PART IV

SENSORY SYSTEMS

18.

GENERAL PRINCIPLES OF SENSORY SYSTEMS

Each sensory system is obviously quite different in the type of stimulation that it responds to and the manner in which environmental stimuli is converted to neuronal signaling. However, there are many principles that can be generalized across sensory systems.

Sensory transduction

Our sensory systems work by converting different types of stimuli in the environment (i.e. visible light, sound waves, chemical molecules) into action potentials in the nervous system. This conversion is called sensory transduction and occurs in all sensory systems.

Sensory receptors

Sensory transduction begins at the sensory receptors. Each sensory system has specialized cells that are able to detect the environmental stimuli. Photoreceptors detect light, chemical receptors in the tongue and nose detect odors and taste, mechanoreceptors detect touch, and hair cells detect sound.

Receptor Potentials

We have learned about postsynaptic potentials in neurons, receptor potentials are similar membrane potential changes that happen in sensory receptors in response to a stimulus.

Receptive fields

Receptive fields are easiest to understand in the visual and somatosensory systems. The receptive field for a neuron is the region of the retina or skin where a stimulus (light or touch) will evoke a response in the neuron. Receptive fields in the auditory system can consist of a certain frequency of sound and/or the location of sound in space.

Receptive fields can vary in size and shape depending on the characteristics of neuron (i.e. type, location in body, location in pathway). Receptive fields become more complex as information travels to the brain.

Lateral Inhibition

Lateral inhibition is a process used by sensory systems to enhance the perception of signals, particularly at edges, points, or other changes in the stimulus. It occurs because overlapping receptive fields can inhibit each other. This inhibition enhances the perceived differences between the stimulus and the area not stimulated.

Neural Coding

There are a number of different ways in which the nervous system encodes complex information. Two that are common within the sensory systems are line coding and population coding.

Labeled Line Coding

In the labeled line coding of information, one cell encodes for one type of sensory quality. Pain is a good example of this. If a pain receptor is activated, the resulting sensation will be pain, regardless of the manner in which the receptor is stimulated. In other words, the sensory neurons are specifically tuned to one sensory stimulus. If that receptor-cell type was dysfunctional, the sensation will not be perceived. For example, there is a mutation that prevents sodium channels in pain receptors (but not other cell types) from working. When this mutation occurs, the subject cannot feel pain.

Population Coding

In populating coding, one cell can encode more than one sensory modality, and it is the combination of many cells that make up the perception. An example of this is color vision. Each color photoreceptor is most sensitive to a specific color (blue, green, or red), but a range of wavelengths can elicit changes in firing rates in the neuron. Therefore, the responses from a population of color photoreceptors must be combined to perceive the full spectrum of color.

Higher level processing of taste and olfaction also uses population coding – sometimes the sense of smell is needed in addition to the sense of taste to fully perceive a flavor. Have you ever been congested from a cold and food just doesn't taste the same? That's due to this combining of the senses for a full perception.

Pathways

In general, the route sensory information takes from the periphery to the central nervous system is similar among most of the systems. Environmental stimuli become encoded by a specialized receptor in the periphery. Information then enters the central nervous system via the spinal cord or brainstem and relays through the thalamus, a structure that sits deep in the forebrain. The only sensory system that does not relay through the thalamus is the olfactory system. The thalamus then sends projections out to the primary cortical regions for each sensory system.

Role of the Thalamus

It's common to hear that sensory information "relays" through the thalamus on the way to the cortex (for example, in the paragraph above). This language can give the impression that the thalamus is only responsible for making sure the sensory signal gets from periphery to the cortex. This greatly underestimates the thalamic role. The thalamus is known to contribute to the processing and modification of the sensory signal.

19.

VISION: THE RETINA

Resources

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

Anatomy of the Retina

The front of the eye consists of the cornea, pupil, iris, and lens. The cornea is the transparent, external part of the eye. It covers the pupil and the iris and is the first location of light refraction. The pupil is the opening in the iris that allows light to enter the eye. The iris is the colored portion of the eye that surrounds the pupil and along with local muscles can control the size of the pupil to allow for an appropriate amount of light to enter the eye. The lens is located behind the pupil and iris. The lens refracts light to focus images on the retina. Proper focusing requires the lens to stretch or relax, a process called accommodation.

The retina is the light-sensitive region in the back of the eye where the photoreceptors, the specialized cells that respond to light, are located. The retina covers the entire back portion of the eye, so it's shaped like a bowl. In the middle of the bowl is the fovea, the region of highest visual acuity, meaning the area that can form the sharpest images. The optic nerve projects to the brain from the back of the eye, carrying information from the retinal cells. Where the optic nerve leaves, there are no photoreceptors since the axons from the neurons are coming together. This region is called the optic disc and is the location of the blind spot in our visual field.

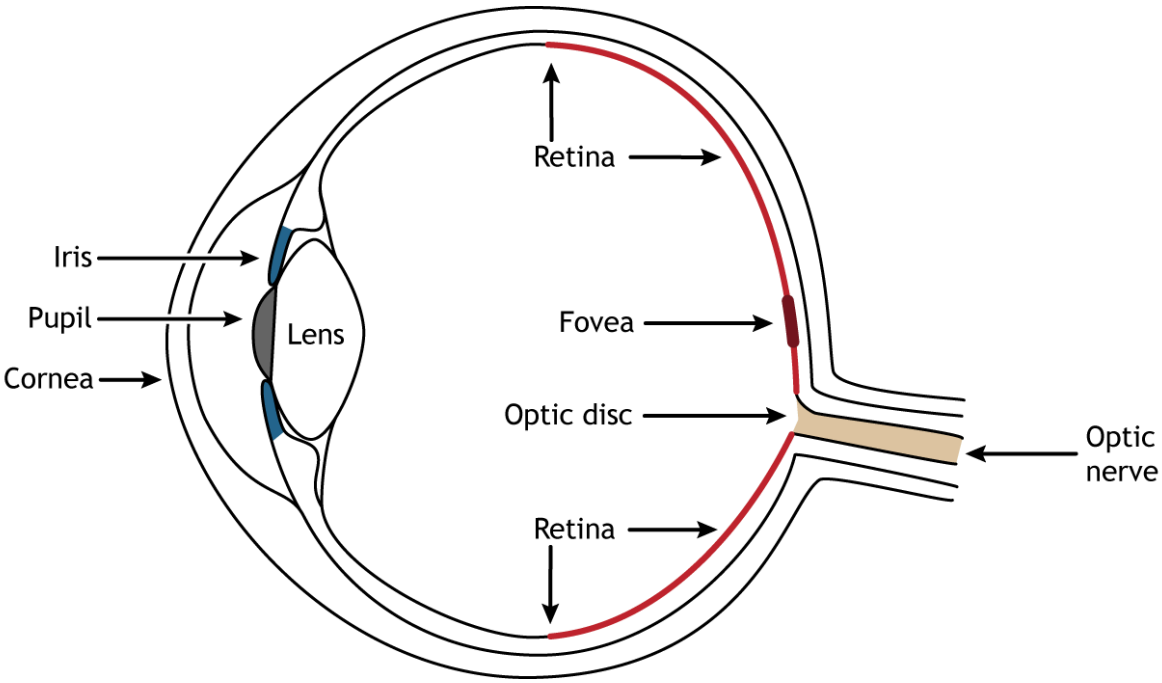


Figure 19.1. Cross section of the eye. The visible regions of the eye include the cornea, pupil (gray region), and iris (blue region). The lens sits behind the pupil and iris. The retina (red line) is located along the back of the eye. The fovea (dark red section) is a small portion of the retina where visual acuity is highest, and the optic disc is located where the optic nerve (tan region) leaves the eye. Details about the functions of each region are in the text. 'Eye Anatomy' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Retinal Cells

In addition to the photoreceptors, there are four other cell types in the retina. The photoreceptors synapse on bipolar cells, and the bipolar cells synapse on the ganglion cells. Horizontal and amacrine cells allow for communication laterally between the neurons.

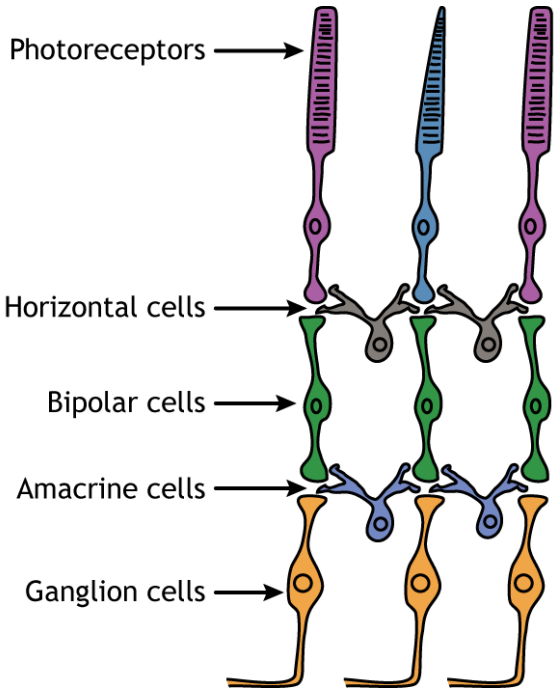


Figure 19.2. There are five cell types in the retina. The photoreceptors synapse on bipolar cells, and the bipolar cells synapse on ganglion cells. The horizonal cells allow for communication between photoreceptors by interacting with the photoreceptor-bipolar cell synapse, and the amacrine cells allow for communication between bipolar cells by interacting at the bipolar cell-ganglion cell synapse. 'Retinal Neurons' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Direction of Information

When light enters the eye and strikes the retina, it must pass through all the neuronal cell layers before reaching and activating the photoreceptors. The photoreceptors then initiate the synaptic communication back toward the ganglion cells.

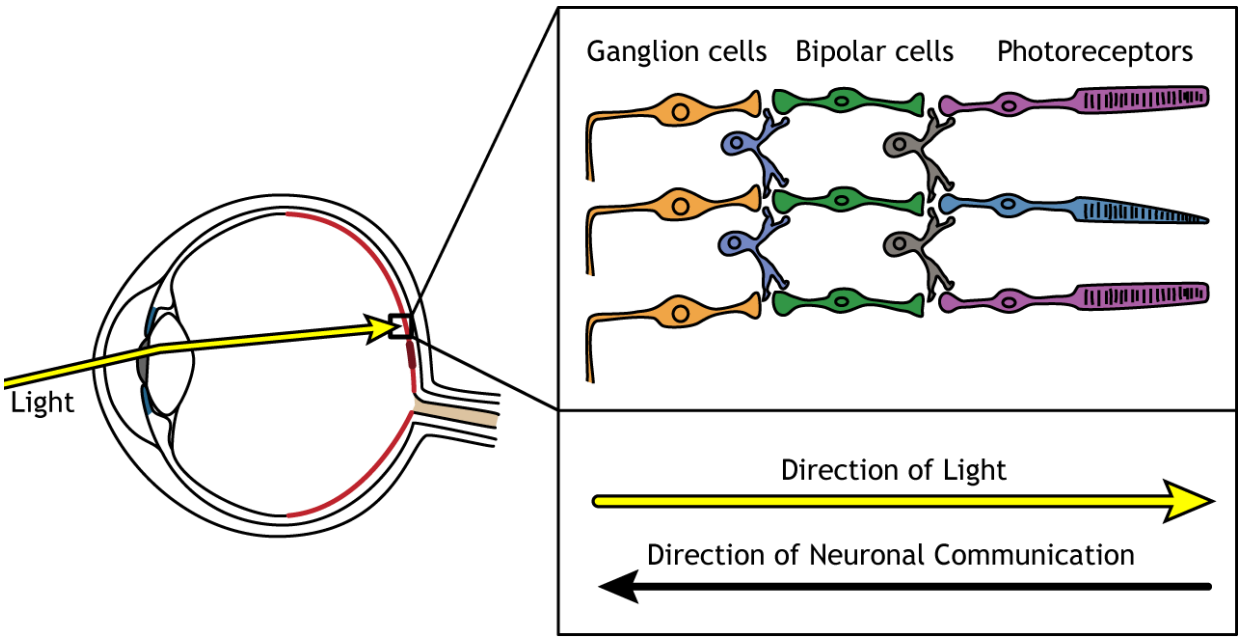


Figure 19.3. When light enters the eye, it must pass through the ganglion and bipolar cell layers before reaching the photoreceptors. The neuronal communication travels in the opposite direction from the photoreceptors toward the ganglion cells. 'Light in the Retina' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Receptors

The photoreceptors are the specialized receptors that respond to light. There are two types of photoreceptors: rods and cones. Rods are more sensitive to light, making them primarily responsible for vision in low-lighting conditions like at night. Cones are less sensitive to light and are most active in daylight conditions. The cones are also responsible for color vision.

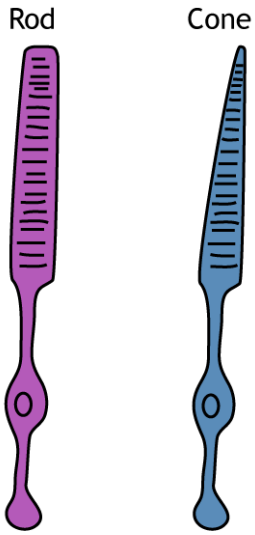


Figure 19.4. The rods and cones have different physical appearances and play separate roles in visual processing. 'Rod and Cone' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Receptor Density

In addition to having different visual functions, the rods and cones are also distributed across the retina in different densities. The cones are primarily found in the fovea, the region of the retina with the highest visual acuity. The remainder of the retina is predominantly rods. The region of the optic disc has no photoreceptors because the axons of the ganglion cells are leaving the retina and forming the optic nerve.

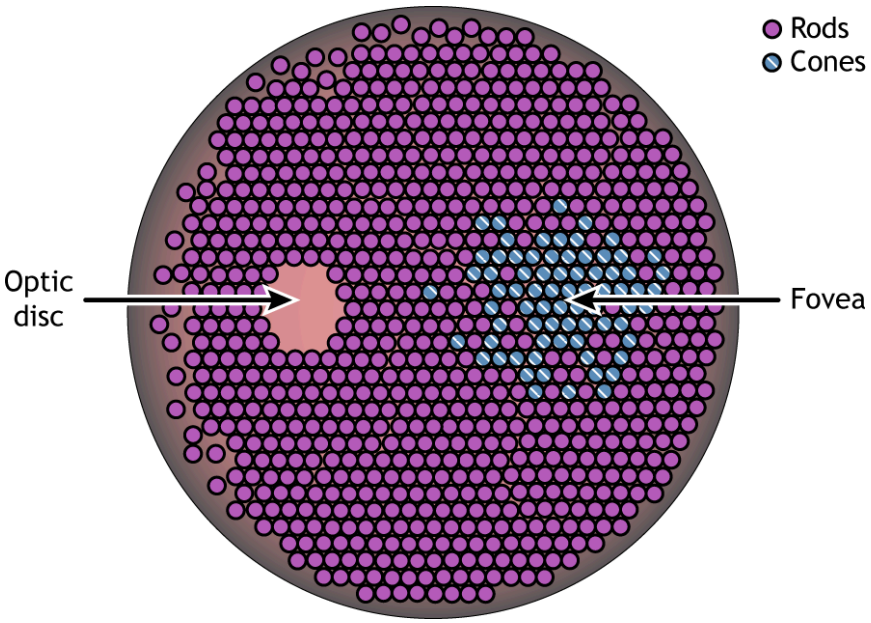


Figure 19.5. Rods and cones are distributed across the retina in different densities. Cones are located at the fovea. Rods are located everywhere else. The optic disc lacks all photoreceptors since the optic nerve fibers are exiting the eye at this location. 'Retinal Receptor Density' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Phototransduction

The photoreceptors are responsible for sensory transduction in the visual system, converting light into electrical signals in the neurons. For our purposes, to examine the function of the photoreceptors, we will A) focus on black and white light (not color vision) and B) assume the cells are moving from either an area of dark to an area of light or vice versa.

Photoreceptors do not fire action potentials; they respond to light changes with graded receptor potentials (depolarization or hyperpolarization). Despite this, the photoreceptors still release glutamate onto the bipolar cells. The amount of glutamate released changes along with the membrane potential, so a hyperpolarization will lead to less glutamate being released. Photoreceptors hyperpolarize in light and depolarize in dark. In the graphs used in this lesson, the starting membrane potential will depend on the initial lighting condition.

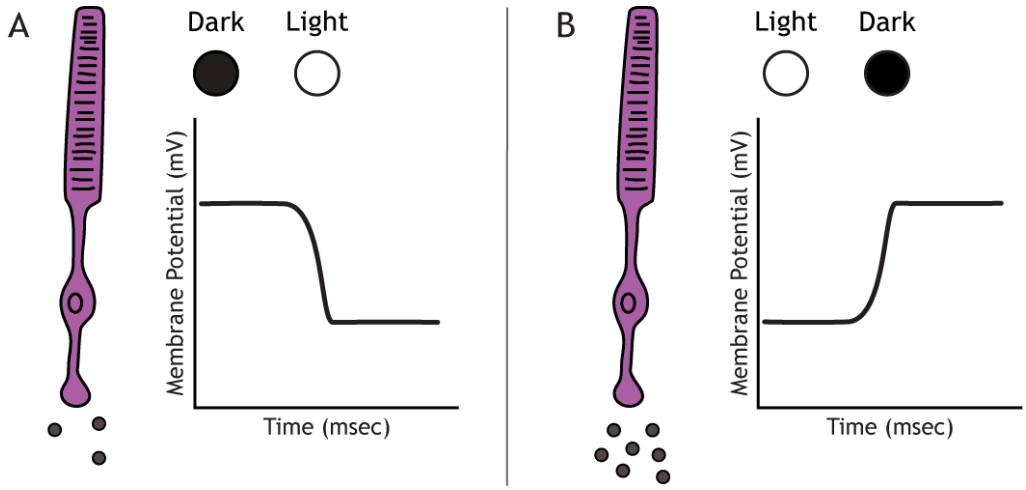


Figure 19.6. Photoreceptors respond with graded potentials when moving from light to dark or vice versa. A) When moving from dark to light, the photoreceptor will hyperpolarize, and glutamate release will decrease. B) When moving from light to dark, the photoreceptor will depolarize, and glutamate release will increase. 'Photoreceptor Receptor Potentials' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

In the dark, the photoreceptor has a membrane potential that is more depolarized than the "typical" neuron we examined in previous chapters; the photoreceptor membrane potential is approximately -40 mV. Photoreceptors have open cation channels that allow the influx of sodium and calcium in the dark. These channels are gated by the presence of cyclic GMP (cGMP), a molecule important in second-messenger cascades that is present in the photoreceptor in the dark.

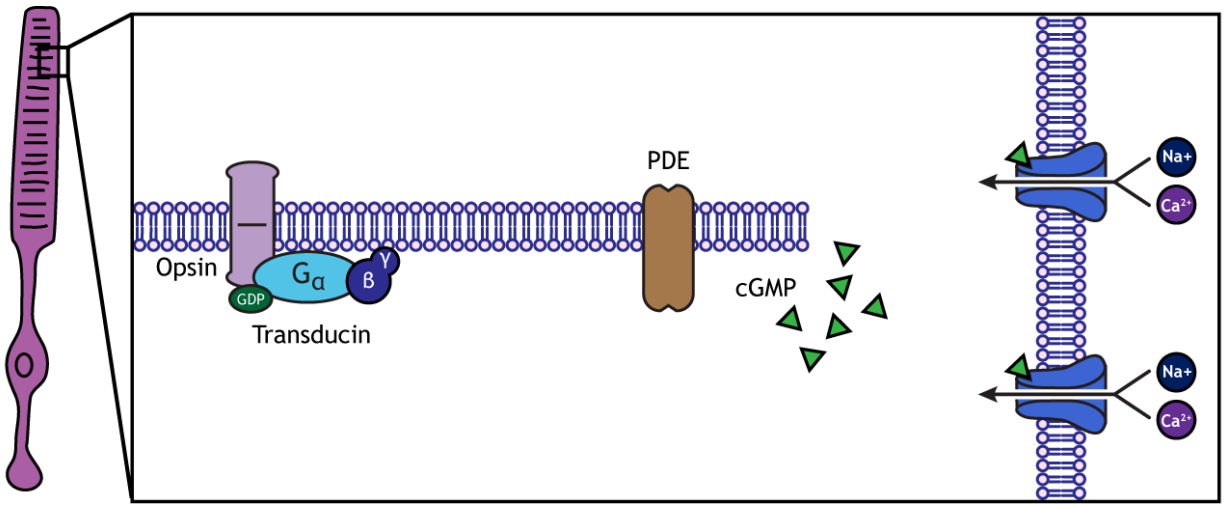


Figure 19.7. In the dark, the photoreceptor is depolarized due to an influx of sodium and calcium through open ion channels that are gated by cGMP. The photoreceptor has high levels of cGMP when it is in the dark. Additionally, the opsin proteins, the G-protein transducin, and phosphodiesterase (PDE) are all inactivated. 'Retinal Dark Current' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

When the photoreceptor moves into the light, the cell hyperpolarizes. Light enters the eye, reaches the photoreceptors, and causes a conformational change in a special protein called an opsin. This change activates a G-protein called transducin, which then activates a protein called phosphodiesterase (PDE). PDE breaks down cGMP to GMP, and the cGMP-gated ion channels that were open in the dark close. The decrease in cation flow into the cell causes the photoreceptor to hyperpolarize.

A video element has been excluded from this version of the text. You can watch it online here: https://openbooks.lib.msu.edu/neuroscience/?p=438

Animation 19.1. Light reaching the photoreceptor causes a conformational change in the opsin protein, which activates the G-protein transducing. Transducin activates phosphodiesterase (PDE), which converts cGMP to GMP. Without cGMP, the cation channels close, stopping the influx of positive ions. This results in a hyperpolarization of the cell. 'Phototransduction' by Casey Henley is

 View static image of animation.

Transmission of Information within Retina

Photoreceptors synapse onto bipolar cells in the retina. There are two types of bipolar cells: OFF and ON. These cells respond in opposite ways to the glutamate released by the photoreceptors because they express different glutamate receptors. Like photoreceptors, the bipolar cells do not fire action potential and only respond with graded postsynaptic potentials.

OFF Bipolar Cells

In OFF bipolar cells, the glutamate released by the photoreceptor is excitatory. OFF bipolar cells express ionotropic glutamate receptors. In the dark, glutamate released by the photoreceptor activates the ionotropic receptors, and sodium can flow into the cell, depolarizing the membrane potential. In the light, the absence of glutamate causes the ionotropic receptors to close, preventing sodium influx, hyperpolarizing the membrane potential.

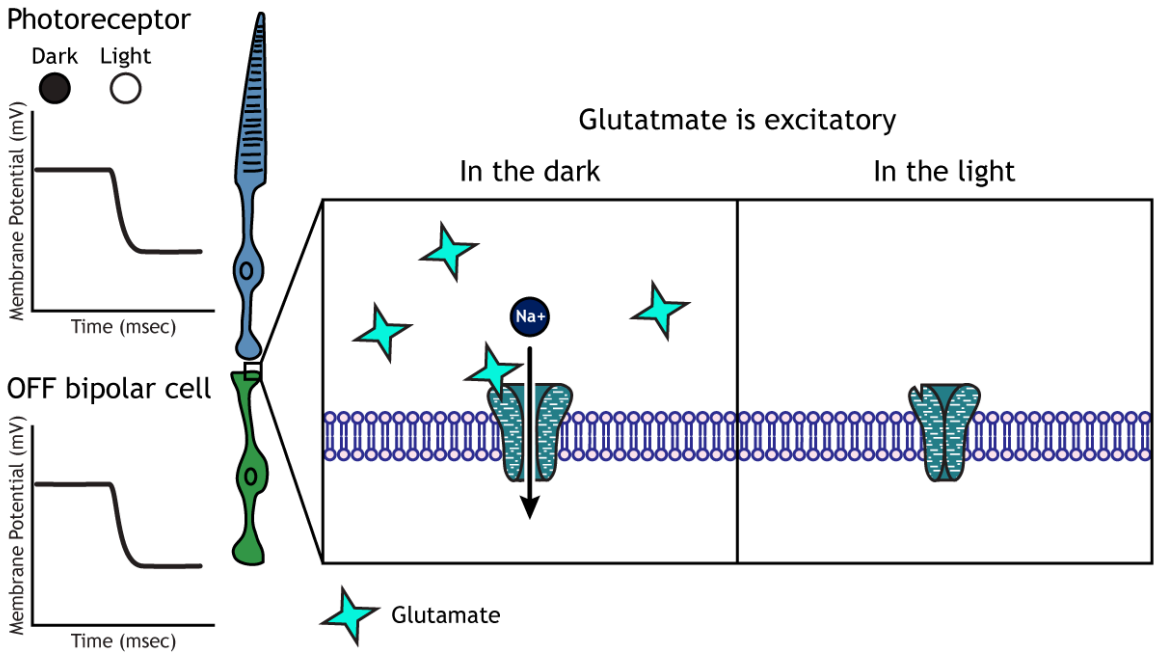


Figure 19.8. Photoreceptors hyperpolarize in light and decrease the amount of released glutamate. Glutamate is excitatory in OFF bipolar cells, opening ionotropic receptors and allowing sodium influx. In the dark, the OFF bipolar cells are depolarized, and in the light the OFF bipolar cells are hyperpolarized. 'Off Bipolar Cells' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

ON Bipolar Cells

In ON bipolar cells, the glutamate released by the photoreceptor is inhibitory. ON bipolar cells express metabotropic glutamate receptors. In the dark, glutamate released by the photoreceptor activates the metabotropic receptors, and the G-proteins close cation channels in the membrane, stopping the influx of sodium and calcium, hyperpolarizing the membrane potential. In the light, the absence of glutamate results in the ion channels being open and allowing cation influx, depolarizing the membrane potential.

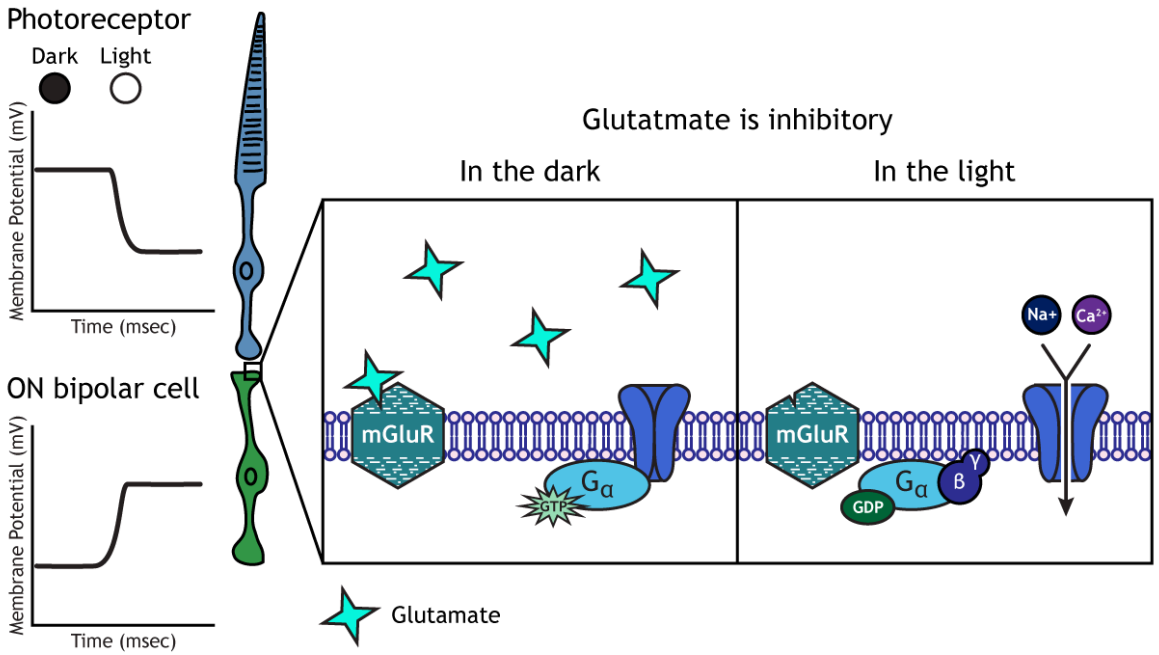


Figure 19.9. Photoreceptors hyperpolarize in light and decrease the amount of released glutamate. Glutamate is inhibitory in ON bipolar cells, activating metabotropic receptors, which closes cation channels. In the dark, the ON bipolar cells are hyperpolarized, and in the light the ON bipolar cells are depolarized. 'ON Bipolar Cells' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Ganglion Cells

OFF and ON bipolar cells synapse on OFF-center and ON-center ganglion cells, respectively. Ganglion cells are the only cell type to send information out of the retina, and they are also the only cell that fires action potentials. The ganglion cells fire in all lighting conditions, but it is the relative firing rate that encodes information about light. A move from dark to light will cause OFF-center ganglion cells to decrease their firing rate and ON-center ganglion cells to increase their firing rate.

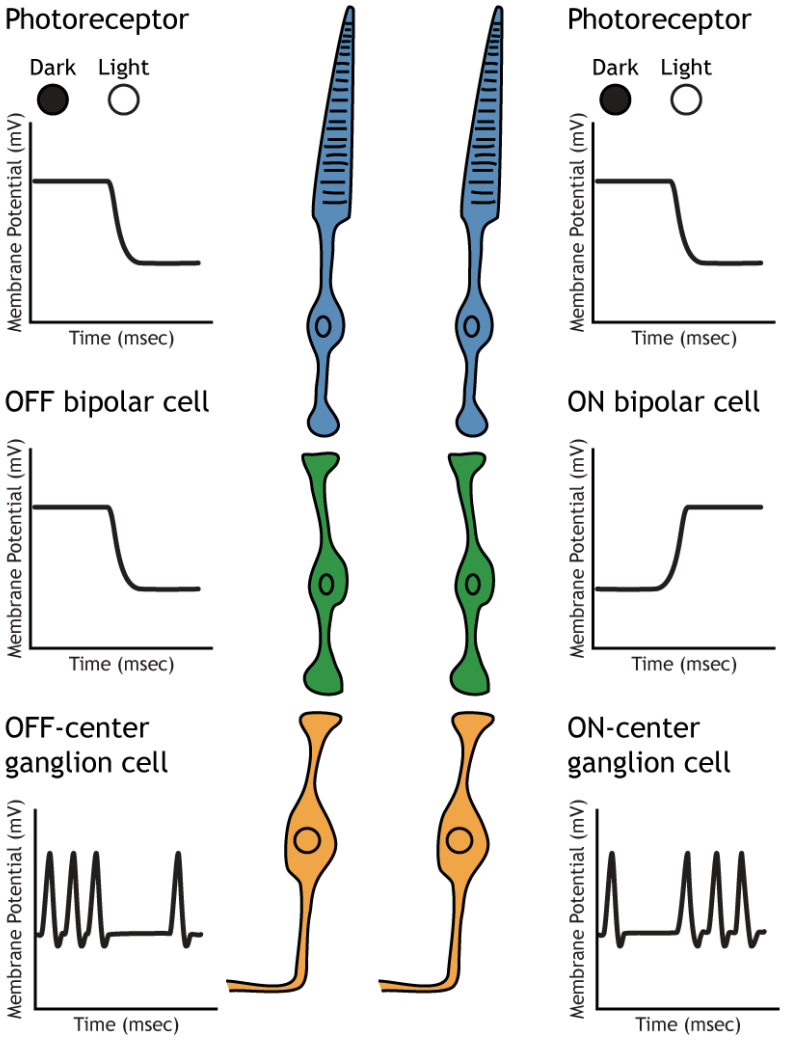


Figure 19.10. A move from dark to light will hyperpolarize all photoreceptors. OFF bipolar cells will also hyperpolarize in light, which will lead to a decreased firing rate in OFF-center ganglion cells. ON bipolar cells will depolarize in light, which will lead to an increased firing rate in ON-center ganglion cells. 'Retinal Ganglion Cells' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Receptive Fields

Each bipolar and ganglion cell responds to light stimulus in a specific area of the retina. This region of retina is the cell's receptive field. Receptive fields in the retina are circular.

Size of the receptive field can vary. The fovea has smaller receptive fields than the peripheral retina.

The size depends on the number of photoreceptors that synapse on a given bipolar cell and the number of bipolar cells that synapse on a given ganglion cell, also called the amount of convergence.

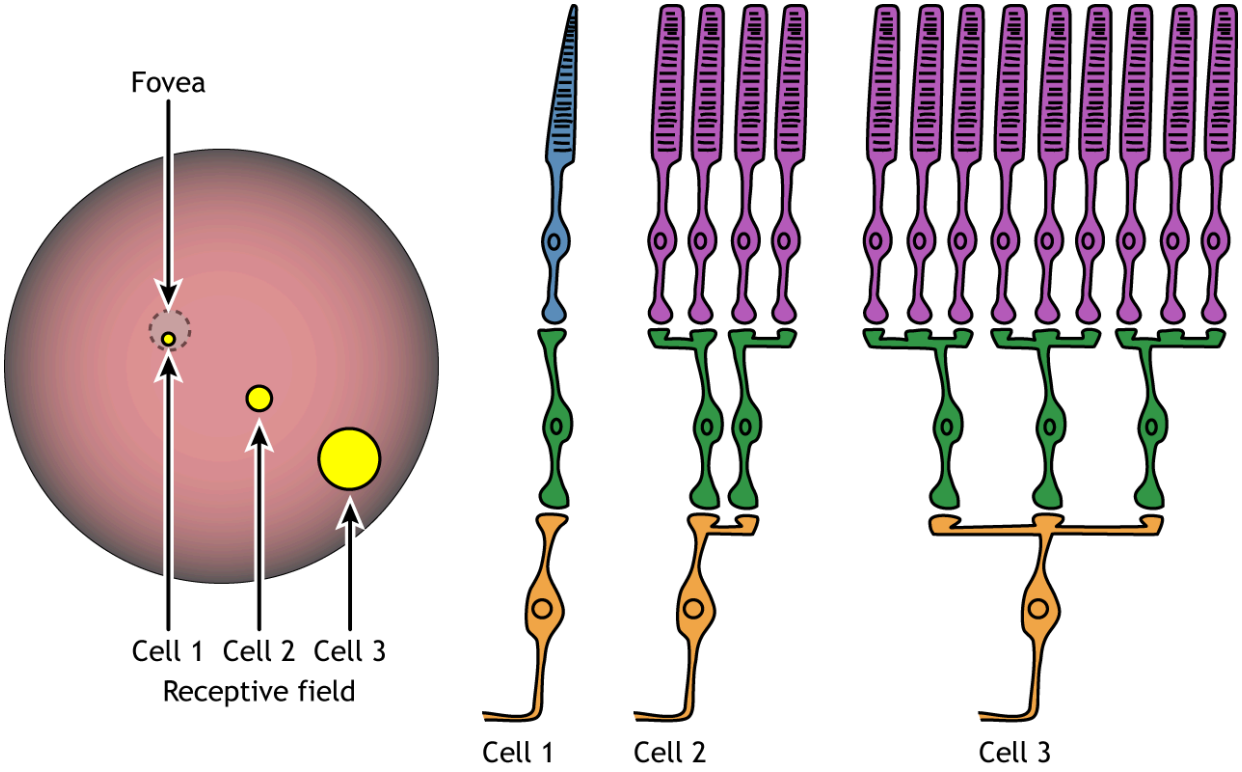


Figure 19.11. Ganglion receptive field sizes can vary depending on location of the bipolar and ganglion cells and the amount of convergence onto those cells. When the photoreceptors are in or near the fovea (Cell 1), the receptive fields are small. In the fovea, each bipolar cell receives input from only one photoreceptor and then synapses on only one ganglion cell. Toward the periphery (Cells 2 and 3), more photoreceptors synapse on each bipolar cell, and more bipolar cells synapse on each ganglion cell, making the surface area of the receptive field larger. 'Retinal Receptive Field' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Receptive Field Example

Let's use an example of an ON bipolar cell to look at the structure of receptive fields in the retina. The bipolar and ganglion cell receptive fields are divided into two regions: the center and the surround. The center of the receptive field is a result of direct innervation between the photoreceptors, bipolar cells, and ganglion cells. If a light spot covers the center of the receptive field, the ON bipolar cell would depolarize, as discussed above; the light hits the photoreceptor, it hyperpolarizes, decreasing glutamate release. Less glutamate leads to less inhibition of the ON bipolar cell, and it depolarizes.

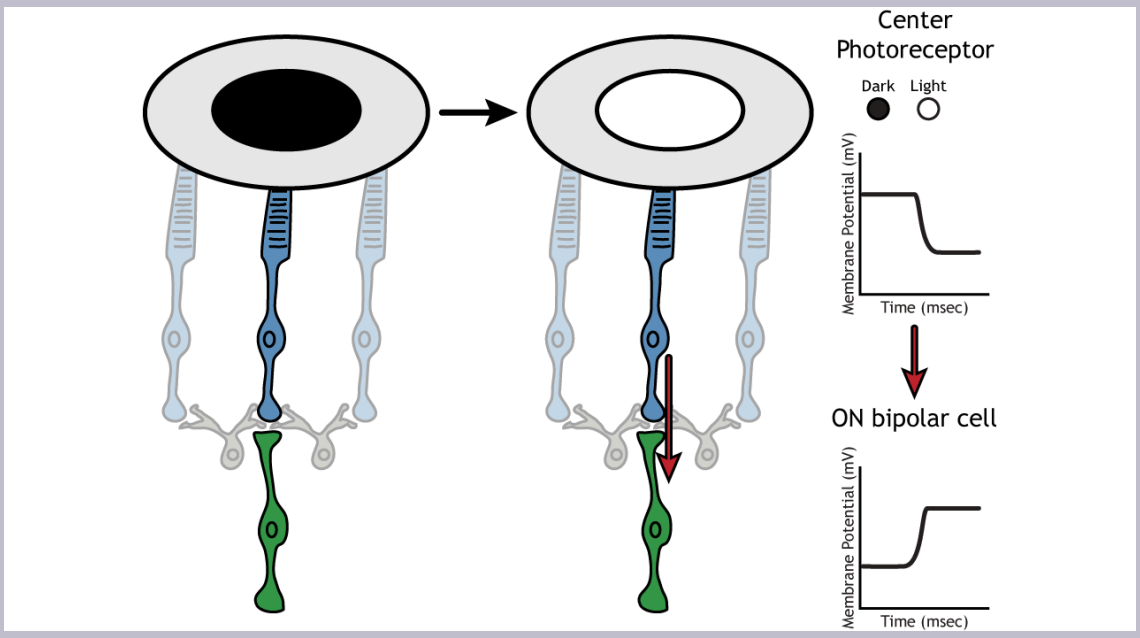


Figure 19.12. A photoreceptor in the center of an ON bipolar cell's receptive field moves from dark to light. The photoreceptor will hyperpolarize, and the ON bipolar cell will depolarize. The red arrows show the direct synaptic communication from photoreceptor to ON bipolar cell. 'Light in Center' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

The surround portion of the receptive field is a result of indirect communication among the retinal neurons via horizontal and amacrine cells. The surround also has an opposing effect on the bipolar or ganglion cell compared to the effect of the center region. If a light spot covers the surround portion, the ON bipolar cell would respond by hyperpolarizing. The light would cause the photoreceptor in the surround to hyperpolarize. This would cause the

horizontal cell to also hyperpolarize. Horizontal cells have inhibitory synaptic effects, so a hyperpolarization in the horizontal cell would lead to a depolarization in the center photoreceptor. The center photoreceptor would then cause a hyperpolarization in the ON bipolar cell. These effects mimic those seen when the center is in dark. So even though the center photoreceptor is not directly experiencing a change in lighting conditions, the neurons respond as if they were moving toward dark.

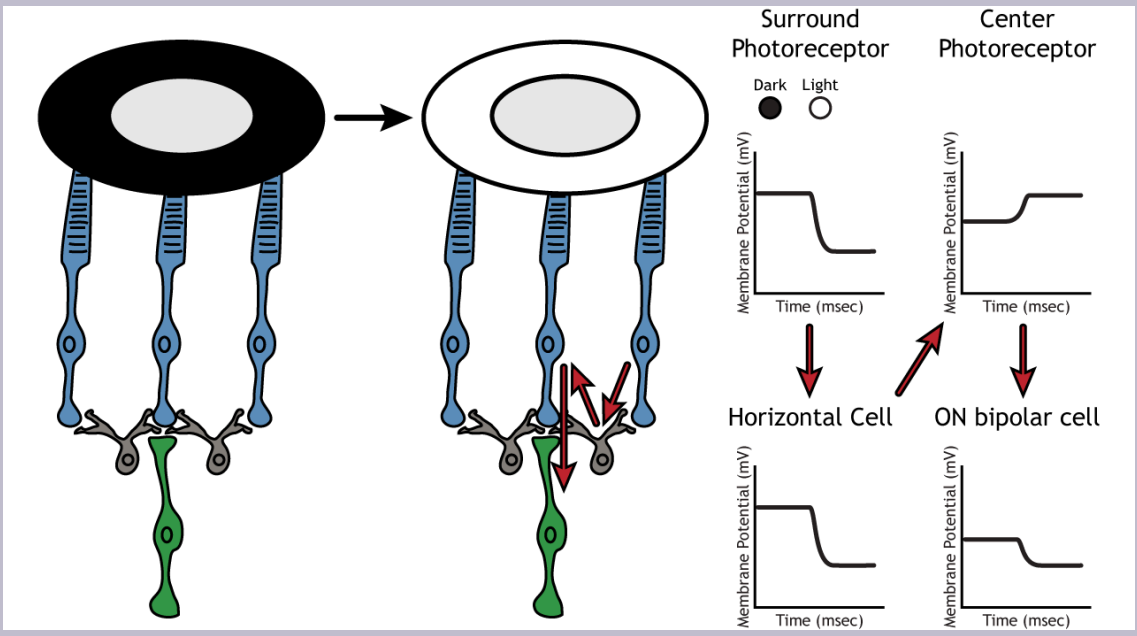


Figure 19.13. A photoreceptor in the surround of an ON bipolar cell's receptive field moves from dark to light. The photoreceptor will hyperpolarize, and the postsynaptic horizontal cell will hyperpolarize. This will cause the center photoreceptor to depolarize, and the ON bipolar cell to hyperpolarize. The red arrows show the indirect synaptic communication between the surround photoreceptor and the ON bipolar cell. The surround photoreceptor synapses on the horizontal cell, which synapses on the center photoreceptor, which synapses on the bipolar cell. 'Light in Surround' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Lateral Inhibition

The center-surround structure of the receptive field is critical for lateral inhibition to occur. Lateral

inhibition is the ability of the sensory systems to enhance the perception of edges of stimuli. It is important to note that the photoreceptors that are in the surround of one bipolar cell would also be in the center of a different bipolar cell. This leads to a direct synaptic effect on one bipolar cell while also having an indirect effect on another bipolar cell.

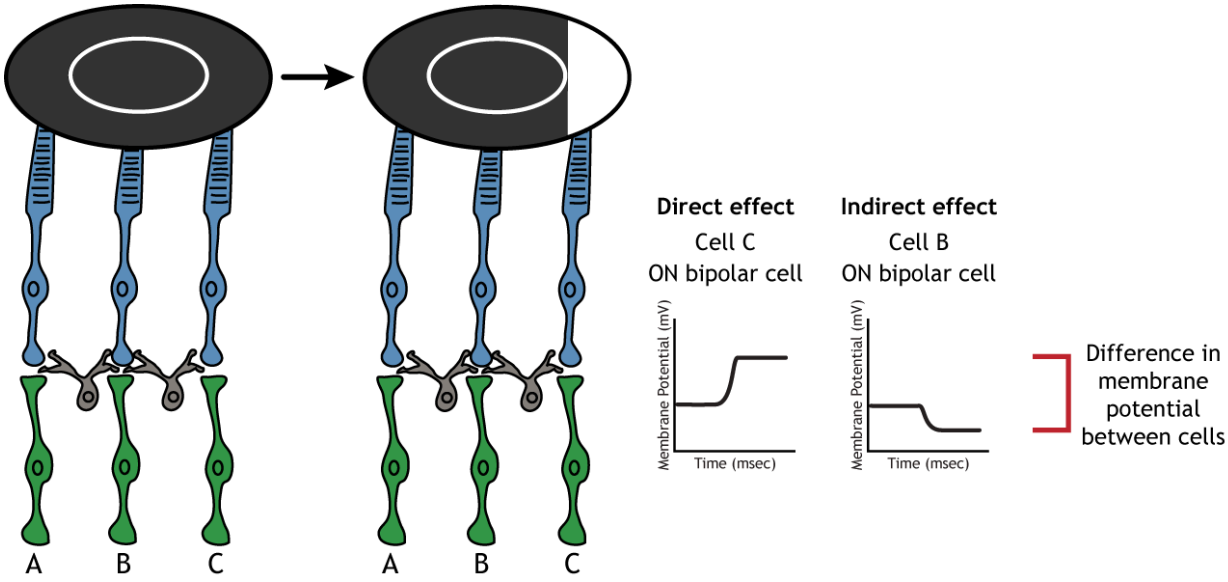


Figure 19.14. An edge of a light stimulus moves into the receptive field surround of ON bipolar cell B. This edge is also falling on the receptive field center of ON bipolar cell C. The light will cause bipolar cell C to depolarize because of the direct synapse with the photoreceptor. The light will also cause bipolar cell B to hyperpolarize because of the indirect synapses through the horizontal cell. This hyperpolarization causes a larger membrane potential difference between cells B and C that would occur if the horizontal cells were absent. The larger membrane potential difference between the cells will lead to an enhancement in the perception between the dark and light side of the edge. 'Lateral Inhibition' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Although some of the images used here will simplify the receptive field to one cell in the center and a couple in the surround, it is important to remember that photoreceptors cover the entire surface of the retina, and the receptive field is two-dimensional. Depending on the level of convergence on the bipolar and ganglion cells, receptive fields can contain many photoreceptors.

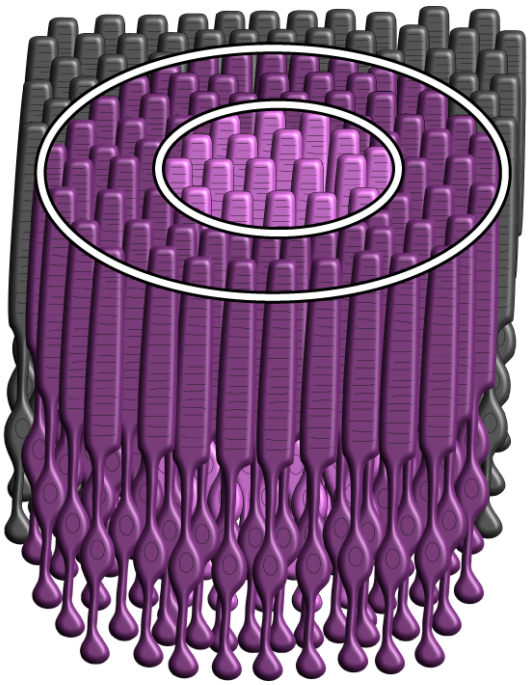


Figure 19.15. The receptive fields exist in two-dimensions along the surface of the retina. Depending on the location of the receptive field, and the amount of convergence that occurs at the bipolar or ganglion cell, the receptive field may contain many photoreceptors. 'Retinal surface' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Key Takeaways

- Photoreceptors and bipolar cells do not fire action potentials
- Photoreceptors hyperpolarize in the light
- ON bipolar cells express inhibitory metabotropic glutamate receptors
- OFF bipolar cells express excitatory ionotropic glutamate receptors
- Receptive fields are circular, have a center and a surround, and vary in size
- Receptive field structure allows for lateral inhibition to occur

Test Yourself!

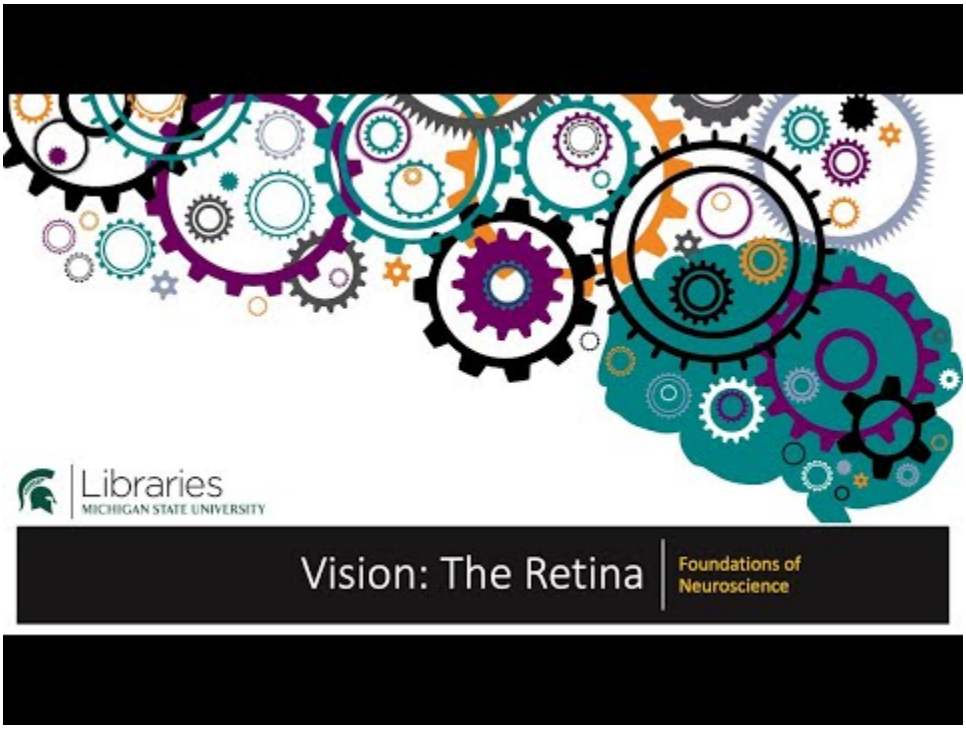
An interactive H5P element has been excluded from this version of the text. You can view it online here:
https://openbooks.lib.msu.edu/neuroscience/?p=438#h5p-18

Additional Review

1. Compare and contrast rods and cones.
2. Compare and contrast the fovea and the optic disc.

Answers

Video Version of Lesson



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20.

VISION: CENTRAL PROCESSING

Visual Fields

Before learning the pathway that visual information takes from the retina to the cortex, it is necessary to understand how the retina views the world around us. The full visual field includes everything we can see without moving our head or eyes.

Resources

- Key Takeaways
- Test Yourself
- Video Version

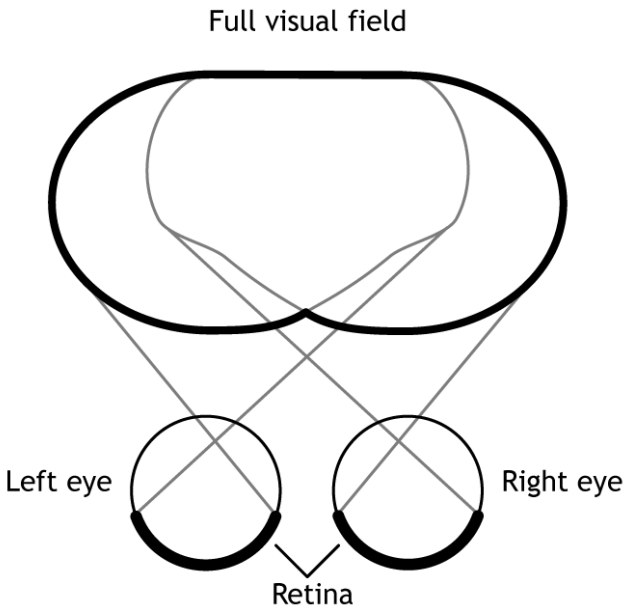


Figure 20.1. The two eyes together can view the entire visual field, which is all the visual space we can see without moving our head or eyes. 'Full Visual Field' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

The full visual field can be divided in a few ways. Each individual eye is capable of seeing a portion of, but not the entire, visual field.

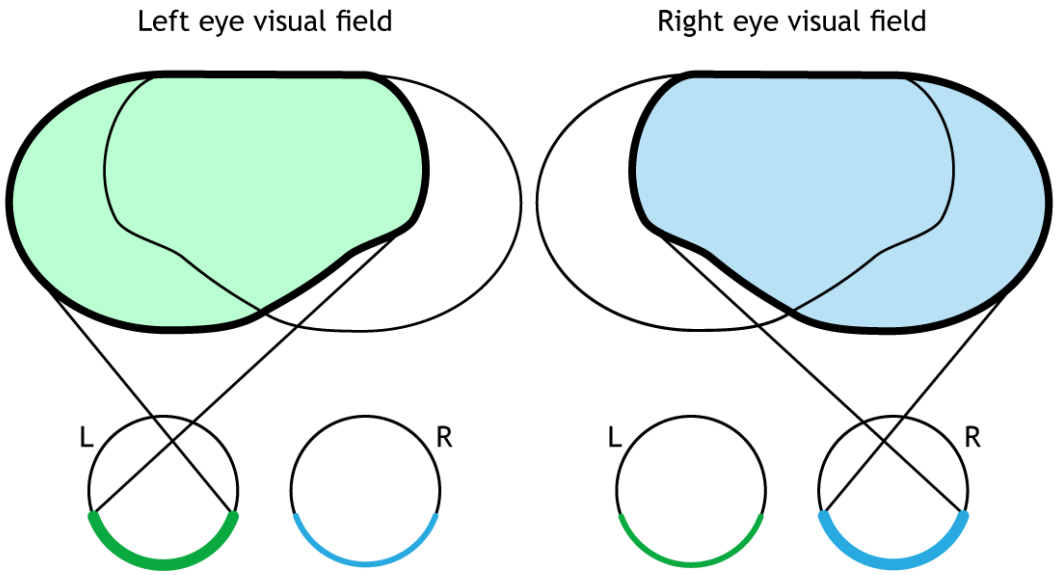


Figure 20.2. Each eye individually can view only a portion of the full visual field. 'Single Eye Fields' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

The full visual field can also be divided into the right and left hemifields. The hemifields range from the most peripheral point to the center point, splitting the full visual field into two equal regions. Both eyes are involved in viewing each hemifield. The fovea separates the retina into two sections: the nasal retina and the temporal retina. The nasal retina is the medial portion that is located toward the nose. The temporal retina is the lateral portion that is located toward the temples and temporal lobe. The nasal retina from one eye along with the temporal retina from the other eye are able to view an entire hemifield.

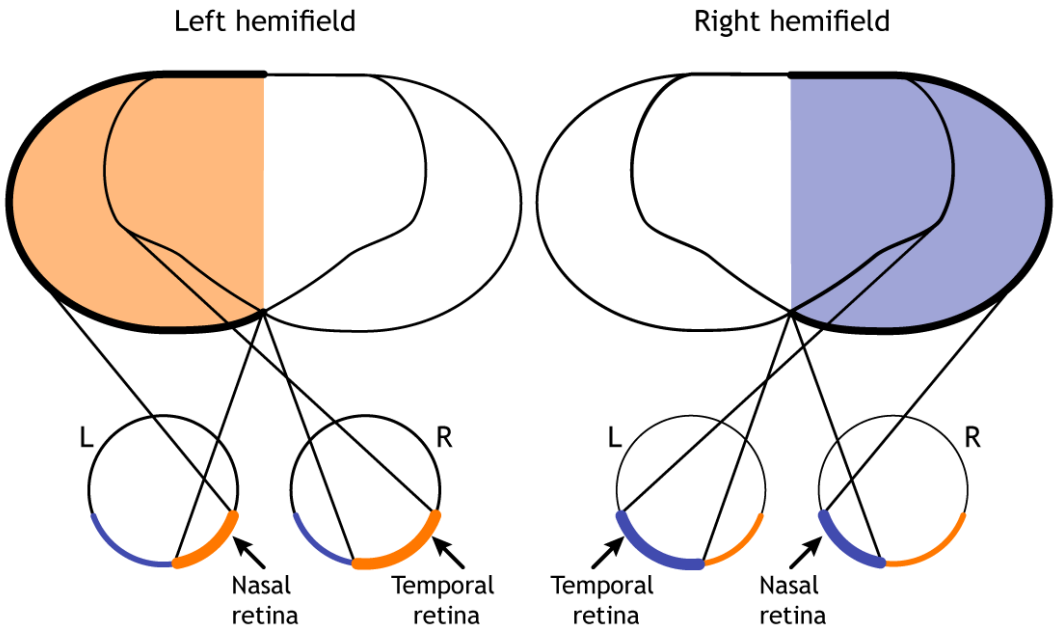


Figure 20.3. The full visual field can be divided into left and right hemifields. Both eyes contribute to viewing these regions. The nasal retina of the left eye and the temporal retina of the right eye view the left hemifield. The nasal retina of the right eye and the temporal retina of the left eye view the right hemifield. 'Visual Hemifields' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Finally, the full visual field can be separated into monocular and binocular regions. Each monocular field is visual space that can only be viewed by one eye. The binocular region is visual space that can be viewed by both eyes.

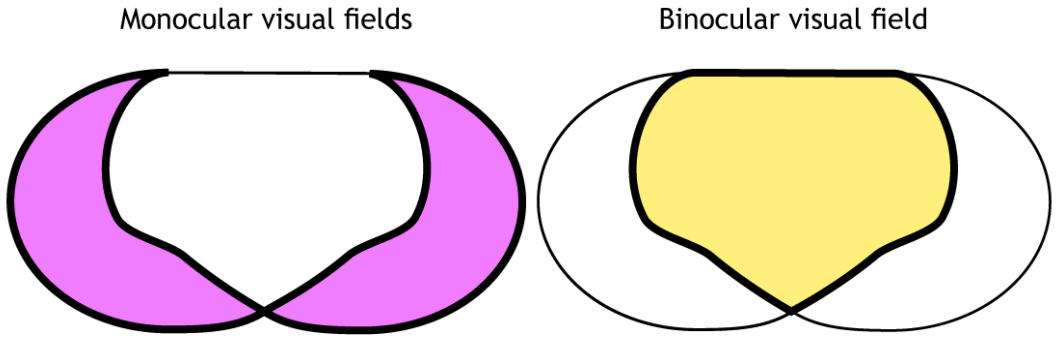


Figure 20.4. Monocular visual fields are viewed by only one eye and are located toward the periphery of the full visual field. The binocular visual field is viewed by both eyes and is located in the center of the full visual field. 'Monocular and Binocular Fields' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Pathway to Brain

Visual information from each eye leaves the retina via the ganglion cell axons at the optic disc, creating the optic nerve. Prior to entering the brain, axons from the nasal portion of each retina cross the midline at the optic chiasm. Since the axons from the nasal retina cross to the opposite side of the nervous system but the temporal retina axons do not, this leads to the brain processing input from the contralateral (opposite side) visual hemifield. Therefore, the right side of the brain receives visual information from the left hemifield and vice versa.

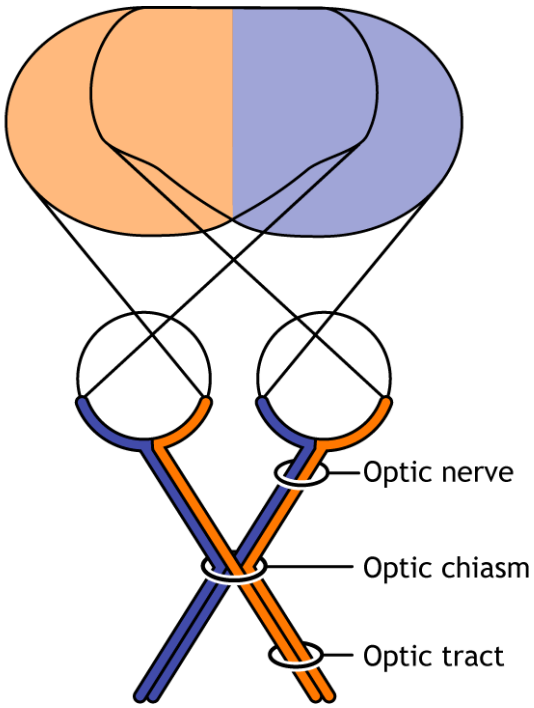


Figure 20.5. Information from each eye is carried away from the retina by the optic nerve. Information perceived by neurons in the nasal retina of each eye crosses the midline at the optic chiasm. Information from the contralateral visual hemifield then travels to the brain. 'Pathway from Retina' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

View the optic nerve (cranial nerve II) using the BrainFacts.org 3D Brain

The optic tract enters the brain and ascends to synapse in the lateral geniculate nucleus of the thalamus. From there, axons project to the primary visual cortex, also called the striate cortex or V1, located in the occipital lobe.

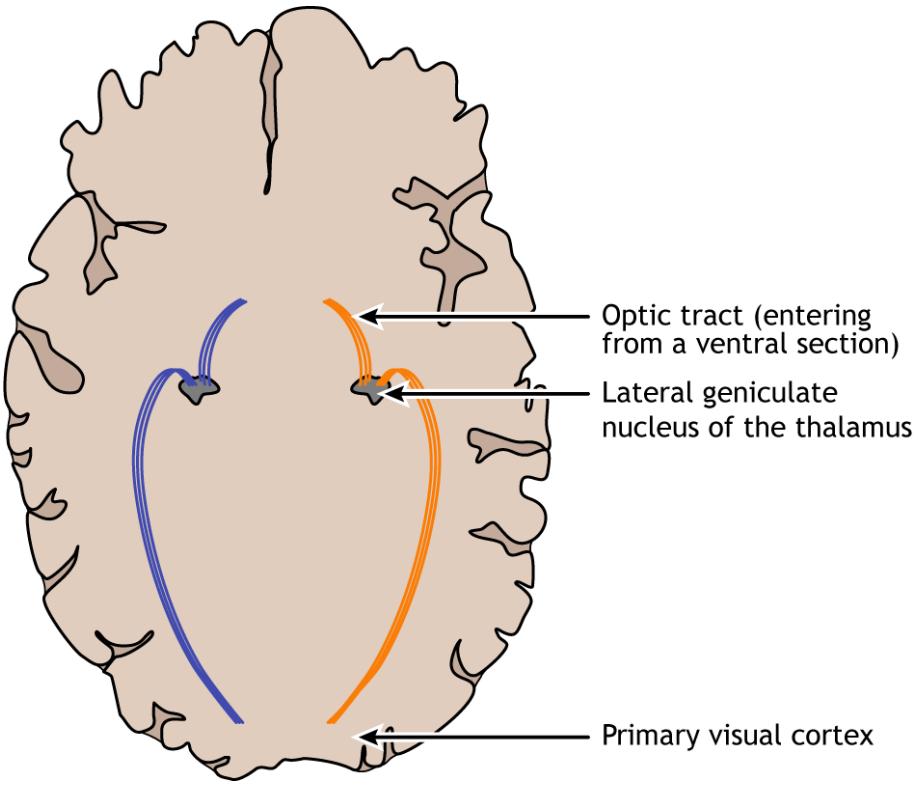


Figure 20.6. A horizontal section of the brain. The optic tract enters the brain and projects dorsally to the thalamus. Information is then sent to the primary visual cortex in the occipital lobe. 'CNS Visual Pathway' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

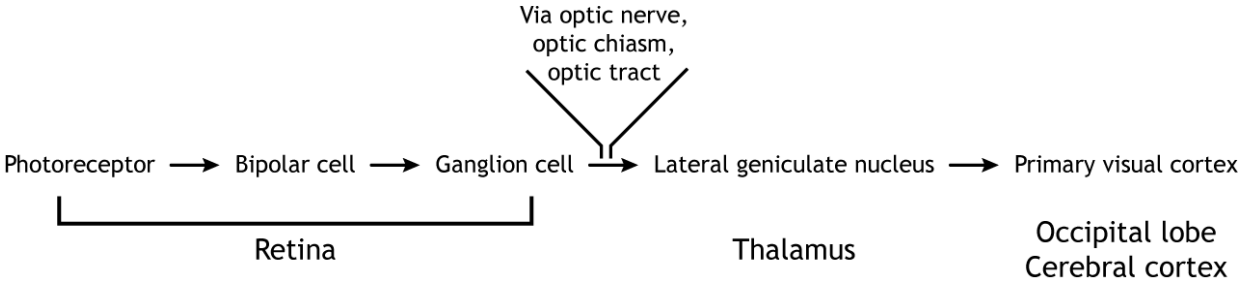


Figure 20.7. Visual information that is sent through the full visual pathway, therefore, moves from photoreceptor to bipolar cell to ganglion cell in the retina. It leaves the retina via the optic nerve, optic chiasm, and optic tract to the lateral geniculate nucleus of the thalamus and then travels to the primary visual cortex. 'Visual Pathway' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

View the thalamus using the BrainFacts.org 3D Brain
View the primary visual cortex using the BrainFacts.org 3D Brain

Receptive Fields

As information moves from the retina to the cortex, receptive fields become larger and more complex. Receptive fields in the thalamus continue to be circular in shape like the receptive fields of the retinal neurons. However, once information reaches the primary visual cortex, these circular receptive fields combine to create receptive fields that are activated by lines.

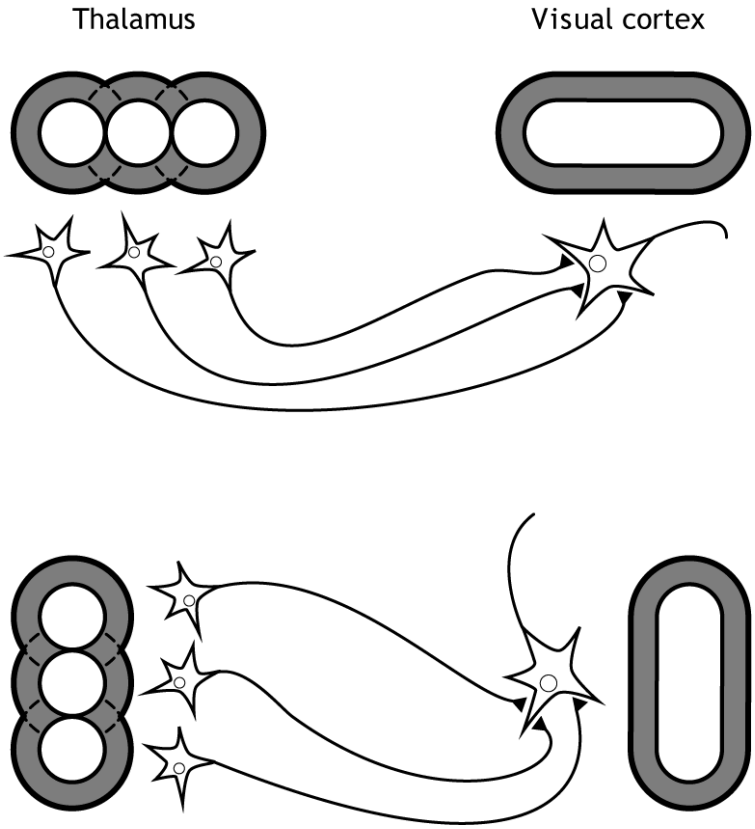


Figure 20.8. Circular receptive fields located in the thalamus combine to form straight receptive fields in the visual cortex. The orientation of the line direction in the visual cortex depends on the location of the thalamic retinal fields. 'CNS Receptive Fields' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

These receptive fields cause neurons in the primary visual cortex to respond best to a line in a specific orientation. The firing rate of the neuron will increase as the line rotates toward the "preferred" orientation. The firing rate will be highest when the line is in the exact preferred orientation. Different orientations are preferred by different neurons.

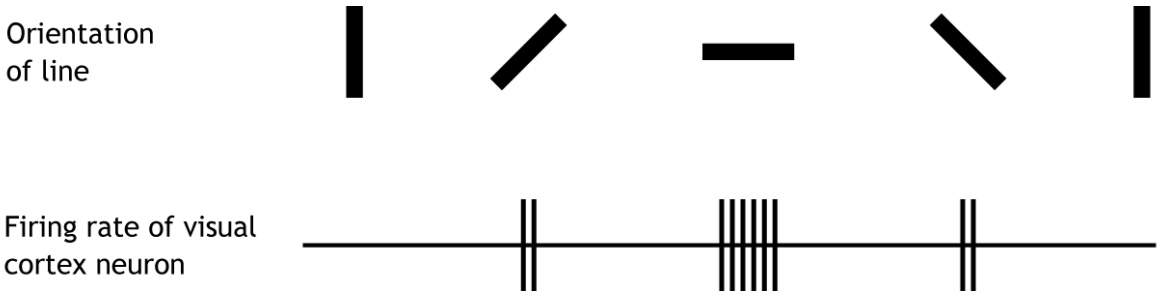


Figure 20.9. Neurons in the primary visual cortex show increased firing rates in response to a preferred line orientation. Lines rotated away from the preferred orientation will not cause activity. 'CNS Receptive Field Responses' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Higher-Level Processing of Sensory Information

Sensory system processing of input does not end upon reaching the primary sensory cortex in any sensory system. Information typically gets sent from the primary sensory cortex to other sensory association regions throughout the brain. The characteristics of sensory information becomes more complex as this higher-level processing occurs.

Post-Striatal Processing

In the visual system, there are two broad streams of information that leave the striate cortex. Information that travels from the primary visual cortex down through the inferior temporal lobe is responsible for determining object recognition, or what an object is. Differentiating between an apple and a person occurs in this stream. Information that travels from the striate cortex up through the parietal lobe is responsible for motion or spatial components of vision.

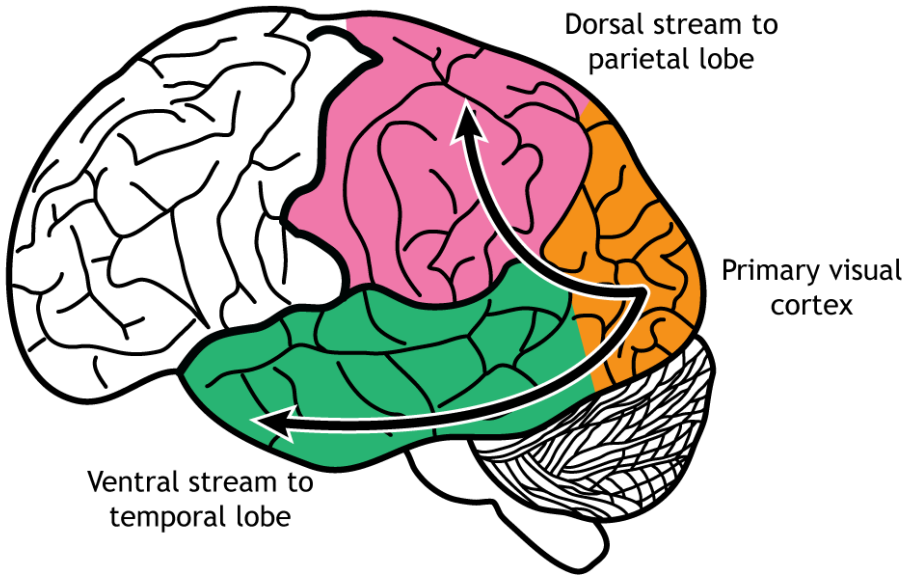


Figure 20.10. Information continues to be processed after reaching the primary visual cortex. The dorsal stream travels to the parietal cortex and is important for spatial components of vision. The ventral stream travels to the temporal lobe and is important for object recognition. 'Visual Streams' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Dorsal Stream

One of the most important regions in the dorsal pathway is region MT, also called V5. In this region, neurons are preferentially activated by a specific direction of movement by an object – for example, left to right or up to down. As an example, remember the receptive fields in the primary visual cortex were activated by lines at a specific orientation. Like that, in V5, the neurons would be activated by lines moving in a specific direction.

As information continues to be processed through the dorsal stream, the neurons become selective for more complex motions. The dorsal stream is also important for processing our actions in response to visual stimulation, for example, reaching for an object in the visual field or navigating around objects while walking.

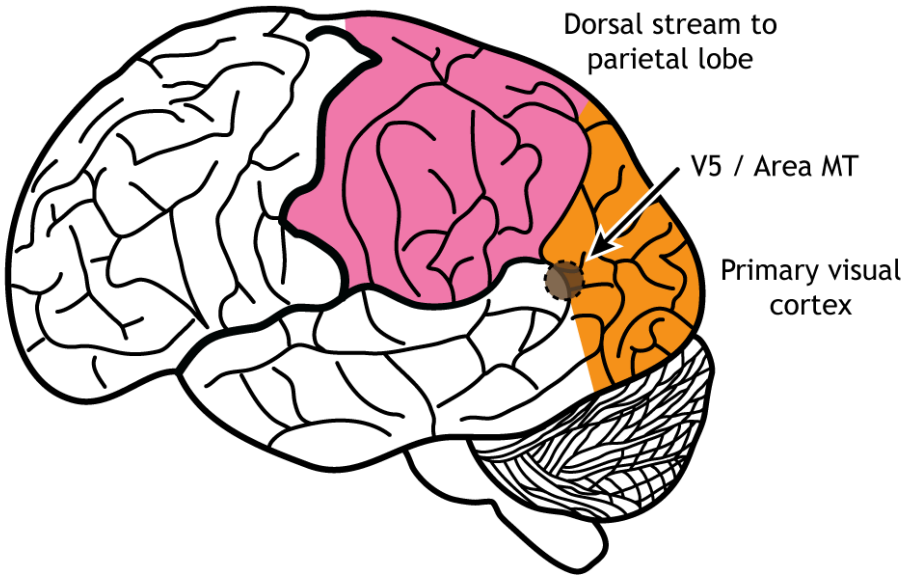


Figure 20.11. Area MT, also called V5, is an early processing region of the dorsal stream through the parietal lobe. Neurons in the region are activated by direction of an object in a specific direction. 'Area MT' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Ventral Stream

Object identification is a key function of our visual system. The ventral visual stream is responsible for this process. Like the more complex activation characteristics of region MT in the dorsal stream, neurons in Area V4 in the ventral stream show more complex receptive fields and show sensitivity to shape and color identification. As visual information continues to be processed through the inferior temporal lobe, differentiation of objects occurs. For example, in a region called the fusiform face area, located in the fusiform gyrus, which lies on the ventral aspect of the temporal lobe, neurons are activated by faces and can be specialized to one specific face.

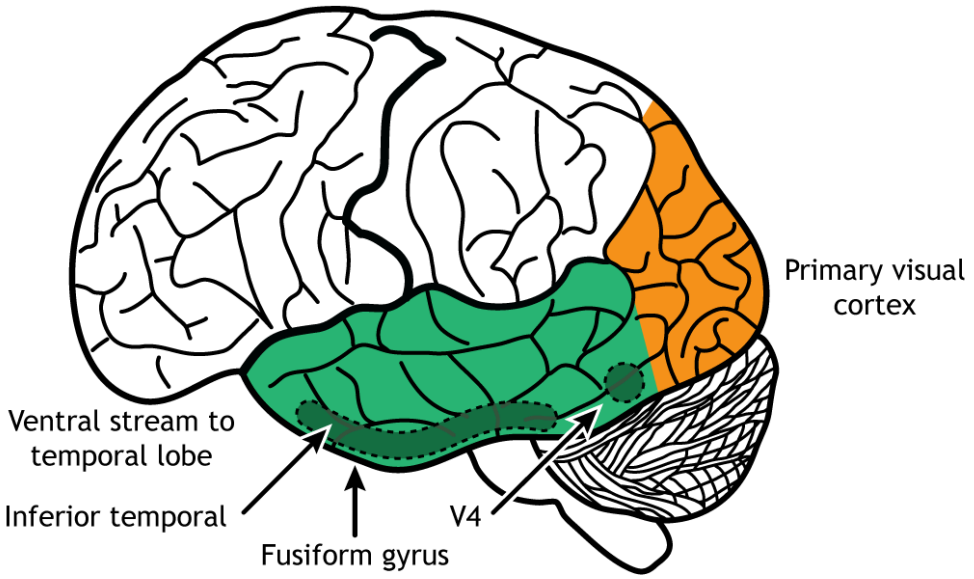


Figure 20.12. The ventral stream is first processed by area V4, which recognizes shapes and color. Information the continues through the inferior temporal lobe and sends information to regions like the fusiform gyrus, which is an area responsible for the recognition of faces. 'Ventral Stream' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

The inferior temporal lobe also makes reciprocal connections with the structures in the limbic system. The limbic system plays an important role in processing emotions and memory, both of which are significant components to visual perception. The amygdala ties visual stimuli with emotions and provides value to objects. A family member will have emotional ties that a stranger will not. The hippocampus is responsible for learning and memory and helps establish memories of visual stimuli.

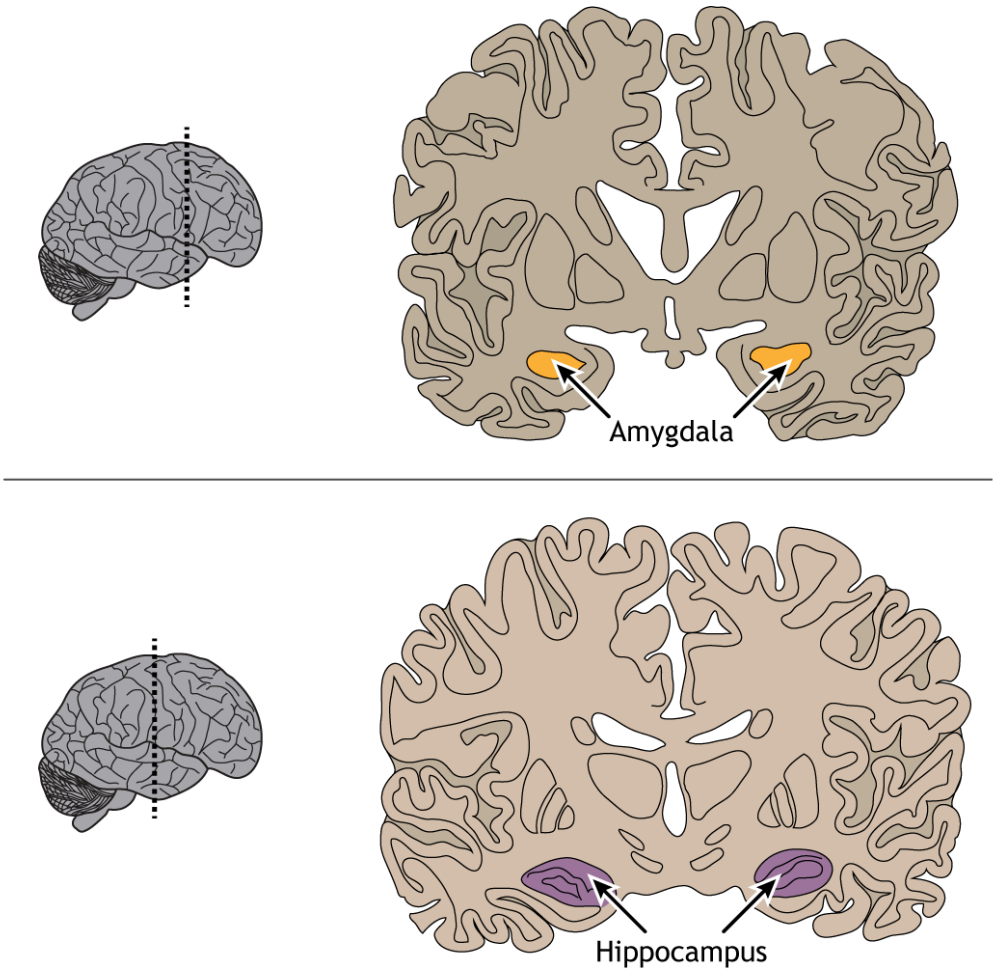


Figure 20.13. The limbic system structures, the amygdala and the hippocampus, also play important roles in visual processing. Both regions are located deep in the temporal lobe and have reciprocal connections with the ventral stream as is it moves through the temporal lobe. 'Deep Temporal Lobe' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

View the amygdala using the BrainFacts.org 3D Brain

View the hippocampus using the BrainFacts.org 3D Brain

Non-Thalamic Pathways

Although most retinal output projects to the lateral geniculate nucleus of the thalamus and then to the primary visual cortex, there are some axons that project to other areas of the brain. A subset of

specialized retinal ganglion cells project to the suprachiasmatic nucleus in the hypothalamus. This region is critical for circadian rhythms and the sleep/wake cycle. Other retinal neurons send axons to the pretectum, a midbrain region that communicates with motor nuclei and is responsible for pupillary control. Finally, other ganglion cells project to the superior colliculus, another midbrain region. This pathway is responsible for movements that will orient the head and eyes toward an object to focus the object in the center of the visual field, the region of highest visual acuity.

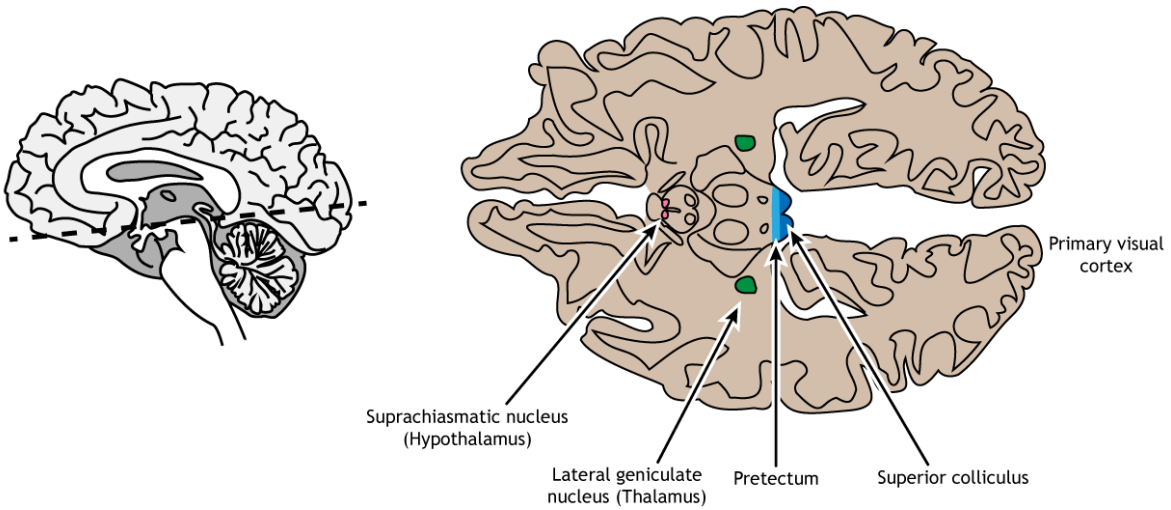


Figure 20.14. In addition to the thalamus, the retinal neurons send projections to other regions of the brain. The suprachiasmatic nucleus (pink) is located in the hypothalamus and is important for biological rhythms. The pretectum (light blue) is a midbrain structure that plays a role in muscle control of the pupil. Finally, the retina projects to the superior colliculus (blue), another midbrain region important in eye and head movements. The lateral geniculate nucleus of the thalamus (green) is also shown. 'Non-Thalamic Retinal Pathways' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

View the hypothalamus using the BrainFacts.org 3D Brain

View the midbrain using the BrainFacts.org 3D Brain

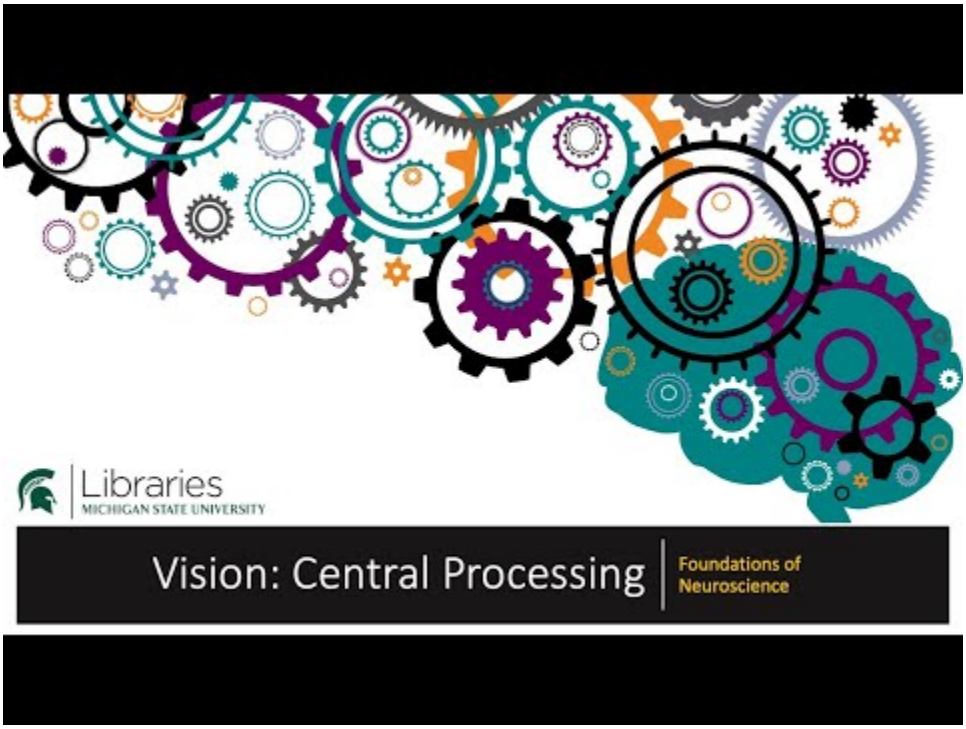
Key Takeaways

- The nasal and temporal retinal regions are responsible for viewing specific regions of the visual field
- Some retinal projections cross the midline at the optic chiasm, causing the left side of the brain to process the right visual hemifield and vice versa
- The retinal axons synapse in the lateral geniculate nucleus of the thalamus. Information then travels to the primary visual cortex
- Receptive fields and the preferred visual stimuli for neuron activation become more complex as information moves through the visual pathway
    - Retinal cells and thalamic neurons have circular receptive fields with inhibitory surround
    - Primary visual cortex neurons have linear receptive fields are are activated by a line in a specific orientation
    - Area MT / V5 is activated by motion in a specific direction
    - Area V4 is activated by specific shapes and colors
    - The fusiform gyrus is activated by faces
- The retina also projects to midbrain regions

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=479#h5p-19

Video Version of Lesson



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21.

SOMATOSENSORY SYSTEMS

Resources

- Key Takeaways
- Test Yourself

The somatosensory system is regulated by receptors that are spread throughout the body and measure a number of different sensory modalities in the body. These sensations can be divided into three main divisions: external stimuli, internal stimuli, and the sense of where the body is in space.

Perception of external stimuli can include the sense of touch (via mechanoreceptors), pain (via nociceptors), and temperature (via thermal receptors). Perception of internal stimuli can include organ (visceral) sensation and pain (via multiple receptor types) and blood chemical composition (via chemoreceptors). Finally, proprioception (via proprioceptors) is the sense of where the body is in space. The ability of an individual to touch their nose easily while their eyes are closed is an example of the proprioception system.

Somatosensory Cell Bodies

All somatosensory receptor neurons have their cell bodies located in the dorsal root ganglion, a structure found just outside the dorsal aspect of the spinal cord. The receptor neurons, also called primary afferent fibers, of the somatosensory system are bipolar neurons, meaning they have one process from the cell body that splits into two branches. One travels to the location of the receptor (e.g. the skin for touch) via the spinal nerves, and one travels into the spinal cord at the dorsal horn via the dorsal root. The axon can either synapse in the spinal cord or ascend to the brain in the dorsal column.

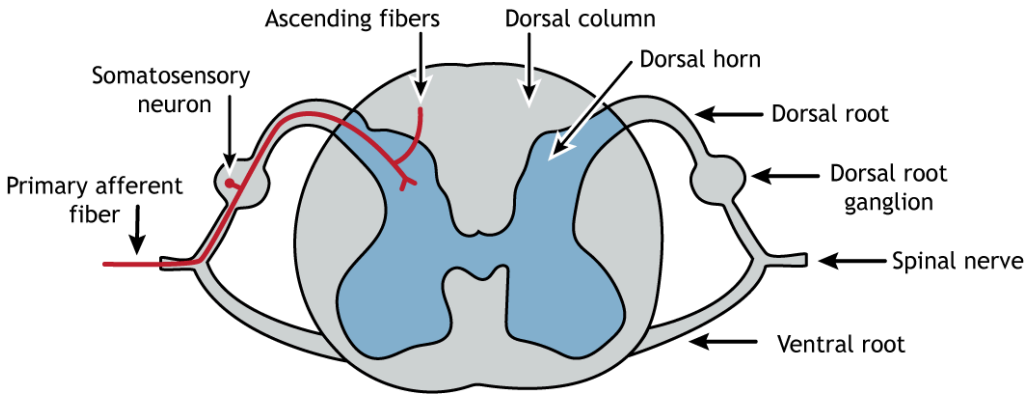


Figure 21.1. Primary afferent fibers travel from the periphery or target organs through the spinal nerve to the dorsal root ganglion where the cell body of the neuron is located. The axons then continue through the dorsal root into the dorsal horn of the spinal cord. Axons can branch and synapse in the spinal cord, or they can ascend to the brain via the dorsal column. 'Somatosensory Spinal Cord' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Primary Afferent Axons

Primary afferent axons are divided into four groups based on size and conduction speed. The groups, unfortunately, have different names depending on if the axons come from the skin (Aα, Aβ, Aδ, and C fibers; examples are touch or pain) or the muscles (Group I, II, III and IV fibers; example is proprioception). The fastest axons are the Aα or Group I type; they have the largest diameter and are heavily myelinated. The next fastest myelinated axons are the Aβ or Group II fibers, followed by the Aδ or Group III fibers. Finally, the C fibers have the smallest diameter, are unmyelinated, and are the slowest at conducting action potentials.

Afferent axon from muscle	Group 1	Group II	Group III	Group IV
Afferent axon from skin	Aα	Aβ	Aδ	C
Diameter (μm)	13-20 (Largest)	6-12	1-5	0.2-1.5 (Smallest)
Conduction speed (m/sec)	80-120 (Fastest)	35-75	5-30	0.5-2 (Slowest)

Table 21.1. Diameter and conduction speed of primary afferent axons. Group I and A alpha have the

largest diameter and fastest speed. Group II and A beta are the next largest and fastest, followed by Group III and A delta. Group IV and C fibers are the slowest and smallest of all axon types.

Different sensory information is sent via the different types of axons. Proprioceptive information from the skeletal muscles is sent to the spinal cord via Group I fibers. Touch information from the mechanoreceptors travels along Aβ fibers. Aδ fibers carry pain and temperature sensation, and C fibers convey information about pain, temperature, itch, and chemoreception.

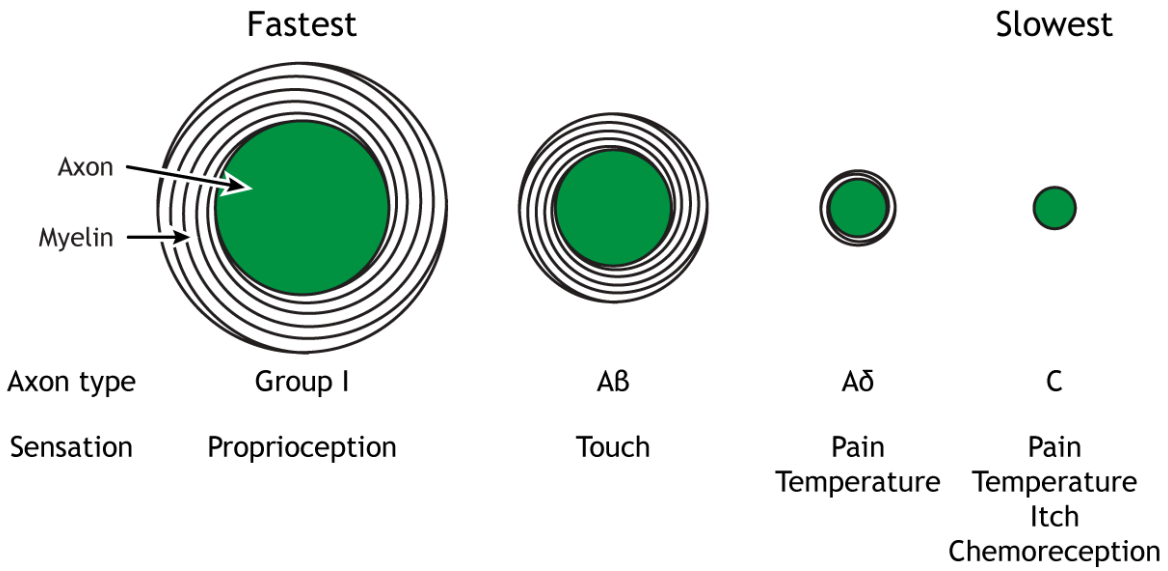


Figure 21.2. Primary afferent fibers differ in diameter and myelination, and therefore have different conduction speeds. A alpha fibers convey proprioception and are the largest and fastest of the axon types. Mechanoreception, or touch, is sent via A beta fibers, the next largest. Some aspects of pain and temperatures are sent by A delta fibers, which have small diameter and little myelination. C fibers are unmyelinated and sensory axons that detect pain, temperature, itch and chemoreception (chemical composition). These are the slowest of the somatosensory axons. 'Somatosensory Axon Types' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Dermatomes

The afferent axons from the dorsal root ganglion enter the spinal cord via the spinal nerves. Axons from nearby regions of the body enter the spinal cord together, and this forms regions of skin that are innervated by the same spinal nerve. These regions are called dermatomes. Damage to a spinal nerve will cause dysfunction along the innervated dermatome. The dermatomes and spinal nerves are divided into 4 groups. The seven cervical spinal segments are the most rostral and are located in the

neck. The twelve thoracic spinal segments are located along the chest and abdomen. The five lumbar segments are located below the thoracic segments, and the five sacral segments are the most caudal.

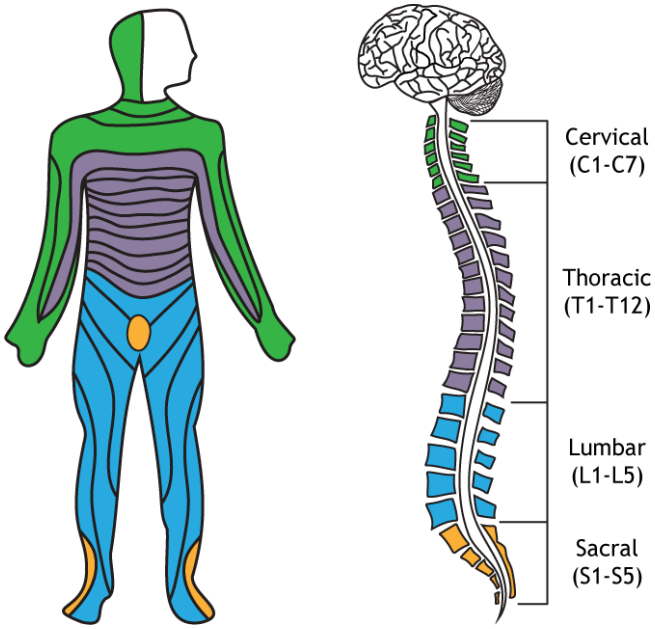


Figure 21.3. Spinal nerves exit the spinal cord and innervate a region of skin called a dermatome. There are five cervical, twelve thoracic, five lumbar, and five sacral spinal segments. 'Dermatomes' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Key Takeaways

- Somatosensory neuron cell bodies are located in the dorsal root ganglion
- Somatosensory primary afferent axons ascend to the brainstem via the dorsal column white matter tract
- Primary afferent axons vary in diameter and myelination, both of which affect action potential speed
- Different somatosensory information is carried by the different sizes afferents

- Dermatomes are the region of skin innervated by one spinal nerve

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=1211#h5p-23

22.

TOUCH: THE SKIN

Touch can come in many forms: pressure, vibration, stretch, motion, edges, points, etc. Receptors in the skin allow for perception of these different characteristics, and when this information is combined in the central nervous system, we are able to determine the location, strength, duration, movement, shape, and texture of the object interacting with the skin.

Resources

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

Receptors

We can feel different modalities of touch because of the presence of specialized sensory receptors, called mechanoreceptors, located in the skin.

The Pacinian corpuscles are located deep in the dermis of the skin and are responsible for perception of vibration.

Ruffini endings detect skin stretch and are also located within the dermis layer of the skin.

The Meissner corpuscles are stimulated by skin motion and are located in the epidermis layer.

The Merkel cells are located at the border between the dermis and epidermis and are specialized to detect edges and points.

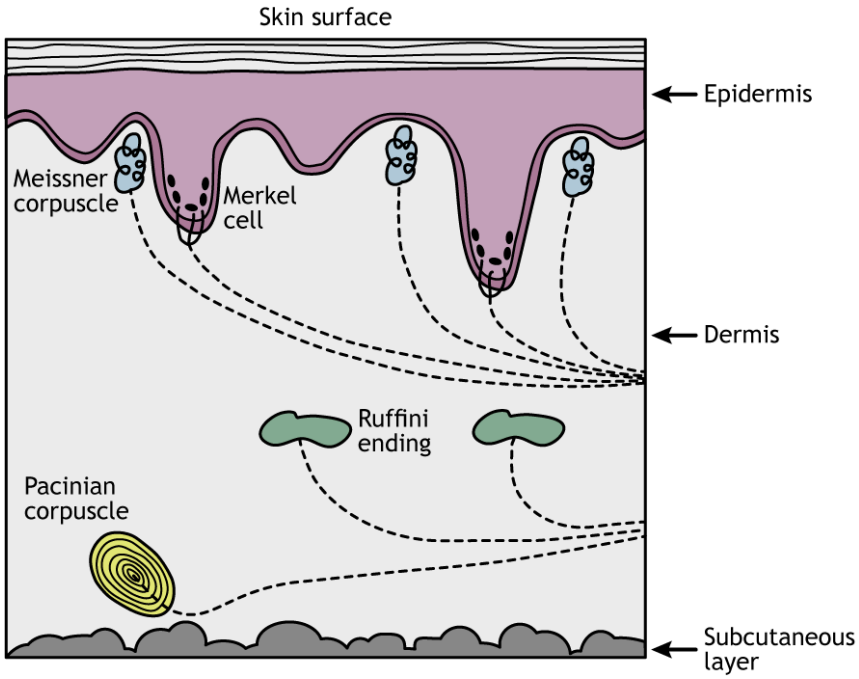


Figure 22.1. The different mechanoreceptor types are located in different regions of the skin and are responsible for perception of different characteristics of a touch timulus. Pacinian corpuscles and Ruffini endings are located deep in the dermis. Meissner corpuscles are located in the dermis near the epidermis, and Merkel cells are located in the epidermis, near the surface of the skin. 'Mechanoreceptors' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Receptive Fields

Each mechanoreceptor responds to a touch stimulus in a specific area of the skin, a region called the receptive field of the receptor. When the receptive field is touched, the mechanoreceptor will be activated.

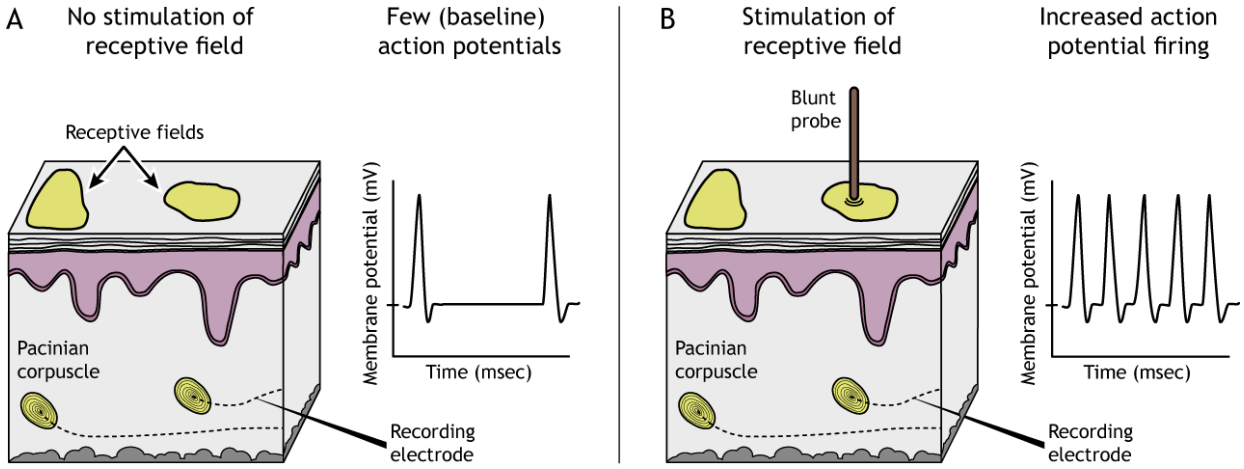


Figure 22.2. Each mechanoreceptor will be activated by a specific region of skin, the receptive field. When no stimulation of the receptive field occurs on the surface of the skin, the mechanoreceptor will show a baseline firing rate. When stimulation of the receptive field occurs, the firing rate of the mechanoreceptor will increase. 'Receptive Field Activation' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Receptive Field Size

Merkel cells and Meissner corpuscles, both of which are located near the skin surface, have small receptive fields. Ruffini endings and Pacinian corpuscles, located deeper in the skin layers, have larger receptive fields than the Merkel cells and Meissner corpuscles.

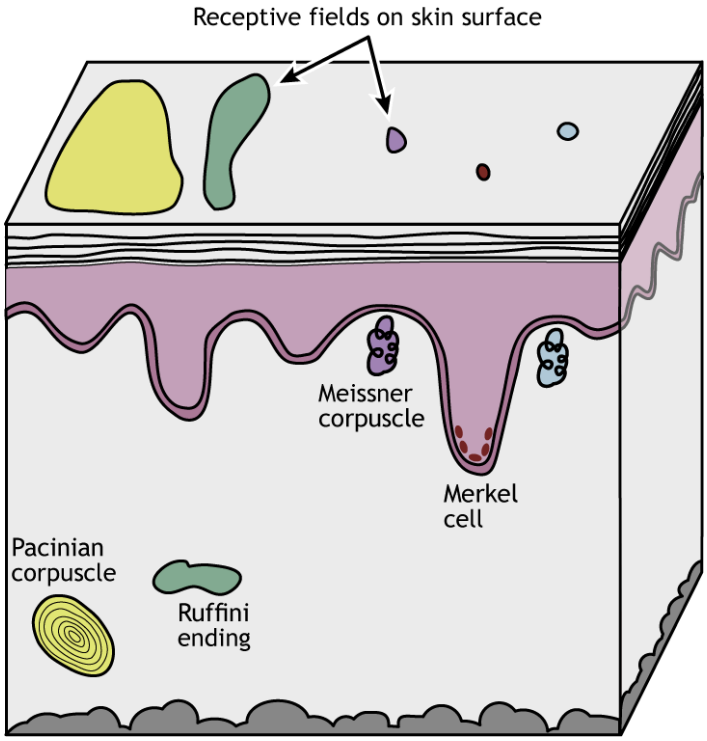


Figure 22.3. Receptive field sizes vary depending on the underlying mechanoreceptor type and location. Merkel cells and Meissner corpuscles have small receptive fields, whereas Pacinian corpuscles and Ruffini endings have large receptive fields. 'Mechanoreceptor Receptive Fields' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Receptive field sizes are different among the different mechanoreceptors, but they also vary among different body regions. Even within one receptor type (e.g. Meissner corpuscles), receptive fields in regions like the fingers or lips are smaller than in regions like the back or leg. This allows us to have finer spatial resolution with locating and identifying objects using our fingers. The smaller receptive fields in these regions are a result of a higher density of receptors in the skin.

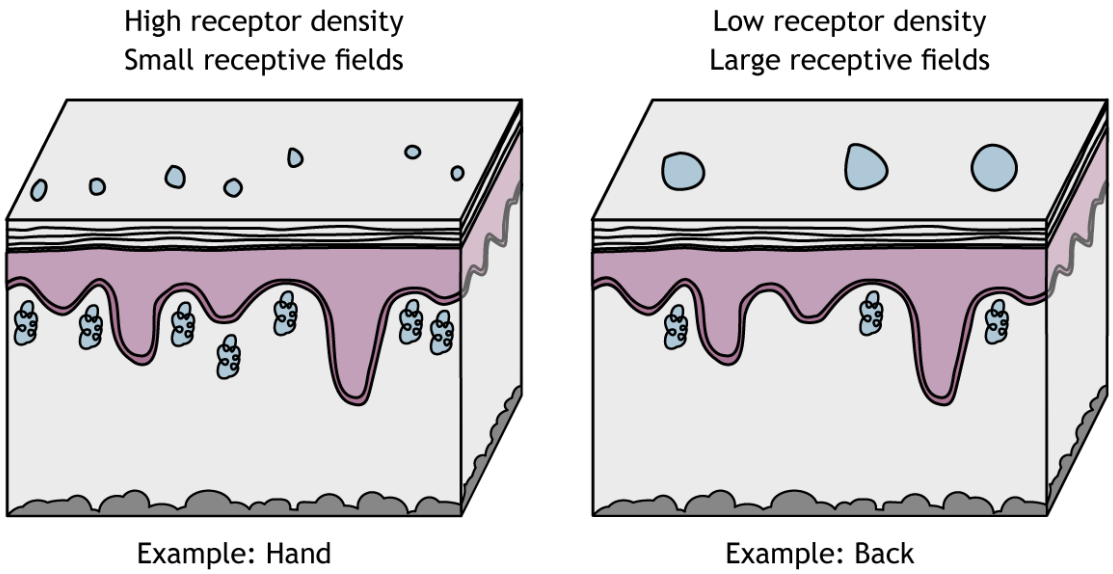


Figure 22.4. Density of mechanoreceptors can affect the size of the receptive field for each receptor. High density leads to smaller receptive fields. Density and receptive field size varies by location on the body. Regions like the hands and face have smaller receptive fields than regions like the back. 'Receptive Field Location' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Two-Point Discrimination

Receptive field sizes are important because they allow us to locate a stimulus on our bodies. Larger receptive fields are not as precise as smaller receptive fields. One measure of receptive field size is two-point discrimination (try it at home!), which determines the minimum distance needed between two stimuli to perceive two separate points on the skin and not one. The hand has a smaller threshold for discerning between two points than does the back, a result of the different sized in receptive fields.

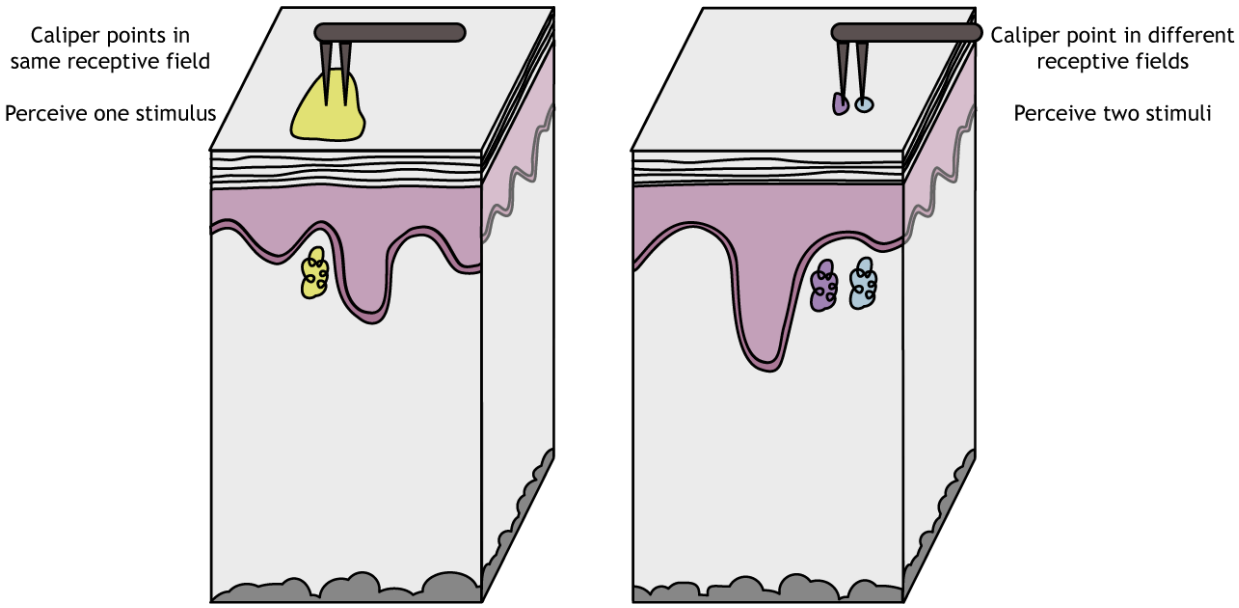


Figure 22.5. The size of the receptive fields affect the sensitivity of the skin, which can be measured by the two-point discrimination test. Tools like calipers or even a paperclip can be used to measure two-point discrimination. If the two points of the caliper feel like one point, they are both activating the same receptive field, indicating the receptive field is large. If, however, it is possible to perceive two separate points on the skin, then the calipers are activating two different receptive fields. 'Two-Point Discrimination' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Adaptation Rate

Another important characteristic of the somatic sensory receptors is that of adaptation rate. Fibers that are slowly adapting show action potential firing throughout the entire time a stimuli is present. Merkel cells and Ruffini endings are both slowly adapting fibers. Slowly adapting fibers are most useful for determining the pressure and shape of a stimulus.

A video element has been excluded from this version of the text. You can watch it online here: https://openbooks.lib.msu.edu/neuroscience/?p=493

Animation 22.1. Slowly adapting mechanoreceptors continuing firing action potentials throughout

the duration of a stimulus. As the stimulus moves from not present, to weak, to strong, the action potential firing of the Ruffini ending fires throughout the entire stimulus. 'Slowly Adapting Receptor' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License. View static image of animation.

Rapidly adapting fibers fire action potentials when a stimulus changes (e.g., starts, stops, gets stronger or weaker) but not when a stimulus is constant. This firing makes rapidly adapting fibers specialized for detecting movement and vibration. Meissner and Pacinian corpuscles are rapidly adapting.

A video element has been excluded from this version of the text. You can watch it online here: https://openbooks.lib.msu.edu/neuroscience/?p=493

Animation 22.2. Rapidly adapting mechanoreceptors firing action potentials when the strength of the stimulus changes. As the stimulus moves from not present, to weak, to strong, the action potential firing of the Pacinian corpuscle only fires when the stimulus changes strength. 'Rapidly Adapting Receptor' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License. View static image of animation.

Sensory Transduction

In previous chapters we discussed ion channels that are gated by voltage changes in the neuron and channels that are gated by neurotransmitters. In the somatosensory system, we find ion channels that are gated by physical distortion or stretch of the membrane. These channels can open by stretch of the membrane itself or indirectly through movement of intra- or extracellular proteins that are linked to the channels. Sodium and calcium flow into the cell, causing both a depolarization and the initiation of second messenger cascades. If enough stimulus is applied, the depolarization reaches threshold of the axon and an action potential is sent toward the spinal cord.

A video element has been excluded from this version of the text. You can watch it online here: https://openbooks.lib.msu.edu/neuroscience/?p=493

Animation 22.3. Mechanoreceptors respond to touch stimuli via stretch-gated non-selective cation channels. The channels can either open due to stretch of the membrane itself which stretches open the channel or due to proteins associated with the channels that pull the channel open. 'Stretch-Gated Ion Channels' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License. View static image of animation.

Key Takeaways

- There are multiple types of mechanoreceptors in the skin that are activated by different types of touch stimuli
- The receptive field size differs among the types of mechanoreceptors
- The adaptation rate differs among the types of mechanoreceptors
- Receptive field is a region of skin that activate a given mechanoreceptor
- Receptive field size for a specific type of mechanoreceptor can vary in size across the body
- Mechanoreceptors express stretch-gated non-selective ion channels that depolarize the cell during sensory transduction

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=493#h5p-21

Additional Review

Describe the relationship between density of receptors, receptive fields, and two-point discrimination.

Answers

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=493

23.

TOUCH: CENTRAL PROCESSING

Receptive Fields and Lateral Inhibition

Resources

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

The receptive fields of the sensory neurons become more complex as information moves up the pathway. We saw in the last lesson that mechanoreceptors have receptive fields that, when touched, activate the neuron. The mechanoreceptors synapse on neurons in the dorsal column, and those neurons have more complex receptive fields. The dorsal column nuclei have receptive fields that are divided into center and surround regions. The center of the receptive field is a result of direct innervation from the mechanoreceptors. If a stimulus touches the skin in the center of a dorsal column neuron's receptive field, the neuron will increase its firing rate. The center / surround structure is like that of bipolar and ganglion cells in the vision system.

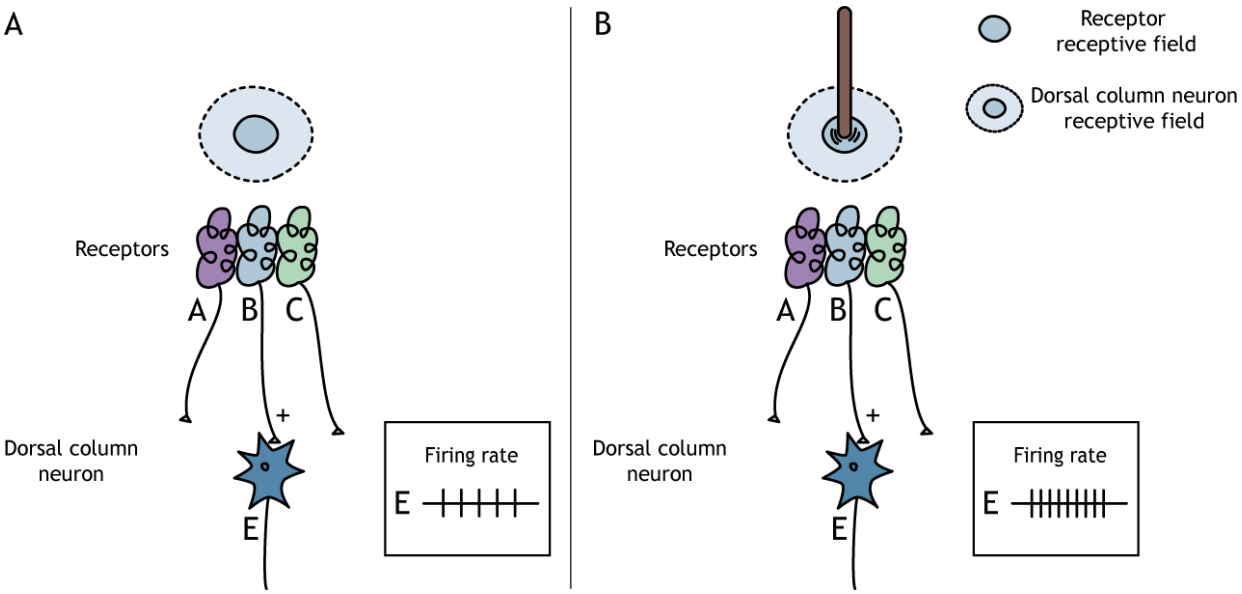


Figure 23.1. The receptive field of a dorsal column neuron has an excitatory center that is generated by the mechanoreceptors that synapse directly on the dorsal column neuron. A) When no stimulus is present, the dorsal column neuron fires at a baseline rate. B) When a stimulus touches the center of the receptive field of Cell E, the firing rate increases. 'Touch Receptive Field Center' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

The surround region of the receptive field is a result of indirect communication between the receptor neurons and the dorsal column neurons via inhibitory interneurons. The surround has an inhibitory effect on the dorsal column neuron. If a stimulus touches the skin in the surround of a dorsal column neuron's receptive field, the neuron will decrease its firing rate.

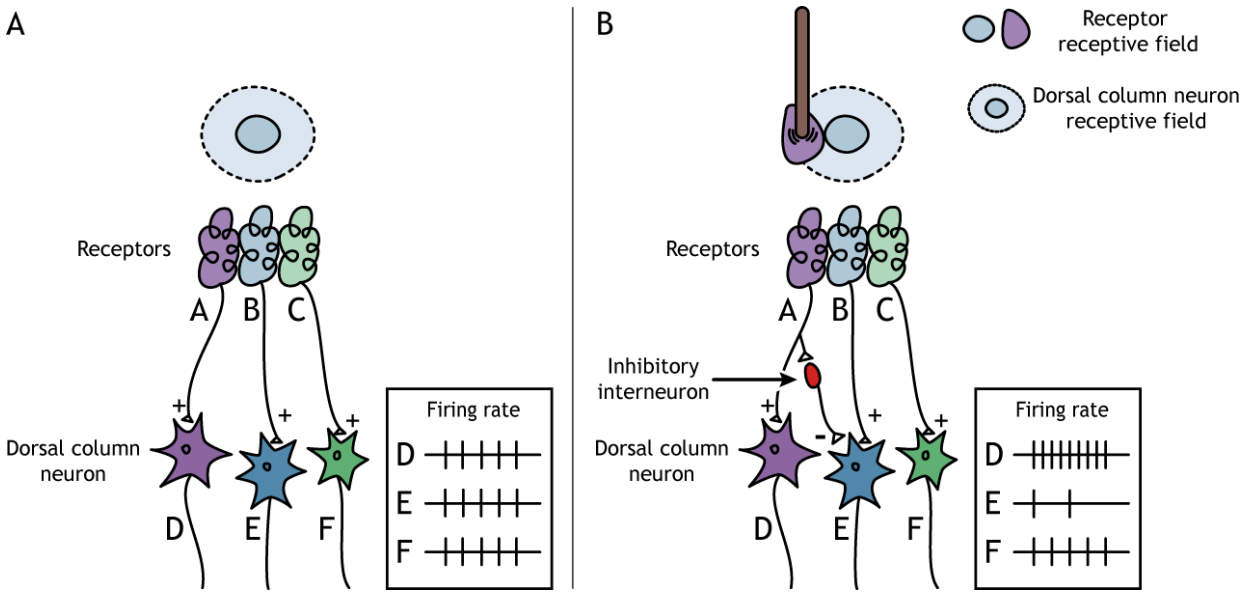


Figure 23.2. The receptive field of a dorsal column nucleus has an inhibitory surround, which is a result of the indirect connections between mechanoreceptors and the dorsal column neuron via inhibitory interneurons. A) When no stimulus is present, the dorsal column neurons fire at a baseline rate. B) When a stimulus touches the surround of the receptive field of Cell E, the firing rate decreases. Note that the stimulus is in the surround of Cell E's receptive field but is also in the center of Cell D, so the firing rate of Cell D will increase. 'Touch Receptive Field Surround' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Lateral Inhibition

The center-surround structure of the receptive field is critical for lateral inhibition to occur. Lateral inhibition is the ability of the sensory systems to enhance the perception of edges of stimuli. At a point or an edge of a stimulus, because of the inhibitory interneurons, the perceived stimulus strength will be enhanced compared to the actual stimulus strength.

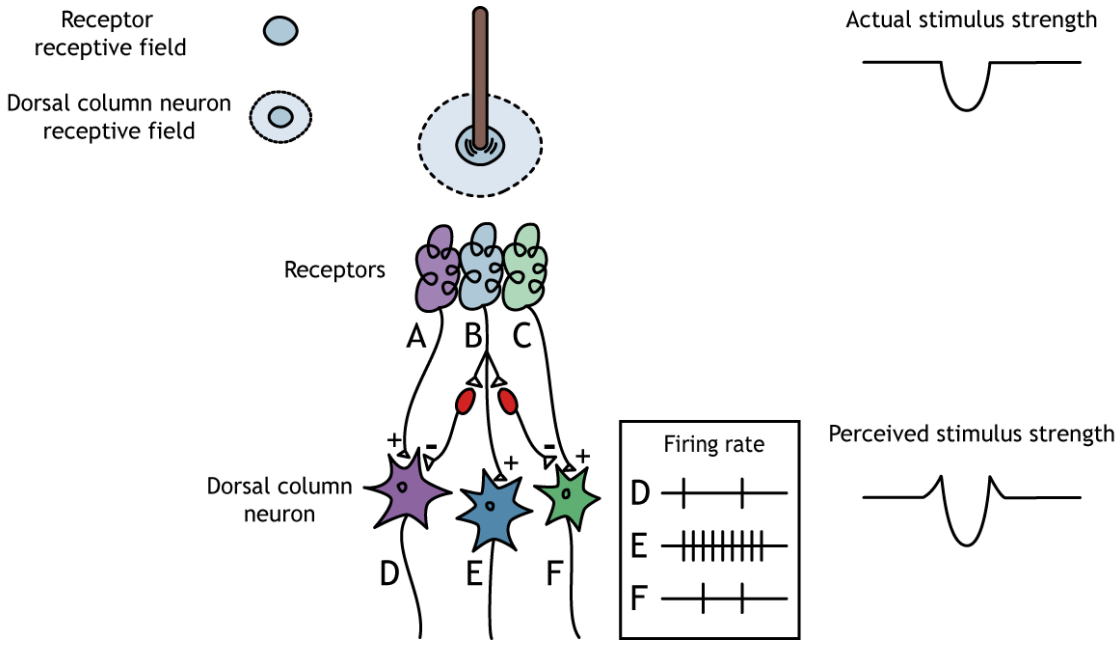


Figure 23.3. Lateral inhibition heightens the perception of edges or points on the skin. The point of a blunt probe pressing on the receptive field of Cell B will cause an increase in the firing rate of Cell E, but will also cause a decrease in the firing rate of Cells D and F. This increases the perceived difference between the point and the area next to the point that is not being stimulated. 'Touch Lateral Inhibition' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Pathway to Brain

Dorsal Column-Medial Lemniscus Pathway

Primary afferent sensory fibers have their cell bodies located in the dorsal root ganglion, a structure that lies just outside of the spinal cord. The axons of these first-order neurons enter the ipsilateral dorsal side of the spinal cord. Some axon collaterals terminate in the spinal cord and are important for reflexes. The main axon branch ascends the spinal cord toward the brain, via the dorsal column, terminating in the dorsal column nuclei located in the brainstem. The axons of sensory neurons in the lower body remain separate from the axons of sensory neurons in the upper body throughout the pathway. These two populations of neurons synapse in different regions of the brainstem. The lower body axons terminate in the gracile nucleus, whereas the upper body axons terminate in cuneate nucleus. Projections from the second-order neurons in the dorsal column nuclei cross the midline, or

decussate, and ascend via a white matter tract called the medial lemniscus. The axons terminate in the ventral posterior lateral nucleus of the thalamus. The thalamic neurons then project to the primary somatosensory cortex located in the postcentral gyrus in the parietal lobe.

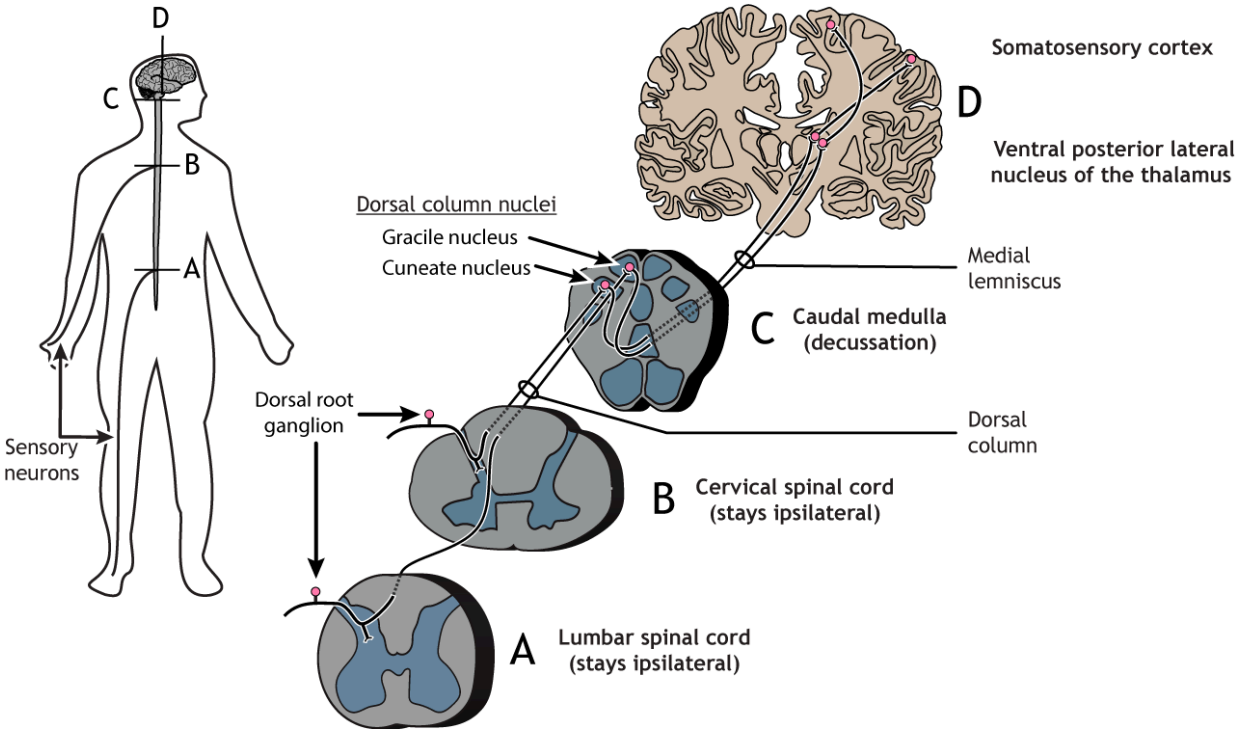


Figure 23.4 Somatosensory information from the neck and body travels through the dorsal column – medial lemniscus pathway, named for structures within the pathway. Axons enter the spinal cord and ascend through the dorsal column to the medulla where decussation, or crossing the midline, occurs. Information continues to the thalamus via the medial lemniscus, and then reaches the somatosensory cortex. Details of the pathway are found in the text. 'Touch Pathway from Body' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

View the thalamus using the BrainFacts.org 3D Brain

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

Trigeminal Pathway

Sensory receptors in the face and head send information to the brain via cranial nerve V, the trigeminal nerve. The first-order neurons have their cell bodies in the trigeminal ganglion, located just

outside of the brainstem, and they project to the ipsilateral trigeminal nucleus in the pons. The second-order neurons cross the midline and project up to the ventral posterior medial nucleus of the thalamus. These neurons then send projections to the face region of the somatosensory cortex.

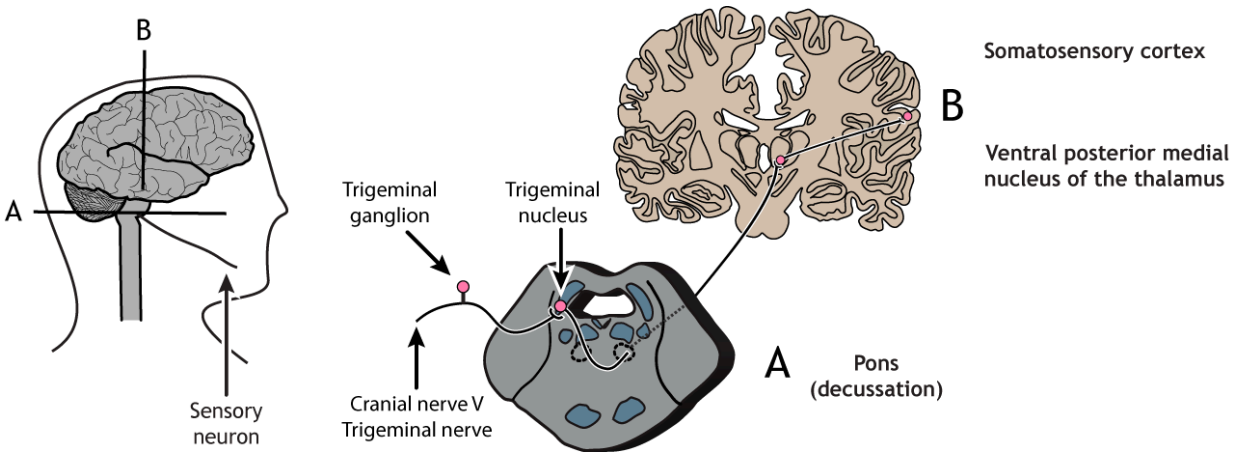


Figure 23.5. Somatosensory information from the head and face travels through the trigeminal pathway. Axons enter the brainstem at the level of the pons and decussate before traveling to the thalamus and somatosensory cortex. Details of the pathway are found in the text. 'Touch Pathway from Face' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

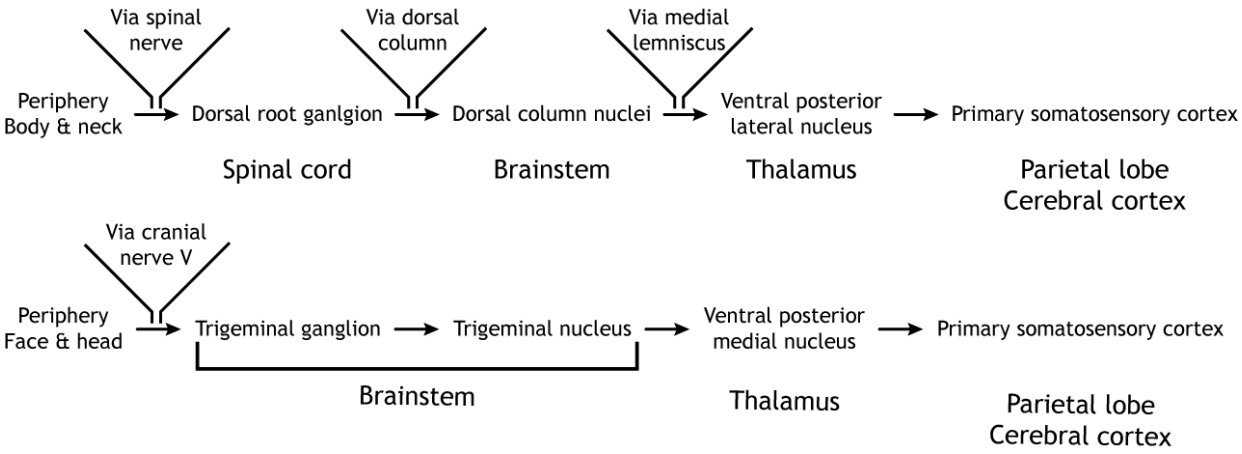


Figure 23.6. To compare the two pathways, sensory information comes in from the periphery. For the body, the peripheral axon branch travels via a spinal nerve to the cell body located in the dorsal root ganglion, which sits just outside the spinal cord. The central axon branch then enters the spinal cord and ascends via the dorsal column to the dorsal column nuclei in the brainstem. The second-order neuron crosses the midline and then projects to the ventral posterior lateral nucleus of the thalamus via the medial lemniscus tract. The thalamic third-order neuron projects to the primary somatosensory cortex in the parietal lobe. For sensory information from the face, the peripheral axon branch travels to the trigeminal ganglion via cranial nerve V. The ganglion sits outside of the brainstem, and the axons then enter the brainstem and synapse on the trigeminal nucleus. The second-order neuron travels to the ventral posterior medial nucleus of the thalamus, and the third-order neuron projects to the primary somatosensory cortex in the parietal lobe. 'Touch Pathways' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Primary Somatosensory Cortex

Anatomy

The primary somatosensory cortex is divided into four regions, each with its own input and function: areas 3a, 3b, 1, and 2. Most touch information from mechanoreceptors inputs to region 3b, whereas most proprioceptive information from the muscles inputs to region 3a. These regions then send and receive information from areas 1 and 2. As processing of somatosensory information continues, the stimuli required to activate neurons becomes more complex. For example, area 1 is involved in sensing texture, and area 2 is involved in sensing size and shape of an object. The posterior parietal cortex, an important output region of the somatosensory cortex, lies caudal to the postcentral gyrus; areas 5 and 7 are downstream structures that continue to process touch.

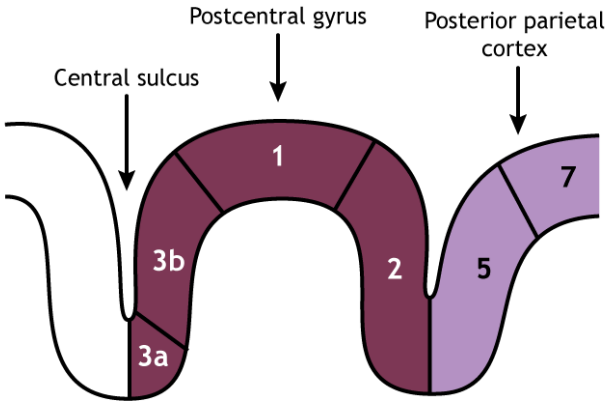


Figure 23.8. The somatosensory cortex, located in the postcentral gyrus, just posterior to the central sulcus, is divided into 4 areas: 3a, 3b, 1, and 2. The posterior parietal cortex, an output region of the somatosensory cortex, lies just posterior to the postcentral gyrus and is divided into areas 5 and 7. 'Postcentral Gyrus' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Somatotopic Map

The receptive fields of each higher order neuron increases in size and complexity, but even cortical neurons are associated with a specific region of the body. Cortical neurons are organized by the region of the body they represent, so neurons that respond to sensation in the fingers are located close to the neurons that respond to sensation in the hand. Remember from above that axons in the dorsal column from the lower body run next to, but remain separate from, the axons from the upper body. This separation, which occurs for all body regions and at all levels of the pathway, creates a somatotopic map of the body in the primary somatosensory cortex. Each area of the somatosensory cortex (Figure 23.7) has its own, but similar, map of the body.

Regions with high receptor density in the skin, and, therefore, fine two-point discrimination, have more cortical space devoted to them. This means that the cortical representation of the body is not true to actual physical proportions. A homunculus is a cartoon representation of what a body would look like if actual body size was proportional to the cortical representation. The hands and lips would be excessively large while the torso, arms, and legs, would be relatively small.

Figure 23.8. The body is mapped onto the somatosensory cortex. Regions with high touch sensitivity, and therefore high mechanoreceptor density, have more cortical space dedicated to their processing. The feet and legs are represented in the medial superior region of the cortex; the face is represented on the lateral side of the cortex; the hand and fingers fall in between. 'Somatotopic map' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Higher-Level Processing of Touch Information

The primary somatosensory cortex sends projections to other parietal lobe regions for higher-level processing of touch information.

Secondary Somatosensory Cortex

The secondary somatosensory cortex (SII) is located in the inferior parietal lobe, just above the lateral fissure. This region, like the dorsal stream of visual processing, is responsible for object recognition, discerning texture, shape, and size. The SII also has receptive fields that represent bilateral regions of the body, so both hemispheres will be activated by touch on either side of the body. The SII sends projections to the posterior parietal cortex, the premotor cortex, the amygdala, and the hippocampus.

Posterior Parietal Cortex

The posterior parietal cortex recognizes touch characteristics like orientation and movement. It is also important for combining the touch and motor components of actions like grasping. The posterior parietal cortex outputs to the frontal motor cortex.

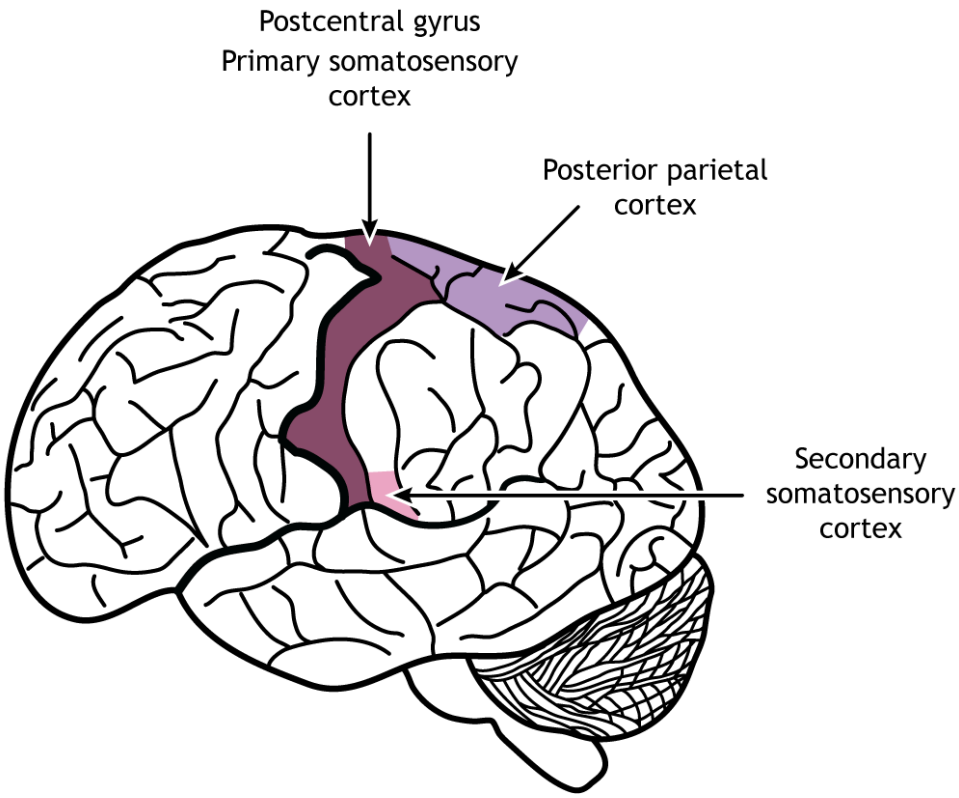


Figure 23.9. The primary somatosensory cortex is located in the postcentral gyrus. The posterior parietal cortex regions important for somatosensory lie caudal to the postcentral gyrus in the superior parietal lobe. The secondary somatosensory cortex is located dorsal to the lateral fissure, caudal to the postcentral gyrus. 'Somatosensory Streams" by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

View the posterior parietal cortex using the BrainFacts.org 3D Brain

Cortical Plasticity

In adulthood, the brain is plastic, meaning synaptic connections can rearrange under certain conditions. Amputation or loss of a finger, for example, will lead to the associated cortical space to be functionally remapped by input from neighboring regions of the hand. The cortical neurons do not die, they begin to be activated by a different region of the body. Likewise, cortical representation can expand with use or practice. Repeated training of certain fingers can lead to an increase in cortical space mapped to those digits. Cortical plasticity is believed to underly the phenomenon of the perception of phantom limbs after amputation. In these cases, subjects that have lost a region of their body can sometimes still "feel" the missing part.

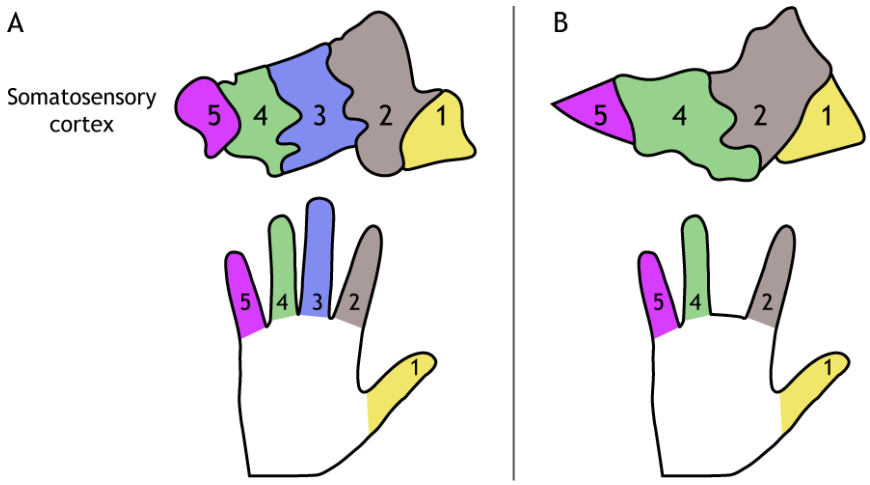


Figure 23.10. It is possible to map cortical space to regions of skin. A) The cortical space mapped to each finger for an imaginary individual is shown as an example. B) If this individual were to lose a finger, in this case digit 3 or the middle finger, and the cortical space was remapped after time had passed, the region that had once responded to touch on digit 3 would instead respond to touch on either digit 2 or 4. The brain does not let that cortical space die or go to waste; it rearranges connections to make use of all the neurons. Based on Merzenich et al., 1984. 'Cortical Plasticity' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Key Takeaways

- Receptive fields become more complex as information moves through the touch pathway
- Lateral inhibition enhances edges and borders by affecting the perceived stimulus strength
- Mechanoreceptor afferents synapse in the dorsal column nuclei in the medulla. Information then decussates and synapses in the ventral posterior nucleus of the thalamus before traveling to the primary somatosensory cortex
    - Sensory axons from the lower body synapses in the gracile nucleus in the dorsal column
    - Sensory axons from the upper body synapses in the cuneate nucleus in the dorsal column
    - Information from the neck and body synapse in the ventral posterior lateral nucleus of the thalamus
    - Information from the head and face synapse in the ventral posterior medial nucleus of the thalamus
- The primary somatosensory cortex is organized in a somatotopic map
- The cortex is plastic and connections can change with experience

Test Yourself!

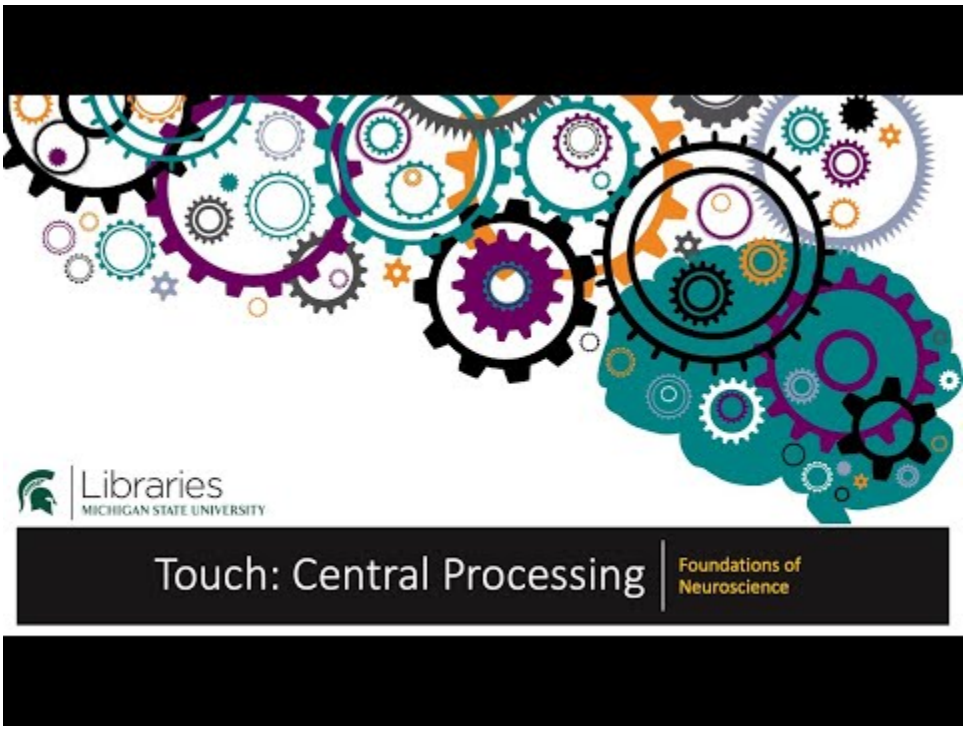
An interactive H5P element has been excluded from this version of the text. You can view it online here:
https://openbooks.lib.msu.edu/neuroscience/?p=512#h5p-22

Additional Review

1. What is the anatomical name of the primary somatosensory cortex?
2. After somatosensory information leaves the brainstem, it must relay through which structure before reaching the primary somatosensory cortex?

Answers

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=512

24.

TASTE

Being able to sense chemicals in the environment through taste and olfaction can help an organism find food, avoid poisons, and attract mates. Humans can perceive five basic tastes: salty, sour, bitter, sweet, and umami. Bitter taste often indicates a dangerous substance like a poison, sweet taste signifies a high energy food, salty taste indicates a substance with high salt content, sour taste indicates an acidic food, and umami taste indicates a high protein food.

Resources

- Key Takeaways
- Test Yourself
- Video Version

Tongue anatomy

The surface of the tongue is covered in small, visible bumps called papillae. Taste buds are located within the papillae, and each taste bud is made up of taste receptor cells, along with supporting cells and basal cells, which will eventually turn into taste receptors cells. The taste cells have a lifespan of approximately two weeks, and the basal cells replace dying taste cells. The taste cells have microvilli that open into the taste pore where chemicals from the food can interact with receptors on the taste cells. Although taste cells are not technically neurons, they synapse and release neurotransmitters on afferent axons that send taste perception information to the brain.

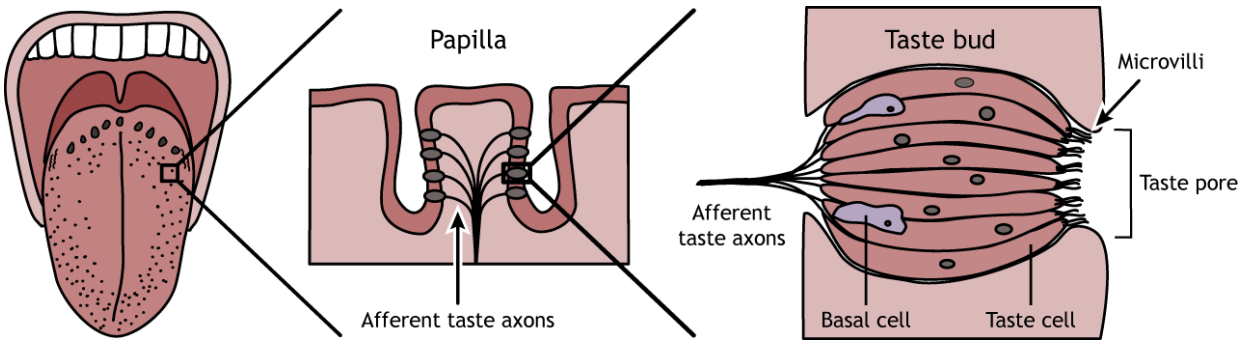


Figure 24.1. The visible bumps on the surface of the tongues are papillae that house taste buds. Taste buds are made up of taste cells and basal cells. The taste cells synapse on afferent axons that send information to the central nervous system. Tastants in food access the taste cells via the taste pore, where the food particles interact with the microvilli of the taste cells. 'Tongue Anatomy' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

The entire tongue is capable of perceiving all five tastes, meaning there are taste receptors for each taste present across the entire surface. However, some regions of the tongue have a slightly lower threshold to respond to some tastes over others. The tip of the tongue is the region most sensitive to sweet, salt, and umami tastes. The sides are most sensitive to sour, and the back of the tongue to bitter tastes.

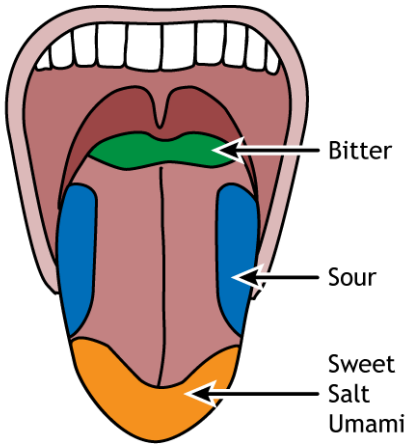


Figure 24.2. Although all tastes can be perceived across the entire tongue, sensitivity levels vary for each taste. The front of the tongue has the lowest threshold for sweet, salt, and umami tastes; the side of the tongue has the lowest threshold for sour tastes, and the back of the tongue has the lowest threshold for bitter tastes. 'Taste Map' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Taste transduction

Salt

Salt taste is mediated by the presence of epithelial sodium channels. These receptors are usually open, and when foods are ingested with high salt concentrations, sodium flows into the cell causing a depolarization. This change in membrane potential opens voltage-gated sodium and calcium channels. The increased calcium influx causes the release of serotonin-filled vesicles. The serotonin acts on the afferent taste axon causing depolarization and action potentials.

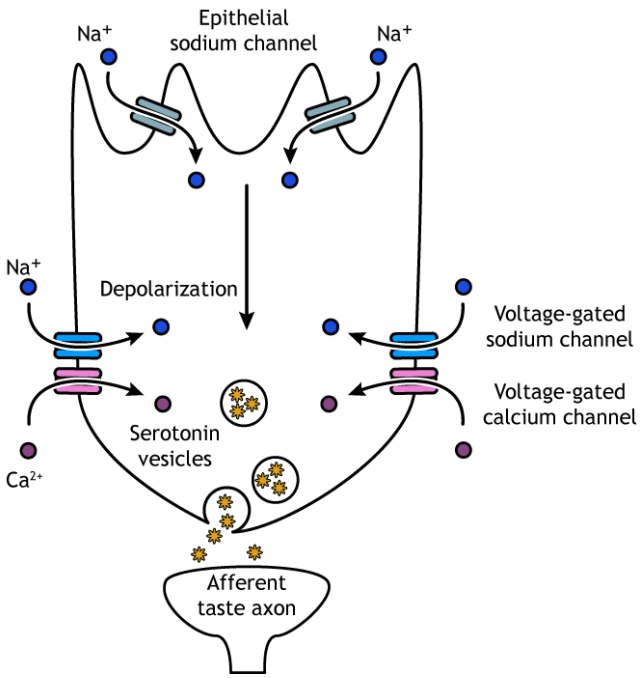


Figure 24.3. When salty foods are ingested, the sodium from the food enters the taste cell via open epithelial sodium channels. The resulting depolarization opens voltage-gated sodium and calcium channels, leading to release of serotonin onto the afferent taste axon. 'Salt Taste Transduction' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Sour

Foods taste sour because of their acidity, and when acids are present in water, they produce hydrogen

ions (protons). The exact mechanism for sour taste transduction has yet to be worked out, but it is believed that protons enter the cell through an ion channel, and then block potassium channels. The decreased efflux of potassium, along with the presence of the protons, depolarizes the cell causing voltage-gated sodium and calcium channels to open. Like salt taste transduction, the increase in intracellular calcium causes release of serotonin into the synapse.

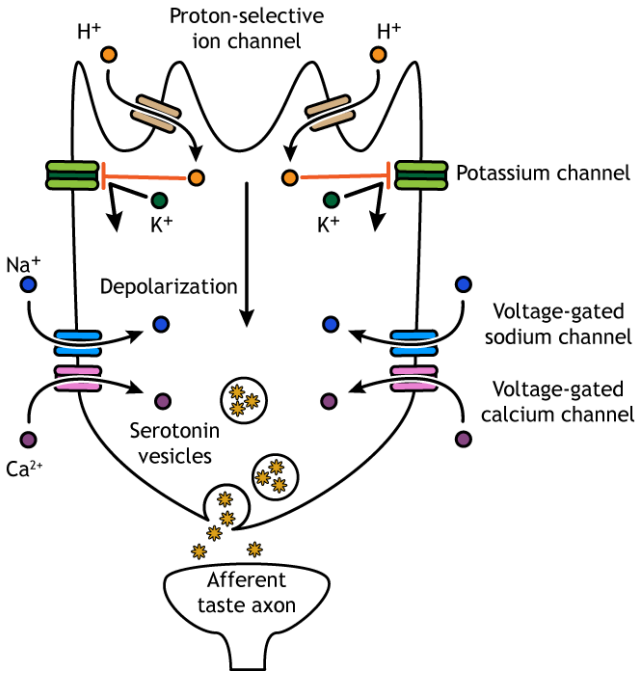


Figure 24.4. When sour foods are ingested, the protons from the acid enter the cell via open ion channels. The protons then block potassium channels. The resulting depolarization opens voltage-gated sodium and calcium channels, leading to release of serotonin onto the afferent taste axon. 'Sour Taste Transduction' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Bitter

Bitter, sweet, and umami compounds all activate taste receptor cells via G-protein coupled receptors. The bitter receptors are from the T2R family of receptor proteins; humans have over 25. Each taste cell can express most or all of the different receptor types, allowing for the detection of numerous molecules, which is important when wanting to avoid dangerous substances like poisons and toxins.

Activation of the G-protein receptor uses a second messenger system to increase intracellular

calcium, which opens ion channels, allowing the influx of sodium. These ion changes depolarize the cell and cause ATP-specific channels to open, allowing ATP to enter the synapse and act on the afferent taste axon.

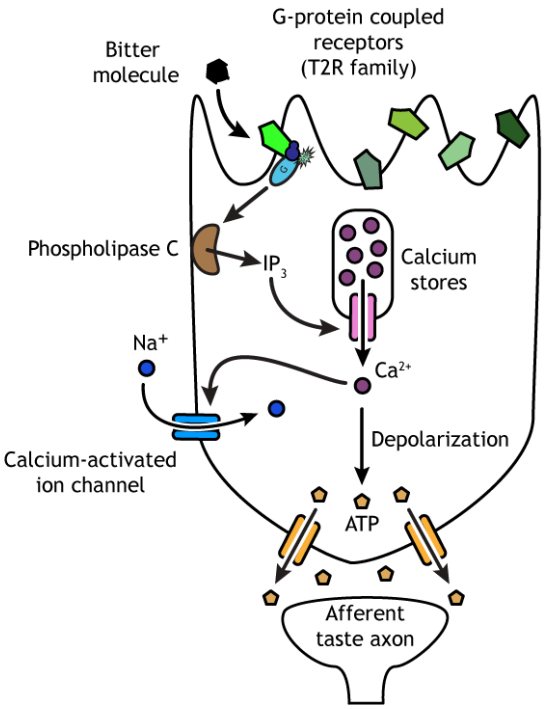


Figure 24.5. Bitter foods activate G-protein receptors, which initiate the phospholipase C second messenger system. IP3 releases calcium from intracellular stores, and the calcium opens ion channels that allow sodium influx. The resulting depolarization causes ATP release onto the afferent taste axon. 'Bitter Taste Transduction' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Sweet

Sweet and umami receptors are comprised of G-protein coupled dimers, meaning two separate proteins function together as one. The receptors are encoded by the T1R family of receptor proteins. Sweet receptors are dimers of the T1R2 and T1R3 proteins. Both proteins need to be present and functioning for activation of a sweet taste cell. Like bitter cells, activation of the G-protein receptor uses a second messenger system to release calcium from intracellular stores and increase the influx of sodium. These ion changes depolarize the cell and cause ATP-specific channels to open, allowing ATP to enter the synapse and act on the afferent taste axon.

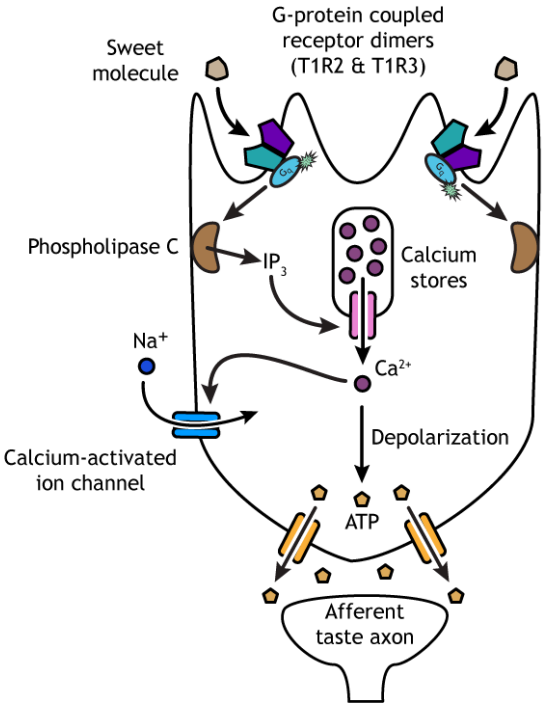


Figure 24.6. Sweet foods activate G-protein receptor dimers, which initiate the phospholipase C second messenger system. IP3 releases calcium from intracellular stores, and the calcium opens ion channels that allow sodium influx. The resulting depolarization causes ATP release onto the afferent taste axon. 'Sweet Taste Transduction' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Umami

Umami receptors are comprised of the T1R3 protein, like the sweet receptor, but it is paired with the T1R1 protein. Once the G-protein coupled receptor is activated, the transduction pathway is the same as bitter and sweet taste cells.

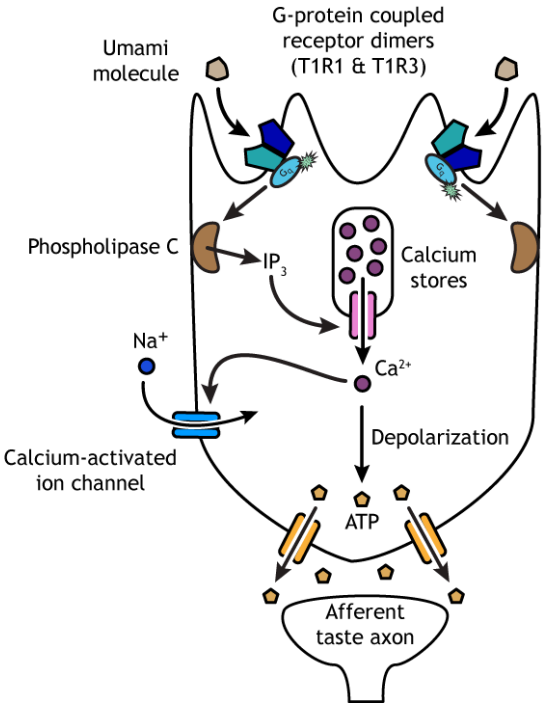


Figure 24.7. Umami compounds activate G-protein receptor dimers, which initiate the phospholipase C second messenger system. IP3 releases calcium from intracellular stores, and the calcium opens ion channels that allow sodium influx. The resulting depolarization causes ATP release onto the afferent taste axon. 'Umami Taste Transduction' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Coding Properties of Taste

Of the five tastes, only two neurotransmitters are used to communicate information to the central nervous system, so how does our brain know what tastes to perceive? The answer is how the information is encoded. Most taste cells use a labeled line coding method, which means that each cell and the related afferent taste axon only responds to one type of taste. For example, bitter cells only express bitter receptors and are only activated by bitter molecules. These bitter taste cells activate bitter sensory neurons and bitter regions of the taste cortex. A small portion of taste cells do use population coding as well, meaning more than one tastant can activate the cell, and perception is based on a combination of multiple cells each with a different response. Most information, however, is encoded via labeled line at the level of the taste cell.

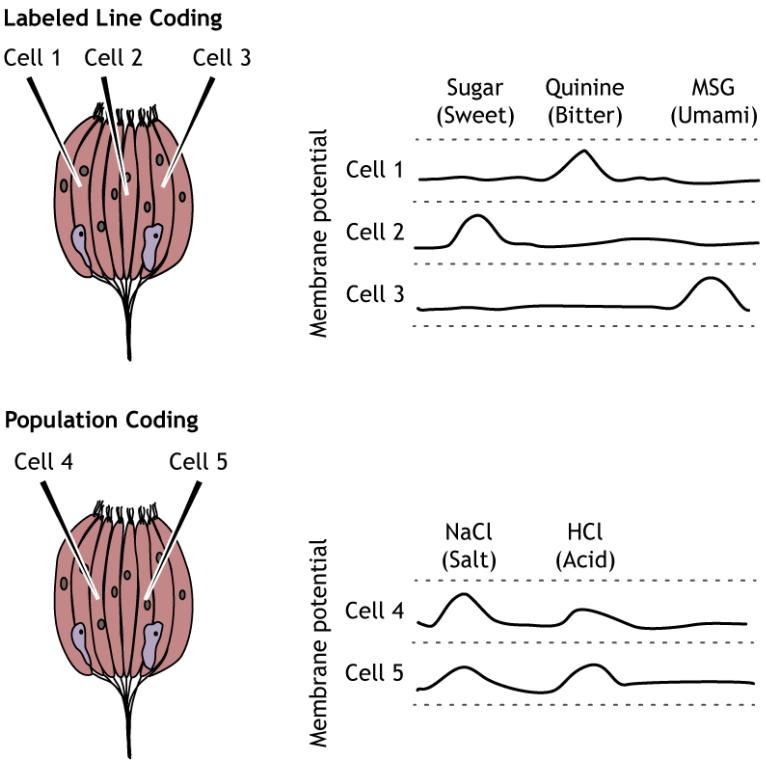


Figure 24.8. Labeled lined coding occurs when one sensation (in this case, a specific taste) leads to activation of the sensory cell. In this example, Cell 1 is activated only by quinine, a bitter compound, Cell 2 is activated only by sugar, a sweet compound, and Cell 3 is activated only by MSG, an umami compound. Most taste cells in the tongue use labeled line coding. Population coding results from broader activation, where multiple sensations can activate a sensory cell and perception is a result of information from a population of cells. In the example, Cells 4 and 5 are activated by both salt and acid compounds. 'Taste Coding' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Mouth and Throat Anatomy

Although taste receptor cells are most prevalent on the tongue, there are other regions of the mouth and throat, including the palate, pharynx, and epiglottis, that also are sensitive to food and play a role in taste perception. The olfactory system is tightly linked to our sense of taste as well, and odorant compounds from food can reach odor receptors in the nasal cavity.

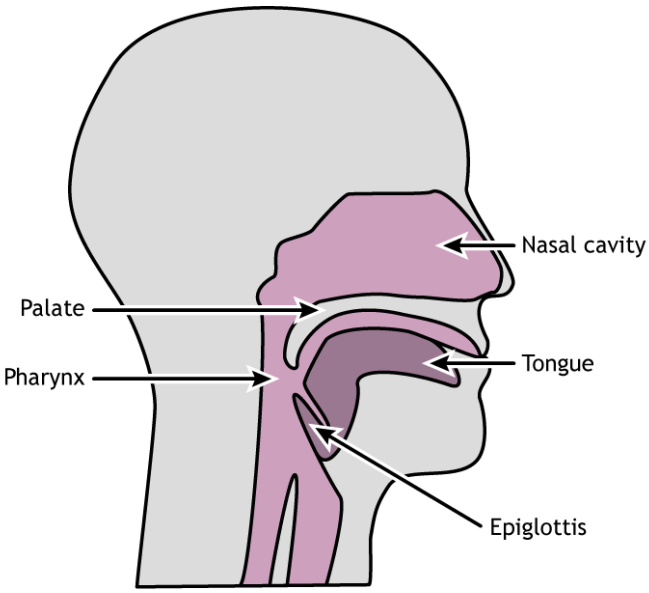


Figure 24.9. The tongue is the primary location for taste receptors cells, but receptors are also located along the palate, pharynx, and epiglottis. Additionally, airborne compounds from food can reach odor receptors in the nasal cavity. The sense of smell plays an important role in the perception of flavor. 'Throat Anatomy' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

Pathway

The tongue is innervated by three cranial nerves. The front two-thirds of the tongue is innervated by cranial nerve VII. The back third is innervated by cranial nerve IX. Finally, the epiglottis and pharynx are innervated by cranial nerve X. All three cranial nerves enter the brainstem at the medulla and synapse in the nucleus of the solitary tract. From there, information is sent to the ventral posterior medial nucleus of the thalamus. Thalamic neurons send projections to the gustatory cortex. The gustatory cortex is located deep in the lateral fissure in a region called the insula. Information processing taste stays primarily on the ipsilateral side of the nervous system. Projections within the brain also exist between the taste regions and the hypothalamus and amygdala.

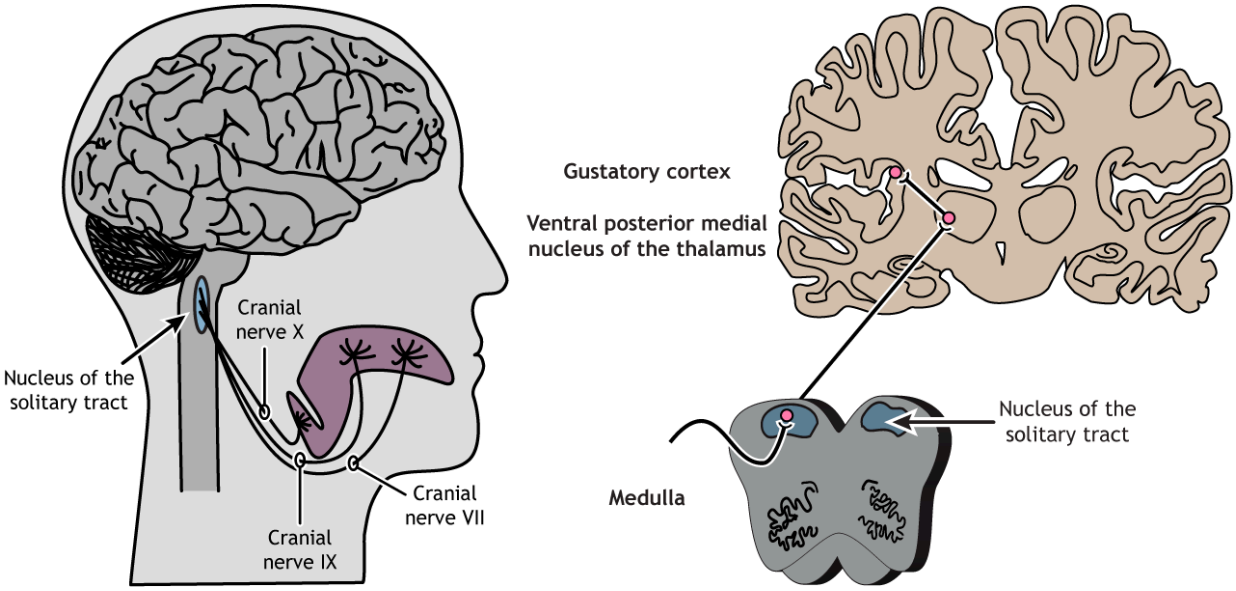


Figure 24.10. Taste information from the tongue travels through cranial nerves VII, IX, and X to the nucleus of the solitary tract in the medulla. Neurons in the brainstem project to the ventral posterior medial nucleus of the thalamus and then on to the gustatory cortex. 'Taste Pathway' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

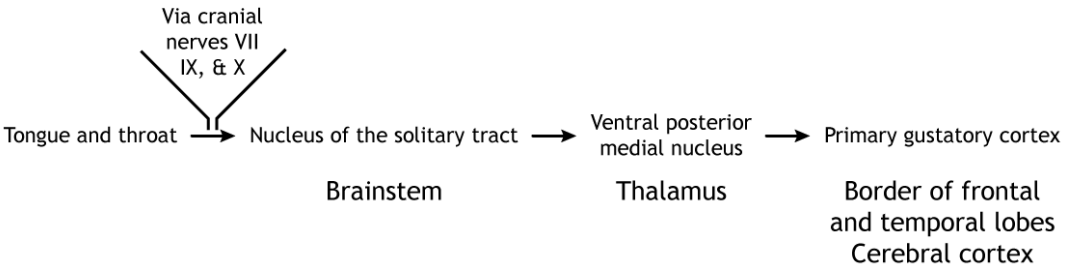


Figure 24.11 Axons from sensory afferents from the tongue and throat travel to the nucleus of the solitary tract in the brainstem via cranial nerves VII, IX, and X. The second-order brainstem neurons project to the ventral posterior medial nucleus of the thalamus. The thalamic third-order neuron projects to the primary gustatory cortex, which is located at the border of the frontal and temporal lobes. 'Taste Pathway' by Casey Henley is licensed under a Creative Commons Attribution Non-Commercial Share-Alike (CC BY-NC-SA) 4.0 International License.

View the facial nerve (cranial nerve VII) using the BrainFacts.org 3D Brain

View the glossopharyngeal nerve (cranial nerve IX) using the BrainFacts.org 3D Brain

View the vagus nerve (cranial nerve X) using the BrainFacts.org 3D Brain

View the thalamus using the BrainFacts.org 3D Brain

Flavor

How do 5 basic tastes turn into the myriad complex taste sensations we experience when eating food? Olfaction plays an important role in the perception of flavor, as do vision and touch. Taste information combines with information from these other sensory systems in the orbitofrontal cortex located in the frontal lobe. This region is believed to be important for the pleasant and rewarding aspects of food. Additionally, as taste is processed in higher-order regions of the CNS, information is combined using population coding mechanisms. Test how your senses combine to create flavor at home!

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

Key Takeaways

- Taste cells express specific taste receptors and are located in taste buds within the papillae
- Salt and sour taste cells rely on ion channels to depolarize the cell and release serotonin
- Bitter, sweet, and umami taste cells rely on G-protein coupled receptors and second messengers that open ATP channels
- At the level of the taste receptor cells, taste is perceived by using labeled line coding
- Multiple regions in the mouth and throat play a role in processing of taste
- Three cranial nerves innervate the tongue and throat
- The cranial nerves synapse in the nucleus of the solitary tract in the medulla. Information then travels to the ventral posterior medial nucleus of the thalamus and then to the gustatory cortex
- To perceive complex flavors, information from other sensory systems is combined with taste information in the orbitofrontal cortex

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=587#h5p-20

Video Version of Lesson

A YouTube element has been excluded from this version of the text. You can view it online here:
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