PART V

MOTOR SYSTEM

25.

SPINAL CONTROL OF MOVEMENT

The motor system controls all of our skeletal muscle movement. There are multiple levels of control. Within the spinal cord, simple reflexes can function without higher input from the brain. Slightly more complex spinal control occurs when central pattern generators function during repetitive movements like walking. The motor and premotor cortices in the brain are responsible for the planning and execution of voluntary movements. And finally, the basal ganglia and cerebellum modulate the responses of the neurons in the motor cortex to help with coordination, motor learning, and balance.

This lesson explores the lowest level of control – spinal reflexes.

Resources

- Key Takeaways
- Test Yourself
- Additional Review
- Video Version

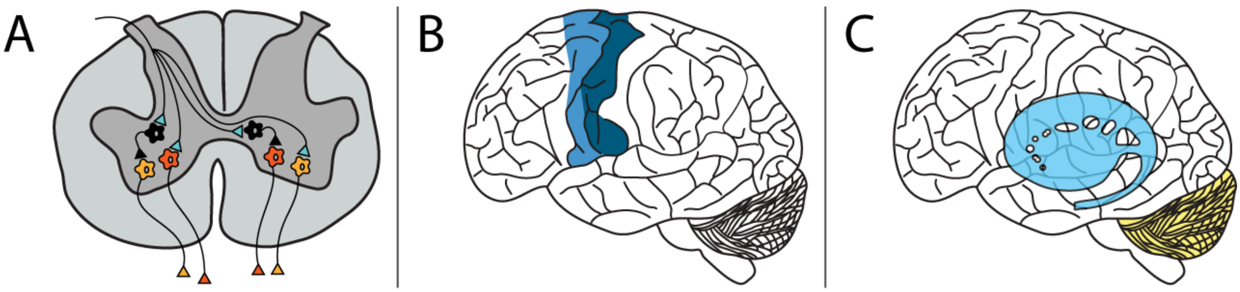


Figure 25.1. Motor output is controlled at multiple levels: A. Spinal cord and spinal neurons, B. Motor (dark blue) and premotor (light blue) cortices, C. Basal ganglia (a subcortical structure shown in light blue) and cerebellum (yellow). 'Motor Control Levels' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Alpha Motor Neurons

Muscle fibers are innervated by alpha motor neurons. The cell bodies of the alpha motor neurons are located in the central nervous system in the ventral horn of the spinal cord. Their axons leave the spinal cord via the ventral roots and travel to the muscle via efferent peripheral spinal nerves.

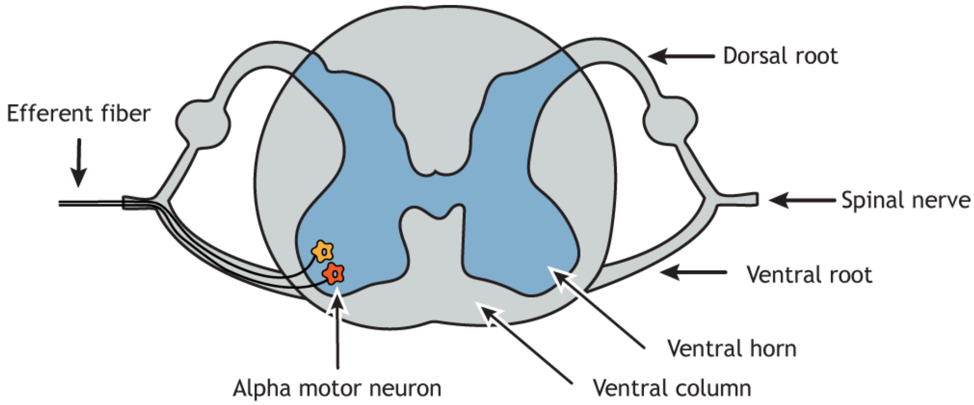


Figure 25.2. Alpha motor neurons are located in the ventral horn of spinal cord. Their axons, which are efferent fibers, travel to the muscles via spinal nerves. 'Alpha Motor Neurons' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

One alpha motor neuron can innervate multiple fibers within one muscle; the axons of a motor neuron can branch to make synaptic contacts with many fibers. A motor neuron and the fibers innervated by it are called a motor unit. The muscle fibers within one motor unit are often spread throughout the muscle to spread the contraction throughout the full muscle.

The group of motor neurons that innervate all the fibers of one muscle is called a motor pool.

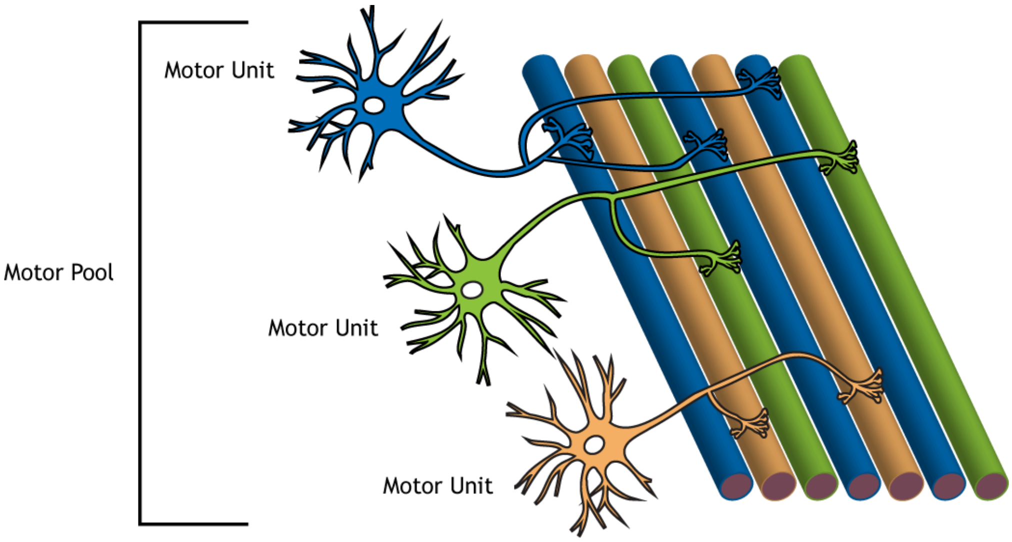


Figure 25.3. Motor neurons can innervate more than one muscle fiber within a muscle. The motor neuron and the fibers it innervates are a motor unit. Three motor units are shown in the image: one blue, one green, one orange. Those three motor units innervate all the muscles fibers in the muscle and are the motor pool for that muscle. 'Motor Unit and Pool'by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Neuromuscular Junction

The neuromuscular junction is one of the largest synapses in the body and one of the most well-studied because of its peripheral location. Acetylcholine is the neurotransmitter released at the neuromuscular junction (NMJ), and it acts upon ligand-gated, non-selective cation channels called nicotinic acetylcholine receptors that are present in postjunctional folds of the muscle fiber. Acetylcholinesterase, an enzyme that breaks down acetylcholine and terminates its action, is present in the synaptic cleft of the neuromuscular junction.

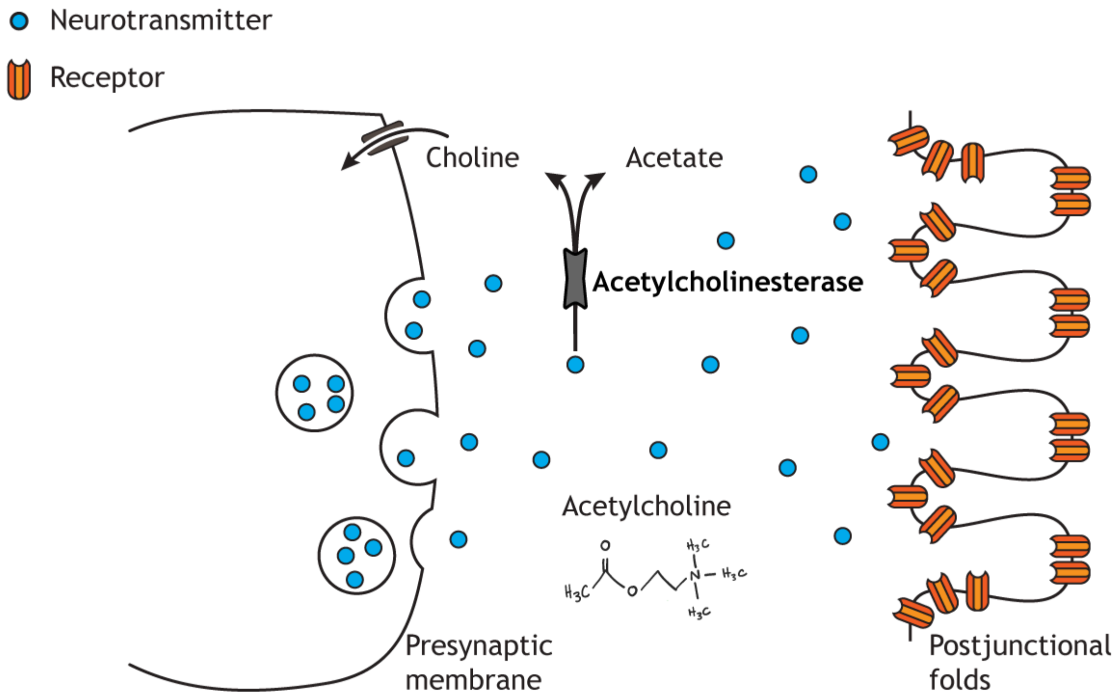


Figure 25.4. The neuromuscular junction (NMJ) is the synapse between a motor neuron and a muscle fiber. Acetylcholine is released at the NMJ and acts on nicotinic acetylcholine receptors located in the postjunctional folds of the muscle fiber. Neurotransmitter action is terminated by breakdown by acetylcholinesterase. 'Neuromuscular Junction' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Nicotinic acetylcholine receptors allow the influx of sodium ions into the muscle cell. The depolarization will cause nearby voltage-gated channels to open and fire an action potential in the muscle fiber. In a healthy system, an action potential in the motor neurons always causes an action potential in the muscle cell. The action potential leads to contraction of the muscle fiber.

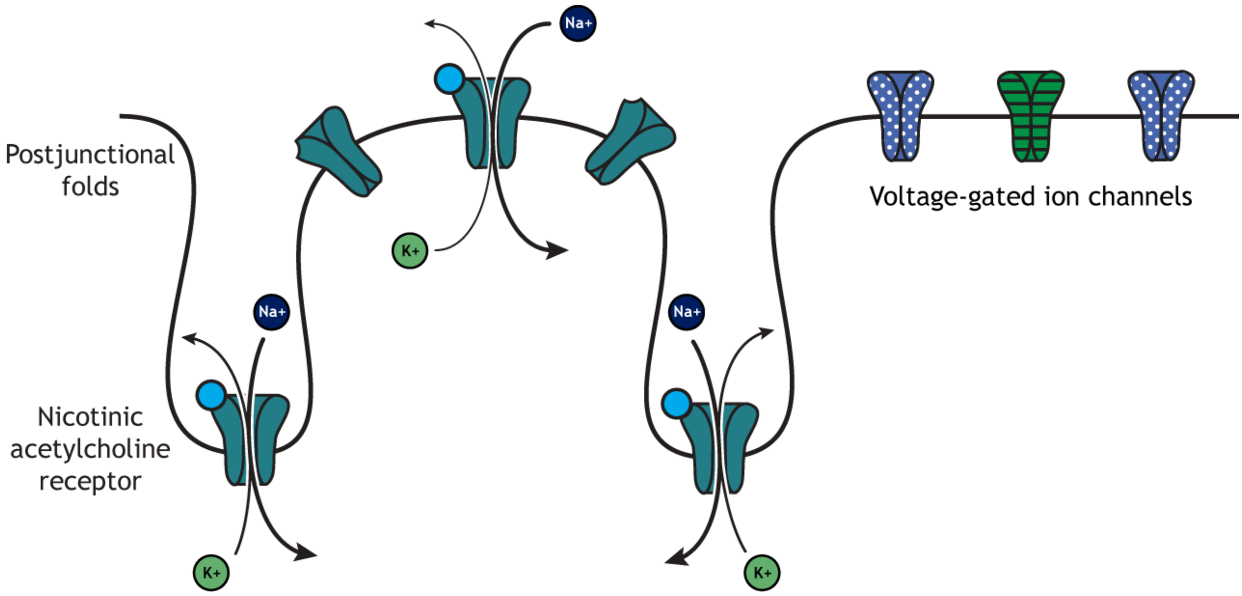


Figure 25.5. The ionotropic nicotinic acetylcholine receptors in the postjunctional folds of the muscle fiber are non-selective cation channels that allow the influx of sodium and the efflux of potassium The depolarization of the cell by the sodium influx will activate nearby voltage-gated ion channels. 'NMJ Ion Flow' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Organization

Like the sensory systems, the motor system is also organized in a topographic fashion. Within the spinal cord, alpha motor neurons that innervate muscles in the arms and legs are located in the lateral portion of the ventral horn, whereas alpha motor neurons that innervate muscles in the trunk are located in the medial portion.

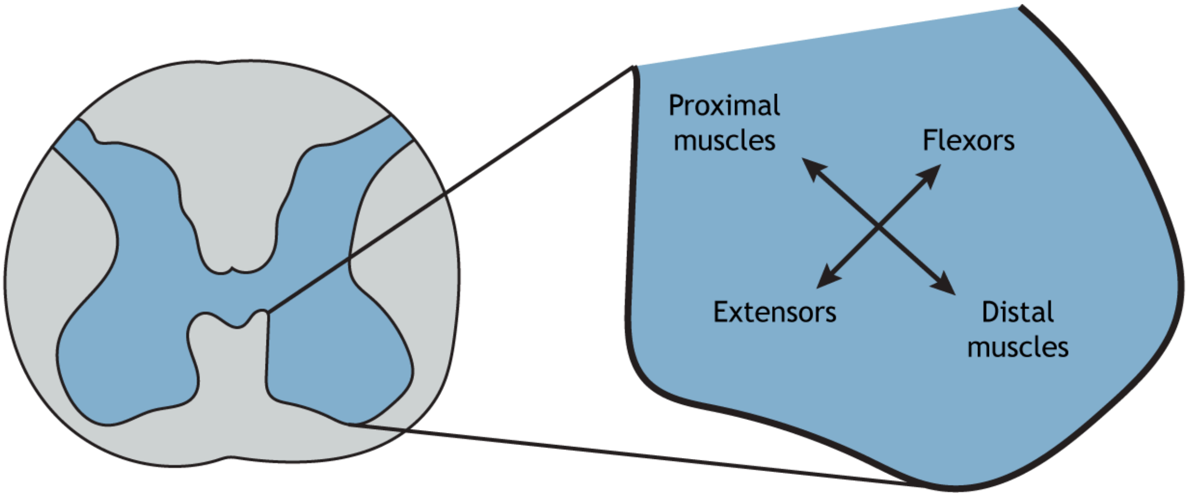


Figure 25.6. The ventral horn is organized in a topographic manner, with proximal muscles (like those in the trunk) located more medially than distal muscles (like the arms or legs). Additionally, motor neurons are organized by function with extensor motor neurons located together and flexor neurons located together. 'Spinal Cord Map' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Sensation

Proprioception is the ability to know where your body is in space and relies on the presence of sensory receptors located within the muscles. Some of these specialized structures are called muscle spindles, and they monitor muscle fiber stretch. Information is relayed to the nervous system via Group I sensory axons, which are large, myelinated fibers. Muscle spindles are important for spinal reflexes.

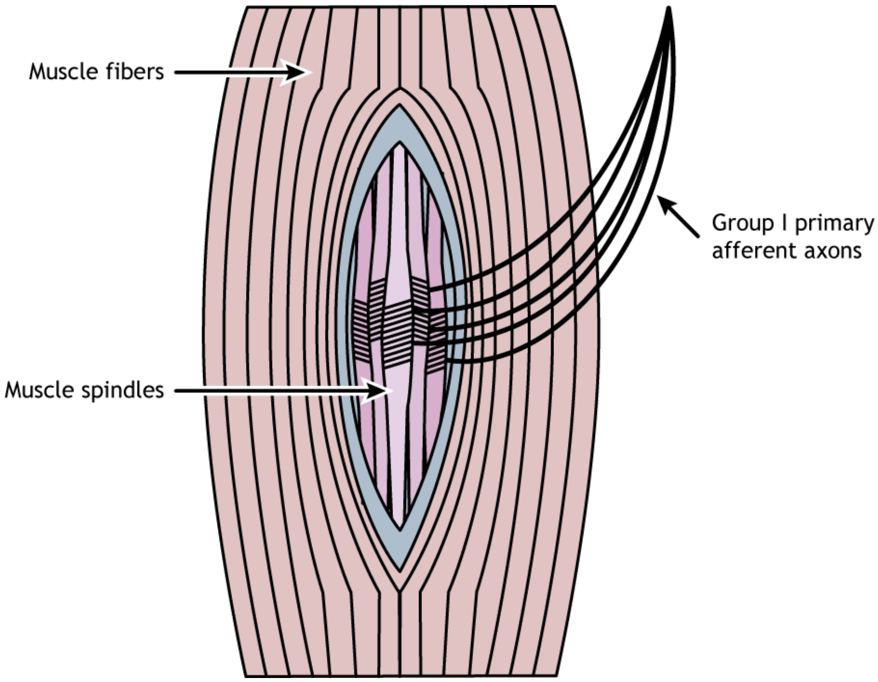


Figure 25.7. Type I primary afferent sensory axons wrap around the fibers within the muscle spindle, located deep in the muscle. When the muscle stretches, these sensory neurons are activated. 'Muscle Spindle' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Reflexes

Stretch (Myotatic) Reflex

The stretch reflex, also called the myotatic, patellar, or knee-jerk reflex, occurs in response to activation of the muscle spindle stretch receptors. The stretch reflex is a common occurrence at a doctor's visit when the doctor taps your knee with a little hammer. This usually results in the lower leg kicking up slightly. The synaptic communication for this reflex takes place completely within the spinal cord and requires no input from the brain.

The knee is tapped on the tendon that connects to the quadriceps muscle. The tendon extends enough to stretch the quadriceps muscle, activating the stretch receptors. Sensory information travels to the dorsal horn of the spinal cord where it synapses on alpha motor neurons that innervate the quadriceps. Activation of the motor neurons contracts the quadriceps, extending the lower leg. This is called monosynaptic communication because there is only one synapse between the sensory input and the motor output.

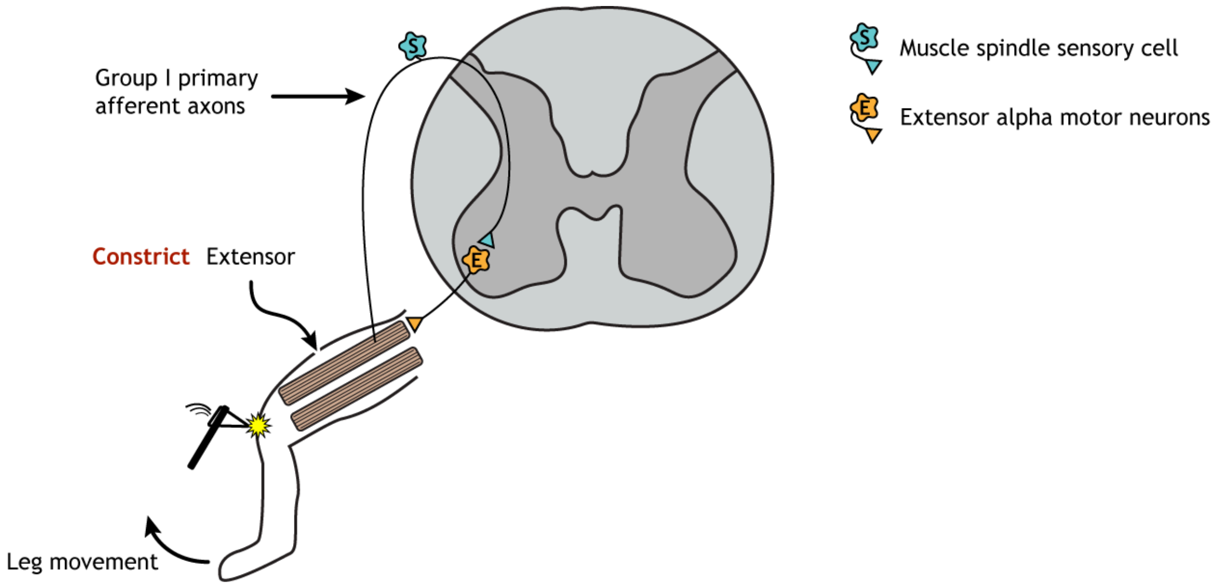


Figure 25.8. When the tendon in the knee is tapped, the extensor muscle is stretched slightly. This stretch activates the Group I sensory afferent axons (blue S neuron in dorsal root ganglion) from the muscle spindles. The sensory neurons synapse on and activate motor neurons (yellow E neuron) that constrict the extensor muscle, causing the leg to kick upward. The stretch reflex is a monosynaptic reflex. 'Stretch Reflex Extensor' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

The sensory neurons also synapse on interneurons within the spinal cord that are inhibitory. These inhibitory interneurons then synapse on alpha motor neurons that innervate the hamstring, the antagonistic flexor muscle to the quadriceps. When these motor neurons are inhibited, the hamstring muscle relaxes, allowing the contraction of the quadriceps to occur with more ease.

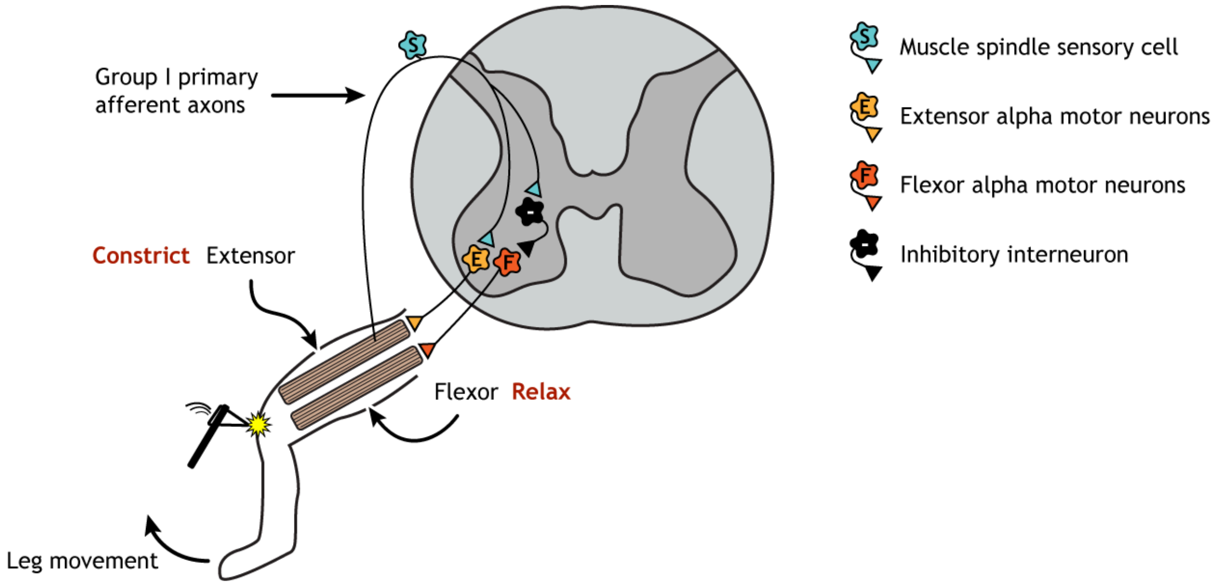


Figure 25.9. In addition to the monosynaptic extensor reflex, the sensory information from the muscle spindle sensory cell (blue S neuron) also activates inhibitory interneurons (black – neuron) in the spinal cord. These interneurons then inhibit the motor neurons (orange F neuron) that innervate the flexor muscle, causing the flexor muscle to relax. This relaxation allows the extensor muscle to kick the leg up with less opposition from the flexor muscle. 'Stretch Reflex' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Withdrawal (Flexor) Reflex

A similar process can be seen in the withdrawal reflex. In this case, instead of an extension, the muscles lead to muscle flexion in response to a stimulus. If, for example, you step on something painful, the reflex will be to lift the injured foot. The sensory information that initiates this reflex is activation of pain receptors, or nociceptors. Like with the stretch reflex, the sensory information enters the spinal cord at the dorsal horn. Unlike the stretch reflex, the withdrawal reflex is a polysynaptic reflex, meaning interneurons are present between the sensory neurons and the motor neurons. Excitatory interneurons communicate with the alpha motor neurons of the flexor muscle, whereas inhibitory interneurons communicate with the alpha motor neurons of the extensor muscle. The behavioral response is flexing of the leg upward (the opposite action of the stretch reflex).

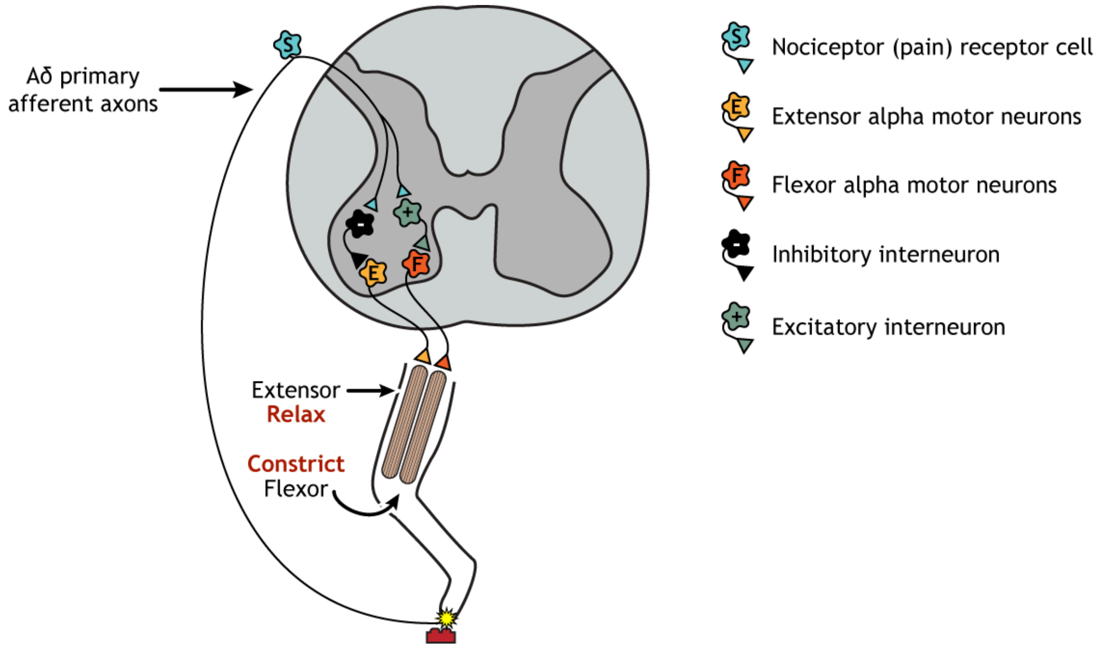


Figure 25.10. Pain information is sent from the periphery to the spinal cord via a nociceptor receptor cell (blue S neuron in dorsal root ganglion). The A delta sensory axons synapse on interneurons within the spinal cord. Excitatory interneurons (green + neuron) activate motor neurons (orange F neuron) that constrict the flexor muscle. Inhibitory interneurons (black – neuron) inhibit motor neurons (yellow E neuron) that innervate and relax the extensor muscle. The leg lifts in response. 'Withdrawal Reflex' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Crossed-Extensor Reflex

Running in parallel to the withdrawal reflex is the crossed-extensor reflex. If you step on something sharp and lift that leg, your other leg needs to be able to support your weight shift, or you would fall. This is accomplished by interneurons that cross the midline of the spinal cord and communicate with motor neurons on the contralateral side of the body. The painful sensory information that initiated the withdrawal reflex also initiates the crossed-extensor reflex. In addition to the ipsilateral interneurons active in the withdrawal reflex, the sensory axons also synapse on excitatory interneurons that cross the midline. These interneurons then synapse on excitatory interneurons that activate the alpha motor neurons of the extensor muscle and inhibitory interneurons that inhibit the alpha motor neurons of the flexor muscle (the opposite configuration to the withdrawal reflex). This leads to the leg extending, providing a stable base for the weight shift.

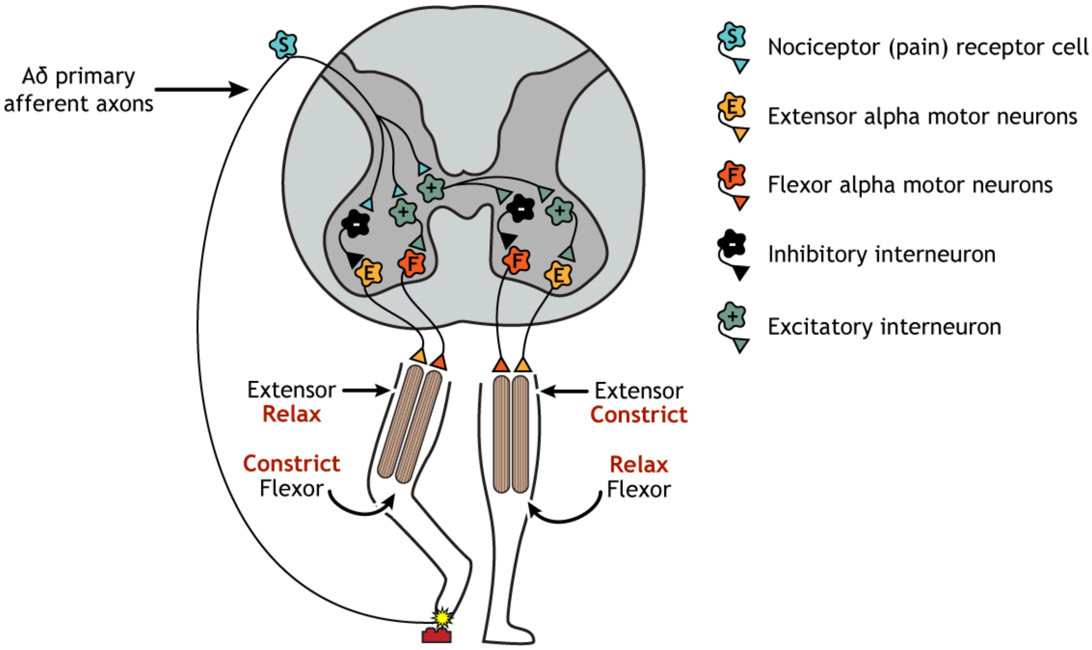


Figure 25.11. If the leg lifts due to the withdrawal reflex, the opposite leg must stabilize via contraction of extensor muscles to balance the body. This is accomplished by excitatory spinal interneurons that cross the midline and communicate the sensory information to the contralateral side of spinal cord. Inhibitory interneurons cause relaxation of the contralateral flexor muscles, and excitatory interneurons cause constriction of the contralateral extensor muscles. 'Crossed-Extensor Reflex' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Central Pattern Generators

Locomotion

Locomotion is one example of a basic, rhythmic movement that requires coordination of a number of muscle groups to work properly (other examples include swimming, flying, respiration, swallowing).

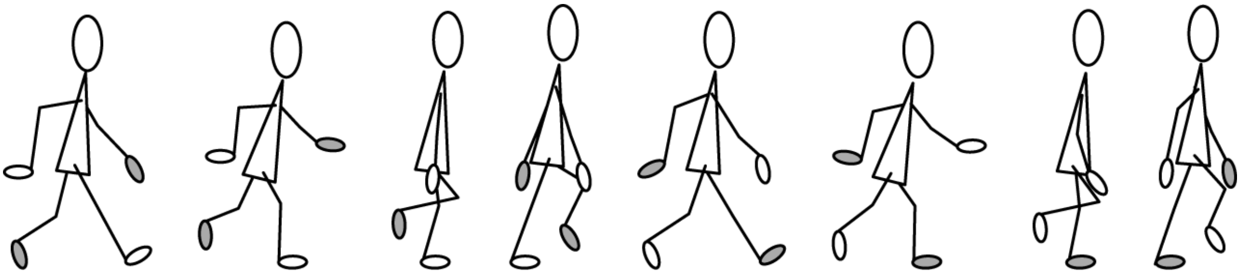


Figure 25.12. Walking cycle of a human. The arms and legs must be coordinated in opposing fashion during locomotion. The gray hand and foot are left side limbs. When one is in front of the body, the other is behind. 'Walking Cycle' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Activity of extensor and flexor muscles in both legs must be coordinated to allow smooth locomotion without falling. These rhythmical movements are controlled at the level of the spinal cord by circuits called central pattern generators. The spinal cord has circuitry that, in the case of walking, moves the legs in opposite patterns. When one leg is lifting up to move forward, the other leg is stable, touching the ground.

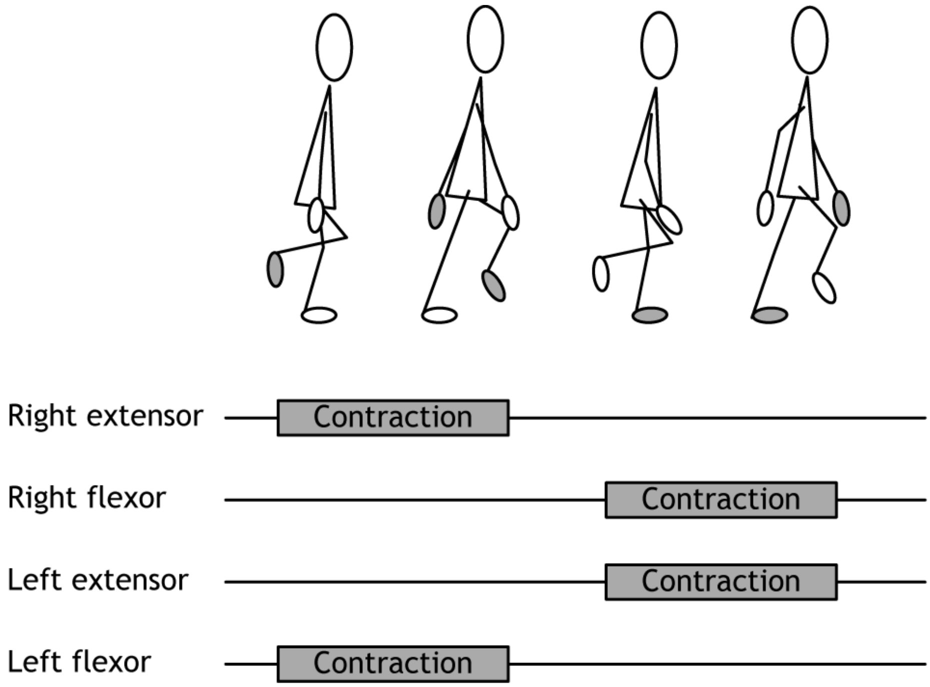


Figure 25.13. While walking, there must be coordinated, reciprocal activation of the extensor and flexor muscles of each leg; as an extensor is contracted (gray bar) the flexor must relax. Additionally, the muscle activation of one leg must be the opposite of the other leg, so the right extensor and the left flexor are activated at the same time. 'Walking Cycle Muscle Activation' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Spinal Circuitry

The control of this system has multiple levels. Neurons themselves may have pacemaker properties that allow for a continuous cycle of depolarization and repolarization. These neurons are then located within multi-cell circuits involving a collection of excitatory and inhibitory interneurons that results in reciprocal inhibition of contralateral muscles. Additional networks of spinal interneurons would cause reciprocal inhibition of ipsilateral antagonistic muscles.

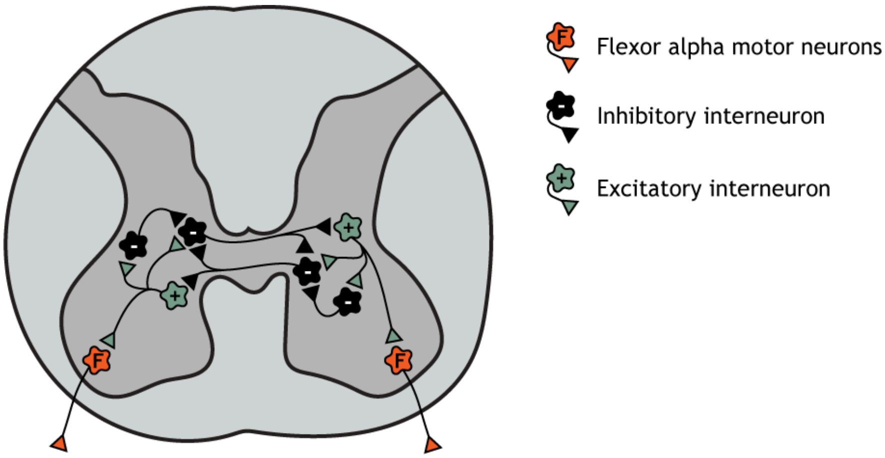


Figure 25.14. Central pattern generators are controlled by interneuron circuitry within the spinal cord. The circuit would require the motor neurons on the opposite side of the spinal cord to be activated in a reciprocal fashion. This is accomplished through a network of excitatory and inhibitory interneurons that allow for the flexor (or extensor) muscle on one side of the body to control while the contralateral muscle relaxes. 'Central Pattern Generator Circuit' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Although the spinal cord is able to control these movements on its own, there is input from both the brainstem and sensory neurons which can have an effect on modulating the pattern of neuronal activity in the spinal cord. For example, when an animal needs to slow down, speed up, or turn away from a danger, for example, those inputs can alter the spinal cord circuit.

Key Takeaways

- Motor neuron cell bodies are located in the ventral horn of the spinal cord
- Motor neuron axons are located in the peripheral nervous system and travel to muscles via spinal nerves
- Acetylcholine is released at the neuromuscular junction and acts upon ionotropic nicotinic acetylcholine receptors

- The spinal cord is topographically organized
- Control of reflexes occurs within the spinal cord and input from the brain is not needed
- Central pattern generators are circuits in the spinal cord that control repetitive, consistent movements like walking

Test Yourself!

An interactive H5P element has been excluded from this version of the text. You can view it online here:
https://openbooks.lib.msu.edu/neuroscience/?p=535#h5p-24

Additional Review

1. What is the difference between a motor unit and a motor pool?

Video Version of Lesson

A YouTube element has been excluded from this version of the text. You can view it online here: https://openbooks.lib.msu.edu/neuroscience/?p=535

26.

PLANNING OF MOVEMENT

There are a number of steps that must take place for voluntary movement to occur. Assessment of the surrounding environment and the body's location in space, followed by determining what action is appropriate, and then initiating that action. We will first focus on the cortical regions involved in planning of voluntary movement.

Resources

- Key Takeaways
- Test Yourself
- Video Version

After work, you sit down on the couch to watch one episode of your favorite show. As the end credits appear, you realize it is now time to head to your study space and start working on class. To do this, you need to leave the couch, grab your computer from the table, get your coffee from the kitchen and head to a different room. All of these voluntary movements take a great deal of processing by the brain. You must assess your surrounding environment and your body's location in it, determine which actions need to be completed, and then actually initiate those actions. In this chapter we will focus on how the planning of voluntary movement occurs.

Cortical Anatomy

Much of the cortex is actually involved in the planning of voluntary movement. Sensory information, particularly the dorsal stream of the visual and somatosensory pathways, are processed in the posterior parietal lobe where Visual, tactile, and proprioceptive information are integrated.

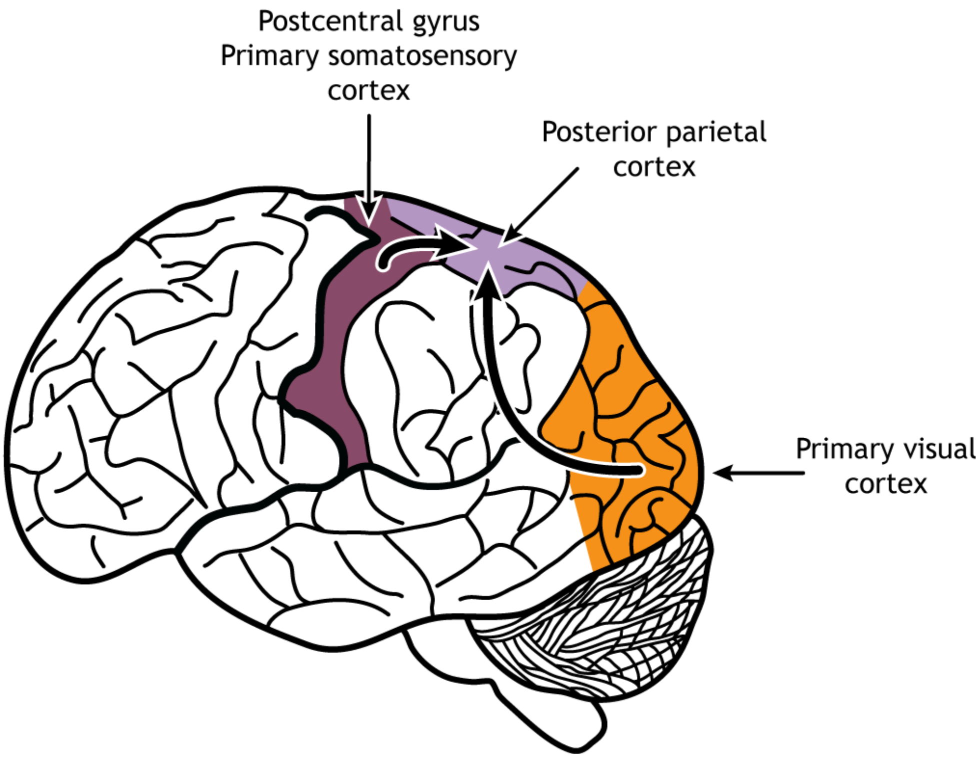


Figure 26.1. Information from multiple sensory systems are processed in the posterior parietal lobe. Projections are sent from the primary somatosensory and primary visual cortices. 'Posterior Parietal by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Connections from the posterior parietal lobe are then sent to both the premotor regions and the prefrontal cortex. The prefrontal cortex, which is located in the front of the brain in the frontal lobe, plays an important role in higher level cognitive functions like planning, critical thinking, and understanding the consequences of our behaviors. The premotor area lies just anterior to the primary motor cortex. This region helps plan and organize movement and makes decisions about which actions should be used for a situation.

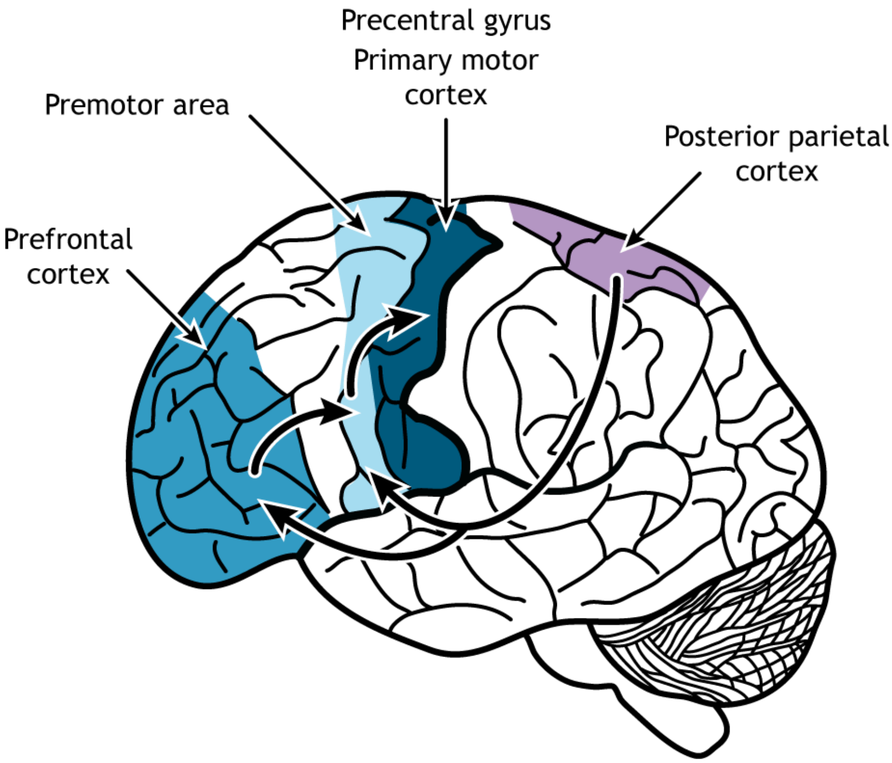


Figure 26.2. Sensory information from the posterior parietal is processed in the prefrontal cortex and premotor area, both located in the frontal cortex. These areas then send information to the primary motor cortex located in the precentral gyrus. 'Motor Regions' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

View the primary motor cortex using the BrainFacts.org 3D Brain

View the premotor cortex using the BrainFacts.org 3D Brain

View the prefrontal cortex using the BrainFacts.org 3D Brain

Role of Premotor Area

The premotor regions do send some axons directly to lower motor neurons in the spinal cord using the same pathways as the motor cortex (see Execution of Movement chapter). However, the premotor cortex also plays an important role in the planning of movement. Two experimental designs have demonstrated this role. Monkeys were trained on a panel that had one set of lights in a row on top and one set of buttons that could also light up in a row on the bottom. The monkeys would watch for a top row light to turn on. This would indicate that within a few seconds, the button directly below would light up. When the button turned on, the monkeys were supposed to push the button.

Therefore, there were two light triggers in the experiment. The first required no motor movement from the monkey but did give the monkey information about where a motor movement would be needed in the near future. The second required the monkey to move to push the button. When brain activity was measured during this study, neurons in the premotor cortex became active when the first light trigger turned on, well before any movement actually took place (Weinrich and Wise, 1928).

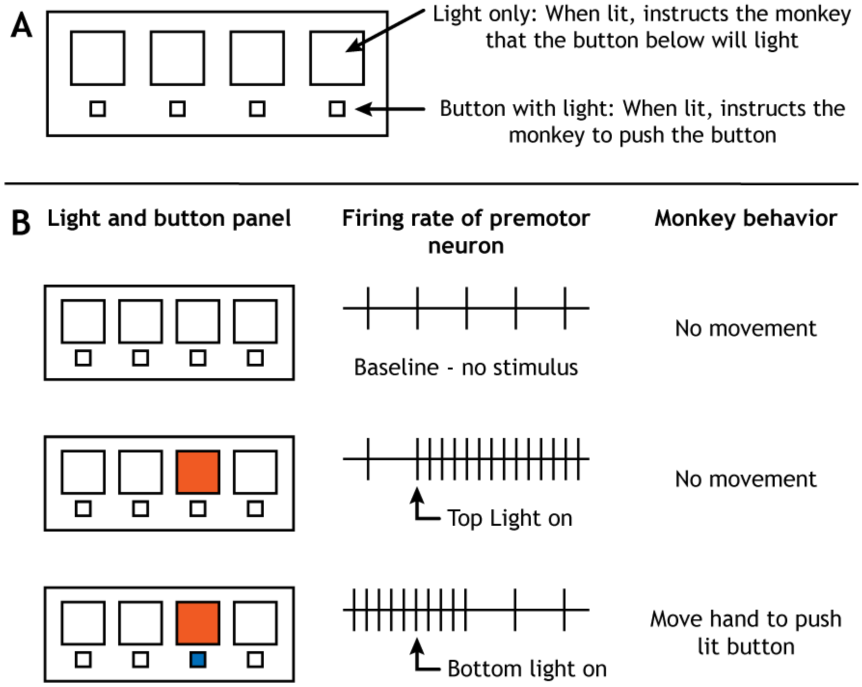


Figure 26.3. (A) Monkeys were trained to use a light panel. When lit, a light located in the top row informed the monkey that the button directly below would light up soon. Shortly after one of the top row lights turned on, the button directly below it would turn on, and the monkey would need to push that button for a reward. (B) When no lights are lit, premotor neurons fire at a baseline rate, and the monkey does not move. Neurons located in the premotor cortex increase action potential firing rate when the top row light turns on, even though the monkey makes no movement. The firing stops shortly after the monkey moves to push the bottom button after it turns on. (Based on Weinrich and Wise, 1928) 'Light Panel Experiment' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

In another experiment, people were trained to move their fingers in a specific pattern. Cerebral blood flow was then measured when they repeated the finger pattern and when they only imagined repeating the finger pattern. When the movement was only imagined and not actually executed, the premotor regions along with parts of the prefrontal cortex were activated (Roland, et al, 1980).

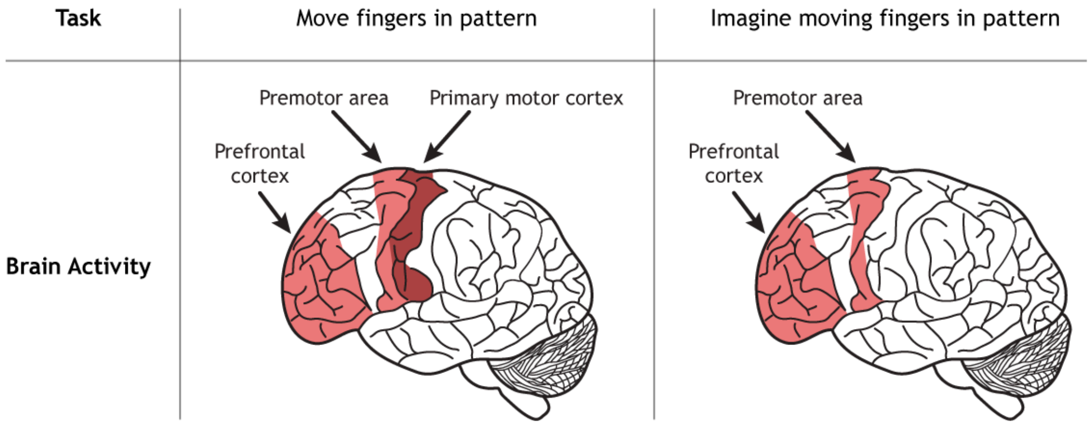


Figure 26.4. People were trained to move their fingers in a pattern. When the pattern was repeated, brain activity was seen in the primary motor cortex, along with the premotor area and prefrontal cortex. When the pattern was only imagined, and no finger movement took place, brain activity was seen in the premotor area and prefrontal cortex. (Based on Roland, et al, 1980) 'Finger Movement Experiment' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

These studies show that the premotor cortex is active prior to the execution of movement, indicating that it plays an important role in the planning of movement. The posterior parietal, prefrontal, and premotor regions, though, also communicate with a subcortical region called the basal ganglia to fully construct the movement plan. The basal ganglia are covered in the next chapter.

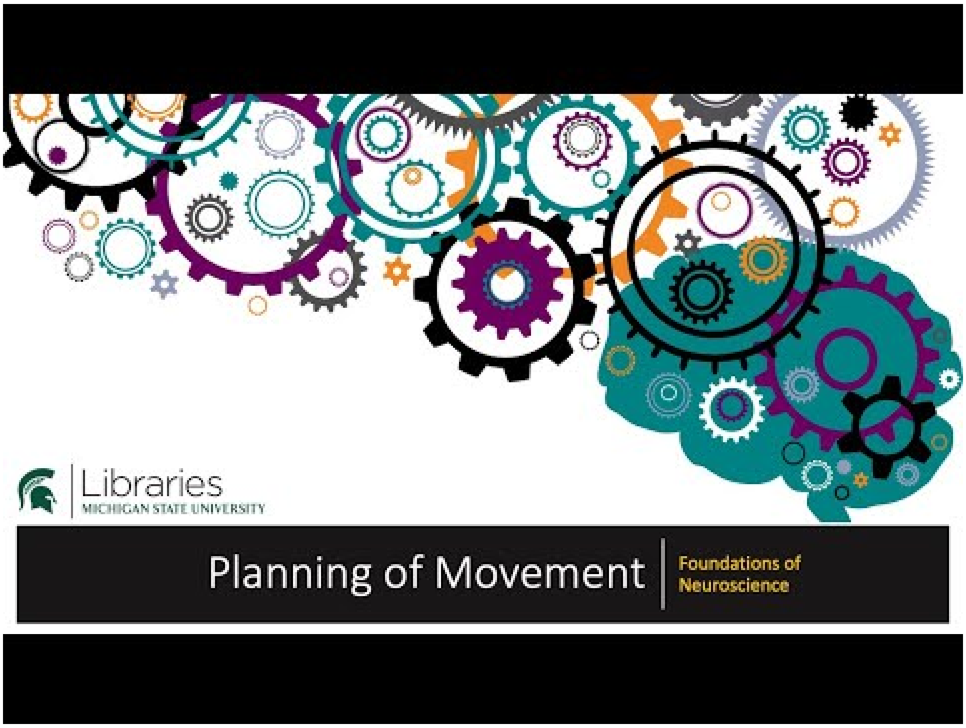
Key Takeaways

- Sensory information is processed in the posterior parietal before being sent to motor regions of the brain
- The prefrontal cortex and premotor cortex are critical for creating a movement plan

Test Yourself!

An interactive H5P element has been excluded from this version of the text. You can view it online here:
https://openbooks.lib.msu.edu/neuroscience/?p=661#h5p-25

Video Version of Lesson



A YouTube element has been excluded from this version of the text. You can view it online here:
https://openbooks.lib.msu.edu/neuroscience/?p=661

References

Roland PE, Larsen B, Lassen NA, Skinhøj E. Supplementary motor area and other cortical areas in organization of voluntary movements in man. J Neurophysiol. 1980 Jan;43(1):118-36. doi: 10.1152/jn.1980.43.1.118. PMID: 7351547.

Weinrich M, Wise SP. The premotor cortex of the monkey. J Neurosci. 1982 Sep;2(9):1329-45. doi: 10.1523/JNEUROSCI.02-09-01329.1982. PMID: 7119878; PMCID: PMC6564318.

27.

BASAL GANGLIA

Resources

- Key Takeaways
- Test Yourself
- Video Version

The basal ganglia are a group of subcortical nuclei, meaning groups of neurons that lie below the cerebral cortex. The basal ganglia is comprised of the striatum, which consists of the caudate nucleus and the putamen, the globus pallidus, the subthalamic nucleus, and the substantia nigra The basal ganglia are primarily associated with motor control, since motor disorders, such as Parkinson's or Huntington's diseases stem from dysfunction of neurons within the basal ganglia. For voluntary motor behavior, the basal ganglia are involved in the initiation or suppression of behavior and can regulate movement through modulating activity in the thalamus and cortex. In addition to motor control, the basal ganglia also communicate with non-motor regions of the cerebral cortex and play a role in other behaviors such as emotional and cognitive processing.

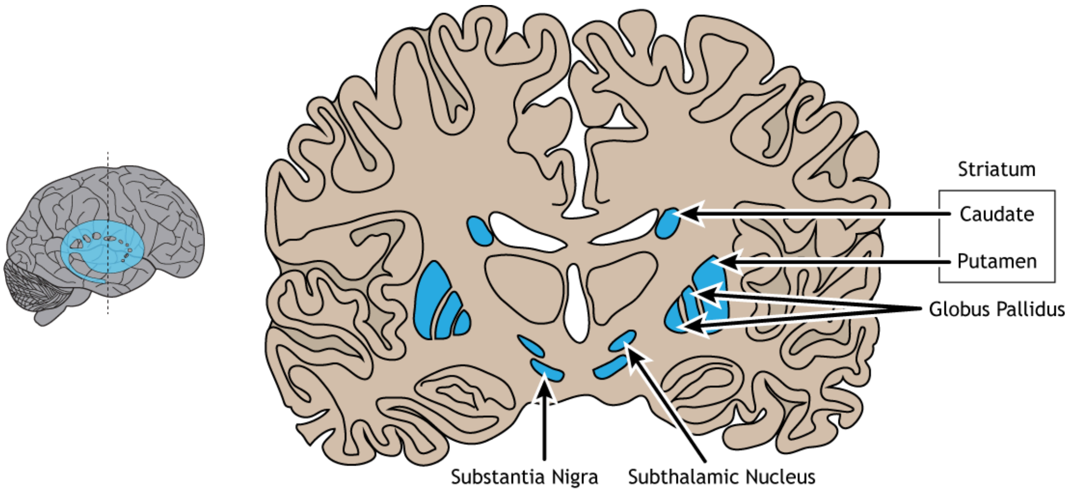


Figure 27.1. The basal ganglia are subcortical structures located at the base of the forebrain. They are comprised of the caudate and putamen, which both make up the striatum, as well as the globus pallidus, substantia nigra, and subthalamic nucleus. 'Basal Ganglia' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

View the basal ganglia using the BrainFacts.org 3D Brain

Basal Ganglia Input

The majority of information processed by the basal ganglia enters through the striatum. The principal source of input to the basal ganglia is from the cerebral cortex. This input is glumatergic and therefore, excitatory. The substantia nigra is also a region with critical projections to the striatum and is the main source of dopaminergic input. Dopamine plays an important role in basal ganglia function. Parkinson's disease results when dopamine neurons in the substantia nigra degenerate and no longer send appropriate inputs to the striatum. Dopamine projections can have either excitatory or inhibitory effects in the striatum, depending on the type of metabotropic dopamine receptor the striatal neuron expresses. Dopamine action at a neuron that expresses the D1 receptor is excitatory. Dopamine action at a neuron that expresses the D2 receptor is inhibitory.

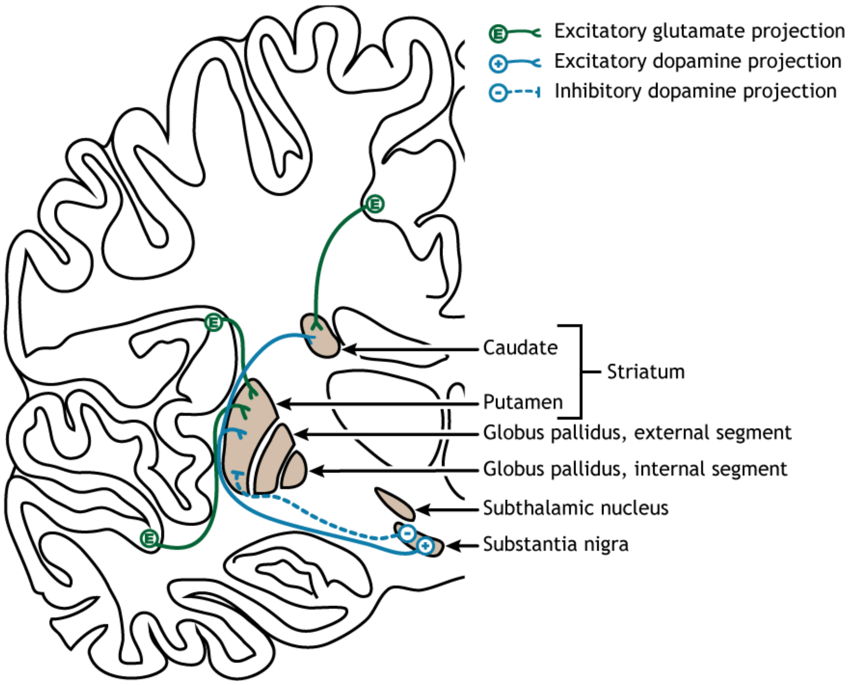


Figure 27.2. Inputs to the basal ganglia enter through the striatum (the caudate and putamen). Cortical projections (shown in green) release glutamate and are excitatory. Substantia nigra projections (shown in blue) release dopamine and can be either excitatory or inhibitory. 'Basal Ganglia Input' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

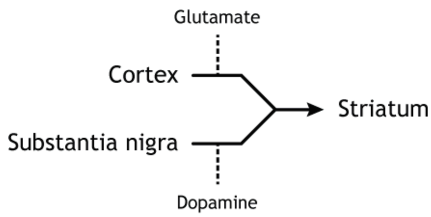


Figure 27.3. The cortex sends glutamate projections to the striatum. The substantia nigra sends dopamine projections to the striatum. 'Basal Ganglia Input – Text' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Basal Ganglia Output

The primary output region of the basal ganglia is the internal segment of the globus pallidus. This region sends inhibitory GABAergic projections to nuclei in the thalamus. This inhibitory output has a tonic, constant firing rate, which allows the basal ganglia output to both increase and decrease depending on the situation. The thalamus then projects back out to the cerebral cortex, primarily to motor areas.

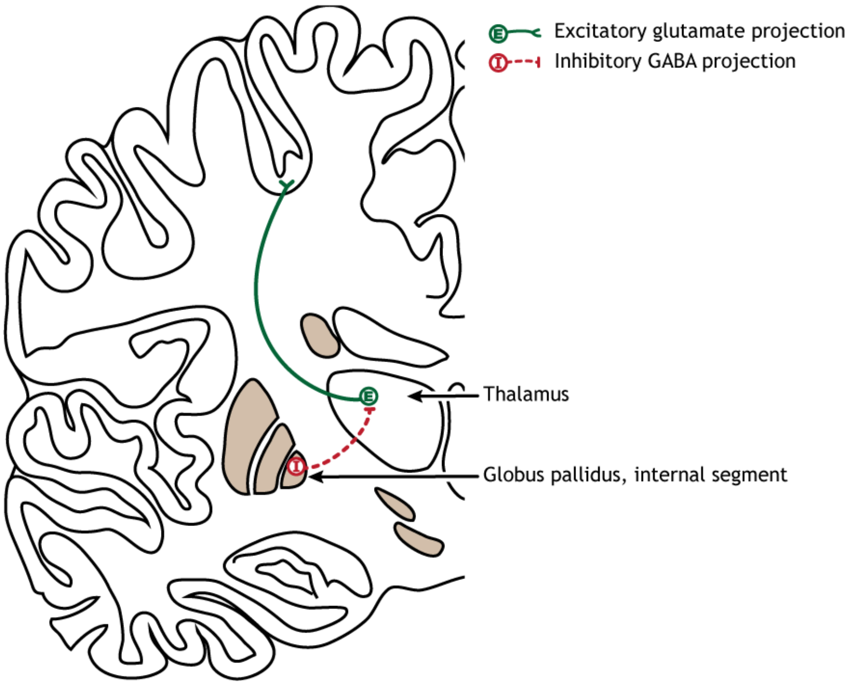


Figure 27.4. Output from the basal ganglia leaves through the internal segment of the globus pallidus. Inhibitory projections (shown in red) release GABA onto the thalamus. Excitatory thalamic projections (shown in green) communicate with the cerebral cortex. 'Basal Ganglia Output' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

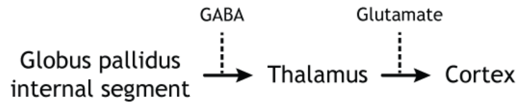


Figure 27.5. The internal segment of the globus pallidus sends GABA projections to the thalamus. The thalamus sends glutamate projections to the cortex. 'Basal Ganglia Output – Text' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Basal Ganglia Internal Processing

Direct Pathway

There are multiple connections within the basal ganglia structures as well. For motor control, there are two main circuits: the direct pathway and the indirect pathway. These circuits have opposing actions when activated by cortical neurons. The circuits are also modulated by dopamine release by the substantia nigra into the striatum. It is believed that the different control mechanisms allow a finely tuned balance between the direct and indirect circuits, which allows for refined control of movement.

The direct pathway begins in the striatum, which sends inhibitory projections to the internal segment of the globus pallidus (GPi). The GPi then sends inhibitory output to the thalamus.

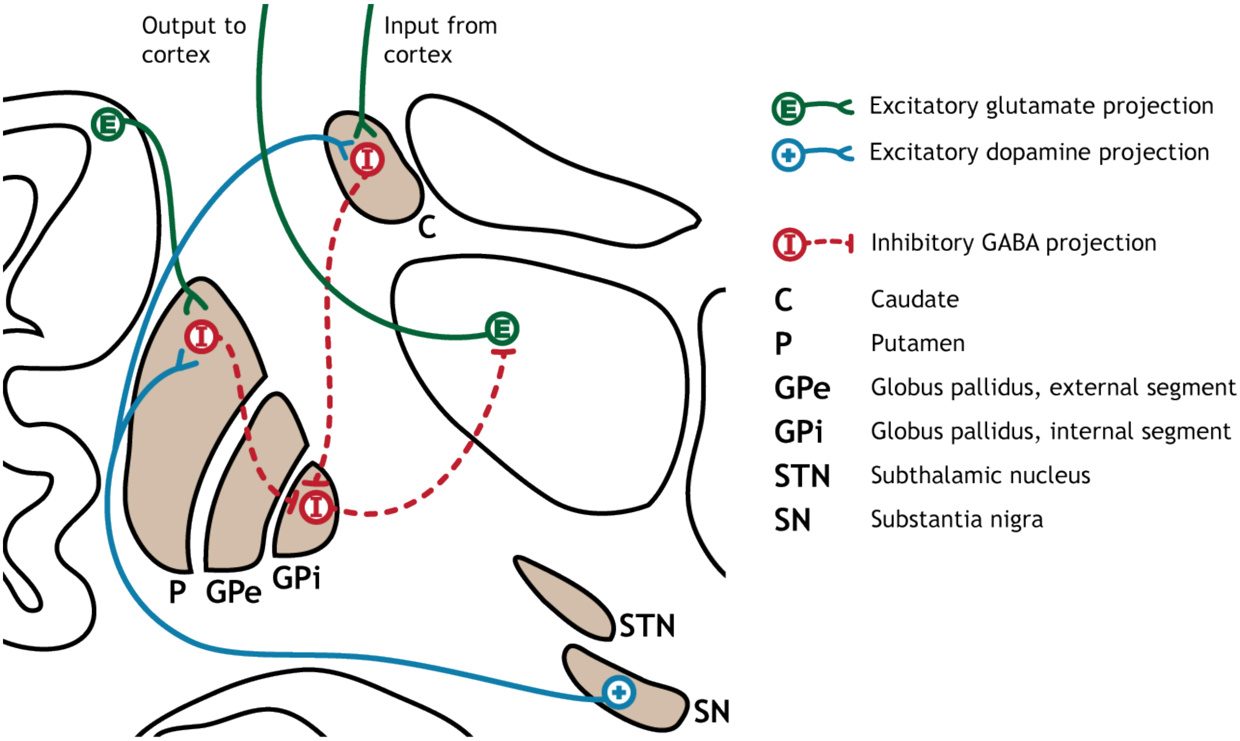


Figure 27.6. The direct pathway in the basal ganglia consists of excitatory input from the cortex via glutamate action or substantia nigra via dopamine action that synapses on inhibitory neurons in the striatum. The striatal neurons project to the internal segment of the globus pallidus (GPi). The GPi then sends inhibitory output to the thalamus. 'Basal Ganglia Direct Pathway' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

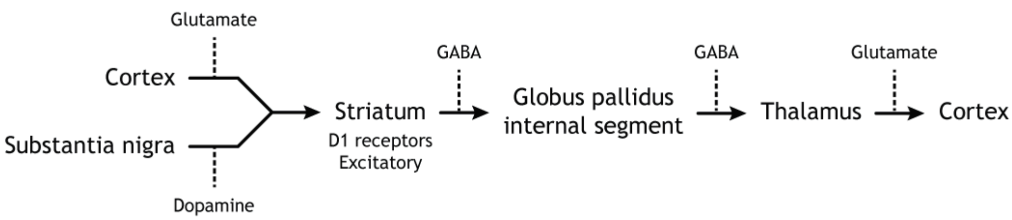


Figure 27.7. The cortex sends glutamate projections to the striatum. The substantia nigra sends dopamine projections to the striatum, which are excitatory, acting on D1 receptors in the neurons involved in the direct pathway. The striatum sends GABA projections to the internal segment of the globus pallidus (GPi). The GPi sends GABA projections to the thalamus. The thalamus sends glutamate projections to the cortex. 'Basal Ganglia Direct Pathway – Text' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Activation of the Direct Pathway

When input from either the cortex or substantia nigra increases in intensity, the direct pathway is activated. The neurons in the striatum involved in the direct pathway express the D1 metabotropic dopamine receptor, and the activation of this receptor is excitatory. Therefore, projections from both the cortex and the substantia nigra activate the neurons in the striatum. Those neurons are inhibitory and release GABA onto the internal segment of the globus pallidus (GPi). As described above, the neurons in the GPi are inhibitory, releasing GABA onto the thalamus. Activation of the striatum neurons inhibit the neurons in the GPi, releasing the inhibition on the thalamus. Inhibition of an inhibitory region is called disinhibition. Therefore, the activation of the direct pathway results in increased output from the thalamus because it is disinhibited.

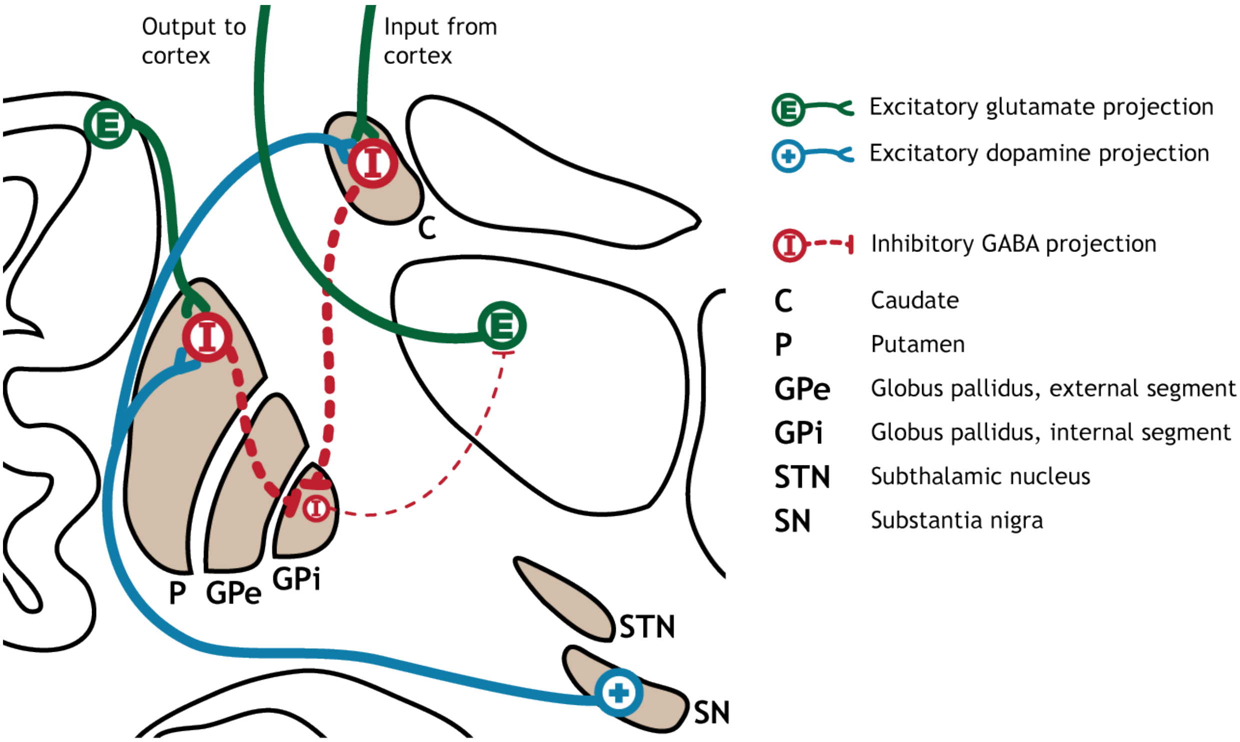


Figure 27.8. Activation of the direct pathway by either increased input from either the cortex or substantia nigra leads to increased inhibitory output from the striatium to the GPi. The inhibition on the GPi leads to less inhibitory input to the thalamus, causing increased output from the thalamus to the cortex. 'Direct Pathway Activation' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

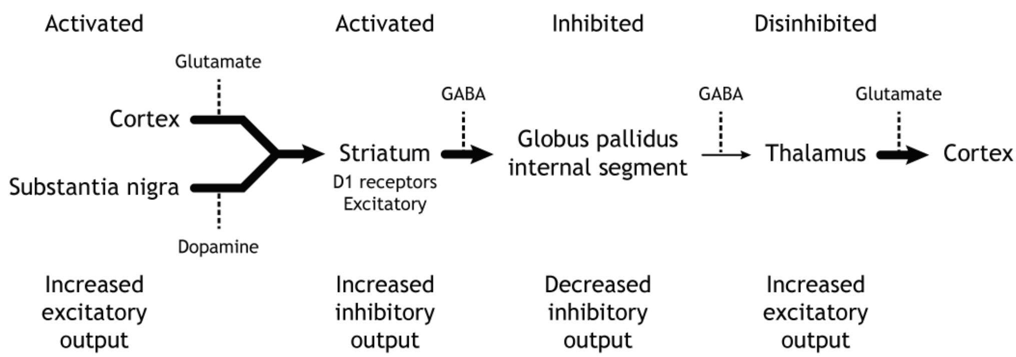


Figure 27.9. When either the cortex or the substantia nigra are activated, they send increased excitatory output to the striatum, which expresses excitatory D1 receptors in the neurons involved in the direct pathway. This input activates the striatum, which sends increased inhibitory projections to the GPi. The inhibited GPi sends decreased inhibitory projections to the thalamus, disinhibiting the thalamus. The thalamus then sends increased excitatory output to the cortex.

Indirect pathway

The indirect pathway is a little more complex. Like the direct pathway, input into the basal ganglia arises from the cortex and substantia nigra, but there are more internal connections within the basal ganglia that what occurs in the direct pathway. Inhibitory neurons in the striatum involved in the indirect pathway project to the external segment of the globus pallidus (GPe). GABA-ergic neurons in the GPe project to the subthalamic nucleus, which then sends excitatory output to the GPi, which outputs to the thalamus.

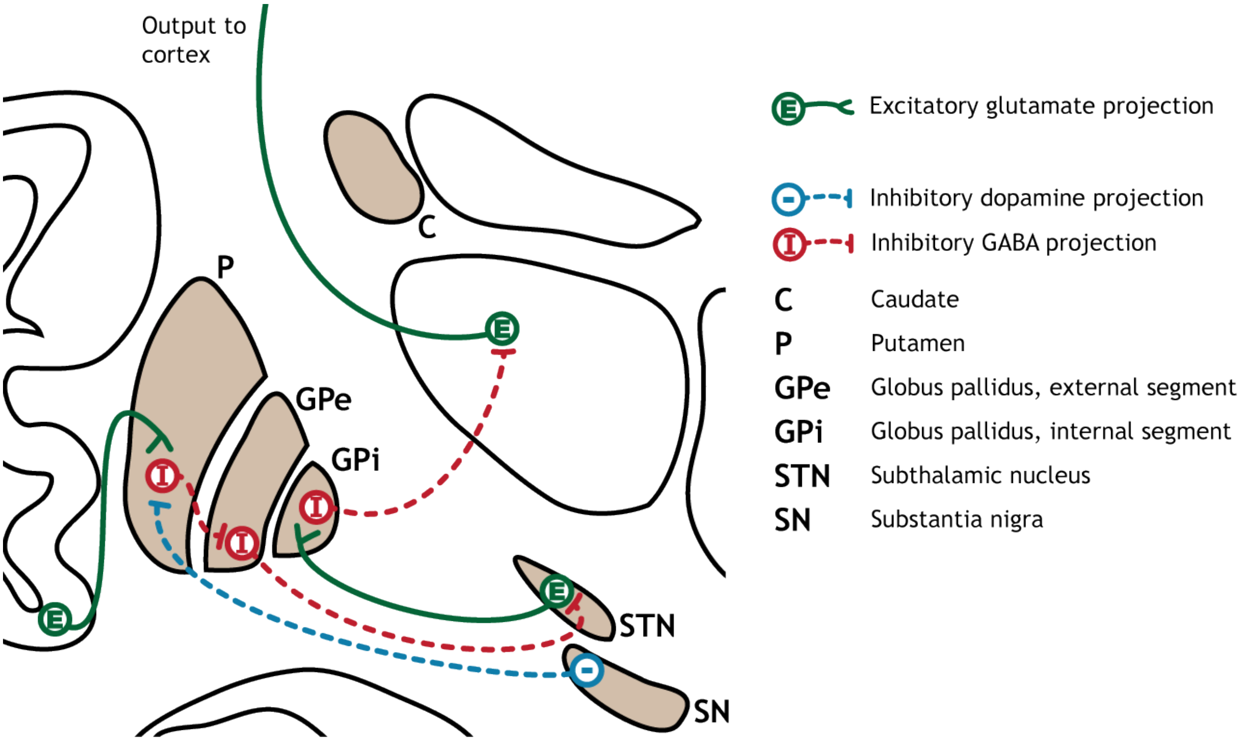


Figure 27.10. The indirect pathway in the basal ganglia consists of excitatory input from the cortex via glutamate action or inhibitory input from the substantia nigra via dopamine action that synapses on inhibitory neurons in the striatum. The striatal neurons project to the external segment of the globus pallidus (GPe). The GPe the sends inhibitory output to the subthalamic nucleus, which had excitatory projections to the GPi. The GPi then sends inhibitory output to the thalamus. 'Basal Ganglia Indirect Pathway' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

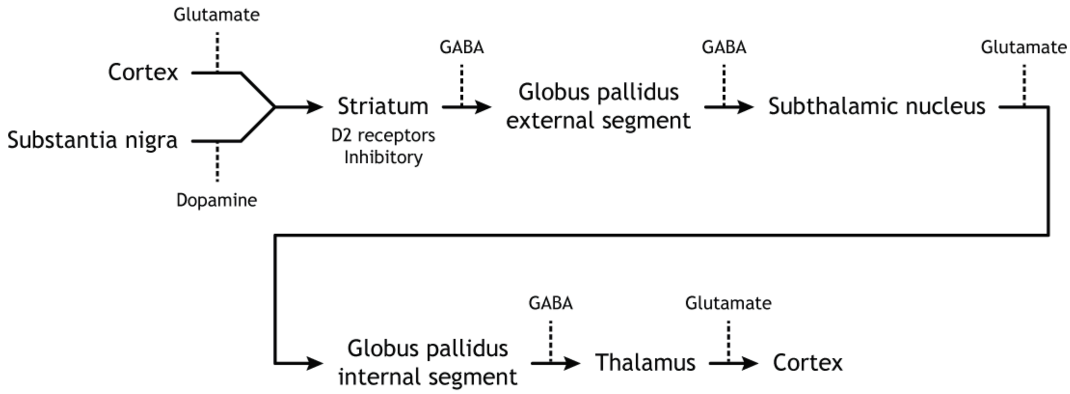


Figure 27.11. The cortex sends glutamate projections to the striatum. The substantia nigra sends dopamine projections to the striatum, which are inhibitory, acting on D2 receptors in the neurons involved in the indirect pathway. The striatum sends GABA projections to the external segment of the globus pallidus (GPe). The GPe sends GABA projections to the subthalamic nucleus. The subthalamic nucleus sends glutamate projections to the GPi. The GPi send GABA projections to the thalamus. The thalamus sends glutamate projections to the cortex. 'Basal Ganglia Indirect Pathway – Text' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Activation of the Indirect Pathway

The indirect pathway is activated by excitatory cortical input, activating the inhibitory striatal neurons. This leads to inhibition of the GPe neurons, resulting in disinhibition of the excitatory neurons in the subthalamic nucleus. The excitatory output from the subthalamic nucleus to the GPi increases inhibition of the thalamus, leading to decreased thalamic output to the cortex.

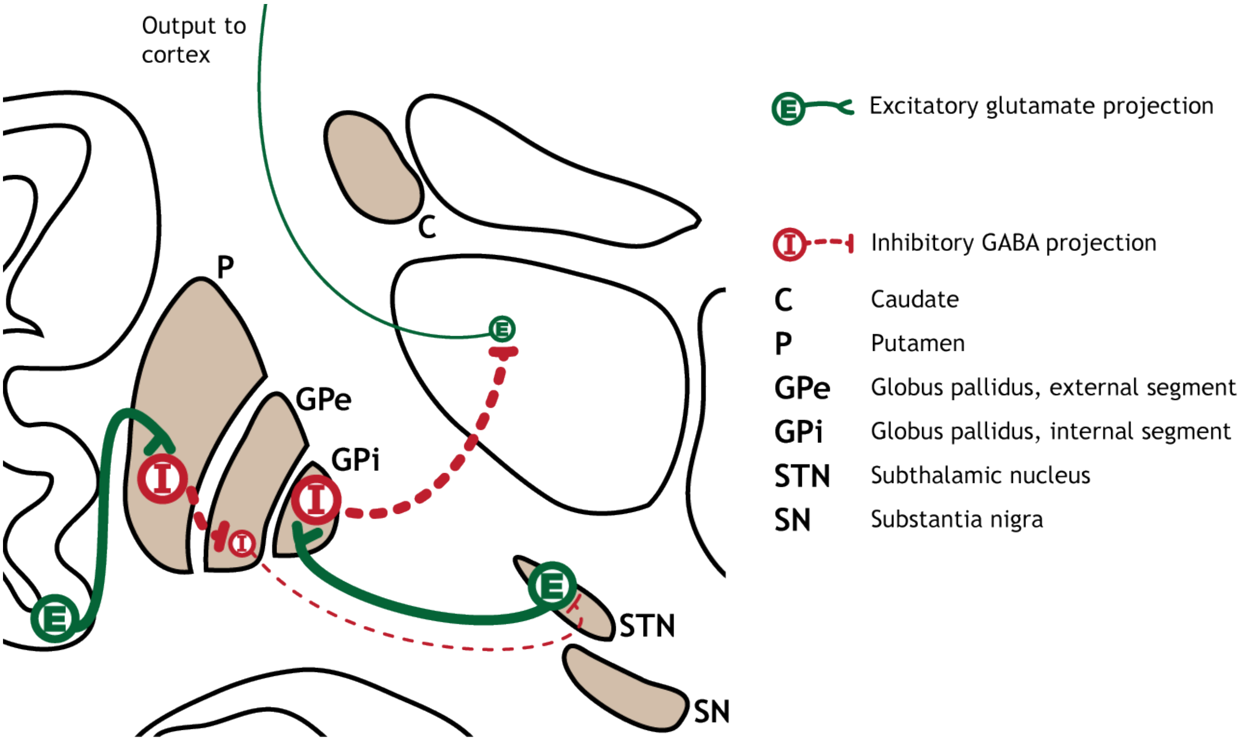


Figure 27.12. Activation of the indirect pathway by excitatory cortical input to the striatum leads to increased inhibitory output to the GPe. The inhibited GPe sends decreased inhibitory output to the subthalamic nucleus, causing increased excitatory output from the subthalamic nucleus to the GPi. Activation of the GPi inhibits the thalamus, resulting in decreased output from the thalamus to the cortex. 'Indirect Pathway Activation' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

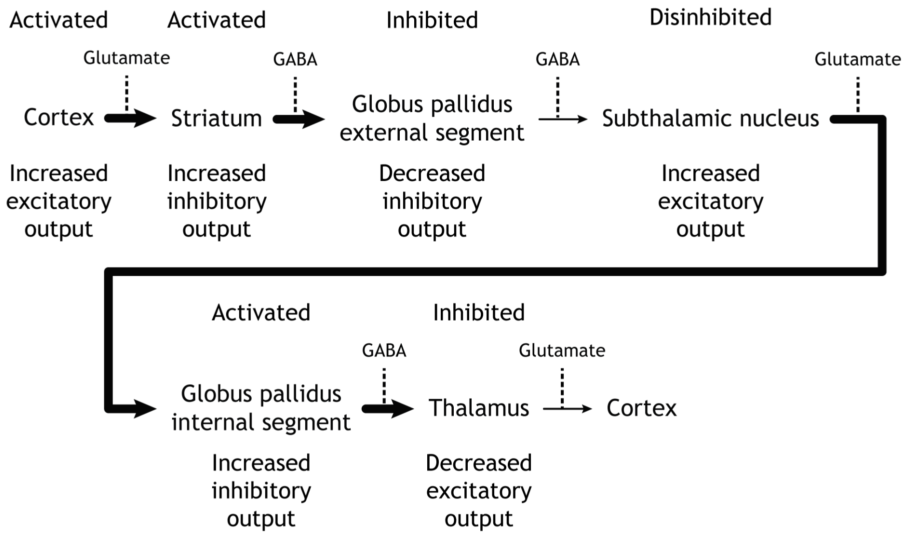


Figure 27.13. When the cortex is activated, it sends increased excitatory output to the striatum. This input activates the striatum, which sends increased inhibitory projections to the GPe. The inhibited GPe sends decreased inhibitory projections to the subthalamic nucleus, disinhibiting the region. The subthalamic nucleus then sends increased excitatory output to the GPi. The activated GPi sends increased inhibitory projections to the thalamus, which sends decreased excitatory output to the cortex. 'Indirect Pathway Activation – Text' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Inhibition of the Indirect Pathway

The indirect pathway can be inhibited by dopamine release from the substantia nigra. The neurons in the striatum involved in the indirect pathway express the D2 metabotropic dopamine receptor. The activation of this receptor is inhibitory. If the indirect pathway is inhibited by dopamine projections from the substantia nigra, the inhibitory striatal neurons are inhibited. This leads to disinhibiton of the GPe neurons, resulting in inhibition of the excitatory neurons in the subthalamic nucleus. This decreased excitatory output to the GPi decreases inhibition of the thalamus, leading to increased thalamic output to the cortex.

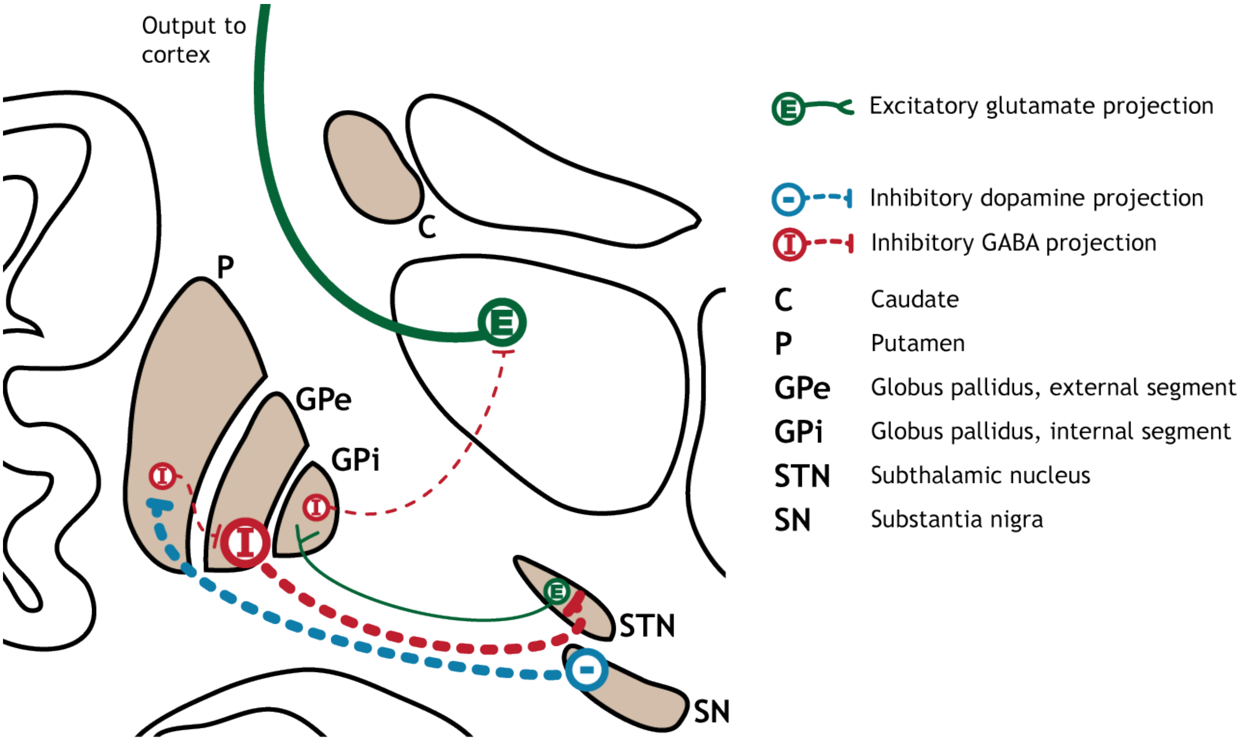


Figure 27.14. Inhibition of the indirect pathway by inhibitory input from the substantia nigra to the striatum leads to decreased inhibitory output to the GPe. The disinhibited GPe sends increased inhibitory output to the subthalamic nucleus, causing decreased excitatory output from the subthalamic nucleus to the GPi. A decrease in activation of the GPi releases the inhibition on the thalamus, resulting in increased output from the thalamus to the cortex. 'Indirect Pathway Inhibition' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

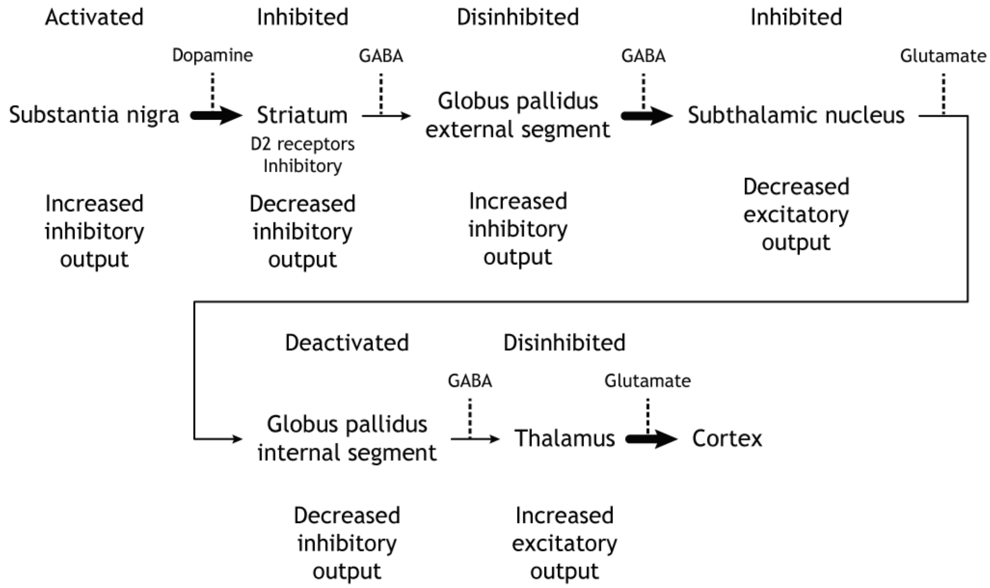


Figure 27.15. When the substantia nigra is activated, it sends increased inhibitory output to the striatum, which expresses inhibitory De receptors in the neurons involved in the indirect pathway. This input inhibits the striatum, which sends decreased inhibitory projections to the GPe. The disinhibited GPe sends increased inhibitory projections to the subthalamic nucleus, inhibiting the region. The subthalamic nucleus then sends decreased excitatory output to the GPi. The deactivated GPi sends decreased inhibitory projections to the thalamus, which sends increased excitatory output to the cortex. 'Indirect Pathway inhibition – Text' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Summary of Internal Processing

To put it all together, there is input to the striatum from two different locations: cortex (glutamate) and substantia nigra (dopamine).

- Cortical activation of the direct pathway leads to increased thalamic output
- Cortical activation of the indirect pathway leads to decreased thalamic output
- Substantia nigra activation (via D1) of the direct pathway leads to increased thalamic output
- Substantia nigra inhibition (via D2) of the indirect pathway leads to increased thalamic output

It is the combination of these pathway that allows for precise control of motor movement.

Loops through the Basal Ganglia

There are multiple circuits that pass through the basal ganglia:

- The motor circuit, which plays a role in voluntary movement
- The oculomotor circuit, which plays a role in eye movement
- The associative circuit, which plays a role in executive functions like behavioral inhibition (preventing impulsive behaviors) planning and problem solving, and mediating socially appropriate behaviors
- The limbic or emotional circuit, which plays a role in the processing of emotion and reward.

Although the circuits each use different circuits within the basal ganglia, the general loop is the same: cortical input to the striatum leads to internal processing within the basal ganglia structures. Basal ganglia output projects from the pallidum to the thalamus, which then projects back to the cortex. It is important to recognize that the basal ganglia plays an important role in a number of functions. For example, medications that are used to treat Parkinson's can sometimes lead to the presentation of impulse control disorders, a result of dopaminergic changes in the limbic loop through the basal ganglia.

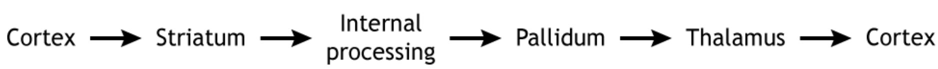


Figure 27.16. Loops through the basal ganglia have different functions but follow the same general circuit. The cortex inputs to the striatum. Internal processing through basal ganglia circuits occurs, and then the output from the pallidum projects to the thalamus, which sends output to the cortex.

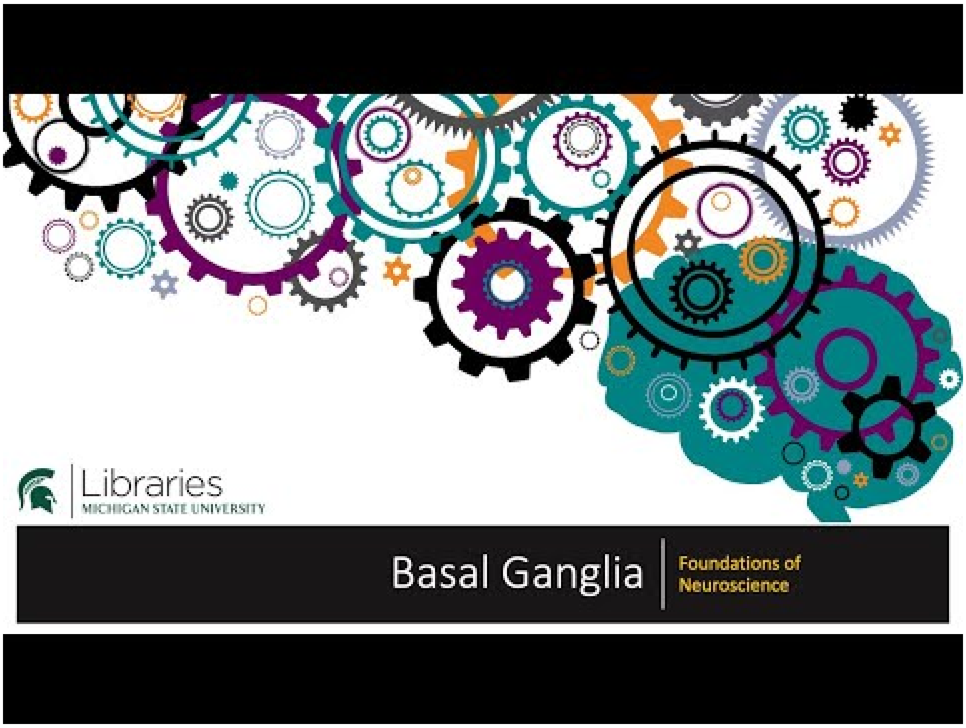
Key Takeaways

- The subcortical basal ganglia nuclei receive information from the cortex and send output to the thalamus
- Motor control through the basal ganglia occurs through both the direct and indirect pathways
- Disinhibition is when an inhibitory region is itself inhibited
- The basal ganglia are best known for their role in motor control but are also critical for emotion and behavioral inhibition

Test Yourself!

An interactive H5P element has been excluded from this version of the text. You can view it online here:
https://openbooks.lib.msu.edu/neuroscience/?p=673#h5p-27

Video Version of Lesson



A YouTube element has been excluded from this version of the text. You can view it online here: https://openbooks.lib.msu.edu/neuroscience/?p=673

28.

EXECUTION OF MOVEMENT

Motor cortex

Once the plan for movement has been created, the primary motor cortex is responsible for the execution of that action. The primary motor cortex lies just anterior to the primary somatosensory cortex in the precentral gyrus located in the frontal lobe.

Resources

- Key Takeaways
- Test Yourself
- Video Version

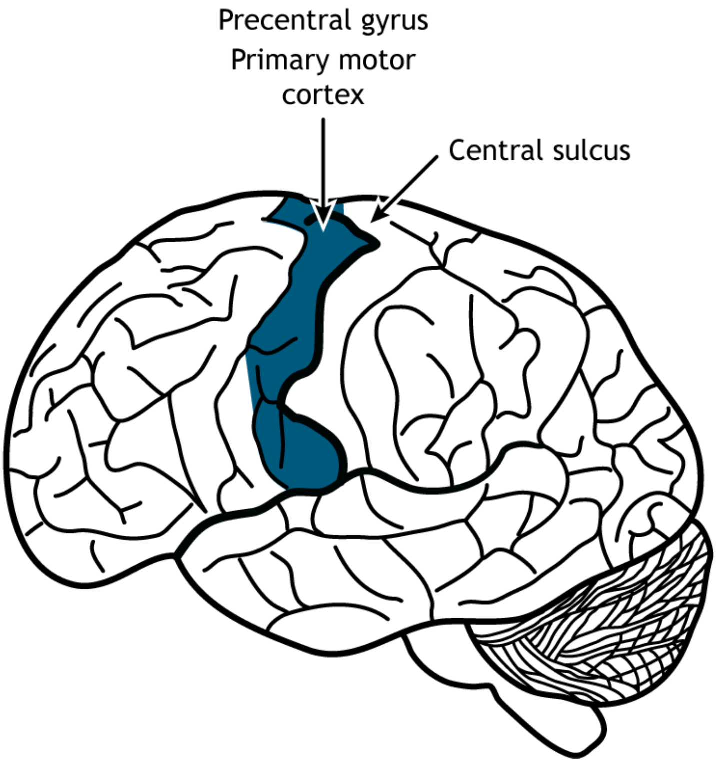


Figure 28.1. The primary motor cortex is located in the frontal lobe in the precentral gyrus, just anterior to the central sulcus. 'Primary Motor Cortex' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Like the somatosensory cortex, the motor cortex is organized by a somatotopic map. However, the motor cortex does not map onto the body in such an exact way as does the somatosensory system. It is believed that upper motor neurons in the motor cortex control multiple lower motor neurons in the spinal cord that innervate multiple muscles. This results in activation of an upper motor neuron causing excitation or inhibition in different neurons at once, indicating that the primary motor cortex is responsible for movements and not simply activation of one muscle. Stimulation of motor neurons in monkeys can lead to complex motions like bringing the hand to the mouth or moving into a defensive position (Graziano et al, 2005).

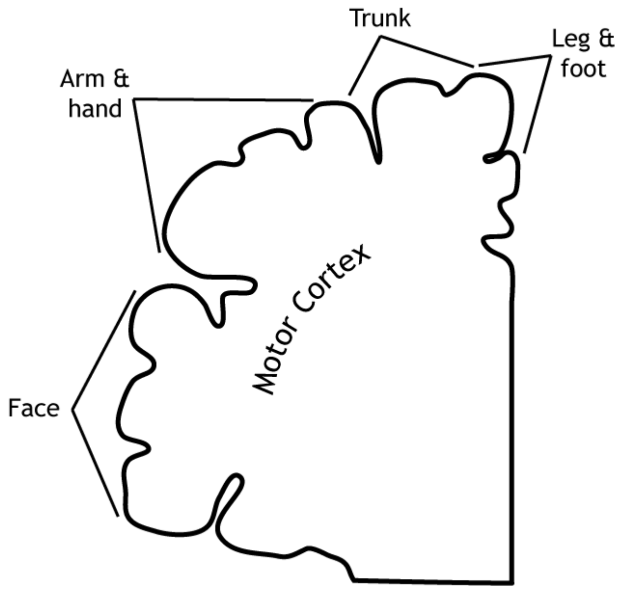


Figure 28.2. The map of the body that exists on the motor cortex is less specific than the somatosensory map because cortical neurons control multiple muscles at the same time. Instead, regions of the cortex are associated with larger body regions, such as the face, arm and hand, trunk, or leg and foot. 'Motor Cortex Map' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Population coding

The motor cortex controls movement by using population coding mechanisms. Upper motor neurons are broadly tuned to a certain movement in a certain direction, meaning firing rate is highest when moving in one direction, but firing also occurs when moving in nearby directions. For example, when a monkey is trained to move its hand toward the left, neurons "tuned" toward left movement will be active immediately before and during the movement. Neurons tuned to other directions will also be active but at lower rates (Georgopoulos, et al, 1982). This means that the firing rate of one specific neuron does not give enough information to know direction of movement. It is the combined firing rates of an entire population of neurons that indicates direction.

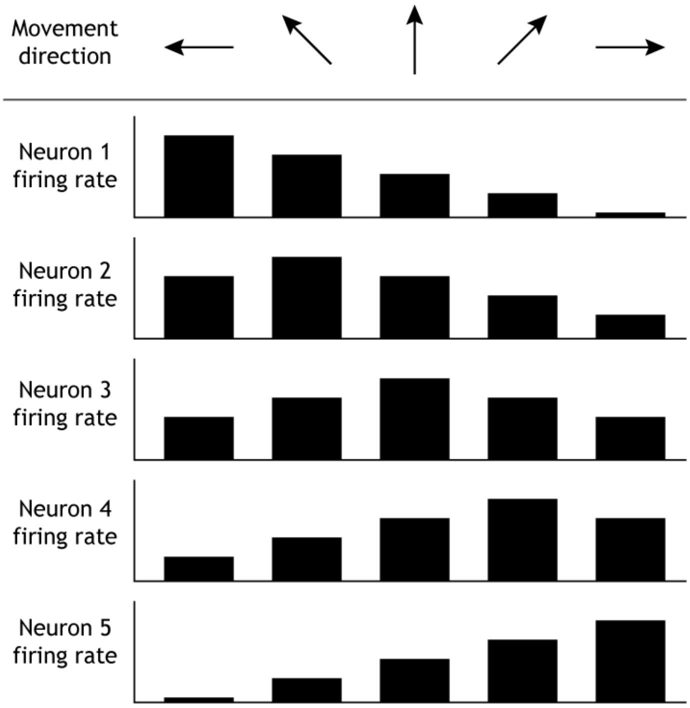


Figure 28.3. Motor movement is coded via population coding in the primary motor cortex. Information from one neuron is not enough to determine the direction of movement; a population of neurons must be used. Some neurons will be "tuned" to fire most rapidly in response to a specific direct. For example, Neuron 1 in the figure shows the highest firing rate when movement of the hand is to the left and a low firing rate when the hand is moving to the right, whereas Neuron 3 fires the most when the movement is forward. The combination of the firing patterns of many neurons provides a precise direction for the movement. 'Population Coding' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Descending Spinal Tracts

There are multiple descending tracts within the spinal cord that send information from the brain to the motor neurons in the ventral horn. The lateral tracts are responsible for carrying information about voluntary movement of the arms and legs. The ventromedial pathways are responsible for carrying information about posture and balance.

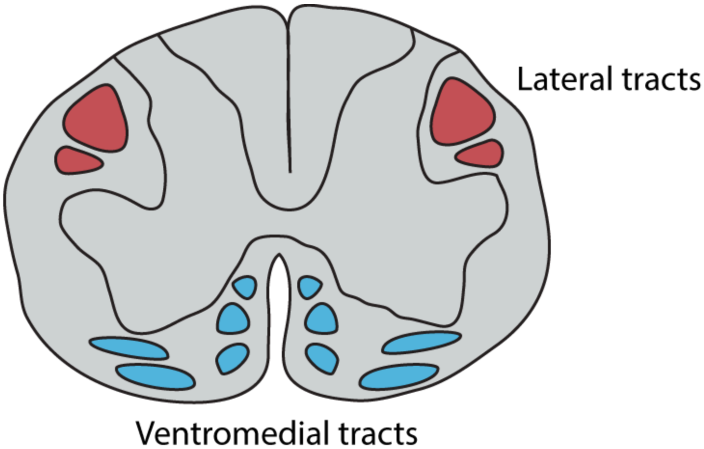


Figure 28.4. The descending motor tracts travel from the brain through the white matter in the spinal cord. The lateral tracts descend in the dorsolateral white matter, and the ventromedial tracts descend in the ventromedial white matter. 'Descending Spinal Tracts' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Lateral Tracts

Coticospinal Tract

The largest of the lateral pathways is the corticospinal tract. This pathway sends information directly from the motor and premotor cortices down to the motor neurons in the spinal cord. Cortical axons travel through the brainstem and then cross the midline at the base of the medulla; like the somatosensory system, the right side of the cortex processes information for the left side of the body and vice versa. In the spinal cord, the axons travel through the lateral column and synapse in the ventral horn on motor neurons that typically innervate distal muscles.

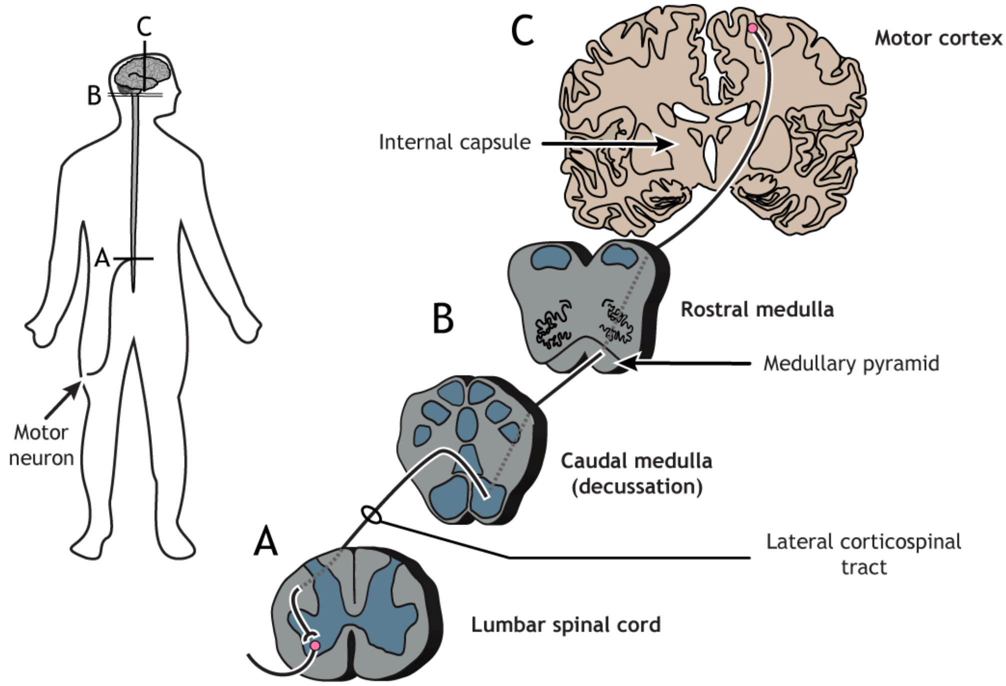


Figure 28.5. Motor information to the arms and legs travels from the primary motor cortex to the medulla via the internal capsule, a white matter structure in the brain. The corticospinal tract passes through the medullary pyramids and then decussates in the caudal medulla. The axons continue traveling through the lateral corticospinal tract and synapse on an alpha motor neurons in the ventral horn of the spinal cord. 'Corticospinal Tract' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Corticobulbar Tract

The corticobulbar tract is another lateral tract and sends motor information to cranial nerves for motor control of the face. This path travels ipsilateral from the cortex into the brainstem where it branches off at the appropriate cranial nerve level in either the pons or the medulla and then innervates cranial nerve neurons bilaterally.

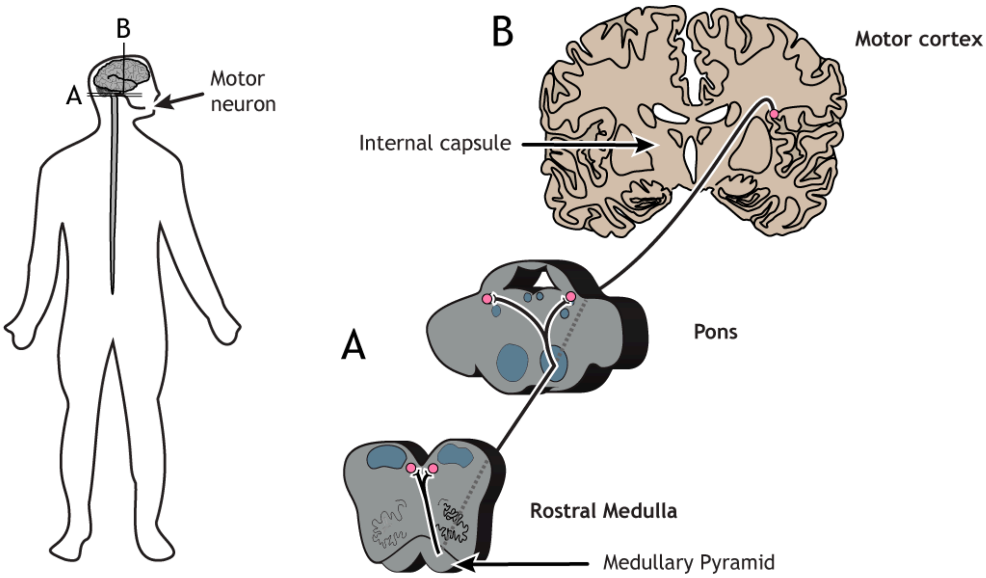


Figure 28.6. Motor information to the face travels from the primary motor cortex through the internal capsule to the pons and medulla where it branches to synapse on cranial nerve nuclei on both sides of the brainstem. 'Corticobulbar Tract' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Ventromedial Tracts

There are four ventromedial pathways that travel in the spinal cord as well. These tracts begin in the brainstem and descend through the ventromedial columns. They receive input from motor areas of the cortex as well as integrating information from multiple sensory regions.

- The vestibulospinal tract is important for head balance as we move. This tract begins in the vestibular nucleus.
- The tectospinal tract is responsible for moving the head in response to visual stimuli. This tract begins in the superior colliculus.
- The two reticulospinal tracts play a role in managing anti-gravity reflexes needed for posture and standing. These tracts begin in the reticular formation.

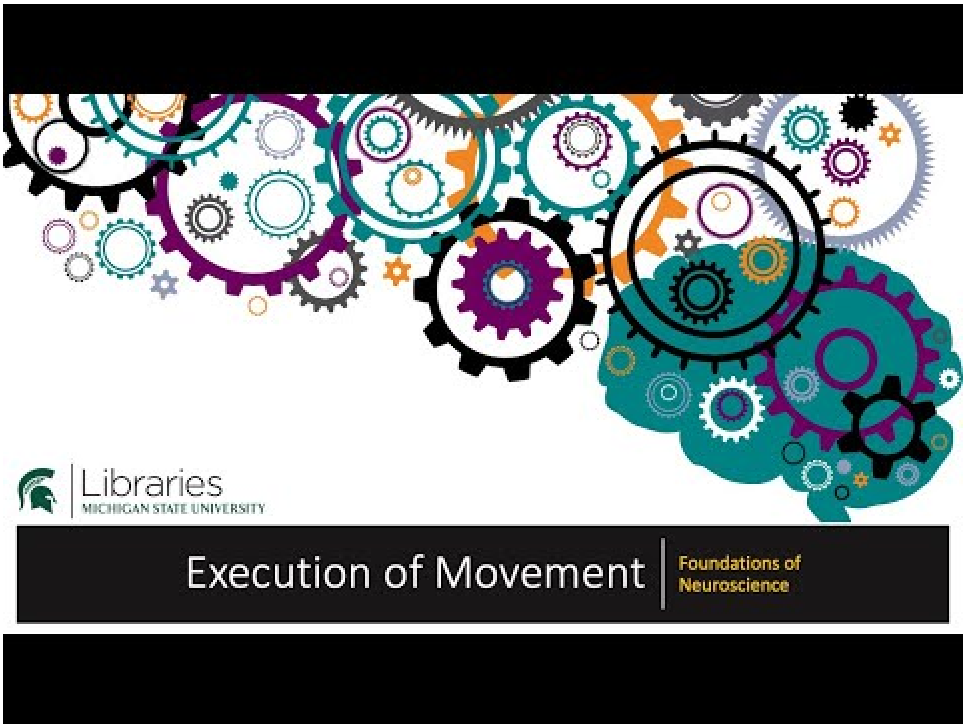
Key Takeaways

- The motor cortex is located in the frontal lobe
- The motor map is not as detailed as the somatosensory homunculus
- The motor cortex uses population coding to encode direction of movement
- The lateral tracts carry information about voluntary movement of the arms and legs
- The ventromedial pathways carry information about posture and balance

Test Yourself!

An interactive H5P element has been excluded from this version of the text. You can view it online here: https://openbooks.lib.msu.edu/neuroscience/?p=684#h5p-28

Video Version of Lesson



A YouTube element has been excluded from this version of the text. You can view it online here: https://openbooks.lib.msu.edu/neuroscience/?p=684

References

Georgopoulos AP, Kalaska JF, Caminiti R, Massey JT. J Neurosci. 1982 Nov;2(11):1527-37.

Graziano et al, 2005 J Neurophysiol 94: 4209-4223.