can be displaced linearly (eg, the scapula on the trunk), adding to the degrees of freedom about a joint.

The off-axis attachment of muscles enhances the flexibility of the skeletal motor system; the same movement can be achieved by activating different combinations of muscles. However, this additional flexibility requires the nervous system to control the unwanted actions. A solution used by the nervous system is to organize relations among selected muscles to produce specific actions. A particular sequence of muscle activations is known as a *muscle synergy,* and movement is produced through the coordinated activation of these synergies. For example, EMG recordings of human subjects suggest that variations of movements with the same general purpose, such as grasping various objects with the hand, reaching and pointing in different directions, or walking and running at several speeds, are controlled by approximately five muscle synergies.

The number of muscles that participate in a movement also varies with the speed of the movement. For example, slow lifting of a load requires only that the muscle torque slightly exceed the load torque (see Figure 31–14), and thus, only the flexor muscle is activated. This strategy is used when lifting a handheld weight with the elbow flexor muscles. In contrast, to perform this movement rapidly with an abrupt termination at an intended joint angle, both the flexor and extensor muscles must be activated. First, the flexor muscle is activated to accelerate the limb in the direction of flexion, followed by activation of the extensor muscle to accelerate the limb in the direction of extension, and finally a burst of activity by the flexor muscle to increase the angular momentum of the limb and the handheld weight in the direction of flexion so that it arrives at the desired joint angle (Figure 31–15B). The amount of extensor muscle activity increases with the speed of the movement.

Increases in movement speed introduce another factor that the nervous system must control: unwanted accelerations in other body segments. Because body parts are connected to one another, motion in one part can induce motion in another. The induced motion is often controlled with lengthening contractions, such as

Figure 31–16 A single muscle can influence the motion about many joints.

A. Muscles that cross one joint can accelerate an adjacent body segment. For example, at the beginning of the swing phase while running, the hip flexor muscles are activated to accelerate the thigh forward (**red arrow**). This action causes the lower leg to rotate backward (**blue arrow**) and the knee joint to flex. To control the knee joint flexion during the first part of the swing phase, the knee extensor muscles are activated and undergo a lengthening contraction to accelerate the lower leg forward (**red arrow**) while it continues to rotate backward (**blue arrow**).

B. Many muscles cross more than one joint to exert an effect on more than one body segment. For example, the hamstring muscles of the leg accelerate the hip in the direction of extension and the knee in the direction of flexion (**red arrows**). During running, at the end of the swing phase, the hamstring muscles are activated and undergo lengthening contractions to control the forward rotation of the leg (hip flexion and knee extension). This strategy is more economical than activating individual muscles at the hip and knee joints to control the forward rotation of the leg.

Direction of force exerted by muscle
Direction of rotation of limb segment

A

B
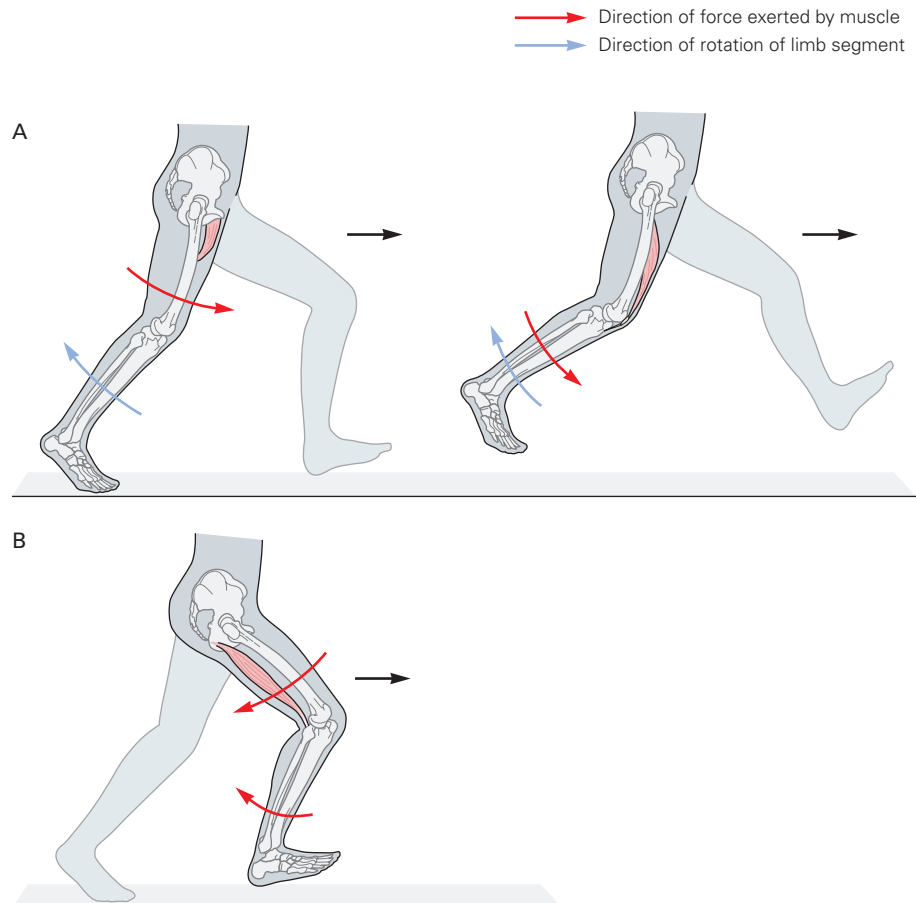
those experienced by thigh muscles during the swing phase of running (Figure 31–16A).

Muscles that span more than one joint can be used to control these motion-dependent interactions between body parts. At the end of the swing phase in running, activation of the hamstring muscles causes both the thigh and lower leg to accelerate backward (Figure 31–16B). If a hip extensor muscle is used to accelerate the thigh backward instead of the hamstring muscles, the lower leg would accelerate forward, requiring activation of a knee flexor muscle to control the unwanted lower leg motion so that the foot could be placed on the ground. Use of the two-joint hamstring muscles is a more economical strategy, but one that can subject the hamstrings to high stresses during fast movements, such as sprinting. The control of such

motion-dependent interactions often involves lengthening contractions, which maximize muscle stiffness and the ability of muscle to resist changes in length.

For most movements, the nervous system must establish rigid connections between some body parts for two reasons. First, as expressed in Newton's law of action and reaction, a reaction force must provide a foundation for the acceleration of a body part. For example, in a reaching movement performed by a person standing upright, the ground must provide a reaction force against the feet. The muscle actions that produce the arm movement exert forces that are transmitted through the body to the feet and are opposed by the ground. Different substrates provide different amounts of reaction force, which is why ice or sand can influence movement capabilities.
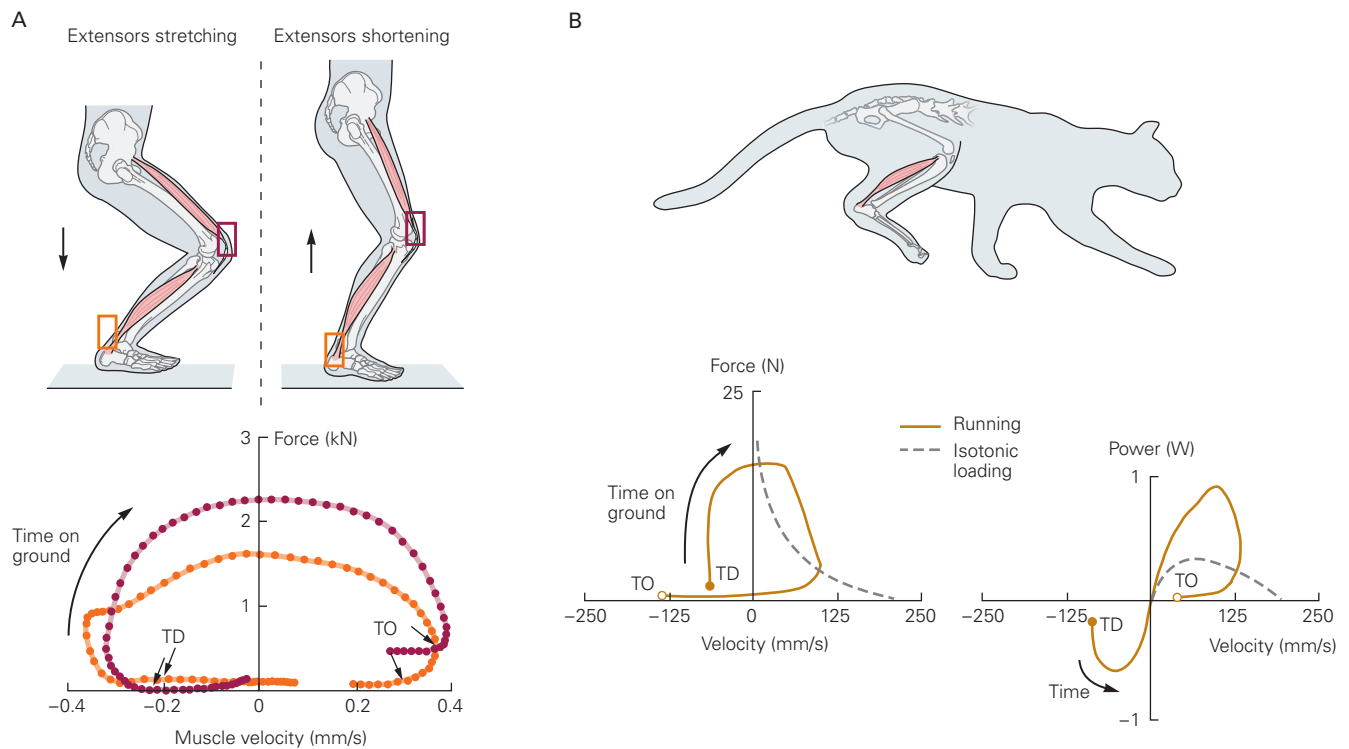
Figure 31–17 An initial phase of negative work augments subsequent positive work performed by the muscle. (Reproduced, with permission, from Finni, Komi, and Lepola 2000. Copyright © 2000, Springer-Verlag; Gregor et al. 1988.)

A. The force in the Achilles tendon (**orange**) and patellar tendon (**purple**) vary during the ground-contact phase of two-legged hopping. The feet contact the ground at touchdown (**TD**) and leave the ground at toe-off (**TO**). For approximately the first half of the movement, the quadriceps and triceps surae muscles lengthen, performing negative work (negative velocity). The muscles perform positive work when they shorten (positive velocity). The sites of force transducer measurements are indicated by rectangles.

B. The force exerted by the soleus muscle of a cat running at moderate speed varies from the instant the paw touches the ground (**TD**) until it leaves the ground (**TO**). The force exerted by the muscle during the shortening contraction (positive velocity) is greater than the peak forces measured when the muscle contracts maximally against various constant loads (isotonic loading). Negative velocity reflects a lengthening contraction in the soleus muscle. The power produced by the soleus muscle of the cat during running is greater than that produced in an isolated-muscle experiment (**dashed line**). The phase of negative power corresponds to the lengthening contraction just after the paw is placed on the ground (**TD**), when the muscle performs negative work.

Second, uncertain conditions are usually accommodated by stiffening the joints through concurrent activation of the muscles that produce force in opposite directions. Coactivation of opposing muscles occurs often when a support surface is unsteady, when the body might experience an unexpected perturbation, or when lifting a heavy load. Because coactivation increases the energetic cost of performing a task, one characteristic of skilled performance is the ability to accomplish a task with minimal activation of muscles that produce opposing actions.

Muscle Work Depends on the Pattern of Activation

Limb muscles in healthy young adults are active 10% to 20% of the time during waking hours. For much of this time, the muscles perform constant-length (*isometric*) contractions to maintain a variety of static body postures. In contrast, muscle length has to change during a movement so that the muscle can perform work to displace body parts. A muscle performs positive work and produces power during a shortening contraction, whereas it performs negative work and absorbs power during a lengthening contraction. The capacity of muscle to do positive work establishes performance capabilities, such as the maximal height that can be jumped.

The nervous system can augment the positive work capacity of muscle by commanding a brief period of negative work before performing positive work. This activation sequence, the *stretch–shorten cycle,* occurs in many movements. When a person jumps in place on two feet, for example, the support phase involves an initial stretch (lengthening) and subsequent shortening of the ankle extensor and knee extensor muscles (Figure 31–17A). The forces in the Achilles and patellar tendons increase during the stretch of the lengthening contraction and reach a maximum at the onset of the shortening phase. As a result, the muscles can perform more positive work and produce more power during the shortening contraction (Figure 31–17B).

Although negative work involves an increase in the length of the muscle, the length of the fascicles in the muscle often remains relatively constant, which indicates that the connective tissue structures are stretched prior to the shortening contraction. Thus, the capacity of the muscle to perform more positive work comes from strain energy that can be stored in the elastic elements of muscle and tendon during the stretch phase and released during the subsequent shortening phase. More strain energy can be stored in long tendons, but short tendons are more advantageous when the movement requires the rapid release of strain energy.

Highlights

1. The basic functional unit for the control of movement by the nervous system is the motor unit, which comprises a motor neuron and the muscle fibers it innervates.

2. The force exerted by a muscle depends in part on the number and properties of the motor units that are activated and the rates at which they discharge action potentials. The key motor unit properties include contraction speed, maximal force, and fatigability, all of which can be altered by physical activity. Motor unit properties vary continuously across the population that innervates each muscle; that is, there are not distinct types of motor units. Due to technological advances, it is becoming possible to characterize the adaptations exhibited by populations of motor units in response to different types of changes in physical activity.

3. Motor units tend to be activated in a stereotypical order that is highly correlated with motor neuron size. The rate at which motor units are recruited during a voluntary contraction increases with contraction speed.

4. The rate at which a motor unit discharges action potentials in response to a given synaptic input can be modulated by descending inputs from the brain stem. The modulatory input is likely critical for establishing the level of excitation in spinal pathways, but this has been difficult to demonstrate in humans.

5. Except at low muscle forces, variation in discharge rate has a greater influence on muscle force than does the number of activated motor units. Moreover, the variability in discharge rate of the motor unit population influences the level of fine motor control.

6. The sarcomere is the smallest element of muscle to include a complete set of contractile proteins. A transient connection between the contractile proteins myosin and actin, known as the cross-bridge cycle, enables muscle to exert a force. The organization of the sarcomeres within a muscle varies substantially and, in addition to motor unit activity, has a major effect on the contractile properties of the muscle.

7. For a given arrangement of sarcomeres, the force a muscle can exert depends on the activation of the cross bridges by Ca^{2+}, the amount of overlap between the thick and thin filaments, and the velocity of the moving filaments. Sarcomere force during lengthening contractions is augmented by a Ca^{2+}-mediated increase in titin stiffness. The force

produced by activated sarcomeres depends on the interactions of three filaments: actin, myosin, and titin.

8. Most of the force generated by activated sarcomeres is transmitted laterally through a network of non-contractile proteins that maintains the alignment of the thick and thin filaments.

9. The functional capability of a muscle depends on the torque that it can exert, which is influenced both by its contractile properties and by the location of its attachments on the skeleton relative to the joint that it spans.

10. To perform a movement, the nervous system activates multiple muscles and controls the torque exerted about the involved joints. The nervous system can vary the magnitude and direction of a movement by altering the amount of motor unit activity, and hence muscle torque, relative to the load acting on the body.

11. Although muscle exerts only a pulling force on the skeleton, it can do so whether the activated muscle shortens or is lengthened by a load torque that exceeds the muscle torque. The force capacity of muscle is greater during lengthening contractions. Motor unit activity differs during shortening and lengthening contractions, but little is known about how the synaptic inputs to motor neurons differ during these two types of contractions.

12. Faster movements elicit motion-dependent interactions between body parts that produce unwanted accelerations. These actions must be controlled by the nervous system to produce an intended movement.

13. The nervous system must coordinate the activity of multiple muscles to provide a mechanical link between moving body parts and the required support from the surroundings. The muscles engaged for each action, such as grasping, reaching, running, and walking, are organized into a few sets that exhibit a stereotypical pattern of activation, but it is not known why particular patterns are preferred.

14. The patterns of muscle activity vary substantially between movements and often include strategies that augment the work capacity of muscles. The patterns can be modified by experience, but little is known about the locus of the adaptations other than that both spinal and supraspinal pathways are involved.

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32

Sensory-Motor Integration in the Spinal Cord

DURING PURPOSEFUL MOVEMENTS the central nervous system uses information from a vast array of sensory receptors to ensure that the pattern of muscle activity suits the purpose. Without this sensory information, movements tend to be imprecise, and tasks requiring fine coordination in the hands, such as buttoning one's shirt, are difficult. The sensory-motor integration that makes the ongoing regulation of movement possible takes place at many levels of the nervous system, but the spinal cord has a special role because of the close coupling in the cord between sensory input and the motor output to the muscles.

Charles Sherrington was among the first to recognize the importance of sensory information in regulating movements. In 1906, he proposed that simple

reflexes—stereotyped movements elicited by activation of receptors in skin or muscle—are the basic units for movement. He also emphasized that all parts of the nervous system are connected and that no part is ever capable of activation without affecting or being affected by other parts. In his words, the simple reflex is a convenient if not a probable fiction.

Laboratory studies of reflexes in animals from the 1950s and onward demonstrated that descending motor pathways and afferent sensory pathways converge on common interneurons in the spinal cord. Later research in intact animals and in humans engaged in normal behavior confirmed that the neural circuitries in the spinal cord take part in conveying and shaping the motor command to the muscles by integrating descending motor commands and sensory feedback signals. Nevertheless, the idea of simple reflexes is convenient for understanding the principles of organization of sensory-motor integration in the spinal cord and of how sensory input to different spinal circuits contributes to movement control.

In this chapter, we explain the principles underlying sensory-motor integration in the spinal cord and describe how this integration regulates movement. For this purpose, we must first have a thorough knowledge of how reflex pathways in the spinal cord are organized.

Reflex Pathways in the Spinal Cord Produce Coordinated Patterns of Muscle Contraction

The sensory stimuli that activate spinal reflex pathways act outside the spinal cord, on receptors in muscles, joints, and skin. By contrast, the neural circuitry responsible for the motor response is entirely contained within the spinal cord. The interneurons in the reflex pathways and the resulting reflexes have traditionally been classified based on the sensory modality and type of sensory fiber that activates the interneurons. As we shall see, this classification is inconsistent with the significant convergence of multiple modalities on common interneurons, but as a starting point, it is still useful to distinguish reflex pathways based on whether the principal sensory input originates from muscle or skin.

The Stretch Reflex Acts to Resist the Lengthening of a Muscle

The simplest and certainly the most studied spinal reflex is the *stretch reflex*, a reflex muscle contraction elicited by lengthening of the muscle. Stretch reflexes

were originally thought to be an intrinsic property of muscles. Early in the 20th century, however, Liddell and Sherrington showed that the stretch reflex could be abolished by cutting either the dorsal or ventral root, thus establishing that these reflexes require sensory input from muscle to spinal cord and a return path to muscle (Figure 32–1A).

We now know that the receptor that senses the change of length is the muscle spindle (Box 32–1) and that the type Ia sensory axon from this receptor makes direct excitatory connections with motor neurons. (The classification of sensory fibers from muscle is discussed in Box 32–2.) The afferent axon also connects to interneurons that inhibit the motor neurons innervating antagonist muscles, an arrangement called reciprocal innervation. This inhibition prevents muscle contractions that might otherwise resist the movements produced by the stretch reflexes.

Sherrington developed an experimental model for investigating spinal circuitry that is especially valuable in the study of stretch reflexes. He conducted his experiments on cats whose brain stems had been surgically transected at the level of the midbrain, between the superior and inferior colliculi. This is referred to as a *decerebrate preparation.* The effect of this procedure is to disconnect the rest of the brain from the spinal cord, thus blocking sensations of pain as well as interrupting normal modulation of reflexes by higher brain centers. A decerebrate animal has stereotyped and usually heightened stretch reflexes, making it easier to examine the factors controlling their expression.

Without control by higher brain centers, descending pathways from the brain stem powerfully facilitate the neuronal circuits involved in the stretch reflexes of extensor muscles. This results in a dramatic increase in tone of the extensor muscle that sometimes can suffice to support the animal in a standing position. In normal animals and humans, owing to the balance between facilitation and inhibition, stretch reflexes are weaker and considerably more variable in strength than those in decerebrate animals.

Neuronal Networks in the Spinal Cord Contribute to the Coordination of Reflex Responses

The Stretch Reflex Involves a Monosynaptic Pathway

The neural circuit responsible for the stretch reflex was one of the first reflex pathways to be examined in detail. The physiological basis of this reflex was examined by measuring the latency of the response in
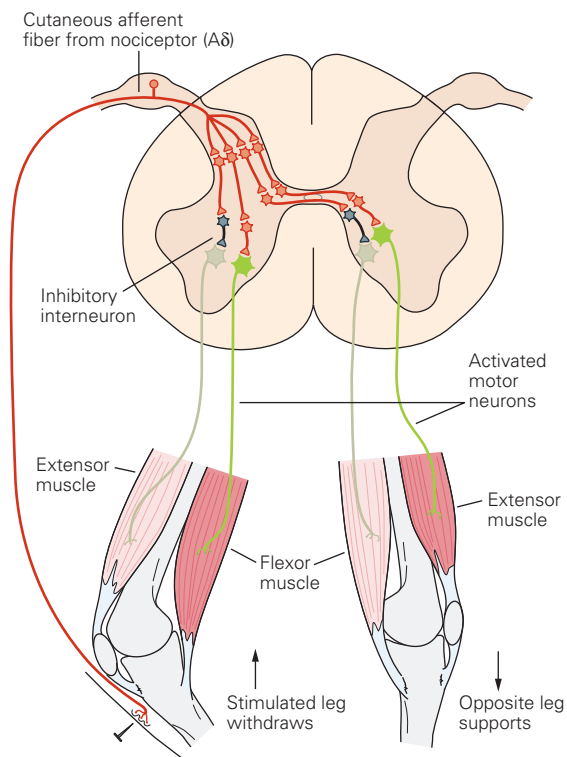
A Monosyaptic pathways (stretch reflex)

B Polysynaptic pathways (flexion reflex)
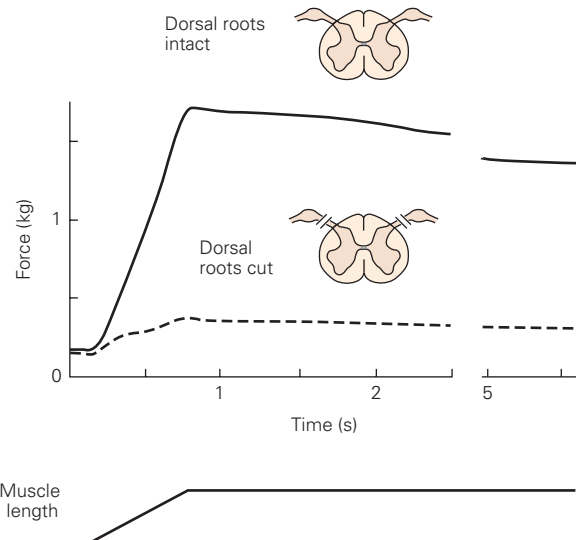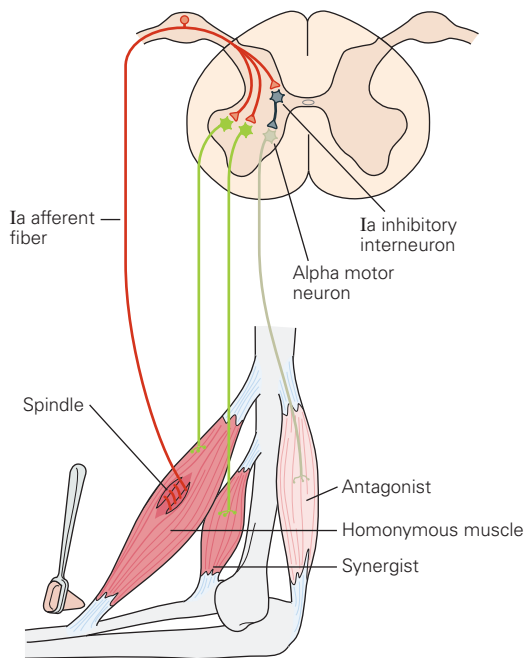
Figure 32–1 Spinal reflexes involve coordinated contractions of numerous muscles in the limbs.

A. In monosynaptic pathways, Ia sensory axons from muscle spindles make excitatory connections on two sets of motor neurons: alpha motor neurons that innervate the same (homonymous) muscle from which they arise and motor neurons that innervate synergist muscles. They also act through interneurons to inhibit the motor neurons that innervate antagonist muscles. When a muscle is stretched by a tendon tap with a reflex hammer, the firing rate in the sensory fiber from the spindle increases. This leads to contraction of the same muscle and its synergists and relaxation of the antagonist. The reflex therefore tends to counteract the stretch, enhancing the spring-like properties of the muscles.

The records on the right demonstrate the reflex nature of contractions produced by muscle stretch in a decerebrate cat. When an extensor muscle is stretched, it normally produces a large force, but it produces a very small force (**dashed line**) after the sensory afferents in the dorsal roots have been severed. (Adapted, with permission, from Liddell and Sherrington 1924.)

B. In polysynaptic pathways, one excitatory pathway activates motor neurons that innervate ipsilateral flexor muscles, which withdraw the limb from noxious stimuli, while another pathway simultaneously excites motor neurons that innervate contralateral extensor muscles, providing support during withdrawal of the limb. Inhibitory interneurons ensure that the motor neurons supplying antagonist muscles are inactive during the reflex response. (Adapted, with permission, from Schmidt 1983.)

Box 32–1 Muscle Spindles

Muscle spindles are small encapsulated sensory receptors that have a spindle-like or fusiform shape and are located within the fleshy part of a muscle. Their main function is to signal changes in the length of the muscle within which they reside. Changes in length of muscles are closely associated with changes in the angles of the joints that the muscles cross. Thus, muscle spindles are used by the central nervous system to sense relative positions of the body segments.

Each spindle has three main components: (1) a group of specialized *intrafusal* muscle fibers with non-contractile central regions; (2) sensory fibers that terminate on the central regions of the intrafusal fibers; and (3) motor axons that terminate on the contractile polar regions of the intrafusal fibers (Figure 32–2A,B).

When the intrafusal fibers are stretched, often referred to as "loading the spindle," the sensory axon endings are also stretched and increase their firing rate. Because muscle spindles are arranged in parallel with the *extrafusal* muscle fibers that make up the main body of the muscle, the intrafusal fibers change in length as the whole muscle changes. Thus, when a muscle is stretched, activity in the sensory axons of muscle spindles increases. When a muscle shortens, the spindle is unloaded and the activity decreases.

The intrafusal muscle fibers are innervated by *gamma* motor neurons, which have small-diameter myelinated axons, whereas the extrafusal muscle fibers are innervated by *alpha* motor neurons, with large-diameter myelinated axons. Activation of gamma motor neurons causes shortening of the polar regions of the intrafusal fibers. This in turn stretches the central region from both ends, leading to an increase in firing rate of the sensory axons or to a greater likelihood that the axons will fire in response to stretch of the muscle. Thus, the gamma motor neurons adjust the sensitivity of the muscle spindles. Contraction of the intrafusal muscle fibers does not contribute significantly to the force of muscle contraction.

The structure and functional behavior of muscle spindles is considerably more complex than this simple description depicts. As a muscle is stretched, the change in length has two phases: a dynamic phase, the period during which length is changing, and a static or steady-state phase, when the muscle has stabilized at a new length. Structural specializations within each component of the muscle spindle enable the sensory axons to signal aspects of each phase separately.

The intrafusal muscle fibers include nuclear bag fibers and nuclear chain fibers. The bag fibers can be classified as dynamic or static. A typical spindle has two or three bag fibers and a variable number of chain fibers, usually about five. Furthermore, the intrafusal fibers receive two types of sensory endings. A single Ia (large diameter) axon spirals around the central region of all intrafusal muscle fibers and serves as the *primary sensory ending* (Figure 32–2B). A variable number of type II (medium diameter) axons spiral around the static bag and chain fibers near their central regions and serve as *secondary sensory endings*.

The gamma motor neurons can also be divided into two classes: Dynamic gamma motor neurons innervate the dynamic bag fibers, whereas the static gamma motor neurons innervate the static bag fibers and the chain fibers.

This duality of structure is reflected in a duality of function. The tonic discharge of both primary and secondary sensory endings signals the steady-state length of the muscle. The primary sensory endings are, in addition, highly sensitive to the velocity of stretch, allowing them to provide information about the speed of movements. Because they are highly sensitive to small changes, the primary endings rapidly provide information about sudden unexpected changes in length, which can be used to generate quick corrective reactions.

Increases in the firing rate of dynamic gamma motor neurons increase the dynamic sensitivity of primary sensory endings but have no influence on secondary sensory endings. Increases in the firing rate of static gamma motor neurons increase the tonic level of activity in both primary and secondary sensory endings, decrease the dynamic sensitivity of primary endings (Figure 32–2C), and can prevent the silencing of primary endings when a muscle is released from stretch. Thus, the central nervous system can independently adjust the dynamic and static sensitivity of the different sensory endings in muscle spindles.

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ventral roots to electrical stimulation of dorsal roots. When the Ia sensory axons innervating the muscle spindles were selectively activated, the reflex latency through the spinal cord was less than 1 ms. This demonstrated that the Ia fibers make direct connections on the alpha motor neurons because the delay at a single synapse is typically 0.5 ms to 0.9 ms (Figure 32–3B). In humans, an analog of the monosynaptic stretch reflex, the Hoffmann reflex, may be elicited by electrical stimulation of peripheral nerves (Box 32–3).