Chapter 12
SENSATIONS

Student Learning Objectives

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2. Describe the location and function of the receptors for tactile, thermal, and pain sensations. 3
3. Identify the receptors for proprioception and describe their functions. 3
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Most of us are aware of sensory input to the central nervous system (CNS) from structures associated with smell, taste, vision, hearing, and balance. Input from structures associated with tactile sensations (touch, pressure, vibration), thermal sensations (warm and cold), pain, proprioceptive sensations (position of body parts), and visceral sensations (conditions within internal organs) are just as important to the maintenance of homeostasis.

OVERVIEW OF SENSATIONS

Objective: Define a sensation and describe the conditions necessary for a sensation to occur.

Consider what would happen if you could not feel the pain of a hot pot handle or an inflamed appendix, or if you could not see, hear, smell, taste, or maintain your balance. In short, if you could not “sense” your environment and make the necessary homeostatic adjustments, you could not survive very well on your own.

Definition of Sensation

Sensation is the conscious or subconscious awareness of external or internal conditions of the body. For a sensation to occur, four conditions must be satisfied:

1. A stimulus, or change in the environment, capable of activating certain sensory neurons, must occur.
2. A sensory receptor must convert the stimulus to nerve impulses.
3. The nerve impulses must be conducted along a neural pathway from the sensory receptor to the brain.
4. A region of the brain must receive and integrate the nerve impulses into a sensation.

A stimulus that activates a sensory receptor may be in the form of light, heat, pressure, mechanical energy, or chemical energy. A sensory receptor responds to a stimulus by altering its membrane’s permeability to small ions. In most types of sensory receptors, the resulting flow of ions across the membrane produces a depolarization called a generator potential. When a generator potential is large enough to reach the threshold level, it triggers one or more nerve impulses that are conducted along the sensory neuron toward the CNS.

Sensory receptors vary in their complexity. The simplest are free nerve endings that have no visible structural specializations (for example, pain receptors). Receptors for other general sensations, such as touch, pressure, and vibration, have encapsulated nerve endings. Their dendrites are enclosed in a connective tissue capsule with a distinctive microscopic structure. Still other sensory receptors consist of specialized, separate cells that synapse with sensory neurons.

Characteristics of Sensations

Conscious sensations or perceptions are integrated in the cerebral cortex. You seem to see with your eyes, hear with your ears, and feel pain in an injured part of your body. This is because sensory impulses from each part of the body arrive in a specific region of the cerebral cortex, which interprets the sensation as coming from the stimulated sensory receptors.

The distinct quality that makes one sensation different from others is its modality. A sensory neuron carries information for one modality only. Neurons relaying impulses for touch, for example, do not also transmit impulses for pain. The specialization of sensory neurons enables nerve impulses from the eyes to be perceived as sight, and those from the ears to be perceived as sounds.

A characteristic of most sensory receptors is adaptation, a decrease in sensation during a prolonged stimulus. Adaptation is caused in part by a decrease in the responsiveness of sensory receptors. As a result of adaptation, the perception of a sensation decreases even though the stimulus persists. For example, when you first step into a hot shower, the water may feel very hot, but soon the sensation decreases to one of comfortable warmth even though the stimulus (the high temperature of the water) does not change. Receptors vary in how quickly they adapt. Rapidly adapting receptors adapt very quickly and are specialized for signaling changes in a particular stimulus. Receptors associated with pressure, touch, and smell are rapidly adapting. Slowly adapting receptors, in contrast, adapt slowly and continue to trigger nerve impulses as long as the stimulus persists. Slowly adapting receptors monitor stimuli associated with body positions and the chemical composition of the blood.

Classification of Sensations

The senses can be grouped into two classes: general senses and special senses.

1. The general senses include both somatic senses (soma- = of the body) and visceral senses. Somatic senses include tactile sensations (touch, pressure, and vibration); thermal sensations (warm and cold); pain sensations; and proprioceptive sensations, which allow perception of both the static positions of limbs and body parts (joint and muscle position sense) and movements of the limbs and head. Visceral senses provide information about conditions within internal organs.
2. The special senses include smell, taste, vision, hearing, and equilibrium (balance).
Classification of Sensory Receptors

Sensory receptors are classified on the basis of their location (exteroceptors, interoceptors, and proprioceptors), the type of stimulus that activates them (mechanoreceptors, thermoreceptors, nociceptors, photoreceptors, and chemoreceptors), and their degree of complexity (simple receptors, complex receptors). Table 12.1 describes each of these categories.

<table>
<thead>
<tr>
<th>A. Location</th>
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<tbody>
<tr>
<td>1. <strong>Exteroceptors</strong> (eks-ter-ō-SEP-tors). Located at or near surface of body; provide information about external environment; transmit sensations of hearing, sight, smell, taste, touch, pressure, temperature, and pain.</td>
</tr>
<tr>
<td>2. <strong>Interoceptors</strong> (in-ter-ō-SEP-tors). Located in blood vessels and viscera; provide information about internal environment; transmit sensations such as pain, pressure, fatigue, hunger, thirst, and nausea from within the body.</td>
</tr>
<tr>
<td>3. <strong>Proprioceptors</strong> (prō-pre-ō-SEP-tors). Located in muscles, tendons, joints, and the internal ear; provide information about body position and movement; transmit information related to muscle tension, position and tension of joints, and equilibrium (balance).</td>
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<th>B. Type of stimulus</th>
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<tr>
<td>1. <strong>Mechanoreceptors</strong>. Detect pressure or stretching; stimuli are related to touch, pressure, proprioception, hearing, equilibrium, and blood pressure.</td>
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<tr>
<td>2. <strong>Thermoreceptors</strong>. Detect changes in temperature.</td>
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<tr>
<td>3. <strong>Nociceptors</strong> (nō-sē-SEP-tors). Detect pain, usually as a result of physical or chemical damage to tissues.</td>
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<td>4. <strong>Photoreceptors</strong>. Detect light in retina of eye.</td>
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<td>5. <strong>Chemoreceptors</strong>. Detect taste in mouth; smell in nose; and chemicals such as oxygen, carbon dioxide, water, and glucose in body fluids.</td>
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<th>C. Degree of complexity</th>
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<tr>
<td>1. <strong>Simple receptors</strong>. Simple structures and neural pathways that are associated with general senses (touch, pressure, heat, cold, and pain).</td>
</tr>
<tr>
<td>2. <strong>Complex receptors</strong>. Complex structures and neural pathways that are associated with special senses (smell, taste, sight, hearing, and equilibrium).</td>
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Classification of Sensory Receptors

Sensory receptors are classified on the basis of their location (exteroceptors, interoceptors, and proprioceptors), the type of stimulus that activates them (mechanoreceptors, thermoreceptors, nociceptors, photoreceptors, and chemoreceptors), and their degree of complexity (simple receptors, complex receptors). Table 12.1 describes each of these categories.

**SOMATIC SENSES**

**Objectives:**
- Describe the location and function of the receptors for tactile, thermal, and pain sensations.
- Identify the receptors for proprioception and describe their functions.

Somatic sensations arise from stimulation of sensory receptors embedded in the skin or subcutaneous layer; in mucous membranes of the mouth, vagina, and anus; in muscles, tendons, and joints; and in the internal ear. The sensory receptors for somatic sensations are distributed unevenly. Some parts of the body surface are densely populated with receptors, whereas other parts contain only a few. The areas with the highest density of sensory receptors are the tip of the tongue, the lips, and the fingertips. Somatic sensations that result from stimulating the skin surface are called **cutaneous sensations** (kyoo-TĀ-nē-us; cutane- = skin).

**Tactile Sensations**

The **tactile sensations** (TAK-til; tact- = touch) are touch, pressure and vibration, and itch and tickle. Itch and tickle sensations are detected by free nerve endings. All other tactile sensations are detected by a variety of encapsulated mechanoreceptors. Tactile receptors in the skin or subcutaneous layer include corpuscles of touch, hair root plexuses, type I and II cutaneous mechanoreceptors, lamellated corpuscles, and free nerve endings (Figure 12.1).

**Touch**

Sensations of touch generally result from stimulation of tactile receptors in the skin or subcutaneous layer. **Crude touch** is the ability to perceive that something has contacted the skin, even though its exact location, shape, size, or texture cannot be deter-
Elongated, encapsulated receptors located deep in the dermis, and in ligaments and tendons as well. Present in the hands and abundant on the soles, they are most sensitive to stretching that occurs as digits or limbs are moved.

### Pressure and Vibration

**Pressure** is a sustained sensation that is felt over a larger area than touch. Receptors that contribute to sensations of pressure include corpuscles of touch, type I mechanoreceptors, and lamellated corpuscles. **Lamellated** or **Pacinian corpuscles** (pa-SIN-e-an) are large oval structures composed of a multilayered connective tissue capsule that encloses a nerve ending (Figure 12.1). Like corpuscles of touch, lamellated corpuscles adapt rapidly. They are widely distributed in the body: in the dermis and subcutaneous layer; in tissues that underlie mucous and serous membranes; around joints, tendons, and muscles; in the periosteum; and in the mammary glands, external genitalia, and certain viscera, such as the pancreas and urinary bladder.

**Vibration** results from rapidly repetitive sensory signals from tactile receptors. The receptors for vibration sensations are corpuscles of touch and lamellated corpuscles.


**Itch and Tickle**

The *itch* sensation results from stimulation of free nerve endings by certain chemicals, such as bradykinin, often as a result of a local inflammatory response. Receptors for the *tickle* sensation are thought to be free nerve endings and lamellated corpuscles. This intriguing sensation typically arises only when someone else touches you, not when you touch yourself. The explanation of this puzzle seems to lie in the impulses that conduct to and from the cerebellum when you are moving your fingers and touching yourself that don’t occur when someone else is tickling you.

**Thermal Sensations**

The sensory receptors for thermal sensations (sensations of heat and cold) consist of two types: cold receptors and warm receptors. Cold receptors are located in the stratum basale of the epidermis. Temperatures between 10° and 40°C (50° to 105°F) activate cold receptors. Warm receptors, located in the dermis, are activated by temperatures between 32° and 48°C (90° to 118°F). Both cold and warm receptors adapt rapidly at the onset of a stimulus but continue to generate some impulses throughout a prolonged stimulus. Temperatures below 10°C and above 48°C stimulate mainly pain receptors, rather than thermoreceptors, producing painful sensations.

**Pain Sensations**

The ability to perceive pain is indispensable for a normal life, providing us with information about tissue-damaging stimuli so we can protect ourselves from greater damage. Pain initiates our search for medical assistance, and our description and indication of the location of the pain may help pinpoint the underlying cause of disease.

The sensory receptors for pain, called nociceptors (nō’-sē-SEP-tors; noci- = harmful), are free nerve endings (Figure 12.1). Pain receptors are found in practically every tissue of the body except the brain, and they respond to several types of stimuli. Excessive stimulation of sensory receptors, excessive stretching of a structure, prolonged muscular contractions, inadequate blood flow to an organ, or the presence of certain chemical substances can all produce the sensation of pain.

During tissue irritation or injury, release of chemicals such as prostaglandins stimulates nociceptors. Nociceptors adapt only slightly or not at all to the presence of these chemicals, which are only slowly removed from the tissues following an injury. This situation explains why pain persists after the initial trauma. If there were adaptation to painful stimuli, irreparable tissue damage could result.

Recognition of the type and intensity of pain occurs primarily in the cerebral cortex. In most instances of somatic pain, the cortex projects the pain back to the stimulated area. If you burn your finger, you feel the pain in your finger, not in your cortex. In most instances of visceral pain, the sensation is not projected back to the point of stimulation. Rather, the pain is felt in the skin overlying the stimulated organ or in a surface area far from the stimulated organ. This phenomenon is called referred pain. It occurs because the area to which the pain is referred and the visceral organ involved are innervated by the same segment of the spinal cord. For example, sensory neurons from the heart as well as from the skin over the heart and left upper limb enter thoracic spinal cord segments T1 to T5. Thus the pain of a heart attack is typically felt in the skin over the heart and along the left arm.

A kind of pain often experienced by patients who have had a limb amputated is called phantom pain. They still experience sensations such as itching, pressure, tingling, or pain in the limb as if the limb were still there. One reason for these sensations is that the remaining proximal portions of the sensory nerves that previously received impulses from the limb are being stimulated by the trauma of the amputation. Stimuli from these nerves are interpreted by the brain as coming from the nonexistent (phantom) limb.

Some pain sensations are inappropriate; rather than warning of actual or impending damage, they occur out of proportion to minor damage or persist chronically for no obvious reason. In such cases, analgesia (an- = without; -algia = pain) or pain relief is needed. Analgesic drugs such as aspirin and ibuprofen (for example, Advil) block formation of the chemicals that stimulate nociceptors. Local anesthetics, such as procaine (Novocain), provide short-term pain relief by blocking conduction of nerve impulses. Morphine and other opiate drugs alter the quality of pain perception in the brain; pain is still sensed, but it is no longer perceived as so unpleasant.

**Proprioceptive Sensations**

Proprioceptive sensations (proprio- = one’s own) inform you, consciously and subconsciously, of the degree to which your muscles are contracted, the amount of tension present in your tendons, the positions of your joints, and the orientation of your head. The receptors for proprioception, called proprioceptors, adapt slowly and only slightly. Slow adaptation is advantageous because your brain must be aware of the status of different parts of your body at all times so that adjustments can be made. Kinesthesia (kin’-es-THE-ze-a; kin- = motion; -esthesia = perception), the perception of body movements, allows you to walk, type, or dress without using your eyes. Proprioceptive sensations also allow you to estimate the weight of objects and determine the amount of effort necessary to perform a task. For example, when you pick up a bag you quickly realize whether it contains feathers or books, and you then exert only the amount of effort needed to lift it.

Proprioceptors are located in skeletal muscles, in tendons, in and around synovial joints, and in the internal ear.

- **Muscle spindles** are delicate proprioceptors that are located between skeletal muscle fibers. When a muscle spindle is stretched, it sends impulses to the CNS, indicating how much and how fast the muscle is changing its length. This information is integrated within the CNS to coordinate muscle activity.
Focus on Wellness

Pain Management—Sensation Modulation

Pain is a useful sensation when it alerts us to an injury that needs attention. We pull our finger away from a hot stove, we take off shoes that are too tight, and we rest an ankle that has been sprained. We do what we can to help the injury heal and meanwhile take over-the-counter or prescription painkillers until the pain goes away.

Pain that persists for longer than two or three months despite appropriate treatment is known as chronic pain. The most common forms of chronic pain are low back pain and headache. Cancer, arthritis, fibromyalgia, and many other disorders are associated with chronic pain. People experiencing chronic pain often experience chronic frustration as they are sent from one specialist to another in search of a diagnosis. Their lives may turn into nightmares of fear and worry.

The goal of pain management programs, developed to help people with chronic pain, is to decrease pain as much as possible, and then help patients learn to cope with whatever pain remains. Because no single treatment works for everyone, pain management programs typically offer a wide variety of treatments from surgery and nerve blocks to acupuncture and exercise therapy. Following are some of the therapies that complement medical and surgical treatment for the management of chronic pain.

Counseling
Pain used to be regarded as a purely physical response to physical injury. Psychological factors are now understood to serve as important mediators in the perception of pain. Feelings such as fear and anxiety strengthen the pain perceptions. Pain may be used to avoid certain situations, or to gain attention. Depression and associated symptoms such as sleep disturbances can contribute to chronic pain. Psychological counseling techniques can help people with chronic pain confront issues such as these that may be worsening their pain.

Relaxation and Meditation
Relaxation and meditation techniques may reduce pain by decreasing anxiety and giving people a sense of personal control. Some of these techniques include deep breathing, visualization of positive images, and muscular relaxation. Others encourage people to become more aware of thoughts and situations that increase or decrease pain or provide a mental distraction from the sensations of pain.

Exercise
People with chronic pain tend to avoid movement because it hurts. Inactivity causes muscles and joint structures to atrophy, which may eventually cause the pain to worsen. Regular exercise and improved fitness helps to relieve pain. Why? Exercise stimulates the production of endorphins, chemicals produced by the body to relieve pain. It also improves self-confidence, can serve as a distraction from pain, and improves sleep quality, which is often a problem for people with chronic pain.

Think It Over

In what part of the nervous system do relaxation techniques have their effect?

- Tendon organs (Golgi tendon organs) are found at the junction of a tendon with a muscle. They protect tendons and their associated muscles from damage due to excessive tension by relaying information about the amount of tension to the CNS.
- Joint kinesthetic receptors are found in and around synovial joints, such as the shoulder, elbow, hip, and knee joints. They respond to pressure, acceleration and deceleration, and excessive strain on a joint.
- Hair cells of the internal ear are proprioceptors that provide information for maintaining balance and equilibrium. Their function is discussed in more detail later in the chapter.

Impulses for conscious proprioception pass along sensory tracts in the spinal cord and are relayed to the primary somatosensory area (postcentral gyrus) in the parietal lobe of the cerebral cortex (see areas 1, 2, and 3, in Figure 10.12 on page 000). Proprioceptive impulses also pass to the cerebellum along spinocerebellar tracts and contribute to subconscious proprioception.
SPECIAL SENSES

Receptors for the special senses—smell, taste, sight, hearing, and equilibrium—are structurally more complex than receptors for general sensations and are organized into familiar receptor organs (nose, tongue, eyes, and ears). The sense of smell is the least specialized, and the sense of sight, the most. Like the general senses, the special senses allow us to detect changes in our environment.

OLFAC TION: SENSE OF SMELL

Objective: Describe the receptors for olfaction and the olfactory pathway to the brain.

In the chemical senses, smell and taste sensations arise from the interaction of molecules with sensory receptors. The nose contains 10 million to 100 million receptors for the sense of smell, or olfaction (ol-FAK-shun; olfact- = smell). Because some nerve impulses for smell and taste propagate to the limbic system, certain odors and tastes can evoke strong emotional responses or a flood of memories.

Structure of the Olfactory Epithelium

The olfactory epithelium occupies the upper portion of the nasal cavity (Figure 12.2a) and consists of three types of cells: olfactory receptors, supporting cells, and basal stem cells (Figure 12.2b). Several cilia called olfactory hairs project from a knob-shaped tip on each olfactory receptor. The olfactory hairs are the parts of the olfactory receptor that respond to odors in the air. Supporting cells provide physical support, nourishment, and electrical insulation for the olfactory receptors, and they help detoxify chemicals that come in contact with the olfactory epithelium. Basal cells lie between the bases of the supporting cells.
and continually undergo cell division to produce new olfactory receptors, which live for only a month or so before being replaced. This process is remarkable because olfactory receptors are neurons, and in general, mature neurons are not replaced. Within the connective tissue that supports the olfactory epithelium are mucus-producing olfactory glands. Mucus moistens the surface of the olfactory epithelium and serves as a solvent for inhaled odorants.

Stimulation of Olfactory Receptors
Many attempts have been made to distinguish among and classify “primary” sensations of smell. Genetic evidence now suggests that individual olfactory receptors respond to hundreds of different scents. Our ability to recognize about 10,000 different scents probably depends on patterns of activity in the brain that arise from activation of many different combinations of olfactory receptors.

Olfactory receptors react to odorant molecules by producing a generator potential that triggers one or more nerve impulses. Only a few molecules of certain substances need be present in air to be perceived as an odor. A good example is the chemical methylmercaptan, which smells like rotten cabbage and can be detected in concentrations as low as \( \frac{1}{25} \) billionth of a milliliter of air. Because the natural gas used for cooking and heating is odorless but lethal and potentially explosive if it accumulates, a small amount of methylmercaptan is added to natural gas to provide olfactory warning of gas leaks. Adaptation (decreasing sensitivity) to odors occurs rapidly. Olfactory receptors adapt by about 50% in the first second or so after stimulation and very slowly thereafter.

The Olfactory Pathway
On each side of the nose, bundles of slender, unmyelinated axons of olfactory receptors extend through holes in the cribiform plate of the ethmoid bone (Figure 12.2b). These bundles of axons form cranial nerve I, the olfactory nerves. They terminate in the brain in the olfactory bulbs, which are located inferior to the frontal lobes of the cerebrum. Within the olfactory bulbs, the axon terminals of olfactory receptors synapse with the dendrites and cell bodies of the next neurons in the olfactory pathway. The axons of the neurons extending from the olfactory bulb form the olfactory tract. The olfactory tract projects to the primary olfactory area in the temporal lobe, where conscious awareness of smells begins. Olfactory impulses also reach the limbic system and the hypothalamus. These pathways probably account for your emotional and memory-evoked responses to odors, such as nausea upon smelling a food that once made you violently ill, or memories of your mother’s kitchen at Thanksgiving upon smelling pumpkin pie. From the temporal lobe, pathways also extend to the frontal lobe. An important region for odor identification is the orbitofrontal area, corresponding to Brodmann’s area 11 (see Figure 10.12 on page 000). People who suffer damage in this area have difficulty identifying different odors.

GUSTATION: SENSE OF TASTE

Objective: Describe the receptors for gustation and the gustatory pathway to the brain.

The other chemical sense, taste or gustation (GUS-tä-shun; gust- = taste), is much simpler than olfaction because only four major classes of stimuli can be distinguished: sour, sweet, bitter, and salty. All other “tastes,” such as chocolate, pepper, and coffee, are combinations of these four, plus the accompanying olfactory sensations. Odors from food pass upward from the mouth into the nasal cavity, where they stimulate olfactory receptors. Because olfaction is much more sensitive than taste, foods may stimulate the olfactory system thousands of times more strongly than they stimulate the gustatory system. When persons with colds or allergies complain that they cannot taste their food, they are reporting blockage of olfaction, not of taste.

Structure of Taste Buds
The receptors for sensations of taste are located in the taste buds (Figure 12.3). The nearly 10,000 taste buds of a young adult are mainly on the tongue, but they are also found on the roof of the mouth, in the throat, and in the larynx (voice box). With age, the number of taste buds declines dramatically. Taste buds are found in elevations on the tongue called papillae (pa-PIL-e), which give the upper surface of the tongue its rough appearance (Figure 12.3a,b). Circumvallate papillae (ser’-kum-VAL-ä) form an inverted V-shaped row at the posterior portion of the tongue. Fungiform papillae (FUN-ji-form) are mushroom-shaped elevations scattered over the entire surface of the tongue. All circumvallate and most fungiform papillae contain taste buds. In addition, the entire surface of the tongue has filiform papillae (FI-ler-form), pointed, threadlike structures that rarely contain taste buds.

Each taste bud is an oval body consisting of three types of epithelial cells: supporting cells, gustatory receptor cells, and basal cells (Figure 12.3c). The supporting cells surround about 50 gustatory receptor cells. A single, long microvillus, called a gustatory hair, projects from each gustatory receptor cell to the external surface through the taste pore, an opening in the taste bud. Basal cells produce supporting cells, which then develop into gustatory receptor cells with a life span of about 10 days. The gustatory receptor cells synapse with dendrites of sensory neurons that form the first part of the gustatory pathway.

Stimulation of Gustatory Receptors
Once a chemical is dissolved in saliva, it enters a taste pore and makes contact with the plasma membrane of the gustatory hairs. The result is a depolarizing potential that stimulates exocytosis of synaptic vesicles containing neurotransmitter from the gustatory receptor cell. Nerve impulses are triggered when these neurotransmitter molecules bind to their receptors on the dendrites.
of the sensory neuron. The dendrites branch profusely and contact many gustatory receptors in several taste buds. Individual gustatory receptor cells may respond to more than one of the four primary tastes, but certain regions of the tongue are more sensitive to particular primary taste sensations (Figure 12.3a). Receptors in the tip of the tongue are highly sensitive to sweet and salty substances, receptors in the posterior portion of the tongue are highly sensitive to bitter substances, and those in the lateral areas of the tongue are most sensitive to sour substances. Complete adaptation (loss of sensitivity) to a specific taste can occur in 1 to 5 minutes of continuous stimulation.

**The Gustatory Pathway**

Three cranial nerves include axons of sensory neurons from taste buds: the facial (VII) nerve, the glossopharyngeal (IX) nerve, and the vagus (X) nerve. Impulses conduct along these cranial nerves to the medulla oblongata. From the medulla, some axons carrying impulses for taste extend to the limbic system and the hypothalamus, whereas others extend to the thalamus. From the thalamus, axons extend to the primary gustatory area in the parietal lobe of the cerebral cortex (see area 43 in Figure 10.12), giving rise to the conscious perception of taste.
The upper and lower eyelids shade the eyes during sleep, protect the eyes from excessive light and foreign objects, and spread lubricating secretions over the eyeballs (by blinking).

The lacrimal apparatus (lacríma = tear) refers to the glands, ducts, canals, and sacs that produce and drain tears (Figure 12.4). The right and left lacrimal glands are each about the size and shape of an almond. They secrete lacrimal fluid (tears) through the lacrimal ducts onto the surface of the upper eyelid. Tears then pass over the surface of the eyeball toward the nose into two lacrimal canals and a nasolacrimal duct, which allow the tears to drain into the nasal cavity (producing a runny nose when you cry).

Tears are a watery solution containing salts, some mucus, and a bacteria-killing enzyme called lysozyme. Tears clean, lubricate, and moisten the portion of the eyeball exposed to the air to prevent it from drying. Normally, tears are cleared away by evaporation or by passing into the nasal cavity as fast as they are produced. If, however, an irritating substance makes contact with the eye, the lacrimal glands are stimulated to oversecrete and tears accumulate. This protective mechanism dilutes and washes away the irritant. In response to parasympathetic stimulation, the lacrimal glands produce excessive tears that may spill over the edges of the eyelids and even fill the nasal cavity with fluid. Humans are unique in their ability to cry to express certain emotions such as happiness and sadness.

Layers of the Eyeball

The adult eyeball measures about 2.5 cm (1 inch) in diameter and is divided into three layers: fibrous tunic, vascular tunic, and retina (Figure 12.5a).
The fibrous tunic is the outer coat of the eyeball consisting of an anterior cornea and a posterior sclera. The cornea (KOR-nē-ā) is a nonvascular, transparent fibrous coat that covers the colored part of the eyeball, the iris. The cornea’s outer surface is covered by an epithelial layer called the conjunctiva, which also lines the eyelid. The sclera (SKLER-ā = hard), the “white” of the eye, is a coat of dense connective tissue that covers all of the eyeball, except the cornea. The sclera gives shape to the eyeball, makes it more rigid, and protects its inner parts.

The cornea bends light rays entering the eyeball to produce a clear image. If the cornea is not curved properly, blurred vision results. A defective cornea can be removed and replaced with a donor cornea of similar diameter, a procedure called a corneal transplant. Corneal transplants are the most successful type of transplantation because corneas do not contain blood vessels and the body is unlikely to reject them.

The vascular tunic is the middle layer of the eyeball and is composed of the choroid, ciliary body, and iris. The choroid (KOR-oyd) is a thin membrane that lines most of the internal surface of the sclera. It contains many blood vessels that help nourish the retina.
Which type of photoreceptor is specialized for vision in dim light and allows us to see shapes and movement? Which type of photoreceptor is specialized for color vision and vision with high acuity?
At the front of the eye, the choroid becomes the ciliary body (SIL-ē-ar-ē). The ciliary body consists of the ciliary processes, folds on the inner surface of the ciliary body whose capillaries secrete a watery fluid called aqueous humor, and the ciliary muscle, a smooth muscle that alters the shape of the lens for near or far vision. The lens, a transparent structure that focuses light rays onto the retina, is constructed of numerous layers of elastic protein fibers. Suspensory ligaments that attach the lens to the ciliary muscle hold the lens in position.

The iris (= colored circle) is the doughnut-shaped colored portion of the eyeball. It consists of circular and radial smooth muscle fibers. The hole in the center of the iris, through which light enters the eyeball, is the pupil. The iris regulates the amount of light passing through the lens. When the eye is stimulated by bright light, the circular muscles of the iris contract and decrease the size of the pupil (constriction). When the eye must adjust to dim light, the radial muscles of the iris relax and the pupil increases in size (dilation) (Figure 12.5b). These muscles of the iris are controlled by the autonomic nervous system (see Table 11.3).

Retina

The third and inner coat of the eyeball, the retina, lines the posterior three-quarters of the eyeball and is the beginning of the visual pathway. An ophthalmoscope allows an observer to peer through the pupil, providing a magnified image of the retina and the blood vessels that cross it. The surface of the retina is the only place in the body where blood vessels can be viewed directly and examined for pathological changes, such as those that occur with hypertension or diabetes mellitus.

The retina consists of a pigment epithelium (nonvisual portion) and a neural portion (visual portion). The pigment epithelium is a sheet of melanin-containing epithelial cells that lies between the choroid and the neural portion of the retina. Melanin in the choroid and in the pigment epithelium absorbs stray light rays, which prevents reflection and scattering of light within the eyeball. As a result, the image cast on the retina by the cornea and lens remains sharp and clear.

The neural portion of the retina is a multilayered structure that develops from brain tissue. It extensively processes visual data before transmitting nerve impulses to the thalamus. Three distinct layers of retinal neurons—the photoreceptor layer, the bipolar cell layer, and the ganglion cell layer—are separated by the outer and inner synaptic layers, where synaptic contacts are made (Figure 12.5c). The two types of cells located in the photoreceptor layer—rod and cone photoreceptors—are highly specialized for detecting light rays. Rods allow us to see in dim light, such as moonlight. Because they do not provide color vision, in dim light we see only shades of gray. Brighter lights stimulate the cones, giving rise to highly acute, color vision. The loss of cone vision causes a person to become legally blind. In contrast, a person who loses rod vision mainly has difficulty seeing in dim light and thus should not, for example, drive at night.

There are about 6 million cones and 120 million rods. Cones are most densely concentrated in the central fovea, a small depression in the center of the macula lutea (MAK-yoo-la LOO-te-a), or yellow spot, in the exact center of the retina. The central fovea is the area of highest visual acuity or resolution (sharpness of vision) because of its high concentration of cones. The main reason that you move your head and eyes while looking at something, such as the words of this sentence, is to place images of interest on your fovea. Rods are absent from the central fovea and macula lutea and increase in numbers toward the periphery of the retina.

From photoreceptors, information flows through the outer synaptic layer to the bipolar cells of the bipolar cell layer, and then from bipolar cells through the inner synaptic layer to the ganglion cells of the ganglion cell layer. The axons of the ganglion cells extend posteriorly to a small area of the retina called the optic disk (blind spot), where they all exit as the optic (II) nerve. Because the optic disk contains no rods or cones, we cannot see an image that strikes the blind spot.

A frequently encountered problem related to the retina is a detached retina, which may occur in trauma, such as a blow to the head. The actual detachment occurs between the neural part of the retina and the underlying choroid. Fluid accumulates between these layers, resulting in distorted vision and blindness. Often, it is possible to surgically reattach the retina.

Interior of the Eyeball

The lens divides the interior of the eyeball into two cavities, the anterior cavity and the vitreous chamber. The anterior cavity lies anterior to the lens and is filled with aqueous humor (A-kwe-us HYOO-mor; aqua = water), a watery fluid similar to cerebrospinal fluid. The aqueous humor is secreted into the anterior cavity from blood capillaries of the ciliary processes. It then drains into the scleral venous sinus (canal of Schlemm), an opening where the sclera and cornea meet, and reenters the blood. The aqueous humor helps maintain the shape of the eye and nourishes the lens and cornea, neither of which has blood vessels.

The second, and larger, cavity of the eyeball is the vitreous chamber. It lies behind the lens and contains a clear, jellylike substance called the vitreous body. This substance helps prevent the eyeball from collapsing and holds the retina flush against the choroid. The vitreous body, unlike the aqueous humor, does not undergo constant replacement. It is formed during embryonic life and is not replaced thereafter.

The pressure in the eye, called intraocular pressure, is produced mainly by the aqueous humor with a smaller contribution from the vitreous body. Intraocular pressure maintains the shape of the eyeball and keeps the retina smoothly pressed against the choroid so the retina is well nourished and forms clear images. Normal intraocular pressure (about 16 mm Hg) is maintained by a balance between production and drainage of the aqueous humor.
### Table 12.2 / Summary of Structures Associated with the Eyeball

<table>
<thead>
<tr>
<th>Structure</th>
<th>Function</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fibrous tunic</strong></td>
<td>Cornea: Admits and refracts (bends) light. Sclera: Provides shape and protects inner parts.</td>
</tr>
<tr>
<td><strong>Vascular tunic</strong></td>
<td>Iris: Regulates amount of light that enters eyeball. Ciliary body: Secretes aqueous humor and alters shape of lens for near or far vision. Choroid: Provides blood supply.</td>
</tr>
<tr>
<td><strong>Retina</strong></td>
<td>Converts light stimuli into nerve impulses. Output to brain is via the optic (II) nerve.</td>
</tr>
<tr>
<td><strong>Lens</strong></td>
<td>Focuses light on the retina.</td>
</tr>
<tr>
<td><strong>Anterior cavity</strong></td>
<td>Contains aqueous humor that helps maintain shape of eyeball and supplies oxygen and nutrients to lens and cornea.</td>
</tr>
<tr>
<td><strong>Vitreous chamber</strong></td>
<td>Contains vitreous body that helps maintain shape of eyeball and keeps retina attached to choroid.</td>
</tr>
</tbody>
</table>
Table 12.2 summarizes the structures associated with the eyeball.

**Image Formation and Binocular Vision**

In some ways the eye is like a camera. Its optical elements focus an image of some object on a light-sensitive “film”—the retina—while ensuring the correct amount of light makes the proper “exposure.” To understand how the eye forms clear images of objects on the retina, we must examine three processes: (1) the refraction or bending of light by the lens and cornea, (2) the change in shape of the lens, and (3) constriction of the pupil.

**Refraction of Light Rays**

When light rays traveling through a transparent substance (such as air) pass into a second transparent substance with a different density (such as water), they bend at the junction between the two substances. This bending is called refraction (Figure 12.6a). About 75% of the total refraction of light occurs at the anterior and posterior surfaces of the cornea. Both surfaces of the lens of the eye further refract the light rays so that they come into exact focus on the retina.

Images focused on the retina are inverted (upside down) (Figure 12.6b,c). They also undergo right-to-left reversal; that is, light from the right side of an object strikes the left side of the retina, and vice versa. The reason the world does not look inverted and reversed is that the brain “learns” early in life to coordinate visual images with the orientations of objects. The brain stores the inverted and reversed images we acquire when we first reach for and touch objects and interprets those visual images as being correctly oriented in space.

When an object is more than 6 meters (20 ft) away from the viewer, the light rays reflected from the object are nearly parallel to one another, and the curvatures of the cornea and lens exactly focus the image on the retina (Figure 12.6b). However, light rays from objects closer than 6 meters are divergent rather than parallel (Figure 12.6c). The rays must be refracted more if they are to be focused on the retina. This additional refraction is accomplished by changes in the shape of the lens, a process called accommodation.

**Accommodation**

A surface that curves outward, like the surface of a ball, is said to be convex. The convex surface of a lens refracts incoming light rays toward each other, so that they eventually intersect. The lens of the eye is convex on both its anterior and posterior surfaces, and its ability to refract light increases as its curvature becomes greater. When the eye is focusing on a close object, the lens becomes more curved and refracts the light rays more. This increase in the curvature of the lens for near vision is called accommodation (Figure 12.6c).

When you are viewing distant objects, the ciliary muscle is relaxed and the lens is fairly flat because it is stretched in all directions by taut suspensory ligaments. When you view a close object, the ciliary muscle contracts, which pulls the ciliary process and choroid forward toward the lens. This action releases tension on the lens, allowing it to become rounder (more convex), which increases its focusing power and causes greater convergence of the light rays. With aging, the lens loses some of its elasticity so its ability to accommodate decreases. At about age 40, people who have not previously worn glasses begin to require them for near vision, such as reading. This condition is called presbyopia (prez-bè-Ô-pé-a; presby- = old; -opia = pertaining to the eye or vision).
The normal eye, known as an *emmetropic eye* (em’-e-TROP-ik; *emmetr-* = according to measure; *-opic* = eye), can sufficiently refract light rays so that a clear image is focused on the retina (Figure 12.7). Many people, however, lack this ability because of refraction abnormalities. For example, they may have an inability to clearly see distant objects, termed *hyper-* (hi-’-per-; *hyper-* = over) or farsightedness (Figure 12.7d,e). Another refraction abnormality is *astigmatism* (a-STIG-ma-tizm), an irregular curvature of either the cornea or the lens.

**Constriction of the Pupil**

Constriction of the pupil is a narrowing of the diameter of the hole through which light enters the eye. It occurs due to constriction of the circular muscles of the iris. This autonomic reflex occurs simultaneously with accommodation and prevents light rays from entering the eye through the periphery of the lens. Light rays entering at the periphery of the lens would not be brought to focus on the retina and would result in blurred vision. The pupil, as noted earlier, also constricts in bright light to limit the amount of light that strikes the retina.

**Convergence**

In humans, both eyes focus on a single object or set of objects, a characteristic called *binocular vision*. This feature of our visual system allows the perception of depth and an appreciation of the three-dimensional nature of objects. When you stare straight ahead at a distant object, the incoming light rays are aimed directly at the pupils of both eyes and are refracted to comparable spots on the two retinas. As you move closer to the object, your eyes must rotate toward the nose if the light rays from the object are to strike comparable points on both retinas. **Convergence** is the name for this automatic movement of the two eyeballs toward the midline, which is caused by the coordinated action of the extrinsic eye muscles. The nearer the object, the greater the convergence needed to maintain binocular vision.

**Stimulation of Photoreceptors**

After an image is formed on the retina by refraction, accommodation, constriction of the pupil, and convergence, light rays must be converted into neural signals. The initial step in this process is the absorption of light rays by the rods and cones of the retina. To understand how absorption occurs, it is necessary to understand the role of photopigments.

A **photopigment** is a substance that can absorb light and undergo a change in structure. The photopigment in rods is called **rhodopsin** (*rhodo-* = rose; *-opsin* = related to vision) and is composed of a protein called **opsin** and a derivative of vitamin A called **retinal**. Rhodopsin is a highly unstable compound in the presence of even very small amounts of light. Any amount of light in a darkened room causes some rhodopsin molecules to split into opsin and retinal and initiate a series of chemical changes in the rods. When the light level is dim, opsin and retinal recombine into rhodopsin so that production keeps pace with breakdown. Rods usually are nonfunctional in daylight, because rhodopsin is split apart faster than it can be re-formed. After going from bright sunlight into a dark room, it takes about 40 minutes before the rods function maximally.

Cones function in bright light and provide color vision. As in rods, absorption of light rays causes breakdown of photopigment molecules. The photopigments in cones also contain retinal, but there are three different opsin proteins. One type of cone photopigment responds best to yellow-orange light, the
second to green, and the third to blue. An individual cone photoreceptor contains just one type of cone photopigment. The cone photopigments re-form much more quickly than the rod photopigment. If there are only three types of color photopigments, why don’t we just see yellow, orange, green, and blue? Just as an artist can obtain almost any color by mixing them on a palette, the cones can code for different colors by differential stimulation. If all three types of cones are stimulated, an object is perceived as white in color; if none is stimulated, the object looks black.

An individual with one type of cone missing from the retina cannot distinguish some colors from others and is said to be colorblind. In the most common type, red-green colorblindness, one cone photopigment is missing. Color blindness is an inherited condition that affects males far more often than females. The inheritance of the condition is discussed in Chapter 24 and illustrated in Figure 24.13.

HEARING AND EQUILIBRIUM

**Objectives:**
- Describe the structures of the external, middle, and internal ear.
- Describe the receptors for hearing and equilibrium and their pathways to the brain.

The ear is a marvelously sensitive structure. Its sensory receptors can convert sound vibrations as small as the diameter of an atom of gold (0.3 nanometers) into electrical signals 1000 times faster than photoreceptors can respond to light. In addition to these incredibly sensitive receptors for sound waves, the ear also contains receptors for equilibrium (balance).

**Structure of the Ear**

The ear is divided into three main regions: the external ear, which collects sound waves and channels them inward; the middle ear, which conveys sound vibrations to the oval window; and the internal ear, which houses the receptors for hearing and equilibrium.

**External Ear**

The external ear collects sound waves and passes them inward (Figure 12.9). It consists of an auricle, external auditory canal, and eardrum. The auricle, the part of the ear that you can see, is a flap of elastic cartilage shaped like the flared end of a trumpet to direct sound waves into the external auditory canal. It is attached to the head by ligaments and muscles. The external auditory canal (audit- = hearing) is a curved tube that extends from the auricle to the eardrum. The canal contains a few hairs and ceruminous glands (se-ROO-mi-nus; cer- = wax), which secrete cerumen (se-ROO-min) (earwax). The hairs and cerumen help prevent foreign objects from entering the ear. The eardrum, also called the tympanic membrane (tim-PAN-ik = drum), is a thin, semitransparent partition between the external auditory canal and the middle ear.
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Middle Ear
The middle ear is a small, air-filled cavity between the eardrum of the external ear and internal ear (Figure 12.9). An opening in the anterior wall of the middle ear leads directly into the auditory (Eustachian) tube, which connects the middle ear with the nasopharynx, the upper part of the throat. Via the auditory tube, air pressure can equalize on both sides of the eardrum. Otherwise, abrupt changes in external or internal air pressure might cause the eardrum to rupture. During swallowing and yawning, the tube opens to relieve pressure, which explains why the sudden pressure change in an airplane may be equalized by swallowing or pinching the nose closed, closing the mouth, and gently forcing air up from the lungs.

Extending across the middle ear and attached to it by means of ligaments are three tiny bones called auditory ossicles (OS-si-kuls) that are named for their shapes: the malleus, incus, and stapes, commonly called the hammer, anvil, and stirrup (Figure 12.9). Equally tiny skeletal muscles control the amount of movement of these bones to prevent damage by excessively loud noises. The stapes fits into a small opening in the thin bony partition between the middle and internal ear called the oval window, where the internal ear begins.

Internal Ear
The internal ear is divided into the outer bony labyrinth and inner membranous labyrinth (Figure 12.10). The bony labyrinth (LAB-i-rinth) is a series of cavities in the temporal bone, including the cochlea, vestibule, and semicircular canals. The cochlea is the sense organ for hearing, whereas the vestibule and semicircular canals are the sense organs for equilibrium and balance. The bony labyrinth contains a fluid called perilymph. This fluid surrounds the inner membranous labyrinth, a series of sacs and tubes with the same general shape as the bony labyrinth. The membranous labyrinth contains a fluid called endolymph.

The vestibule is the oval-shaped middle part of the bony labyrinth. The membranous labyrinth in the vestibule consists of two sacs called the utricle (YOO-tri-kul = little bag) and saccule (SAK-yool = little sac). Behind the vestibule are the three bony semicircular canals. The anterior and posterior semicircular canals are both vertical and the lateral canal is horizontal.
What structures separate the external ear from the middle ear? the middle ear from the internal ear?
One end of each canal enlarges into a swelling called the **am-\textipa{pol-la}** (am-\textipa{pol-la} = little jar). Inside the bony semicircular canals are the **semicircular ducts**, which connect with the utricle of the vestibule.

A transverse section through the **cochlea** (KOK-lè-a = snail’s shell), a bony spiral canal that resembles a snail’s shell, shows that it is divided into three channels: the **scala vestibuli** that begins near the oval window, the **scala tympani** that ends at the **round window** (a membrane-covered opening directly below the oval window), and the **cochlear duct**. Between the cochlear duct and the scala vestibuli is the **vestibular membrane**. Between the cochlear duct and scala tympani is the **basilar membrane**.

Resting on the basilar membrane is the **spiral organ (organ of Corti)**, the organ of hearing (Figure 12.10b). The spiral organ consists of **supporting cells** and **hair cells**. The hair cells, the receptors for auditory sensations, have long processes at their free ends that extend into the endolymph of the cochlear duct. The hair cells are in contact with one of two branches of the vestibulocochlear (VIII) nerve, the cochlear branch. The **tectorial membrane** (tector- = covering), a flexible gelatinous membrane, covers the hair cells.

**Sound Waves**

*Sound waves*, the stimuli that we perceive as sounds, originate and spread out from a vibrating object much the same way that waves travel over the surface of water. The sounds heard most acutely by human ears are from sources that vibrate at frequencies between 500 and 5000 cycles per second. The entire range of human hearing extends from 20 to 20,000 cycles per second.

The frequency of vibration (the speed at which the sound waves vibrate) is its **pitch**. The greater the frequency, the higher the pitch. The greater the force of the vibration, the louder the sound. Intensity or loudness (the size of the sound wave) is measured in **decibels (dB)**. The point at which a person can just detect sound from silence is 0 dB. Rustling leaves have a decibel rating of 15, normal conversation 45, crowd noise 60, a vacuum cleaner 75, and a pneumatic drill 90. Prolonged exposure to sounds over 90 dB (loud music, jet planes, even some vacuum cleaners) damages hair cells of the spiral organ and causes hearing loss. The louder the sounds, the quicker the loss. If bystanders can hear the music you are listening to through headphones, the sound intensity is in the damaging range.

**Physiology of Hearing**

The hair cells convert a mechanical force into an electrical signal. When the hairs at the top of the cell are moved in one direction, the hair cell membrane depolarizes, causing release of neurotransmitter molecules that trigger nerve impulses in sensory neurons that synapse with the hair cell at its base (Figure 12.10b). Bending of the hairs in the opposite direction allows repolarization or even hyperpolarization to occur, thus reducing neurotransmitter release from the hair cells and decreasing the frequency of nerve impulses in the sensory neurons.

The events involved in stimulation of hair cells by sound waves are as follows (Figure 12.11):

1. The auricle directs sound waves into the external auditory canal.
2. Sound waves striking the eardrum cause it to vibrate. The distance and speed of its movement depend on the intensity and frequency of the sound waves. More intense (louder) sounds produce larger vibrations. The eardrum vibrates slowly in response to low-frequency (low-pitched) sounds and rapidly in response to high-frequency (high-pitched) sounds.
3. The central area of the eardrum connects to the malleus, which also starts to vibrate. The vibration is transmitted from the malleus to the incus and then to the stapes.
4. As the stapes moves back and forth, it pushes the oval window in and out.
5. The movement of the oval window sets up fluid pressure waves in the perilymph of the cochlea. As the oval window bulges inward, it pushes on the perilymph of the scala vestibuli.
6. The fluid pressure waves are transmitted from the scala vestibuli to the scala tympani and eventually to the round window, causing it to bulge into the middle ear. (See 9 in Figure 12.11.)
7. As the pressure waves deform the walls of the scala vestibuli and scala tympani, they also push the vestibular membrane back and forth, creating pressure waves in the endolymph inside the cochlear duct.
8. The pressure waves in the endolymph cause the basilar membrane to vibrate, which moves the hair cells of the spiral organ against the tectorial membrane. Bending of the hairs ultimately leads to the generation of nerve impulses in sensory neurons within the cochlear branch of the vestibulocochlear nerve (see Figure 12.10b).

Sound waves of various frequencies cause specific regions of the basilar membrane to vibrate more intensely than others. In other words, each segment of the basilar membrane is “tuned” for a particular pitch. High-intensity (loud) sound waves cause greater vibration of the basilar membrane, which leads to a higher frequency of nerve impulses reaching the brain. Louder sounds also may stimulate a larger number of hair cells.

**Auditory Pathway**

Sensory neurons in the cochlear branch of each vestibulocochlear (VIII) nerve terminate in the cochlear nuclei of the medulla oblongata on the same side of the brain. From there, axons carrying auditory impulses project to other nuclei in the medulla, on both sides of the brain. Slight differences in the timing of impulses arriving from the two ears at these nuclei allow us to locate the source of a sound. From the medulla, axons ascend to the midbrain, then to the thalamus, and finally to the primary auditory area in the temporal lobe (areas 41 and 42 in Figure 10.12 on page 000). Because many auditory axons cross over, the right and left primary auditory areas receive nerve impulses from both ears.
Physiology of Equilibrium

You learned about the anatomy of the internal ear structures for equilibrium in the previous section. In this section we will cover the physiology of balance, or how you are able to stay on your feet after tripping over your roommate’s shoes. There are two types of equilibrium (balance). One kind, called **static equilibrium**, refers to the maintenance of the position of the body relative to the force of gravity. The second kind, **dynamic equilibrium**, is the maintenance of body position in response to sudden movements such as rotation, acceleration, and deceleration. Collectively, the receptor organs for equilibrium, which include the saccule, utricle, and membranous semicircular ducts, are called the **vestibular apparatus** (ves-TIB-yoo-lar).

**Saccule and Utricle**

The walls of the saccule and the utricle contain small, thickened regions called **maculae** (MAK-yoo-le; macula = spot). The two maculae, oriented perpendicular to one another, are the receptor organs for static equilibrium. They provide sensory information on the position of the head in space and help maintain appropriate posture and balance. They also contribute to some aspects of dynamic equilibrium by detecting linear acceleration and deceleration, such as the sensations you feel while in an elevator or a car that is speeding up or slowing down.

Like the spiral organ of the inner ear, the maculae consist of two kinds of cells: **hair cells** and **supporting cells** (Figure 12.12). Hair cells contain long, hairlike extensions of the cell membrane. Floating over the hair cells is a thick, jellylike substance called the **otolithic membrane**. Calcium carbonate crystals, called **otoliths** (oto- = ear; -liths = stones), are arranged in a layer over the entire surface of the otolithic membrane.

The otolithic membrane sits on top of the macula. If you tilt your head forward, the membrane (and the otoliths) is pulled by gravity and slides over the hair cells in the direction of the tilt. This stimulates the hair cells and triggers nerve impulses that conduct along the **vestibular branch** of the vestibulocochlear (VIII) nerve (see Figure 12.9).

**Membranous Semicircular Ducts**

The three membranous semicircular ducts lie at right angles to one another in three planes (see Figure 12.10a). This positioning permits detection of rotational acceleration or deceleration. The dilated portion of each duct, the ampulla, contains a small elevation called the **crista** (Figure 12.13). Each crista contains a
Figure 12.12 Location and structure of receptors in the maculae of the right ear. Both sensory neurons (blue) and motor neurons (red) synapse with the hair cells. Movements of the otolithic membrane stimulate the hair cells.

What is the function of the maculae?
With which type of equilibrium are the membranous semicircular ducts, the utricle, and the saccule associated?
group of hair cells and supporting cells covered by a mass of gelatinous material called the cupula. When the head moves, the attached membranous semicircular ducts and hair cells move with it. However, the endolymph within the membranous semicircular ducts is not attached and lags behind due to its inertia. As the moving hair cells drag along the stationary endolymph, the hairs bend. Bending of the hairs leads to nerve impulses that conduct along the vestibular branch of the vestibulocochlear (VIII) nerve. The nerve impulses follow the same pathways as those for static equilibrium and are eventually sent to the muscles that must contract to maintain body balance and posture.

**Equilibrium Pathways**

Most of the axons of the vestibular branch of the vestibulocochlear (VIII) nerve enter the brain stem and then extend to the medulla or the cerebellum, where they synapse with the next neurons in the equilibrium pathways. From the medulla, some axons conduct nerve impulses along the cranial nerves that control eye movements and head and neck movements. Other axons form a spinal cord tract that conveys impulses for regulation of muscle tone in response to head movements. Various pathways among the medulla, cerebellum, and cerebrum enable the cerebellum to play a key role in maintaining static and dynamic equilibrium. The cerebellum continuously receives sensory information from the utricle and saccule. In response, the cerebellum makes adjustments to the signals going from the motor cortex to specific skeletal muscles to maintain equilibrium and balance.

Table 12.3 summarizes the structures of the ear related to hearing and equilibrium.

Now that our exploration of the nervous system is completed, you can appreciate the many ways that this system contributes to homeostasis of other body systems by examining Focus on Homeostasis: The Nervous System. Next, in Chapter 13, we will see how the hormones released by the endocrine system also help maintain homeostasis of many body processes.
<table>
<thead>
<tr>
<th>Body System</th>
<th>Contribution of Nervous System</th>
</tr>
</thead>
<tbody>
<tr>
<td>For all body systems</td>
<td>Together with hormones from the endocrine system, nerve impulses provide communication and regulation of most body tissues.</td>
</tr>
<tr>
<td>Integumentary system</td>
<td>Sympathetic nerves of the autonomic nervous system (ANS) control contraction of smooth muscles attached to hair follicles and secretion of perspiration from sweat glands.</td>
</tr>
<tr>
<td>Skeletal system</td>
<td>Nociceptors (pain receptors) in bone tissue warn of bone trauma or damage.</td>
</tr>
<tr>
<td>Muscular system</td>
<td>Somatic motor neurons receive instructions from motor areas of the brain and stimulate contraction of skeletal muscles to bring about body movements; reticular formation sets level of muscle tone.</td>
</tr>
<tr>
<td>Endocrine system</td>
<td>Hypothalamus regulates secretion of hormones from anterior and posterior pituitary; ANS regulates secretion of hormones from adrenal medulla and pancreas.</td>
</tr>
<tr>
<td>Cardiovascular system</td>
<td>Cardiovascular center in the medulla oblongata provides nerve impulses to ANS that govern heart rate and the forcefulness of the heartbeat; nerve impulses from ANS also regulate blood pressure and blood flow through blood vessels.</td>
</tr>
<tr>
<td>Lymphatic and immune system</td>
<td>Certain neurotransmitters help regulate immune responses; activity in nervous system may increase or decrease immune responses.</td>
</tr>
<tr>
<td>Respiratory system</td>
<td>Respiratory areas in brain stem control breathing rate and depth; ANS helps regulate diameter of airways.</td>
</tr>
<tr>
<td>Digestive system</td>
<td>ANS and enteric nervous system (ENS) help regulate digestion; parasympathetic division of ANS stimulates many digestive processes.</td>
</tr>
<tr>
<td>Urinary system</td>
<td>ANS helps regulate blood flow to kidneys, thereby influencing the rate of urine formation; brain and spinal cord centers govern emptying of urinary bladder.</td>
</tr>
<tr>
<td>Reproductive system</td>
<td>Hypothalamus and limbic system govern a variety of sexual behaviors; ANS brings about erection of penis in males and clitoris in females and ejaculation of semen in males; hypothalamus regulates release of anterior pituitary hormones that control gonads (ovaries and testes); nerve impulses elicited by touch stimuli from suckling infant cause release of oxytocin and milk ejection in nursing mothers.</td>
</tr>
</tbody>
</table>
Cataracts
A common cause of blindness is a loss of transparency of the lens known as a cataract. The lens becomes cloudy (less transparent) due to changes in the structure of the lens proteins. Cataracts often occur with aging but may also be caused by injury, excessive exposure to ultraviolet rays, certain medications (such as long-term use of steroids), or complications of other diseases (for example, diabetes). People who smoke also have increased risk of developing cataracts. Fortunately, sight can usually be restored by surgical removal of the old lens and implantation of an artificial one.

Glaucoma
In glaucoma, the most common cause of blindness in the United States, a buildup of aqueous humor within the anterior cavity causes an abnormally high intraocular pressure. Persistent pressure results in a progression from mild visual impairment to irreversible destruction of the retina, damage to the optic (II) nerve, and blindness. Because glaucoma is painless, and because the other eye initially compensates to a large extent for the loss of vision, a person may experience considerable retinal damage and loss of vision before the condition is diagnosed.

Macular Degeneration
Macular degeneration, the leading cause of blindness in individuals over age 75, is irreversible deterioration of the retina in the region of the macula, ordinarily the area of most acute vision. Initially, a person may experience blurring and distortion at the center of the visual field. Smokers have a threefold greater risk of developing macular degeneration than nonsmokers.

Deafness
Deafness is significant or total hearing loss. Sensorineural deafness is caused by either impairment of hair cells in the cochlea or damage of the cochlear branch of the vestibulocochlear (VIII) nerve. This type of deafness may be caused by atherosclerosis, which reduces blood supply to the ears; repeated exposure to loud noise, which destroys hair cells of the spiral organ; or certain drugs such as aspirin and streptomycin. Conductive deafness is caused by impairment of the external and middle ear mechanisms for transmitting sounds to the cochlea. It may be caused by otosclerosis, the deposition of new bone around the oval window; impacted cerumen; injury to the eardrum; or aging, which often results in thickening of the eardrum and stiffening of the joints of the auditory ossicles.

Ménière’s Disease
Ménière’s disease (mä-NYARZ) results from an increased amount of endolymph that enlarges the membranous labyrinth. Among the symptoms are fluctuating hearing loss (caused by distortion of the basilar membrane of the cochlea) and roaring tinnitus (ringing). Vertigo (a sensation of spinning or whirling) is characteristic of Ménière’s disease. Almost total destruction of hearing may occur over a period of years.

Otitis Media
Otitis media is an acute infection of the middle ear caused primarily by bacteria and associated with infections of the nose and throat. Symptoms include pain; malaise (discomfort or uneasiness); fever; and a reddening and outward bulging of the eardrum, which may rupture unless prompt treatment is received (this may involve draining pus from the middle ear). Bacteria from the nasopharynx passing into the auditory tube are the primary cause of all middle ear infections. Children are more susceptible than adults to middle ear infections because their auditory tubes are shorter, wider, and almost horizontal, which decreases drainage.

MEDICAL TERMINOLOGY AND CONDITIONS

Amblyopia (am’-blé-Ô-pé-ä; ambly- = dull or dim) The loss of vision in a functionally normal eye that, because of muscle imbalance, cannot focus in synchrony with the other eye.

Blepharitis (blef’-a-RI-tis; blepharos = eyelid; itis = inflammation of) An inflammation of the eyelid.

Conjunctivitis (pink eye) An inflammation of the conjunctiva; the type caused by bacteria such as pneumococci, staphylococci, or Hemophilus influenzae is very contagious and more common in children. Conjunctivitis may also be caused by irritants, such as dust, smoke, or pollutants in the air, in which case it is not contagious.

Keratitis (ker’-a-THI-tis; kerat- = cornea) An inflammation or infection of the cornea.

Labyrinthitis (lab’-i-rin-THIH-tis) An inflammation of the internal ear.

Myringitis (mir’-in-JIH-tis; myringa = eardrum) An inflammation of the eardrum; also called tympanitis.

Night blindness The lack of normal night vision; most often it is caused by vitamin A deficiency.

Nystagmus (nis-TAG-mus; nystagm- = nodding or drowsy) A rapid involuntary movement of the eyeballs, possibly caused by a disease of the central nervous system. It is associated with conditions that cause vertigo.

Otitis (o-TAL-jë-ä; oto = ear; algia = pain) Earache.

Ptosis (TÖ-sis; fall) Falling or drooping of the eyelid. (This term is also used for the slipping of any organ below its normal position.)

Retinoblastoma (ret’-i-nö-blas-TÖ-ma; blast = bud; oma = tumor) A tumor arising from immature retinal cells; it accounts for 2% of childhood cancers.

Scotoma (skö-TÖ-ma; scotoma = darkness) An area of reduced or lost vision in the visual field. Also called a blind spot (other than the normal blind spot or optic disk).

Strabismus (stra-BIZ-mus) An imbalance in the extrinsic eye muscles that cannot be controlled voluntarily. In convergent strabismus (cross eye), the visual axes converge. In divergent strabismus (walleye), the visual axes diverge.

Trachoma (tra-KÖ-ma) A serious form of conjunctivitis and the greatest single cause of blindness in the world, caused by the bacterium Chlamydia trachomatis. The disease produces an excessive growth of subconjunctival tissue and invasion of blood vessels into the cornea, which progresses until the entire cornea is opaque.
Overview of Sensations (p. 2)
1. Sensation is the conscious or subconscious awareness of external and internal conditions of the body.
2. The conditions for a sensation to occur are reception of a stimulus by a sensory receptor, conversion of the stimulus into a nerve impulse, conduction of the impulse to the brain, and integration of the impulse by a region of the brain.
3. When stimulated, most sensory receptors produce a depolarizing potential called a generator potential.
4. Sensory impulses from each part of the body arrive in specific regions of the cerebral cortex.
5. Adaptation is a decrease in sensation during a prolonged stimulus. Some receptors are rapidly adapting, whereas others are slowly adapting.
6. Modality is the distinct quality that makes one sensation different from others.
7. Two general classes of senses are general senses, which include somatic senses and visceral senses, and special senses, which include the modalities of smell, taste, vision, hearing, and equilibrium (balance).
8. Receptors can be classified by location as exteroceptors, interoceptors, and proprioceptors.
9. Receptors can be classified by the type of stimulus they detect as mechanoreceptors, thermoreceptors, nociceptors, photoreceptors, and chemoreceptors.

Somatic Senses (p. 3)
1. Somatic sensations that result from stimulating the skin surface are called cutaneous sensations. They include tactile sensations (touch, pressure, vibration, itch, and tickle), thermal sensations (heat and cold), and pain. Receptors for these sensations are located in the skin, subcutaneous layer, and mucous membranes of the mouth and anus.
2. Receptors for touch include corpuscles of touch (Meissner corpuscles), hair root plexuses, type I cutaneous mechanoreceptors (Merkel disks), and type II cutaneous mechanoreceptors (Ruffini corpuscles). Receptors for pressure and vibration are lamellated (Pacinian) corpuscles. Tickle and itch sensations result from stimulation of free nerve endings.
3. Thermoreceptors, free nerve endings in the epidermis and dermis, adapt to continuous stimulation.
4. Pain receptors (nociceptors) are free nerve endings that are located in nearly every body tissue.
5. Referred pain is felt in the skin near or away from the organ sending pain impulses.
6. Phantom pain is the sensation of pain in a limb that has been amputated.
7. Proprioceptors inform us of the degree to which muscles are contracted, the amount of tension present in tendons, the positions of joints, and the orientation of the head.
8. The proprioceptors include muscle spindles, tendon organs (Golgi tendon organs), joint kinesthetic receptors, and hair cells of the internal ear.

Olfaction: Sense of Smell (p. 7)
1. The olfactory epithelium in the upper portion of the nasal cavity contains olfactory receptors, supporting cells, and basal cells.
2. In olfactory reception, an odor molecule is dissolved in mucus and received by an olfactory receptor, which causes development of a generator potential and one or more nerve impulses.
3. Adaptation to odors occurs quickly.
4. Axons of olfactory receptors form the olfactory (I) nerves, which convey nerve impulses to the olfactory bulbs, olfactory tracts, limbic system, and cerebral cortex (temporal and frontal lobes).

Gustation: Sense of Taste (p. 10)
1. The receptors for gustation, the gustatory receptor cells, are located in taste buds.
2. To be tasted, substances must be dissolved in saliva.
3. The four primary tastes are salty, sweet, sour, and bitter.
4. Gustatory receptor cells trigger impulses in cranial nerves VII (facial), IX (glossopharyngeal), and X (vagus). Impulses for taste conduct to the medulla oblongata, limbic system, hypothalamus, thalamus, and the primary gustatory area in the parietal lobe of the cerebral cortex.

Vision (p. 10)
1. Accessory structures of the eyes include the eyebrows, eyelids, eyelashes, the lacrimal apparatus, and extrinsic eye muscles.
2. The lacrimal apparatus consists of structures that produce and drain tears.
3. The eyeball has three layers: (a) fibrous tunic (sclera and cornea), (b) vascular tunic (choroid, ciliary body, and iris), and (c) retina.
4. The retina consists of pigment epithelium and a neural portion (photoreceptor layer, bipolar cell layer, and ganglion cell layer).
5. The anterior cavity contains aqueous humor; the vitreous chamber contains the vitreous body.
6. Image formation on the retina involves refraction of light rays by the cornea and lens, which focus an inverted image on the central fovea of the retina.
7. For viewing close objects, the lens increases its curvature (accommodation), and the pupil constricts to prevent light rays from entering the eye through the periphery of the lens.
8. Improper refraction may result from myopia (nearsightedness), hypermetropia (farsightedness), or astigmatism (irregular curvature of the cornea or lens).
9. Movement of the eyeballs toward the nose to view an object is called convergence.
10. The first step in vision is the absorption of light rays by photopigments in rods and cones (photoreceptors). Stimulation of the rods and cones then activates bipolar cells, which in turn activate the ganglion cells.
11. Nerve impulses arise in ganglion cells and conduct along the optic (II) nerve, through the optic chiasm and optic tract to the thalamus. From the thalamus, the next axons in the visual pathway extend to the primary visual area in the occipital lobe of the cerebral cortex.
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Hearing and Equilibrium (p. 17)

1. The external ear consists of the auricle and external auditory canal. The eardrum (tympanic membrane) separates the external ear from the middle ear.
2. The middle ear consists of the auditory (Eustachian) tube, ossicles, oval window, and round window.
3. The internal ear consists of the bony labyrinth and membranous labyrinth. The internal ear contains the spiral organ (organ of Corti), the organ of hearing.
4. Sound waves enter the external auditory canal, strike the eardrum, pass through the ossicles, strike the oval window, set up pressure waves in the perilymph, strike the vestibular membrane and scala tympani, increase pressure in the endolymph, vibrate the basilar membrane, and stimulate hair cells in the spiral organ.
5. Hair cells convert mechanical vibrations into depolarization of the hair cell membrane, which releases neurotransmitter that can initiate nerve impulses in sensory neurons.

SELF-QUIZ

1. You enter a sauna and it feels awfully hot, but soon the temperature feels comfortably warm. What have you experienced?
   a. damage to your thermoreceptors
   b. sensory adaptation
   c. a change in the temperature of the sauna
   d. inactivation of your thermoreceptors
   e. damage to the parietal lobe
2. The unique quality that makes one sensation different from others is its
   a. generator potential
   b. modality
   c. adaptability
   d. action potential
   e. classification of receptors
3. Match each receptor with its function.
   ___ a. color vision
   ___ b. taste
   ___ c. smell
   ___ d. dynamic equilibrium
   ___ e. vision in dim light
   ___ f. stretch in a muscle
   ___ g. static equilibrium
   ___ h. pressure
   ___ i. fine touch
   ___ j. detects pain
   a. lamellated (Pacinian) corpuscle
   B. type I cutaneous mechanoreceptor
   C. rod photoreceptor
   D. nociceptor
   E. gustatory receptor cell
   F. olfactory receptor
   G. muscle spindle
   H. maculae
   I. cristae
   J. cones
4. The spiral organ (organ of Corti)
   a. contains hair cells
   b. is responsible for equilibrium
   c. is filled with perilymph
   d. is another name for the auditory (Eustachian) tube
   e. transmits auditory nerve impulses to the brain
5. Equilibrium and the activities of muscles and joints are monitored by
   a. olfactory receptors
   b. nociceptors
   c. tactile receptors
   d. proprioceptors
   e. thermoreceptors
6. Sensory neurons in the cochlear branch of the vestibulocochlear (VIII) nerve terminate in the medulla oblongata. Auditory signals then pass to the midbrain, thalamus, and temporal lobes.
7. Static equilibrium is the orientation of the body relative to the pull of gravity. The maculae of the utricle and saccule are the sense organs of static equilibrium.
8. Dynamic equilibrium is the maintenance of body position in response to rotation, acceleration, and deceleration. The maculae of the utricle and saccule and the cristae in the membranous semicircular ducts are the sense organs of dynamic equilibrium.
9. Most vestibular branch axons of the vestibulocochlear (VIII) nerve enter the brain stem and terminate in the medulla and pons; other axons extend to the cerebellum.
10. You are seated at your desk and drop your pencil. As you lean over to retrieve it, what is occurring in your internal ear?
    a. The hair cells on the macula are responding to changes in static equilibrium.
    b. The hair cells in the cochlea are responding to changes in dynamic equilibrium.
    c. The cristae of each semicircular duct are responding to changes in dynamic equilibrium.
d. The cochlear branch of the vestibulocochlear (VIII) nerve begins to transmit nerve impulses to the brain.
e. The auditory (Eustachian) tube makes adjustments for varying air pressures.

11. A generator potential
   a. results from the change in the receptor's membrane permeability to ions
   b. is the same as an action potential
   c. is a type of modality
   d. results when there is a decreased sensitivity of receptors to a stimulus
   e. is a region of the brain that integrates nerve impulses into sensations

12. Which of the following is NOT true concerning nociceptors?
   a. They respond to stimuli that may cause tissue damage.
   b. They consist of free nerve endings
   c. They can be activated by excessive stimuli from other sensations.
   d. They are found in virtually every body tissue except the brain.
   e. They adapt very rapidly.

13. Match the following:

   ___ a. focuses light rays onto
       ___ b. regulates the amount of light
        ___ c. contains aqueous humor
        ___ d. contains blood vessels that
        ___ e. produce tears
        ___ f. dense connective tissue that
        ___ g. contains photoreceptors

   A. sclera
   B. choroid
   C. lacrimal glands
   D. lens
   E. retina
   F. iris
   G. anterior cavity

14. Which of the following is NOT a function of tears?
   a. moisten the eye
   b. wash away eye irritants
   c. destroy certain bacteria
   d. lubricate the eye
   e. provide nutrients to the cornea

15. Transmission of vibrations (sound waves) from the tympanic membrane to the oval window is accomplished by
   a. nerve fibers
   b. tectorial membrane
   c. the auditory ossicles
   d. the endolymph
   e. the auditory (Eustachian) tube

16. Which of the following structures refracts light rays entering the eye?
   a. cornea   b. sclera   c. pupil   d. retina   e. conjunctiva

17. Your 45-year-old neighbor has recently begun to have difficulty reading the morning newspaper. You explain that this condition is known as _______ and is due to _______.
   a. myopia, inability of his eyes to properly focus light on his retinas
   b. night blindness, a vitamin A deficiency
   c. binocular vision, the eyes focusing on two different objects
   d. astigmatism, an irregularity in the curvature of the lens
   e. presbyopia, the loss of elasticity in the lens

18. Damage to cells in the central fovea would interfere with
   a. dynamic equilibrium
   b. accommodation
   c. visual acuity
   d. ability to see in dim light
   e. intraocular pressure

19. Place the following events concerning the visual pathway in the correct order:
   1. Nerve impulses exit the eye via the optic (II) nerve.
   2. Optic tract axons terminate in the thalamus.
   3. Light reaches the retina.
   4. Rods and cones are stimulated.
   5. Synapses occur in the thalamus and continue to the primary visual area in the occipital lobe.

   a. 4, 1, 2, 5, 6, 3   b. 5, 4, 1, 3, 2, 6   c. 3, 4, 6, 1, 5, 2
   d. 3, 4, 6, 1, 2, 5   e. 3, 4, 5, 6, 1, 2

20. Place the following events of the auditory pathway in the correct order:
   1. Hair cells in the spiral organ bend as they rub against the tectorial membrane.
   2. Movement in the oval window begins movement in the perilymph.
   3. Nerve impulses exit the ear via the vestibulocochlear (VIII) nerve.
   4. The eardrum and auditory ossicles transmit vibrations from sound waves.
   5. Pressure waves from the perilymph cause bulging of the round window and formation of pressure waves in the endolymph.

   a. 4, 2, 5, 1, 3   b. 4, 5, 2, 3, 1   c. 5, 3, 2, 4, 1
   d. 3, 4, 5, 1, 2   e. 2, 4, 1, 5, 3
1. When you first enter a chemistry lab the odors are quite strong. After several minutes, the odor in the lab is barely noticeable. Has something happened to the odors or has something happened to you?

2. Cliff works the night shift and sometimes falls asleep in A & P class. What is the effect on the structures in his internal ear when his head falls backward as he slumps in his seat?

3. A medical procedure used to improve vision involves shaving thin layers off the cornea. How could this procedure improve vision?

4. The optometrist put drops in Kate’s eyes during her eye exam. When Kate looked in the mirror after the exam, her pupils looked very large, and her eyes were sensitive to the bright light. How did the eye drops produce this effect on Kate’s eyes?

**ANSWERS TO FIGURE QUESTIONS**

**12.1** Corpuscles of touch (Meissner corpuscles) are abundant in the fingertips, palms, and soles.

**12.2** From the olfactory bulbs, impulses conduct into the olfactory tracts.

**12.3** The gustatory pathway: gustatory receptors → cranial nerves VII, IX, and X → medulla oblongata → thalamus → primary gustatory area in the parietal lobe of the cerebral cortex.

**12.4** Tears contain water, salts, some mucus, and lysozyme. Tears clean, lubricate, and moisten the eyeball.

**12.5** Rods are specialized for vision in dim light and allow us to see shapes and movement; cones are specialized for color vision and acute vision.

**12.6** During accommodation, the ciliary muscle contracts, suspensory ligaments slacken, and the lens becomes more rounded (convex) and refracts light more.

**12.7** Presbyopia is the loss of elasticity in the lens that occurs with aging.

**12.8** Structures carrying visual impulses from the retina: axons of ganglion cells → optic (II) nerve → optic chiasm → optic tract → thalamus → primary visual area in occipital lobe of the cerebral cortex.

**12.9** The receptors for hearing and equilibrium are located in the internal ear: cochlea (hearing) and semicircular ducts (equilibrium).

**12.10** The eardrum (tympanic membrane) separates the external ear from the middle ear. The oval and round windows separate the middle ear from the internal ear.

**12.11** Hair cells convert a mechanical force (stimulus) into an electrical signal (depolarization and repolarization of the hair cell membrane).

**12.12** The maculae are the receptors for static equilibrium and also contribute to dynamic equilibrium.

**12.13** The membranous semicircular ducts, the utricle, and the saccule function in dynamic equilibrium.