

| THE BRAIN AND CRANIAL NERVES

Sensory Nerves

Once any sensory cell transduces a stimulus into a nerve impulse, that impulse has to travel along axons to reach the CNS. In many of the special senses, the axons leaving the sensory receptors have a **topographical** arrangement, meaning that the location of the sensory receptor relates to the location of the axon in the nerve. For example, in the retina, axons from RGCs in the fovea are located at the center of the optic nerve, where they are surrounded by axons from the more peripheral RGCs.

Spinal Nerves

Generally, spinal nerves contain afferent axons from sensory receptors in the periphery, such as from the skin, mixed with efferent axons travelling to the muscles or other effector organs. As the spinal nerve nears the spinal cord, it splits into dorsal and ventral roots. The dorsal root contains only the axons of sensory neurons, whereas the ventral roots contain only the axons of the motor neurons. Some of the branches will synapse with local neurons in the dorsal root ganglion, posterior (dorsal) horn, or even the anterior (ventral) horn, at the level of the spinal cord where they enter. Other branches will travel a short distance up or down the spine to interact with neurons at other levels of the spinal cord. A branch may also turn into the posterior (dorsal) column of the white matter to connect with the brain. For the sake of convenience, we will use the terms ventral and dorsal in reference to structures within the spinal cord that are part of these pathways. This will help to

underscore the relationships between the different components. Typically, spinal nerve systems that connect to the brain are **contralateral**, in that the right side of the body is connected to the left side of the brain and the left side of the body to the right side of the brain.

Cranial Nerves

Cranial nerves convey specific sensory information from the head and neck directly to the brain. For sensations below the neck, the right side of the body is connected to the left side of the brain and the left side of the body to the right side of the brain. Whereas spinal information is contralateral, cranial nerve systems are mostly **ipsilateral**, meaning that a cranial nerve on the right side of the head is connected to the right side of the brain. Some cranial nerves contain only sensory axons, such as the olfactory, optic, and vestibulocochlear nerves. Other cranial nerves contain both sensory and motor axons, including the trigeminal, facial, glossopharyngeal, and vagus nerves (however, the vagus nerve is not associated with the somatic nervous system). The general senses of somatosensation for the face travel through the trigeminal system.

| Central Processing

By the end of this section, you will be able to:

- Describe the pathways that sensory systems follow into the central nervous system
- Differentiate between the two major ascending pathways in the spinal cord
- Describe the pathway of somatosensory input from the face and compare it to the ascending pathways in the spinal cord
- Explain topographical representations of sensory information in at least two systems
- Describe two pathways of visual processing and the functions associated with each

Sensory Pathways

Specific regions of the CNS coordinate different somatic processes using sensory inputs and motor outputs of peripheral nerves. A simple case is a reflex caused by a synapse between a dorsal sensory neuron axon and a motor neuron in the ventral horn. More complex arrangements are possible to integrate peripheral sensory information with higher processes. The important regions of the CNS that play a role in somatic processes can be separated into the spinal cord brain stem, diencephalon, cerebral cortex, and subcortical structures.

Spinal Cord and Brain Stem

A sensory pathway that carries peripheral sensations to the brain is referred to as an **ascending pathway**, or ascending tract. The various sensory modalities each follow specific pathways through the CNS. Tactile and other somatosensory stimuli activate receptors in the skin, muscles, tendons, and joints throughout the entire body. However, the somatosensory pathways are divided into two separate systems on the basis of the location of the receptor neurons. Somatosensory stimuli from below the neck pass along the sensory pathways of the spinal cord, whereas somatosensory stimuli from the head and neck travel through the cranial nerves—specifically, the trigeminal system.

The **dorsal column system** (sometimes referred to as the dorsal column–medial lemniscus) and the **spinothalamic tract** are two major pathways that bring sensory information to the brain (**Figure 14.19**). The sensory pathways in each of these systems are composed of three successive neurons.

The dorsal column system begins with the axon of a dorsal root ganglion neuron entering the dorsal root and joining the dorsal column white matter in the spinal cord. As axons of this pathway enter the dorsal column, they take on a positional arrangement so that axons from lower levels of the body position themselves medially, whereas axons from upper levels of the body position themselves laterally. The dorsal column is separated into two component tracts, the **fasciculus gracilis** that contains axons from the legs and lower body, and the **fasciculus cuneatus** that contains axons from the upper body and arms.

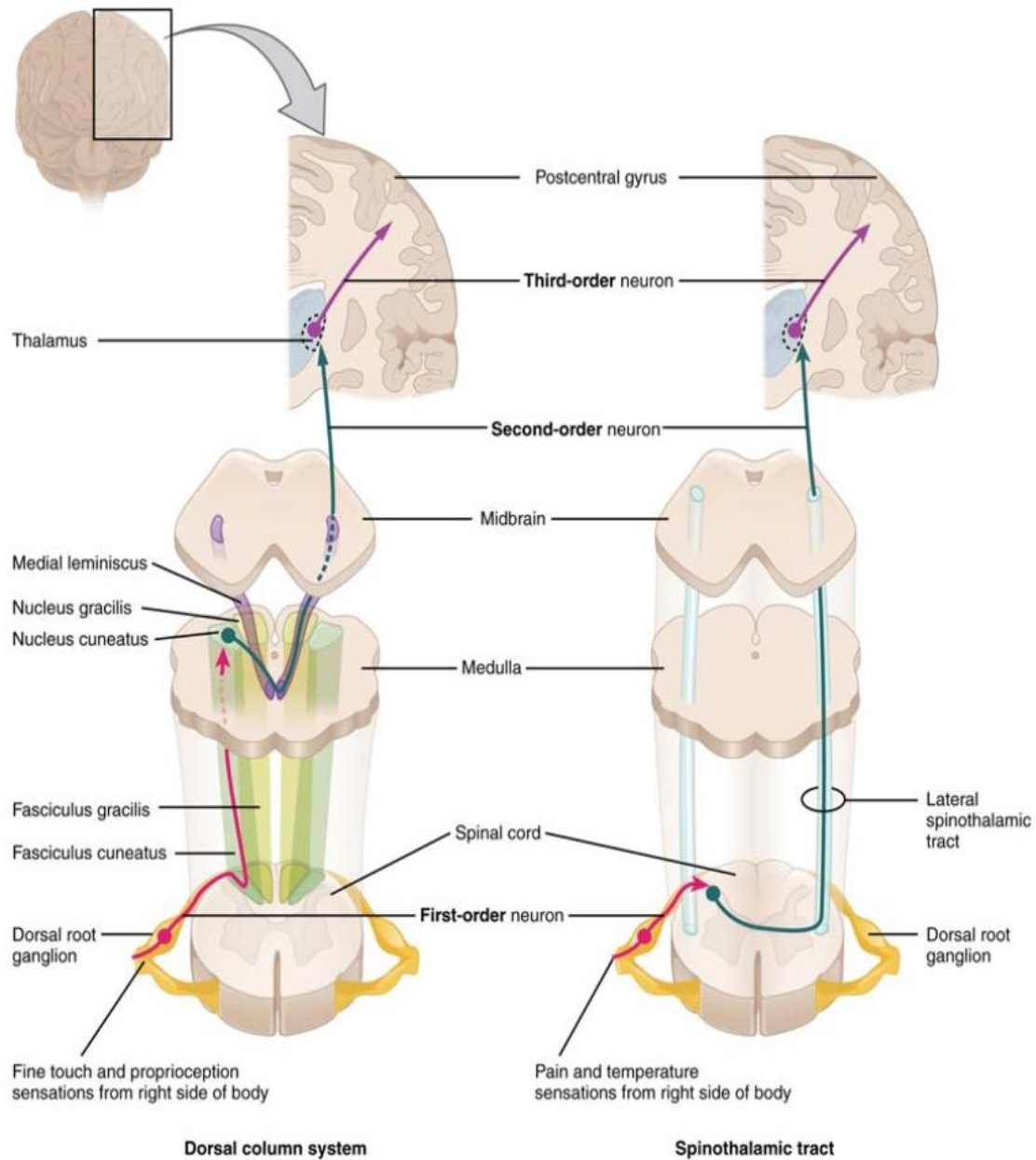
The axons in the dorsal column terminate in the nuclei of the medulla, where each synapses with the second neuron in their respective pathway. The **nucleus gracilis** is the target of fibers in the fasciculus gracilis, whereas the **nucleus cuneatus** is the target of fibers in the fasciculus cuneatus. The second neuron in the system projects from one of the two nuclei and then **decussates**, or crosses the midline of the medulla. These axons then continue to ascend the brain stem as a bundle called the **medial lemniscus**. These axons terminate in the thalamus, where each synapses with the third neuron in their respective pathway. The third neuron in the system projects its axons to the postcentral gyrus of the cerebral cortex, where somatosensory stimuli are initially processed and the conscious perception of the stimulus occurs.

The spinothalamic tract also begins with neurons in a dorsal root ganglion. These neurons extend their axons to the dorsal horn, where they synapse with the second neuron in their respective pathway. The name “spinothalamic” comes from this second neuron, which has its cell body in the spinal cord gray matter and connects to the thalamus. Axons from these second neurons then decussate within the spinal cord and ascend to the brain and enter the thalamus, where each synapses with the third neuron in its respective pathway. The neurons in the thalamus then project their axons to the spinothalamic tract, which synapses in the postcentral gyrus of the cerebral cortex.

These two systems are similar in that they both begin with dorsal root ganglion cells, as with most general sensory information. The dorsal column system is primarily responsible for touch sensations and proprioception, whereas the spinothalamic tract pathway is primarily responsible for pain and temperature sensations. Another similarity is that the second neurons in both of these pathways are contralateral, because they project across the midline to the other side of the brain or spinal cord. In the dorsal column system, this decussation takes place in the brain stem; in the spinothalamic pathway, it takes place in the spinal cord at the same spinal cord level at which the information entered. The third neurons in the two pathways are essentially the same. In both, the second neuron synapses in the thalamus, and the thalamic neuron projects to the somatosensory cortex.

Figure 14.19 Ascending Sensory Pathways of the Spinal Cord The dorsal column system and spinothalamic tract are the major ascending pathways that connect the periphery with the brain.

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The trigeminal pathway carries somatosensory information from the face, head, mouth, and nasal cavity. As with the previously discussed nerve tracts, the sensory pathways of the trigeminal pathway each involve three successive neurons. First, axons from the trigeminal ganglion enter the brain stem at the level of the pons. These axons project to one of three locations. The **spinal trigeminal nucleus** of the medulla receives information similar to that carried by spinothalamic tract, such as pain and temperature sensations. Other axons go to either the **chief sensory nucleus** in the pons or the **mesencephalic nuclei** in the midbrain. These nuclei receive information like that carried by the dorsal column system, such as touch, pressure, vibration, and proprioception. Axons from the second neuron decussate and ascend to the thalamus along the trigeminothalamic tract. In the thalamus, each axon synapses with the third neuron in its respective pathway. Axons from the third neuron then project from the thalamus to the primary somatosensory cortex of the cerebrum.

The sensory pathway for gustation travels along the facial and glossopharyngeal cranial nerves, which synapse with neurons of the **solitary nucleus** in the brain stem. Axons from the solitary nucleus then project to the **ventral posterior nucleus** of the thalamus. Finally, axons from the ventral posterior nucleus project to the gustatory cortex of the cerebral cortex, where taste is processed and consciously perceived.

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The sensory pathway for audition travels along the vestibulocochlear nerve, which synapses with neurons in the cochlear nuclei of the superior medulla. Within the brain stem, input from either ear is combined to extract location information from the auditory stimuli. Whereas the initial auditory stimuli received at the cochlea strictly represent the frequency—or pitch—of the stimuli, the locations of sounds can be determined by comparing information arriving at both ears.

Sound localization is a feature of central processing in the auditory nuclei of the brain stem. Sound localization is achieved by the brain calculating the **interaural time difference** and the **interaural intensity difference**. A sound originating from a specific location will arrive at each ear at different times, unless the sound is directly in front of the listener. If the sound source is slightly to the left of the listener, the sound will arrive at the left ear microseconds before it arrives at the right ear (Figure 14.20). This time difference is an example of an interaural time difference. Also, the sound will be slightly louder in the left ear than in the right ear because some of the sound waves reaching the opposite ear are blocked by the head. This is an example of an interaural intensity difference.

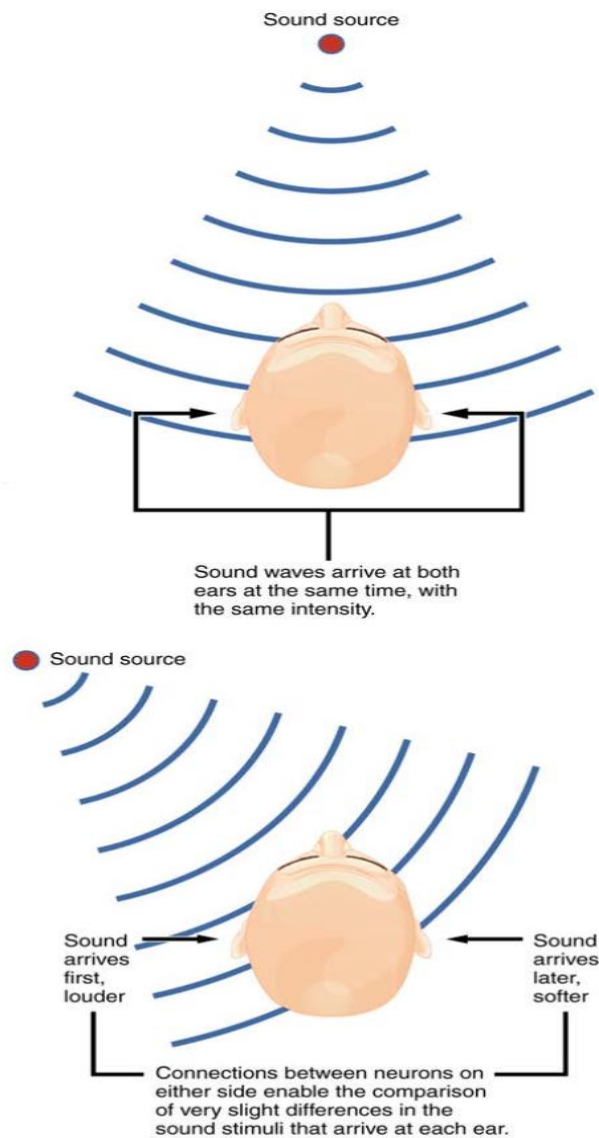


Figure 14.20 Auditory Brain Stem Mechanisms of Sound Localization Localizing sound in the horizontal plane is achieved by processing in the medullary nuclei of the auditory system. Connections between neurons on either side are able to compare very slight differences in sound stimuli that arrive at either ear and represent interaural time and intensity differences.

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Auditory processing continues on to a nucleus in the midbrain called the **inferior colliculus**. Axons from the inferior colliculus project to two locations, the thalamus and the **superior colliculus**. The **medial geniculate nucleus** of the thalamus receives the auditory information and then projects that information to the auditory cortex in the temporal lobe of the cerebral cortex. The superior colliculus receives input from the visual and somatosensory systems, as well as the ears, to initiate stimulation of the muscles that turn the head and neck toward the auditory stimulus.

Balance is coordinated through the vestibular system, the nerves of which are composed of axons from the vestibular ganglion that carries information from the utricle, saccule, and semicircular canals. The system contributes to controlling head and neck movements in response to vestibular signals. An important function of the vestibular system is coordinating eye and head movements to maintain visual attention. Most of the axons terminate in the **vestibular nuclei** of the medulla.

Some axons project from the vestibular ganglion directly to the cerebellum, with no intervening synapse in the vestibular nuclei. The cerebellum is primarily responsible for initiating movements on the basis of equilibrium information.

Neurons in the vestibular nuclei project their axons to targets in the brain stem. One target is the reticular formation, which influences respiratory and cardiovascular functions in relation to body movements. A second target of the axons of neurons in the vestibular nuclei is the spinal cord, which initiates the spinal reflexes involved with posture and balance. To assist the visual system, fibers of the vestibular nuclei project to the oculomotor, trochlear, and abducens nuclei to influence signals sent along the cranial nerves. These connections constitute the pathway of the **vestibulo-ocular reflex (VOR)**, which compensates for head and body movement by stabilizing images on the retina (**Figure 14.21**). Finally, the vestibular nuclei project to the thalamus to join the proprioceptive pathway of the dorsal column system, allowing conscious perception of equilibrium.

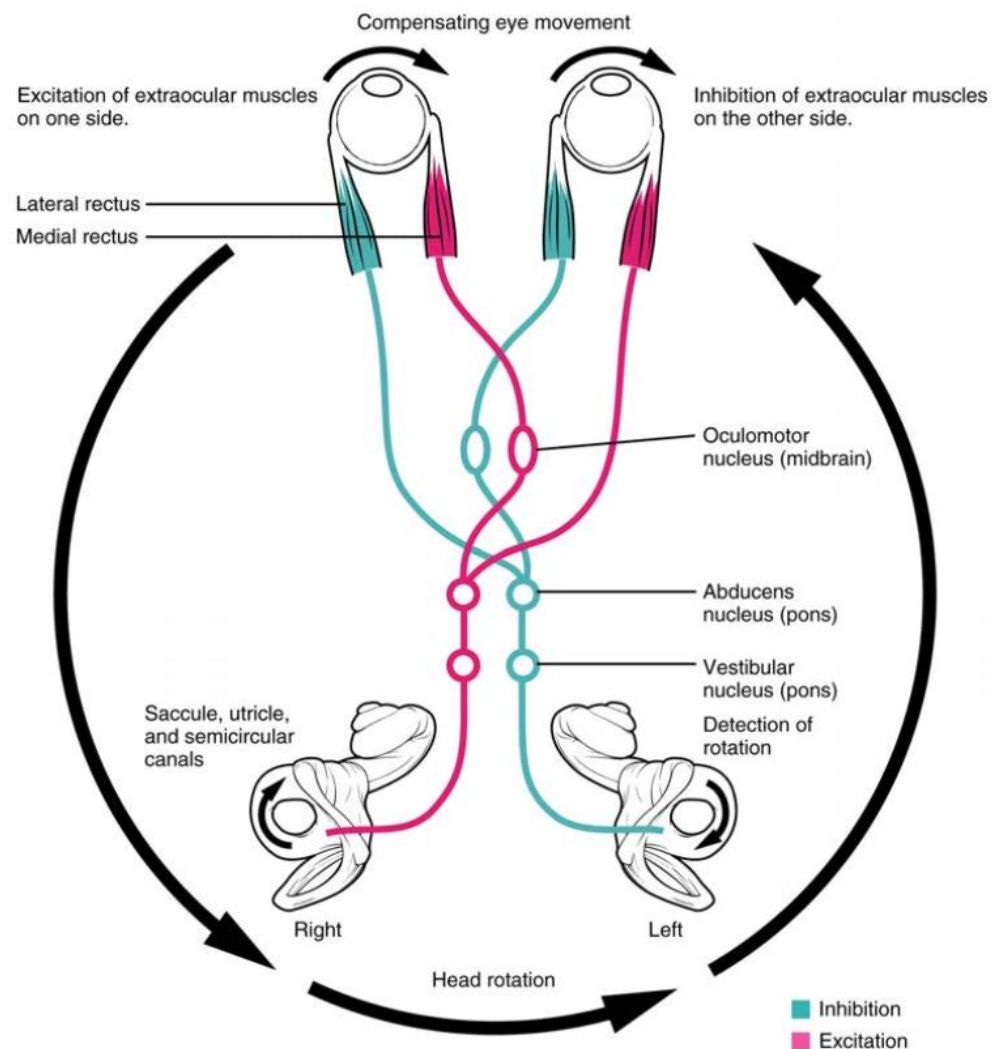


Figure 14.21 Vestibulo-ocular Reflex Connections between the vestibular system and the cranial nerves controlling eye movement keep the eyes centered on a visual stimulus, even though the head is moving. During head movement, the eye muscles move the eyes in the opposite direction as the head movement, keeping the visual stimulus centered in the field of view.

The connections of the optic nerve are more complicated than those of other cranial nerves. Instead of the connections being between each eye and the brain, visual information is segregated between the left and right sides of the visual field. In addition, some of the information from one side of the visual field projects to the opposite side of the brain. Within each eye, the axons projecting from the medial side of the retina decussate at the **optic chiasm**. For example, the axons from the medial retina of the left eye cross over to the right side of the brain at the optic chiasm. However, within each eye, the axons projecting from the lateral side of the retina do not decussate. For example, the axons from the lateral retina of the right eye project back to the right side of the brain. Therefore the left field of view of each eye is processed on the right side of the brain, whereas the right field of view of each eye is processed on the left side of the brain (**Figure 14.22**).

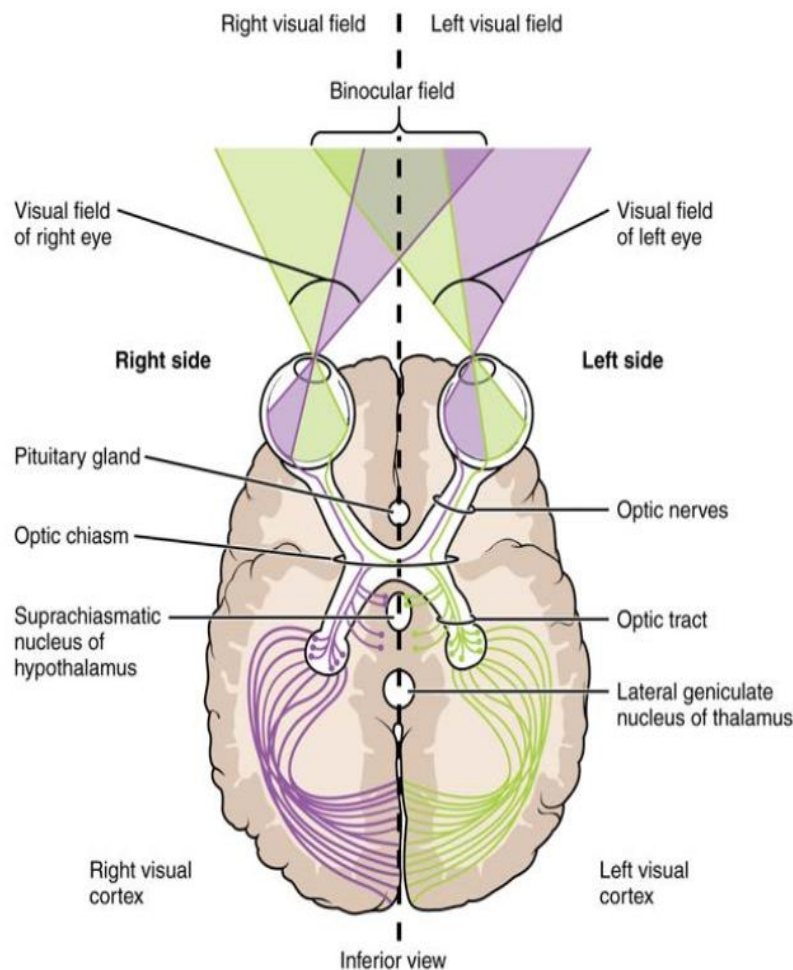


Figure 14.22 Segregation of Visual Field Information at the Optic Chiasm Contralateral visual field information from the lateral retina projects to the ipsilateral brain, whereas ipsilateral visual field information has to decussate at the optic chiasm to reach the opposite side of the brain.

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A unique clinical presentation that relates to this anatomic arrangement is the loss of lateral peripheral vision, known as bilateral hemianopia. This is different from “tunnel vision” because the superior and inferior peripheral fields are not lost. Visual field deficits can be disturbing for a patient, but in this case, the cause is not within the visual system itself. A growth of the pituitary gland presses against the optic chiasm and interferes with signal transmission. However, the axons projecting to the same side of the brain are unaffected. Therefore, the patient loses the outermost areas of their field of vision and cannot see objects to their right and left.

Extending from the optic chiasm, the axons of the visual system are referred to as the **optic tract** instead of the optic nerve. The optic tract has three major targets, two in the diencephalon and one in the midbrain. The connection between the eyes and diencephalon is demonstrated during development, in which the neural tissue of the retina differentiates from that of the diencephalon by the growth of the secondary vesicles. The connections of the retina into the CNS are a holdover from this developmental association. The majority of the connections of the optic tract are to the thalamus—specifically, the **lateral geniculate nucleus**. Axons from this nucleus then project to the visual cortex of the cerebrum, located in the occipital lobe. Another target of the optic tract is the superior colliculus.

In addition, a very small number of RGC axons project from the optic chiasm to the **suprachiasmatic nucleus** of the hypothalamus. These RGCs are photosensitive, in that they respond to the presence or absence of light. Unlike the photoreceptors, however, these photosensitive RGCs cannot be used to perceive images. By simply responding to the absence or presence of light, these RGCs can send information about day length. The perceived proportion of sunlight to darkness establishes the **circadian rhythm** of our bodies, allowing certain physiological events to occur at approximately the same time every day.

Diencephalon

The diencephalon is beneath the cerebrum and includes the thalamus and hypothalamus. In the somatic nervous system, the thalamus is an important relay for communication between the cerebrum and the rest of the nervous system. The hypothalamus has both somatic and autonomic functions. In addition, the hypothalamus communicates with the limbic system, which controls emotions and memory functions.

Sensory input to the thalamus comes from most of the special senses and ascending somatosensory tracts. Each sensory system is relayed through a particular nucleus in the thalamus. The thalamus is a required transfer point for most sensory tracts that reach the cerebral cortex, where conscious sensory perception begins. The one exception to this rule is the olfactory system. The olfactory tract axons from the olfactory bulb project directly to the cerebral cortex, along with the limbic system and hypothalamus.

The thalamus is a collection of several nuclei that can be categorized into three anatomical groups. White matter running through the thalamus defines the three major regions of the thalamus, which are an anterior nucleus, a medial nucleus, and a lateral group of nuclei. The anterior nucleus serves as a relay between the hypothalamus and the emotion and memory-producing limbic system. The medial nuclei serve as a relay for information from the limbic system and basal ganglia to the cerebral cortex. This allows memory creation during learning, but also determines alertness. The special and somatic senses connect to the lateral nuclei, where their information is relayed to the appropriate sensory cortex of the cerebrum.

Cortical Processing

As described earlier, many of the sensory axons are positioned in the same way as their corresponding receptor cells in the body. This allows identification of the position of a stimulus on the basis of which receptor cells are sending information. The cerebral cortex also maintains this sensory topography in the particular areas of the cortex that correspond to the position of the receptor cells. The somatosensory cortex provides an example in which, in essence, the locations of the somatosensory receptors in the body are mapped onto the somatosensory cortex. This mapping is often depicted using a **sensory homunculus** (Figure 14.23).

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The term homunculus comes from the Latin word for “little man” and refers to a map of the human body that is laid across a portion of the cerebral cortex. In the somatosensory cortex, the external genitals, feet, and lower legs are represented on the medial face of the gyrus within the longitudinal fissure. As the gyrus curves out of the fissure and along the surface of the parietal lobe, the body map continues through the thighs, hips, trunk, shoulders, arms, and hands. The head and face are just lateral to the fingers as the gyrus approaches the lateral sulcus. The representation of the body in this topographical map is medial to lateral from the lower to upper body. It is a continuation of the topographical arrangement seen in the dorsal column system, where axons from the lower body are carried in the fasciculus gracilis, whereas axons from the upper body are carried in the fasciculus cuneatus. As the dorsal column system continues into the medial lemniscus, these relationships are maintained. Also, the head and neck axons running from the trigeminal nuclei to the thalamus run adjacent to the upper body fibers. The connections through the thalamus maintain topography such that the anatomic information is preserved. Note that this correspondence does not result in a perfectly miniature scale version of the body, but rather exaggerates the more sensitive areas of the body, such as the fingers and lower face. Less sensitive areas of the body, such as the shoulders and back, are mapped to smaller areas on the cortex.

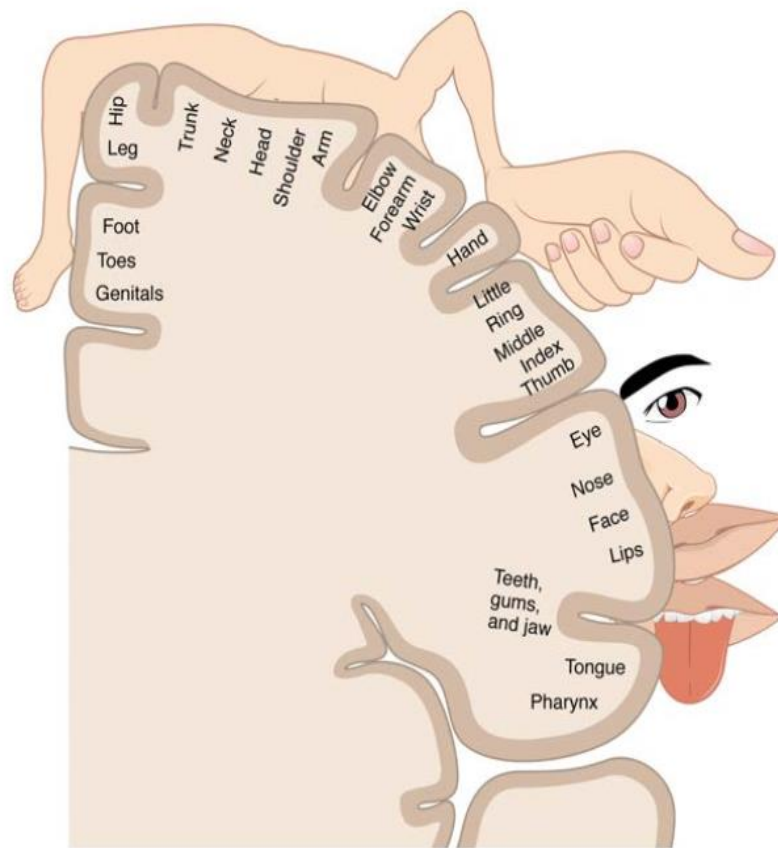


Figure 14.23 The Sensory Homunculus A cartoon representation of the sensory homunculus arranged adjacent to the cortical region in which the processing takes place.

Likewise, the topographic relationship between the retina and the visual cortex is maintained throughout the visual pathway. The visual field is projected onto the two retinæ, as described above, with sorting at the optic chiasm. The right peripheral visual field falls on the medial portion of the right retina and the lateral portion of the left retina. The right medial retina then projects across the midline through the optic chiasm. This results in the right visual field being processed in the left visual cortex. Likewise, the left visual field is processed in the right visual cortex (see [Figure 14.22](#)). Though the chiasm

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is helping to sort right and left visual information, superior and inferior visual information is maintained topographically in the visual pathway. Light from the superior visual field falls on the inferior retina, and light from the inferior visual field falls on the superior retina. This topography is maintained such that the superior region of the visual cortex processes the inferior visual field and vice versa. Therefore, the visual field information is inverted and reversed as it enters the visual cortex—up is down, and left is right. However, the cortex processes the visual information such that the final conscious perception of the visual field is correct. The topographic relationship is evident in that information from the foveal region of the retina is processed in the center of the primary visual cortex. Information from the peripheral regions of the retina are correspondingly processed toward the edges of the visual cortex. Similar to the exaggerations in the sensory homunculus of the somatosensory cortex, the foveal-processing area of the visual cortex is disproportionately larger than the areas processing peripheral vision.

In an experiment performed in the 1960s, subjects wore prism glasses so that the visual field was inverted before reaching the eye. On the first day of the experiment, subjects would duck when walking up to a table, thinking it was suspended from the ceiling. However, after a few days of acclimation, the subjects behaved as if everything were represented correctly. Therefore, the visual cortex is somewhat flexible in adapting to the information it receives from our eyes (**Figure 14.24**).

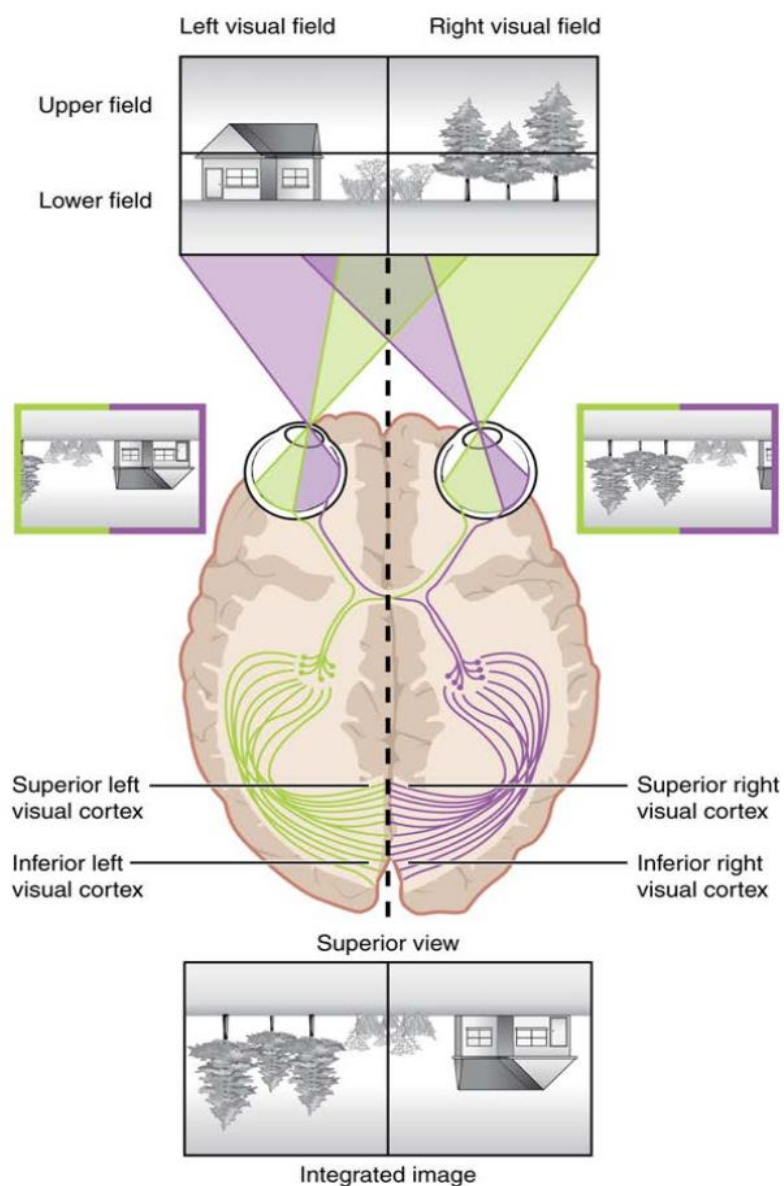


Figure 14.24 Topographic Mapping of the Retina onto the Visual Cortex The visual field projects onto the retina through the lenses and falls on the retinae as an inverted, reversed image. The topography of this image is maintained as the visual information travels through the visual pathway to the cortex.

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The cortex has been described as having specific regions that are responsible for processing specific information; there is the visual cortex, somatosensory cortex, gustatory cortex, etc. However, our experience of these senses is not divided. Instead, we experience what can be referred to as a seamless percept. Our perceptions of the various sensory modalities—though distinct in their content—are integrated by the brain so that we experience the world as a continuous whole.

In the cerebral cortex, sensory processing begins at the **primary sensory cortex**, then proceeds to an **association area**, and finally, into a **multimodal integration area**. For example, the visual pathway projects from the retinae through the thalamus to the primary visual cortex in the occipital lobe. This area is primarily in the medial wall within the longitudinal fissure. Here, visual stimuli begin to be recognized as basic shapes. Edges of objects are recognized and built into more complex shapes. Also, inputs from both eyes are compared to extract depth information. Because of the overlapping field of view between the two eyes, the brain can begin to estimate the distance of stimuli based on **binocular depth cues**.

There are two main regions that surround the primary cortex that are usually referred to as areas V2 and V3 (the primary visual cortex is area V1). These surrounding areas are the visual association cortex. The visual association regions develop more complex visual perceptions by adding color and motion information. The information processed in these areas is then sent to regions of the temporal and parietal lobes. Visual processing has two separate streams of processing: one into the temporal lobe and one into the parietal lobe. These are the ventral and dorsal streams, respectively (**Figure 14.26**). The **ventral stream** identifies visual stimuli and their significance. Because the ventral stream uses temporal lobe structures, it begins to interact with the non-visual cortex and may be important in visual stimuli becoming part of memories. The **dorsal stream** locates objects in space and helps in guiding movements of the body in response to visual inputs. The dorsal stream enters the parietal lobe, where it interacts with somatosensory cortical areas that are important for our perception of the body and its movements. The dorsal stream can then influence frontal lobe activity where motor functions originate.

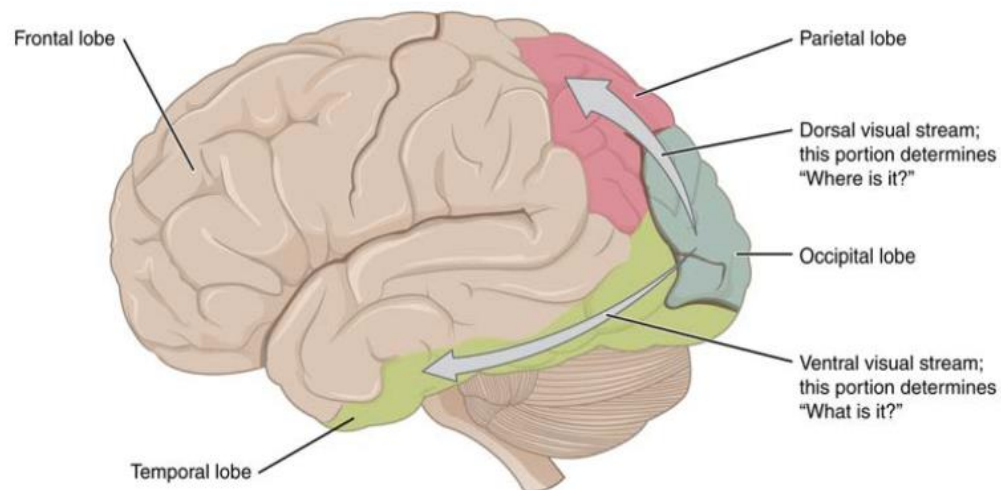


Figure 14.26 Ventral and Dorsal Visual Streams From the primary visual cortex in the occipital lobe, visual processing continues in two streams—one into the temporal lobe and one into the parietal lobe.

| Motor Responses

By the end of this section, you will be able to:

- List the components of the basic processing stream for the motor system
- Describe the pathway of descending motor commands from the cortex to the skeletal muscles
- Compare different descending pathways, both by structure and function
- Explain the initiation of movement from the neurological connections
- Describe several reflex arcs and their functional roles

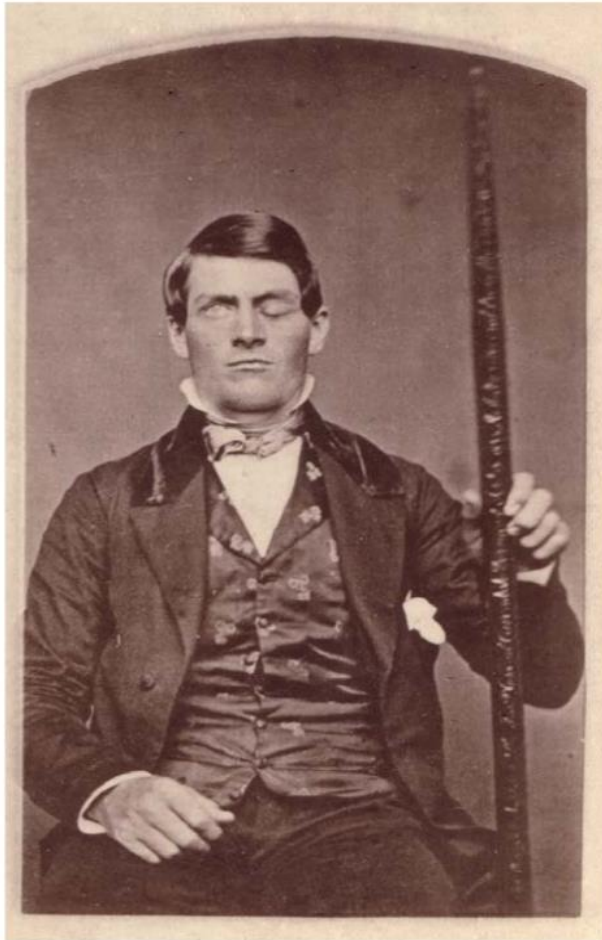
The defining characteristic of the somatic nervous system is that it controls skeletal muscles. Somatic senses inform the nervous system about the external environment, but the response to that is through voluntary muscle movement. The term “voluntary” suggests that there is a conscious decision to make a movement. However, some aspects of the somatic system use voluntary muscles without conscious control. One example is the ability of our breathing to switch to unconscious control while we are focused on another task. However, the muscles that are responsible for the basic process of breathing are also utilized for speech, which is entirely voluntary.

Cortical Responses

Let’s start with sensory stimuli that have been registered through receptor cells and the information relayed to the CNS along ascending pathways. In the cerebral cortex, the initial processing of sensory perception progresses to associative processing and then integration in multimodal areas of cortex. These levels of processing can lead to the incorporation of sensory perceptions into memory, but more importantly, they lead to a response. The completion of cortical processing through the primary, associative, and integrative sensory areas initiates a similar progression of motor processing, usually in different cortical areas.

Whereas the sensory cortical areas are located in the occipital, temporal, and parietal lobes, motor functions are largely controlled by the frontal lobe. The most anterior regions of the frontal lobe—the prefrontal areas—are important for **executive functions**, which are those cognitive functions that lead to goal-directed behaviors. These higher cognitive processes include **working memory**, which has been called a “mental scratch pad,” that can help organize and represent information that is not in the immediate environment. The prefrontal lobe is responsible for aspects of attention, such as inhibiting distracting thoughts and actions so that a person can focus on a goal and direct behavior toward achieving that goal.

The functions of the prefrontal cortex are integral to the personality of an individual, because it is largely responsible for what a person intends to do and how they accomplish those plans. A famous case of damage to the prefrontal cortex is that of Phineas Gage, dating back to 1848. He was a railroad worker who had a metal spike impale his prefrontal cortex (**Figure 14.27**). He survived the accident, but according to second-hand accounts, his personality changed drastically. Friends described him as no longer acting like himself. Whereas he was a hardworking, amiable man before the accident, he turned into an irritable, temperamental, and lazy man after the accident. Many of the accounts of his change may have been inflated in the retelling, and some behavior was likely attributable to alcohol used as a pain medication. However, the accounts suggest that some aspects of his personality did change. Also, there is new evidence that though his life changed dramatically, he was able to become a functioning stagecoach driver, suggesting that the brain has the ability to recover even from major trauma such as this.



(a)



(b)

Figure 14.27 Phineas Gage The victim of an accident while working on a railroad in 1848, Phineas Gage had a large iron rod impaled through the prefrontal cortex of his frontal lobe. After the accident, his personality appeared to change, but he eventually learned to cope with the trauma and lived as a coach driver even after such a traumatic event.

Secondary Motor Cortices

In generating motor responses, the executive functions of the prefrontal cortex will need to initiate actual movements. One way to define the prefrontal area is any region of the frontal lobe that does not elicit movement when electrically stimulated. These are primarily in the anterior part of the frontal lobe. The regions of the frontal lobe that remain are the regions of the cortex that produce movement. The prefrontal areas project into the secondary motor cortices, which include the **premotor cortex** and the **supplemental motor area**.

Two important regions that assist in planning and coordinating movements are located adjacent to the primary motor cortex. The premotor cortex is more lateral, whereas the supplemental motor area is more medial and superior. The premotor area aids in controlling movements of the core muscles to maintain posture during movement, whereas the supplemental motor area is hypothesized to be responsible for planning and coordinating movement. The supplemental motor area also manages sequential movements that are based on prior experience (that is, learned movements). Neurons in these areas are most active leading up to the initiation of movement. For example, these areas might prepare the body for the movements necessary to drive a car in anticipation of a traffic light changing.

Adjacent to these two regions are two specialized motor planning centers. The **frontal eye fields** are responsible for moving the eyes in response to visual stimuli. There are direct connections between the frontal eye fields and the superior colliculus. Also, anterior to the premotor cortex and primary motor cortex is **Broca's area**. This area is responsible for controlling movements of the structures of speech production. The area is named after a French surgeon and anatomist who studied patients who could not produce speech. They did not have impairments to understanding speech, only to producing speech sounds, suggesting a damaged or underdeveloped Broca's area.

Primary Motor Cortex

The primary motor cortex is located in the precentral gyrus of the frontal lobe. A neurosurgeon, Walter Penfield, described much of the basic understanding of the primary motor cortex by electrically stimulating the surface of the cerebrum. Penfield would probe the surface of the cortex while the patient was only under local anesthesia so that he could observe responses to the stimulation. This led to the belief that the precentral gyrus directly stimulated muscle movement. We now know that the primary motor cortex receives input from several areas that aid in planning movement, and its principle output stimulates spinal cord neurons to stimulate skeletal muscle contraction.

The primary motor cortex is arranged in a similar fashion to the primary somatosensory cortex, in that it has a topographical map of the body, creating a motor homunculus (see [Figure 14.23](#)). The neurons responsible for musculature in the feet and lower legs are in the medial wall of the precentral gyrus, with the thighs, trunk, and shoulder at the crest of the longitudinal fissure. The hand and face are in the lateral face of the gyrus. Also, the relative space allotted for the different regions is exaggerated in muscles that have greater innervation. The greatest amount of cortical space is given to muscles that perform fine, agile movements, such as the muscles of the fingers and the lower face. The “power muscles” that perform coarser movements, such as the buttock and back muscles, occupy much less space on the motor cortex.

Descending Pathways

The motor output from the cortex descends into the brain stem and to the spinal cord to control the musculature through motor neurons. Neurons located in the primary motor cortex, named **Betz cells**, are large cortical neurons that synapse with lower motor neurons in the spinal cord or the brain stem. The two descending pathways travelled by the axons of Betz cells are the **corticospinal tract** and the **corticobulbar tract**. Both tracts are named for their origin in the cortex and their targets—either the spinal cord or the brain stem (the term “bulbar” refers to the brain stem as the bulb, or enlargement, at the top of the spinal cord).

These two descending pathways are responsible for the conscious or voluntary movements of skeletal muscles. Any motor command from the primary motor cortex is sent down the axons of the Betz cells to activate upper motor neurons in either the cranial motor nuclei or in the ventral horn of the spinal cord. The axons of the corticobulbar tract are ipsilateral, meaning they project from the cortex to the motor nucleus on the same side of the nervous system. Conversely, the axons of the corticospinal tract are largely contralateral, meaning that they cross the midline of the brain stem or spinal cord and synapse on the opposite side of the body. Therefore, the right motor cortex of the cerebrum controls muscles on the left side of the body, and vice versa.

The corticospinal tract descends from the cortex through the deep white matter of the cerebrum. It then passes between the caudate nucleus and putamen of the basal nuclei as a bundle called the **internal capsule**. The tract then passes through the midbrain as the **cerebral peduncles**, after which it burrows through the pons. Upon entering the medulla, the tracts make up the large white matter tract referred to as the **pyramids** ([Figure 14.28](#)). The defining landmark of the medullary-spinal border is the **pyramidal decussation**, which is where most of the fibers in the corticospinal tract cross over to the opposite side of the brain. At this point, the tract separates into two parts, which have control over different domains of the musculature.

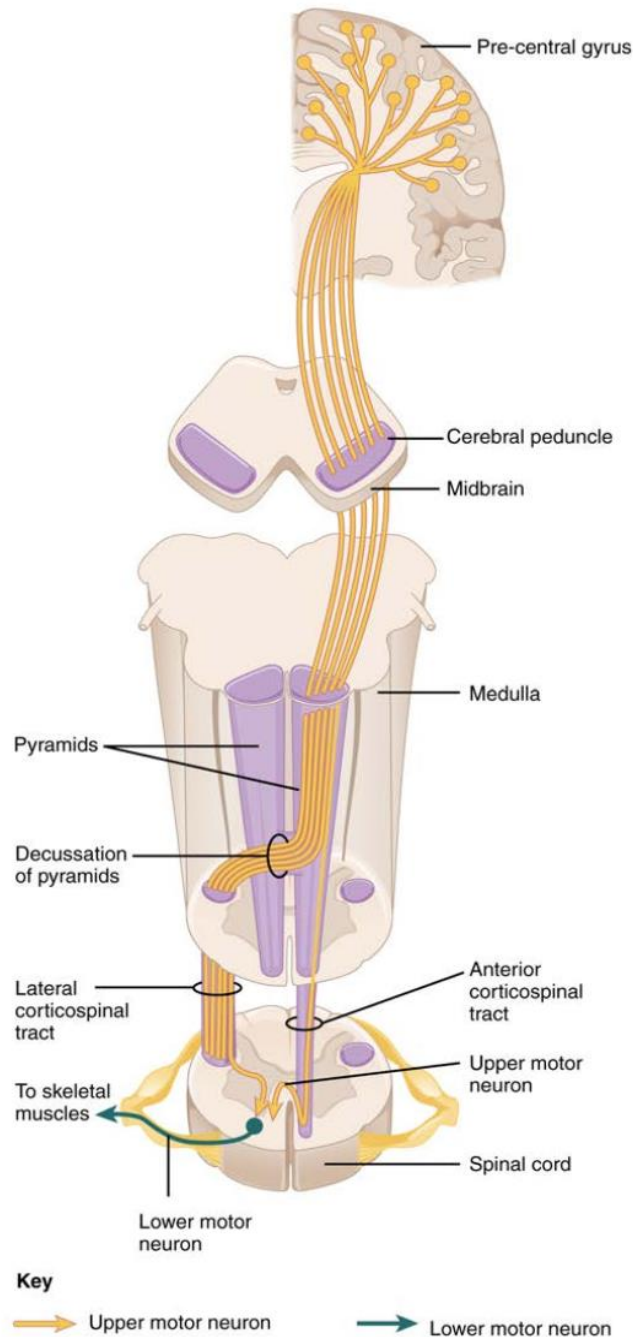


Figure 14.28 Corticospinal Tract The major descending tract that controls skeletal muscle movements is the corticospinal tract. It is composed of two neurons, the upper motor neuron and the lower motor neuron. The upper motor neuron has its cell body in the primary motor cortex of the frontal lobe and synapses on the lower motor neuron, which is in the ventral horn of the spinal cord and projects to the skeletal muscle in the periphery.

Appendicular Control

The **lateral corticospinal tract** is composed of the fibers that cross the midline at the pyramidal decussation (see **Figure 14.28**). The axons cross over from the anterior position of the pyramids in the medulla to the lateral column of the spinal cord. These axons are responsible for controlling appendicular muscles.

This influence over the appendicular muscles means that the lateral corticospinal tract is responsible for moving the muscles of the arms and legs. The ventral horn in both the lower cervical spinal cord and the lumbar spinal cord both have wider ventral horns, representing the greater number of muscles controlled by these motor neurons. The **cervical enlargement** is particularly large because there is greater control over the fine musculature of the upper limbs, particularly

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of the fingers. The **lumbar enlargement** is not as significant in appearance because there is less fine motor control of the lower limbs.

Axial Control

The **anterior corticospinal tract** is responsible for controlling the muscles of the body trunk (see **Figure 14.28**). These axons do not decussate in the medulla. Instead, they remain in an anterior position as they descend the brain stem and enter the spinal cord. These axons then travel to the spinal cord level at which they synapse with a lower motor neuron. Upon reaching the appropriate level, the axons decussate, entering the ventral horn on the opposite side of the spinal cord from which they entered. In the ventral horn, these axons synapse with their corresponding lower motor neurons. The lower motor neurons are located in the medial regions of the ventral horn, because they control the axial muscles of the trunk.

Because movements of the body trunk involve both sides of the body, the anterior corticospinal tract is not entirely contralateral. Some collateral branches of the tract will project into the ipsilateral ventral horn to control synergistic muscles on that side of the body, or to inhibit antagonistic muscles through interneurons within the ventral horn. Through the influence of both sides of the body, the anterior corticospinal tract can coordinate postural muscles in broad movements of the body. These coordinating axons in the anterior corticospinal tract are often considered bilateral, as they are both ipsilateral and contralateral.

Extrapyramidal Controls

Other descending connections between the brain and the spinal cord are called the **extrapyramidal system**. The name comes from the fact that this system is outside the corticospinal pathway, which includes the pyramids in the medulla. A few pathways originating from the brain stem contribute to this system.

The **tectospinal tract** projects from the midbrain to the spinal cord and is important for postural movements that are driven by the superior colliculus. The name of the tract comes from an alternate name for the superior colliculus, which is the tectum. The **reticulospinal tract** connects the reticular system, a diffuse region of gray matter in the brain stem, with the spinal cord. This tract influences trunk and proximal limb muscles related to posture and locomotion. The reticulospinal tract also contributes to muscle tone and influences autonomic functions. The **vestibulospinal tract** connects the brain stem nuclei of the vestibular system with the spinal cord. This allows posture, movement, and balance to be modulated on the basis of equilibrium information provided by the vestibular system.

The pathways of the extrapyramidal system are influenced by subcortical structures. For example, connections between the secondary motor cortices and the extrapyramidal system modulate spine and cranium movements. The basal nuclei, which are important for regulating movement initiated by the CNS, influence the extrapyramidal system as well as its thalamic feedback to the motor cortex.

The conscious movement of our muscles is more complicated than simply sending a single command from the precentral gyrus down to the proper motor neurons. During the movement of any body part, our muscles relay information back to the brain, and the brain is constantly sending “revised” instructions back to the muscles. The cerebellum is important in contributing to the motor system because it compares cerebral motor commands with proprioceptive feedback. The corticospinal fibers that project to the ventral horn of the spinal cord have branches that also synapse in the pons, which project to the cerebellum. Also, the proprioceptive sensations of the dorsal column system have a collateral projection to the medulla that projects to the cerebellum. These two streams of information are compared in the cerebellar cortex. Conflicts between the motor commands sent by the cerebrum and body position information provided by the proprioceptors cause the cerebellum to stimulate the **red nucleus** of the midbrain. The red nucleus then sends corrective commands to the spinal cord along the **rubrospinal tract**. The name of this tract comes from the word for red that is seen in the English word “ruby.”

A good example of how the cerebellum corrects cerebral motor commands can be illustrated by walking in water. An original motor command from the cerebrum to walk will result in a highly coordinated set of learned movements. However, in water, the body cannot actually perform a typical walking movement as instructed. The cerebellum can alter the motor command, stimulating the leg muscles to take larger steps to overcome the water resistance. The cerebellum can make the necessary changes through the rubrospinal tract. Modulating the basic command to walk also relies on spinal reflexes, but the cerebellum is responsible for calculating the appropriate response. When the cerebellum does not work properly, coordination and balance are severely affected. The most dramatic example of this is during the overconsumption of alcohol. Alcohol inhibits the ability of the cerebellum to interpret proprioceptive feedback, making it more difficult to coordinate body movements, such as walking a straight line, or guide the movement of the hand to touch the tip of the nose.

Ventral Horn Output

The somatic nervous system provides output strictly to skeletal muscles. The lower motor neurons, which are responsible for the contraction of these muscles, are found in the ventral horn of the spinal cord. These large, multipolar neurons have a corona of dendrites surrounding the cell body and an axon that extends out of the ventral horn. This axon travels through the ventral nerve root to join the emerging spinal nerve. The axon is relatively long because it needs to reach muscles in the periphery of the body. The diameters of cell bodies may be on the order of hundreds of micrometers to support the long axon; some axons are a meter in length, such as the lumbar motor neurons that innervate muscles in the first digits of the feet.

The axons will also branch to innervate multiple muscle fibers. Together, the motor neuron and all the muscle fibers that it controls make up a motor unit. Motor units vary in size. Some may contain up to 1000 muscle fibers, such as in the quadriceps, or they may only have 10 fibers, such as in an extraocular muscle. The number of muscle fibers that are part of a motor unit corresponds to the precision of control of that muscle. Also, muscles that have finer motor control have more motor units connecting to them, and this requires a larger topographical field in the primary motor cortex.

Motor neuron axons connect to muscle fibers at a neuromuscular junction. This is a specialized synaptic structure at which multiple axon terminals synapse with the muscle fiber sarcolemma. The synaptic end bulbs of the motor neurons secrete acetylcholine, which binds to receptors on the sarcolemma. The binding of acetylcholine opens ligand-gated ion channels, increasing the movement of cations across the sarcolemma. This depolarizes the sarcolemma, initiating muscle contraction. Whereas other synapses result in graded potentials that must reach a threshold in the postsynaptic target, activity at the neuromuscular junction reliably leads to muscle fiber contraction with every nerve impulse received from a motor neuron. However, the strength of contraction and the number of fibers that contract can be affected by the frequency of the motor neuron impulses.

Reflexes

This chapter began by introducing reflexes as an example of the basic elements of the somatic nervous system. Simple somatic reflexes do not include the higher centers discussed for conscious or voluntary aspects of movement. Reflexes can be spinal or cranial, depending on the nerves and central components that are involved. The example described at the beginning of the chapter involved heat and pain sensations from a hot stove causing withdrawal of the arm through a connection in the spinal cord that leads to contraction of the biceps brachii. The description of this withdrawal reflex was simplified, for the sake of the introduction, to emphasize the parts of the somatic nervous system. But to consider reflexes fully, more attention needs to be given to this example.

As you withdraw your hand from the stove, you do not want to slow that reflex down. As the biceps brachii contracts, the antagonistic triceps brachii needs to relax. Because the neuromuscular junction is strictly excitatory, the biceps will

contract when the motor nerve is active. Skeletal muscles do not actively relax. Instead the motor neuron needs to “quiet down,” or be inhibited. In the hot-stove withdrawal reflex, this occurs through an interneuron in the spinal cord. The interneuron’s cell body is located in the dorsal horn of the spinal cord. The interneuron receives a synapse from the axon of the sensory neuron that detects that the hand is being burned. In response to this stimulation from the sensory neuron, the interneuron then inhibits the motor neuron that controls the triceps brachii. This is done by releasing a neurotransmitter or other signal that hyperpolarizes the motor neuron connected to the triceps brachii, making it less likely to initiate an action potential. With this motor neuron being inhibited, the triceps brachii relaxes. Without the antagonistic contraction, withdrawal from the hot stove is faster and keeps further tissue damage from occurring.

Another example of a withdrawal reflex occurs when you step on a painful stimulus, like a tack or a sharp rock. The nociceptors that are activated by the painful stimulus activate the motor neurons responsible for contraction of the tibialis anterior muscle. This causes dorsiflexion of the foot. An inhibitory interneuron, activated by a collateral branch of the nociceptor fiber, will inhibit the motor neurons of the gastrocnemius and soleus muscles to cancel plantar flexion. An important difference in this reflex is that plantar flexion is most likely in progress as the foot is pressing down onto the tack. Contraction of the tibialis anterior is not the most important aspect of the reflex, as continuation of plantar flexion will result in further damage from stepping onto the tack.

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Another type of reflex is a **stretch reflex**. In this reflex, when a skeletal muscle is stretched, a muscle spindle receptor is activated. The axon from this receptor structure will cause direct contraction of the muscle. A collateral of the muscle spindle fiber will also inhibit the motor neuron of the antagonist muscles. The reflex helps to maintain muscles at a constant length. A common example of this reflex is the knee jerk that is elicited by a rubber hammer struck against the patellar ligament in a physical exam.

A specialized reflex to protect the surface of the eye is the **corneal reflex**, or the eye blink reflex. When the cornea is stimulated by a tactile stimulus, or even by bright light in a related reflex, blinking is initiated. The sensory component travels through the trigeminal nerve, which carries somatosensory information from the face, or through the optic nerve, if the stimulus is bright light. The motor response travels through the facial nerve and innervates the orbicularis oculi on the same side. This reflex is commonly tested during a physical exam using an air puff or a gentle touch of a cotton-tipped applicator.

KEY TERMS

- alkaloid** substance, usually from a plant source, that is chemically basic with respect to pH and will stimulate bitter receptors
- amacrine cell** type of cell in the retina that connects to the bipolar cells near the outer synaptic layer and provides the basis for early image processing within the retina
- ampulla** in the ear, the structure at the base of a semicircular canal that contains the hair cells and cupula for transduction of rotational movement of the head
- anosmia** loss of the sense of smell; usually the result of physical disruption of the first cranial nerve
- anterior corticospinal tract** division of the corticospinal pathway that travels through the ventral (anterior) column of the spinal cord and controls axial musculature through the medial motor neurons in the ventral (anterior) horn
- aqueous humor** watery fluid that fills the anterior chamber containing the cornea, iris, ciliary body, and lens of the eye
- ascending pathway** fiber structure that relays sensory information from the periphery through the spinal cord and brain stem to other structures of the brain
- association area** region of cortex connected to a primary sensory cortical area that further processes the information to generate more complex sensory perceptions
- audition** sense of hearing
- auricle** fleshy external structure of the ear
- Betz cells** output cells of the primary motor cortex that cause musculature to move through synapses on cranial and spinal motor neurons
- Broca's area** region of the frontal lobe associated with the motor commands necessary for speech production
- basilar membrane** in the ear, the floor of the cochlear duct on which the organ of Corti sits
- binocular depth cues** indications of the distance of visual stimuli on the basis of slight differences in the images projected onto either retina
- bipolar cell** cell type in the retina that connects the photoreceptors to the RGCs
- capsaicin** molecule that activates nociceptors by interacting with a temperature-sensitive ion channel and is the basis for "hot" sensations in spicy food
- cerebral peduncles** segments of the descending motor pathway that make up the white matter of the ventral midbrain
- cervical enlargement** region of the ventral (anterior) horn of the spinal cord that has a larger population of motor neurons for the greater number of and finer control of muscles of the upper limb
- chemoreceptor** sensory receptor cell that is sensitive to chemical stimuli, such as in taste, smell, or pain
- chief sensory nucleus** component of the trigeminal nuclei that is found in the pons
- choroid** highly vascular tissue in the wall of the eye that supplies the outer retina with blood
- ciliary body** smooth muscle structure on the interior surface of the iris that controls the shape of the lens through the zonule fibers
- circadian rhythm** internal perception of the daily cycle of light and dark based on retinal activity related to sunlight
- cochlea** auditory portion of the inner ear containing structures to transduce sound stimuli
- cochlear duct** space within the auditory portion of the inner ear that contains the organ of Corti and is adjacent to the scala tympani and scala vestibuli on either side

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cone photoreceptor one of the two types of retinal receptor cell that is specialized for color vision through the use of three photopigments distributed through three separate populations of cells

contralateral word meaning “on the opposite side,” as in axons that cross the midline in a fiber tract

cornea fibrous covering of the anterior region of the eye that is transparent so that light can pass through it

corneal reflex protective response to stimulation of the cornea causing contraction of the orbicularis oculi muscle resulting in blinking of the eye

corticobulbar tract connection between the cortex and the brain stem responsible for generating movement

corticospinal tract connection between the cortex and the spinal cord responsible for generating movement

cupula specialized structure within the base of a semicircular canal that bends the stereocilia of hair cells when the head rotates by way of the relative movement of the enclosed fluid

decussate to cross the midline, as in fibers that project from one side of the body to the other

dorsal column system ascending tract of the spinal cord associated with fine touch and proprioceptive sensations

dorsal stream connections between cortical areas from the occipital to parietal lobes that are responsible for the perception of visual motion and guiding movement of the body in relation to that motion

encapsulated ending configuration of a sensory receptor neuron with dendrites surrounded by specialized structures to aid in transduction of a particular type of sensation, such as the lamellated corpuscles in the deep dermis and subcutaneous tissue

equilibrium sense of balance that includes sensations of position and movement of the head

executive functions cognitive processes of the prefrontal cortex that lead to directing goal-directed behavior, which is a precursor to executing motor commands

external ear structures on the lateral surface of the head, including the auricle and the ear canal back to the tympanic membrane

exteroceptor sensory receptor that is positioned to interpret stimuli from the external environment, such as photoreceptors in the eye or somatosensory receptors in the skin

extraocular muscle one of six muscles originating out of the bones of the orbit and inserting into the surface of the eye which are responsible for moving the eye

extrapyramidal system pathways between the brain and spinal cord that are separate from the corticospinal tract and are responsible for modulating the movements generated through that primary pathway

fasciculus cuneatus lateral division of the dorsal column system composed of fibers from sensory neurons in the upper body

fasciculus gracilis medial division of the dorsal column system composed of fibers from sensory neurons in the lower body

fibrous tunic outer layer of the eye primarily composed of connective tissue known as the sclera and cornea

fovea exact center of the retina at which visual stimuli are focused for maximal acuity, where the retina is thinnest, at which there is nothing but photoreceptors

free nerve ending configuration of a sensory receptor neuron with dendrites in the connective tissue of the organ, such as in the dermis of the skin, that are most often sensitive to chemical, thermal, and mechanical stimuli

frontal eye fields area of the prefrontal cortex responsible for moving the eyes to attend to visual stimuli

general sense any sensory system that is distributed throughout the body and incorporated into organs of multiple other systems, such as the walls of the digestive organs or the skin

gustation sense of taste

gustatory receptor cells sensory cells in the taste bud that transduce the chemical stimuli of gustation

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hair cells mechanoreceptor cells found in the inner ear that transduce stimuli for the senses of hearing and balance

incus (also, anvil) ossicle of the middle ear that connects the malleus to the stapes

inferior colliculus last structure in the auditory brainstem pathway that projects to the thalamus and superior colliculus

inferior oblique extraocular muscle responsible for lateral rotation of the eye

inferior rectus extraocular muscle responsible for looking down

inner ear structure within the temporal bone that contains the sensory apparatus of hearing and balance

inner segment in the eye, the section of a photoreceptor that contains the nucleus and other major organelles for normal cellular functions

inner synaptic layer layer in the retina where bipolar cells connect to RGCs

interaural intensity difference cue used to aid sound localization in the horizontal plane that compares the relative loudness of sounds at the two ears, because the ear closer to the sound source will hear a slightly more intense sound

interaural time difference cue used to help with sound localization in the horizontal plane that compares the relative time of arrival of sounds at the two ears, because the ear closer to the sound source will receive the stimulus microseconds before the other ear

internal capsule segment of the descending motor pathway that passes between the caudate nucleus and the putamen

interoceptor sensory receptor that is positioned to interpret stimuli from internal organs, such as stretch receptors in the wall of blood vessels

ipsilateral word meaning on the same side, as in axons that do not cross the midline in a fiber tract

iris colored portion of the anterior eye that surrounds the pupil

kinesthesia sense of body movement based on sensations in skeletal muscles, tendons, joints, and the skin

lacrimal duct duct in the medial corner of the orbit that drains tears into the nasal cavity

lacrimal gland gland lateral to the orbit that produces tears to wash across the surface of the eye

lateral corticospinal tract division of the corticospinal pathway that travels through the lateral column of the spinal cord and controls appendicular musculature through the lateral motor neurons in the ventral (anterior) horn

lateral geniculate nucleus thalamic target of the RGCs that projects to the visual cortex

lateral rectus extraocular muscle responsible for abduction of the eye

lens component of the eye that focuses light on the retina

levator palpebrae superioris muscle that causes elevation of the upper eyelid, controlled by fibers in the oculomotor nerve

lumbar enlargement region of the ventral (anterior) horn of the spinal cord that has a larger population of motor neurons for the greater number of muscles of the lower limb

macula enlargement at the base of a semicircular canal at which transduction of equilibrium stimuli takes place within the ampulla

malleus (also, hammer) ossicle that is directly attached to the tympanic membrane

mechanoreceptor receptor cell that transduces mechanical stimuli into an electrochemical signal

medial geniculate nucleus thalamic target of the auditory brain stem that projects to the auditory cortex

medial lemniscus fiber tract of the dorsal column system that extends from the nuclei gracilis and cuneatus to the thalamus, and decussates

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- medial rectus** extraocular muscle responsible for adduction of the eye
- mesencephalic nucleus** component of the trigeminal nuclei that is found in the midbrain
- middle ear** space within the temporal bone between the ear canal and bony labyrinth where the ossicles amplify sound waves from the tympanic membrane to the oval window
- multimodal integration area** region of the cerebral cortex in which information from more than one sensory modality is processed to arrive at higher level cortical functions such as memory, learning, or cognition
- neural tunic** layer of the eye that contains nervous tissue, namely the retina
- nociceptor** receptor cell that senses pain stimuli
- nucleus cuneatus** medullary nucleus at which first-order neurons of the dorsal column system synapse specifically from the upper body and arms
- nucleus gracilis** medullary nucleus at which first-order neurons of the dorsal column system synapse specifically from the lower body and legs
- odorant molecules** volatile chemicals that bind to receptor proteins in olfactory neurons to stimulate the sense of smell
- olfaction** sense of smell
- olfactory bulb** central target of the first cranial nerve; located on the ventral surface of the frontal lobe in the cerebrum
- olfactory epithelium** region of the nasal epithelium where olfactory neurons are located
- olfactory sensory neuron** receptor cell of the olfactory system, sensitive to the chemical stimuli of smell, the axons of which compose the first cranial nerve
- opsin** protein that contains the photosensitive cofactor retinal for phototransduction
- optic chiasm** decussation point in the visual system at which medial retina fibers cross to the other side of the brain
- optic disc** spot on the retina at which RGC axons leave the eye and blood vessels of the inner retina pass
- optic nerve** second cranial nerve, which is responsible visual sensation
- optic tract** name for the fiber structure containing axons from the retina posterior to the optic chiasm representing their CNS location
- organ of Corti** structure in the cochlea in which hair cells transduce movements from sound waves into electrochemical signals
- osmoreceptor** receptor cell that senses differences in the concentrations of bodily fluids on the basis of osmotic pressure
- ossicles** three small bones in the middle ear
- otolith** gelatinous substance in the utricle and saccule of the inner ear that contains calcium carbonate crystals and into which the stereocilia of hair cells are embedded
- outer segment** in the eye, the section of a photoreceptor that contains opsin molecules that transduce light stimuli
- outer synaptic layer** layer in the retina at which photoreceptors connect to bipolar cells
- oval window** membrane at the base of the cochlea where the stapes attaches, marking the beginning of the scala vestibuli
- palpebral conjunctiva** membrane attached to the inner surface of the eyelids that covers the anterior surface of the cornea
- papilla** for gustation, a bump-like projection on the surface of the tongue that contains taste buds

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photoisomerization chemical change in the retinal molecule that alters the bonding so that it switches from the 11-*cis*-retinal isomer to the all-*trans*-retinal isomer

photon individual “packet” of light

photoreceptor receptor cell specialized to respond to light stimuli

premotor cortex cortical area anterior to the primary motor cortex that is responsible for planning movements

primary sensory cortex region of the cerebral cortex that initially receives sensory input from an ascending pathway from the thalamus and begins the processing that will result in conscious perception of that modality

proprioception sense of position and movement of the body

proprioceptor receptor cell that senses changes in the position and kinesthetic aspects of the body

pupil open hole at the center of the iris that light passes through into the eye

pyramidal decussation location at which corticospinal tract fibers cross the midline and segregate into the anterior and lateral divisions of the pathway

pyramids segment of the descending motor pathway that travels in the anterior position of the medulla

receptor cell cell that transduces environmental stimuli into neural signals

red nucleus midbrain nucleus that sends corrective commands to the spinal cord along the rubrospinal tract, based on disparity between an original command and the sensory feedback from movement

reticulospinal tract extrapyramidal connections between the brain stem and spinal cord that modulate movement, contribute to posture, and regulate muscle tone

retinal ganglion cell (RGC) neuron of the retina that projects along the second cranial nerve

retinal cofactor in an opsin molecule that undergoes a biochemical change when struck by a photon (pronounced with a stress on the last syllable)

retina nervous tissue of the eye at which phototransduction takes place

rhodopsin photopigment molecule found in the rod photoreceptors

rod photoreceptor one of the two types of retinal receptor cell that is specialized for low-light vision

round window membrane that marks the end of the scala tympani

rubrospinal tract descending motor control pathway, originating in the red nucleus, that mediates control of the limbs on the basis of cerebellar processing

sacculle structure of the inner ear responsible for transducing linear acceleration in the vertical plane

scala tympani portion of the cochlea that extends from the apex to the round window

scala vestibuli portion of the cochlea that extends from the oval window to the apex

sclera white of the eye

semicircular canals structures within the inner ear responsible for transducing rotational movement information

sensory homunculus topographic representation of the body within the somatosensory cortex demonstrating the correspondence between neurons processing stimuli and sensitivity

sensory modality a particular system for interpreting and perceiving environmental stimuli by the nervous system

solitary nucleus medullar nucleus that receives taste information from the facial and glossopharyngeal nerves

somatosensation general sense associated with modalities lumped together as touch

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special sense any sensory system associated with a specific organ structure, namely smell, taste, sight, hearing, and balance

spinal trigeminal nucleus component of the trigeminal nuclei that is found in the medulla

spinothalamic tract ascending tract of the spinal cord associated with pain and temperature sensations

spiral ganglion location of neuronal cell bodies that transmit auditory information along the eighth cranial nerve

stapes (also, stirrup) ossicle of the middle ear that is attached to the inner ear

stereocilia array of apical membrane extensions in a hair cell that transduce movements when they are bent

stretch reflex response to activation of the muscle spindle stretch receptor that causes contraction of the muscle to maintain a constant length

submodality specific sense within a broader major sense such as sweet as a part of the sense of taste, or color as a part of vision

superior colliculus structure in the midbrain that combines visual, auditory, and somatosensory input to coordinate spatial and topographic representations of the three sensory systems

superior oblique extraocular muscle responsible for medial rotation of the eye

superior rectus extraocular muscle responsible for looking up

supplemental motor area cortical area anterior to the primary motor cortex that is responsible for planning movements

suprachiasmatic nucleus hypothalamic target of the retina that helps to establish the circadian rhythm of the body on the basis of the presence or absence of daylight

taste buds structures within a papilla on the tongue that contain gustatory receptor cells

tectorial membrane component of the organ of Corti that lays over the hair cells, into which the stereocilia are embedded

tectospinal tract extrapyramidal connections between the superior colliculus and spinal cord

thermoreceptor sensory receptor specialized for temperature stimuli

topographical relating to positional information

transduction process of changing an environmental stimulus into the electrochemical signals of the nervous system

trochlea cartilaginous structure that acts like a pulley for the superior oblique muscle

tympanic membrane ear drum

umami taste submodality for sensitivity to the concentration of amino acids; also called the savory sense

utricle structure of the inner ear responsible for transducing linear acceleration in the horizontal plane

vascular tunic middle layer of the eye primarily composed of connective tissue with a rich blood supply

ventral posterior nucleus nucleus in the thalamus that is the target of gustatory sensations and projects to the cerebral cortex

ventral stream connections between cortical areas from the occipital lobe to the temporal lobe that are responsible for identification of visual stimuli

vestibular ganglion location of neuronal cell bodies that transmit equilibrium information along the eighth cranial nerve

vestibular nuclei targets of the vestibular component of the eighth cranial nerve

vestibule in the ear, the portion of the inner ear responsible for the sense of equilibrium

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vestibulo-ocular reflex (VOR) reflex based on connections between the vestibular system and the cranial nerves of eye movements that ensures images are stabilized on the retina as the head and body move

vestibulospinal tract extrapyramidal connections between the vestibular nuclei in the brain stem and spinal cord that modulate movement and contribute to balance on the basis of the sense of equilibrium

visceral sense sense associated with the internal organs

vision special sense of sight based on transduction of light stimuli

visual acuity property of vision related to the sharpness of focus, which varies in relation to retinal position

vitreous humor viscous fluid that fills the posterior chamber of the eye

working memory function of the prefrontal cortex to maintain a representation of information that is not in the immediate environment

zonule fibers fibrous connections between the ciliary body and the lens