Control of Movement

Control of Movement

Organization of the Motor Systems

The motor systems are organized hierarchically on three control levels: the spinal cord, the descending systems of the brain stem, and the motor areas of the *cortex*. Each level sends descending information to the skeletal muscles (red arrows) and receives sensory information relevant to its function (white arrows) in feedback loops.

At the level of the spinal cord, the lowest level of the hierarchy, neuronal circuits coordinate between *proprioceptive* information (reports on muscle tension and location) and motor neurons that innervate skeletal muscles. These circuits mediate numerous rhythmic motor patterns (such as walking) and reflexes (such as the stretch reflex). The next level, the brain stem, also receives proprioceptive information and projects information to the skeletal muscles through the medial and lateral tracts. At the highest cortical level, feedback loops connect sensory and associative cortical areas with motor cortex areas. These pathways are important for the planning and control of voluntary motor activities.

Two additional subcortical systems, the *cerebellum* and the *basal ganglia*, receive information from the cortex and return information to the motor cortex via the thalamus. The cerebellum also receives information from the brain stem and returns information to it. The cerebellum is involved in motor learning, synchronization of fast and coordinated movements, maintaining posture and balance, and the coordination and refinement of planned movements. The main function of the basal ganglia is to supervise body, limb, and eye movements.

Motor information arriving from all three levels converges on motor neurons that innervate the skeletal muscles.

Muscles and Their Receptors

Overview

The human body contains three types of muscles: skeletal muscles, smooth muscles, and cardiac muscles. The following illustration shows skeletal muscles of the human arm. Most skeletal muscles are attached to bones at each end by tendons, which are strong strips of connective tissue. Contraction of flexor muscles produces flexion, the drawing in of a limb; contraction of extensor muscles produces the opposite motion, extension, which opens the joints.

The skeletal muscles are innervated by motor (efferent) neurons and sensory (afferent) neurons. There are two types of motor neurons: alpha motor neurons, which cause skeletal muscles to contract, and gamma motor neurons, which regulate the sensitivity of muscle spindles. There are also two types of sensory neurons: the Ia afferent neuron, which carries information about muscle length from the muscle spindle, and the Ib efferent neuron, which conveys information about muscle tension from the Golgi tendon organ.)

The illustration presents an arm with three exposed muscles: a flexor muscle (incorporating a *muscle spindle*), which draws in the arm; a synergist muscle, which supports the flexor muscle; and an extensor muscle, which opens the arm joint. When the flexor and synergist muscles contract, the extensor muscle relaxes, and vice versa.

Muscle
Skeletal muscles are made up of many muscle fibers and are usually connected to the bones by tendons. Their contraction allows maintenance of body posture, limb movement, and execution of delicate and complex movements of the hands and fingers.

Muscle Spindle
The muscle spindle is a sensory organelle within the muscle that senses muscle length. The spindle consists of three main elements: a group of muscle fibers of limited contraction ability, known as the intrafusal muscle fibers; Ia *afferent* axons , which carry information about spindle length to the spinal cord; and gamma motor axons, which regulate spindle sensitivity to muscle length. These elements are contained in a connective tissue envelope that forms a spindle-like capsule.

Muscle Tendon
The tendon is a white fibrous cord made of dense connective tissue. This tissue is made of parallel collagen fibers aligned in the same direction as the muscle fibers. The tendon is flexible, yet has great resistance to being stretched. It is the tendon that connects the muscle to the bone.

Golgi Tendon Organ
The Golgi tendon organ is a sensory organ located at the junction of muscle and tendon. The Golgi tendon organ senses muscle tension. It consists of a number of collagen fibers innervated by Ib *afferent* axons that wrap around and between the collagen fibers. When the tendon is stretched, the Ib afferent axons are compressed by the collagen fibers, causing them to fire. Thus, sensory information about muscle tension is carried to the spinal cord. The Golgi tendon organ protects the tendons and the muscles from being overloaded (see the: “Control of Muscle Contraction”).

Ia Afferent Neuron
The Ia afferent neuron innervates the muscle spindle. Neural impulses travel fast in a Ia large-diameter myelinated axon. Its cell body is located in the dorsal root ganglion, and its axon ending spirals around the central region of the intrafusal fibers. When the muscle lengthens, the intrafusal fibers are stretched and the Ia neuron is excited. Ia fibers innervate motor neurons, located in the ventral horn, either directly or via interneurons.

Ib Afferent Neuron
The Ib *afferent* neuron innervates the Golgi tendon organ. Its cell soma is located in the dorsal root ganglion, while its axon ending wraps around and between the collagen fibers of the tendon organ. When the tendon is stretched, the Ib axons are compressed by the collagen fibers, causing them to fire. The activation of Ib neurons inhibits motor neurons in the spinal cord.

Alpha Motor Neuron
The alpha motor neuron innervates the muscle fibers. It receives input from sensory feedback from the muscles, as well as directly from the brain. The soma of the motor neuron is located in the *ventral* horn of the spinal cord gray matter. Its myelinated axon extends via the ventral root of the spinal cord to innervate a number of extrafusal muscle fibers. The innervation ratio between an alpha motor neuron and extrafusal muscle fibers is associated with the precision of muscular control. Muscles that control precise movements, such as movements of the fingers or eyes, have a small innervation ratio (approximately one alpha motor axon for ten fibers), whereas muscles that control gross motor movements, such as movements of the leg, have a large innervation ratio (approximately one axon to a few hundred fibers). A motor unit consists of a single alpha motor neuron and the total number of extrafusal muscle fibers innervated by it.

Ventral Root
The ventral root is a bundle of motor *axons* extending from the *spinal cord*. Cell *somas* of these axons are located within the ventral horn of the *gray matter* of the spinal cord. Axons of the ventral roots project motor information to muscles and glands of the body. The ventral root and the dorsal root join together to form the spinal nerve.

Dorsal Root
The *dorsal* root is a bundle of sensory axons that enter the spinal cord. The somas of these axons are located in the dorsal root ganglion. These axons bring sensory information from the skin, muscles, and viscera. The dorsal root and the ventral root join together to form the spinal nerve.

Detailed Anatomy

The Muscle
Skeletal muscles are composed of groups of muscle fibers. A single muscle fiber consists of *myofibrils*, which are overlapping strands of *actin* and *myosin*. It is the sliding of actin on myosin that provides the physical basis for muscular contraction.

The illustration presents a skeletal muscle and a tendon. In the upper right hand corner you'll find a button with a magnifying glass icon marked with a plus sign. Moving the cursor over the button will mark a section of the muscle with a red box. Clicking on the button will zoom into the marked section; additional clicks will further zoom into muscle structures, allowing inspection of muscle details. In order to return to previous windows, click the button with a magnifying glass icon marked with a minus sign.

Skeleltal muscle
Skeletal muscles are made up of many muscle fibers and are usually connected to the bones by tendons. Their contraction allows maintenance of body posture, limb movement, and execution of delicate and complex movements of the hands and fingers.

Muscle Tendon
The tendon is a white fibrous cord made of dense connective tissue. This tissue is made of parallel collagen fibers aligned in the same direction as the muscle fibers.

The tendon is flexible, yet has great resistance to being stretched. It is the tendon that connects the muscle to the bone.

Fasciculus (bundle) of Muscle Fiber
Muscle fibers are organized within the muscle in bundles of 10-100 fibers, which lie parallel to each other and are wrapped in connective tissue.

Muscle Fiber
The muscle fiber is a cylindrical multi-nuclear cell with a diameter of 10-100 micrometers and a typical length of 100 micrometers. The muscle fiber is made of many cells that fuse together during embryonic development, which explains why it has multiple nuclei. Most nuclei are located in the cell periphery, in the region of the sarcolemma (the muscle fiber membrane), and far from the contracting elements. The muscle fiber transduces chemical energy into a skeletal muscle contraction, and the contraction causes movement in those organs to which the muscles are attached.

Sarcolemma
The sarcolemma is the membrane of the muscle fiber. Axons of alpha motor neurons innervate the *end-plate*, a specialized region of the muscle membrane. Action potentials reaching the *terminal boutons* of an alpha motor neuron release acetylcholine (ACh) in the end-plate region. Acetylcholine binds to nicotinic receptors on the surface of the sarcolemma, which leads to the opening of sodium channels and to development of an excitatory postsynaptic potential in the muscle fiber called the end-plate potential.

Myofibril (Muscle Fibril)
Myofibrils are the contractile elements of skeletal muscles. They are found within the muscle fiber and contain smaller structures called myofilaments. There are two types of myofilaments: thin filaments made of *actin* and thick filaments made of *myosin*. Areas of overlapping actin and myosin appear under the microscope as dark strips, as compared to the bright areas of no overlapping. Because of the alternating light and dark strips arranged across the muscle, skeletal muscles are also called striated muscles.

Z Discs
Z discs are plate-shaped regions in myofibrils separating the basic contractile element of the striated muscle, called sarcomeres. The Z discs are connected on both sides to filaments of actin.

Actin
Thin filaments consist of a twisted double-braided chain of actin molecules. These molecules are connected to Z discs at one end, while their other ends overlap with myosin fibers. The surface of the actin molecule is covered with calcium binding sites and myosin binding sites. When a muscle fiber is excited, calcium binds to actin molecules, exposing myosin-binding sites on actin molecules. The myosin head binds to the actin and bends, leading to muscular contraction.

Myosin
Myosin is a large and complex molecule that has a head and a tail" area (see magnification). The tails join each other and create thick filaments from which the

heads (cross bridges) extrude toward the thin filaments (actin). When a muscle fiber is excited, calcium binds to actin molecules, exposing myosin-binding sites on actin molecules. The myosin head binds to the actin and bends, pulling the actin molecules toward the center of the sarcomere, thus bringing the Z discs closer to each other and shortening the length of the sarcomere. The simultaneous shortening of thousands of sarcomeres in the muscle ultimately leads to its contraction (see the "Muscle Contraction" animation).

Sarcomere
The filaments inside a myofibril do not extend the entire length of a muscle fiber. They are arranged in compartments called sarcomeres. The sarcomere is the basic functional unit of the striated muscle and is located between the Z discs in a myofibril. During muscle contraction, the myosin slides over the actin and changes the sarcomere's length.

Sarcoplasmic Reticulum
The sarcoplasmic reticulum is a system of membranes that surrounds the myofibrils. It consists of liquid-filled tubes and sacs containing calcium *ions*. An action potential reaching the muscle fibers spreads through channels called T tubules and causes the release of calcium ions from the sarcoplasmic reticulum. This leads to the contraction of the muscle fibers. The muscle relaxes when the calcium is absorbed by the sarcoplasmic reticulum (see the "Muscle Contraction" animation).

T Tubules
T-tubules form a network of channels that connect the sarcolemma (the muscle fiber membrane) with the sarcoplasmic reticulum. An action potential that develops on the surface of the sarcolemma spreads through the T tubules and causes the release of calcium ions from the sarcoplasmic reticulum (see the "Muscle Contraction" animation clip).

The Muscle Spindle

The muscle spindle is a sensory organelle within the muscle that senses muscle length. The spindle consists of three main elements: a group of muscle fibers of limited contraction ability, known as the intrafusal muscle fibers; Ia afferent axons, which carry information about spindle length to the spinal cord; and gamma motor axons, which regulate spindle sensitivity to muscle length. These elements are contained in a connective tissue envelope that forms a spindle-like capsule.

Fibrous Capsule
The fibrous capsule is the connective tissue that envelops the intrafusal muscle fibers and creates a spindle-like capsule—wide at the center and narrower at both ends.

Intrafusal Muscle Fibers
The intrafusal muscle fibers are thin fibers within the muscle spindle. The ends of Ia afferent axons spiral around the center of the intrafusal muscles, while gamma motor axons innervate their contractile polar regions.

Ia Afferent Axons
The Ia *afferent* neuron is a sensory neuron that innervates the muscle spindle. Neural impulses travel fast in a Ia large-diameter myelinated axon. Its cell body is located in

the *dorsal root ganglion*, and its axon ending spirals around the central region of the intrafusal fibers. When the muscle lengthens, the intrafusal fibers are stretched and the Ia neuron is excited. Ia fibers innervate motor neurons, located in the *ventral* horn, either directly or via interneurons.

Gamma Motor Neurons
Gamma motor neurons extend from the ventral horn of the spinal cord; and innervate the contractile polar regions of intrafusal muscle fibers. When the muscle contracts the intrafusal muscle fibers relax, leading to decreased sensitivity of the muscle spindles. Activation of the gamma motor neurons causes the poles of the intrafusal muscle fibers to contract, thus ensuring that the spindle remains sensitive to the muscle length (see the "Control of Muscle Contraction" animation).

The Golgi Tendon Organ
The Golgi tendon organ is a sensory *organelle* located at the junction of muscle and tendon. The Golgi tendon organ senses muscle tension. It consists of a number of collagen fibers innervated by Ib *afferent* axons that wrap around and between the collagen fibers. When the tendon is stretched, the Ib afferent axons are compressed by the collagen fibers, causing them to fire. Thus, sensory information about muscle tension is carried to the *spinal cord*. The tendon organ protects the tendons and the muscles from being overloaded.

The Golgi Tendon Capsule
The Golgi tendon capsule is a thin connective tissue located at the junction of muscle fiber and tendon. The capsule contains braided bundles of collagen fibers and is innervated by a single group of Ib afferent neurons.

Ib Afferent Neuron
The Ib afferent neuron innervates the Golgi tendon organ. Its cell soma is located in the *dorsal root ganglion*, while its axon ending wraps around and between the collagen fibers of the tendon organ. When the tendon is stretched, the Ib afferent axons are compressed by the collagen fibers, causing them to fire. The activation of Ib neurons inhibits motor neurons in the spinal cord.

Collagen Fibers
Collagen fibers are connective fibers between the tendon and the muscle fibers. They are organized in bundles of braids along the length of the Golgi tendon organ. When the tendon is stretched, the Ib afferent axons are compressed by the collagen fibers, causing them to fire.

Muscle Fibers
Many parallel muscle fibers of the skeletal muscles enter the Golgi tendon capsule via a narrow aperture and connect to collagen fibers arising from the tendon.

Muscle Tendon
The tendon is a white fibrous cord made of dense connective tissue. This tissue is made of parallel collagen fibers aligned in the same direction as the muscle fibers. The tendon is flexible, yet has great resistance to being stretched. It is the tendon that connects the muscle to the bone.

The Spinal Cord

The spinal cord serves as a conduit for the flow of information to and from the brain. In addition, the spinal cord contains neuronal circuits that mediate numerous rhythmic motor patterns (such as walking) and reflexes (such as the stretch reflex). The spinal cord is organized in segments. Each segment serves as the origin of two pairs of nerve roots, called the dorsal and ventral roots. The *dorsal roots* contain only sensory axons, while the *ventral roots* contain only motor axons.

The illustration presents an alpha motor neuron (*efferent*) and an Ia *afferent* neuron. The "butterfly" at the center of the spinal cord is the gray matter, which consists mainly of cell somas (hence its color). The left half of the butterfly depicts an image of the upper body. This representation includes the somatotopic organization of the ventral horn. Neurons along the sides of the gray matter innervate the distal muscles, those far away from the center of the body, such as those of the hand. Cells in the medial parts of the gray matter innervate the axial muscles, those at the center of the body, such as the chest muscles. Surrounding the gray matter is the white matter, which includes ascending axon tracts (in blue) or descending axon tracts (in red).

Gray Matter

The gray matter is made of cell bodies that give it its grayish color. It is found in the center of the spinal cord and has a butterfly shape. Each of the butterfly wings includes two horns: a dorsal horn and a ventral horn. The dorsal horn receives sensory input from the dorsal root, while the ventral horn comprises somas of *motor neurons* that extend their axons through the ventral roots. The intermediate area between the two roots includes interneurons, neurons with short axons or no axons, whose processes are contained within the central nervous system.

Ventral Root

The ventral root is a bundle of motor *axons* extending from the spinal cord. Cell somas of these axons are located within the ventral horn of the gray matter of the spinal cord. Axons of the ventral roots project motor information to muscles and glands of the body. The ventral root and the dorsal root join together to form the spinal nerve.

Dorsal Root

The dorsal root is a bundle of sensory axons that enter the spinal cord. The somas of these axons are located in the dorsal root ganglion. These axons bring sensory information from the skin, muscles, and viscera. The dorsal root and the ventral root join together to form the spinal nerve.

Ia Afferent Neuron

The Ia *afferent* neuron innervates the *muscle spindle*. Neural impulses travel fast in a Ia large-diameter *myelinated* axon. Its cell body is located in the dorsal root ganglion, and its axon ending spirals around the central region of the intrafusal fibers. When the muscle lengthens, the intrafusal fibers are stretched and the Ia neuron is excited. Ia fibers innervate motor neurons, located in the ventral horn, either directly or via interneurons.

Alpha Motor Neuron

The alpha motor neuron innervates the muscle fibers. It receives input from sensory

feedback from the muscles, as well as directly from the brain. The *soma* of the motor neuron is located in the ventral horn of the spinal cord gray matter. Its myelinated axon extends via the ventral root of the spinal cord to innervate a number of extrafusal muscle fibers. The innervation ratio between an alpha motor neuron and extrafusal muscle fibers is associated with the precision of muscular control. Muscles that control precise movements, such as movements of the fingers or eyes, have a small innervation ratio (approximately one alpha motor axon for ten fibers), whereas muscles that control gross motor movements, such as movements of the leg, have a large innervation ratio (approximately one axon to a few hundred fibers). A motor unit consists of a single alpha motor neuron and the total number of extrafusal muscle fibers innervated by it.

Descending Tracts in the White Matter
Most of the descending *tracts* are found in the lateral and ventral columns of the white matter in the spinal cord; they carry motor information from the cortex and the brain stem. These tracts transmit the information to motor neurons located in the gray matter of the spinal cord.

Ascending Tracts in the White Matter
Ascending tracts are mostly found in the dorsal and lateral columns of the white matter. The ascending tracts convey somatosensory information relating to contact, pressure, temperature, and pain, as well as information from skeletal joints and skeletal muscles. There are two main ascending tracts: the dorsal column (or medial lemniscal pathway), and the anterolateral (or spinothalamic) pathway.

Innervation of Distal Limb Muscles
Motor tracts descending in the ventral column of the spinal cord mostly innervate distal ("distal" means far from the center of the body) muscles of the limbs. These muscles control delicate and precise movements of the hands and fingers. The cell bodies of the motor neurons that innervate distal muscles are located at the lateral-ventral horn and the intermediate area of the spinal cord gray matter.

Innervation of Axial and Proximal Muscles
Descending motor tracts in the medial column of the spinal cord mostly innervate axial muscles (those at the center of the body), and proximal muscles (at the neck and shoulder). These muscles primarily control body posture and balance. The cell bodies of the motor neurons that innervate these muscles are located at the medial-ventral horn of the spinal cord gray matter.

Muscle Contraction

Muscle Contraction
The animation presents a muscle fiber section with myofibrils wrapped in sarcoplasmic reticulum and T tubules around them. The sarcoplasmic reticulum has been removed from part of the lower myofibril, revealing the alternating light and dark strips made up of *myosin* and *actin* proteins. The myofibril is divided into segments by Z discs. Two Z discs and the segment in between compose a sarcomere, which is the basic contractile unit of striated muscles. Also presented is a terminal bouton of an alpha motor neuron , which synapses on the sarcolemma at the neuromuscular junction.

First Segment – Development of an Action Potential in Muscle Fibers
An action potential, marked with red dots, arrives from the *spinal cord* through the axon of an alpha motor neuron and reaches the *terminal bouton* that synapse with the muscle fiber. The *neurotransmitter* acetylcholine (ACh) is released into the synaptic cleft, crosses the synapse, and binds to receptors on the surface of the sarcolemma. This leads to the opening of sodium channels and the development of an excitatory postsynaptic potential in the muscle (EPSP or end-plate potential). When the threshold of excitation is reached an action potential is generated. The action potential spreads along the T tubules throughout the sarcoplasmic reticulum of the muscle fiber.

Second Segment –Muscle Contraction
A magnification of a small area of the myofibril is shown, including part of the sarcoplasmic reticulum, and a sarcomere composed of actin and myosin filaments in between two Z discs.

The excitatory potential spreads through the T tubules and causes the release of calcium ions from reservoirs in the sarcoplasmic reticulum (represented by purple arrows). The release of calcium causes myosin heads to bind to the actin molecules. Following binding, the myosin heads bend, pulling the actin molecules toward the center of the sarcomere, thus bringing the Z discs closer to each other and shortening the length of the sarcomere. The simultaneous shortening of thousands of sarcomeres in the muscle ultimately leads to its contraction.

Third Segment –Sliding Filament Mechanism
Further magnification shows a single actin filament, attached to a Z disc on one end, and a single myosin filament. An ADP molecule is attached to the myosin head, which is known as a cross bridge.

Calcium ions released from the sarcoplasmic reticulum bind to the actin, exposing myosin binding sites. The myosin head binds to actin, and an ADP molecule is detached from the myosin. Following binding, the myosin heads bend, causing the actin molecules to slide toward the center of the sarcomere, thus bringing the Z discs closer to each other and shortening the length of the sarcomere. As long as the myosin head, or cross bridge, binds to the actin the muscle remains contracted. When the bending is complete, an ATP molecule (an energy-rich molecule) binds to the myosin head, causing it to disengage the actin. The process repeats and the muscular contraction continues as long as calcium and ATP are present. When calcium is absorbed by the sarcoplasmic reticulum, the contraction stops and the muscle relaxes. In the absence of ATP, the cross bridges cannot disengage the actin. This is why the muscles stiffen after death—a state called rigor mortis.

Twitch and Tetanus
One means by which the force of a muscle contraction is graded is the rate of *motor neuron* firing. A brief muscle fiber contraction is induced by a single action potential in an *alpha motor neuron*. This brief contraction is the basic muscle contraction unit, called a twitch. The duration of a twitch is far longer than that of an action potential. An action potential lasts about 1–3 milliseconds, while the time required for a muscle fiber to contract and relax is approximately 10–100 milliseconds. Thus, an increase in

the firing frequency of an alpha motor neuron allows the forces of successive twitches to summate. When the firing rate is high enough, the forces produced by each twitch add until a sustained maximal contraction is reached—this condition is called tetanus.

The illustration presents muscle fiber tension (upper green trace) as a function of the firing rate of an alpha motor neuron (lower green trace). The firing frequency is measured in Hertz (Hz) units (1 Hz = 1 cycle per second). Clicking the check boxes presents the change in muscle tension as a function of the neural firing rate. Four stages of muscular contraction are presented—individual twitch, summation of twitches, unfused tetanus, and fused tetanus.

Successive Twitches
Low frequency firing of an alpha motor neuron leads to successive twitches in the muscle fiber. The muscle fiber fully relaxes between successive twitches.

Summation of Successive Twitches
An increase in the firing frequency of the neuron (20 Hz) leads to summation of twitches and to an increase in muscular force. The muscle fiber does not relax completely between contractions, but rather begins to relax and immediately contracts again.

Unfused Tetanus
When the firing rate is higher (80 Hz), the muscle fiber tension rises quickly and almost reaches its peak force. The muscle fiber goes into a state of prolonged contraction, called unfused tetanus, in which individual twitches can still be distinguished.

Fused Tetanus
When the firing rate is very high (100 Hz), the force produced in the muscle increases progressively to a steady maximum value. This is called fused tetanus, because individual twitches can no longer be distinguished.

Control of Muscle Contraction

The animation presents a cross-section of the *spinal cord*, an exposed muscle fiber, and a muscle spindle. Two types of sensory neurons originate in the muscle and enter the spinal cord via the *dorsal* horn: Ia afferent neuron (in purple) originates in the muscle spindle, and Ib afferent neuron (in blue) originates in the muscle tendon. Two types of motor neurons originate in the ventral horn of the spinal cord and innervate the muscle fiber: alpha motor neuron (light green) innervates the extrafusal muscle fiber, and gamma motor neuron (dark green) innervates the intrafusal muscle fiber. An interneuron (white) is located between the Ib afferent neuron and the alpha motor neuron. The spinal cord is also innervated by neurons arriving from the brain (marked in red). The animation also shows a flexed hand, which changes its posture in relation to the length of the muscle.

First Segment – The Stretch Reflex
A weight is added to a flexed hand, causing the hand to stretch downward. As a result, the muscle and the muscle spindle are stretched. Stretching the intrafusal muscle excites the Ia afferent neuron. The action potentials enter the spinal cord through the

dorsal horn and excite an alpha motor neuron in the ventral horn. The firing rate of the motor neuron is increased, resulting in contraction of the extrafusal muscle. The hand flexes again and almost returns to its original posture. As the intrafusal muscle fibers relax, the firing rate of the Ia afferent neuron is decreased, leading to a reduction in the firing rate of the alpha motor neuron.

Second Segment – Flexion of the Hand
A command to flex the hand is sent by the brain through a descending tract in the spinal cord (neural fiber marked 1) to the alpha motor neuron. The firing rate of the alpha motor neuron increases, leading to contraction of the extrafusal muscle fibers and to further flexion of the hand. The intrafusal fibers go slack, and the firing rate in the Ia afferent neuron decreases.

Third Segment –Intrafusal Muscle Fiber Sensitivity
The brain sends another command through a descending *tract* in the spinal cord (neural fiber marked 2), activating the *gamma motor neuron*. This activation causes contraction and shortening of the polar regions of the intrafusal fibers, without any change in the extrafusal fibers' length. The contraction of the intrafusal fibers increases the firing rate of the Ia *afferent* neuron, which in turn excites the alpha motor neuron, resulting in contraction of the extrafusal muscle and in additional flexion of the hand.

Fourth Segment – Muscle Relaxation
The additional flexion of the hand increases the tension in the muscle tendons (marked by a red color in the tendon). Stretching the tendon leads to activation of the Golgi tendon organ, which in turn excites the Ib afferent neuron. Action potentials from the Ib neuron enter the spinal cord and excite an interneuron that inhibits the alpha motor neuron. The inhibition is marked in blue within the *soma* of the alpha motor neuron. As the alpha motor neuron stops firing, the muscle relaxes and elongates, and the hand is extended.

Spinal Reflexes

The Stretch Reflex

The stretch reflex is a negative feedback loop to resist changes in muscle length. The illustration shows an arm holding an empty cup, with three exposed muscles: the flexor, including a *muscle spindle*; the synergist muscle, controlling the same joint with a similar action; and the extensor, also called the antagonist muscle, that has an opposite action. Also shown are a cross-section of the spinal cord; a Ia *afferent* axon (in blue), which innervates the muscle spindle of the flexor muscle; and three alpha motor neurons innervating the three muscles. The Ia axon excites alpha motor neurons (in purple and dark green), which innervate the flexor and synergist muscles. The Ia axon also excites an interneuron (white), which inhibits the alpha motor neuron (in light green) of the antagonist muscle.

First Segment – Stretching of the Flexor Muscle
The cup is suddenly filled with water, causing the hand to stretch downward. The flexor muscle and its spindle are stretched. The stretching causes the Ia afferent neuron to fire at a higher frequency. The action potentials enter the spinal cord

through the *dorsal* horn.

Second Segment – Excitation of the Flexor and Synergetic Muscles
The Ia afferent neuron excites alpha motor neurons that innervate the flexor and synergist muscles. At the same time, the Ia afferent neuron excites an interneuron, which inhibits the alpha motor neuron of the antagonist muscle. This inhibition is represented by a blue color in the cell *soma* and a minus sign alongside it.

Third Segment – Contraction of the Flexor and Synergetic Muscles
The increased rate of firing in the alpha motor neurons leads to contraction of the flexor and synergist muscles. At the same time, inhibition of the alpha motor neuron causes the antagonist muscle to relax. When the flexor and synergist muscles contract, the hand flexes and almost returns to its original posture.

Spinal Control of Walking

Although walking is a voluntary action, once initiated it does not require coordination by the brain. When we walk, we are generally unaware of the changing movements of our feet as they move us forward. This allows us to carry out additional activities while walking, such as talking, listening, and even reading. The automatic and easy nature of walking can be attributed to local spinal circuits that coordinate the contraction of muscles used in walking. These neural circuits in the spinal cord are known as locomotion pattern generators.

The following video clip shows a recording of neuronal circuit activity in the spinal cord of a rat. These circuits serve as locomotion pattern generators. The recording was taken from an isolated lumbar area of the spinal cord (recorded from the L3 segment). The upper trace is from the left *ventral* horn, innervating the left leg, and the lower trace is from the right ventral horn, innervating the right leg. Once walking is initiated, circuits in the spinal cord generate rhythmic activity. As the white line shows, this rhythmic activity involves alternating excitation of motor neurons that innervate the left leg (as shown in the upper trace) followed by excitation of motor neurons that innervate the right leg (in the lower trace). Thus, walking is coordinated at the level of the spinal cord, without intervention from the brain. Other spinal pattern generators are responsible for carrying out automatic motor activities, such as chewing and swimming.
(Movie provided by Lev-Tov, A., Medical School, The Hebrew University of Jerusalem, Jerusalem, Israel.)

Descending Motor Tracts

Tracts of nerve fibers descend from the cortex and the brain stem along the *white matter* of the spinal cord. These tracts convey motor information to neurons that have their cell bodies in the ventral horn of the *gray matter*. These neurons control skeletal muscles. The descending tracts are grouped functionally in distinct medial and lateral positions in correspondence with the somatotopic organization of motor nuclei within the gray matter. The most medial part of the ventral horn contains *motor neuron* pools that innervate the axial muscles and proximal muscles of the limbs; whereas the lateral part contains motor neurons that innervate the distal muscles of the limbs.

Descending motor tracts in the lateral columns of the spinal cord terminate in the lateral part of the ventral horn and innervate distal muscles (muscles far from the center of the body, such as arm and fingers).

Descending motor tracts in the medial columns of the spinal cord terminate in the medial part of the ventral horn and innervate proximal muscles (muscles close to the trunk, such as the shoulders) and axial muscles (muscles at the center of the body, such as the back muscles).

Selecting each check box presents a tract descending from the cortex or the brain stem. The red lines in the small schematic picture on the bottom left indicate the planes and position of each brain section.

Descending Tracts from the Cerebral Cortex

Lateral Corticospinal Tract

The corticospinal tract, also known as the pyramidal tract, originates in the *primary motor cortex* and terminates in the spinal cord. At the level of the medulla oblongata the tract splits into two branches that take different spinal paths: 90 percent of the axons cross to the contralateral side of the medulla and form the lateral corticospinal tract; the remaining 10 percent continue on the ipsilateral side and form the ventral corticospinal tract.

Axons of the lateral corticospinal tract descend through the internal capsule and proceed through the cerebral peduncles to the pyramids in the ipsilateral side of the medulla oblongata. At the medulla, the axons cross to the contralateral side of the brain (decussation), descending within the lateral column of the white matter in the spinal cord. The name “pyramidal tract” refers to the pyramidal shape of the axon bundles decussating at the ventral surface of the medulla. The lateral corticospinal tract conveys motor information to *distal* skeletal muscles, mainly controlling voluntary movements of the arms, hands, and fingers.

Ventral Corticospinal Tract

The *ventral* corticospinal tract originates in the *primary motor cortex* and the supplementary motor area. It descends through the internal capsule and the cerebral peduncles to the medulla oblongata. The axons in this tract continue to descend on the same side of the brain to create a column in the medial-ventral part of the *white matter* of the spinal cord. The column terminates in the gray matter of the spinal cord, where some of the axons decussate and innervate motor neurons in the *contralateral* side. The ventral corticospinal tract conveys information to both *axial* and *proximal* skeletal muscles, mainly controlling movement of the neck and the axial skeletal muscles

.

Corticobulbar Tract

The corticobulbar tract, like the corticospinal tract, begins at the primary motor cortex. The tract receives information from both the premotor cortex and the somatosensory cortex. The tract descends through the internal capsule of the brain and terminates in the nuclei of the cranial nerves (such as the facial nerve nucleus) at the pons and the medulla. The corticobulbar tract is mainly responsible for movements of the eyes, jaws, and tongue, as well as speech production and facial expressions.

Descending Tracts from the Brain Stem

Tectospinal Tract

The tectospinal tract extends from the superior colliculi in the brain stem, crosses to the contralateral side at the tegmentum, and descends down the medial-*ventral* part of the *spinal cord*. This tract conveys motor information to the *axial* and *proximal* skeletal muscles and coordinates neck and eye movements in response to visual information.

Vestibulospinal Tracts

There are two vestibulospinal tracts, the ventral and the medial, which extend from the vestibular nuclei in the brain stem. These tracts innervate motor neurons on both sides of the spinal cord and are important for maintaining balance and controlling head and neck movements.

Reticulospinal Tract

The reticulospinal tract conveys motor information from the reticular formation in the brain stem to the spinal cord. This tract innervates motor neurons of axial skeletal muscles, which are important in maintaining muscle tonus and controlling automatic movements such as posture, breathing, coughing, and sneezing.

Rubrospinal Tract

The rubrospinal tract extends from the *red nucleus* in the midbrain. At the tegmentum it crosses to the contralateral side of the brain (decussation) and descends in the lateral column of the spinal cord. The tract innervates *distal* muscles, controlling voluntary movements of the limbs.

Primary Motor Cortex

The Motor Homunculus

The primary motor cortex is located in the precentral gyrus of the frontal lobe. Stimulation experiments (including those in awake humans) have shown that activation of neurons located in certain parts of the primary motor cortex leads to the movement of specific body parts. Neurons in the motor cortex are somatotopically organized, so that adjacent body parts are represented in adjacent cells in the *cortex*. The illustration presents a motor homunculus—a somatotopic map of the body as represented on the surface of the motor cortex (a similar map also exists in the somatosensory system, where it is called the sensory homunculus). The somatotopic organization can be seen on a cross-section of the primary motor cortex (on the left) and in the homunculus figure (on the right). Notice that different body parts are represented disproportional to their actual size. The parts of the body used in tasks requiring precision and fine control (the face, hands, and tongue) have a proportionately larger representation in the homunculus. Parts of the body used in gross movements (such as the back) are represented by a relatively small area of the motor cortex and therefore appear smaller in the homunculus. Roll the cursor over various body parts and see how the areas that innervate these organs light up in the primary motor cortex.

Population Vector

Each neuron in the primary motor cortex responds maximally to a movement in a certain direction. The response gradually decreases as the direction of movement diverges from the preferred direction.

The video clip shows a recording of a large number of neurons in the primary motor cortex of a monkey. The monkey is using its hand to trace the course of a spiraling point of light. The direction of the monkey's hand movement is traced by the white line. Blue rays extend from the head of the white line, with a single yellow ray at their center. Each of the blue rays represents the vector of a single neuron. The direction of the vector indicates the preferred orientation of the cell, while its length indicates the firing rate at a given direction of movement. The yellow ray at the center represents "the population vector"—the average vector of the entire population of neurons responding to a certain direction of the hand movement (i.e., the average of all the blue vectors).

As can be seen, there is a high degree of correspondence between the direction of movement (the white line) and the population vector (the yellow ray). It can be concluded that a voluntary movement is associated not only with the activity of individual neurons, but also with the activity of a large population of cells in the primary motor cortex. Each neuron "points" to its preferred direction of movement (vector) and responds to the actual direction with a certain firing rate. The weighted average of the response of all the vectors determines the actual direction of movement.
(Movie provided by Schwartz, A., The Neuroscience Institute San Diego, CA.)

Brain Control of Movement

Higher Order Motor Areas

Detailed Anatomy
The motor cortex plays a central role in the performance of voluntary movements. It consists of three main areas: the primary motor cortex, the premotor cortex, and the supplementary motor cortex. Each of these areas sends information directly to the spinal cord through the corticospinal tract (also called the *pyramidal tract*), or indirectly via subcortical areas and the brain stem. The premotor cortex and the supplementary motor cortex are responsible for the planning and coordination of complex movements. These areas receive information from the posterior parietal cortex and from the anterior associative areas in the prefrontal lobe, and convey information to the primary motor cortex. The primary motor cortex receives input from the somatosensory cortex, which is necessary for coordination and refinement of voluntary movements.

Primary Motor Cortex
The primary motor cortex is located in the *frontal lobe*, anterior to the central sulcus. It directly controls voluntary movements and executes planned movements. The primary motor cortex receives direct input from the somatosensory cortex regarding the precise location of the body and limbs, *proprioception*, and touch sensation. It

also receives indirect information from other sensory modalities, including visual and auditory information. This information provides fast sensory feedback when carrying out motor activities and is important in the production of delicate and precise movements.

Primary Somatosensory Cortex
The primary somatosensory cortex is located in the postcentral gyrus, posterior to the central sulcus. Tracts extending from the *spinal cord* provide this area with sensory information relating to muscle tonus, joint position, pressure, and touch. The sensory information is transferred from the primary somatosensory cortex to the associative somatosensory cortex and the primary motor cortex. Sensory information helps coordinate and refine voluntary movements.

Premotor Cortex
The premotor cortex plays a role in the control of proximal and axial muscles. These muscles are important for the initial orientation of the body and limbs toward a target.

The premotor cortex also participates in the control of movement through visual and somatosensory cues that arrive from the posterior parietal cortex (see the video clip "Preparation for Movement"). The premotor cortex sends its output to the primary motor cortex, the *brain stem* (to the reticulospinal tract, in particular), and the spinal cord.

Supplementary Motor Area
The supplementary motor area is involved in the planning of complex movement sequences, such as turning the body in a certain direction or opening and closing the hand. Direct neural pathways extend from this area to the spinal cord, innervating proximal muscles. The innervation of distal muscles by the supplementary motor area is carried out indirectly through the primary motor cortex. Studies based on brain imaging, such as PET scans, have shown that the supplementary motor area is activated both during the performance of complex movements and during mental activities wherein the subject only imagines that he/she carries out such movements.

Posterior Parietal Cortex
The posterior parietal cortex receives input from the somatosensory cortex and visual cortex and sends output to the premotor cortex and the supplementary motor area. The posterior parietal cortex is also *somatotopically organized*. Patients with lesions in this area experience difficulty in reaching objects under visual guidance, a syndrome called optic ataxia. (See video clip "Optic Ataxia" in the subsection "Brain Lesions in the Visual Cortex.")

The Premotor Cortex: Preparation for Movement
The premotor cortex participates in the control of movement through visual and somatosensory cues arriving from the posterior parietal cortex. The video clip presents a recording of the activity in the premotor cortex of a monkey. The response of the neuron is recorded by means of a microelectrode. The neural activity (action potentials) is translated into auditory signals, so that a sequence of action potentials sounds like a barrage. This recording reveals neurons in the premotor cortex that are activated during preparation for movement, but not during movement itself.

The monkey is presented with a panel with five light bulbs. At the beginning of the experiment, all five light bulbs turn on momentarily, after which all turn off except for the one in the center. Then, a light bulb on the side briefly turns on, indicating the target. The monkey's task is to press the target, but only after the central light has turned off.

When the target goes on, the monkey begins to plan its hand motion toward the target, and the recorded neuron fires a barrage of action potentials. The action potentials stop when the central light goes off and the monkey begins to reach for the target. Thus, the particular neuron recorded in the premotor cortex is active during the preparation of the action rather than during the action itself.

The Basal Ganglia

Neural Connections

Basal Ganglia

The basal ganglia are a group of subcortical nuclei located in the white matter surrounding the lateral *ventricles*. They constitute an important component of the motor system, receiving input from diverse regions of the cerebral cortex and projecting their output back to the frontal cortex via the thalamus. Some of our knowledge concerning the motor function of the basal ganglia comes from the study of neural diseases affecting them, such as Parkinson's disease and Huntington's chorea.

The illustration presents a frontal section of the brain and a diagram showing the input-output organization of the basal ganglia. Also shown are connections within the basal ganglia. The red arrows mark excitatory neural connections, while the blue arrows mark inhibitory connections. Selecting the check boxes at the bottom of the diagram presents input sources, intraconnections, and the output of the basal ganglia.

Basal Ganglia Input

The striatum, the input area of the basal ganglia, receives excitatory and inhibitory input from diverse regions of the cerebral cortex. It receives excitatory input from the cortex, particularly from the motor cortex and the somatosensory cortex. And it also receives excitatory and inhibitory dopaminergic input from the substantia nigra. The striatum is divided into two nuclei: the caudate nucleus and the putamen.

Intraconnections within the Basal Ganglia

The *striatum* projects the information to the inner segment of the globus pallidus(Gp_i), the major output pathway of the basal ganglia. The information is projected along two neural pathways—a direct and an indirect pathway. The direct pathway conveys inhibitory information from the striatum to the Gp_i. The indirect pathway projects through the external segment of the globus pallidus (Gp_e) and through the subthalamus to the Gp_i. Activity in this pathway results in excitation of the Gp_i by the means of inhibition-of-inhibition. Thus, the direct pathway inhibits the Gp_i, while the indirect pathway excites it. Dopaminergic input arriving at the striatum from the *substantia nigra* amplifies the inhibitory message of the direct pathway (through D1-type dopamine receptors) and reduces the excitatory message of the indirect passage (through D2-type dopamine receptors). Thus, dopaminergic input from the substantia nigra results in increased inhibition of the Gp_i.

Basal Ganglia Output

The Gp_i, the main output source of the basal ganglia, projects to the ventral-lateral nucleus (VL) and the ventral-anterior nucleus (VA) of the thalamus. From there, the information proceeds to motor areas in the frontal cortex. Inhibition of the Gp_i removes its inhibitory effect on the thalamus and results in increased excitatory input from the thalamus to the motor areas.

Thus, the projection from the cortex to the basal ganglia and back completes a neural circuit that allows the basal ganglia to regulate the excitation level of motor areas. This level of excitation is important for the initiation and termination of movements. Impairment of this circuit may result in inhibition of the motor cortex, as happens in Parkinson's disease; or in over-excitation, as is the case in Huntington's chorea.

Parkinson's Disease

Parkinson's disease is characterized by motor disturbances including muscular rigidity, slowness of movement, a resting tremor, postural instability, and difficulty in initiating movements. The disease may also be associated with cognitive defects. The video clip presents the difficulties of a Parkinson's patient while trying to initiate a movement. The patient finds it hard to start walking in the room and uses his walking cane to initiate the walking movement. Once he begins moving, he quickly walks a few small steps, stops, then starts moving again. The difficulties involved in initiating a movement are also evident when he is requested to turn around and return to the other side of the room. The second part of the clip shows the rigidity and uncontrollable resting tremor in his limbs.

The difficulties Parkinson's patients experience arise from degeneration of dopaminergic neurons in the pathway between the substantia nigra and striatum (the nigro-striatal pathway). In a healthy person, these neurons project from the substantia nigra to the striatum in the basal ganglia and inhibit the inner segment of the globus pallidus (Gp_i). (See also the "Basal Ganglia" subsection.) Dopamine deficiency in Parkinson's patients leads to over-excitation of the Gp_i and subsequently to a decreased excitation of the motor cortex. The low level of cortical excitation causes difficulties in movement initiation and termination. The limb rigidity and instability typical of Parkinson's patients are also related to over-activity of the Gp_i and to the ensuing inhibition of motor nuclei in the *brain stem*.

Parkinson's patients are treated with L-DOPA, the precursor of dopamine. This drug increases the production and release of dopamine in the nigro-striatal pathway, and in this way partly compensates for the degeneration of dopaminergic neurons projecting to the striatum. Elevated levels of dopamine in the striatum partially alleviate the symptoms of Parkinson's disease. Sometimes, however, this beneficial effect is short-lived. Moreover, the drug is liable to cause severe side-effects. A number of new treatments are currently being considered. One is based on transplantation of fetal dopaminergic nerve cells in the striatum in an attempt to reestablish the secretion of dopamine. Another treatment is based on surgical destruction of the Gp_i area, which is over-active in Parkinson's patients. Patients that underwent such an operation achieved a considerable improvement for a number of years.
(Movie provided by Ivry, R., Department of Psychology, University of California, Berkeley, CA.)

The Cerebellum

Neural Connections

Cerebellum

The cerebellum is a large structure located dorsally to the brain stem pons. The cerebellum ("little brain") resembles the structure of the cerebrum. It comprises two *hemispheres*, separated by a mid-area called the vermis. A cortex with many folds covers the cerebellum. Underneath the cortex are a number of deep cerebellar nuclei. The cerebellum plays a key role in movement and regulating the functions of the descending motor pathways. It is important for the execution of fast, coordinated movements. It also participates in motor learning and in maintaining posture and equilibrium. Damage to the cerebellum causes jumpy, jerky, and non-coordinated movements.

The cerebellum can be divided into three functional systems: the spinocerebellum system, the cerebrocerebellum system, and the vestibulocerebellum system. Each system consists of a region of the cerebral cortex and one or more deep nuclei.

Spinocerebellum System

The spinocerebellum system receives somatosensory information from the spinal cord, which is *somatotopically organized*. The input reaches the cerebellar cortex at the vermis and at the intermediate hemispheres. The cortical areas project to two groups of deep cerebellar nuclei: the interposed nuclei and the fastigial nucleus. These deep nuclei also receive direct information from the spinal cord.

The output of this system projects to nuclei in the *brain stem* and the midbrain, as well as to the motor cortex. Through this system the cerebellum controls the ongoing execution of limb movement.

Cerebrocerebellum System

The cerebrocerebellum system receives input from sensory and motor cortical areas via nuclei in the pons. The input reaches the lateral cerebellar hemispheres, and from there it is projected back to the dentate nucleus, a deep nucleus in the cerebellum. The dentate nucleus also receives information directly from the cortex.

The output of this system is projected to the thalamus and from there to the motor cortex and premotor cortex. The neural circuit through which information is projected from the cortex to the cerebellum and back allows the cerebrocerebellum system to participate in the planning and monitoring of movements.

Vestibulocerebellum System

The vestibulocerebellum system receives information relating to body balance and equilibrium from the vestibular nerve and the vestibular nuclei in the *brain stem*. The input reaches the flocculonodular lobe of the cerebellum, and from there it is projected back to the vestibular nuclei. The vestibular nuclei also receive direct information from the vestibular nerve.

The output of the vestibulocerebellum system is projected to vestibular nuclei in the brain stem. Through this system the cerebellum coordinates between head and eye movements and controls body equilibrium while standing and walking.

Cerebellar Atrophy

The video clip presents a patient with a cerebellar atrophy syndrome, caused by an accidental lesion to the lateral hemisphere of the cerebellum. The syndrome is manifested in an inability to perform continuous and precise reaching movements toward a target. When the patient is requested to touch his nose with his hand, he produces a decomposed movement (comprised of discrete movements of the shoulder, elbow, and wrist), rather than a coordinated, smooth movement. Moreover, the closer the hand gets to the nose, the greater its tremors.

Lesions to the lateral hemisphere of the cerebellum also impair the synchronization of fast ballistic movements. Ballistic movements (such as tossing or throwing) take place so fast that they cannot be modified and redirected once the action is initiated. It is therefore necessary to pre-plan the entire sequence of required muscular movements and ensure that each and every muscle operates at the appropriate timing. When rapidly reaching for a target, the cerebellum synchronizes the alternating activity of flexor and extensor muscles. In the video clip, when the patient is asked to quickly track the physician's finger, he makes an exaggerated movement, overshooting the target. The imprecise ballistic movement arises from his difficulty in synchronizing the action of flexor and extensor muscles.
(Movie provided by Ivry, R., Department of Psychology, University of California, Berkeley, CA.)