

# 4.4 Spinal Reflexes

## Learning Objectives

- Define “reflex”
- List four spinal reflexes
- Describe the withdrawal reflex and draw a “wiring diagram” that explains it
- Explain why two different interneurons are required for the withdrawal reflex
- Describe the crossed-extensor reflex
- Draw a “wiring diagram” to explain the crossed-extensor reflex
- Describe the myotatic reflex
- Distinguish between extrafusal and intrafusal muscle fibers
- Distinguish between primary and secondary afferent information arising from the muscle spindle
- Draw a “wiring” diagram to explain the myotatic reflex
- Explain how the gamma efferent system maintains muscle spindle sensitivity during contraction
- Describe the function of the Golgi tendon organs and the inverse myotatic reflex
- Describe what is meant by the “final common pathway” in motor control
- List the major tracts of axons from higher centers that modulate spinal reflexes and control lower motor neurons

## A REFLEX IS A STEREOTYPED MUSCULAR RESPONSE TO A SPECIFIC SENSORY STIMULUS

The word “reflex” derives from “reflection” meaning a mirror image of an event or stimulus. Thus the spinal reflexes are processes that cause sensory stimuli to be “reflected” onto the musculature without the involvement of conscious deliberation. The “stereotype” means that the reflexes always occur in the same manner and no training is required. These reflexes result from hardwired connections that are the same in all humans and in most mammals. We will discuss four basic reflexes:

1. The withdrawal reflex
2. The crossed-extensor reflex
3. The myotatic reflex
4. The inverse myotatic reflex.

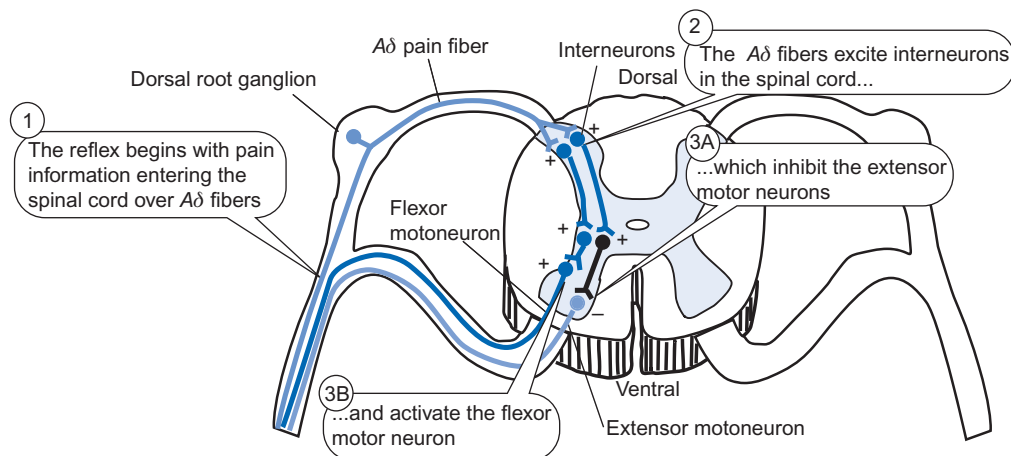
## THE WITHDRAWAL REFLEX PROTECTS US FROM PAINFUL STIMULI

A painful stimulus in a limb extremity causes us to reflexly withdraw the limb from the stimulus, protecting it from further harm. Withdrawal is accomplished by activation of the **flexor muscles** and inactivation of the **extensor muscles**, and the coordination of these is accomplished by the spinal cord.

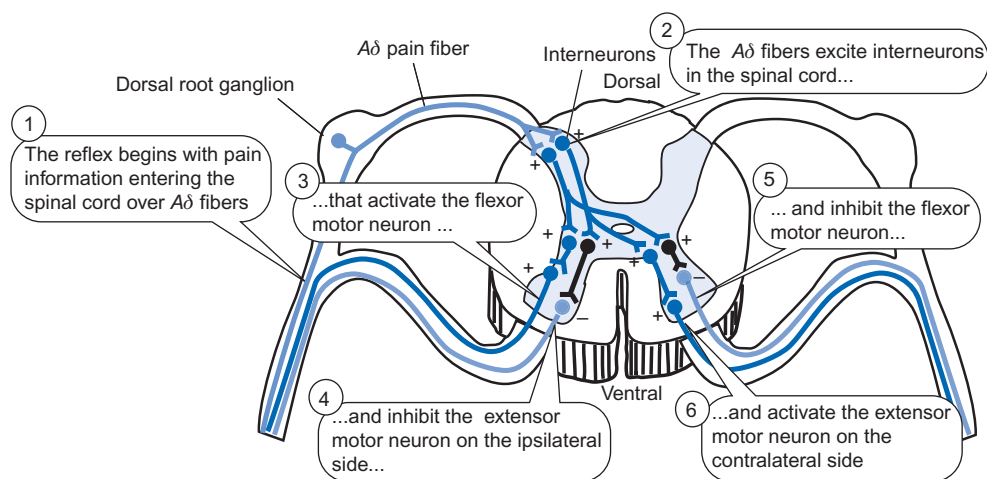
Sensory neurons entering the spinal cord synapse on interneurons in the dorsal horn of the spinal cord, which subsequently make polysynaptic connections to the large  $\alpha$  motor neurons that reside in the ventral horn of the cord and control the flexor muscles. At the same time, interneurons also synapse on inhibitory interneurons that innervate the motor neurons for the extensor muscles. In this way, painful sensory input activates the flexor muscle and relaxes the extensors. The wiring diagram for this reflex is shown in [Figure 4.4.1](#). A minimum of two interneurons are required to transform the excitatory input of the interneuron into an inhibitory one. The  $\alpha$  motor neurons all have the same set of receptors for neurotransmitters. Since the interneuron produces only one set of neurotransmitters, it cannot simultaneously excite the flexor’s motor neuron and inhibit the extensor’s. Instead, it must activate another interneuron that uses a different neurotransmitter to inhibit the extensor motor neuron.

## THE CROSSED-EXTENSOR REFLEX USUALLY OCCURS IN ASSOCIATION WITH THE WITHDRAWAL REFLEX

If we step on a sharp piece of glass, withdrawal of the affected leg requires the cooperation of the opposite leg to maintain balance. If the affected limb is an arm, the arm on the contralateral side to the pain will extend rather than flex, in an effort to move the body away from the source of the pain. The flexion of the limb on the side of the pain is the withdrawal reflex. **The reflex extension of the limb on the opposite side is called the crossed-extensor reflex.** The mechanism is similar to that of the withdrawal reflex: interneurons form excitatory and inhibitory connections to the appropriate motor neurons. A circuit diagram for the crossed-extensor reflex is shown in [Figure 4.4.2](#). The net effect of any pathway can be determined by multiplying the signs of



**FIGURE 4.4.1** Wiring diagram for the withdrawal reflex. Fast pain fibers make connections with an interneuron in the spinal cord. There is always at least one and there may be more interneurons between the primary afferent fiber and the motor neurons. Excitation of the interneuron passes on to the flexor motor neurons, while other interneurons inhibit the extensor muscles.



**FIGURE 4.4.2** The crossed-extensor reflex. A strong nociceptive stimulus elicits the withdrawal reflex on the ipsilateral side. At the same time, fibers cross over the cord to synapse onto excitatory interneurons that activate the extensor motor neuron and inhibitory interneurons for the flexor muscles. Thus, activation of the sensory afferents causes a withdrawal on the ipsilateral side and an extension on the contralateral side.

activation (+) or inhibition (-). Thus, pain activates the ipsilateral (meaning the same side) flexion (+ × + × + = +) and inhibits extensors (+ × + × - = -); it inhibits contralateral (the opposite side) flexion (+ × + × - = -) and activates contralateral extension (+ × + × + = +).

## THE MYOTATIC REFLEX INVOLVES A MUSCLE LENGTH SENSOR, THE MUSCLE SPINDLE

The **myotatic reflex** is the **muscle stretch reflex**. A classical example of this is the knee-jerk reflex. Striking the patellar ligament (connecting the patella to the tibial tuberosity) on a flexed, but relaxed knee joint with a rubber mallet causes the quadriceps to stretch. The stretch is sensed and the information carried to the cord, resulting in activation of the muscle, causing

the knee to extend. The process begins with the sensor for muscle length, the muscle spindle.

## THE MUSCLE SPINDLE IS A SPECIALIZED MUSCLE FIBER

The regular muscle fibers are called **extrafusal** fibers, and the activation and contraction of these fibers are discussed in Chapters 3.4–3.7. Interspersed among these fibers are small encapsulated sensory receptors that have a fusiform or spindle shape. The entire apparatus is called the **muscle spindle**, and its job is to inform the central nervous system (CNS) of the contractile state of the muscle by sending afferent impulses to the spinal cord when the muscle spindle is stretched. The muscle spindle consists of a group of fine muscle fibers, called **intrafusal muscle fibers**, 4–10 mm long, whose central portions are not contractile.

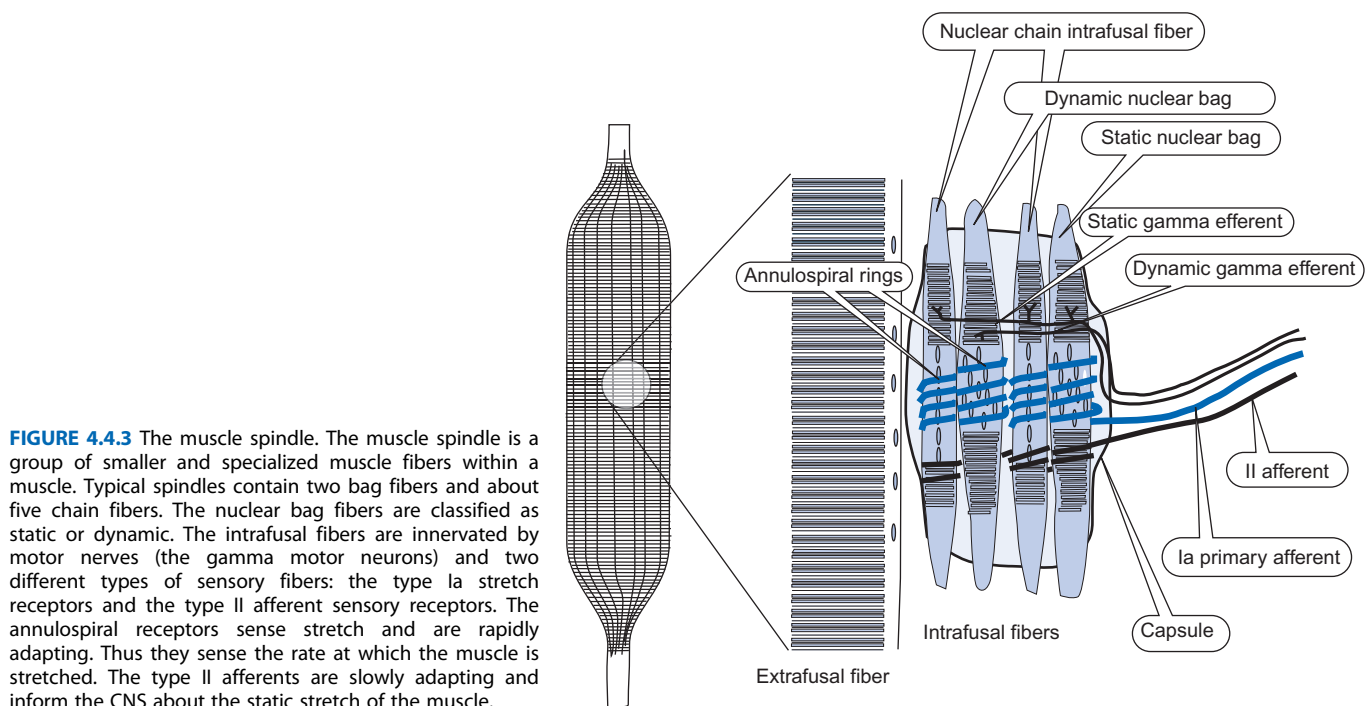
Typically the connective tissue **capsule** encloses two different types of intrafusal fibers. The **nuclear chain** intrafusal fibers have a set of aligned nuclei in the center. The **nuclear bag** fibers have a clump of nuclei randomly arrayed in a bag-like structure in the center of the intrafusal fiber. Typically a spindle has two to three nuclear bag fibers and about five nuclear chain fibers. There are also two distinct types of afferent sensory fiber endings. Large myelinated nerves termed **Ia** or **primary afferents** surrounds the central portion of all of the intrafusal muscle fibers. This nerve ending forms a coiled structure called the **annulospiral ring**. Stretching this nerve ending activates **stretch-activated channels** in its surface that depolarize the neuron and therefore increase its firing rate. Lengthening the muscles stretches these receptors and increases the firing rate. Shortening of the muscle alleviates stretch of these receptors and their firing rate decreases. Thus, the firing rate of the intrafusal sensory nerve is related to the stretch of the muscle relative to the muscle spindle. The nuclear bags actually come in two varieties: "static bags" and "dynamic bags". The static nuclear bag and nuclear chain fibers receive a second kind of innervation, classified as **II afferents**. These innervate the juxtaequatorial regions of the intrafusal fibers. The II afferents consist of medium myelinated fibers that adapt slowly. Their tonic activity carries information about the static muscle length. In addition to these sensory receptors, each intrafusal fiber is innervated with a motor neuron, the **gamma motor efferent**, that controls the length of the intrafusal fiber by activating its contractile mechanism just as an ordinary motor neuron would. This has the effect of maintaining the sensitivity of the muscle spindle when muscles contract. The arrangement is shown schematically in Figure 4.4.3.

## THE MYOTATIC REFLEX IS A MONOSYNAPTIC REFLEX BETWEEN Ia AFFERENTS AND THE $\alpha$ MOTOR NEURON

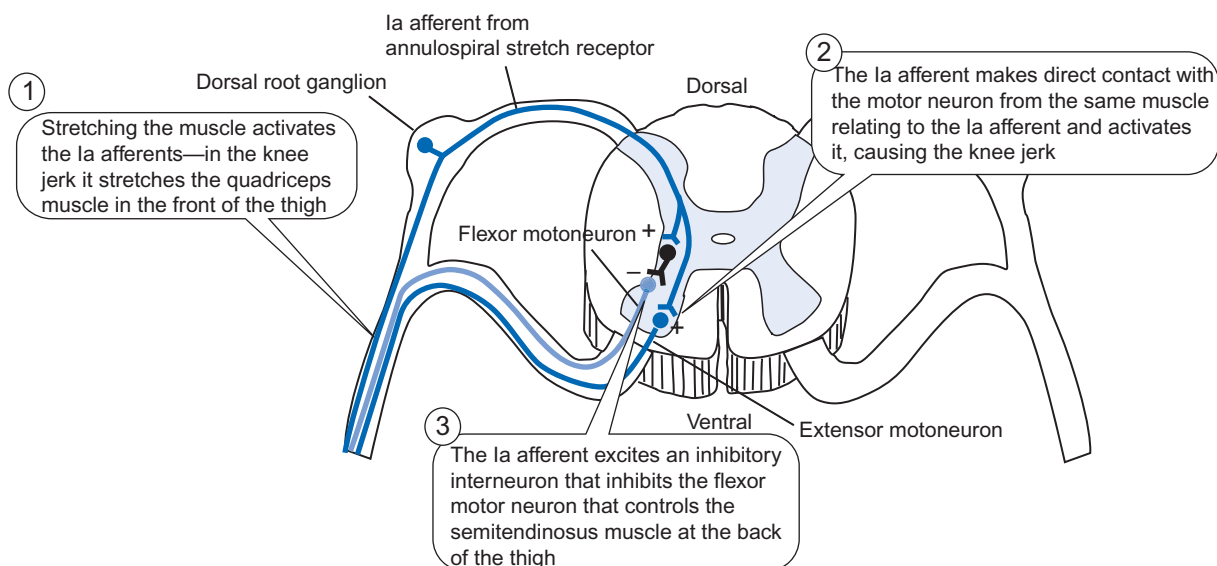
The myotatic reflex is the "knee-jerk" reflex in which a muscle contracts in direct response to its stretch. It is typically elicited by tapping on the tendon of a muscle, which deforms the tendon and stretches the muscle. Ia afferents of the muscle spindles sense the stretch and make direct connections to the  $\alpha$  motor neurons that innervate the muscle. The increased rate of firing upon stretch causes excitation of the  $\alpha$  motor neuron and a contraction of the muscle. Because the stretch is short-lived, so is the excitation of the Ia afferent and so is the excitation of the  $\alpha$  motor neuron, and a short twitch of the muscle is observed. The wiring of this reflex is shown in Figure 4.4.4.

The purpose of the myotatic reflex is to resist changes in muscle length. This is useful when one is trying to maintain the position of a limb during purposeful work or in maintaining posture, but it is counter-productive during purposeful movements when the muscles must contract while their antagonist member relaxes. Thus, this system is over-ridden during purposeful movements. At other times, the reflex can be enhanced. Its strength can be facilitated or depressed by inputs from the motor cortex.

The myotatic reflex relies on excitation of the  $\alpha$  motor neuron by input from the Ia afferents. Their ability to depolarize the motor neuron to produce action potentials depends on the resting membrane potential of the motor neuron, which in turn can be influenced by other



**FIGURE 4.4.3** The muscle spindle. The muscle spindle is a group of smaller and specialized muscle fibers within a muscle. Typical spindles contain two bag fibers and about five chain fibers. The nuclear bag fibers are classified as static or dynamic. The intrafusal fibers are innervated by motor nerves (the gamma motor neurons) and two different types of sensory fibers: the type Ia stretch receptors and the type II afferent sensory receptors. The annulospiral receptors sense stretch and are rapidly adapting. Thus they sense the rate at which the muscle is stretched. The type II afferents are slowly adapting and inform the CNS about the static stretch of the muscle.



**FIGURE 4.4.4** The circuitry of the myotatic reflex. Increased firing of the annulospiral stretch receptor of the Ia muscle spindle afferents activates the muscle, here denoted as the extensor muscle. In the knee-jerk reflex this corresponds to the quadriceps muscle. Simultaneously, the stretch receptor synapses on an interneuron that inhibits the antagonistic muscle, which in this case is a flexor muscle, the semitendinosus. In this way, stretch of the muscle is accompanied by contraction of the muscle and relaxation of its antagonist.

connections in the cord and from higher centers. Usually it is possible to enhance the knee-jerk reflex by **Jendrassik's maneuver**. In this maneuver, the subject interlocks the fingers of the two hands and tries to pull the hands apart while resisting the movement. This isometric exercise increases the general outflow from the cerebral motor cortex, depolarizing a variety of motor neurons and thereby facilitating the myotatic reflex.

### THE GAMMA MOTOR SYSTEM MAINTAINS TENSION ON THE INTRAFUSAL FIBERS DURING MUSCLE CONTRACTION

The primary and secondary sensory receptors of the muscle spindle are stretch receptors. The rapidly adapting annulospiral sensors encode the rate of stretch, whereas the slowly adapting secondary sensors encode the static length of the muscle. During contractions, the extrafusal fibers shorten and so the tension on the intrafusal fibers disappears. To maintain the tension on the stretch receptors, the  $\gamma$  efferent system simultaneously activates the intrafusal fibers with the extrafusal fibers so that the stretch receptors are tight enough to remain able to report stretch. Thus, the  $\gamma$  efferent system maintains the sensitivity of the muscle spindle stretch receptors over the range of muscle lengths that occur during contraction and relaxation. The cell bodies of the  $\gamma$  motoneurons are located in the ventral horn of spinal cord, like those of the  $\alpha$  motor neurons. The  $\gamma$  efferent motor system is shown in Figure 4.4.5.

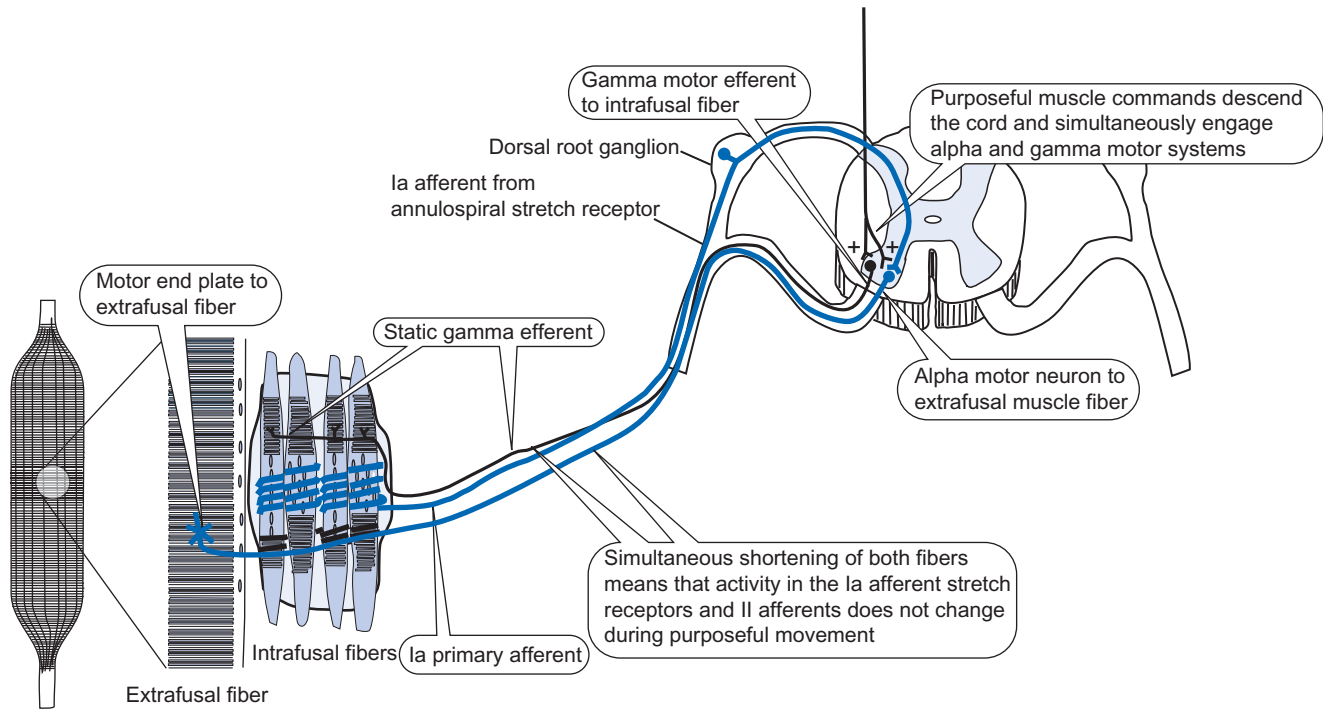
Coactivation of the  $\gamma$  efferents also helps activate the muscles. While under tension, the Ia and II fibers return

action potentials to the cord to facilitate the  $\alpha$  motor neurons. When the muscle contracts, this facilitation would disappear because the Ia and II fibers would decrease their firing rates. Coactivation of the intrafusal fibers solves this problem.

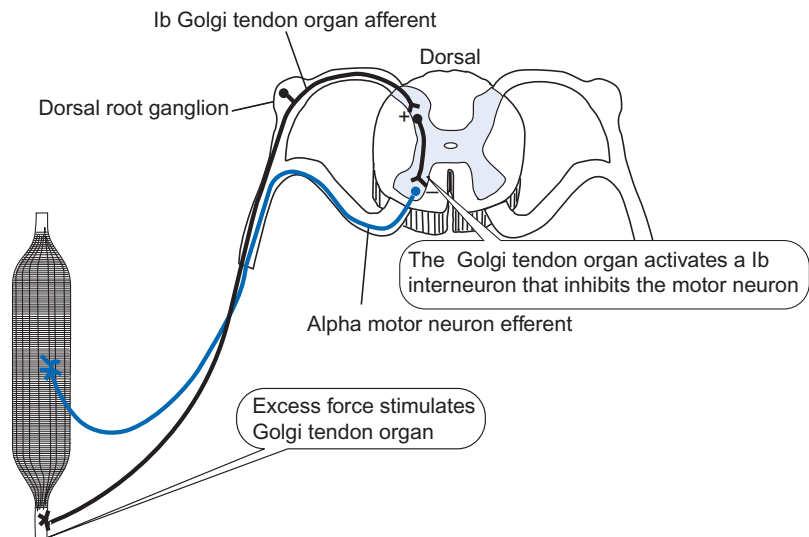
### THE INVERSE MYOTATIC REFLEX INVOLVES SENSORS OF MUSCLE FORCE IN THE TENDON

Stretch receptors called **Golgi tendon organs** are found within the collagen fibers of tendons and within joint capsules. They are generally located in series with the muscle rather than the parallel arrangement of the intrafusal muscle fibers. Therefore, the stretch of the tendons reflects the force on the tendon that is developed by all of the muscle, and the firing rate of the Golgi tendon organ encodes muscle force rather than stretch, even though it actually senses stretch. The action potentials are carried to the spinal cord over **type Ib afferent fibers**, which are large myelinated fibers. The sensory neurons synapse in the cord on interneurons which then make connections to  $\alpha$  motor neurons. In this way, high force development that could injure muscles can be prevented by relaxation of the muscle. This reflex, which connects high force in the Golgi tendon organs with relaxation, is the opposite of the myotatic reflex, the stretch reflex, in which stretch elicits a reflex contraction. Thus, this reflex is called the **inverse myotatic reflex** even though the muscle is not necessarily stretched. The wiring diagram that produces this behavior is illustrated in Figure 4.4.6.

Table 4.4.1 summarizes the afferent and efferent inputs relating to control of muscle function.



**FIGURE 4.4.5** Coactivation of the  $\gamma$  efferent system with the  $\alpha$  motor neurons. Command signals from the motor cortex activate  $\alpha$  motor neurons. Simultaneously,  $\gamma$  efferents are activated so that the intrafusal fibers contract along with the muscle, thereby preserving sensitivity of the stretch receptors during contraction. In this way, the CNS can remain informed of the rate of muscle shortening through sensory inputs from the Ia stretch receptors on the muscle spindles, and the stretch receptors do not inhibit purposeful movement. Some connections are only partially shown for clarity.



**FIGURE 4.4.6** Wiring of the inverse myotatic reflex. Sensors in the tendon, the Golgi tendon organ, are activated upon stretch of the tendon, which requires considerable force. These sensors synapse on interneurons in the spinal cord that inhibit further activity of the motor neurons innervating the muscle. This relaxation of the muscle prevents damage from excess force.

## THE SPINAL CORD POSSESSES OTHER REFLEXES AND INCLUDES LOCOMOTOR PATTERN GENERATORS

The spinal reflexes discussed above are only part of the story. There are a variety of other reflexes such as the **placing reflex**, which helps maintain posture and support. The placing reflex refers to the reaction to tactile stimuli applied to the back of the paw of lower animals. The reaction is to flex the limb and then swing it forward and extend it. For example, a twig touching the

dorsum of the foot during its swing phase results in the foot being lifted over the twig. In humans, this is the reaction upon stubbing one's toe: the affected limb is flexed and then rapidly swung forward and extended to catch the falling body. This is a far more complicated reflex than what we have already discussed. It involves a complex sequence of motor neuron activation and inhibition.

The spinal cord also possesses **central pattern generators** that are the basis of gait. Lower animals, because of their quadrupedal locomotion, show distinct differences



**TABLE 4.4.1** Summary of the Afferent and Efferent Fibers to Skeletal Muscle Involved in the Spinal Reflexes and Control of Muscle Function

<b>Afferents</b>				
Receptor	Axon	Axon Diameter ( $\mu\text{m}$ )	Conduction Velocity ( $\text{m s}^{-1}$ )	Function
Primary muscle spindle	Ia	12–20	70–120	Rate of length change
Secondary muscle spindle	II	4–12	20–70	Static length
Golgi tendon organ	Ib	12–18	70–110	Muscle tension
<b>Efferents</b>				
Motor neuron	Target	Axon Diameter ( $\mu\text{m}$ )	Conduction Velocity ( $\text{m s}^{-1}$ )	
$\alpha$ Motor neuron	Extrafusal muscle	8–13	40–80	Voluntary control
$\gamma$ Motor neuron	Intrafusal muscle	3–8	20–50	Adjust spindle sensitivity

in gaits from walking, trotting, pacing, and galloping. Humans also show differences in gait but, because of our bipedal locomotion, the differences center on speed of movement rather than differences in the sequence of flexion and extension of four legs. In the gallop, for example, the two hind legs are simultaneously or nearly simultaneously extended to push the animal forward. Out of phase with the extension of the hind legs is the extension and then flexion of the forelegs to pull the animal forward. In bipedal motion this would become a hop, which is extraordinarily inefficient locomotion. Humans pay for their bipedal locomotion by being one of the slowest animals around. The advantage is that it frees the hands to throw a sharp rock or a spear at much higher velocities than locomotion.

Experiments with lower animals show that part of locomotion control resides in pattern generators located in the spinal cord. When the thoracic spinal cord of a cat is cut, severing all connections to the lower motor neurons from higher centers in the brain, and the cat is suspended in a sling above a treadmill, the animal can still raise and place the hind legs, and this motion will keep pace as the treadmill is accelerated. Thus, the basic circuitry for movement of the hind legs resides in the spinal cord.

## THE SPINAL CORD CONTAINS DESCENDING TRACTS THAT CONTROL LOWER MOTOR NEURONS

The cell bodies of the **lower motor neurons** reside in the ventral horn of the spinal cord and provide the only direct neural control of skeletal muscle. All of the reflexes, and all voluntary control of muscle, act through their effects on these relatively small number of motor neurons. We have already discussed the spinal reflexes. In addition, voluntary and unconscious higher control of muscle descend in bundles from the cerebral cortex and brainstem down the spinal cord to make synapses onto interneurons and motor neurons within the spinal cord. Sherrington coined the term “final common path” to describe the motor neurons that innervate the muscles because all of the variety of reflex activities and all complex behavior involving skeletal

muscles must eventually be directed to these lower motor neurons.

The descending tracts are named first from their point of origin and secondly from their termination. In addition, tracts are named for their specific anatomical location. Thus the descending tracts controlling the lower motor neurons are as follows:

### LATERAL CORTICOSPINAL TRACT

This tract originates in the cerebral cortex and descends to the lower motor neurons in the spine. Hence it is a corticospinal tract. In addition, it descends the spinal cord in the lateral aspect. As we will see in Chapter 4.5, the motor and premotor areas of the cerebral cortex in front of the central sulcus forms this tract, which crosses the midline (**decussates**) to descend on the lateral aspect of the contralateral spinal cord. The axons make synapses with interneurons and motor neurons within the cord. The fibers in this tract control motor neurons for the muscles of the distal extremities. Thus, damage to this pathway results in the loss of fine motor skills.

### RUBROSPINAL TRACT

The **red nucleus** is a structure in the midbrain from which the rubrospinal tract originates. It receives inputs from the motor cortex and from the cerebellum. The fibers cross over the midline and descend in the rubrospinal tract, terminating primarily on interneurons within the spinal cord.

### VENTRAL CORTICOSPINAL TRACT

This tract also originates from the premotor and motor cortex and descends the ventral contralateral spinal cord. These fibers control motor neurons for axial and proximal muscles and so are involved in posture and gross motor movements.

### LATERAL VESTIBULOSPINAL TRACT

As its name implies, the lateral vestibulospinal tract originates in the **lateral vestibular nucleus**. These fibers receive inputs from the ipsilateral vestibular apparatus

(see Chapter 4.5), which informs the brain about balance. The tract descends without crossing to make connections to medial motor neurons that control postural muscles on the axis of the body. The tract is involved in the reaction of the muscles to gravity and thus it helps maintain posture.

### MEDIAL VESTIBULOSPINAL TRACT

The medial vestibulospinal tract originates from the **medial vestibular nucleus**, which in turn receives inputs from the vestibular apparatus and from stretch receptors in the muscles of the head and neck. The tract descends ipsilaterally to make contact with interneurons and motor neurons within the thoracic spinal cord to help position the torso relative to gravity and the head during movements.

### TECTOSPINAL TRACT

The tectospinal tract originates in the **superior colliculus**, which is part of the **tectum**, or roof of the midbrain. The

tract crosses the midline before descending to the upper cervical spinal cord. It receives inputs from the eyes and ears and serves to coordinate the positioning of the head and eyes in relation to auditory and visual targets.

### PONTINE RETICULOSPINAL TRACT

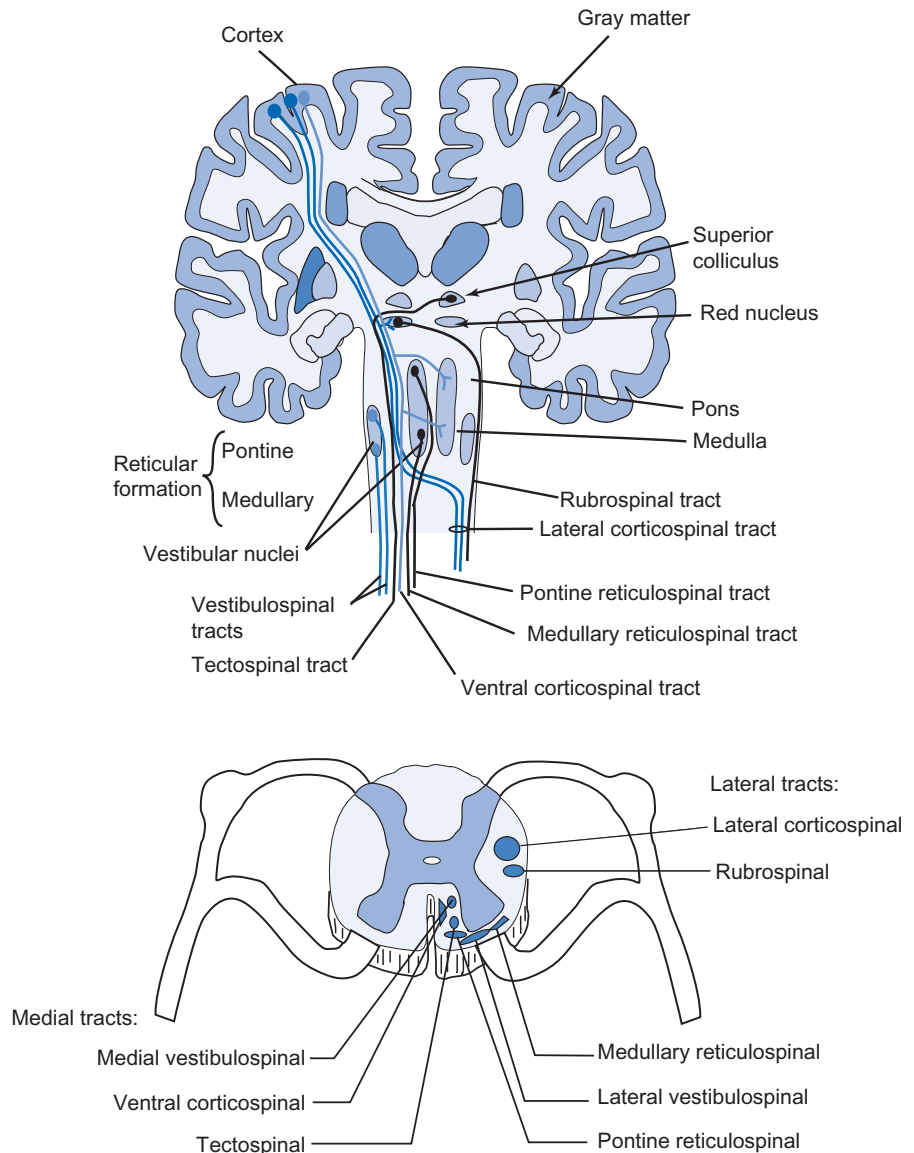
The pontine reticulospinal tract begins in part of the **reticular formation** located in the pons. It descends ipsilaterally and terminates on interneurons that control medial extensor motor neurons. This tract is largely excitatory.

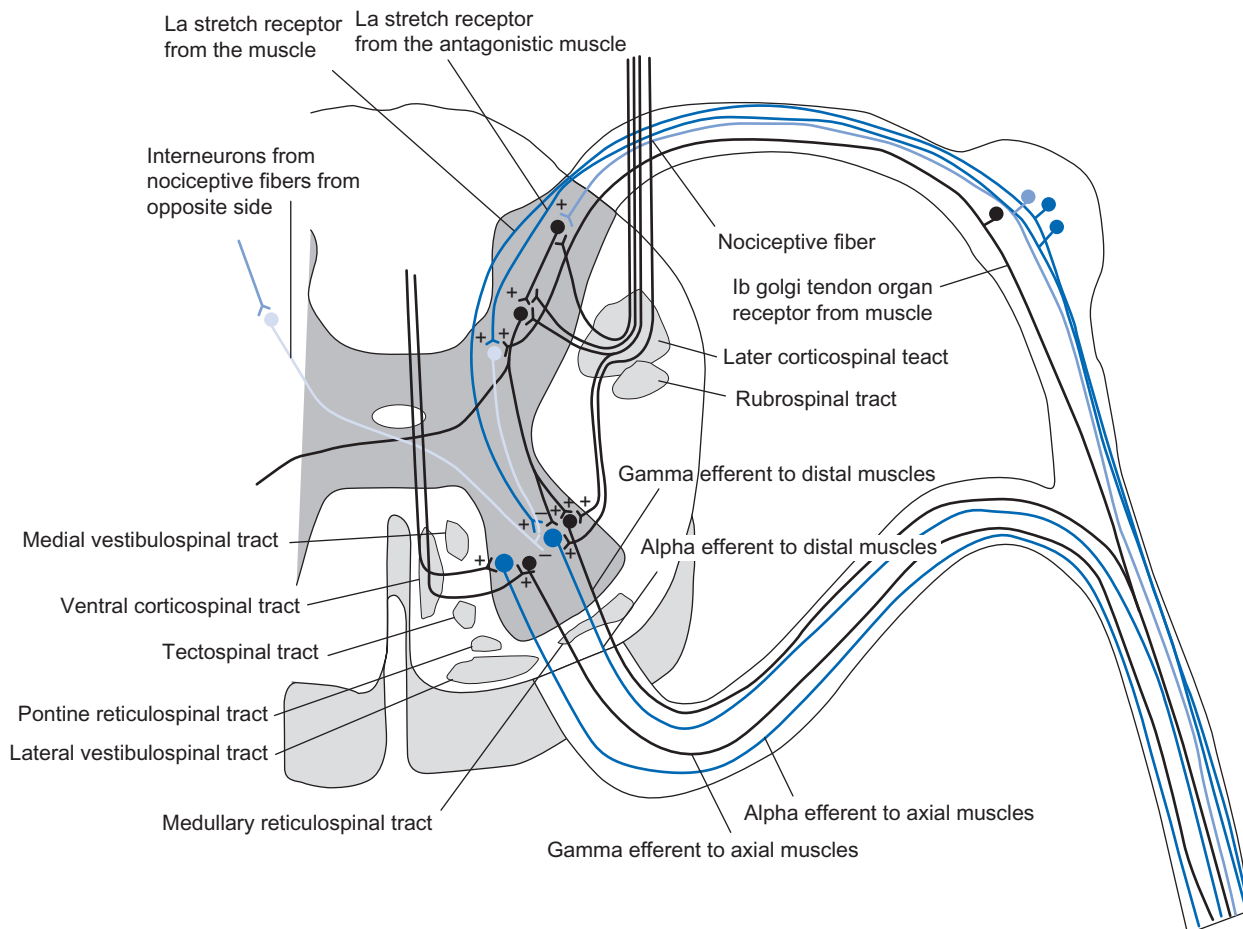
### MEDULLARY RETICULOSPINAL TRACT

This tract is similar to the pontine reticulospinal tract except that it originates in the part of the reticular formation located in the medulla. It is largely inhibitory, and it serves to balance the excitatory drive of the pontine reticulospinal tract.

The anatomical pathways for these tracts are shown in Figure 4.4.7.

**FIGURE 4.4.7** Major descending motor pathways. The lateral tracts supply motor neurons located in the lateral portion of the ventral horn of the spinal cord that control the distal muscles of the limbs. The medial tracts supply motor neurons located in the medial portion of the ventral horn of the spinal cord. These control the axial and proximal muscles. Cells in the primary motor cortex send axons to the contralateral spinal cord in the lateral corticospinal tract. These send collaterals to the red nucleus located in the midbrain. Cells in the red nucleus also send fibers to the contralateral spinal cord in the rubrospinal tract. Some primary motor neurons do not cross over; they form the ventral corticospinal tract. These neurons in the ventral corticospinal tract send collaterals to the contralateral reticular formation, from which axons descend ipsilaterally, forming the pontine reticulospinal tract and the medullary reticulospinal tract. The vestibular nuclei send axons down the spinal cord ipsilaterally, forming the lateral vestibulospinal tract and the medial vestibulospinal tract. The vestibular nuclei receive inputs from the vestibular apparatus, which senses gravity, and so these tracts are involved in postural responses to gravity. The superior colliculus is part of the tectum, or roof of the midbrain, and it receives inputs from both the eyes and the ears. It sends axons down the contralateral spinal cord in the tectospinal tract. It is involved in moving the head and eyes in search of auditory or visual targets. The lower part of the figure indicates the approximate location of these tracts on one side of the spinal cord. These tracts are symmetrically placed on both sides of the spinal cord, but for clarity only one side is shown.





**FIGURE 4.4.8** Convergence of pathways controlling lower motor neurons. **The flexor muscles alone are shown for clarity.** The  $\alpha$  motor neurons receive inputs from the stretch receptors (Ia fibers) located in the intrafusal fibers of the muscle. These directly activate the  $\alpha$  motor neurons in a monosynaptic pathway. The  $\alpha$  motor neurons also receive inputs from the Ia stretch receptors of the antagonistic muscle, which synapse on an interneuron which then inhibits the motor neuron. Afferent Ib fibers from the Golgi tendon organs make a polysynaptic, inhibitory connection to the  $\alpha$  motor neuron. Nociceptive fibers from the ipsilateral side make a polysynaptic excitatory connection to  $\alpha$  motor neurons for the flexors and an inhibitory connection to motor neurons of the extensors, which are not shown. The nociceptors from the contralateral side synapse onto interneurons within the cord. These send fibers across the cord to have opposite effects on the contralateral  $\alpha$  motor neurons. Inputs from the higher centers in the nervous system descend in the tracts indicated. Only those inputs from the corticospinal tracts are shown. The lateral corticospinal tract predominantly activates muscles in the limb extremities. The ventral corticospinal tract provides input to  $\alpha$  motor neurons that control the axial muscles.

## ALL OF THE INPUTS TO THE LOWER MOTOR NEURONS FORM INTEGRATED RESPONSES

All of the reflexes that we have discussed, and all of the descending tracts with their attendant activity, are simultaneously active to varying degrees. Thus the response of the motor neurons depends on the relative intensity of the inputs from all of these different sources. A simplified version of all of these combined inputs is shown diagrammatically in Figure 4.4.8.

## SUMMARY

Strong stimuli applied to the body are *reflected* back in a muscular response. These reflexes are stereotypical and hardwired. The withdrawal reflex refers to the withdrawing of a limb upon painful stimulation of the skin of

the limb. The pain information is carried by A $\delta$  pain fibers that synapse onto interneurons within the spinal cord. These in turn make synapses on the motor neurons of both the flexors and extensors. Pain activates the flexors and inhibits the extensors.

The crossed-extensor reflex generally occurs with the withdrawal reflex and refers to the extension of the opposite limb. Here interneuron connections cross over to the other side of the spinal cord, but now contralateral pain activates extensors and inhibits flexors. The withdrawal reflex and crossed-extensor reflex are polysynaptic but occur entirely within the spinal cord. Input from higher centers may facilitate or inhibit reflexes but they cannot eliminate them.

Muscles have receptors for stretch and force. Extrafusal muscle fibers comprise the bulk of muscle and forms the major force-generating structure. Intrafusal muscle fibers are buried in the muscle and they contain afferent



receptors for stretch, but they also contain contractile elements. Nuclear bag and nuclear chain fibers both contribute to the afferents. Primary Ia fibers report on dynamic stretch; they innervate the dynamic nuclear bag fibers. Group II afferents are receptors that report on the static stretch of the muscle; these innervate static nuclear bag fibers and all of the nuclear chain fibers. Rapid stretch of the intrafusal fibers sends action potentials to the spinal cord, where Ia fibers make a monosynaptic activation of  $\alpha$  motor neurons that innervate the same muscle as the Ia afferents. The stretch receptors also inhibit the antagonist muscles. The stretch reflex is called the myotatic reflex.

Gamma motor neurons innervate intrafusal fibers and control their contraction. Contraction of a muscle relieves stretch on the parallel intrafusal fibers and this defacilitates muscle contraction and also removes the effectiveness of the receptors as stretch receptors. Simultaneous coactivation of the  $\alpha$  motor neurons and  $\gamma$  motor neurons during purposeful movements preserves the sensitivity of the stretch receptors during contraction.

The Golgi tendon organs are arranged in series with the muscle, and they inform the CNS of the force developed by the muscle. When force is excessive, afferent activity on the Ib Golgi tendon organ afferents inhibits further  $\alpha$  motor neuron activity. This reflex is called the inverse myotatic reflex.

Spinal reflexes form the basis of movement, but more complicated locomotion circuits are present in the spinal cord. Although these locomotion pattern generators play an important role in movement, purposeful movement requires motor commands from higher centers in the CNS. The  $\alpha$  motor neurons are the sole

conduit for excitation of muscles, and all commands pass through this final common pathway. These are the lower motor neurons. Purposeful control of the lower motor neurons is provided by upper motor neurons in the cortex. Many tracts of axons descend the cord to control the lower motor neurons and the interneurons in the cord. These tracts are named for their location in the spinal cord and for the origin and terminus of the axons. The lateral corticospinal tract, for example, is located in the lateral aspect of the cord and connects neurons in the cortex with those in the spinal cord. Other tracts provide input from vision and balance sensory systems.

## REVIEW QUESTIONS

1. What is a reflex?
2. What sensory information elicits a withdrawal reflex?
3. Why are interneurons necessary for the withdrawal reflex?
4. What is the crossed-extensor reflex? Why is it necessary to inhibit antagonistic muscles during operation of the reflexes?
5. Which reflex is the only monosynaptic reflex? Would you expect this reflex to be faster or slower?
6. What is a muscle spindle? What afferents carry what information to the spinal cord? Are you conscious of this information? Why is it necessary for muscle spindles to have contractile ability?
7. Which spinal tracts do not cross over from their origin?
8. What is the purpose of the inverse myotatic reflex?
9. What is a locomotor pattern generator?