainly to sources extrinsic to the limb, including descending and propriospinal sources, it has also been suggested that feedback from within the limb can alter the pattern of activity during locomotion. For example, the semitendinosus and posterior biceps femoris muscles exhibit a double bursting pattern, one burst occurring at the transition from extension to flexion (i.e. swing initiation), and another at the transition from flexion to extension (i.e. terminal swing) (Smith et al. 1993; Krouchev et al. 2006; Markin et al. 2012). This pattern is not observed during fictive locomotion, where there is usually only a single burst at the beginning of flexion (locomotor-like patterns of muscle nerve activity in a paralyzed, decerebrate animal) (Markin et al. 2012). Since there is little or no feedback during fictive locomotion, the second burst has been attributed to feedback from within the limb. The role of intrinsic proprioceptive pathways in regulating patterns of muscular activity remains to be fully explored.

As discussed here, the functions of proprioceptive pathways can best be understood in terms of the regulation of whole limb mechanics. Until recently most studies of the proprioceptive pathways focused on measuring the output of individual muscles or individual or populations of neurons. However measuring whole limb properties such as limb stiffness can provide a metric more appropriate for the framework described here. We have recently adapted methods used to quantify endpoint stiffness in the upper extremity by Eric Perreault et al. (2004, 2008; Krutky et al. 2013) to the cat fore- and hindlimbs in an effort to more directly link proprioceptive pathways with whole limb mechanics. Moreover, a computational model can be extremely useful in connecting and synthesizing the experimental data from the previous more modular approach with experimental data from the current whole limb approach. A model incorporating the full 3 dimensional representation of muscular action of a feline hindlimb was originally developed by Thomas Burkholder (Burkholder and Nichols 2000, 2004) and later ported to the Neuromechanic software environment (Bunderson et al. 2012), see also Chap. 1 in this book (Bunderson and Bingham 2015). Using this model whole limb properties such as limb stability (Bunderson et al. 2008) and endpoint stiffness (Bunderson et al. 2010) have been obtained. We are currently utilizing this model to understand the integrated function of proprioceptive pathways.

3.3 Transformation of Muscular Mechanics by Autogenic Feedback

The analysis of proprioceptive feedback begins with the actions of autogenic (self) feedback on the muscle of origin. The most familiar and thoroughly studied example of autogenic feedback is the autogenic stretch reflex (Liddell and Sherrington 1924). The stretch reflex includes monosynaptic feedback from primary spindle afferents to motoneurons as well as possible contributions from group II muscle afferents (Stuart et al. 1970; Stauffer et al. 1976; Sypert et al. 1980; Munson et al. 1982). The original functional hypothesis for this reflex was the “Follow-Up Length Servo Hypothesis” (Merton 1953) based on length as the controlled variable. Subsequent work as well as more recent thinking about what variables are controlled by the nervous system (Stein 1982) justified rejection of this hypothesis (Houk 1972a). The current understanding of this and other proprioceptive pathways requires a more comprehensive understanding of the mechanics of movement and muscle physiology. Indeed, knowledge of the interactions between neural feedback and intrinsic muscle mechanics is crucial to the understanding of motor control (Nichols et al. 1999b; Dickinson et al. 2000; Huyghues-Despointes et al. 2003a, b; Sponberg et al. 2011).

Skeletal muscles have complex mechanical properties. Both length-tension and force-velocity relationships depend critically on the rate at which motor units are activated (Joyce et al. 1969; Rack and Westbury 1969). Furthermore, skeletal muscle exhibits “thixotropic” properties, such that the responses of the muscle to a given length change are altered by prior movement (Kirsch et al. 1994; Proske and Morgan 1999; Campbell and Moss 2000; Huyghues-Despointes et al. 2003b). Complementary history-dependence is also exhibited by muscle spindle receptors (Haftel et al. 2004; Nichols and Cope 2004). Finally, short-range stiffness represents the initial response of a muscle to length change, with higher stiffness than the muscle presents subsequently (Joyce et al. 1969; Rack and Westbury 1974; Malamud et al. 1996; Cui et al. 2008). Short-range stiffness provides a response to perturbations before the central nervous system can react (Dickinson et al. 2000; Nishikawa et al. 2007; Daley et al. 2009). However, short-range stiffness depends on background force, so it provides a relatively small contribution under conditions of quiet standing. Neural mechanisms are required to decouple stiffness and force.

Autogenic length feedback transforms both the steady-state and transient properties of muscle in ways that are appropriate for motor control. Steady-state properties intrinsic to the muscle are determined predominantly by muscle length, rate of motor unit activation (Rack and Westbury 1969) and level of motor unit recruitment (Boskov and Heckman 1996; Nichols et al. 1999a). The rates of activation of motor units are usually subtetanic (Grillner and Udo 1971), and force output is relatively smooth due to the asynchronous activation of motor units (Rack and Westbury 1969). At physiological rates, the force-length relationship maintains a positive slope throughout the normal range of movement (Rack and Westbury 1969), so that muscular stiffness remains positive and non-zero (Fig. 3.1). The stiffness of the muscle scales according to the level of recruitment, since motor units are arranged mechanically in parallel (Fig. 3.1). As more motor units are recruited, both force and stiffness increase.

An important function of proprioceptive length feedback is to decouple force and stiffness, so that muscles can present a substantial stiffness to disturbances even at low background forces. Despite the presence of feedback, the muscle may present a stiffness no greater than that provided by intrinsic properties when all motor units are recruited, but this level of stiffness is independent of operating point on the force-length plane. The length-tension curves illustrated in Fig. 3.1 represent those of fixed populations of motor units in the absence of feedback, and those of the muscle when feedback was present (two cases with different slopes are shown). For any given operating point in the force-length plane, the stiffness with feedback

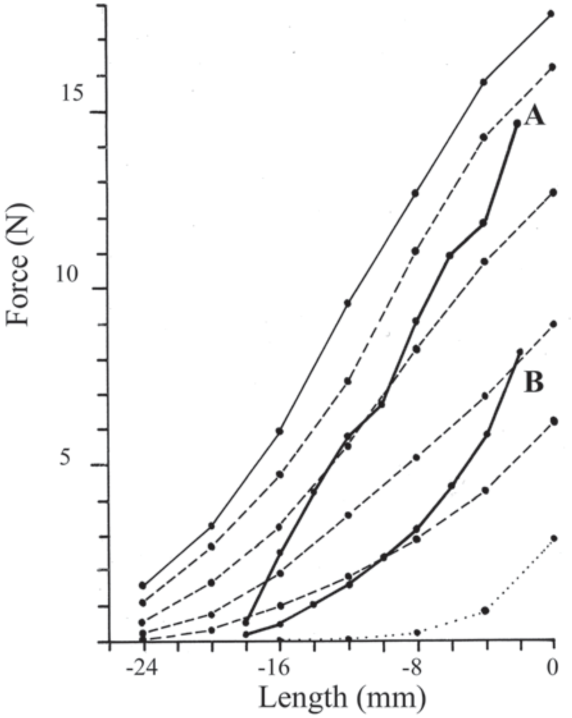

Fig. 3.1 *Transformation of steady-state mechanics of the feline soleus muscle by autogenic feedback*. The two heavy solid lines (A, B) represent force-length relationships obtained at different times in one animal in the unanesthetized decerebrate state. The muscle was held at each length for 30 s. The intrinsic force-length relationships of fixed populations of motor units were obtained by stimulating progressively larger groups of ventral root filaments at 8 pps after transecting the ventral roots. This rate was selected as the firing rate observed during steady force production in this muscle (Grillner and Udo 1971). Intermediate groups are shown as *dashed lines* and 100 % of the population is shown as the *light solid line*. Each data point was obtained by stimulating the muscle at a given length, and length was then changed during the inactive period between stimuli. The *dotted line* denotes the relationship for the inactive muscle. Zero length denotes the maximum physiological extension determined while the muscle was still connected to the calcaneus. Note that all force-length relationships have positive slopes across the physiological range of the muscle lengths. Autogenic feedback increases the stiffness of the muscle at each operating point in the force-length plane by the recruitment of additional motor units. The relative contributions of intrinsic stiffness and autogenic feedback can be estimated as the difference in slopes at the points of intersection of *dashed* and *heavy solid lines*. The stiffness of the regulated muscle can change under different states of the spinal cord, as illustrated by the different slopes of curves A and B. In different preparations (Nichols 1974) or with different levels of stimulation of Dieter's nucleus (Feldman and Orlovsky 1972), the threshold of activation of the muscle can change. Threshold and slope can therefore be controlled independently of background force, so that the muscle can present substantial stiffness even if background force is low. Data were adapted from a thesis (Nichols 1974)

exceeds the intrinsic stiffness. At longer lengths and higher levels of recruitment, however, the intrinsic properties make a larger contribution to the total stiffness. The force-length relationships in the presence of feedback can also shift along the length axis (Feldman and Orlovsky 1972), representing different thresholds of activation due to different command signals to the motor neuron pool, with no substantial changes in slope. The slope can change, however, under different behavioral conditions and in response to descending control signals (Nichols and Steeves 1986), as also shown in Fig. 3.1. The length-tension characteristic with lower slope was observed during the same experiment due to spontaneous changes in the state of the preparation. While intrinsic muscular stiffness depends on the level of activation and consequently force, the stiffness and threshold of the muscle with local feedback can vary independently of background force. This principle is a basis for the Equilibrium Point Hypothesis of motor control (Feldman and Levin 1995). As motor units are recruited, the rate of firing of recruited units also increases (Monster and Chan 1977). The intrinsic properties of muscle are therefore somewhat more complicated than portrayed in Fig. 3.1, but the transformation brought about by feedback is similar to what is shown.

When the length of an active muscle is changed, the initial response is determined by the intrinsic properties. This initial response coincides with short-range stiffness (Joyce et al. 1969), followed by a complex interaction between the intrinsic properties and autogenic feedback. The importance of short-range stiffness is that this mechanical response occurs before any changes in motor unit recruitment due to feedback and is therefore responsible for the initial response of the body to disturbing forces. Short-range stiffness is subject, therefore, to the scaling of stiffness with background force. During quiet standing, background force is low, so the response to postural perturbations is dominated by contributions of feedback. At high forces, the intrinsic properties including short-range stiffness contribute substantially to the mechanical response (Nichols and Houk 1976).

Short-range stiffness and the remainder of the intrinsic response are dependent upon movement history, as illustrated in Fig. 3.2, and this dependence has a profound influence on the contributions of feedback to the mechanical properties of muscle (Huyghues-Despointes et al. 2003b). When a contracting muscle is stretched following a period of isometric contraction, the stiffness decreases following the short range, a phenomenon known as yielding (Joyce et al. 1969; Nichols and Houk 1976). In the presence of autogenic feedback, the yield is compensated by additional recruitment of motor units (Fig. 3.2, upper left panel), resulting in a response that more closely resembles a linear viscoelastic response (Nichols and Houk 1976). If stretch is preceded by release, the yield is reduced in relation to the magnitude of the shortening. If the release is large enough, no yield is observed. The contribution of feedback is complementary, preserving the viscoelastic character of the intrinsic response. In this case, the contribution of feedback is nil, and there is no real distinction between the short and longer-range stiffnesses. It appears that this remarkable control strategy arises from the history dependence of muscle spindle receptors (Haftel et al. 2004; Nichols and Cope 2004).

In the above examples, the “spring constant” of the muscle is determined by feedback, with intrinsic properties contributing variable amounts depending upon conditions, including level of recruitment, length and previous mechanical history. As stated above, the available evidence suggests that the critical autogenic feedback

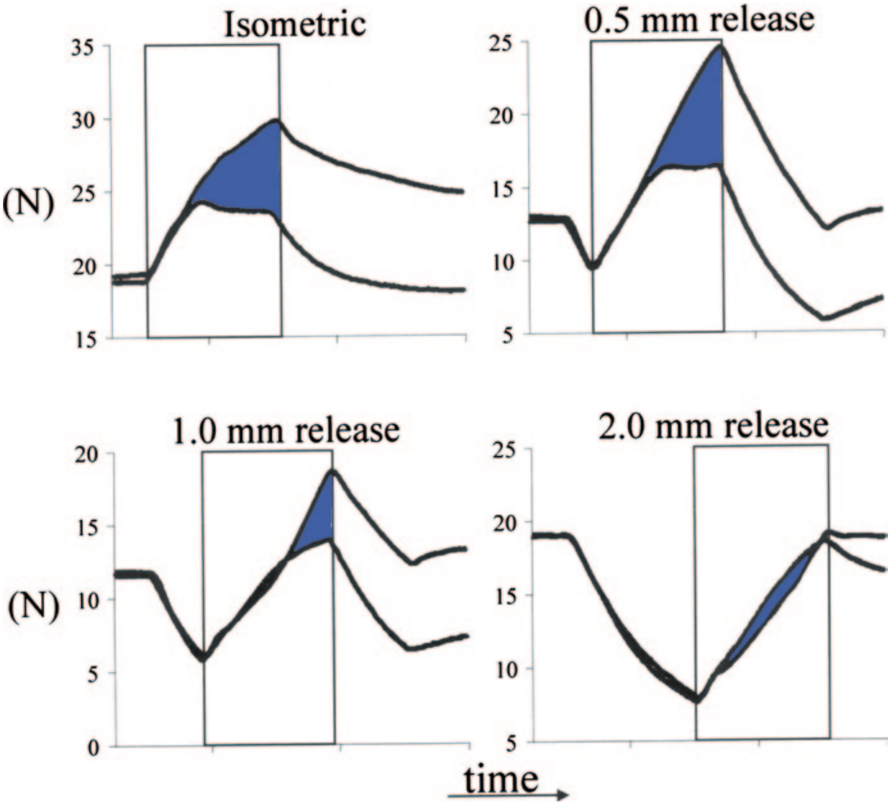

Fig. 3.2 *Transformation of the transient mechanical properties of muscle by autogenic feedback*. The intrinsic response of the deafferented right feline soleus muscle in a decerebrate cat is compared to the response of the muscle with intact autogenic feedback during stretch. Intrinsic responses were obtained by reinnervation of the right muscle approximately 1 year prior to the experiment. Motor units were reinnervated during this time, but autogenic feedback was blocked by a process of synaptic stripping (Bullinger et al. 2011). The data in each panel represents the responses of the two muscles during activation by crossed-extension reflexes. For the responses illustrated in each successive panel, muscle stretch (2 mm) was preceded by muscle shortening of the given amplitude. The differences between intrinsic responses and those with intact feedback are indicated by the shaded areas, allowing an estimate of the relative contributions of intrinsic properties and feedback. With no prior stretch, autogenic feedback increased muscular stiffness and compensated for the yield in the intrinsic response. As the prior release was increased, the yield diminished and the contribution of feedback progressively diminished, conserving the resultant response of the muscle. The feedback compensated for amplitude and history dependent nonlinearities of the muscle. Adapted from Huyghues-Despointes et al. (2003b)

is from the muscle spindle receptor. During different behaviors, other sources of feedback contribute to the mechanical response. During locomotion for example, inertial loads become greater, and greater stiffness is desirable. As stated above, excitatory force feedback is enabled and projects primarily autogenically (Ross 2006). This feedback serves to increase muscular stiffness, but based on force rather than length. This arrangement is advantageous for muscles in which tendon compliance is such that the length changes of muscle fascicles do not correspond to the length changes of the muscle-tendon unit. Indeed, during level walking, the fascicles of the medial gastrocnemius muscle actually shorten during weight acceptance while the muscle tendon unit is lengthening (Hoffer et al. 1989). Since forces in the tendon are increasing, excitatory force feedback still reinforces muscular contraction even in the face of decreasing length feedback. There is also evidence that in muscles not exhibiting excitatory force feedback during locomotion, autogenic inhibition (Granit 1950) is expressed (Ross 2006), presumably reducing stiffness slightly. It is not clear what functional advantage this would have, but may simply be a byproduct of mobilization of the force feedback system.

These data indicate that autogenic length feedback transforms the properties of the muscle to present spring-like characteristics (with nonlinear damping) with variable length threshold, while autogenic force feedback may be responsible for determining the magnitude of muscular stiffness in a task dependent manner. Some of the complex mechanical properties of muscle, such as short-range stiffness and thixotropy, are incorporated into the response, while others, such as the dependence of stiffness on force, are compensated. In order to represent these interactions, suitably sophisticated models of muscle are needed. The available computational models of muscle systems utilize various modifications of "Hill-type" muscle models that in some cases capture important steady-state and transient muscle properties (Lin and Crago 2002a, b). However, these models by and large do not represent the history-dependent properties of muscles and spindle receptors described above. More mechanistically based models would help to overcome this difficulty. Moreover, Hill-type models are commonly used to represent the dependencies of force on length and velocity, but these models, with some exceptions (for example Lin & Crago), are often based on unphysiological conditions of activation. Hill-type models also do not usually represent short-range stiffness (but see Lin & Crago). Hill-type models are a useful starting point for ongoing locomotion, but for more complex behaviors involving changes in speed and direction or sudden initiation of movement, more realistic, mechanistic models will be necessary.

3.4 Organization of Heterogenic Feedback

The functions of proprioceptive feedback can best be appreciated by considering the attachments and moment arms of individual muscles. The interpretation of autogenic and intermuscular (heterogenic) pathways is critically dependent upon an understanding of the anatomical context. In this section we will discuss proprioceptive pathways in this anatomical context. Insight into the anatomical context can be obtained from two types of studies that were initiated in order to understand the actions of muscles in three dimensions.[2] For the distal musculature, the torques

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[2] In the analysis of proprioceptive feedback for muscles crossing the hip and the knee (Eccles and Lundberg 1958a), actions out of the sagittal plane were acknowledged, but functions of specific

exerted by the major distal muscles during electrical stimulation (Lawrence and Nichols 1999a, b) and their moment arms (Young et al. 1993) have been documented. In another approach, the muscular actions during electrical simulation were measured as the reaction forces on the ground (Honeycutt and Nichols 2014). These latter measurements agree substantially with predictions from the Burkholder computational model (Burkholder and Nichols 2004). A table providing a qualitative description of the actions of muscles crossing the hip and knee based on several sources is available (Nichols et al. 1999a).

It should be noted that connective tissues, including tendon and fascia, are important components of the peripheral motor apparatus and can also influence limb mechanics. Tendons provide mechanical buffering during locomotion (Griffiths 1991; Roberts and Konow 2013), and in some cases result in shortening of the muscle fibers while the muscle-tendon unit is lengthening (Hoffer et al. 1989; Prilutsky et al. 1996; Maas et al. 2009; Konow et al. 2012). Fascia provides an additional route for force transmission (Maas et al. 2005; Stahl 2010). Connective tissue, including tendon and fascia, together with muscle and bone forms a complex mechanical network that has been described as a tensegrity structure (Silva et al. 2010). Muscle fibers work within this mechanical network and produce movement by altering the patterns of force within it.

Individual muscles or portions of muscles (English and Weeks 1987; Carrasco et al. 1999) influence joint stiffness by virtue of their attachments and routes of force transmission between these attachments. Individual muscles can cross one or more joints and one or more axes of rotation. Muscles contribute to the stiffness of joints by virtue of their resultant stiffness (the sum of intrinsic stiffness and contributions from proprioceptive pathways) and the moment arm of the muscle at the spanned joint. For example, the FHL muscle exerts substantial plantarflexion torque and therefore stiffness at the ankle joint, while its strong synergist FDL (Eccles et al. 1957a; Bonasera and Nichols 1994) exerts relatively little due to the differences in moment arms at the ankle (Lawrence et al. 1993; Lawrence and Nichols 1999a). The greater moment arm for ankle plantarflexion by FHL can explain the very different activation patterns of these two muscles (O'Donovan et al. 1982), where FHL presumably contributes to ankle stiffness during stance. This example also illustrates the fact that the presence of strong connections through Ia afferents does not underlie patterns of muscular activity, since both muscles are strong Ia synergists with very different patterns of activity.

Multiarticular muscles provide mechanical coupling across joints. The gastrocnemius muscles (MG and LG) have greater moment arms for plantarflexion at the ankle and therefore contribute preferentially to ankle joint stiffness, but also impart a flexor moment to the knee. During locomotion, the expression of excitatory force feedback combined with length feedback greatly enhances this mechanical coupling in addition to increasing the stiffness of the ankle. The distal attachment of MG also couples plantarflexion with abduction, promoting postural stability and

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muscles were still expressed in terms of flexion and extension. Later work underscored the necessity of incorporating muscular actions in three dimensions (Macpherson 1988b).

contributing to the initiation of turning (Lawrence et al. 1993; Nichols et al. 1993; Lawrence and Nichols 1999a, b). Several proximal muscles produce combinations of multiarticular and biaxial torques. PSOAS, ADF and GRAC provide combinations of hip extension or flexion and adduction, while BFA and BFP provide abduction in addition to knee flexion. The tensor fascia lata muscle, which is not included in our model as yet, provides flexion and abduction of the hip. Examples of relatively uniaxial actions include the vastus muscles, providing knee extension due to the patellar mechanism.

In order to represent the relationships between muscles and to understand the functions of heterogenic feedback, we utilized a model constructed in Neuromechanic (Bunderson et al. 2012; Bunderson and Bingham 2015) to generate a "similarity matrix" similar to that originally constructed by Dr. Thomas Burkholder (Nichols et al. 2002). The similarity matrix provides a quantification of the mechanical similarity between any two muscles. In our model, the mechanics of the feline hindlimb are described by seven degrees of freedom (DOF), including three at the hip, two at the knee and two at the ankle. 31 muscles are represented in the model and the mechanical action of each muscle is represented by a seven element moment arm vector corresponding to these seven DOF. The a_{ij} element of the similarity matrix A (Fig. 3.3) is calculated as the angle between the moment arm vectors for muscle i and muscle j, shifted and scaled to vary between −1 (for perfect mechanical antagonists) and 1 (for perfect mechanical agonists)

$$a_{ij} = 1 - \frac{1}{\pi}\cos^{-1}\left(\frac{\vec{v}_i \cdot \vec{v}_j}{\left\|\vec{v}_i\right\|\left\|\vec{v}_j\right\|}\right).$$

The rationale for the order in which muscles are listed on the rows and columns is given by the dendrogram at the right of Fig. 3.3. The dendrogram is the result of a cluster analysis performed in Matlab (Mathworks, Natick MA). The 31 similarity comparisons between a single muscle and all other muscles were used as the observation set and the Euclidean distance between observation sets for each muscle was used to form the hierarchical cluster tree shown in the dendrogram in Fig. 3.3. These clusters denote the mechanically synergistic and antagonistic groups. Although the vector directions are biased toward the dominant actions of the muscles, it should be kept in mind that most muscles have complex actions, and in some cases a given pair may have both synergistic and antagonistic relationships (for example, ST and BFP).

The similarity matrix shows the synergistic groupings near the diagonal and the antagonistic groupings mainly distant from the diagonal. Note that the triceps surae muscles (LG, MG, SOL) group with PLAN and FHL. Even though FHL and FDL insert into the same tendons to the toes, they fall into two different mechanical synergies since their actions at the ankle differ substantially. The group of biarticular and biaxial muscles crossing the hip and ankle form the largest mechanically synergistic group. Note that ST and BFP are represented as synergistic, although they do have opposing actions in the frontal plane (Nichols et al. 1999a). Within this group,

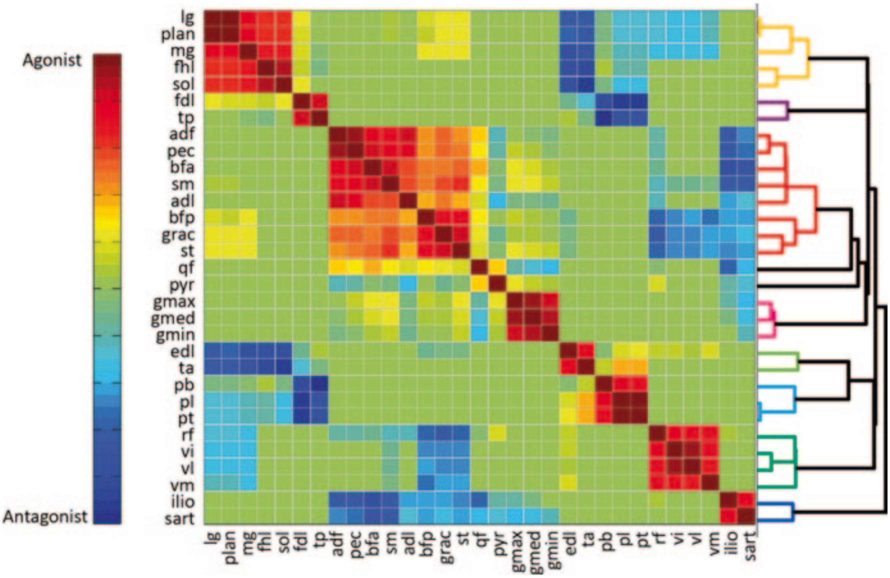

Fig. 3.3 *The similarity between the moment arms of any two muscle pairs of the feline hindlimb model at a quiet standing posture is shown here in a symmetric matrix*. The colors depict a continuum ranging from completely agonistic muscles (*dark red*) to completely antagonistic muscles (*dark blue*) with a midpoint where muscle pairs have no shared joint actions (*light green*). The order of the muscles in the rows and columns was chosen based on a cluster analysis (dendrogram at *right*) that groups muscles according to their normalized moment arm vector. The different colors of the terminal branches of the dendrogram show ten clusters identified in the analysis. Four clusters can be identified with primarily ankle actions including a plantar flexor cluster (LG, PLAN, MG, FHL, SOL), ankle adductor cluster (FDL, TP), ankle abductor cluster (PB, PL, PT), and ankle extensor cluster (EDL, TA). The quadriceps (RF, VI, VL, VM) and gluteal (GMAX, GMED, GMIN) muscles form two additional clusters. Two muscles, PYR muscle and QF, had sufficiently different moment arm vectors to each warrant their own individual "cluster". ILIO and SART formed a hip flexor group and the remaining muscles (ADF, PEC, BFA, SM, ADL, BFP, GRAC, ST) formed the largest group as hip extensors

one can discern at least two subgroups, namely, the "hamstrings muscles" (BFP, ST, GRAC) with strong actions at the knee and another subgroup acting predominantly at the hip (ADF, PEC, BFA, SM, ADL) (cf. Rossignol 1996). The five remaining synergistic groups are the gluteus muscles (Gmax, Gmed, Gmin), the pretibial flexors (TA, EDL), the peroneus muscles (PB, PL, PT), the quadriceps (RF, VI, VL, VM) and the group consisting of ILIO and SART. Note that TA and EDL are synergistic with PL as both produce dorsiflexion, but not with PB since PB is neutral with respect to the flexion/extension direction (Lawrence et al. 1993; Lawrence and Nichols 1999a). Therefore the synergistic groups of pretibial flexors and peroneus muscles have some overlap. There is a region of weak synergism between the biarticular ankle extensors (MG, LG, PLAN) and the hamstrings muscles (BFP, GRAC, ST). Our model does not yet distinguish the two divisions of SART (Eccles and Lundberg 1958b; Hoffer et al. 1987).

The antagonist groupings fall in two regions of the matrix. One grouping relates the ankle extensors to the pretibial flexors, the ankle stabilizers (TP and FDL to PB), and the long toe flexors and extensors (FHL, FDL) to the pretibial flexors. The gastrocnemius muscles (MG, LG) and PLAN, but not SOL, are mechanically dissimilar to the quadriceps. SOL is the only one of the triceps surae that does not cross the knee, and therefore does not share a common joint with the quadriceps muscles. The other region representing antagonistic relationships can be divided into two parts. In one, the “hamstrings” muscles (BFP, ST, GRAC) are antagonistic to the quadriceps. The other part consists of mechanical antagonism between hip flexors (ILIO & SART) and the other biarticular and biaxial muscles crossing the hip and knee. These mechanical relationships reflect the anatomy considering both articulation and axis of rotation of each muscle. It is important to note that the similarity matrix provides a snapshot of the mechanical similarity of muscles at a given posture and that for dynamic tasks such as locomotion where the posture can vary substantially there may be a reordering of clusters. Such varying relationships for different limb spacing during quiet standing are suggested by changes in the organization of directionally tuned force responses to perturbations of the support surface (Macpherson 1994; Honeycutt and Nichols 2010).

3.4.1 Heterogenic Length Feedback

The distribution of length feedback from group Ia spindle afferents (Fig. 3.4a) generally corresponds to the synergistic and antagonistic mechanical groupings, although the neural connections are more restricted than the mechanical connections (Fig. 3.3). The illustrated connections represent a compendium of results from the papers of Eccles et al. (1957a, b; Eccles and Lundberg 1958b) and more recent papers (Nichols and Koffler-Smulevitz 1991; Bonasera and Nichols 1994, 1996; Nichols 1999; Wilmink and Nichols 2003; Ross and Nichols 2009). As is well known, the triceps surae muscles form a synergistic group (Eccles et al. 1957a; Nichols 1999). Interestingly, MG provides substantially greater Ia input to LG than the reverse, which has consequences for directional tuning of LG during postural responses. MG torque at the ankle has a strong abduction component (Lawrence and Nichols 1999a). Therefore, the directional tuning of LG corresponds approximately to the directional tuning of MG (Honeycutt and Nichols 2014). Although a powerful ankle plantarflexor, PLAN has only weak Ia connections to LG and SOL perhaps related to its additional actions at the toes. FHL is somewhat paradoxical in that it has no known Ia connections to the triceps surae or PLAN (Eccles et al. 1957a), despite the fact that it shares mechanical actions with these muscles; FDL and FHL both flex the toes and are strong Ia synergists, but do not share action at the ankle. Although the activation patterns of these two muscles are very different during locomotion, the proprioceptive link suggests that they would be coactivated in response to dorsiflexion of the toes at the onset of stance.

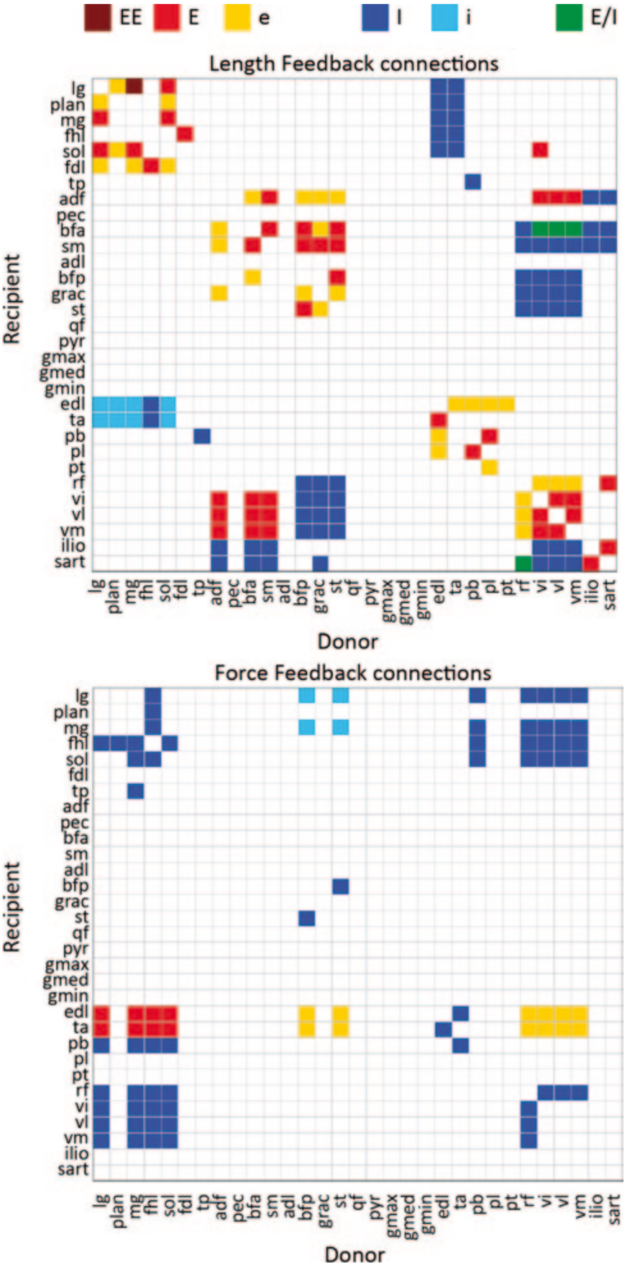

Fig. 3.4 *The short latency reflex interactions between muscles of the feline hindlimb described in these sections are summarized in two matrices dividing the interactions between length and force dependencies*. Very strong, strong, and weak excitatory interactions are depicted in *dark red, red*, and *yellow* respectively. Strong and weak inhibitory interactions are depicted in *dark blue* and cyan respectively. The interactions marked in *green* (from RF to SART and from the vastus muscles to BF) represent data from Eccles et al. (1957b) where different motoneurons in the same motor pool received either inhibitory or excitatory inputs from the stimulated nerves. Note that some muscles received both length and inhibitory force feedback from other muscles. The dominant effect is then force dependent

Other mechanical synergies are also associated with Ia linkages, such as the pretibial flexors, the peroneus muscles, and the group consisting of ILIO and SART. The quadriceps group forms a Ia synergy, but the linkages between RF and the vastus muscles are somewhat weaker than between the vastus muscles. The weaker synergies between vastus muscles and RF presumably reflect the differences in activation patterns and functions of these two groups (Engberg and Lundberg 1969) rather than any differences in the direction of endpoint forces (Honeycutt and Nichols 2014). A large Ia synergy (Fig. 3.4a) corresponds to the mechanical synergy linking the complex muscles causing hip extension, knee flexion, adduction and abduction at the hip (Fig. 3.3). One can also discern subgroupings corresponding to the hamstrings muscles (BFP, GRAC, ST) and to muscles that primarily extend the hip (ADF, PEC, BFA, SM). Members of these two subgroups correspondingly show two distinct patterns of endpoint forces in both horizontal and sagittal planes (Honeycutt and Nichols 2014). Identification of the hamstrings as a distinct subgroup is further justified by the connection of these muscles through the crural fascia to the calcaneus (van Ingen Schenau 1994; Stahl 2010). The predominantly hip extensor subgroup also forms a Ia synergy. The Ia linkages among the members of the gluteus group have not been studied to our knowledge, and therefore these linkages are not represented.

Although most Ia linkages for hind limb muscles represent close mechanical synergies (Fig. 3.3), there is one prominent example of a Ia linkage that crosses joints, namely, a unidirectional link from VI to SOL (Eccles et al. 1957a; Wilmink and Nichols 2003). VI and SOL are both single joint extensors, crossing the knee and ankle, respectively, and show no mechanical synergy (Fig. 3.3). The vastus muscles also share Ia feedback with ADF and receive excitation from SM and BFA, all hip extensors (Eccles and Lundberg 1958b). Apparently due to technical limitations, it was not specified whether all three vasti project to ADF, or only VI (“crureus”).

Muscles are also linked by reciprocal Ia inhibition (Fig. 3.4a), although these linkages do not represent all the examples of mechanical dissimilarity (Fig. 3.3). These linkages include the triceps surae muscles and FHL with the TA & EDL, hamstrings with the quadriceps muscles, and BFA & SM with ILIO & SART. Linkages are also apparent for ADF with ILIO and SART, and vastus muscles with ILIO and SART. These linkages all correspond to mechanical dissimilarity, and involve joints common to both muscle groups. The linkage between RF and SART is represented as mixed. RF is linked by excitation to lateral SART, which extends the knee, and by inhibition to medial SART, that flexes the knee. Note that inhibition between the vastus muscles and ILIO represents an example of cross-joint inhibition. The quadriceps muscles are mechanically dissimilar to MG, LG and PLAN for action at the knee (Fig. 3.3), but these groups are not linked by reciprocal inhibition. Further, adductors and abductors of the hip are not linked by reciprocal inhibition (Eccles and Lundberg 1958b).

At the ankle, the reciprocal inhibition between triceps surae muscles and TA & EDL is stronger in the direction TA & EDL to triceps surae, but is balanced between TP and PB (Bonasera and Nichols 1994), two important ankle stabilizing muscles that are coactivated during stance. This reciprocal inhibition has the effect of stiffening the ankle in the frontal plane during stance. Although FDL and FHL are strong Ia synergists, only FHL shares reciprocal inhibition with TA & EDL, presumably because FHL, but not FDL, has a strong action at the ankle (Lawrence and Nichols 1999a).

3.4.2 Implications for the Myotatic Unit Hypothesis

The distribution of excitatory and inhibitory Ia feedback generally reflects mechanical synergism and antagonism, respectively, but the connections in many cases are inconsistent with the myotatic unit hypothesis (cf. Eccles and Lundberg 1958b). The presence of monosynaptic linkages or inhibition across joints and the projection of excitation and inhibition to more than one muscle group are examples of patterns not consistent with the hypothesis. Even in the distal hind limb, one can find examples of muscles that form strong Ia linkages with a synergist (e.g. FHL & FDL) but do not share inhibition with direct antagonists (e.g. FDL).

The myotatic unit has also been considered a basis for synergistic activation of muscles (Caicoya et al. 1999). However, there are numerous examples of muscular activation patterns that do not correspond to patterns of length feedback. For example, the ankle stabilizers are linked by reciprocal inhibition, but yet are coactivated during stance. The strong reciprocal inhibition during cocontraction provides increased stiffness in the frontal plane (Nichols and Koffler-Smulevitz 1991; Bonasera and Nichols 1996). Furthermore, cutaneous pathways (e.g. sural nerve) can simultaneously activate MG and inhibit LG and SOL, even though these muscles are closely linked by Ia afferents (LaBella et al. 1989; LaBella and McCrea 1990; Nichols et al. 1993). Finally, FDL and FHL are recruited according to very different patterns during locomotion (O'Donovan et al. 1982) and yet are strong Ia synergists. We conclude from these observations that length feedback helps to regulate limb mechanics rather than providing a basis for muscular activation patterns, and that this regulatory system operates at the level of the limb rather than at the level of single joints.

3.4.3 Heterogenic Force Feedback

These results have been drawn from the studies of Eccles et al. (1957b) and more recent studies (Bonasera and Nichols 1994, 1996; Wilmink and Nichols 2003). Most heterogenic pathways from Golgi tendon organs are inhibitory during conditions of steady force production and during locomotion (Ross and Nichols 2009), but some excitatory pathways exist also (Fig. 3.4b). Heterogenic inhibition between major muscle groups is found principally between the quadriceps muscles, the triceps surae muscles, and FHL. FHL is a particularly powerful source of inhibitory feedback (Bonasera and Nichols 1994). Eccles et al. (1957b) reported that FDL was a powerful source of inhibition to other muscles, but more recent results indicate that this inhibition emerges from FHL while FDL provides relatively little force feedback (Bonasera and Nichols 1994). Since the studies of Eccles et al. depended upon electrical stimulation of muscle nerves, it may have been difficult to distinguish contributions of these two synergists. There is also some inhibition from the hamstrings muscles to MG and LG. Therefore, force dependent inhibition appears to link the major antigravity muscles across the joints of the limb. Inhibition across axes of rotation is found between PB and the triceps surae. Force related excitation was found in a single direction from the triceps surae and FHL to TA & EDL, which is complementary to the relatively weak reciprocal inhibition in this direction. Observation of these excitatory connections may have been responsible for the suggestion of the "inverse myotatic reflex mechanism" (Laporte and Lloyd 1952). According to Eccles et al. (1957b), however, TA and EDL receive excitation from a number of extensor muscles across the limb, so this system is not localized in the manner of length feedback. Therefore, the concept of the "inverse myotatic reflex mechanism" proposed by Laporte and Lloyd is not generalizable to the whole limb and does not parallel the organization of length feedback.

Heterogenic inhibition was also found within muscle groups. The weak Ia excitation between the vastus muscles and RF is complemented by mutual force dependent inhibition. Within the triceps surae group, inhibition is found projecting from MG and to some extent from LG to SOL, but not generally in the reverse direction (Nichols 1999). Finally, force-related inhibition was found between EDL and TA and between ST and BFP. These pathways are force-dependent, so the inhibitory linkages across joints and axes of rotation are likely to become more important during movements than during quiet standing.

3.4.4 Magnitude and Directionality

Recent studies, consistent with an earlier report (see Table 3.1 from Eccles et al. (1957b)), indicate that the magnitude of heterogenic inhibition varies considerably across preparations (Bonasera and Nichols 1994; Lyle, Niazi, Tuthill and Nichols, unpublished), in different tasks (Nichols et al. 2014) and following spinal cord injury (Niazi et al. 2012), while the strength of length feedback remains relatively constant over tasks. In addition, inhibitory force feedback appears to have a directional bias. During locomotion on a level treadmill, heterogenic inhibition follows a proximal to distal gradient (Ross and Nichols 2009) in which inhibition is stronger from the quadriceps to the triceps surae muscles to FHL. In various non-locomoting preparations, this gradient, its reverse or balanced inhibition may be observed (Bonasera and Nichols 1994; Lyle and Nichols 2014). Following spinal cord injury, the greater strength of force feedback is from FHL to the triceps surae muscles or the quadriceps. Returning to the original hypothesis of Houk (1972a) in which length and force feedback are integrated for the regulation of muscular stiffness, and its extrapolation to the regulation of limb stiffness, the different gradients of force feedback that have been observed suggest the stiffness of the limb measured at the endpoint as well as the distribution of stiffnesses across the joints are regulated by the central nervous system. Our recent results suggest further that force feedback constitutes an important mechanism for modulating limb stiffness.

3.5 Summary and Discussion

In this chapter we have attempted to assemble information about the organization of proprioceptive circuits for the cat spinal cord where connections to specific muscles could be identified. The main sources of this information are the extensive studies of Eccles et al. on group I pathways using electrically evoked afferent responses recorded intracellularly from motoneurons in anesthetized animals, and the more recent mechanographic studies using unanesthetized decerebrate animals. These two series of studies, where the same muscle combinations were used, are largely compatible. We propose that an important advantage of the mechanographic method—which involves evoking afferent responses with muscle stretch (i.e. physiological input) and recording the net population effect as force responses (i.e. physiological output)—is the closer approximation of reality affording more salient functional inferences. However, it remains difficult to interpret the function of individual pathways in many cases, and even more difficult to perceive how these pathways function together as an integrated whole. Current work utilizing robotic perturbations to calculate endpoint stiffness ellipsoids is anticipated to provide insight concerning the integrated role of proprioceptive pathways at the whole limb level. We believe that a more complete picture of the integrated pathways will come through mathematical modeling of the neuromusculoskeletal system, where the contributions of various components can be systematically tested. In a neuromechanical modeling environment, de novo limb controllers can be constructed based on theories derived from experimental observations and the features of that controller as well as the performance of the limb under that control can be compared with experimentally observed features and behavior. For example, by extending the insights of James Houk (that the integration of length and force feedback act as regulators of muscle stiffness) to the entire limb we can construct an integrated feedback system that regulates whole limb stiffness and compare the performance and features of that feedback system with the experimental observations.

3.5.1 Summary of Intrinsic Properties of the Musculoskeletal System

Understanding the actions of proprioceptive pathways requires knowledge of the intrinsic properties of the musculoskeletal system. Muscles have complex mechanical properties, such as nonlinear viscosity, and stiffness that depends on amplitude of perturbation, background force, and movement history. Properties such as intrinsic stiffness are advantageous for posture and movement, while others appear to be compensated (yielding and the dependence of stiffness on background force level and length). Muscles transmit forces through an elastic network consisting largely of tendons and fascia that provide filtering and distribution of forces across different joints. Energy storage and dissipation occurs through the elasticity of connective tissue elements and viscous muscle. The mechanical actions of each muscle depend on these routes of force transmission and on the location of their attachments through fascia or tendon. Finally, each limb segment has inertial properties that have a major impact on motor coordination.

3.5.2 General Principles of Organization and Action of Individual Pathways: Length Feedback

Pathways arising from muscle spindle receptors are stimulated by length changes in muscles, and primarily by muscle stretch that occurs during tasks involving eccentric muscular work such as downslope walking. Autogenic length feedback decouples force and stiffness so that muscles can respond vigorously to length change when starting with minimal levels of muscular recruitment, as occurs in response to postural disturbances during quiet standing, and also compensate for certain other nonlinear properties of muscle. The excitatory length feedback shared by close synergists would seem to have similar actions to autogenic length feedback, and function to increase the stiffness of shared joints or mechanically coupled joints spanned by the muscles.

There are also several examples of short latency excitation between muscles crossing different joints. In the case of VI to SOL, there are not parallel pathways from VL and VM to SOL, even though all these muscles are technically single joint. This might suggest that this short-latency connection could be related to motor unit type. However, ADF and other hip extensor muscles linked to the quadriceps by short-latency excitation are heterogeneous in fiber-type composition, and it has been argued elsewhere that proprioceptive linkages are related to articulation rather than motor unit type (Wilmink and Nichols 2003). It is therefore not clear what principle determines the VI to SOL connection. However, it is interesting that VL and VM are connected to fascia and therefore have more possibility of myofascial force transmission than VI. This neuronal pathway from VI to SOL therefore might constitute a neural pathway that parallels the mechanical coupling of VM and VL to the distal limb.

Inhibitory effects of length feedback, usually referred to as reciprocal inhibition, appear to have the effect of increasing joint stiffness. The reciprocal inhibition shared by PB and TP, two ankle stabilizers in the frontal plane, clearly enhances stiffness in the frontal plane since these muscles are coactivated during stance. For multi-joint muscles, the strict reciprocal relationships are not so clear. In the distal limb, TA & EDL receive inhibition from several muscles crossing various combinations of joints (MG, LG, PLAN, SOL, FHL), even though the different pairings share some antagonistic action. Although reciprocal inhibition generally links muscles having antagonistic actions, this is not always the case as illustrated by inhibitory pathways from the quadriceps to BFA and other hip extensors, in addition to the expected inhibitory linkages of quadriceps with knee flexors. These heterogenic connections of length feedback illustrate that the idea of the myotatic unit is rarely realized in the feline hind limb.

By virtue of the actions of length feedback to mediate vigorous muscle reflex responses at low background forces, the associated pathways are important for balance and stability during tasks such as quiet standing. Indeed, the directional tuning of initial muscular activations in response to perturbations of the support surface observed in intact animals (Macpherson 1988a, b) can be explained by short-latency length feedback and limb anatomy, both experimentally and computationally (Honeycutt et al. 2009, 2012; Bunderson et al. 2010; Honeycutt and Nichols 2010). That is, the principal direction of the tuning curve for each muscle opposes the direction of force produced by stimulation of that muscle (Honeycutt and Nichols 2014). The synergy structure during postural perturbations (Torres-Oviedo et al. 2006) is therefore explained in part by the anatomical organization of the limb. The magnitude of muscular responses is, however, likely to be determined also by integrated feedback from other limbs (Ting et al. 1998; Zehr et al. 2009; Hayes et al. 2012; Stevenson et al. 2013), as well as by the relative strengths of length feedback between muscles and length feedback across joints.

3.5.3 General Principles of Organization and Action of Individual Pathways: Force Feedback

Force feedback is expected to influence muscular action in response to perturbations and also in response to active contractile force due to central commands. Force feedback can be quite powerful at low background forces (FHL to triceps surae and quadriceps), but is generally force and task dependent, unlike length feedback. Autogenic excitation from Golgi tendon organs (MG and LG) is observed only during locomotion, and given that it is observed mainly in the biarticular members of the triceps surae, presumably functions to increase mechanical coupling between the knee and ankle by increasing the stiffness of these muscles. Autogenic inhibition in muscles not exhibiting excitation is also amplified during locomotion (Ross 2006). Although heterogenic inhibition is observed under static conditions as well as locomotion, its magnitude is subject to the specific task (Tuthill and Nichols 2009; Nichols et al. 2014).

The distribution of force feedback also differs considerably from the distribution of length feedback. The major anti-gravity groups are linked across joints and axes of rotation by inhibitory force feedback (quadriceps, triceps surae and FHL; triceps surae, PB and FHL) and force dependent inhibition links muscles with different articulation or axes of rotation within the major groups (RF and vastus muscles; MG and SOL; TA and EDL; TA and PB; ST and BFP). Within the major groups, one finds mixtures of length dependent excitation and force dependent inhibition, where the balance between the two sources of feedback depends on background tension (e.g. MG contributes excitation to SOL at lower forces that is gradually replaced by inhibition at higher background forces) (Nichols 1999). TA & EDL also receive heterogenic excitation from many muscles in the limb (e.g. triceps, Q, PB & ST) (Eccles et al. 1957b). The functions of the excitatory pathways onto TA & EDL are unknown, but it is interesting that reciprocal inhibition from the triceps surae to TA & EDL is considerably weaker than the reverse direction, and it is in this weaker direction that the force dependent excitation is found. The force dependence of these pathways suggests that these muscle groups are more tightly linked under dynamic conditions. Work is in progress to incorporate these pathways into the feline hind limb model to better understand their integrative action. It should be born in mind that confining the analysis to individual limbs provides an incomplete picture of the neuromechanical system. These proprioceptive pathways also influence muscular activation in other limbs (Ting et al. 1998; Zehr et al. 2009; Hayes et al. 2012; Stevenson et al. 2013). Interlimb communication will be important to include in future versions of the model.

3.5.4 Integration of Intrinsic Mechanical Properties, Length and Force Feedback During Functional Tasks

The relative contributions of mechanical and proprioceptive pathways to the regulation of limb dynamics are challenging to determine under most experimental conditions. It is fruitful nonetheless to seek this critical knowledge if we are to understand the causes of movement impairment in the presence of musculoskeletal and neurological disorders. We propose, based on the principles discussed previously, some hypotheses concerning the regulation of limb dynamics for the contrasting locomotor tasks of locomotion and landing from a fall. Locomotion occurs over a range of speeds over which inertial influences and overall loading varies, whereas landing is characterized by exaggeration of segment inertial disparity and high loading. Sense can be made of the actions of many of the individual proprioceptive pathways previously discussed during these tasks, but there are some seemingly conflicting actions as well.

There are several problems associated with managing the mechanics of multisegmented limbs during locomotion, besides provision of the appropriate sequencing of muscles. Movements of the individual joints should be coordinated so as to maintain muscles within ranges of motion that optimize force and torque production. Indeed, disruption of proportional coordination between the ankle and knee is observed following the loss of proprioceptive feedback from the triceps surae muscles (Abelew et al. 2000; Maas et al. 2007). In addition, the disparity in inertia between the proximal and distal limb segments, and intersegmental dynamics need to be compensated when inertial effects become important, such as during trotting and running. For example, during interaction with the ground, the lighter distal segments potentially would absorb more of the perturbation than the heavier proximal segments. During swing, the inertia of the distal segments can lead to unwanted relative motions of the distal and proximal segments. The limb stiffness must also be appropriate to the task for shock absorption and efficient use of energy (Ferris and Farley 1997; Farley et al. 1998; Ferris et al. 1998; Daley et al. 2006).

The roles of some pathways in the regulation of stiffness, in the regulation of gravitational forces, and in inertial compensation are apparent. During the weight acceptance phase of stance (E2), TP and PB are coactive, stiffening the ankle in the transverse plane, and the reciprocal inhibition between these two muscles reinforces this stabilization. The knee and the ankle are mechanically coupled by the biarticular MG and LG, reinforced by excitatory force feedback. This mechanical coupling helps to reduce the effects of inertial disparity between the limb segments. The moment arms for MG and LG are greater at the ankle than at the knee (Lan and Crago 1992), so these muscles contribute to weight support, propulsion and ankle stiffness. Ankle stiffness also receives a contribution from the substantial reciprocal inhibition from TA & EDL. Unlike the balanced reciprocal inhibition between TP and PB, there is relatively little reciprocal inhibition from the triceps surae onto TA & EDL. The stronger reciprocal inhibition from the pretibial flexors onto triceps surae seems to be correlated with the direction of gravity: it is focused on the muscles that are stretched under the weight of the body (Nichols and Koffler-Smulevitz 1991). Stiffness at the knee is presumably similarly regulated by autogenic feedback and reciprocal inhibition between the quadriceps muscles and knee flexors (BFP, GRAC, ST). Since the knee flexors and RF cross the hip as well, mechanical coupling between knee and hip is provided.

Superimposed on this system of length feedback, force feedback provides an additional source of mechanical coupling, stiffness regulation and inertial compensation under dynamic conditions, since force feedback is itself force dependent. As discussed earlier, autogenic force feedback can be excitatory during locomotion. Force dependent excitation in MG and LG during locomotion (Ross and Nichols 2009) contributes to ankle stiffness and coupling between ankle and knee. In contrast, heterogenic force feedback appears to be predominantly inhibitory. The integration of this more global feedback with length feedback helps to determine limb stiffness and the distribution of stiffness across the component joints.

Heterogenic force feedback between major muscle groups can contribute to inertial compensation and the distribution of limb stiffness. The distal limb is the site of direct interaction with the environment, so one might expect that the impedance of the distal joints of the limb might be less than that of the proximal joints in order to provide a moderately compliant interface. Since the distal limb segments have smaller mass than the more proximal segments, impedance due to inertia is therefore non-uniform in the appropriate direction based on limb mechanics. As discussed previously, the strong Ib inhibition from what we believe is FHL (i.e., reported as FDL) onto the triceps surae and quadriceps muscles in the anesthetized state (Eccles et al. 1957b) would tend to compensate for this non-uniformity in impedance when the anti-gravity muscles, including FHL, are activated during stance. The regulatory mechanism(s) mediating the balance between limb inertia and the gradient of force feedback is unknown, but is anticipated to have an important influence on task-specific limb mechanics. In the unanesthetized, non-locomoting decerebrate animal, the directionality of inhibitory force feedback was distal to proximal in some preparations, the opposite in others and more balanced in the remainder (Bonasera and Nichols 1994), so it may be that the effects of inertial non-uniformity on impedance at different joints are reinforced for some tasks and compensated for others by variations in the strength of Ib inhibition.

Interestingly, strong distal to proximal inhibition has been consistently observed after acute and chronic spinal hemisection (Niazi et al. 2012). This observation, along with the findings of Eccles et al. (1957b), suggests that the distal to proximal gradient of inhibition is the default state of the spinal cord that is then modulated according to the specific task, such as walking (Ross and Nichols 2009). During stepping on a level treadmill in the unanesthetized decerebrate animal, inhibitory feedback was found to be stronger from proximal to distal muscles (Ross and Nichols 2009). During relatively slow walking, inertial effects should be relatively small so that the proximal to distal gradient of force feedback would ensure that the distal limb segment would be appropriately compliant. It is predicted then that during rapid locomotion, or landing from jump, inhibitory feedback would be reweighted so as to influence proximal muscles to compensate for the effects of non-uniform inertia. As noted above, proximal to distal inhibitory feedback can be upregulated during downslope walking to reduce the impedance of distal joints even more. This hypothesis that *force feedback is engaged for inertial compensation and limb stiffness* remains to be validated using computational modeling and experiment.

A potential role for the excitatory force feedback observed between muscles of propulsion and the pretibial flexors (Eccles et al. 1957b; Nichols 1989) is suggested by a consideration of limb mechanics during locomotion. During E3 and into the initial stages of swing, especially for more rapid locomotion, there is coactivation of RF, BFP, ST and TA (Rossignol 1996). It is possible that the activity of TA is reinforced or even mediated during that time by the force-related excitation from the hamstrings muscles and RF. The hamstrings muscles may aid in propulsion through the crural fascia during E3 (Stahl 2010), but then continue with knee flexion as swing progresses. Their activity would also reinforce the action of TA to flex the ankle during the subsequent swing phase (Rossignol 1996). This role of force feedback may be viewed as an "assistance" rather than resistance and would promote the reversal in the direction of limb movement between stance and swing.

As discussed above, intrinsic mechanical properties of the limb and proprioceptive pathways have an important role in regulating joint dynamics in a task dependent manner for locomotion. Landing from a jump, which involves rapid deceleration of total body center of mass through eccentric muscular control of the limb segments in a distal to proximal sequence, is an additional motor task that highlights the complex motor control synergy between intrinsic musculotendon properties and proprioceptive circuits. The act of landing from a height has been studied in animals (Prochazka et al. 1977; McKinley et al. 1983; Abraham and Loeb 1985; Konow et al. 2012) and in humans (Ferris and Farley 1997; McDonagh and Duncan 2002; Santello 2005; Galindo et al. 2009; Lyle et al. 2013). Landing involves higher loads and angular velocities of the limb segments (particularly the distal segments with lower inertia) that necessitate rapid control of joints as compared to locomotion. The rapidity by which the peak forces are experienced (typically within 50–60 ms) indicates that intrinsic musculotendon properties, feedforward muscle activation and sensory feedback mediated by spinal pathways is primarily responsible for deceleration of body center of mass.

The assumed global goal for the nervous system during landing is to smoothly decelerate the center of mass by regulating whole limb stiffness to act as a brake. Animals and humans possess a remarkable ability to modulate limb stiffness across a wide spectrum of loading and surface conditions (Ferris and Farley 1997; Ferris et al. 1998; Dickinson et al. 2000; Daley et al. 2006; Perreault et al. 2008; Krutky et al. 2013). While the details of how this is accomplished remains an open question, it is clear that intrinsic musculotendon properties coupled with feedforward activation of muscles prior to foot contact functions to resist the initial impact due to delays in sensory feedback (Prochazka et al. 1977; McKinley et al. 1983; Abraham and Loeb 1985; Konow et al. 2012). In addition to the complex mechanical properties of muscle, evidence indicates that tendons can act as a mechanical buffer (Griffiths 1991; Prilutsky et al. 1996; Roberts and Konow 2013) by delaying and reducing the velocity of active lengthening of muscle fascicles in response to the rapid joint flexion during landing (Konow et al. 2012). This intrinsic property has been proposed to protect muscles from damage (Griffiths 1991; Konow et al. 2012; Roberts and Konow 2013) and perhaps preserves a favorable force-velocity relation for muscle action (Griffiths 1991; Prilutsky et al. 1996). The rapid flexion of the distal segment (e.g. ankle) additionally imposes mechanical coupling of the ankle and knee joints due to stretching the gastrocnemius for example (Zajac 1993; Prilutsky and Zatsiorsky 1994).

Rapid flexion and high loads characteristic of landing indicate proprioceptive length and force feedback contribute to regulation of whole limb stiffness with short delays occupied by short-range stiffness. As previously discussed, length feedback from muscle spindles contribute to limb stiffness primarily at the joint level but also reinforce segment coupling in cases such as autogenic feedback to gastrocnemius and likely rectus femoris (Prilutsky and Zatsiorsky 1994). Interestingly, a burst of activation from FHL and FDL are both observed after foot contact (Abraham and Loeb 1985) likely attributed to rapid toe dorsiflexion and the strong Ia connections between them. The synergy observed by these muscles during landing is in contrast to dissimilar activations of these muscles during locomotion (see above).

We propose that inhibitory force feedback would best match the task goal of attenuating impact forces by being distributed such that inhibition is strongest from distal to proximal muscles. The clear advantage of this organization is an explicit compensation for the effects of non-uniform inertia. Functionally, this would serve the purpose of increasing the compliance of the knee and hip and thus facilitate energy absorption by the more massive proximal knee and hip extensor muscles. In support of the distal to proximal concept, Prochazka et al. (1977), examining landing in cats, proposed that a reduction in lateral gastrocnemius activation for a short period immediately after impact was due to force dependent inhibition from toe flexors. Alternatively, landing and other rapid deceleration maneuvers could achieve a distal to proximal inhibitory force feedback gradient simply from the mechanics of the task, which is characterized by a distal to proximal sequencing of joint flexion and peak net joint moments. That is, landing involves rapid flexion of the toe and ankle such that toe and ankle flexor muscles presumably could begin inhibiting the proximal muscles at the knee prior to or coincident with rising force in the quadriceps muscles for example.

It argued that functions of proprioceptive feedback may be understood by considering their role in regulating the magnitude and distribution of limb stiffness through the interaction of length and force feedback. Evidence also suggests that the balance of length and force feedback can be altered in a task-specific manner by modulation of force feedback. Force feedback becomes more important under dynamic conditions and can compensate or reinforce the effects of non-uniform inertia of the limb segments. These hypotheses are qualitative and deduced by a review of the experimental evidence, but remain to be directly validated by further experiment and simulation. Work is currently in progress utilizing Neuromechanic to validate these hypotheses. It should be noted that the forgoing analysis assumes that the actions of these pathways are focused on the limb of origin of the proprioceptive signals. It may well be that projections of these pathways to other limbs must be considered to provide a more complete understanding of their *integrative actions*.

Acknowledgements This work was supported by NIH grants NS20855 and HD 32571 to TRN and 1F32NS080393-01A1 to MAL.

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