Section Two: Chapter 11: The General and Special Senses

How do we know that it is cold outside, or that the dog is barking again, or that some really nice coffee is being made? Our senses tell us!

In physiology, **senses** are the capacity within our body that enables us to **detect** information in the world around us. We use our senses to inform us about internal or external stimuli. It is always incoming sensory information. The faculty of **sensation** by our body systems is integrated with our stored information within the body to generate **perception** of the specific information. This allows us to associate meaning to sensations and put them into context.

Here is an example of how the perception of the senses in the opening sentence above would enable a person to respond appropriately: It **feels cold** outside so I'd better find a **warm jacket** because I need to go out there since I can **hear the dog** asking to play. I can **see** the coffee brewing, and it **smells** great so it's likely to **taste** great too**.**

- **Sensation** is input about the physical world obtained by our sensory receptors. It involves the physical stimulation of the sensory receptor.

- **Perception** is the process of selecting, creating and organizing meaningful patterns from raw sensory information. This is a process by which we give meaning to these sensations and puts them into context. In other words, senses are the physiological basis of perception.

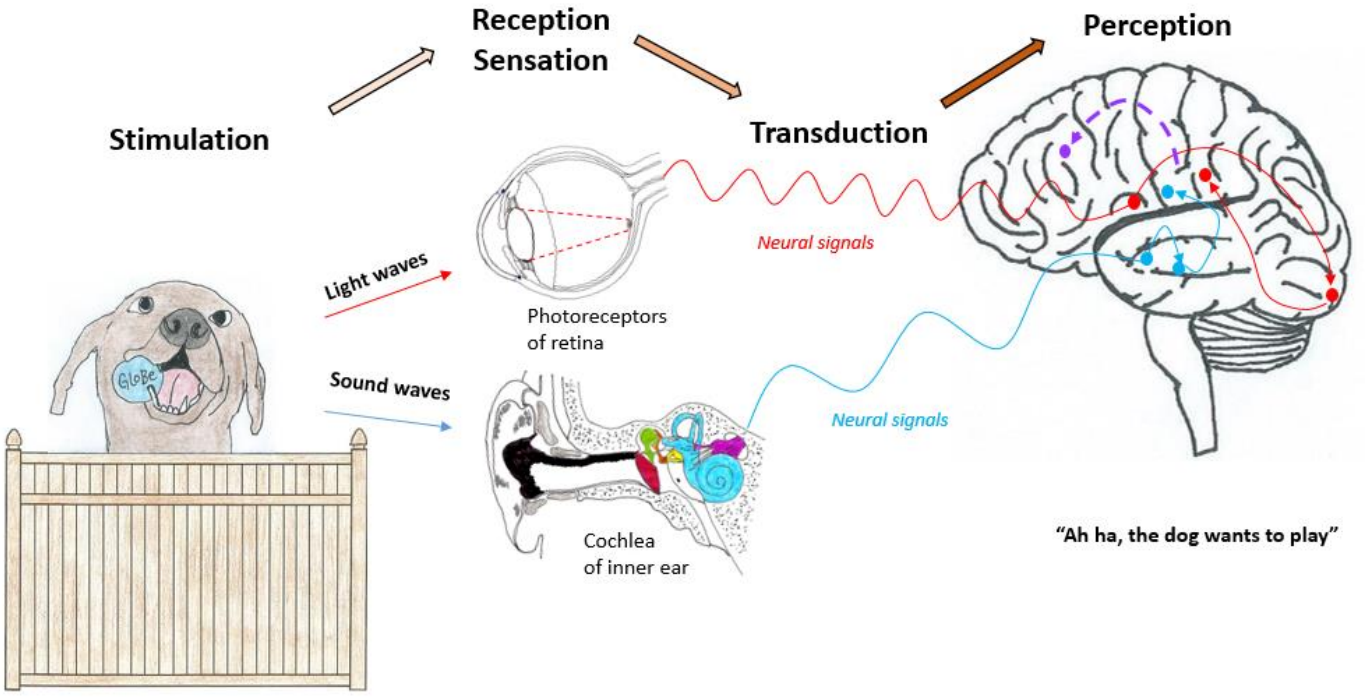


Figure 11.1. Shown above is the process of sensation from the initial stimuli of seeing and hearing the dog making noise all the way to its perception. The various sensations are detected by the body's receptors. The various types of energy from the stimuli are then transduced into electrical neural signals and delivered to specific brain regions for the perception of the original stimuli. This enables a process of association and placing stimuli in context for meaning in order to contemplate the information and maybe form a response to it.

There are General Senses and Special Senses

General senses are distributed throughout the body and have receptor cells within structures of other organs. They and are associated with the various aspects of touch, activity and position of body parts. They also **lack special sense organs**. The general senses are **pain**, **temperature**, **touch**, **pressure**, **vibration**, and **proprioception**. Touch receptors are found throughout the body, but particularly in the skin. For example, mechanoreceptors are present not only in the skin, but also in muscles, the walls of blood vessels and in the lungs. Proprioception or kinesthesia refers to the body's ability to sense movement, action, and location how where the body is in space.

Special senses are **vision**, **audition** (sound), **equilibrioception** (balance or equilibrium), **olfaction** (smell) and **gustation** (taste). Special senses **have specialized organs** that detect and process stimuli. They transduce the energy and send signals to specific brain regions which lead to the perception of that sensation.

Special sense have elaborate and effective specialized sense organs and structures for processing information: The **eyes** process visual information; **ears** process auditory information; the **semi-circular canals** and **vestibular complex** process balance information; the **nasal cavity** process olfactory information; and the **tongue and mouth** process taste information

Various Classifications of Sensory Receptors

There are still valid debates about how many senses there, in some part due to a broad interpretation of the definition of a sense. There are also many ways to classify sensory receptors. For instance, they can be classified by the type of energy they detect (modality), where the origin of the stimulus comes from (outside or within the body), and if they are a general or a special sense.

There is no preferred way to categorize sensory receptors and there is much cross over in each category. For example, the receptors for the **olfaction** are classified as a type of ***chemoreceptor***, and also as an ***exteroceptor***, because its source is external to the body. Being aware of the important and commonly used systems of classification is useful because it enable us to fully describe all of the characteristics about the receptors involved and also some insight into the sense and how it triggered and perceived in the body. Show below are some basic details of three classifications systems for sensory receptors: **A)** by the **Modality**; **B)** by the **Origin** and **C)** whether it is **General** or **Special**.

Sensory Receptor Classifications

A) By **Modality** (type of stimulus energy to which each is most sensitive):

- **Mechanoreceptors** - stimulated by the physical deformation of the plasma membrane caused by touch, pressure, stretch, tension or vibration. Can also be called stretch receptors.

- **Thermoreceptors** - stimulated by changes in temperature (heat and cold).

- **Nociceptors** - pain receptors, stimulated by physical or chemical damage to tissue. Damage can result from trauma, ischemia (reduced blood flow) or excessive heat and chemicals.

- **Photoreceptors** - stimulated by light or changes in light intensity (in retina of the eyes).

- **Chemoreceptors** - stimulated by chemicals, including food, odors, and molecules in body fluids.

B) By **Origin** of their stimuli:

- **Exteroceptors** - detect changes **external** to the body, including surface receptors (e.g., for touch, temperature and cutaneous pain). They also include receptors for vision, hearing, taste and smell.

- **Interoceptors** or **Viscероceptors** - these detect stimuli that originate in the **internal** organs (viscera); they are responsible for feeling visceral pain, nausea, stretch and pressure.

- **Proprioceptors** - detect changes in the **position** of the body and movement of the body or its parts. They are located in muscles, tendons, joint capsules and the inner ear.

- **Surface pain** – this can be accurately located. Visceral pain is **referred pain**, which is typically poorly localized. For example, heart pain felt in the shoulder and arm, a tooth ache can be felt as a pain in the neck.

C) By **General** or **Special** categories:

- **General Senses** (somatic or somatosensory senses) have receptors that are widely distributed in the body rather than limited to specific locations. These receptors occur in the skin, muscles, tendons, joint capsules and viscera (internal organs). They detect touch, pressure, stretch, heat, cold and pain, as well as other stimuli that we are not consciously aware of, such as blood pressure and chemistry of body fluids. These receptors can be extremely sensitive, but they lack any complex special sense organs that define special sense receptors.

- **Special Senses** have receptors which are very complex and incorporate highly specialized sense organs. They are limited to the head and innervated by cranial nerves. There are 5 special senses: **1)** Vision, **2)** Hearing, **3)** Equilibrium (Balance), **4)** Olfaction (Smell), and **5)** Gustation (Taste).

Sense Organs - Sensory Receptors

A **sensory receptor** is a specialized ending of a sensory neuron that detects a specific stimulus that has a distinct form of energy. When sensory receptors are stimulated, they send sensations to the CNS. Receptors can range from simple nerve endings of a sensory neuron (e.g., pain, touch), to a complex combination of nervous, epithelial, connective and muscular tissue (e.g., the eyes).

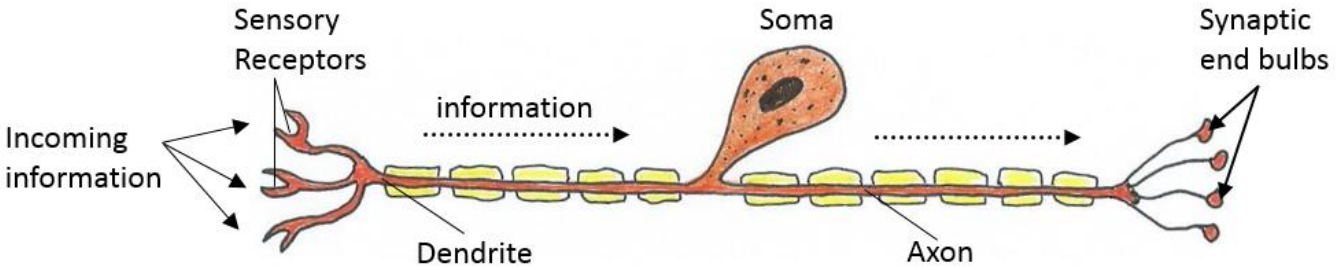


Figure 11.2 Above is a diagram of a sensory neuron with sensory information being detected by sensory receptors located at the incoming end of the neuron. These receptors transduce the energy detected from stimuli and convert it to an electrical signal (an action potential). This information travels along the axon and delvers its signal to the central nervous system via the synaptic end bulbs with the release of neurotransmitters.

Transduction from Sensation to Electrical Signal

The function of a sensory receptor is to act as a **transducer**. Transducers convert one form of **energy** into another. In the human body, sensory receptors convert **stimulus energy** into electrical impulses called **action potentials**. The frequency and duration of action potential firing gives meaning to the information coming in from a specific receptor.

The key element for the sensory system is the translation of a **sensory signal** to an **electrical signal**. This is what **transduction** is in the body – and it takes place at the sensory receptor level. Just think of some every day sensations like pushing a pin into a surface with the tip of your finger. With that example, we can assess that the sensation starts with the physical changes from the distention of the surface of the finger (see **Figure 11.3** below). On the cellular level, it is the detection of this mechanical deformation of the tissue that triggers a type of **mechanoreceptor** which is part of the specialized ending of a sensory neuron (= a sensory receptor!). Recall from the neurophysiology section there are three types of gated ion channels, and these neurons contain **mechanically gated ion channels**.

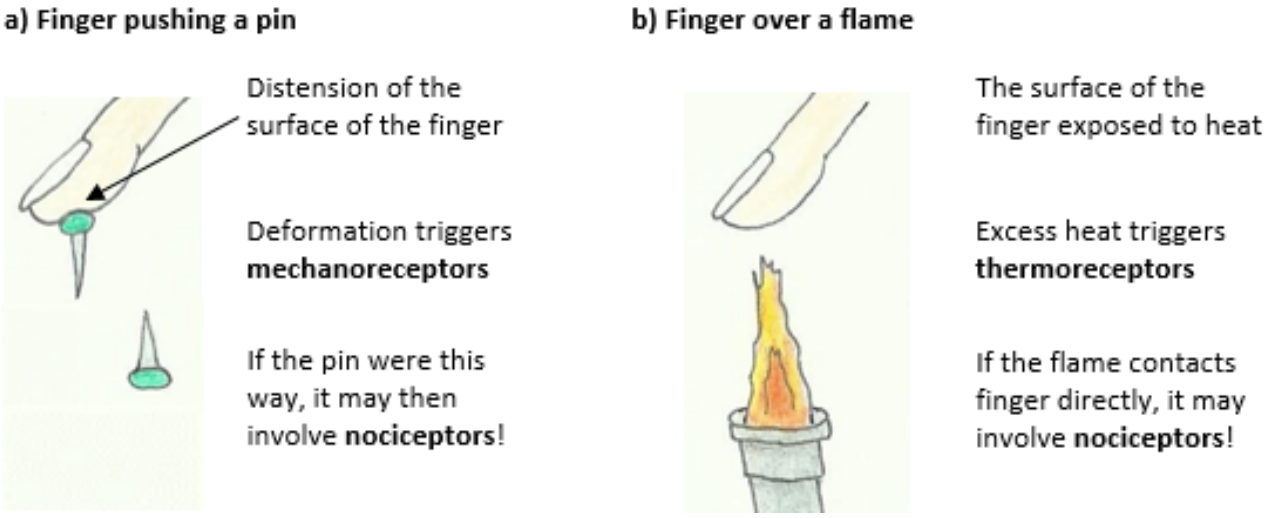


Figure 11.3 Shows **a)** the physical distention in a finger pushing a pin into a surface, the mechanoreceptors in the finger tissue detected this change. If the pin were the other way and pricked the finger causing tissue damage, chemical released would be detected by nociceptors which indicate pain. In **b)** the stimulus is now heat and thermoreceptors in the same finger detect this. Direct contact of the finger with the flame may cause tissue damage, and again, the chemical damages would be detected by nociceptors and indicate pain.

Receptor Potentials – to Signal CNS

Regardless of the specific sensory receptors, they all exhibit **receptor potentials**, these are **graded potentials.** As discussed in the neurophysiology section, the magnitude of a graded (receptor) potential will vary depending on the **strength of the stimulus**. On a macro level, the louder the horn honks the more likely you are to hear it. Same for the micro level of a receptor stimulus. The stronger the stimulus, the greater the strength of the intracellular signal this stimulus will send. If the magnitude of depolarization of the sensory neuron is sufficient, the membrane potential for that neuron will reach **threshold** and the neuron will fire an **action potential**. Neurons communicate in action potentials, therefore when the sensory neuron fires its action potential the duration and frequency of this signal will also play a role in interpreting the signal and conveying it.

The example below in **Figure 11.4** shows a mechanoreceptor for touch located in a fingertip. When there is a stimulus, something that causes physical distention of the surface of the finger, this is detected by **mechanoreceptors** that have **mechanically gated ion channels** on their membranes, when these ion channels open due to mechanical stress, ions enter and **depolarize the membrane**, sending a signal to the soma (cell body) of the sensory neuron. If the stimulus is sufficient, it will cause the sensory neuron to have an **action potential** and transmit the nature of this stimulus in the 'language' of actions potentials in order to convey information to the CNS where it can process it for perception.

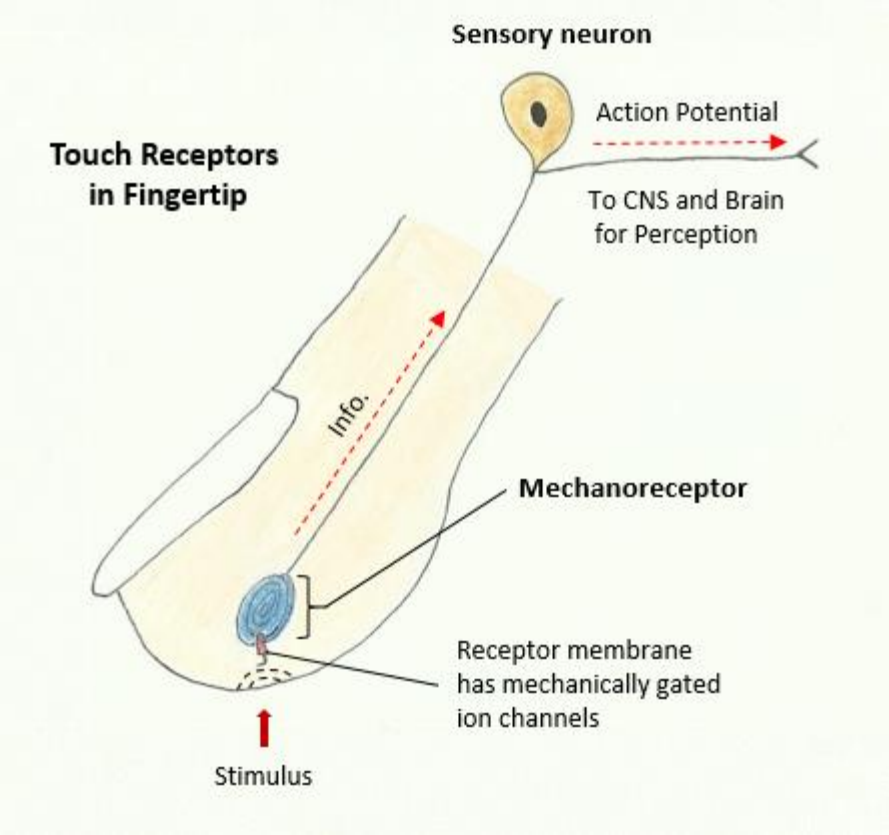
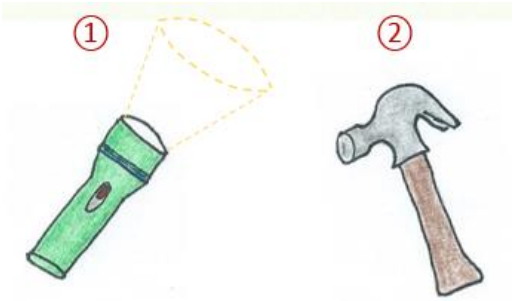


Figure 11.4 The mechanoreceptors in the fingertip are stimulated when the mechanically gated ion channels on the receptor membrane are triggered to open from the physical distention of the tissue. Since sensory receptors are specialized endings of sensory neurons, if the stimulus is strong enough (and the right modality) the sensory neuron will fire an action potential to relay the information to the central nervous system (brain or spinal cord).

The various senses operate somewhat differently from each other because they are specialized according to the **type of stimulus** they sense. This is a type of **receptor specificity**. As will become more and more clear, sound receptors, touch receptors, light receptors, taste receptors, etc., are all activated by different stimuli.

Receptors normally respond to only one type of stimuli, or sensory **modality** (see further discussion below), and that is referred to as the **adequate stimulus** for that receptor. Which of the two options to the right do you think would be the adequate stimulus for the mechanoreceptors in the fingertip in **Figure 11.4** above? Would light trigger the mechanically gated ion channels? Or would that hammer engaged in a mistimed swing be the adequate stimulus? Yes, it's the hammer!



Similarly, **light** receptors are not sensitive to **sound** or **touch**. The receptors for light are structured to be sensitive exclusively to light information. There are times however, when an **inadequate stimulus** may provoke a response. For example, if a person is unfortunate enough to be hit in the eye with a baseball they forgot to catch, it is possible for that person to "see stars" as a consequence of the stimulation of the **photoreceptors** with a mechanical stimulus. The photoreceptors prefer the **adequate stimulus** of **light energy**, but in this instance they attempt to convey this mechanical energy they received.

In addition, **various stimuli** can be integrated at higher levels in the brain for **enhanced perception**. A good example of this the additional taste discrimination that occurs with olfaction, which is the sense of smell. You may be surprised to learn that if you plug your nose and taste a fruit flavored food, it is most often not really possible to distinguish (without any other clues) the difference between a lemon or a lime, peach and mango, etc. Once the nose is unplugged and the vapor of the food can also be detected by the olfactory receptors on the roof of the nasal cavity, highly specific taste discrimination can be made. With the additional powers of olfaction working synergistically with taste buds of the tongue, people can detect a hint of strawberry, or a dash of ginger in a dish once the ability to detect fragrances is added to the mix.

We will now examine the various types of receptors for the array of stimuli we encounter. Then we will discuss how these send signals inward to the CNS, and how they are integrated for perception.

The Kinds of Information Transmitted by Sensory Receptors

Sensations, which are obtained by the physical stimulation of our sensory receptors, are relayed in our body constantly, because the ability to detect important information is critical to maintain balance. We have briefly discussed sensations like seeing and hearing a dog barking, pushing pins in with our finger, tasting a lemon or lime, but there are also many other sensations that are detected subconsciously, that is, that we are not consciously aware. For instance, the levels of glucose in our blood stream are meticulously regulated, yet most often we are not consciously aware of that. Same with blood pressure, balance, etc.

In the following section below, the way that sensory receptors transmit their information will be discussed. The details of important concepts such as what an adequate stimulus means, the threshold of a receptor, and the components of the signaling, like modality, location, intensity and duration are covered.

There are many ways to classify sensory receptors, but a general overview is shown here below:

- Chemoreceptors: Stimulated by changes in the chemical concentration of substances.
- Mechanoreceptors: Stimulated by changes in pressure, movement or distention of membrane.
- Nociceptors (Pain): Stimulated by tissue damage.
- Osmoreceptors: Stimulated by variations in osmolarity of body fluids.
- Photoreceptors: Stimulated by light energy.
- Thermoreceptors: Stimulated by changes in temperature.

Information about Receptor Transmission

An **adequate stimulus** is a particular form of energy to which a receptor is most responsive. For example, thermoreceptors are more sensitive to temperature than to pressure. Receptors can respond to most other forms of energy, if the intensity is high enough. The **threshold** of a receptor is the minimum stimulus required to activate that receptor.

Sensory receptors transmit **four** kinds of information - modality, location, intensity and duration.

1. Modality - describes the type of stimulus (or the sensation) that it produces. A stimulated receptor typically elicits the same perception in the brain. For example, impulses from the optic nerve arrive at the visual cortex and are interpreted as light. Thus, a blow to the eye (the *inadequate stimulus* of pressure) will be perceived as light even though no light has entered the eye.

2. Location - the location of a stimulus detection is s*ensory projection,* the ability of the brain to identify the site of the stimulation. The precision with which the location of a stimulus is perceived is called ***acuity***.

3. Intensity - refers to the strength of the signal that is detected by the receptors. If a stimulus intensity increases it can be encoded in three ways: **1)** increasing action potential rate **2)** recruitment of more nerve fibers; **3)** activating nerve fibers with higher thresholds.

4. Duration – describes the way that a nerve fiber changes its rate of action potential firing over time. Some receptors fire briefly when a stimulus begins and then become 'silent' and fire again briefly when the stimulus ends (e.g., corpuscles of touch). Other receptors fire more continually, but all sensory receptors exhibit some **adaptation**.

Adaptation occurs when the receptors continue to be stimulated over a long period of time and in response to this, the frequency of action potential firing declines. Adapting to the hot water of a shower is an example of sensory receptor adaptation. In terms of adaptation, there are **phasic receptors** and **tonic receptors** (see receptor potential graphs in **Figure 11.6**).

- **Phasic receptors** generate a burst of action potentials when first stimulated; then they quickly adapt and stop transmitting impulses even if the stimulus continues. Receptors for touch and smell are examples of phasic receptors.

- **Tonic receptors** are slow to adapt and generate nerve impulses continually. Proprioceptors (for balance) and baroreceptors (for blood pressure) are examples of tonic receptors.

Somatosensory Receptor Classification

The Somatosensory System is the part of the sensory system concerned with the conscious perception of touch, pressure, pain, temperature, position, movement, and vibration, which arise from the muscles, joints, skin, and fascia. A somatosensory pathway will typically consist of three neurons: primary, secondary, and tertiary. In the periphery, the primary neuron is the **sensory receptor** that detects sensory stimuli, like touch or temperature. As shown in **Table 11.1** below, there are several ways to classify the various somatosensory receptors in the body.

Table 11.1 Shows a summary of somatosensory receptors that are in the skin and mostly concerned with temperature, touch and pain. They can be classified by modality, type, adaptation and receptor field size.

Sensory Modality	General Type of Receptor	Specific Receptor Name	Adaptation	Receptor Field Size
Touch	Mechanoreceptor	Meissner's Corpuscles	Rapid	Small
Bending of hair	Mechanoreceptor	Hair follicle Receptor	Rapid	Small
Pressure	Mechanoreceptor	Pacinian Corpuscles	Rapid	Large
Skin stretch	Mechanoreceptor	Ruffini's End Organ	Slow	Large
Light touch	Mechanoreceptor	Merkel's Disk	Slow	Small
Tickle and Itch	Mechanoreceptor	Free Nerve Endings	Slow	Small
Heat	Thermoreceptor	Free Nerve Endings	Rapid	Small
Cold	Thermoreceptor	Krause's End Bulbs	Rapid	Small
Polymodal Pain	Mechanical Thermoreceptor Chemoreceptor	Free Nerve Endings	Slow	Large
Thermal Pain	Thermoreceptor	Free Nerve Endings	Rapid	Small

Somesthetic Sensations means the same things as somatosensory, which are the senses associated with the **surface of the body** that are detected by the **somatosensory receptors** listed in **Table 11.1** above. Let's review the various somatosensory receptors

Mechanoreceptors detect pressure, force and vibration. These include:

- **Meissner's Corpuscles** - this is a type of nerve ending in the skin that is responsible for sensitivity to light touch and low-frequency vibration. They are very superficial in the dermis.
- **Hair Follicle Receptor** - bending the hair distorts the receptor ending that is wrapped around the hair follicle, this generates a receptor potential. These are rapidly adapting and are more sensitive to something brushing across the skin rather than pressure.
- **Pacinian Corpuscles** – are large encapsulated onion-shaped receptors located deep in the dermis. They detect transient pressure and high-frequency vibration.
- **Ruffini's End Organ** - is a slowly adapting mechanoreceptor located in glabrous (hairless) and hairy skin, between the dermal papillae and the hypodermis. This spindle-shaped receptor is sensitive to skin stretch, contributing control of finger position and movement. It can also act as thermoreceptors.
- **Merkel's Disk** - are slow-adapting, un-encapsulated nerve endings that respond to light touch, highly abundant in fingertips, extending up into the epidermis of skin with hair and glabrous skin.

- **Free Nerve Endings** - are the most common nerve endings in skin, and these fibers are stimulated by both mechanical and heat stimulation thus are sensitive to hot and cold, and to light touch.

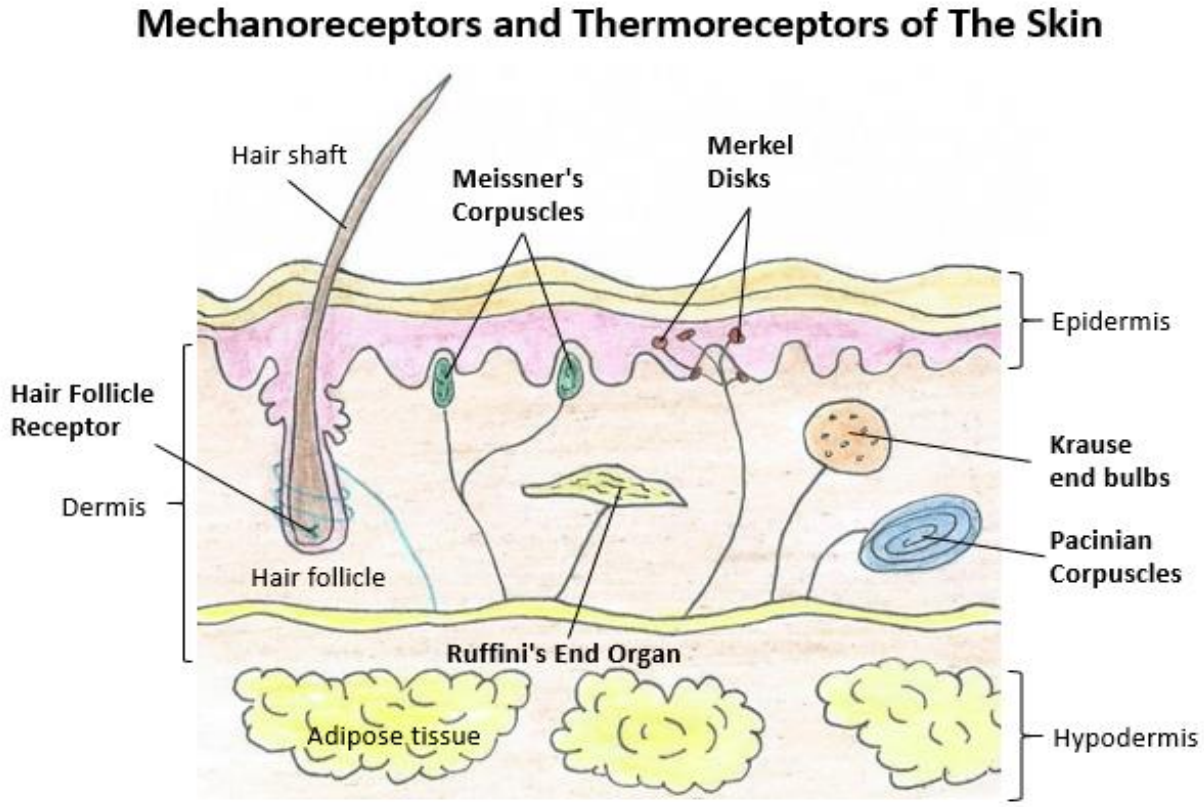


Figure 11.5 The skin has numerous mechanoreceptors and thermoreceptors dispersed around all aspects of it. Shown here are the major receptors including Meissner's and Pacinian corpuscles, hair follicle receptors, Ruffini's end organ, Merkel disks and Krause end bulbs. Free Nerve Endings (not shown) are also widespread for pain, itch and tickle sensations.

Thermoreceptors: These respond to the temperature of receptor endings themselves.

- **Warm receptors** are continuously active at constant temperatures above neutral skin temperature, around 85° F and have a maximum response around 106°F to 115°F (41°C to 46 °C), increasing action potentials as the temperature increases.

- **Cold receptors** respond to temperatures between 41° F and 70° F (5°C to 20°C) with increasing action potentials as the temperature falls. These cold receptors respond to decreases in skin temperature over a range of, and discharge most vigorously at skin temperatures around 25°C.

- **Krause end bulbs** are encapsulated oval bodies found in the conjunctiva of the eye, in the mucous membrane of the lips and tongue, in the epineurium of nerve trunks and in skin.

Both warm and cold receptors respond rapidly to temperature changes and show **rapid adaptation**. The brain uses the relative changes in the responses of hot and cold receptors to interpret the temperature of the environment.

Nociceptors: These transduce potentially harmful stimuli that we perceive as pain. These consist of free nerve endings. There are three types of nociceptors:

- **Mechanical** - respond to intense mechanical stimuli.
- **Thermal** - respond to intense heat.
- **Polymodal** – these are dynamic and respond to a wide range of noxious and non-noxious cutaneous and/or visceral stimuli. They are nociceptive neurons that respond to a variety of noxious stimuli including mechanical, intense heat (thermal) and chemicals released from damaged tissue.

Proprioceptors: These are receptors that give information about body position. These receptors are located in muscles, tendons, ligaments, joints and skin. They provide body-sense sensations.

Receptor Adaptation

Receptor adaptation is the decline of the electric responses, or the **receptor potential**, of a receptor (neuron) over time, with continued presence of an appropriated stimulus of constant strength. The change in firing response is apparent as a gradual decrease in the frequency of spikes generated within the receptor neuron.

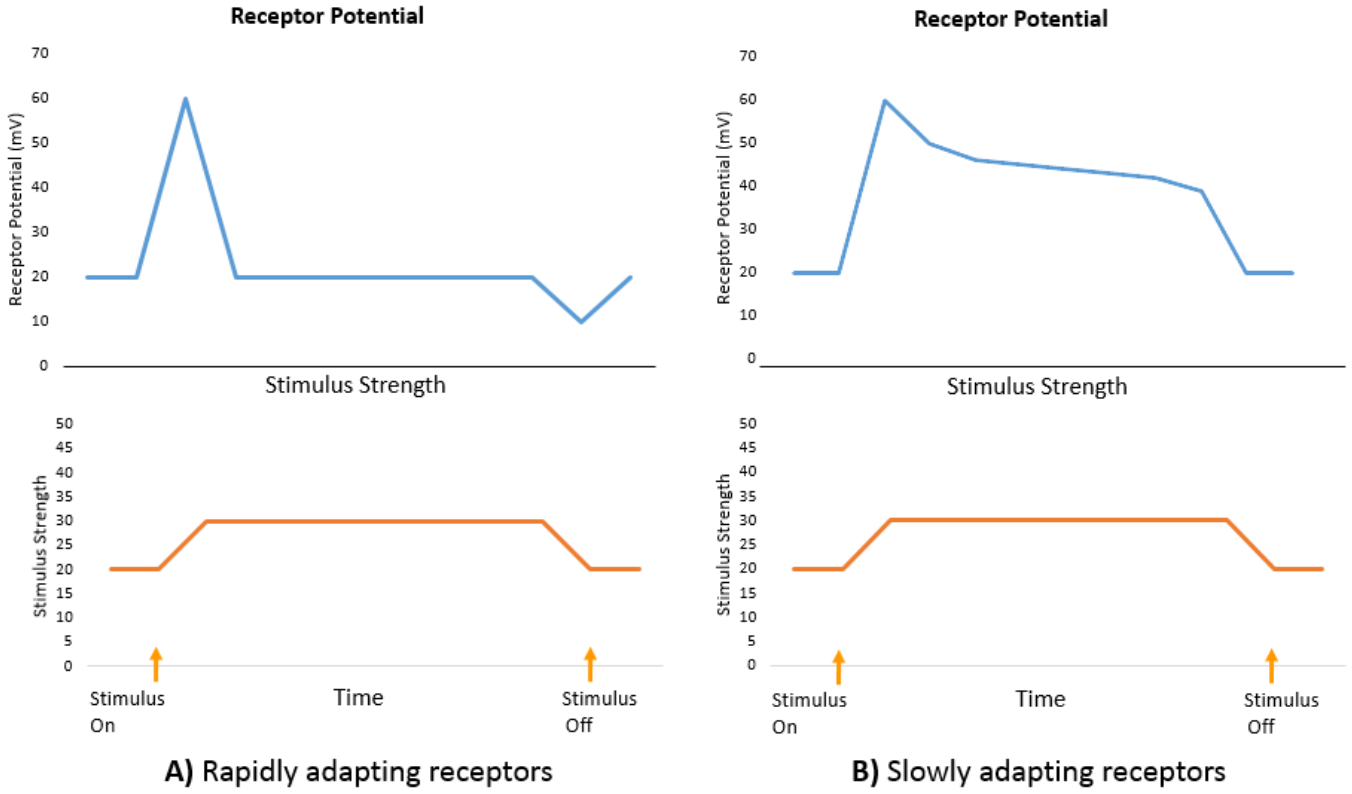


Figure 11.6 Show above are recordings of receptor responses (receptor potential) to a constant stimulus. The **A)** rapidly adapting or phasic receptors adapt quickly to this stimulus. Notice the stimulation is constant but soon after the initial spike in firing receptor potentials, it quickly returns to the baseline value prior to stimulation. There is a transient dip in firing when the signal stops, as this cessation is detected. The **B)** slowly adapting or tonic receptors show little adaptation in response to the prolonged stimulus. There is a slight drop off after the initiation of the stimulus, but the receptor potential is continuously firing throughout the stimulation.

The concept of adaptation is similar to a receptor being able to ignore something that remains present. Some receptors can ignore constant signals very quickly, they are termed **rapidly adapting** (or **phasic**) receptors, while other receptors never really stop paying attention to the stimulus; these are called **slowly adapting** (or **tonic**) receptors.

Rapidly adapting (phasic) receptors adapt quickly (ph = F, for ***fast***!). These receptors are designed to detect changes in stimuli *intensity* (rather than *duration*). If the stimulus intensity suddenly changed, they would begin to fire again.

Slowly adapting (tonic) receptors display little adaptation in response to prolonged stimulus. These types of receptors are important for monitoring parameters that should not be ignored in the body, like blood pressure and proprioceptors used to maintain balance. These receptors are for coding the intensity of a stimulus for its entire duration.

Receptor Experiment: Take a Cold Shower

A good example of **phasic** (fast) adapting receptors in action can be experienced if you take a cold shower! When you turn on the cold water it will feel very **COLD**… especially at first. But hang in there. After a relatively short time, about 10 to 20 seconds (but you need to be in that shower, OK, not at the sides of it), your thermoreceptors begin to adapt to that stimulus even if it remains the same (still cold) temperature. Therefore, as you continue on in your cold shower, it will still be cold, but it will not really feel *that* cold anymore, as you adapt to it.

Of course the experiment could also test the adaptation to the hot water of a shower – but the health benefits are not near as useful as the cold water! Consulting **Table 11.1**, there are several touch receptors that are rapidly adapting. Think of putting a moderately heavy backpack on and walking around for an hour. Soon, if it's not too heavy, the mechanoreceptors will ignore this constant pressure and you may forget you have it on. This is confirmed when you go into a store and turn around, knocking over a display because you forgot about the bulky backpack physically attached to you. The physical presence of clothes, and other things that are worn are also adapted to quickly.

Somatosensory Cortex

The sensations from the body, **somatosensory** sensations, regardless of location in the body, will all go to the somatosensory cortex of the **parietal lobe** of the brain, specifically the post-central gyrus. Like the primary motor cortex of the precentral gyrus, primary somatosensory cortex of the postcentral gyrus is arranged as a **homunculus**, (see **Figure 11.7**), showing the body regions represented disproportionately in terms of size, however, the area occupied in the brain is indicative of the complexity of sensory sensations detected by that region of the body

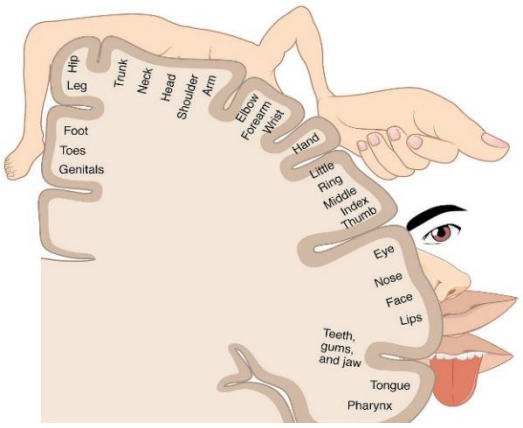


Figure 11.7. The homunculus within the primary somatosensory cortex located on the precentral gyrus. This is the region of the brain related to somatic (body) perceptions.

The route that all sensory information takes from the body to the brain, goes via the **thalamus**, and is then relayed from the thalamus to the cerebral cortex. The only exception to this rule is the sense of **olfaction** (smell) which travels via the hypothalamus and limbic system.

Sensory Units

As described and listed in **Table 11.1**, there are different types of somatosensory receptors and they can be classified in a number of different ways. Whatever the classification, and be they mechanoreceptors, thermoreceptors, nociceptors, chemoreceptors or photoreceptors, etc., they operate as integrated units.

With regard to sensory receptors there are a variety of ways that sense can be detected, but often regardless of the sensation, they the sensory neurons are a part of a sensory unit. A **sensory unit** is defined as a single nerve axon and all the sensory receptors which transmit information to it (see **Figure 11.8** below).

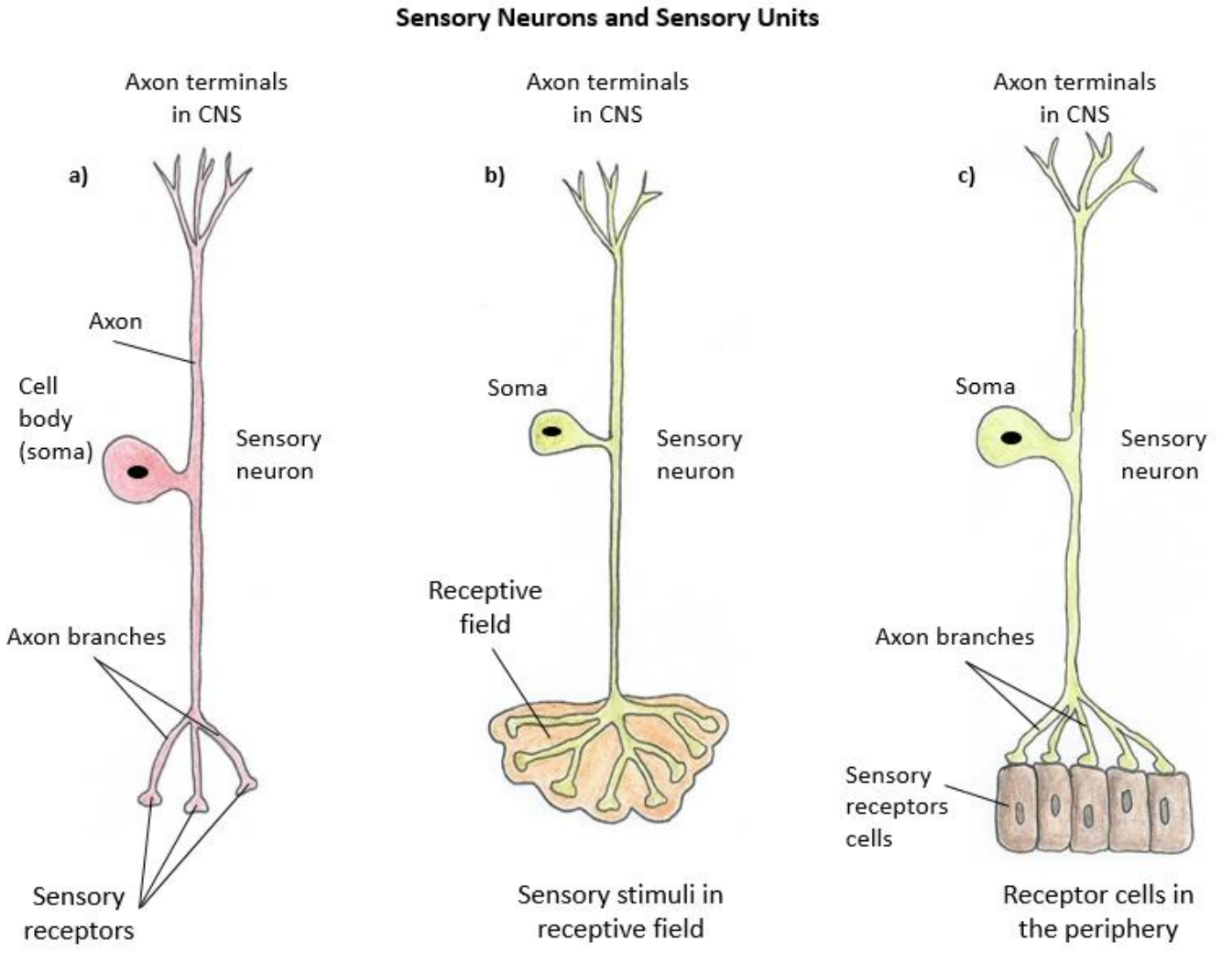


Figure 11.8 In transmitting information from the periphery to the central nervous system, sensory neurons function as an integral part of sensory units. In **a)** the endings of the sensory neuron are receptors specialized for detecting specific types of energy. In **b)** the sensory neuron establishes a receptive field to which the nerve endings are sensitive within. And in **c)** the actual receptors in the periphery may be highly specialized receptor cells that are integrated with the axon branches of a sensory neuron.

Receptive Fields

In terms of detection of sensations in the periphery, **receptive fields** play an important role in sensation and perception. A receptive field is a **region** in the periphery within which stimuli can influence the sensory cell's electrical activity. Therefore, it is directly related to the **sensitivity of an area**.

Receptive fields are found all over the body, including regions of skin on the body's surface, in muscles, joints, in internal organs, in the hair cells of the cochlea, on the retina of the eye, and on the tongue. The size of the receptive fields' correlates to sensory sensitivity of the area, and the variations in the sensitivity of skin is a good example to show this.

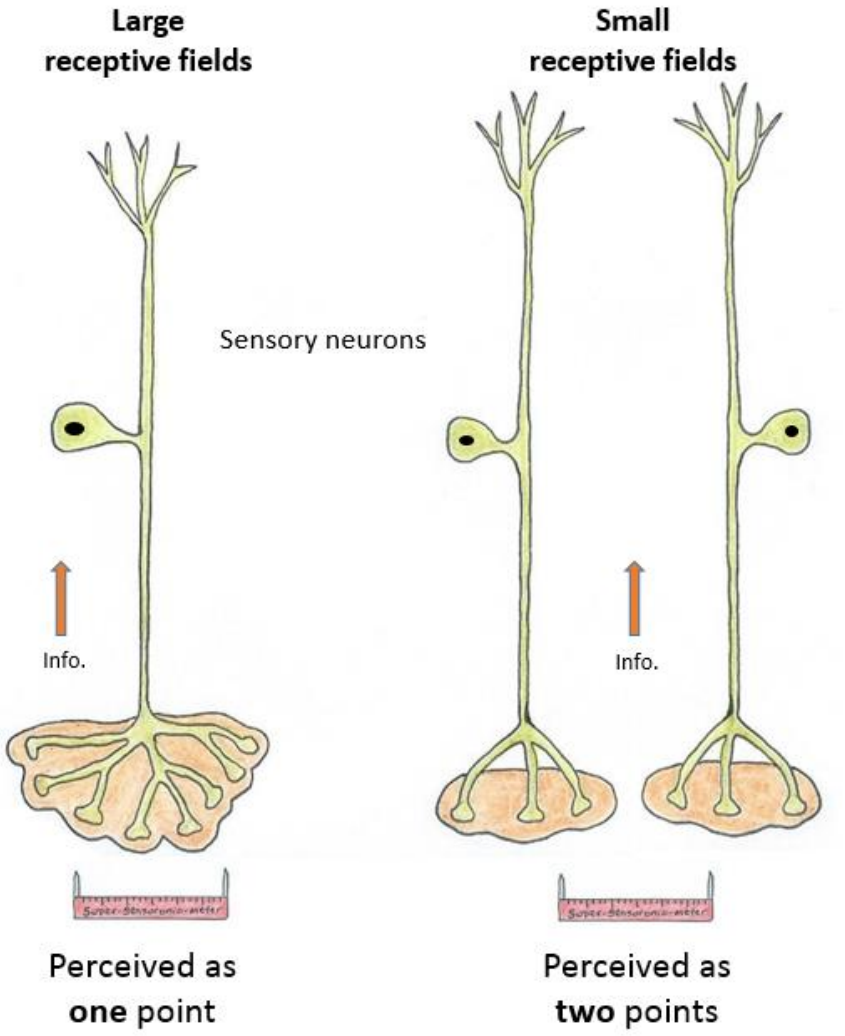
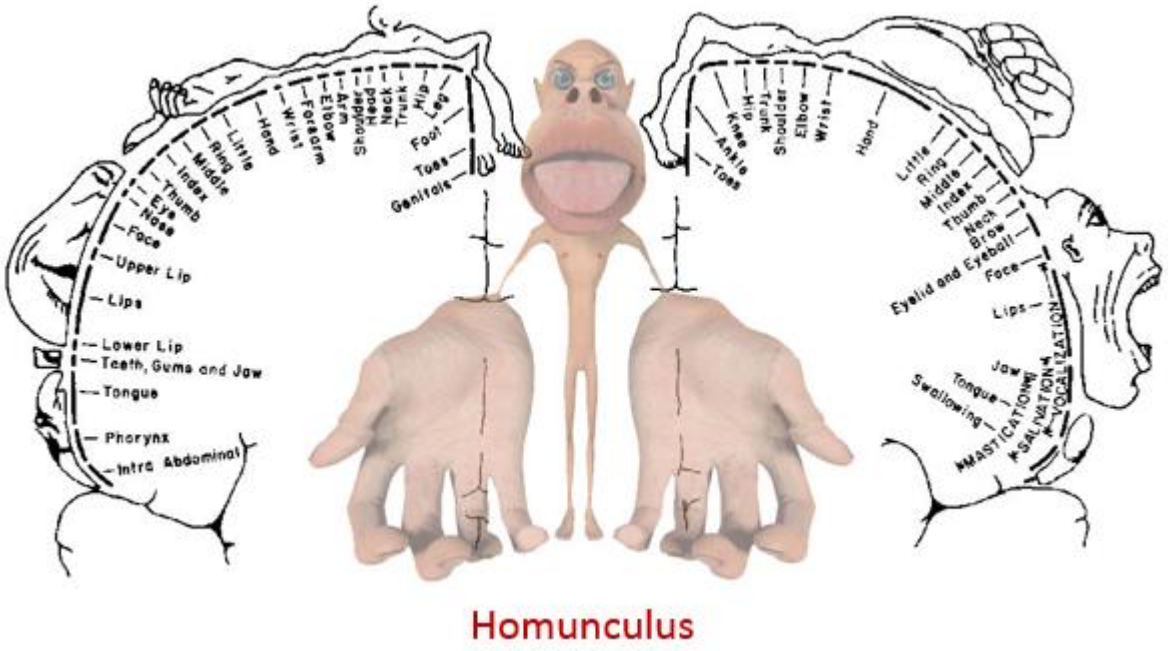


Figure 11.9 The spatial resolution to light-touch stimulation can be evaluated by measuring an area using a two-point discrimination threshold, and the calipers seen at the bottom are set at the same distance for each example. On the left is a sensory neuron with a large receptive field, and the two points of the calipers cannot be distinguished as separate. On the right, the receptive fields of adjacent sensory neurons are smaller and the two points of the calipers are distinguished as two separate points. Thus the smaller the receptive fields, the greater the sensitivity.

In the human body sensations felt via the skin are very important. In terms of touch sensitivity for skin and **receptive fields**, not surprisingly it is the fingertips that have very small receptive fields which provides **a very high spatial resolution** (see **Figure 11.9** above). Comparatively, it is actually the torso or trunk of the body that is the least sensitive area of the body, this region has the largest receptive fields and thus the **lowest spatial resolution**. The reason why **fingertips** have such small receptive fields is because this allows for finer spatial resolution in locating and identifying objects with our fingers. The smaller receptive fields in these regions are a result of a higher density of receptors in the skin. Each fingertip has more than **3,000** touch receptors, mostly responsive to pressure. Can you guess which of your fingers is the most

sensitive? It is the **index finger** (pointer finger, forefinger), think about how you use it for fine discernment more than the other fingers.

If you think the finger tips are super sensitive, it turns out the most sensitive skin on the body is on the **lips** of the face. They are about **100 times** more sensitive than fingertips, with over **one million** different nerve endings. Recall the homunculus from the primary somatosensory cortex below… notice how the lips, tongue and fingertips are the most exaggerated in terms of size, indicating the much greater sensitivity of these regions and the extensive cortical brain area that is dedicated to the perception from these areas of the body.



Homunculus

Figure 11.10 Shown above is the homunculus (meaning 'little man') that is a representation of a small human being within the brain areas. This is commonly used in anatomy and physiology to describe the relationship between the body regions and the space occupied by that body region on the primary somatosensory cortex (postcentral gyrus of parietal lobe) on the left, and on the primary motor cortex (precentral gyrus of frontal lobe) on the right.

Pathways to Sensory Perception

The sensory neurons are the *first-order* of the afferent pathway to the brain for perception of senses. As seen above, the sensory neuron works as a sensory unit to collect stimuli received by receptors across the body. There are essentially three orders of neurons as the sensory information is transmitted to the brain.

- **The first-order neurons** radiate out into the periphery, bit the soma or nerve cell body is located in the **dorsal root ganglia**. This sends afferent fibers through the two dorsal columns, the gracile tract (fasciculus) and the cuneate tract (fasciculus).

- **The second-order neurons** send their axons from the spinal cord or brainstem to the **thalamus**. The nerve cell bodies of second-order neurons are usually located in the spinal cord or brainstem.

- **The third-order neurons** carry signals from the thalamus to the primary **sensory cortex**. These are usually located in **relay nuclei** of the thalamus. Numerous second-order neurons synapse on a single third-order neuron. The relay nuclei process the information they receive via local interneurons, which may be excitatory or inhibitory.

- **The fourth-order neurons** are within the cerebral cortices for the sensory information being processed. For example, for the touch pathway, the fourth-order neurons are in the primary somatosensory cortex, located of the postcentral gyrus of the parietal lobe. For the visual pathway, they are located in primary visual cortex of the occipital lobe, etc.

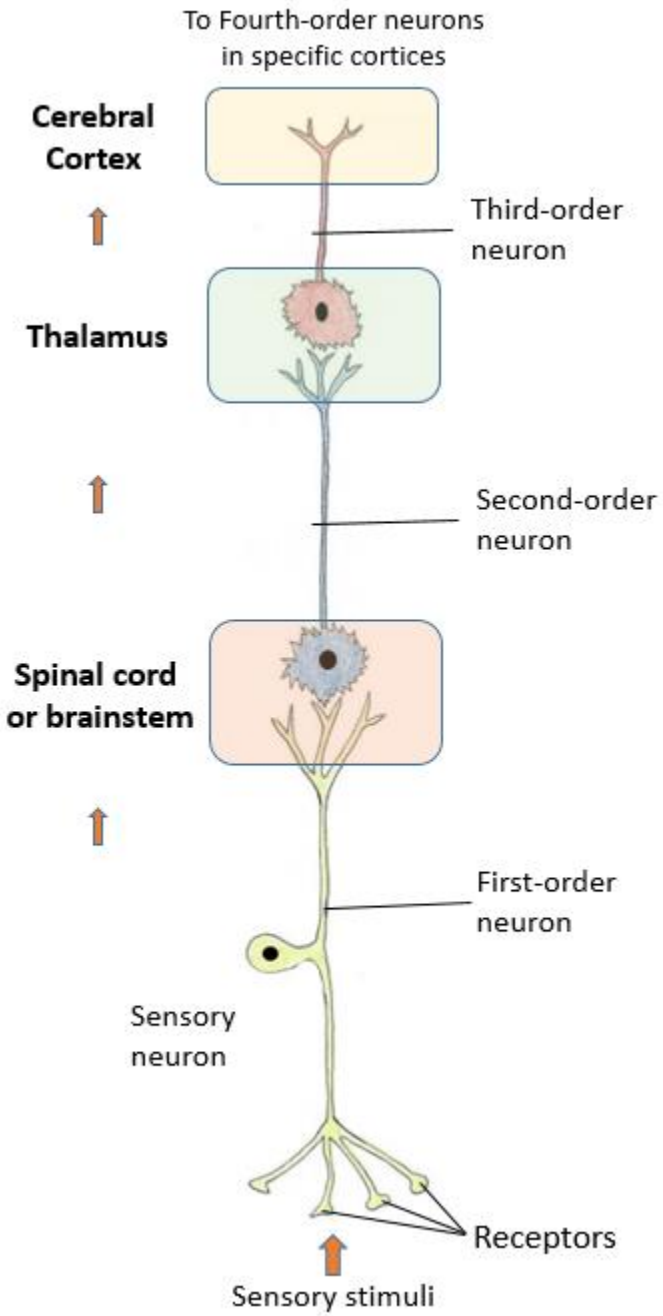


Figure 11.11 The pathway to perception is shown with the sequence of first, second and third-order neurons as they deliver sensory information to specific regions of the cerebral cortex, depending on the type of sensory information processed. Within the cerebral cortices, fourth-order neurons interact with association areas to integrate context and meaning of the information.

Perception is the interpretation of a sensation, which integrates context, relevance and meaning. Perception requires activation of sensory receptors, however, it is the **higher levels of the brain**, in particular the **cerebral cortex** that perceptions are formed. Within the brain, various sensory stimuli are distinguished, and they may be amplified or toned down. Recall that all sensory input are routed through the **thalamus** on their way to the appropriate region of the cortex, with the exception of olfaction (sense of smell). As sensory information leaves the thalamus, it is directed to the specific area of the cortex that is dedicated to processing that particular sense.

There is much consistency in how individuals interpret sensory information, for example if we think of the color '**sky blue**', most have similar renderings of what that color is. Or the sound of a trumpet compared to a violin. The taste of a green apple compared to a mango. There are variations between individuals in terms of interpretations of perception, because placing meaning to the information is based on experience, relevance and familiarity, in order to make sense of what you are seeing, hearing, tasting etc. Another example is cultural differences; for instance what is the reference point to the taste that is 'spicy' and what is not? It will be impacted by the style of foods in various cultures. Other individual differences may arise as a result of different tolerances, for example to pain, or tickling. The sensitivity of the receptors will have a role in this aspect of perception.

Specifics of Incoming Sensory Pathways

Due to **decussation** (crossing over) of nerve fibers, all sensations detected and incoming from the left side of the body go to the thalamus and cerebral cortex on the right side, and vice versa, in that the hemispheres of the brain receive and send signals to the opposite sides of the body.

The 2 main somatosensory pathways are: **1)** the dorsal **column-medial lemniscal** pathway, and **2)** the **spinothalamic** tract.

1) Dorsal Column-Medial Lemniscal Pathway. This pathway handles information from **mechanoreceptors** and **proprioceptors**. The first-order peripheral neurons enter the spinal cord at the **dorsal root**. Then the main axons **ascend** the spinal cord on the same side (ipsilateral) in the dorsal column, ending in the dorsal column nuclei of the **medulla oblongata**, where they synapse with second-order neurons. These neurons cross over to the opposite (contralateral) side of the medulla in the **medial lemniscus** which is formed by the crossings of the internal arcuate fibers, and ascend into the **thalamus**. Finally the third order neurons transmit information from the thalamus to the **somatosensory cortex**.

2. Spinothalamic Tract. This is responsible for transmission of information from **thermoreceptors** and **nociceptors**. The first-order peripheral neurons enter the spinal cord through the **dorsal root** and may **ascend** or **descend** along Lissauer's tract (about a few spinal segments) then synapsing with second-order neurons in the **dorsal horn**. The second-order neurons cross to the contralateral (opposite) side of spinal cord and ascend in the anterolateral quadrant of the spinal cord through the brainstem to the **thalamus**. Again, the third-order neurons in the thalamus ascend to the **somatosensory cortex** (see **Figure 11.11** above).

Pain Perception

Signals that involve pain, although often unpleasant, are very important warning signs, signals that enable us to avoid stimuli or actions that are damaging. Also, pain perception can prevent further damage to tissue that has already been injured.

The Pain Response

The stimulation of nociceptors triggers the pain perception pathway and causes the perception of pain. Nociceptor stimulation also causes autonomic nervous system (ANS) responses, prompts feelings of fear and anxiety, and also activates withdrawal reflexes.

Two Types of Pain Transmission

a) Fast pain: This is perceived as an easily localized, sharp, pricking sensation and is transmitted by the A delta (**Aδ**) fibers (12 to 30 m/sec).

b) Slow pain: This is perceived as a poorly localized, dull, aching sensation and is transmitted by **C** fibers (0.2 to 1.3 m/sec).

There are **different axon diameters** in the human body (see neurophysiology chapter), with the Aα fibers being the largest diametrically, and the Aβ and Aδ being smaller (in touch, pressure and cold thermoreceptors). Finally C axons are the smallest (in nociceptors and warmth receptors), with the slowest signaling. As seen in the neurotransmitter chapter, **substance P** is released for communication in first and second order neurons, as it involves the transmission of pain perception. The information that travels along the spinothalamic tract provides information about the location and type of pain. Pain afferents also ascend along pathways that influence the behavioral and emotional aspects of pain.

The Visceral Senses

Visceral senses are the perception of the presence of the **internal organs** (viscera) in the body. These internal organs are predominantly located in the chest, such as the heart and lungs, as well as the abdomen, such as the liver, pancreas, stomach, intestines, kidneys or bladder. The **conscious sensations** arising from the viscera can include an organ filling (like the stomach or bladder), a sensation of bloating and distension, dyspnea (difficulty breathing), and nausea from various regions in the gastrointestinal tract.

Table 11.2 Shows a summary of visceral receptors within organs. These sensory receptors can be classified by modality, type of receptor, and specific receptors.

Classification	Sensory Modality	General Type of Receptor	Specific Name of Receptor
Visceral Senses	Blood Pressure	Mechanoreceptor	Aortic Arch, Carotid Sinus
	Blood Chemistry	Chemoreceptor	Aortic and Carotid Bodies
	Plasma Oncotic Pressure	Chemoreceptor	Osmoreceptors
	Plasma Temperature	Thermoreceptor	(Hypothalamus)
	Pain	Nociceptor	Hypothalamus
		(Chemoreceptor)	Free Nerve Endings

In addition to these sensations listed in **Table 11.2** above, there are also or reflex sensations and sensations of pain in these organs, which may be indicative of damage or injury. Generally speaking, visceral receptors are often free nerve endings in the various organs.

Visceral Pain and Referred Pain

Generally, stimulation of nociceptors in the viscera produces a pain called **referred pain**. It is called referred pain because it is ***referred to a body surface***. Referred pain is due to second order neurons receiving input from both somatic and visceral afferents. The impulses coming from the second-order neurons is interpreted by the somatosensory cortex as coming from the somatic afferents.

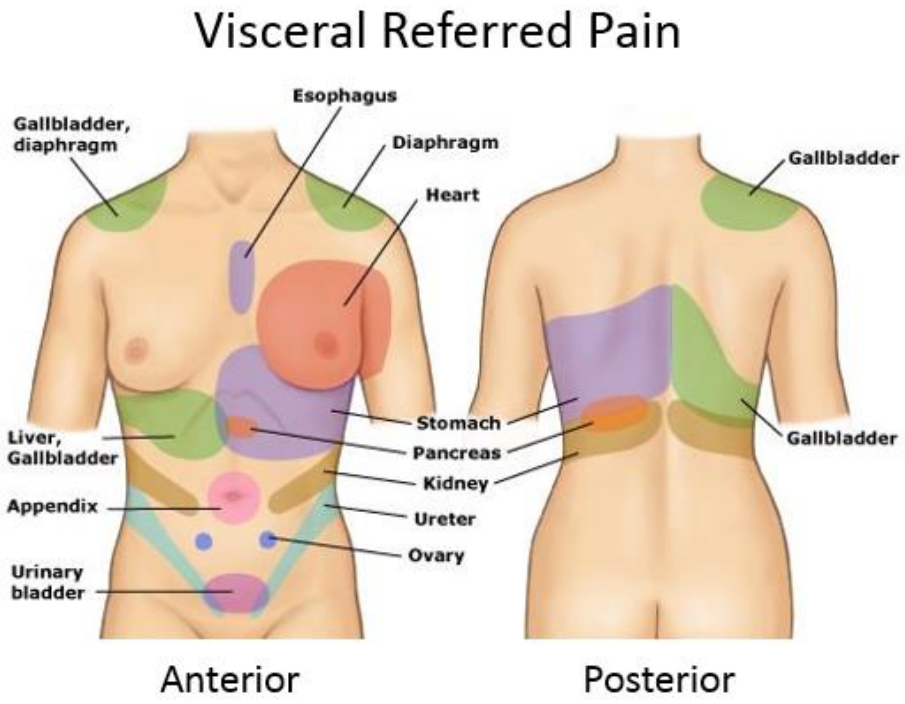


Figure 11.12 Referred pain is when the pain felt in one part of the body that is actually caused by pain or injury in another part of the body. For example, an injured gallbladder could cause shoulder pain, or a heart attack triggers pain in the left arm.

Special Senses

Humans have five special senses: vision, hearing, equilibrium (balance and body position), olfaction (smell) and gustation (taste). Special senses have **specialized sense organs** that are complex in their structure and function in order to gather the various forms of sensory information and change or transduce it into nerve impulses. Just as for the general sense, the receptors for the special senses capture the sensation and send it to the brain for processing and perception of the sensation. **Table 11.3** below gives an overview of the five special sense, their general type of receptor and their specific name.

Table 11.3. Shows a summary of special receptors. These sensory receptors can be classified by modality, type of receptor, adaptation and receptor field size.

Classification	Sensory Modality	General Type of Receptor	Specific Name of Receptor
Special Senses	Low intensity of Light	Photoreceptor	Rods (Black and White)
	High intensity of Light	Photoreceptor	Cones (Color)
	Sound	Mechanoreceptor	Inner Ear (Hair Cells)
	Equilibrium	Chemoreceptor	Inner Ear (Vestibular)
	Smell (olfaction)	Chemoreceptor	Nasal Mucosa (Vomeronasal Organ)
	Taste (gustation)	Chemoreceptor	Taste Buds (Papillae of Tongue)

Summary of the 5 Senses

Vision is the special sense of sight based on the transduction of light stimuli received through the eyes. The eyes are located within either orbit in the skull. The eyelids, with lashes at their leading edges, help to protect the eye from abrasions by blocking particles that may land on the surface of the eye.

Hearing is a mechanical sense. It turns physical movement into the electrical signals, translating these vibrations into what we experience as the world of sound. The diversity of sounds we can hear typically ranges from 20Hz (cycles/second) to 20,000Hz.

Balance, equilibrium or equilibrioception, is the perception of balance and spatial orientation. The vestibular system (inside the inner ear) is made up of three semicircular canals and two otolith organs, the utricle and the saccule, that perceive body motion and orientation. These perceptions contribute to your sense of equilibrium (state of physical balance) and helps prevent us from falling over when standing or moving.

Olfaction is the sensation of smell that results from the detection of odorous substances aerosolized in the environment.

Gustation is the sense of taste, produced or stimulated when a substance in the mouth reacts with chemoreceptors on taste buds in the oral cavity, mostly on the tongue.

The Eyes and Vision

The two **eyes** are is encompassed the bony orbits of the skull and further protected pads of fat cushions. **Vision** is the special sense of sight based on the transduction of light stimuli received through the eyes.

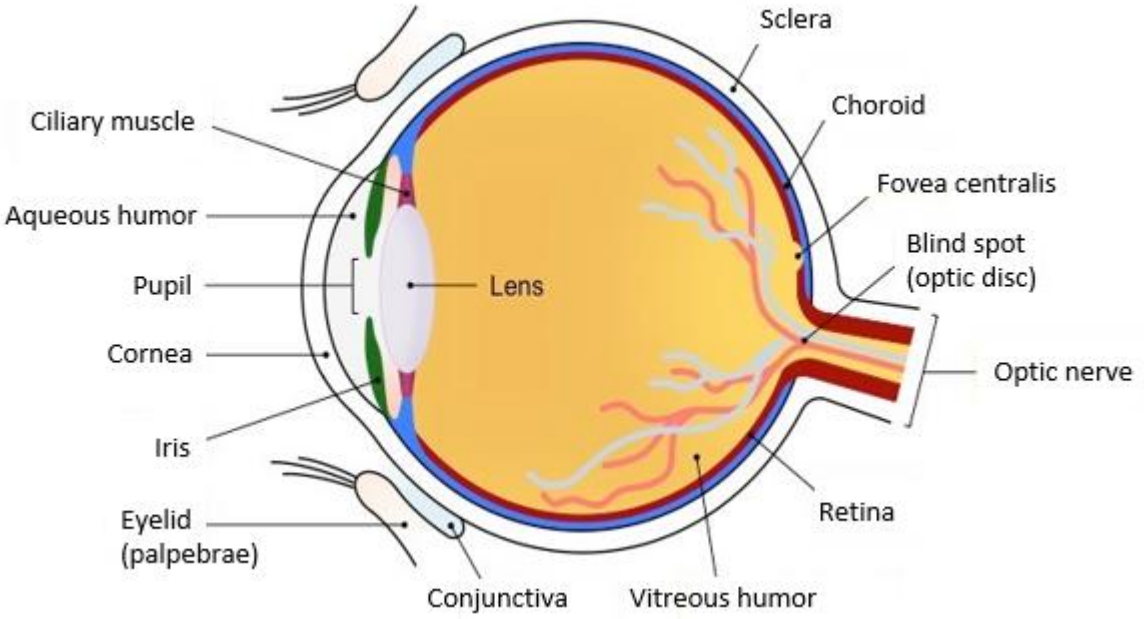


Figure 11.13 The eye is the organ of sight and shown above are a number of the important components of the eyeball. This include the cornea, iris, pupil, ciliary muscle, conjunctiva, lens, sclera, choroid, retina, fovea, optic disc (blind spot), optic nerve, vitreous and aqueous humor.

Structure of the Eyeball

The eyeball has three layers, or tunics.

1) The outermost **fibrous tunic** consists of the sclera and cornea. Sclera means hard and is a tough protective structure, it is the "whites" of the eye. The cornea is the clear front window of the eye that allows light to enter and focuses the light into the eye.

2) The middle **vascular tunic** contains the choroid, the ciliary body with the ciliary muscle, and the iris. The choroid is the vascular supply to the eye and provides nutrients prevents the scattering light within the eye. The ciliary muscles of the ciliary body control lens shape; the iris is the colored part of the eye it controls the size of the hole in the middle of it called the pupil. Changes in the diameter of the pupil control the amount of light that is let into the eye.

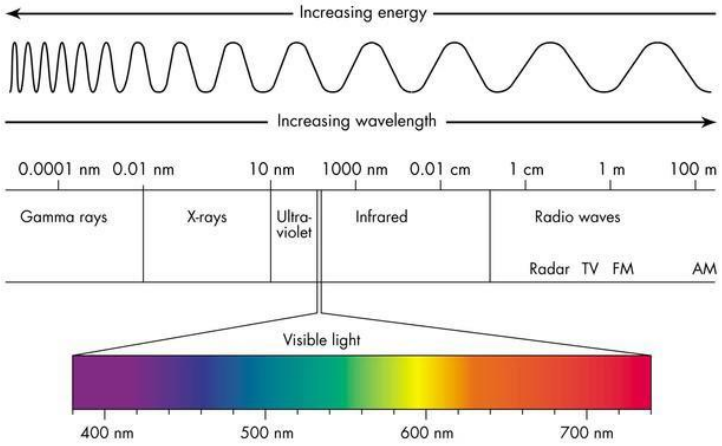
3) The **neural tunic** is the retina, and this consists of an outer pigmented layer and an inner nervous layer. The neural layer contains **photoreceptors** (rods and cones), **bipolar cells**, and g**anglion cells**. Ganglion cell axons form the optic nerve, which exits via the optic disc ("blind spot"). The outer segments of the photoreceptors contain the light-absorbing pigment in membrane-bounded discs.

The portion of the eye behind the lens is called the **posterior cavity**, and contains **vitreous humor** which is a gel-like fluid, similar to, and named after a grape, that is located between the **retina** and the **lens** it gives the eyeball its shape and helps support the eye structures and keep the retina in place.

The portion of the eye in front of the lens is called the **anterior cavity**, it is filled with **aqueous humor**, a filtrate from ocular capillaries in the ciliary body, which flows through the **anterior chamber** to the **posterior chamber** (not cavities!) and is drained into the **scleral venous sinus**, or the **canal of Schlemm**. Aqueous humor is a major factor in maintaining **intraocular pressure**. The biconvex **lens** is suspended within the eye by the suspensory ligaments attached to the ciliary body, enabling it's thickness to be changed and therefore adjusting the refractory structure (light focusing ability) of the eye.

The Physiology of Vision

The visible light we see is made up of wavelengths of the electromagnetic spectrum that excite the photoreceptors. The ray of light is refracted (bent) when passing from one transparent medium to another of different density, or when it strikes a curved surface. This is an important aspect of how the eye handles light. A concave lens disperses light, whereas a convex lens converges light and bring its rays to a focal point.



As light passes through the eye, it is refracted or bent by the cornea and the lens and focused on the retina (in particular on the **macula lutea** of the **fovea centralis** where the cones have their highest density). The cornea accounts for most of the refraction, and the lens allows rapid active focusing for different distances. Focusing for near vision requires **accommodation** (thickening of the lens), pupillary constriction, and convergence of the eyeballs. All three of these reflex action are controlled by the oculomotor nerve (cranial nerve III). Focusing for distance vision requires no special movements of the eye structures.

The Retina

The innermost layer of the eye, the retina, is where the photoreceptors reside. There are two types of photoreceptors: The rods give black and white vision under low light conditions; and the cones give color vision in bright light.

Rods respond to low-intensity light and provide night and peripheral vision. There are there different types of cone cells, and they are bright-light, high-discrimination receptors that provide for color vision. In order to view any object precisely, it must be focused on the cone-rich **fovea centralis**.

There are three layers in the retina. The **inner layer** (deep to middle of eyeball) contains **ganglion cells**; the **middle layer** contains **bipolar cells**; and the **outer layer** contains the photoreceptors, the **rods** and **cones**. There are also **amacrine** and **horizontal cells** present, and their function is to modulate communication by engaging in lateral inhibition (see **Figure 11.14** below).

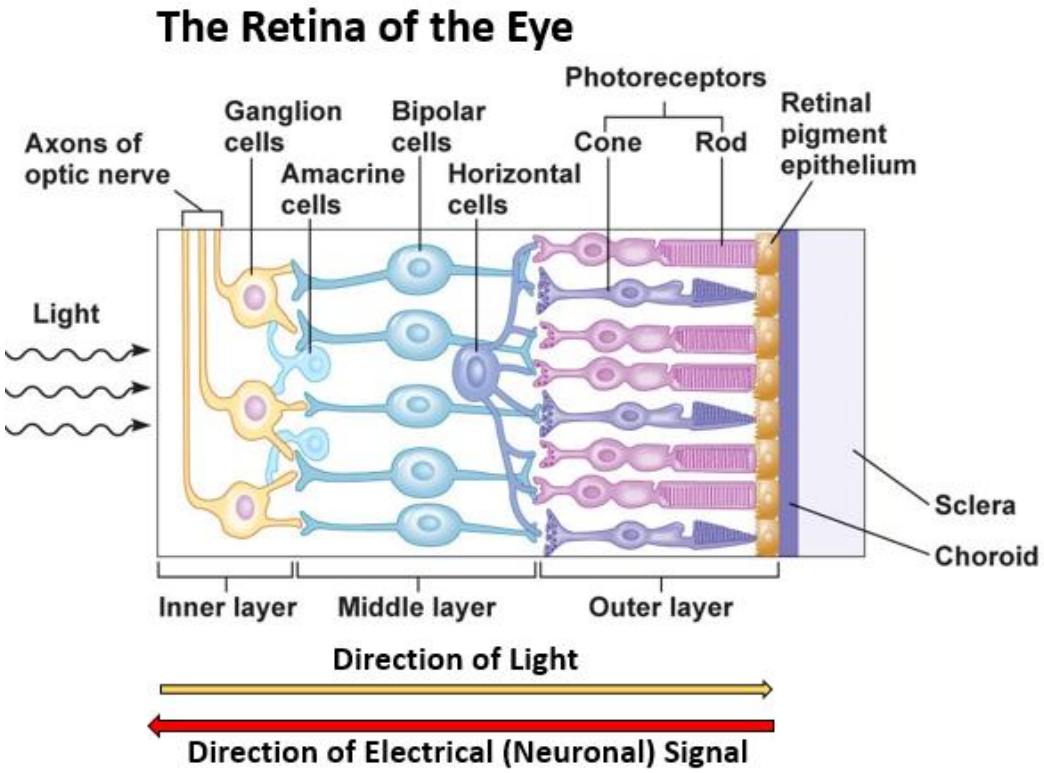
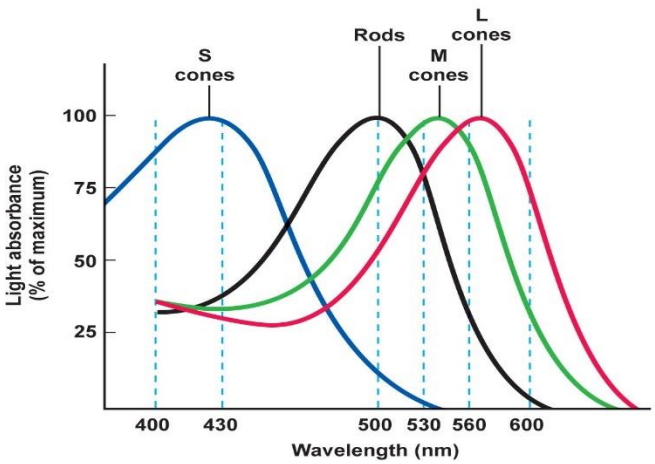


Figure 11.14 Seen here is the retina with its three layers: The inner layer with the ganglion cells; the middle layer with bipolar cells; and the outer layer with the photoreceptors, the rods and cones. There are also amacrine and horizontal cells that function to restrain excess signaling with lateral inhibition. Note that the direction that light travels is the opposite of the direction that the electrical signals travel, as that process starts in the photoreceptors (rods and cones), to the bipolar cells, and finally the ganglion cells whose processes leaving the retina form the optic nerve.

Phototransduction

Since the receptors for light energy are the rods and the cones, it is these cells that convert light to electrical signals. **Rods** are sensitive to light in a **wide spectrum** but is most sensitive to the blue-green range. Rods are highly sensitive and can respond to a single photon.



Cones respond best to more narrow ranges of wavelengths, and are not as sensitive as rods:

S (**blue**) cones - peak sensitivity at 430 nm
M (**green**) cones - peak sensitivity at 530 nm
L (**red**) cones - peak sensitivity at 560 nm

There are about **120 million rods** and about **6 million cones** in the human retina. The cones are not as sensitive to light as the rods. However, cones are most sensitive to **one of three different colors (green, red or blue)**. Signals from the cones are sent to the brain which then translates these messages into the perception of color.

Both photoreceptors can be divided into outer and inner segments (see **Figure 11.15**.). The outer segment contains folds of the cell membrane (disks). It is these membranes that contain molecules which absorb light. The inner segment contains the cell nucleus, organelles and the synaptic terminal, where they communicate with the bipolar cells.

There are four different kinds of photoreceptors each containing a different photopigment that absorbs light.

The photopigment of the **rods** is **rhodopsin**. It is associated with a G protein called transducin and the enzyme phosphodiesterase which degrades cyclic GMP (cGMP).

There are three different types photopigment the three kinds of cones. The photopigments contains a light absorbing portion **retinal** and a protein called **opsin**. It is the type of opsin that determines which wavelengths of light will be optimally absorbed by the retinal.

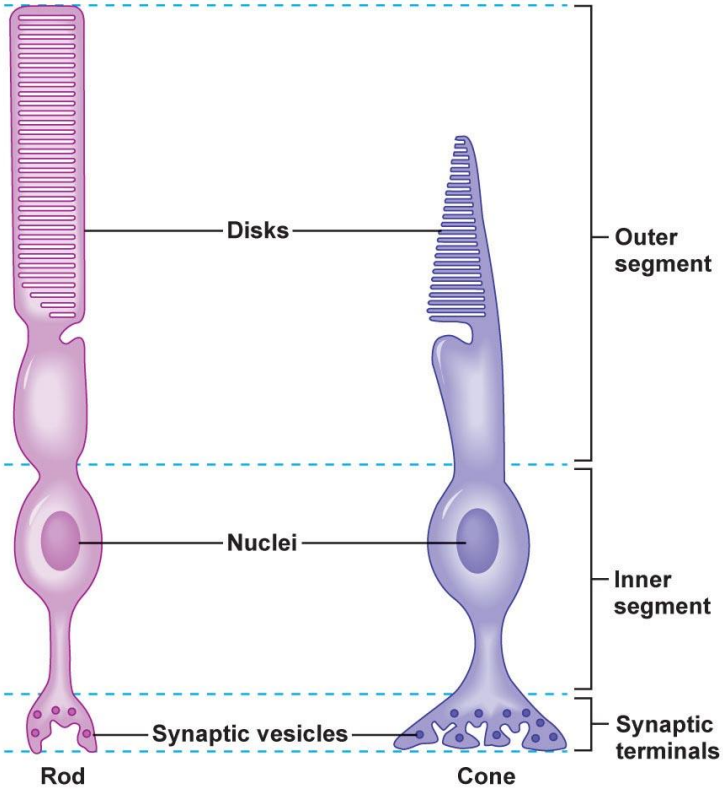
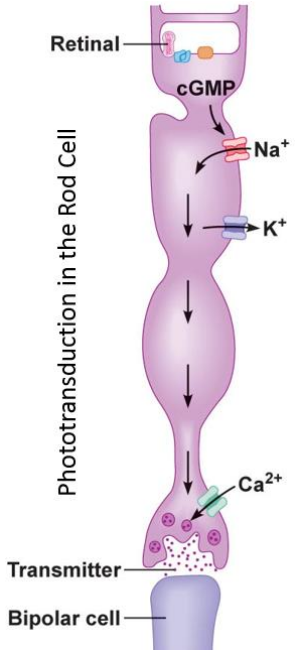


Figure 11.15 Shown here are the two types of photoreceptors in the retina, rods and cones. Rods are responsible for vision at low light levels (scotopic vision). Cones are active at higher light levels (called photopic vision), and are capable of color vision and responsible for high spatial acuity.

The process of **phototransduction** of **rhodopsin** involves many mechanisms and ions that we have encountered before.

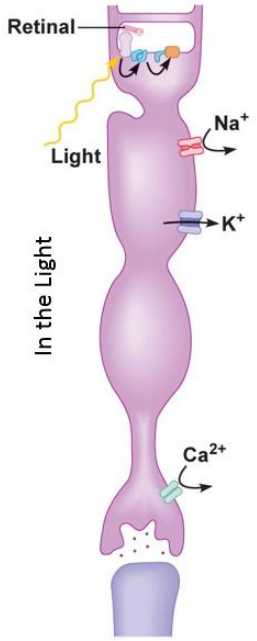
1) In the Dark:

- The levels of cGMP become high in the cytoplasm and this opens sodium channels in the membrane of the outer segment.
- There is an influx of Na+ and an efflux of K+ and this depolarizes the membrane.
- The depolarization spreads to the inner segment.
- This depolarization then opens Ca2+ channels.
- There is an influx of Ca2+, this triggers the release of Glutamate by exocytosis from vesicles.
- The glutamate then diffuses across to the bipolar cell and causes a graded potential there.



2) In the Light:

- As the ligh enters it iis absorbed by rhodopsin. **Retinal** changes shape and is released by **opsin**. This creates **bleached opsin** that activates **transducin**.
- The activated transducin activates the enzyme **phosphodiesterase**, which breaks down **cGMP**.
- This decreased cGMP causes Na^+ channels to close and **stops the influx of Na^+**.
- However, the K^+ channel remains open and K^+ continues to leak out, hyperpolarizing the membrane.
- This hyperpolarization spreads to the inner segment of the cell and closes the Ca^{2+} channels.
- This results in lower Ca^{2+} lelvels in the cell.
- Lower Ca^{2+} means less glutamate is released.
- The graded potential in bipolar cells decreases.



Photoreceptors Bleaching in Light

When exposed to bright light, rhodopsin becomes bleached and opsin is in its active form. No more light can be absorbed. If a person is in a dark room, the rods that are bleached will not be sensitive to light.If tehre is dim light, the retinal and opsin re-associate, and rhodopsin becomes sensitive to light again.

In the Cones

The three types of cones all contain **retinal**, but each has a different type of opsin. Each cone type responds optimally to one color of light: red, blue, or green. The biochemistry of cone function is similar to that of rods that have been described above.

During light adaptation, photopigments are bleached and rods are inactivated; then, as cones begin to respond to high intensity light, high-acuity vision ensues. In dark adaptation, cones cease functioning, and visual acuity decreases; rod function begins when sufficient rhodopsin has accumulated.

The Visual Pathway

It is the **ganglion cells** that transmit the electrical signals to the brain via action potentials. Thus, the visual pathway to the brain begins with the **optic nerve** (cranial N I), which are the axons of the ganglion cells as they exit the retina. The pair of optic nerves leave each eye and combine in front of the brainstem to form the **optic chiasm**. Here there is a 50/50 crossover of fibers from the medial half of each retinal field cross over and continue on in the optic tracts to the thalamus. Thalamic neurons project to the optic cortex via the optic radiation. Fibers also project from the retina to the midbrain **pretectal nuclei** and the **superior colliculi**, and to the **suprachiasmatic nucleus** of the hypothalamus.

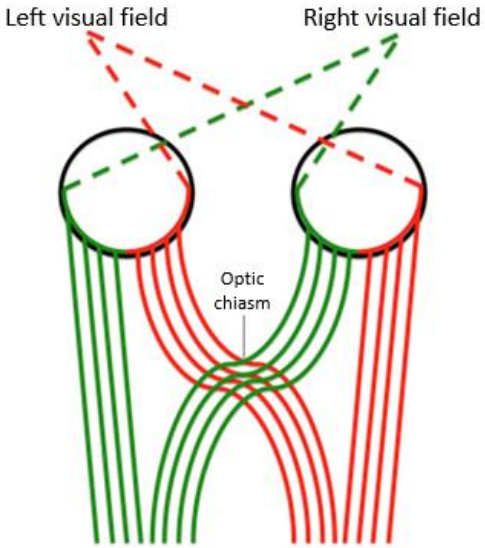


Figure 11.16 The image at right shows how information from both left and right visual fields are detected by each eye, However, at the optic chiasm the crossing fibers ensure that images from the left visual field all go to the right hemisphere and images from the right visual field all go to the left hemisphere.

After visual information arrives at the optic chiasm, input from the left visual field goes to the right side of the brain and vice versa. The fibers that continue from the **optic chiasm** to the **lateral geniculate nucleus** of the thalamus due so in the **optic tract**. At the lateral geniculate nucleus synapses are formed with neurons that arc out in the **optic radiations** and go to the **visual cortex**. The visual field is mapped onto the cortex in a topographic organization. An effective overview of the visual information pathway is displayed directly below in **Fig. 11.17**, starting from the capturing of the image by the visual fields of both eyes, all the way to the end of perceiving it in the occipital lobe and placing that information into context.

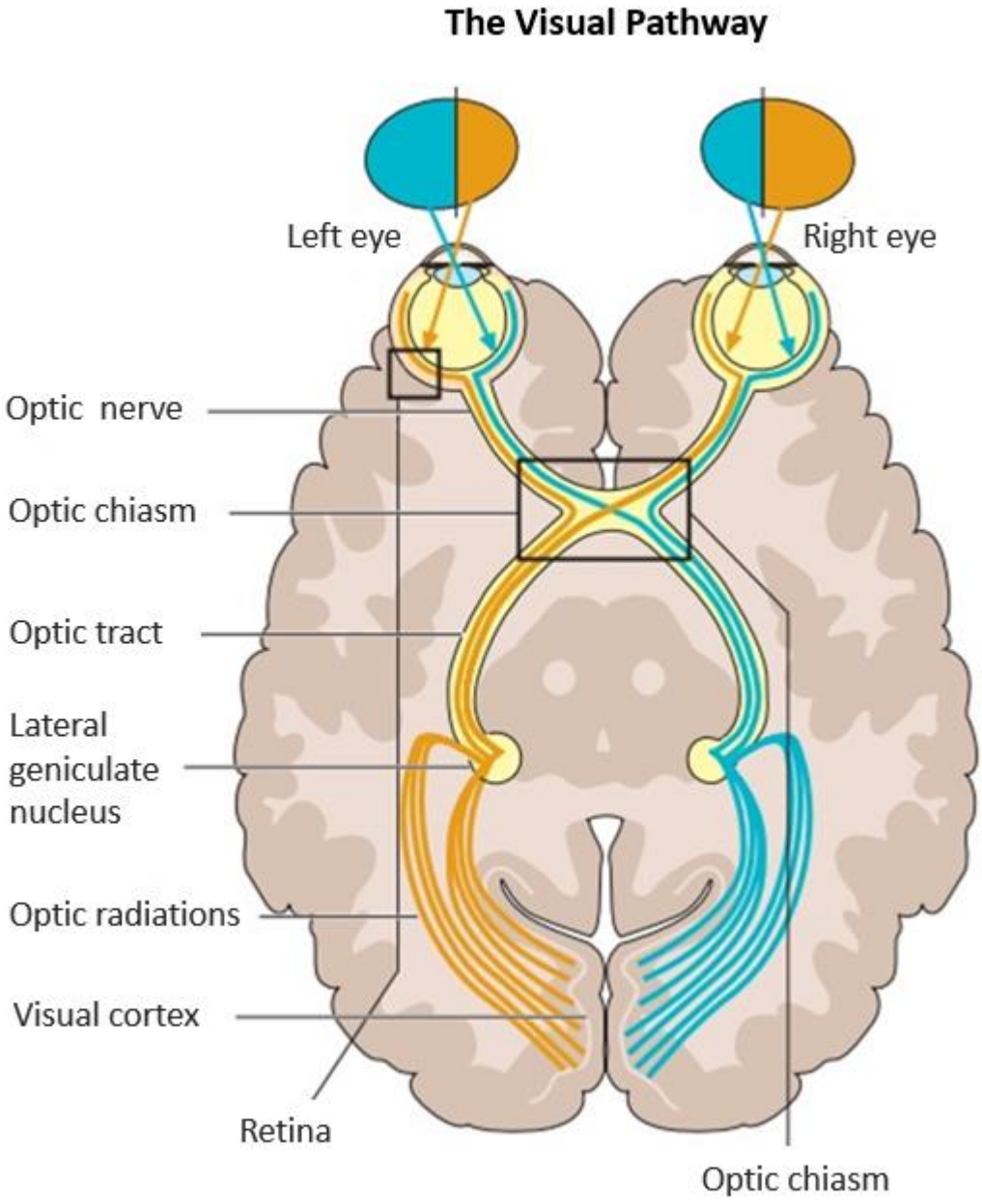


Figure 11.17 Shown here is the visual pathway from the image falling on the retina and detected by the optic nerve, where the information crosses over and split from each eye 50-50 at the optic chiasm, conveyed along the optic tract, to the lateral geniculate nucleus of the thalamus and delivered to the visual cortex via the optic radiations.

Parallel Processing

Information about the different qualities of the stimuli from each point in the visual field, such as shape, color, and movement are transmitted by parallel pathways to the **primary visual cortex** where this information is interpreted. The visual association areas of the occipital lobe is where context of images can be obtained. Visual processing also proceeds anteriorly in the "what" and "where" processing streams via the temporal and parietal lobes, respectively.

Depth Perception

The **stereoscopic vision** created by two separated yet forward facing eyes means that most areas of the right and left visual fields are detected by **both eyes**, but also that each eye receives a slightly different view of the visual field. These views are fused by the **optic cortices** to provide for **depth perception**. Also in the brain, these differences are converted into three dimensional images.

Common Vision Problems

Two of the most common visual problems are **myopia** (nearsightedness) and **hyperopia** (farsightedness). Another is called **presbyopia**. In all three conditions, the eyes fail to focus images correctly on the retina, resulting in blurred vision.

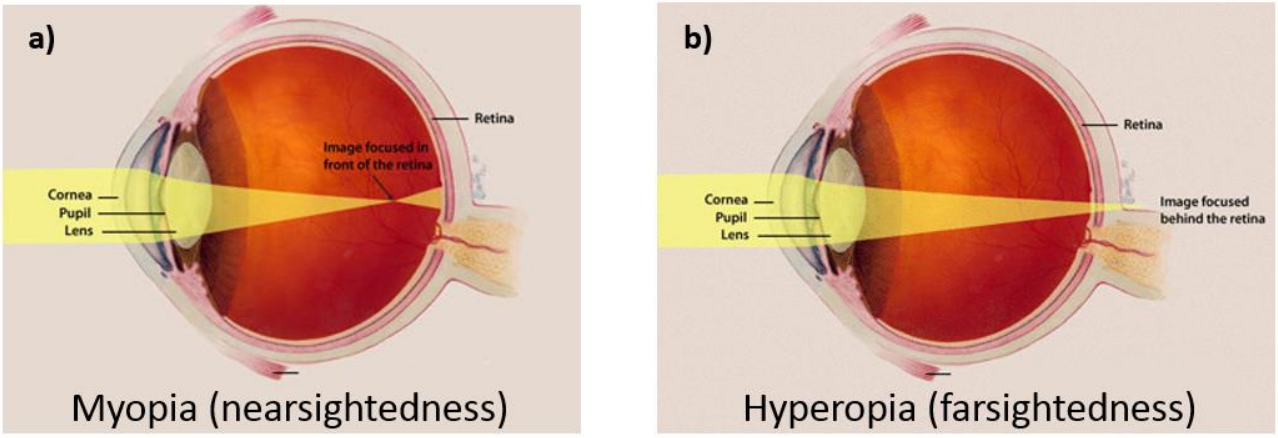
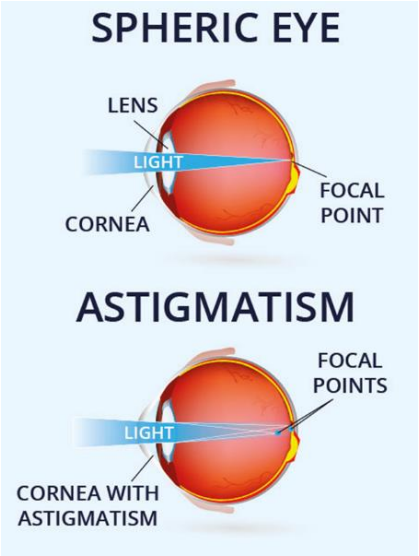


Figure 11.18 If a person has **a)** myopia (nearsightedness), the image is focused in front of the retina, resulting in distant objects appearing out of focus. In a person who has **b)** hyperopia (farsightedness), the image focuses at a point somewhere behind the retina, causing close objects to appear blurry.

Myopia (nearsightedness) occurs when the light entering the eye does not directly focus *on* the retina, but *in front* of it (see **Figure 11.18 a**). As a result, distant objects may appear out of focus, but near objects are not affected. This may occur if the eyeball is elongated from front to back, or if the cornea is too curved. Myopia can be corrected with the use of corrective lenses, either eyeglasses or contact lenses.

Hyperopia (farsightedness) happens when the light entering the eye does not directly focus *on* the retina but *behind* it, (see **Figure 11.18 b**). This causes close objects to appear out of focus, but far objects are not affected. Hyperopia may occur if the eyeball is too short from front to back, or if the lens is not curved enough.



Presbyopia is a vision problem associated with aging, in which the eye gradually loses its ability to focus on close objects. The precise origin of presbyopia is not known for certain, but evidence suggests that the lens may become less elastic with age, causing the muscles that control the lens to lose power as people grow older. Most people use corrective lenses to focus on close objects.

Astigmatism is a common and generally treatable imperfection in the curvature of the eye that causes blurred distance and near vision. Astigmatism occurs when either the front surface of the eye (cornea) or the lens inside the eye has mismatched curves.

Sound and Your Ears

Sound may be more complex that most realize. Sound travels as **waves** in a medium (air, liquid, solid), and sound can be described as longitudinal, mechanical and pressure waves.

- **Longitudinal** - is a wave in which the motion of the medium's particles is **parallel** to the direction of the energy transport of the sound wave.

- **Mechanical** - is a sound wave that moves through a medium by **displacing** particles in a chain reaction. The displacement of one particle, pushes or pulls nearby molecules, causing them to be displaced from their equilibrium. This transports mechanical vibrations throughout the medium as is moves.

- **Pressure** - sound waves consist of **compressions** (increase in density) and **rarefactions** (decrease in density), therefore regions fluctuate between low and high-pressure patterns.

If we settle for a mixture of all of the above descriptions, sound can be described as **mechanical** waves caused by gaseous (liquid or solid) molecules in motion that have **pressure** patterns of compression and rarefactions and can also have **parallel direction**.

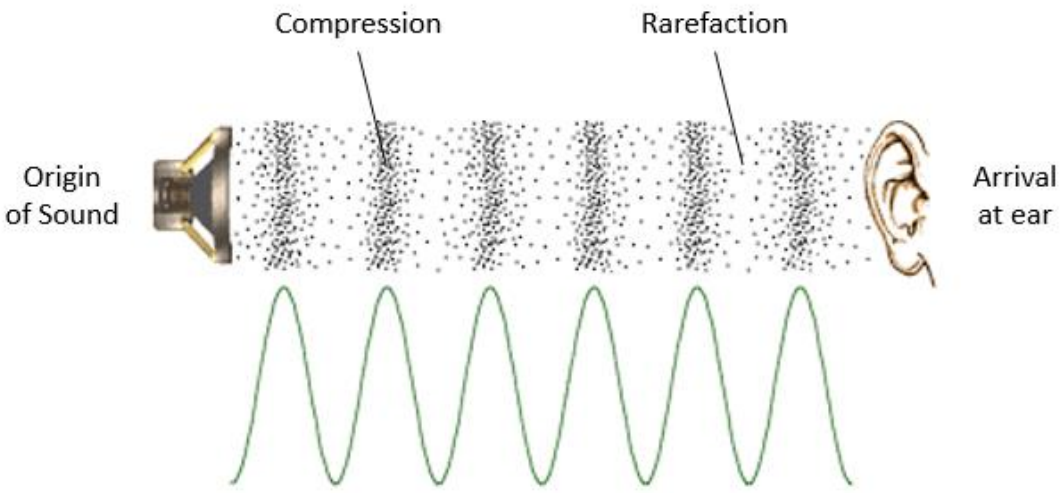


Figure 11.19 This image shows sound travelling through the air and mechanically displacing the particles of the medium creating regions of compression (high density) and rarefaction (low density) in a pressure pattern with direction parallel to the movement from origin to recipient (ear). Sound waves in air (and any fluid medium) are longitudinal waves because particles of the medium through which the sound is transported vibrate parallel to the direction that the sound wave moves.

In our bodies, vibrations create **sound waves** which move through mediums such as air, water or solid structures before reaching our ears. Since the ability to conduct sound depends on the density of the medium, it is solids that are better conductors than liquids, and liquids that are better conductors than gases. The speed of sound in the air (at sea level) is around **767 miles per hour** or 1,230 kilometers per hour. When traveling through water, sound moves over four times faster than through air. That is about **3,000** miles per hour in water. This is one reason why a **humpback whale** singing in the Caribbean can be heard by a fellow whale off the west coast of Ireland more than 4,000 miles away. Who needs the internet? Wales don't!

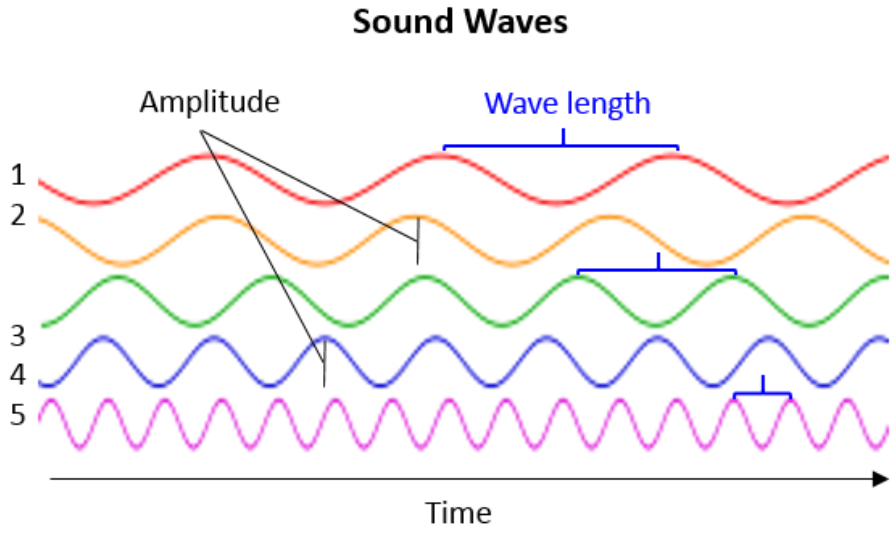


Figure 11.20 Examples of how sound waves of different wavelengths might look. The amplitude (height of the wave) is an index for the loudness of the sound. All of these waves have the same amplitude, thus loudness. Where they differ is in the lengths of the wave cycle over time, or the wavelength. This is the frequency of the wave which is an index of the pitch of the sound. Wave #1 has about 3 wave lengths, whereas wave #5 has about 14 wavelengths in the same time period, thus wave #5 has a higher frequency or pitch that wave #1.

Properties of Sound

Two very important properties or qualities that sound has are ***pitch*** **(wave length)** and ***loudness*** **(amplitude)**.

- ***Pitch*** describes how high or low a tone is and depends upon the **frequency of vibration**. Higher frequencies gives higher tones and lower frequencies give lower tones. It is measured in length.

- ***Loudness*** of a sound depends upon the **amplitude of vibration**, which means the size of the sound wave. The greater the amplitude of the sound wave, the louder the sound. It is measured in decibels.

The pitch of a sound can be thought of in terms of music, as the note of the sound. This is determined by the frequency of sound waves and the frequency is measured by the number of waves per second or **Hertz** (Hz). The average range of hearing is from 20 Hz to 20,000 Hz, with the greatest sensitivity in humans existing in the 1,000 Hz to 4,000 Hz range.

The loudness of a sound (amplitude) is due to differences in the densities of compressed and rarified areas, which creates smaller or larger sized waves. The loudness of sound is expressed in decibels (db) on a logarithmic scale. The hearing apparatus of our ears vibrate in a similar way to the original source of the vibration, allowing us to hear many different sounds. Dogs can hear higher frequencies than humans, thus they hear noises we can't. It is believed the loudest sounds made by any animal are the whistles of the blue whale, measured at up to **188 decibels** – that's a million times more intense than a jet engine, which is only about **120-140 decibels**, since the decibel scale is exponential!

Sound Perception and Hearing

Hearing (auditory perception) is the ability to perceive sound by detecting vibrations – which are changes in the pressure of the surrounding medium through time. The **ear** is our organ of **sound**. Sound may be heard through solid, liquid, or gaseous matter. Sounds waves hit the ear drum (tympanic membrane) and cause it to vibrate at a certain rate in accordance with the frequency (pitch) and amplitude (loudness) of the sound. The inability to hear is called **deafness**; it can be mild or profound, temporary or permanent. Normal hearing ranges from **0 to 20** dB in all frequencies.

The Ear

The human ear contains sense organs that serve two quite different functions: **1)** for hearing and **2)** for equilibrium and postural coordination. The focus in this section is on the elements of the ear related to hearing sounds. The structure of the ear has three distinguishable regions, they are the:

- **Outer ear**: This portion consists of the usually visible **auricle** (also called pinna) which captures the sound waves and directs them into the external auditory meatus, leading to the flexible tympanic membrane (eardrum).
- **Middle ear**: This portion contains the three auditory ossicles, which transfer the vibrations of the eardrum into waves in the fluid and membranes of the inner ear, the **malleus**, **incus** and **stapes**, which resemble a hammer, anvil and stirrup respectively. The malleus is attached to the tympanic membrane and this is where the sound waves from the eardrum are transformed into vibrations, this is transferred to the incus and finally to the stapes which is attached to the **oval window** of the cochlea. The three auditory ossicles act as a system of **levers** and **amplify** sound

vibrations coming from the eardrum, passing them on to oval window of the inner part of the ear, where the stapes pushes against.

- **Inner ear**: It is the inner ear that houses the **cochlea** (meaning shell, because it looks like a snail's shell) and the semicircular canals (involved in balance). It is the snail-shaped cochlea that translates the information in the vibrations from the middle ear and fires electrical signals along the **cochlear** (auditory) **nerve** to the brain for the perception of the sounds

Sound Conduction

It takes greater pressure to produce waves in the fluid of the cochlear than in the air of the outer ear. The ear amplifies the pressure wave in the air by two means:

1) The three **auditory ossicles** are arranged to function as a series of **levers**. The movement of the malleus causes a lesser movement of greater force of the incus which in turn causes a lesser movement of greater force of the stapes. The oval plate of the stapes then presses on the fluid at the oval window of the cochlear duct with an even greater force, producing a pressure wave in the fluid.

2) The diameter of the tympanic membrane is much larger than the membrane on the oval window, therefore, the pressure on the larger surface translates to an exponentially larger pressure on the smaller surface. This is the power of the lever system is being able to amplify very soft sounds.

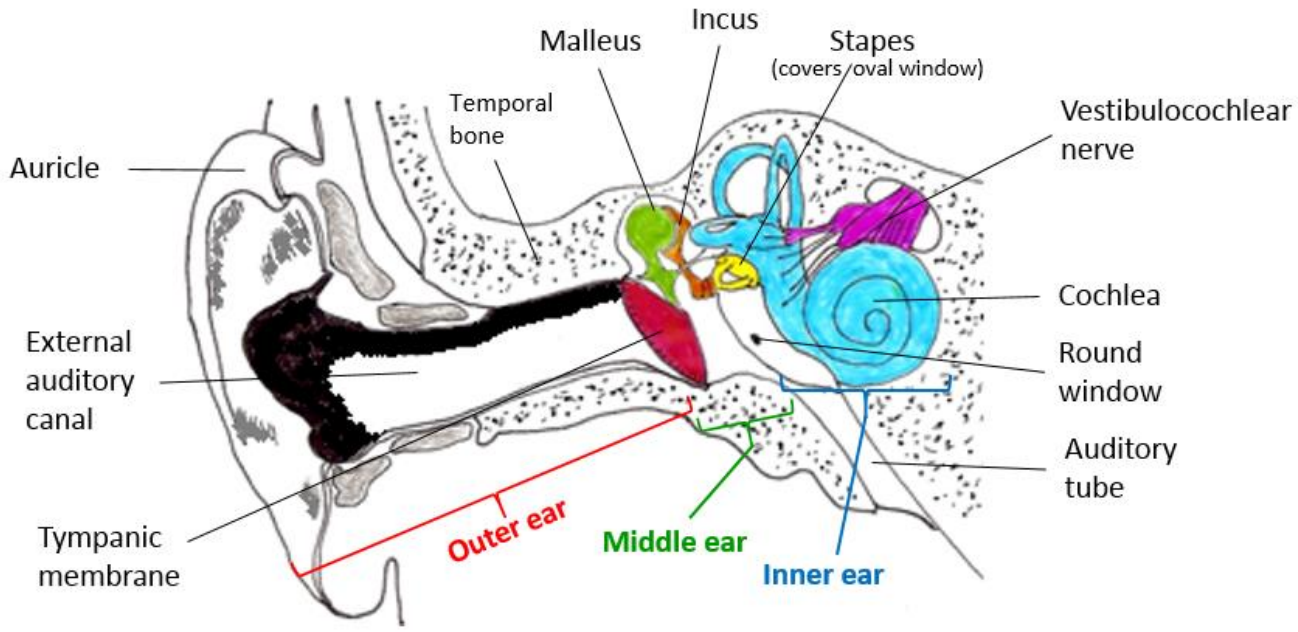


Figure 11.21 The drawing shows the structures of the outer (red bracket), middle (green bracket) and inner ear (blue bracket). Each region has its specific role in the processing of sound.

The Cochlea

The cochlear scalae (chambers) contain two types of fluid, perilymph and endolymph. **Perilymph** is an extracellular fluid found within the scala tympani and scala vestibuli of the cochlea, it has an ionic composition comparable to plasma and cerebrospinal fluid. **Endolymph** is found inside the scala media or cochlear duct, and has a unique composition of very high in K^+ and low in Na^+, not found elsewhere in the body.

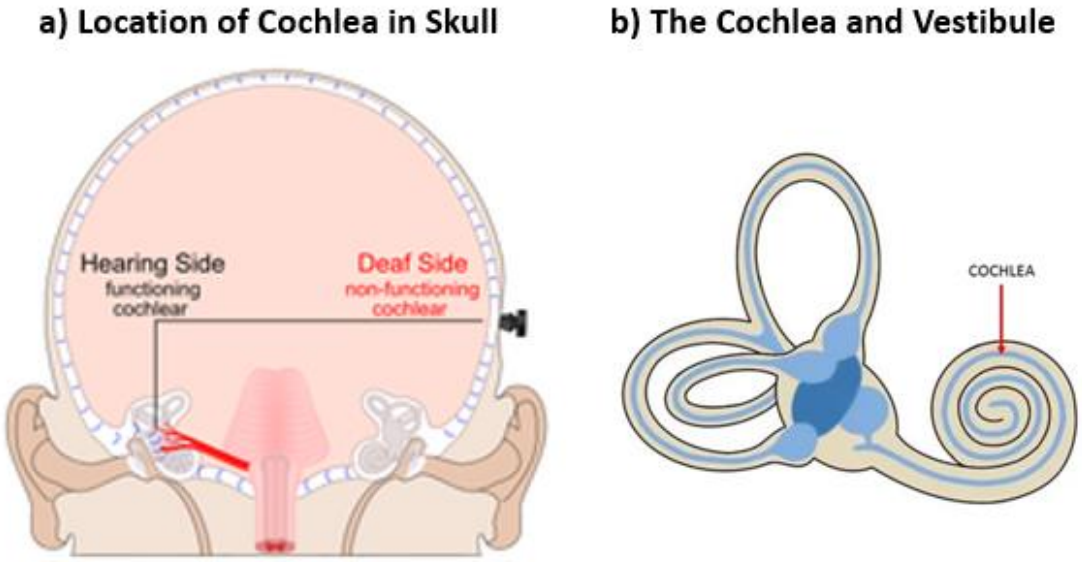


Figure 11.20 The image **a)** shows the location of the left and right cochleae within the skull (which is facing forward). The image **b)** shows a closer view of the structural relationship between the cochlea (for hearing) and the vestibule (for balance).

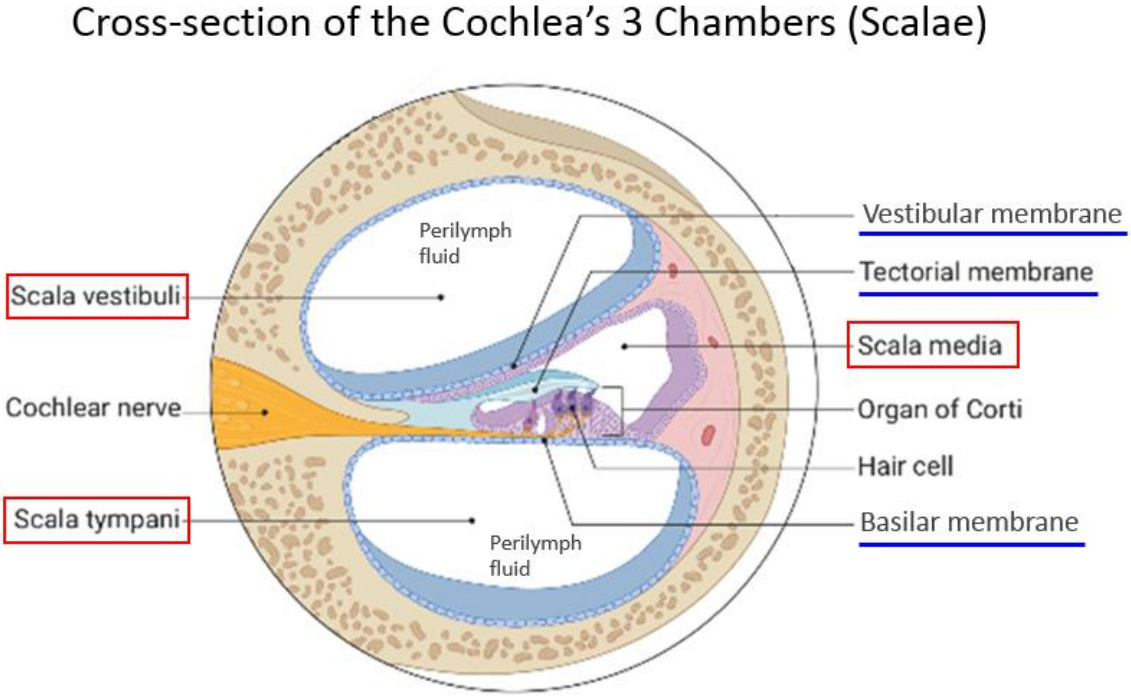


Figure 11.21 The structures of the cochlea of the inner ear is shown in cross section, revealing the three fluid filled chambers, the scalae vestibuli, media and tympai, and the three membranes involved in the conduction and reception (at the hair cells) of the sensation of sound.

The Organ of Corti – the Organ of Hearing

At the heart of capturing and transducing sound stimuli is the **organ of Corti** (an eponym for anatomist Alfonso Corti, who first described it in 1851). As seen in **Figure 11.21** above and zoomed in at image to the right **Figure 11.22**, it sits atop the basilar membrane and contains hair cells, with the overlaying tectorial membrane that moves with sound waves, and alters the **stereocilia** atop the hair cells which are embedded in the tectorial membrane.

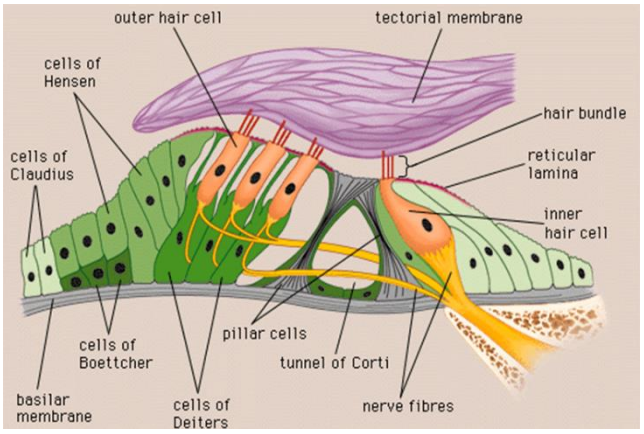


Figure 11.22 Shows details of the organ of Corti.

The arrival of sound waves at the **oval window** cause pressure waves in the **endolymph** of the cochlear duct (see **Figure 11.23** below). The basilar membrane moves relative to the tectorial membrane in which the stereocilia of hair cells is embedded. This causes the **stereocilia to bend**. The distortion of stereocilia causes **K^+ channels** to either open or close. Because the concentration of K^+ in endolymph is higher than that in the cell, the opening of K^+ channels causes the cell to **depolarize** as K^+ rushes in. The closing of these channels cause **hyperpolarization**.

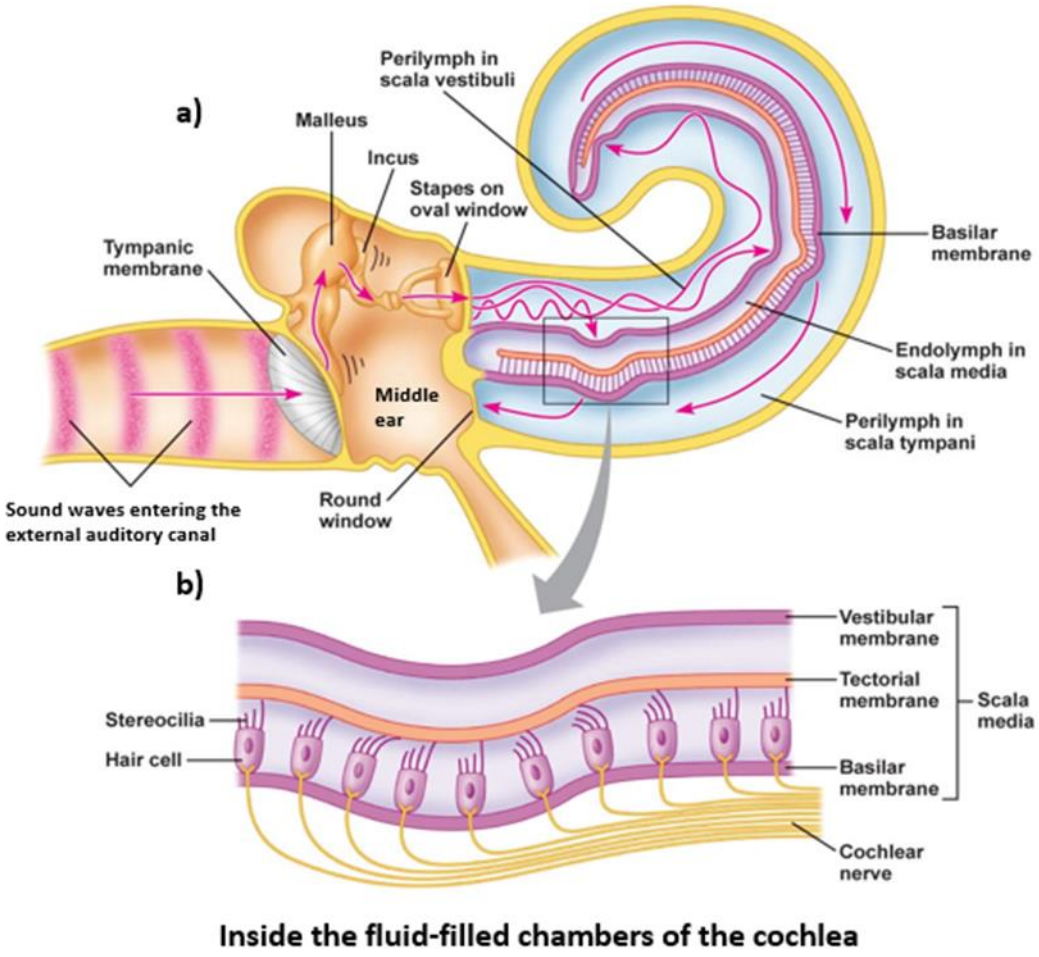


Figure 11.23 As shown in **a)** the sound waves hit the tympanic membrane, then are amplified by the auditory ossicles in the middle ear, and then conducted into the fluid filled chambers of the cochlea. In **b)**, the wave like movement of the tectorial membrane in the cochlea trigger the stereocilia of the hair cells to bend and fire action potentials. Notice the hair cell processes lead out and become the cochlear nerve.

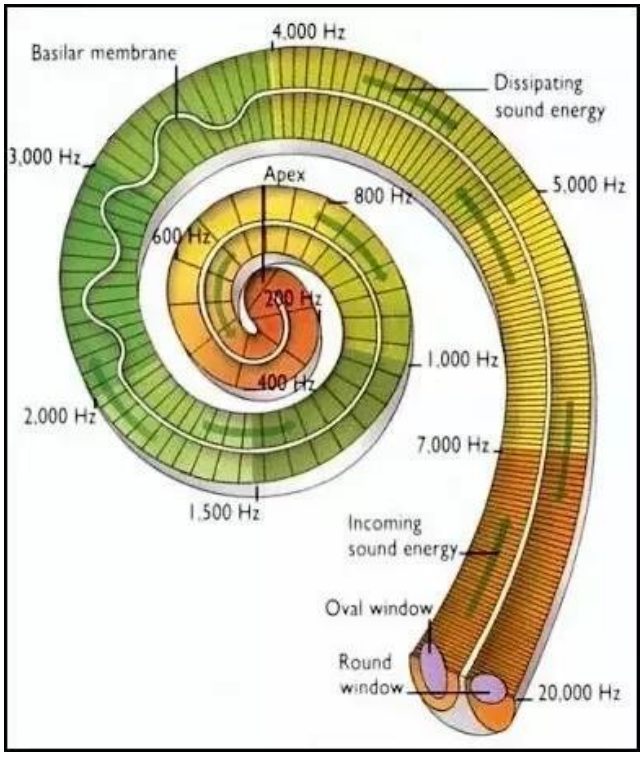
The stereocilia are arranged in decreasing sizes and are connected by elastic protein filaments. When the hair cell is at rest, the K^+ channels are partially open and partial depolarization causes the Ca^{2+} channels to open. The influx of Ca^{2+} (as we have seen) results in the release of the neurotransmitter **glutamate** from the hair cell, which in turn causes neurons of the cochlear nerve to fire action potentials.

When stereocilia bend **toward** the direction of the tallest stereocilia the increased tension on stereocilia open the K^+ channels more, **increasing** depolarization. This increases Ca^{2+} entry and neurotransmitter release and the frequency of action potentials in afferent neurons. When stereocilia bend **away** from the tallest stereocilia K^+ channels close, **decreasing** depolarization close and the results are opposite.

Sound Intensity and Pitch

The greater the intensity (**loudness**) of sound the **greater the bending of the stereocilia**. The larger the variations in transmitter release produces greater variations in action potentials in the afferent neurons.

The Fibonacci helical spiral of the cochlea plays a vital part in sound translation. The hair cells are tuned to different sound pitches based, in part, on their locations along the cochlea's spiral coil, and the number and the length of their stereocilia stimulated. The basilar membrane of the cochlea varies in structure over its length with the membrane being narrow and stiff near the oval and round windows and wider and more flexible near the **helicotrema**, or tip of the spiral cochlea.



High frequency sounds cause greater deflection of the basilar membrane where it is narrow and stiff, and lower frequency sounds produce greater deflection where the basilar membrane is loose and flexible. The pitch of sound is coded by **where along the basilar membrane the greatest deflection occurs** (see **Figure 11.24** to right). The range of human hearing perception is commonly
As seen the human cochlea allows the perception nearly 10 octaves, with a resolution of 1/230 octave from 3 Hz at 1000 Hz.

Figure 11.24 Seen to the right is the cochlea in sagittal section, enabling a view of the inner chambers from the oval and round windows which are separated by the basal membrane. This drawing displays how the cochlea is capable of exceptional sound analysis, for coding both frequency and intensity of sound. The higher pitch (frequency) sounds 20,000Hz, are detected closer to the windows, and lower pitch sounds are detected approaching the apex (20Hz).

The Neural Pathways for Sound

The afferent neurons travel in the **cochlear nerve** (cranial nerve VIII) with frequency of action potential coding intensity of sound. In the brainstem afferent neurons synapse with second-order neurons in the **cochlear nuclei** that travel to the **medial geniculate nucleus** of the thalamus. Third-order neurons travel to the **auditory cortex** of the **temporal lobe**. The frequency of sound is mapped out in the auditory cortex

in a tonotopic manner, meaning **tones** close to each other in terms of frequency are represented in neighboring regions in the brain.

Auditory processing is analytic, meaning that each tone is perceived separately. The pitch perception is related to the position of the excited hair cells along the basilar membrane. The intensity perception is related to the basilar membrane mobility, if it is increased, then the frequency of impulse transmission to the cortex is enhanced. Cues for sound localization of where sound is coming from include the intensity and timing of sound arriving at each ear.

Homeostatic Imbalances of Hearing

Conduction deafness results from interference with conduction of sound vibrations to the fluids of the inner ear. Hearing loss affects people of all ages and can be caused by many different factors. The three basic categories of hearing loss are sensorineural hearing loss, conductive hearing loss and mixed hearing loss. There are also levels of hearing loss, from mild-moderate to severe and profound hearing loss.

- **Sensorineural deafness** reflects damage to neural structures.
- **Tinnitus** is an early sign of sensorineural deafness; it may also result from the use of certain drugs.
- **Ménière's** syndrome is a disorder of the membranous labyrinth. Symptoms include tinnitus, deafness, and vertigo. Excessive endolymph accumulation is the suspected cause.

Equilibrium and Balance

In addition to transducing sound, the inner ear also detects acceleration of the body and the position of the head in relation to the rest of the body. The motions of acceleration are changes in linear speed, and angular acceleration, or rotation. Keeping the physical body in balance (literally) although substantially regulated by automatic responses, relies on input from several areas of the body, in contrast to the other special senses. Information from the inner ear, the eyes, the muscles and joints in your leg and spine assist in us maintaining our posture and prevent us from losing our balance and falling.

The inner ear has two parts, the cochlea as we have seen above, for hearing, and the vestibular system for **balance**. The vestibular system is made up of a network of looped tubes, three in each ear, called the **semicircular canals**. They loop off a central area called the **vestibule** and this system is key in maintaining balance.

Balance and Spatial Body Perception

The ears are also responsible for the sense of balance. Balance is the ability to sense and maintain an appropriate body position. The semicircular canals inside the ear (see the figure above) contain fluid that moves when the head changes position. Tiny hairs lining the semicircular canals sense movement of the fluid. In response, they send nerve impulses to the vestibular nerve, which carries the impulses to the brain. The brain interprets the impulses and sends messages to the peripheral nervous system, which triggers contractions of skeletal muscles as needed to maintain balance.

The Vestibular System (Apparatus)

The vestibular system, like the auditory system, uses hair cells for detection of changes, however, the hair cells are excited differently. The **vestibular labyrinth** has five vestibular receptor organs in the inner ear to assist in maintaining balance and equilibrium. They are: the **utricle** and the **saccule;** which both provide

information about linear acceleration; and the three **semicircular canals**, the anterior, posterior and lateral semicircular canals, which render information about **angular** motion of the head.

The **utricle** is more sensitive to **horizontal** acceleration (think of being in a car as it slows down).

The **saccule** is more sensitive to vertical acceleration (think of being in an elevator and it goes up).

The Semicircular Canals Maintain Dynamic Equilibrium
The three **semicircular canals** detect changes in head position and movement:

> **Anterior**: detects forward and back head movement, like nodding of the head.
> **Posterior**: detects head tilt like tipping the head toward the shoulders (similar to the head gesture dogs make when they do not understand you).
> **Lateral (Horizontal)**: detects horizontal movement of head, such as swiveling the head side to side, for example when making the 'no' gesture.

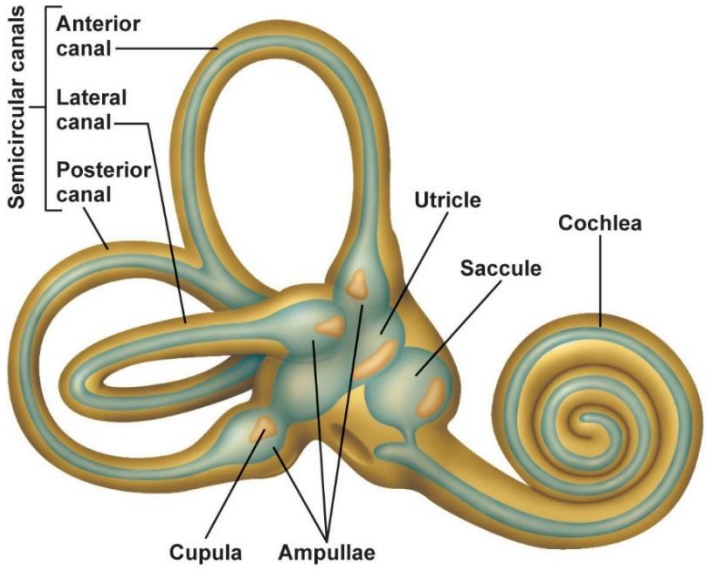


Figure 11.25 The vestibular apparatus of the inner ear is shown, with utricle, saccule, and the anterior, posterior and lateral semicircular canals.

The Utricle and the Saccule Maintained Static Equilibrium

Static equilibrium is maintained by **utricle** and the **saccule**, this means **linear acceleration**. If you are moving forward or backward (utricle) or moving up or down (saccule), it is the position of the head that permits the central nervous system to maintain stability and posture when the body and head are not moving. It is detected by mechanoreceptors which are present in the vestibule of the inner ear.

- The **utricle** detects **linear acceleration forward and backward**, it is more sensitive to **horizontal** acceleration. Think of the feeling of motion experienced when you are a passenger in a car on a flat surface and it suddenly speeds up or slows down. That is the utricle conveying this type of change in horizontal acceleration

- The **saccule** detects **linear acceleration up and down**, it is more sensitive to **vertical** acceleration. Think of the feeling of motion experienced when you are in an elevator and it goes up down quickly. That sensation is relayed by the saccule.

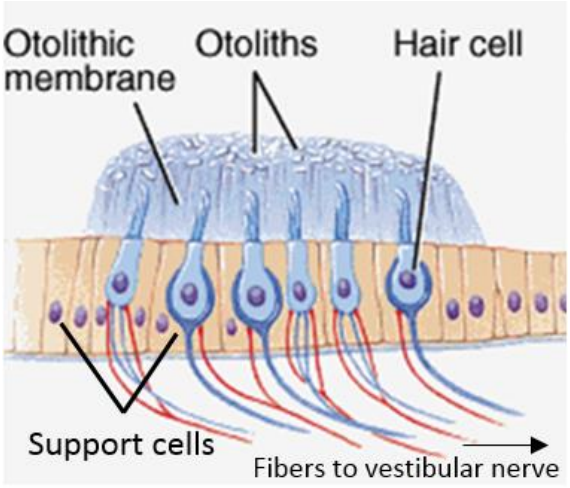


Figure 11.26. Shows the relationship between the otolithic membrane, the hairs cells and the support cells of the utricle and sccule.

Linear Acceleration Utricle and Saccule

The **hair cells** in the utricle and saccule reside under a **gelatinous layer** and their **stereocilia** projecting into that gelatin. Embedded in this gelatin are calcium carbonate crystals, similar to tiny rocks, called **otoliths**. So it's true, we all have rocks in our head. When the head is tilted for example, from the body being moved rapidly in one direction, the crystals continue to be **pulled straight down** by gravity, but the new angle of the head causes the gelatin to shift, thereby **bending the stereocilia**. The bending of the stereocilia stimulates specific neurons to fire and signal the brain that the head is being **tilted**, allowing for the maintenance of balance during these actions.

The receptors for static equilibrium are the **maculae** of the **saccule** and **utricle**. The utricle and saccule are mostly made macula **tissue (plural = maculae), which is composed of hair cells surrounded by support cells** (see **Figure 11.26** above). The stereocilia of the hair cells extend into a viscous gel called the otolith. The otolith contains calcium carbonate crystals, making it denser and giving it greater inertia than the macula. In this way, gravity will cause the otolith to move separately from the macula in response to head movements. Tilting the head causes the otolith to slide over the macula in the direction of the pull of the movement. The moving otolith layer bends the sterocilia stimulating various hair cells to **depolarize** while others **hyperpolarize**. The exact coordinates of the head tilt is interpreted and calculated by the brain on the basis of the pattern of hair-cell depolarization. It is **motions of the head** that cause the otoliths to pull on the **hair cells**, stimulating the **vestibular nerve** branch, which signals the position of the head with respect to the rest of the body.

The Semicircular Canals

The fluid-filled semicircular canals are tubular loops set at oblique angles, arranged in three spatial planes, anterior (forward/backward), posterior (tilt side to side) and lateral (rotate left and right).

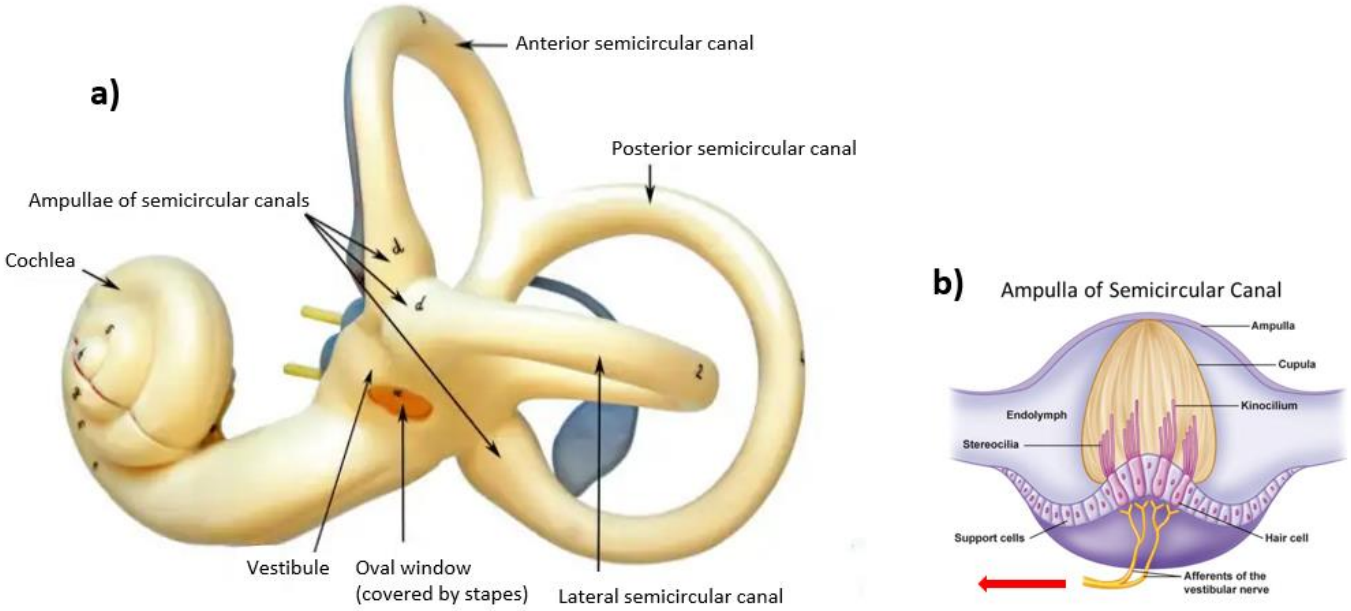


Figure 11.27 Shows **a)** the arrangement of the vestibular complex, with the three semicircular canals (anterior, posterior and lateral). Each of the three semicircular canals have their own ampulla, shown in **b)**, with stereocilia on the hair cells embedded in the cupula surrounded by endolymph. The triggering of the hair cells coordinates with specific angular changes of the head, sending afferent signals via the vestibular neve (red arrow).

The base of each canal has a swelling that contains a cluster of hair cells. The hairs project into a gelatinous cap, the cupula, where they monitor **angular acceleration** and **deceleration** from **rotation**. For example, these would be stimulated by turning your head, driving a car around a corner, or falling forward.

Two of the semicircular canals, the anterior and posterior, lie at about **45º angles** to the horizontal axis of the body, while one canal lies **horizontally** to the perpendicular axis to the body, called the lateral or horizontal semicircular canal. When the brain processes input from **all three canals together**, it can detect angular acceleration or deceleration in **three dimensions**. When the head turns, the fluid in the canals shifts, thereby bending stereocilia and sending signals to the brain. When the acceleration or deceleration stops, the movement of the fluid within the canals also slows or stops.

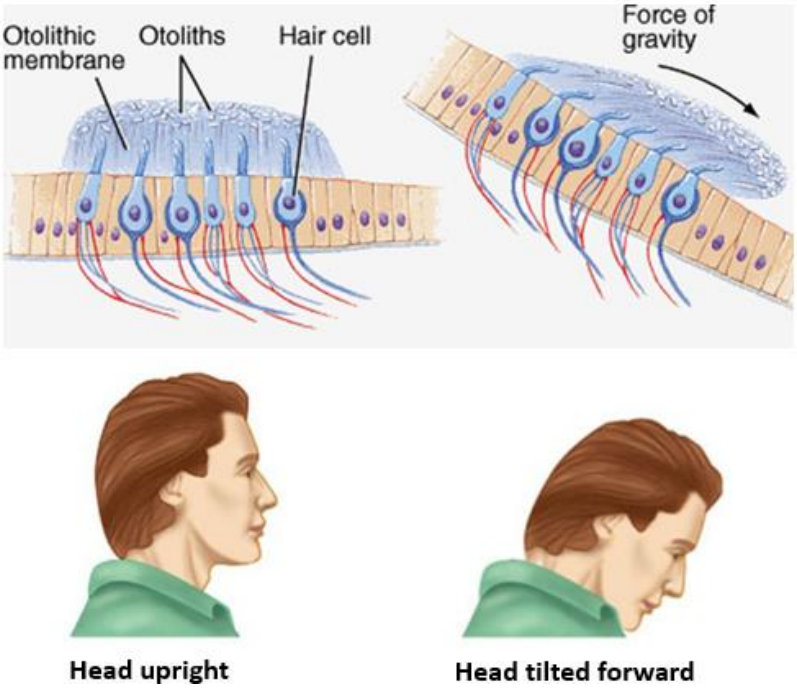


Figure 11.28 When the head is moved from upright to tilting forward, the otoliths of the anterior: semicircular canal moves with gravity and also causes the gelatin to shift, thereby bending the stereocilia of the hair cells, sending signals to the brain about the tilted forward the head, so we can keep our balance.

It is analogous to sitting on a train holding a glass of water. When the train is in constant steady motion, the water will be stable in the glass and will not splash out. However, if the train suddenly significantly began to stop (decelerate), the water in the glass would splash forward (like the movement of the otoliths). Or, if the train accelerated abruptly, the water would splash backwards onto you! The key is that these structures do not detects speeds, they are receptors that detect ***changes*** in acceleration.

Higher Processing

The hair cells from the each component of the vestibular apparatus (the utricle, saccule, and semicircular canals) signal through **bipolar neurons** to the **cochlear nucleus** in the **medulla oblongata**. These cochlear neurons then send descending projections to the spinal cord and ascending projections to the **pons**, **thalamus**, and **cerebellum**. The connections made with the cerebellum are extremely important, particularly for postural reflexes. The **proprioceptors** that are located throughout the body bring information about where the various parts currently are into the cerebellum. Here in the 'little brain' not only coordinated body movements, but is also (throughout life) creates routines to maximize efficiency of recovery of you should start to lose your balance, in order to protect us from falling or to minimize the damage if the fall occurs, ignominiously or elegantly. Think of walking along the sidewalk, tripping on a crack and how automatically your arms may flail out to re-establish your balance. If someone is walking on a tightrope (see image above at right), the relative positions of body parts play an integral role in maintaining equilibrium.

The signals from the vestibular apparatus also projection into the **temporal cortex**, which is related to the feelings of dizziness from excessive spinning. The projections to ANS areas of the brainstem are involved in **motion sickness**. Additional projections into the **primary somatosensory cortex** help to monitor the subjective measurements of the external world and guide movement of self through it. In those with certain damage to the vestibular area of the somatosensory cortex can see vertical objects in the outside environment as being tilted. The last critical element is that the vestibular signals project to various extrinsic eye muscles to comprehensively coordinate head and eye movements.

Olfaction - The Sense of Smell

The Olfactory Epithelium and the Sense of Smell

The olfactory epithelium is located in the roof of the **nasal cavity** (see **Figure 11.29** below). The receptor cells are ciliated bipolar neurons. Their axons are the filaments of the **olfactory nerve** (cranial nerve I). Individual olfactory neurons show a range of responsiveness to different chemicals. Olfactory cells bearing the same odorant receptors synapse in the same glomerulus type. Olfactory neurons are excited by volatile chemicals (molecules in gaseous form) that bind to receptors in the olfactory cilia.

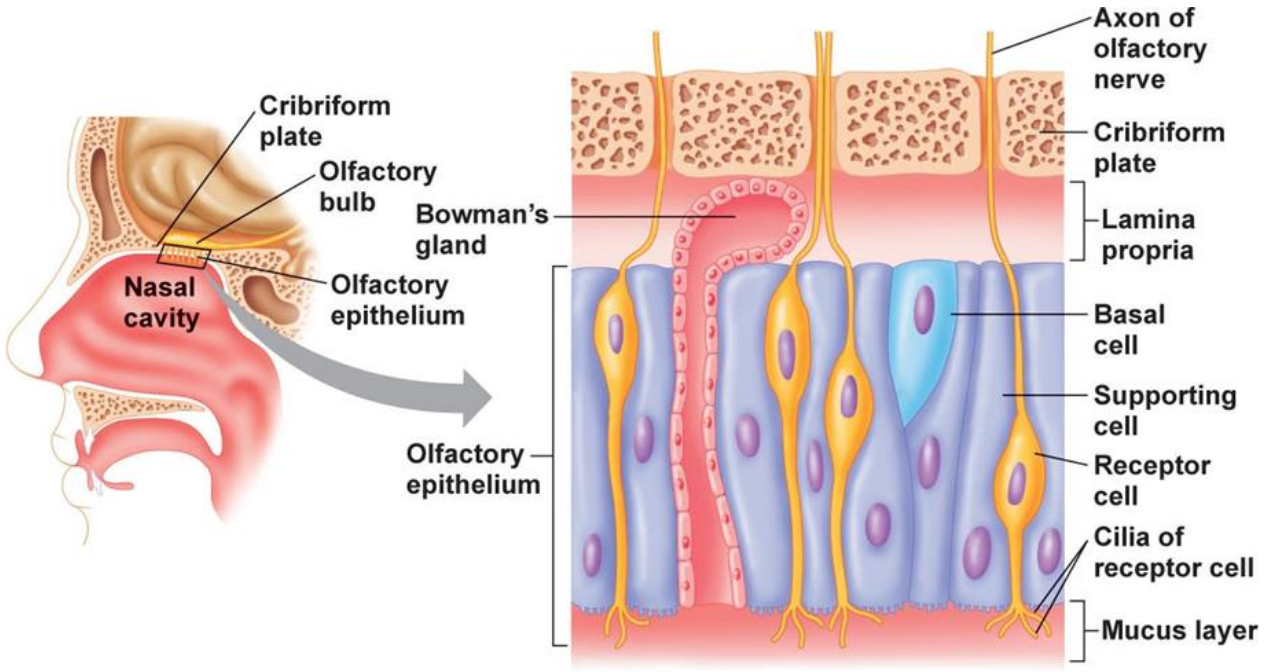


Figure 11.29 As seen in the magnified image on the right, the olfactory epithelium in the nasal cavity consists of supporting cells, basal cells and olfactory receptor cells. The basal cells are essentially stem cells that replace the olfactory receptor cells that have the cilia extending into the mucous layer. The Bowman's gland shown are located in the lamina propria of the olfactory membrane and open into the mucus layer. The mucus produced from these glands is what continually keeps the olfactory surface moist.

Olfactory Signal Transduction

The odorant molecules must be is a vapor state, to be inhaled into the nasal cavity. Once there they dissolve in mucus membrane present and bind to **chemoreceptors**. This binding to membrane receptors and activates a **G protein**. The G protein activates the intracellular enzyme **adenylate cyclase**, which takes ATP and makes **cAMP** is, which is a 2nd messenger inside the cell.

The elevated levels of cAMP bind and to and open both Na^+ and Ca^{2+} channels causing **depolarization** of the receptor cells The influx of Ca^{2+} also causes Cl^- channels to open and Cl^- to exit from the cell, causing further depolarization, and if the membrane depolarization is great enough, action potentials are triggered and send signals up into the olfactory bulb. The

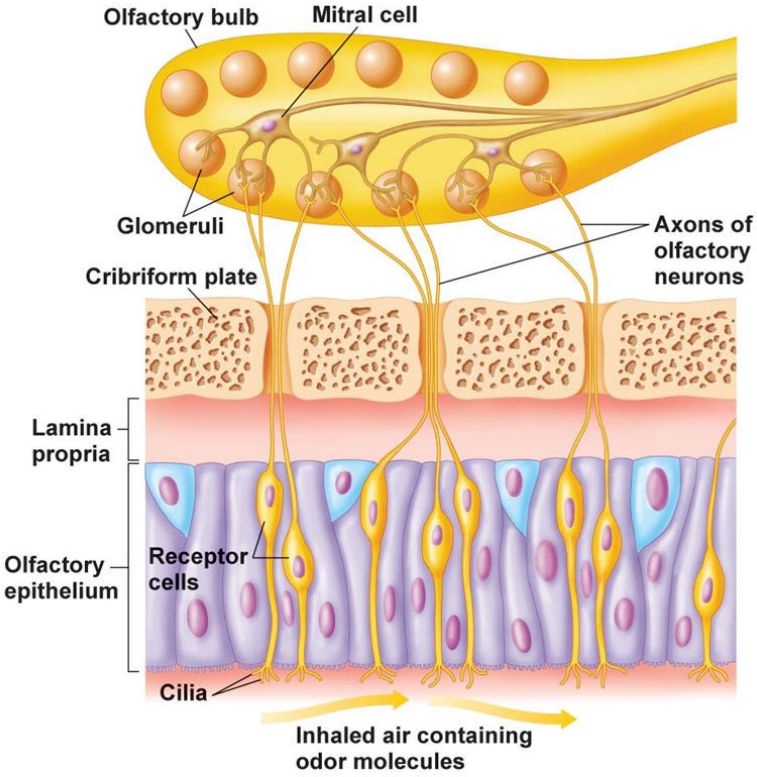


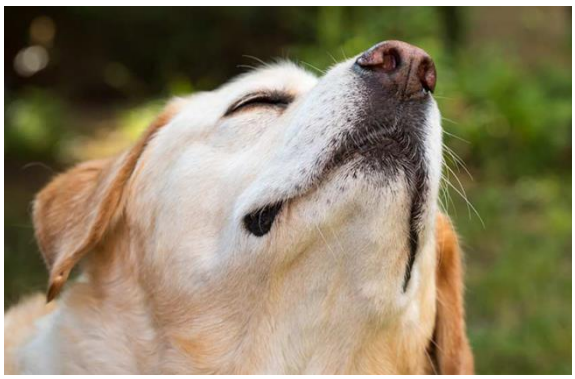
Figure 11.30 Olfactory epithelium in the nasal cavity consists of supporting cells, basal cells and olfactory receptor cells. Basal cells replace olfactory receptor cells.

Neural Pathway for Olfaction

The receptors cells in the olfactory epithelium have processes that create the **olfactory nerve**. The axons of these neurons synapse with second-order neurons called **mitral cells** and release the neurotransmitter **glutamate** within structures called **glomeruli** (the same name as the structure in the kidneys, meaning 'ball of yarn'). These structures help to create the bulbous **olfactory bulb** that sits upon the cribriform plate of the ethmoid bone of the skull. The second-order neurons form the **olfactory tract** which goes to the **olfactory tubercle**. From here, the olfactory information, unlike the other special senses, bypasses the thalamus and either goes to the **olfactory cortex** concerned with the discrimination of smells, or to the **limbic system** for triggering olfactory-driven behaviors, such as sexual behaviors.

Smelling Sensitivity

All odors we perceive are molecules in the air, in fact, if a substance does not release gaseous molecules into the air it will have no smell to us. Also, if the olfactory system does not have a receptor to bind and recognizes a specific molecule, it will also have no smell to us. We have approximately **350 olfactory receptor subtypes** that are able to work in various combinations and allow us to sense about **10,000 different odors**. If that seems like a lot, hold on.



Most of us have experienced that **dogs** have a very good sense of smell. True, dogs are able detect fragrances about 300 times better than humans can. Knew it! However, did you know that **bears** have even more olfactory receptors than dogs! For instance, the scent-detecting portion of a grizzly bear's nose is one hundred times bigger than that of human's. To put things into perspective, bears are known to be able to smell **100 times better than dogs**.

Now, hold on to your trunks, because although bears are very sensitive and charming, it is the **elephant** who has more olfactory receptors than any other mammal. Apparently, they can sniff out food several miles away, and can detect water sources up to 12 miles (19 km) away.

Snakes also do well in terms of having a strong sense of smell, which they use to make up for their poor eyesight and limited hearing. While they smell scents through their nose, this sense is heightened by a pair of organs located at the roof of their mouth, called the **vomer-nasal** organ, which humans also possess.

When mammals live in water, it seems their sense of smell usually diminishes, and a good example is the cetaceans, which are **whales** and **dolphins**. The **humpback whale** to the right has very little sense of smell, in common with dolphins. At the same time these animals have incredible hearing abilities in the water. This is a good example of **sensory trade-offs**, which often occurs when a reduction or absence of a sensory modality specialization in one sensory modality may lead to the enhancement and augmentation of other sensory modalities.

Gustation - The Sense of Taste

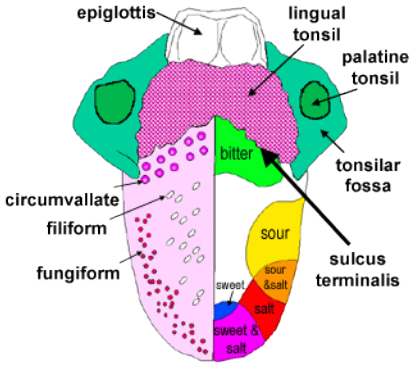
Gustation, or the sense of **taste** is the special sense associated with the **tongue**. The **taste buds** for gustation are located on the tongue, though there are others taste receptors distributed throughout the oral cavity and in the pharynx (through), but predominantly they are on the **tongue papillae**., these are raised bumps called (singular papilla) that contain the structures for **gustatory transduction**.

Gustatory cells, the receptor cells of the taste buds, have **gustatory hairs** (**microvilli**) that serve as the receptor. The gustatory cells are excited by the binding of chemicals to receptors on their microvilli.

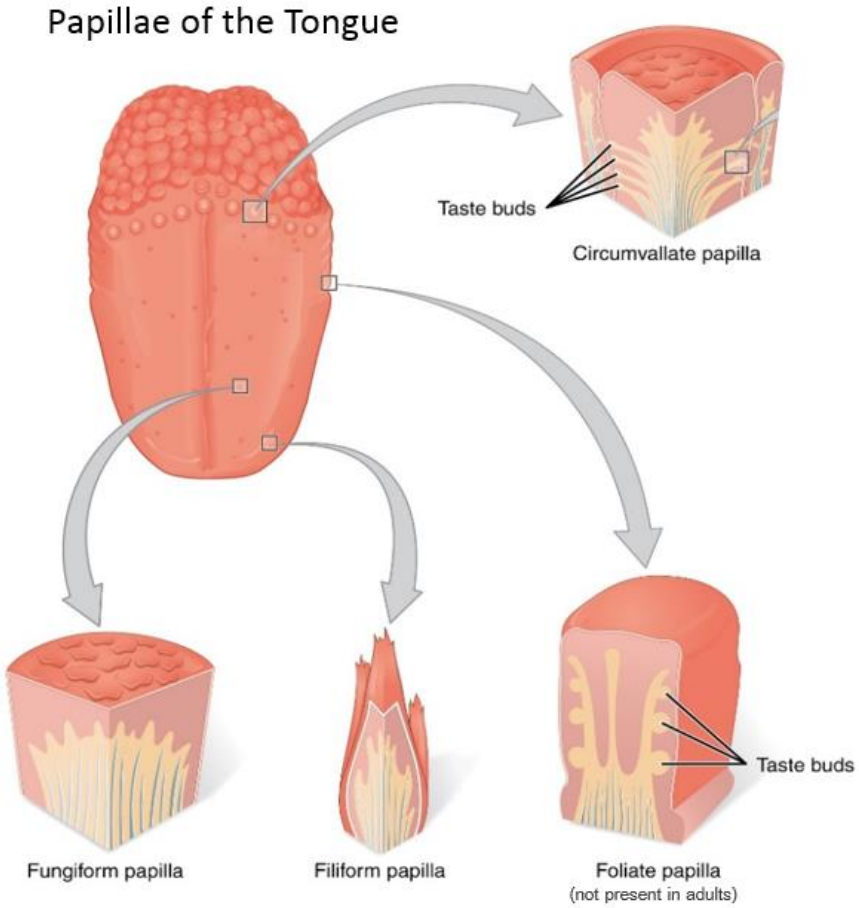
The Papillae of the Tongue

There are three main types of papillae, based on appearance. They are:

1. Circumvallate (to surround)
2. Filiform (filum - thread like)
3. Fungiform (mushroom like)
4. ~~Foliate (lead shaped)~~ Not really present!



The most numerous of the lingual papillae are the **filiform papillae**. They are fine, small, cone-shaped papillae covering most of the dorsum of the tongue. They are responsible for giving the tongue its texture and are responsible for the sensation of **touch**.



The **circumvallate papillae** contain taste buds along the sides of whorls and are located in the posterior third of the tongue in the shape of a V (see **Figure 11.31** left and above).

The **fungiform papillae** are raised lingual structures which contain taste buds. They vary in number due to their relative sensitivity to a range of factors that may affect the dorsum (upper exposed surface of the tongue of the tongue), mostly concentrated on the sides and the tip of the tongue. The **foliate papillae** are much less numerous than the types, and many contend that adult humans do not have any of these papillae. If they are found at all, they are at the dorsolateral (back and side) corners of the tongue, where they define the edges of a series of grooves

Figure 11.31 Shown here is the tongue and the four different types of papillae present on its surface; the circumvallate, the foliate, the filiform, and the fungiform. Note that the foliate papilla is not present in human adults.

Tastes

Gustatory cells, the receptor cells of the taste buds, have **gustatory hairs** (**microvilli**) that serve as the receptor. The gustatory cells are excited by the binding of chemicals to receptors on their microvilli (see **Figure 11.31** below).

There are **five recognized basic taste qualities—sweet**, **sour**, **salty**, **bitter** and **umami**. Umami is a Japanese word that means 'delicious taste'" and is often translated to mean savory. Recent studies suggest there may also be a sixth taste for **lipids** (fat).

Interestingly, the savory umami taste is attributable to the taste of the amino acid **L-glutamate**. This is why **monosodium glutamate** (MSG) is often used in food preparation, to enhance the savory taste of those foods. The use of flavor enhancers such as MSG, especially prevalent in processed 'snack foods', is known to also stimulate appetite, in addition to having the effect of not being able to stop eating the item. It was MSG that was used in 1950's experiments to make study animals obese to measure the effects of diet pills. The significant problem with adding high levels of flavor enhancers such as MSG, is that it contains **glutamate** which is an **excitatory** neurotransmitter. After digestion, this enters the blood stream, and although the brain is protected by the **blood brain barrier**, there are parts of the hypothalamus which lack this protective layer in order to incorporate the hypothalamic-hypophyseal portal system (see chapter 12). This means that certain regions of the hypothalamus are vulnerable to the effects of high levels of glutamate from substances ingested, and in these instances glutamate can act as an **excitotoxin**, as it can over-excite tissue response to it.

On the surface of the tongue are the various papillae. Within those papillae are **taste buds** nestled in between lingual epithelium.
There is a shallow dip called a **taste pore** that leads to the hair-like specialized **gustatory receptor cells** for the transduction of taste stimuli (see **Figure 11.31** at right). The lower **basal cells** are not involved in tasting, but these differentiate into taste receptor cells. There is a high turn-over of taste receptor cells, they are replaced about every 10 days.

These taste **receptor cells** are sensitive to the chemicals contained within foods that are dissolved in **saliva**. When the chemicals bind, and trigger the receptor cell, they release the neurotransmitter **acetylcholine** (ACh) predominantly, which is release is in proportion to the amount of the chemical stimulus form the substance. The release of neurotransmitters from the gustatory cells on the tongue activates the sensory component of the **facial**, **glossopharyngeal**, and **vagus** cranial nerves.

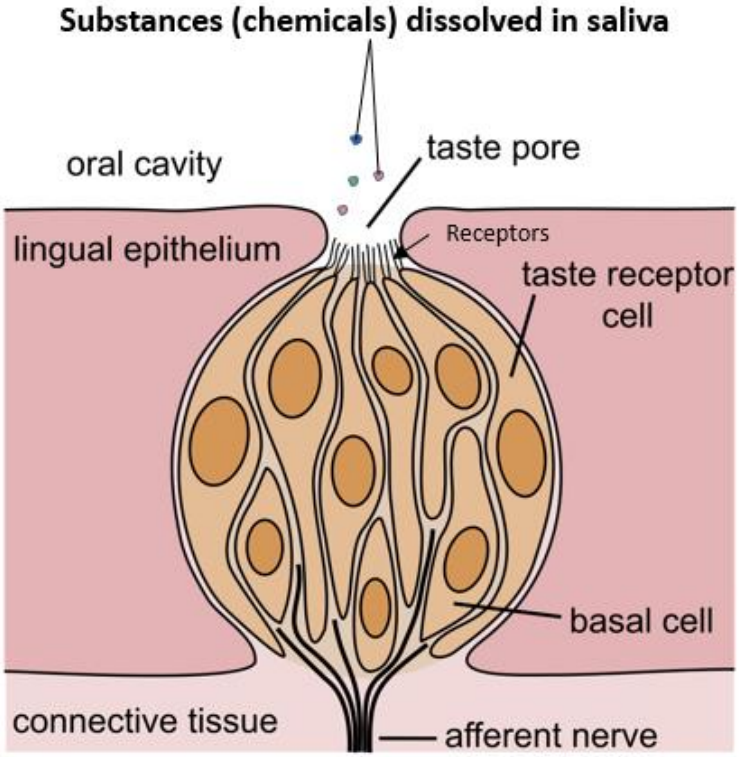


Figure 11.32 This is an example of gustatory receptor cells within a taste bud. The chemical substances dissolved in the oral cavity, move into the pore and stimulated the gustatory hair cell receptors.

As chemicals in food make contact with the **taste receptor**, the specific types of chemicals bind with taste receptor cells, and generate nerve impulses that travel through afferent nerves to the CNS. There are separate taste receptors for sweet, salty, sour, bitter, and savory tastes. The taste sense is served by cranial nerves VII, IX, and X, which send impulses to the solitary nucleus of the medulla. From there, impulses are sent to the **thalamus** and the **gustatory cortex** on the anterior *insula lobe* and the frontal operculum on the **frontal lobe**.

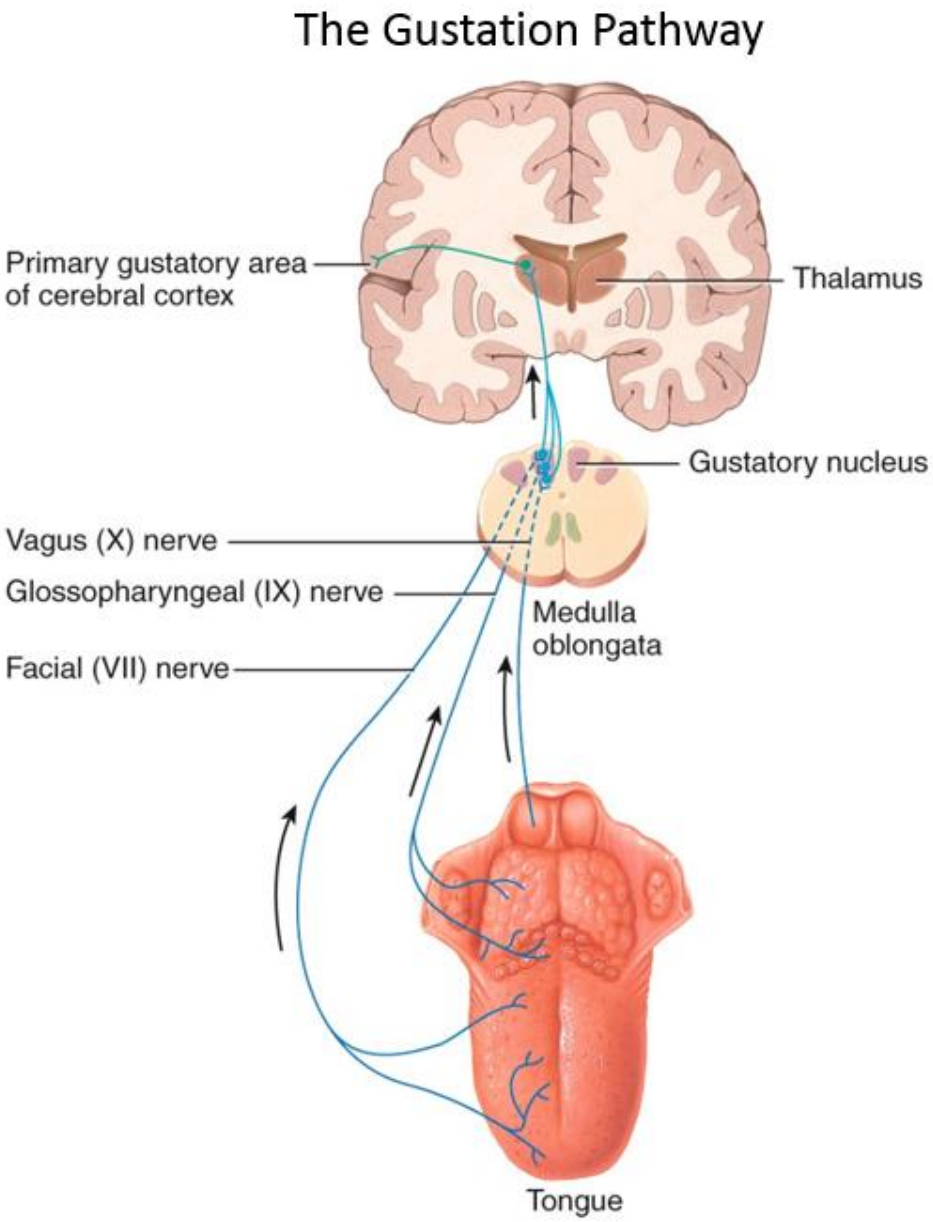


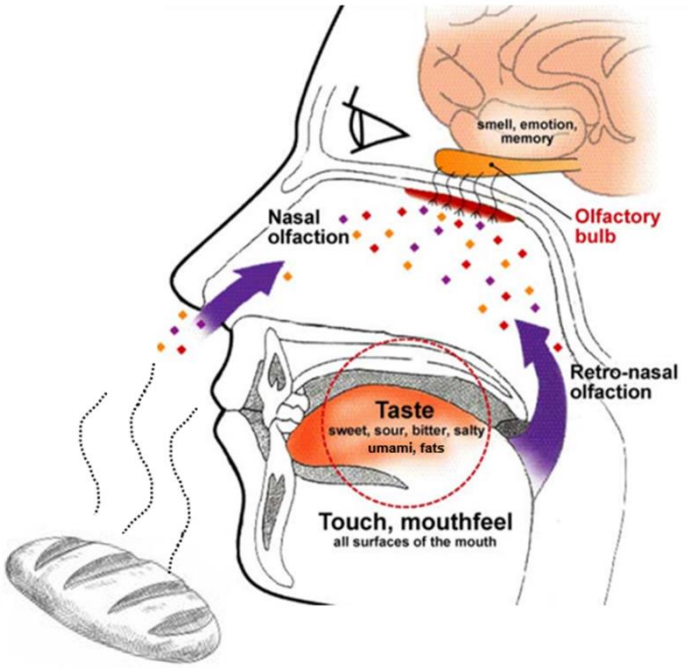
Figure 11.33 The gustation (taste) pathway from the chemoreceptors on the tongue, the gustatory nuclei of the medulla, through the gateway to the cerebrum of the thalamus and finally to the primary gustatory cortex predominantly of the insula lobe. Note that there are three cranial nerves that bring in gustatory information (taste sensation) from the tongue, they are the facial N. (VII), the glossopharyngeal N. (IX) and the vagus N (X) from different regions of the tongue.

The senses of taste and olfaction both rely on the detect chemicals, thus the receptors used are **chemoreceptors**. Both types of chemoreceptors send nerve impulses to the brain along sensory nerves, and the brain “tells” us what we are tasting or smelling.

Taste Discrimination With and Without Olfactory Sensation

The sensations of taste (gustation) and smell (olfaction) are detected by **chemoreceptors**. As we have seen, the epithelial surface of the tongue contains taste receptors which are specialized cells grouped into barrel-shaped structures called **taste buds**. As we also know, the receptors for the sense of smell are located in the olfactory cells in the mucous membrane lining of the upper portion of the nasal cavity. Only volatile substances (gaseous molecules) in solution can stimulate these receptors.

The gaseous particles enter the nasal cavity by diffusion from the circulating air in the external environment. Glands that surround olfactory cells secrete fluid in which the particles dissolve and this solution acts as a chemical stimulus to a nerve impulse (see **Figure 11.34** below).



Does taste sensation depends on the ability to smell? If a person bites a lemon, the solution in the mouth stimulates chemoreceptors on the tongue. The chemicals act as the *stimuli* to activate *chemoreceptors*. Once activated, they send signals to specific regions of the brain that recognize and interpret the stimulus. Although there are only five basic modalities for taste (**sour**, **sweet**, **salt, bitter, umami and lipids**), the combination of these together with the sense of olfaction, provides a wide variety of different sensory experiences regarding gustation or taste.

Figure 11.34 Odorants stimulate receptor proteins found on hair-like cilia at the tips of the sensory cells, a process that initiates a neural response. Ultimately, messages about taste and smell converge, allowing us to detect the detailed specific flavors of food. Acquiring information related to scent through the back of the mouth is called retro-nasal olfaction, and via the nostrils is called ortho-nasal olfaction. Both methods influence flavor; aromas such as vanilla, for example, can cause something perceived as sweet to taste sweeter.

Pheromones

There are substances called **pheromones** that are produced and released into the outside environment by an individual and received by another individual of the same species.

In humans the detection of this signal can affect the behavior or physiology of other people. The detection of pheromones varies, while some can be consciously perceived with a discernable scent, others are not consciously recognized as fragrances the way we experience other odors. Humans have innate responses to other individuals and much information can be transmitted by signals like **pheromones**. The brain and other organs respond to pheromones which can trigger many responses, such as bonding between mother and child, or between companions in various relationships. For example, **oxytocin** functions both as a **hormone** (within an individual's body), and as a **pheromone** for communication between two or more individuals, in such a way as to strengthen emotional bonds between people.

Scent Glands

There are modified apocrine sweat glands at specific locations in the body, such as the axilla (under arms) the inguinal regions (groin) and the anus. There are also sebaceous (oil) glands prevalent in hair-bearing skin, which produce 'odorless' secretions. When **pheromones** are emitted from sweat glands, these can be referred to as **scent glands**, as they play an important role in sexual attraction, sexual repulsion, mother-infant bonding, menstrual cycles, and more. The 'dormitory syndrome' can is seen when women who live in close proximity together experience synchronization of their menstrual cycles.

We'd perhaps all like to think that our cats adore us and that when they rub their cheek against our leg it's a sign of unrelenting affection. Sure. Keep in mind that this is their method for the application of their pheromones to mark their territory. It is sweet that they want to mark you as theirs.

Certain pheromones are **attractants** to potential mates, others are **repellants** to potential competitors of the same sex, and still others play roles in interpersonal attachment. Some pheromones can also influence the timing of puberty, modify reproductive cycles, and even prevent embryonic implantation.

The sex pheromones that play a role in the attraction that one individual might feel for another is where the notion of having "chemistry" with someone is very literal. Here is an example. The molecule **androstenol** is derived from **testosterone** and is a putative sex pheromone for both males and females. Specifically**,** *androstenol* is the scent produced by <u>fresh male sweat</u>, deemed attractive to females. Whereas, after this sweat is exposed to oxygen it converts into *androstenone* and becomes <u>stale sweat</u>, and this is not typically perceived as very pleasant by females. But wait, there's more. This androstenone in stale sweat can smell like either **urine** or **vanilla**, depending on the genetic make-up of the *smeller*, not due to the fragrance produced by the *smellee*. Thus, some people will perceive androstenone as a foul odor (like stale urine or strong sweat), whilst others will find the fragrance to be a sweet and pleasant scent, similar to that of a vanilla wafer. Still others will not be able to smell it at all.

Urine

Vanilla

Appealing Fragrances

There are some similarities and differences between Men and Women with regard to the fragrances that are generally appealing to them. In general here are the top fragrances for each.

Men: Vanilla, licorice, citrus (orange), pumpkin pie, lavender, cinnamon.
Women: Vanilla, peppermint, sandalwood, coffee, lavender, cinnamon.

Testosterone is a key element in the sex pheromones. **Zinc** (Zn) is mineral that has been proven to increase testosterone levels. Since we cannot make this mineral, we need to get it from foods that contain it, such as: Oysters, Shellfish, Wheat germ, Wheat bran, Chicken, Peanuts, Eggs, and Milk. This is a reminder that what we eat is important as it serves as a potential basis for many of the chemicals we manufacture in our bodies for a multitude of functions.

The topic of pheromones can be complex, and this form of communication is particularly important in many animal species, where there are several different types of pheromones which can be released from urine, from sweat, or as glandular secretions. Now the question is how are these signals detected? By specialized **receptors** of course.

Vomeronasal Organ

The vomeronasal organ (VNO), also called Jacobson's organ, is an accessory olfactory organ situated on the anterior inferior (front lower) third of the nasal septum (see Fig X below). It is composed of a blind sac with a duct opening anteriorly connecting to the nasal cavity. It is very sensitive to **pheromones**, and when molecules dissolve in the mucosa of the nasal cavity, they enter the VNO where the pheromone molecules among them bind with the specialized **pheromone receptors**. This region can have a rich vascular and glandular network for relaying the signals.

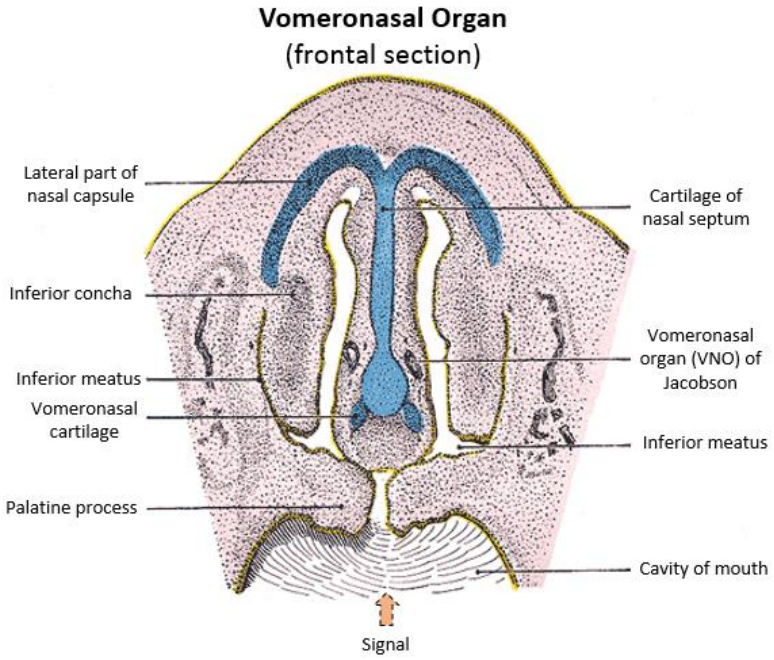


Figure 11.35 Seen above in a frontal section of the nasal cavity, the vomeronasal organ (VNO) is located in the basal portion of the nasal septum. It functions as a component the olfactory system to detect pheromones from other people. These substances can be detected consciously as having a fragrance, and they can also be undetectable consciously, either way they activate the receptors in the VNO. Often pheromones contain information that can trigger behavioral changes or responses to other individuals.

Neural and Synaptic Pruning

There is a natural process of removing excessive, irrelevant synapses in neural networks at various stages of development, and this referred to as **neural or synaptic pruning**. It involves the reduction of both

neurons and synapses. Neural pruning commences near the time of birth and continues into the mid-20s. This process of synapse elimination occurs at various phases between early childhood and the onset of puberty in humans.

The concept of synaptic and neuronal pruning is akin to pruning plants in the garden. This action reduces the spread of connections of a plant, but strengthens the base and foundation of connections. The key is to have many neuronal connections **prior** to pruning, and the most effective way to have a highly interconnected nervous system is to be **active and engaged** with reality from a very young age. Constant positive stimulation causes synapses to grow and become permanent. However, if a young child receives limited stimulation or attention, the nervous and sensory system will maintain fewer of those connections.

The Damaging Effect of watching TV

A mountain of evidence demonstrates that children watching television or using screen viewing devices before the age of 18 months will have lasting **negative effects** on a host of their cognitive abilities. These include language development, reading skills, and short term memory. It also contributes to problems with sleep and attention. In addition, large periods of time spent watching TV degrades the cohesiveness of any family. Negative effects include inhibiting children's social development by diminishing the number of conversations between them and their family members.

The natural, healthy and most effective way for a child to develop is from interacting with other healthy people whose faces can be fully seen (i.e., without a face mask on) to show the full range of human facial expressions of emotion. It is literally damaging to all involved to engage in fearful face covering which inhibits natural breathing, causing hypoxia and hypercapnia (see respiratory section), in addition to the subconscious hiding of oneself and your identity behind a mask. Just like being in an irresponsible mob, or making unkind comments anonymously online, hiding behind a facemask out of irrational fear creates hollow people who can be easily transformed in their behavior by the 'new normal' of unhealthy practices employed vindictively out of fear and anxiety.

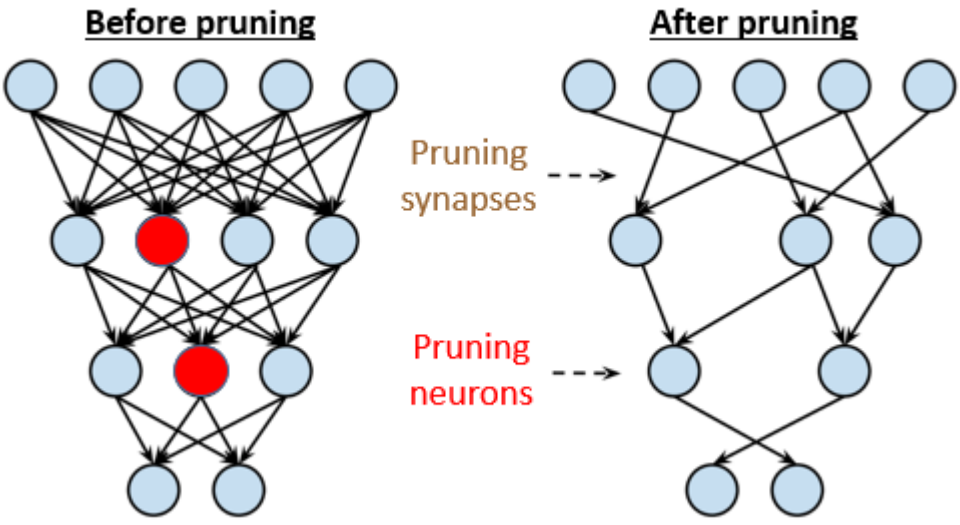


Figure 11.36 On the left, the diagram shows the highly interconnected arrangement of having many associations of synapses between neurons in the developing brain before pruning. On the diagram to the right shows the reduction in the number of synapses and neurons after pruning has occurred.

Old, unused synapses and neurons that are no longer used or useful are removed in the brain during pruning, thus it is critical maintenance that must be done. However, when the process is not done properly, it can lead to other issues.

Too much neural pruning: Removing too many of the pathways will limit the ability of the brain to make the interconnections that allow for sophisticated thinking and intentionally linking concepts that have an underlying association or relationship. This type of situation can be seen in **autism**, with people who show a limited ability to interconnect ideas. For example, those who have a limited capacity to understand analogies or idiomatic expressions, or who cannot empathize with other.

Too little neural pruning: Although it may sound like a great idea that your brain circuitry is heavily interconnected, this arrangement can be similar to having an overloaded circuit board, where there is too much information to process. If not enough reducing of the synapses occurs during development, the massive interconnections that exist in an early developing brain will persist. Conditions like synesthesia (see below) are thought to be an example of reduced synaptic pruning, such that the perception of colors may also involve notes of a musical tone. Great artists, those with a good sense of humor, or who understand cryptic metaphors etc., are likely have greater synaptic circuitry, but they may also find it too difficult to focus on specific issues or tasks.

Examples of Combining of Various Senses or Loss of Perception

Synesthesia

The word 'synesthesia' has origin in Greek 'syn' meaning union, and aesthesis, meaning sensation. Therefore it means '**a union of the senses**'.

At the crux of synesthesia is the experience of one sensory stimulus through the prism of a different stimulus. For example, it may involve **hearing** music and **seeing** colors in your mind is an example of synesthesia. For instance, the note C may have a blue color. Or having colors visualize specific numbers or letters of the alphabet. According to researchers, the most common form of synesthesia is **colored hearing**. This is when sounds, music or voices can be seen as colors. Often it is reported seeing sounds internally, in "the mind's eye".

It may be that about 1 in 2,000 people are 'synesthetes', but it may be that 1 in 300 people have some degree of the condition. Much is unknown about this overlapping of sensory perceptions, but it is thought that it involves highly integrated neuronal networking throughout the brain. The limbic system is also central to the synesthetic experiences, as it is contains structures primarily responsible for regulating related our emotional responses to sensations.

One of the rarest types of synesthesia **lexical–gustatory synesthesia**, or **taste** synesthesia. It involves people who have associations between **words** and **tastes**, causing individuals to experience an automatic and highly consistent taste/smell with certain spoken words and written language (as well as some colors and emotions).

Prosopagnosia

The condition of **prosopagnosia** is also known as **face blindness**, because people cannot recognize people's faces. The origin of the word is from the Greek **prosopa**, meaning 'faces', and **agnosia** (the prefix a meaning 'without' and gnosis 'knowing'), so the term literally means '**not knowing faces**'. Often, all other sensory input yields accurate perceptions, therefore this is a **failure of sensory perception** in the brain, and not a failure of sensory input. It seems to affect people from birth and persists and has varying degrees of severity, with some who may not even recognize their own face.

A study suggest may involve the **anterior fusiform gyrus of the temporal lobe**, where it is not developed enough. This region of the brain is concerned with the recognition of visual stimuli and may be where facial recognition occurs. It's hard enough not paying attention to a face or a name, but not being able to perceive faces must be a very challenging experience. However, people with this condition often use their **other sense** as cues to recognize people they see. The sound of a person's voice is incredibly distinctive. Their gait (manner of walking), hair color, fragrances, clothes can also assist in indicating who they are.

Macular Degeneration of Retina

The most common cause of **blindness** is age related **macular degeneration.** About 196 million people are affected worldwide. The disease occurs with the death of a layer of cells called retinal pigment epithelium, which normally provides nutrients and other support to the macula of the eye.

The **macula lutea** is an oval-shaped pigmented area near the center of the retina which has the density of **cone photoreceptors** (for color). These specialized in high visual acuity. When the epithelial cells die and the macula is no longer supported or nourished, the macula also starts to die, including the cone photoreceptors. Patients experience a black spot in the center of their vision, and as the disease progresses, the black spot grows outward. Patients eventually lose the ability to read and even to recognize familiar faces before developing total blindness.

A great idea is to look after your eyes, rather than hope for some creepy transplant from who knows what source! Adequate blood supply is key, so avoid all the risk factors that would block your arteries, such as refined sugar, alcohol, birth control pills, smoking (anything!) trans fats (not saturated, they are excellent for your health!), etc.

The Stroop Effect

This is a simple phenomenon that indicates how the brain processes information. A psychologist John Ridley Stroop first described this in the 1930s. The Stroop effect is a phenomenon that occurs when **you must say the color of a word but not the name of the word**. It becomes a difficult experience to name a physical color when it is used to spell the name of a different color. For example, blue might be printed in red and you must say the color rather than the word!

Reflexes

Reflexes are rapid, automated, stereotyped responses to sensory stimuli that are usually protective. Reflexes do not require higher brain activity, that is, they can be considered a "subconscious" or “involuntary” action.

Voluntary response follow the same basic neural pathway but with varying integrations centers that enable conscious control.

Concluding this section we examine the concept of **feedback mechanisms** for reflex actions and apply them to many of the special senses we have already discussed

A ‘**reflex arc**’ is just an automated feedback loop, and a common example is illustrated below. It shows the all the components of the feedback loops form the introductory section. This time it is a painful stimulus that starts to reflex. Someone left a tack face up on the lawn, darn it! Shown below is an example of the ‘withdrawal reflex’, which involves a rapid, automatic withdrawal of the limb experiencing a painful stimulus. This s a type of ***polysynaptic spinal reflex***.

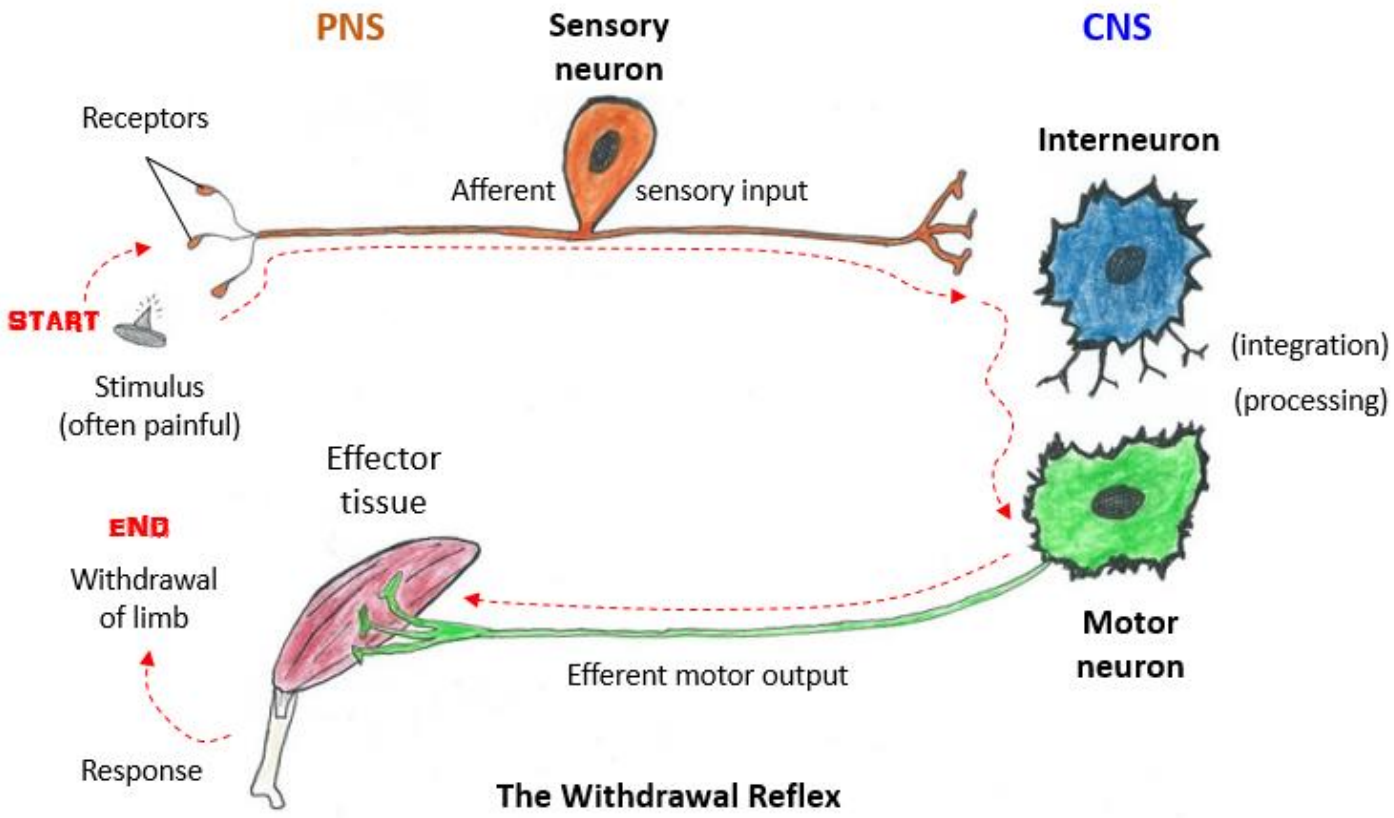
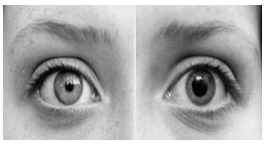


Figure 11.37 This arc shown above, starts, as they always do, with a stimulus. The damage caused by the tack triggers nociceptors, which are specialized endings of the sensory neuron, sends incoming sensory signals into the central nervous system (CNS) communicating with interneurons. A process of integration and information processing occurs here and then the motor neuron takes the command efferent information back out into the peripheral nervous system (PNS) to the effector tissue, in this case, skeletal muscle and the response is a withdrawal of the body part that is in danger.

Pupillary Reflexes

Adaptation to changes in light intensity.

The pupil is the hole in the iris (the colored portion of the eye) and it controls the amount of light that can enter the eye (shown in **Figure 11.38** below). The iris is complex and is composed of two different arrangements of contractile tissue in order to change the diameter of the pupil. They are: **1) sphincter muscle** on the inner aspect (also known as the pupillary sphincter); and **2)** the **radial muscle**.



- The **sphincter muscle** when contracted closes down and constricts the pupil.
- The **radial muscle** when contracted pulls the pupil open, dilating the pupil.

The **pupillary light reflex** controls the diameter of the pupil and therefore regulates intensity of light entering the eye. This pupillary reflex is in response to the **intensity** (luminance) of the light that falls on the ganglion cells of the retina in the back of the eye, thereby assisting in **adaptation** of vision to various levels of lightness. What happens, **automatically**, is that when there is high light intensity, sphincter muscle contracts decreasing pupillary diameter via the parasympathetic division of the ANS, to protect the retina. When the light levels are low, the radial muscle contracts, which opens up the pupil during low light levels. Increasing pupillary diameter via the sympathetic division of the ANS, in order to improve vision, especially distant focus.

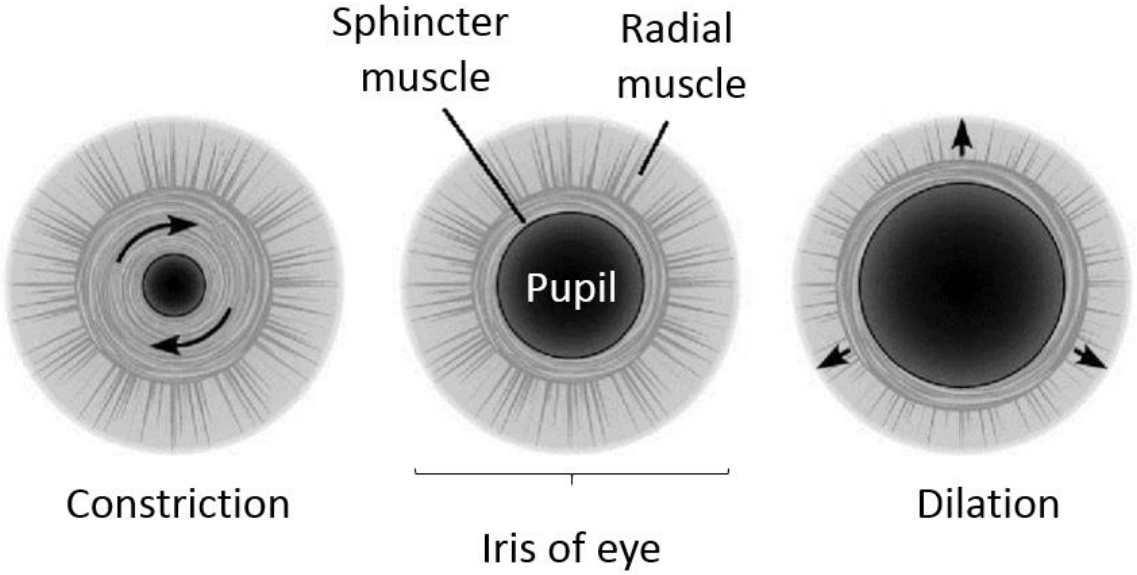


Figure 11.38 The pupil is the hole in the center of the iris, which is the colored part of the eye and contains contractile tissue. On the left, the sphincter muscle contracts creating a smaller pupillary diameter in response to high intensity of light. On the right, the radial muscle contracts, which opens up the pupil during low light levels.

The pupillary light reflex is **consensual**, meaning even if only one eye receives the stimulus, both eyes will respond in the same way. In terms of medical terminology with reference to the pupil of the eye. **Myosis** means constriction of the pupil. **Mydriasis** means dilation of the pupil.

Corneal Reflex

The eye are important to protect, and there are other reflexes. For instance the "corneal reflex" is also known as the **blink reflex**. It is triggered by stimulation of the cornea and can also be stimulated by loud sounds, which are greater than 40–60 dB. The corneal reflex uses the trigeminal nerve (cranial nerve V) as its afferent loop, and the facial nerve (cranial nerve VII) as its efferent loop.

Gag Reflex
The gag reflex (pharyngeal reflex) is a contraction of the back of the throat triggered by an object touching the roof of your mouth, the back of your tongue, the area around your tonsils, or the back of your throat.

Sneeze Reflex
A sneeze (or sternutation) is expulsion of air from the lungs through the nose and mouth, most commonly caused by the irritation of the nasal mucosa. Most of these reflexes (sneeze, vomit, gag, and cough) are coordinated via cranial nerves and processed through the medulla oblongata (see CNS section).

Vomit Reflex
Vomiting is a protective reflex, which may be triggered by a wide variety of gastrointestinal or higher brain centers. The three components of vomiting are 1) nausea, 2) retching ("dry heaves"), and 3) emesis, which is ejection of contents from the stomach through the mouth.

Cough Reflex
The cough reflex is protective of the airways and lungs against aspiration (breathing in foreign objects into the lungs), inhaled irritants, particulates and pathogens and clears the air spaces of accumulated secretions. The forceful coughing is initiated by afferent vagal nerves.

Review Questions for Chapter 11: The General and Special Sense

1. A sensation is:
- **a)** The perception of a signal.
- **b)** Input obtained by sensory receptors.
- **c)** The selection creation and organization of meaningful patterns from sensory information.
- **d)** The process of detecting different types of energy (stimuli) in our brains

2. In terms of sensory receptor classification by origin of stimuli, olfaction is:
- **a)** An exteroceptor
- **b)** A chemoreceptor
- **c)** A mechanoreceptor
- **d)** An interoceptor
- **e)** A visceroceptor

3. The function of a sensory receptor is to act as a/an _____.
- **a)** electrical signal
- **b)** frequency modifier
- **c)** transducer
- **d)** action potential

4. In terms of adaptation, baroreceptors that detect blood pressure _____.
- **a)** detect pressure
- **b)** are tonic
- **c)** are phasic
- **d)** are fast to adapt

5. A Ruffini's end organ detects _____; while Krause's end bulbs detect _____.
- **a)** stretching pain; heat
- **b)** pressure; cold
- **c)** bending of hair; heat
- **d)** light touch; tickle or itch
- **e)** skin stretch; cold

6. The choroid of the eye is:
- **a)** A gland that secretes fluid to lubricate the eye and wash away foreign particles.
- **b)** The 'white of the eye' – an opaque, fibrous, protective layer.
- **c)** A layer containing arteries and veins that contains the black pigment melanin.
- **d)** The thin lining of the eye that contains rods, cones and ganglion cells.
- **e)** A thin layer of epithelium that lines the eyelid and covers the sclera.

7. Which of the following anatomical structures would <u>not</u> be found in the ear?
- **a)** olfactory glomerulus
- **b)** cochlea
- **c)** tympanic membrane
- **d)** incus
- **e)** semicircular canal

8. Which of the following cranial nerves does <u>not</u> transmit taste information to the brain?
- **a)** Vagus nerve
- **b)** Facial nerve
- **c)** Glossopharyngeal nerve
- **d)** Trochlear nerve

9. About how many different odorant receptor subtypes are believed to exist in the human nose?
- **a)** 35
- **b)** 100
- **c)** 350
- **d)** 4,000
- **e)** 10,000

10. The structure(s) associated with sensing changes in the position of the head are:
- **a)** The ossicles
- **b)** The cochlea
- **c)** The fovea
- **d)** The incus and stapes
- **e)** The semicircular canals

Answers in Appendix B