

### 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*.

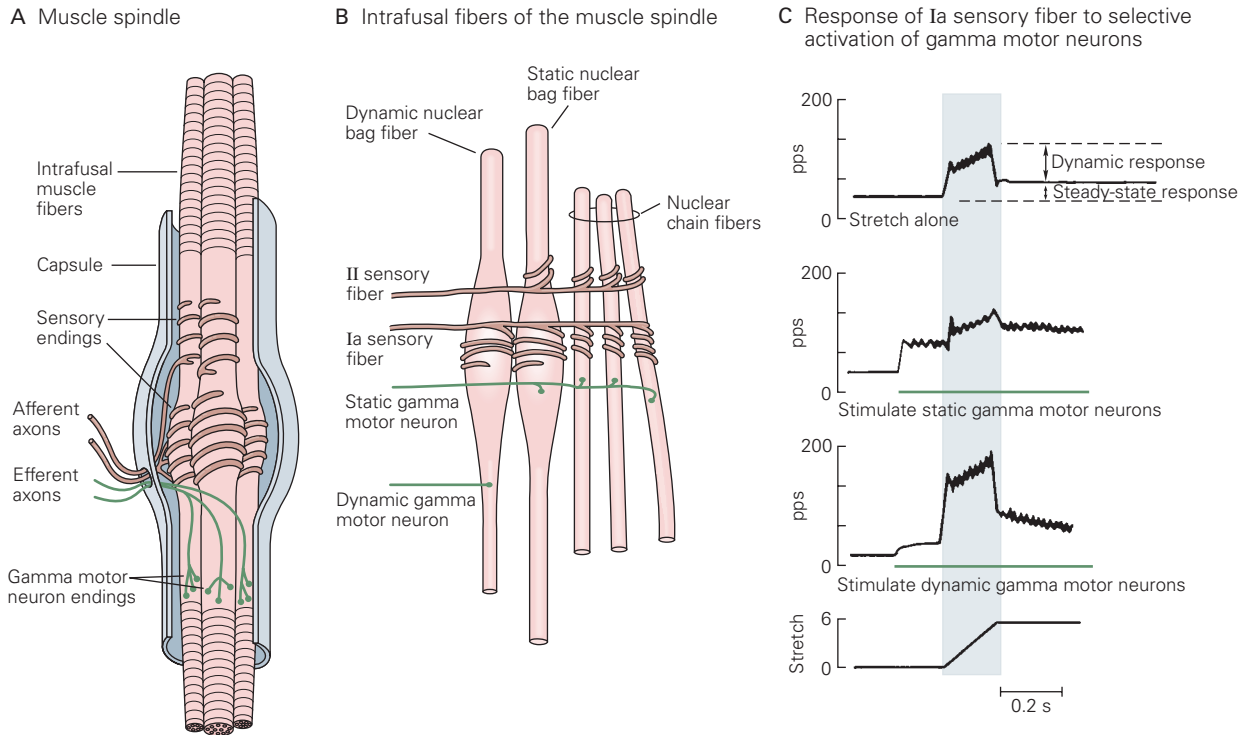
The gamma motor neurons can also be divided into two classes: Dynamic gamma motor neurons innervate the dynamic bag fibers, whereas the static gamma motor neurons innervate the static bag fibers and the chain fibers.

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.

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).



**Figure 32-2** The muscle spindle detects changes in muscle length.

**A.** The main components of the muscle spindle are intrafusal muscle fibers, sensory axon endings, and motor axon endings. The intrafusal fibers are specialized muscle fibers with central regions that are not contractile. Gamma motor neurons innervate the contractile polar regions of the intrafusal fibers. Contraction of the polar regions pulls on the central regions of the intrafusal fiber from both ends. The sensory endings spiral around the central regions of the intrafusal fibers and are responsive to stretch of these fibers. (Adapted, with permission, from Hulliger 1984. Copyright © Springer-Verlag 1984.)

**B.** The muscle spindle contains three types of intrafusal fibers: dynamic nuclear bag, static nuclear bag, and nuclear chain fibers. A single Ia sensory axon innervates all three types of fibers, forming a primary sensory ending. Type II sensory axons innervate the nuclear chain fibers

and static bag fibers, forming a secondary sensory ending. Two types of motor neurons innervate different intrafusal fibers. Dynamic gamma motor neurons innervate only dynamic bag fibers; static gamma motor neurons innervate various combinations of chain and static bag fibers. (Adapted, with permission, from Boyd 1980. Copyright © 1980. Published by Elsevier Ltd.)

**C.** Selective stimulation of the two types of gamma motor neurons has different effects on the firing of the Ia sensory fibers from the spindle. Without gamma stimulation, the Ia fiber shows a small dynamic response to muscle stretch and a modest increase in steady-state firing. When a static gamma motor neuron is stimulated, the steady-state response of the Ia fiber increases but the dynamic response decreases. When a dynamic gamma motor neuron is stimulated, the dynamic response of the Ia fiber is markedly enhanced, but the steady-state response gradually returns to its original level. (Adapted, with permission, from Brown and Matthews 1966.)

The pattern of connections of Ia fibers to motor neurons can be shown directly by intracellular recording. Ia fibers from a given muscle excite not only the motor neurons innervating that same (*homonymous*) muscle but also the motor neurons innervating other

(*heteronymous*) muscles with a similar mechanical action.

Lorne Mendell and Elwood Henneman used a computer enhancement technique called *spike-triggered averaging* to determine the extent to which the action

### Box 32–2 Classification of Sensory Fibers From Muscle

Sensory fibers are classified according to their diameter. Axons with larger diameters conduct action potentials more rapidly than those with smaller diameters (Chapters 9 and 18). Because each class of sensory receptors is innervated by fibers with diameters within a restricted range, this method of classification distinguishes to some extent the fibers that arise from different types of receptor organs. The main groups of sensory fibers from muscle are listed in Table 32–1.

The organization of reflex pathways in the spinal cord has been established primarily by electrically stimulating the sensory fibers and recording evoked responses in different classes of neurons in the spinal cord. This method of activation has three advantages over natural stimulation. The timing of afferent input

can be precisely established; the responses evoked in motor neurons and other neurons by different classes of sensory fibers can be assessed by grading the strength of the electrical stimulus; and certain classes of receptors can be selectively activated.

The strength of the electrical stimulus required to activate a sensory fiber is measured relative to the strength required to activate the fibers with the largest diameter because these fibers have the lowest threshold for electrical activation. The thresholds of most type I fibers usually range from one to two times that of the largest fibers (with Ia fibers having, on average, a slightly lower threshold than Ib fibers). For most type II fibers, the threshold is 2 to 5 times higher, whereas types III and IV have thresholds in the range of 10 to 50 times that of the largest sensory fibers.

**Table 32–1** Classification of Sensory Fibers From Muscle

Type	Axon	Receptor	Sensitivity to
Ia	12–20 $\mu\text{m}$ myelinated	Primary spindle ending	Muscle length and rate of change of length
Ib	12–20 $\mu\text{m}$ myelinated	Golgi tendon organ	Muscle tension
II	6–12 $\mu\text{m}$ myelinated	Secondary spindle ending	Muscle length (little rate sensitivity)
II	6–12 $\mu\text{m}$ myelinated	Nonspindle endings	Deep pressure
III	2–6 $\mu\text{m}$ myelinated	Free nerve endings	Pain, chemical stimuli, and temperature (important for physiological responses to exercise)
IV	0.5–2 $\mu\text{m}$ nonmyelinated	Free nerve endings	Pain, chemical stimuli, and temperature

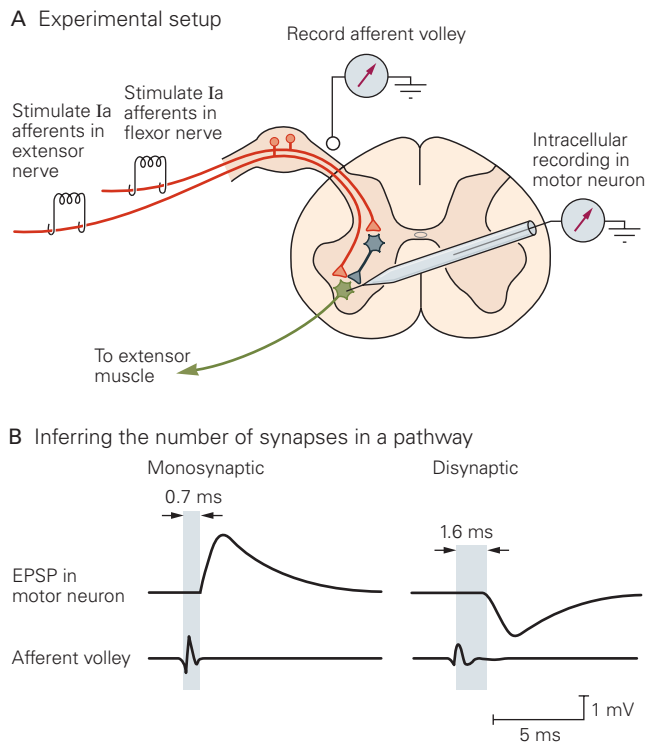
potentials in single Ia fibers are transmitted to a population of spinal motor neurons. They found that individual Ia axons make excitatory synapses with all homonymous motor neurons innervating the medial gastrocnemius of the cat. This widespread divergence effectively amplifies the signals of individual Ia fibers, leading to a strong excitatory drive to the muscle from which they originate (*autogenic excitation*).

The Ia axons in reflex pathways also provide excitatory inputs to many of the motor neurons innervating synergist muscles (up to 60% of the motor neurons of some synergists) (Figure 32–1A). Although widespread, these connections are not as strong as the connections to homonymous motor neurons.

The Ia fibers also send inhibitory signals via the *Ia inhibitory interneurons* to the alpha motor neurons innervating antagonistic muscles. This disynaptic inhibitory pathway is the basis for reciprocal innervation: When a muscle is stretched, its antagonists relax.

### Gamma Motor Neurons Adjust the Sensitivity of Muscle Spindles

Activity of muscle spindles may be modulated by changing the level of activity in the gamma motor neurons, which innervate the intrafusal muscle fibers of muscle spindles (Box 32–1). This function of gamma motor neurons, often referred to as the fusimotor



**Figure 32-3** The number of synapses in a reflex pathway can be inferred from intracellular recordings.

**A.** An intracellular recording electrode is inserted into the cell body of a spinal motor neuron that innervates an extensor muscle. Stimulation of Ia sensory fibers from flexor or extensor muscles produces a volley of action potentials at the dorsal root.

**B. Left:** When Ia fibers from an extensor muscle are stimulated, the latency between the recording of the afferent volley and the excitatory postsynaptic potential (EPSP) in the motor neuron is only 0.7 ms, approximately equal to the duration of signal transmission across a single synapse. Thus, it can be inferred that the excitatory action of the stretch reflex pathway is monosynaptic. **Right:** When Ia fibers from an antagonist flexor muscle are stimulated, the latency between the recording of the afferent volley and the inhibitory postsynaptic potential in the motor neuron is 1.6 ms, approximately twice the duration of signal transmission across a single synapse. Thus, it can be inferred that the inhibitory action of the stretch reflex pathway is disynaptic.

system, can be demonstrated by selectively stimulating the alpha and gamma motor neurons under experimental conditions.

When only alpha motor neurons are stimulated, the firing of the Ia fiber from the muscle spindle pauses during contraction of the muscle because the muscle is shortening and therefore unloading (slackening) the spindle. However, if gamma motor neurons are activated at the same time as alpha motor neurons, the pause is eliminated. The contraction of the intrafusal fibers by the gamma motor neurons keeps the spindle

under tension, thus maintaining the firing rate of the Ia fibers within an optimal range for signaling changes in length, whatever the actual length of the muscle (Figure 32-5). This *alpha-gamma co-activation* is recruited for many voluntary movements because it stabilizes the sensitivity of the muscle spindles.

In addition to the axons of gamma motor neurons, collaterals of alpha motor neuron axons sometimes innervate the intrafusal fibers. Axons that innervate both intrafusal and extrafusal muscle fibers are referred to as *beta* axons. Beta axon collaterals provide the equivalent of alpha-gamma coactivation. Beta innervation in spindles exists in both cats and humans, although it is unquantified for most muscles.

The forced linkage of extrafusal and intrafusal contraction by the beta fusimotor system highlights the importance of the independent fusimotor system (the gamma motor neurons). Indeed, in lower vertebrates, such as amphibians, beta efferents are the only source of intrafusal innervation. Mammals have evolved a mechanism that frees muscle spindles from complete dependence on the behavior of their parent muscles. In principle, this uncoupling allows greater flexibility in controlling spindle sensitivity for different types of motor tasks.

This conclusion is supported by recordings in spindle sensory axons during a variety of natural movements in cats. The amount and type of activity in gamma motor neurons are set at steady levels, which vary according to the specific task or context. In general, activity levels in both static and dynamic gamma motor neurons (Figure 32-2B) are set at progressively higher levels as the speed and difficulty of the movement increase. Unpredictable conditions, such as when the cat is picked up or handled, lead to marked increases in activity in dynamic gamma motor neurons and thus increased spindle responsiveness when muscles are stretched. When an animal is performing a difficult task, such as walking across a narrow beam, both static and dynamic gamma activation are at high levels (Figure 32-6).

Thus, the nervous system uses the fusimotor system to fine-tune muscle spindles so that the ensemble output of the spindles provides information most appropriate for a task. The task conditions under which independent control of alpha and gamma motor neurons occurs in humans have not yet been clearly established.

### The Stretch Reflex Also Involves Polysynaptic Pathways

The monosynaptic Ia pathway is not the only spinal reflex pathway activated when a muscle is stretched. Type II sensory fibers from muscle spindles are also activated. These discharge tonically depending on

### Box 32-3 The Hoffmann Reflex

The characteristics of the monosynaptic connections from Ia sensory fibers to spinal motor neurons in humans can be studied using an important technique introduced in the 1950s and based on early work by Paul Hoffmann. This technique involves electrically stimulating the Ia sensory fibers in a peripheral nerve and recording the reflex electromyogram (EMG) response in the homonymous muscle. The response is known as the *Hoffmann reflex*, or H-reflex.

The H-reflex is readily measured in the soleus muscle, an ankle extensor. The Ia fibers from the soleus and its synergists are excited by an electrode placed above the tibial nerve behind the knee (Figure 32-4A). The response recorded from the soleus muscle depends on stimulus strength. At low stimulus strengths, a pure H-reflex is evoked, for the threshold for activation of the Ia fibers is lower than the threshold for motor axons. Increasing the stimulus strength excites the motor axons innervating the soleus, producing two successive responses.

The first results from direct activation of the motor axons, and the second is the H-reflex evoked by stimulation of the Ia fibers (Figure 32-4B). These two components of the evoked EMG are called the M-wave and H-wave. The H-wave occurs later because it results from signals that travel to the spinal cord, across a synapse, and back again to the muscle. The M-wave, in contrast, results from direct stimulation of the motor axon innervating the muscle.

As the stimulus strength is increased still further, the M-wave continues to become larger and the H-wave progressively declines (Figure 32-4C). The decline in the H-wave amplitude occurs because action potentials in the motor axons propagate toward the cell body (antidromic conduction) and cancel reflexively evoked action potentials in the same motor axons. At very high stimulus strengths, only the M-wave persists.

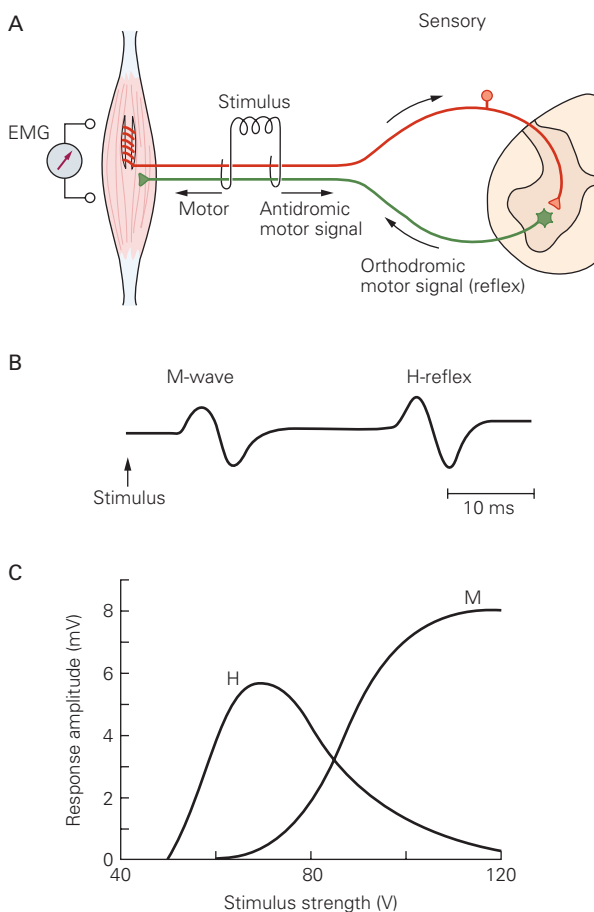
**Figure 32-4** The Hoffmann reflex.

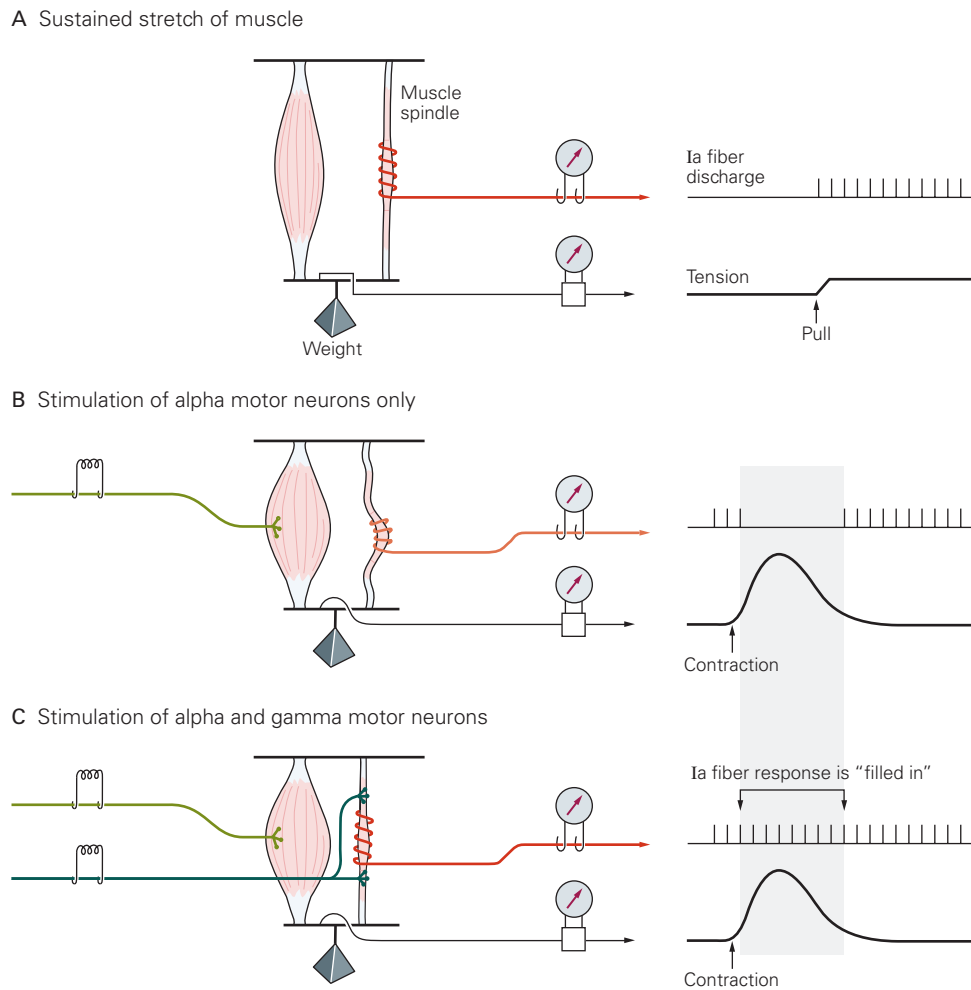
**A.** The Hoffmann reflex (H-reflex) is evoked by electrically stimulating Ia sensory fibers from muscle spindles. The sensory fibers excite alpha motor neurons, which in turn activate the muscle. When a mixed nerve is used, the motor neurons axons may also be activated directly.

**B.** At intermediate stimulus strengths, an M-wave precedes the H-wave (H-reflex) in the electromyogram (EMG).

**C.** As the stimulus strength increases, the orthodromic motor neuron spikes generated reflexively by the spindle sensory fibers are obliterated by antidromic spikes initiated by the electrical stimulus in the same motor axons.

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**Figure 32-5** Activation of gamma motor neurons during active muscle contraction maintains muscle spindle sensitivity to muscle length. (Adapted, with permission, from Hunt and Kuffler 1951.)

**A.** Sustained tension elicits steady firing in the Ia sensory fiber from the muscle spindle (the two muscle fibers are shown separately for illustration only).

**B.** A characteristic pause occurs in the discharge of the Ia fiber when the alpha motor neuron is stimulated, causing a brief

contraction of the muscle. The Ia fiber stops firing because the spindle is unloaded by the contraction.

**C.** Gamma motor neurons innervate the contractile polar regions of the intrafusal fibers of muscle spindles (see Figure 32-2A). If a gamma motor neuron is stimulated at the same time as the alpha motor neuron, the spindle is not unloaded during the contraction. As a result, the pause in discharge of the Ia sensory fiber that occurs when only the alpha motor neuron is stimulated is "filled in" by the response of the fiber to stimulation of the gamma motor neuron.

muscle length and gamma motor neuron activity (Box 32-1) and connect to different populations of excitatory and inhibitory interneurons in the spinal cord.

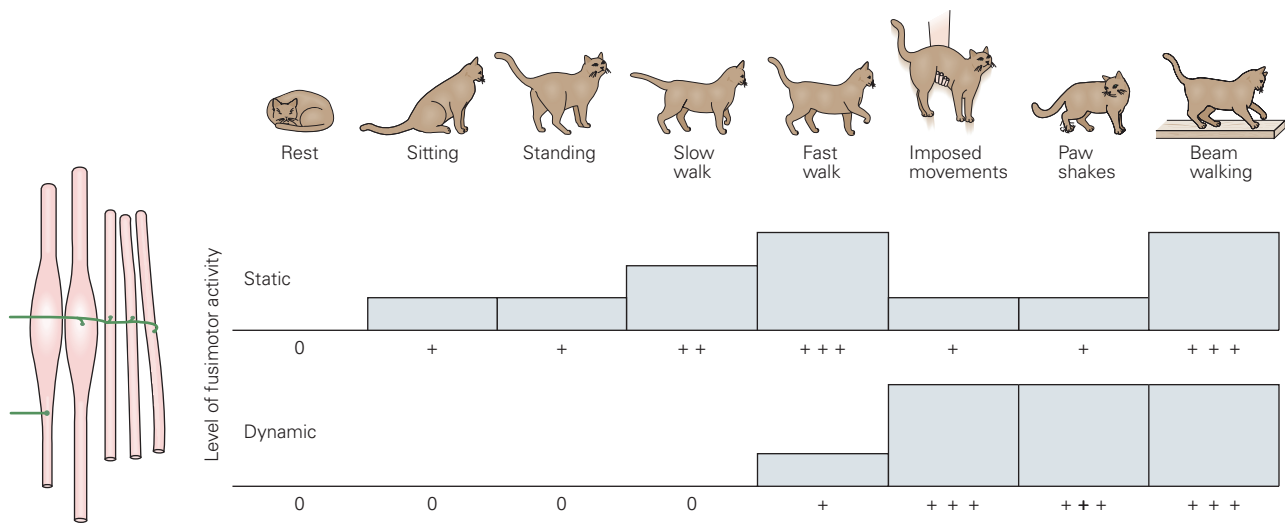
Some of the interneurons project directly to the spinal motor neurons, whereas others have more indirect connections. Because of the slower conduction velocity of type II sensory fibers and the signal relay through interneurons, the muscular responses elicited by group II fibers are smaller, more variable, and delayed compared to the monosynaptic stretch reflex. Some of the interneurons activated by group II fibers send

axons across the midline of the spinal cord and give rise to crossed reflexes. Such connections that cross the midline are important for coordination of bilateral muscle activity in functional motor tasks.

### Golgi Tendon Organs Provide Force-Sensitive Feedback to the Spinal Cord

Stimulation of Golgi tendon organs or their Ib sensory fibers in passive animals produces disynaptic inhibition of homonymous motor neurons (*autogenic*





**Figure 32-6** The level of activity in the fusimotor system varies with the type of behavior. Only static gamma motor neurons are active during activities in which muscle length changes slowly and predictably. Dynamic gamma motor

neurons are activated during behaviors in which muscle length may change rapidly and unpredictably. (Adapted, with permission, from Prochazka et al. 1988.)

inhibition) and excitation of antagonist motor neurons (reciprocal excitation). Thus, these effects are the exact opposite of the responses evoked by muscle stretch or stimulation of Ia sensory axons.

This autogenic inhibition is mediated by *Ib inhibitory interneurons*. These inhibiting interneurons receive their principal input from Golgi tendon organs, sensory receptors that signal the tension in a muscle (Box 32-4), and they make inhibitory connections with homonymous motor neurons. However, stimulation of the Ib sensory fibers from tendon organs in active animals does not always inhibit homonymous motor neurons. Indeed, as we shall see later, stimulation of tendon organs may in certain conditions excite homonymous motor neurons.

One reason that the reflex actions of the sensory axons from tendon organs are complex in natural situations is that the Ib inhibitory interneurons also receive input from the muscle spindles, cutaneous receptors, and joint receptors (Figure 32-8A). In addition, they receive both excitatory and inhibitory input from various descending pathways.

Golgi tendon organs were first thought to have a protective function, preventing damage to muscle. It was assumed that they always inhibited homonymous motor neurons and that they fired only when tension in the muscle was high. We now know that these receptors signal minute changes in muscle tension, thus providing the nervous system with precise information about the state of a muscle's contraction.

The convergent sensory input from tendon organs, cutaneous receptors, and joint receptors to the Ib inhibitory interneurons (Figure 32-8A) may allow for precise spinal control of muscle force in activities such as grasping a delicate object. Additional input from cutaneous receptors may facilitate activity in the Ib inhibitory interneurons when the hand reaches an object, thus reducing the level of muscle contraction and permitting a soft grasp.

As is the case with the Ia fibers from muscle spindles, the Ib fibers from tendon organs form widespread connections with motor neurons that innervate muscles acting at different joints. Therefore, the connections of the sensory fibers from tendon organs with the Ib inhibitory interneurons are part of spinal networks that regulate movements of whole limbs.

### Cutaneous Reflexes Produce Complex Movements That Serve Protective and Postural Functions

Most reflex pathways involve interneurons. One such reflex pathway is that of the flexion-withdrawal reflex, in which a limb is quickly withdrawn from a painful stimulus. Flexion-withdrawal is a protective reflex in which a discrete stimulus causes all the flexor muscles in that limb to contract coordinately. We know that this is a spinal reflex because it persists after complete transection of the spinal cord.

The sensory signal of the flexion-withdrawal reflex activates divergent polysynaptic reflex pathways. One

### Box 32-4 Golgi Tendon Organs

Golgi tendon organs are slender encapsulated structures approximately 1 mm long and 0.1 mm in diameter located at the junction between skeletal muscle fibers and tendon. Each capsule encloses several braided collagen fibers connected in series to a group of muscle fibers.

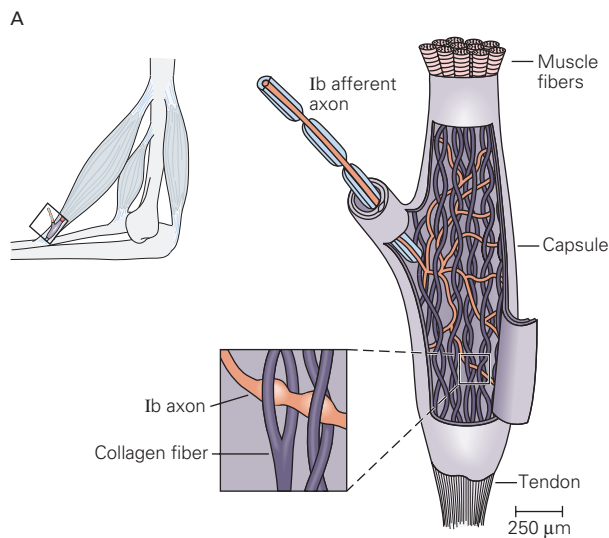
Each tendon organ is innervated by a single Ib axon that branches into many fine endings inside the capsule; these endings become intertwined with the collagen fascicles (Figure 32-7A).

Stretching of the tendon organ straightens the collagen fibers, thus compressing the Ib nerve endings and causing them to fire. Because the nerve endings are so

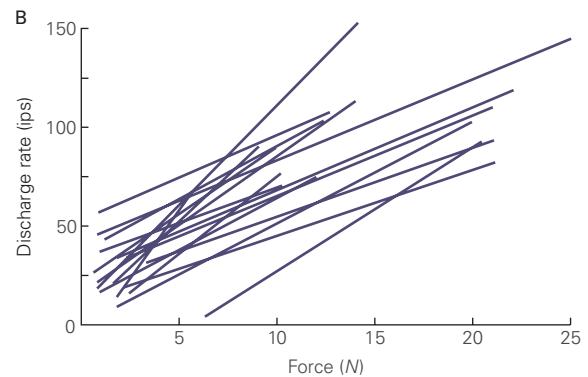
closely associated with the collagen fibers, even very small stretches of the tendons can compress the nerve endings.

Whereas muscle spindles are most sensitive to changes in length of a muscle, tendon organs are most sensitive to changes in muscle tension. Contraction of the muscle fibers connected to the collagen fiber bundle containing the receptor is a particularly potent stimulus to a tendon organ. The tendon organs are thus readily activated during normal movements. This has been demonstrated by recordings from single Ib axons in humans making voluntary finger movements and in cats walking normally.

Studies in anesthetized animal preparations have shown that the average level of activity in the population of tendon organs in a muscle is a good index of the total force in a contracting muscle (Figure 32-7B). This close agreement between firing frequency, and force is consistent with the view that the tendon organs continuously measure the force in a contracting muscle.



**Figure 32-7A** When the Golgi tendon organ is stretched (usually because of contraction of the muscle), the Ib afferent axon is compressed by collagen fibers (see enlargement) and its rate of firing increases. (Adapted, with permission, from Schmidt 1983; inset adapted, with permission, from Swett and Schoultz 1975.)



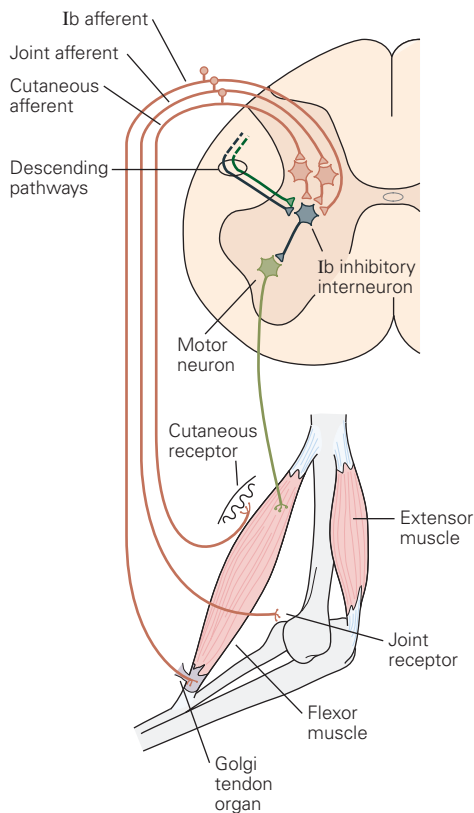
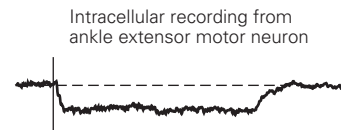
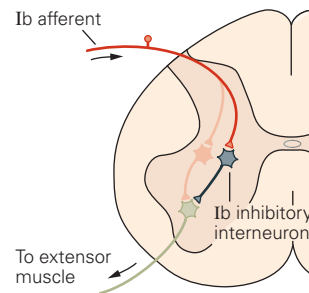
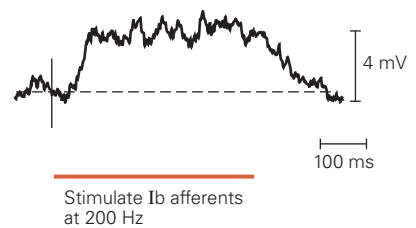
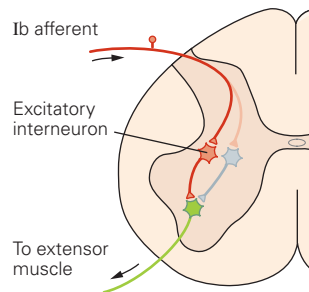
**Figure 32-7B** The discharge rate of a population of Golgi tendon organs signals the force in a muscle. Linear regression lines show the relationship between discharge rate and force for Golgi tendon organs of the soleus muscle of the cat. (Adapted, with permission, from Crago, Houk, and Rymer 1982.)

excites motor neurons that innervate flexor muscles of the stimulated limb, whereas another inhibits motor neurons that innervate the limb's extensor muscles (Figure 32-1B). This reflex can produce an opposite effect in the contralateral limb, that is, excitation of extensor motor neurons and inhibition of flexor motor neurons. This *crossed-extension reflex* serves to enhance postural support during withdrawal of a foot from a

painful stimulus. Activation of the extensor muscles in the opposite leg counteracts the increased load caused by lifting the stimulated limb. Thus, flexion-withdrawal is a complete, albeit simple, motor act.

Although flexion reflexes are relatively stereotyped, both the spatial extent and the force of muscle contraction depend on stimulus intensity. Touching a stove that is slightly hot may produce moderately



**A Convergence onto Ib interneurons****B Reversal of action of Ib afferents****Resting****Locomotion**

**Figure 32–8** The reflex actions of Ib sensory fibers from Golgi tendon organs are modulated during locomotion.

**A.** The Ib inhibitory interneuron receives input from tendon organs, muscle spindles (not shown), joint and cutaneous receptors, and descending pathways.

**B.** The action of Ib sensory fibers on extensor motor neurons is reversed from inhibition to excitation when walking is initiated. When the animal is resting, stimulation of Ib fibers

from the ankle extensor muscle inhibits ankle extensor motor neurons through Ib inhibitory interneurons, as shown by the hyperpolarization in the record. During walking, the Ib inhibitory interneurons are inhibited while excitatory interneurons that receive input from Ib sensory fibers are facilitated by the command system for walking, thus opening a Ib excitatory pathway from the Golgi tendon organs to motor neurons.

fast withdrawal only at the wrist and elbow, whereas touching a very hot stove invariably leads to a forceful contraction at all joints, leading to rapid withdrawal of the entire limb. The duration of the reflex usually increases with stimulus intensity, and the contractions produced in a flexion reflex always outlast the stimulus.

Because of the similarity of the flexion-withdrawal reflex to stepping, it was once thought that the flexion reflex is important in producing contractions of flexor muscles during walking. We now know, however, that a major component of the neural control system for walking is a set of intrinsic spinal circuits that do not require sensory stimuli (Chapter 33). Nevertheless, in mammals, the intrinsic spinal circuits that control

walking share many of the interneurons involved in flexion reflexes.

### Convergence of Sensory Inputs on Interneurons Increases the Flexibility of Reflex Contributions to Movement

The Ib inhibitory interneuron is not the only interneuron that receives convergent input from many different sensory modalities. An enormous diversity of sensory information converges on interneurons in the spinal cord, enabling them to integrate information from muscle, joints, and skin.

Interneurons activated by groups I and II sensory fibers have received special attention. It was thought