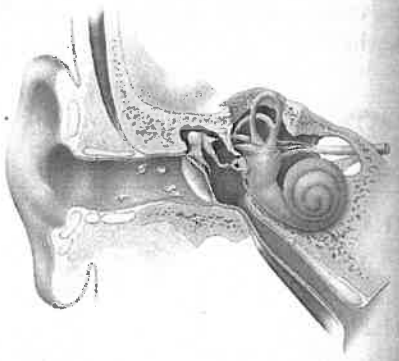
chapter 12

SOMATIC SENSES AND SPECIAL SENSES



did you know?

Some things improve with age, but hearing is not one of them. Damage to the hair cells that convert sound waves into nerve impulses accumulates over a lifetime, and by the time hearing loss is discovered, irreversible damage has already occurred. Exposure to excessive noise is the most common cause of hair cell damage. Damage increases with both the intensity and duration of exposure. The hair cells appear to be less traumatized by short periods of loud noise, such as a fire alarm going off, than by chronic exposure to moderately loud noise, such as the noise of vacuum cleaners, power tools, engines, and loud music.

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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 an oncoming car, hear a baby's cry, smell smoke, taste your favorite dessert, or maintain your balance on a flight of stairs. In short, if you could not "sense" your environment and make the necessary homeostatic adjustments, you could not survive very well on your own.

looking back to move ahead . . .

- **Sensory Nerve Endings and Sensory Receptors in the Skin (page 100)**
- **Somatic Sensory Pathways (page 259)**

OVERVIEW OF SENSATIONS

OBJECTIVE • Define a sensation and describe the conditions needed for a sensation to occur.

Most of us are aware of sensory input to the central nervous system (CNS) from structures associated with smell, taste, vision, hearing, and balance. These five senses are known as the ***special senses***. The other senses are termed ***general senses*** and include both somatic senses and visceral senses. ***Somatic senses*** (*somat-* = of the body) include tactile sensations (touch, pressure, and vibration); thermal sensations (warm and cold); pain sensations; and proprioceptive sensations (joint and muscle position sense and movements of the limbs and head). ***Visceral senses*** provide information about conditions within internal organs.

Definition of Sensation

Sensation is the conscious or subconscious awareness of changes in the external or internal environment. 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. A stimulus that activates a sensory receptor may be in the form of light, heat, pressure, mechanical energy, or chemical energy.
2. A *sensory receptor* must convert the stimulus to an electrical signal, which ultimately produces one or more nerve impulses if it is large enough.
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.

Characteristics of Sensations

As you have learned in Chapter 10, ***perception*** is the conscious awareness and interpretation of sensations and is primarily a function of 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 nerve 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. A given sensory neuron carries information for one type of sensation only. Neurons relaying impulses for touch, for example, do not also conduct 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 the strength of a 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 may fade or disappear 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. Receptors associated with pressure, touch, and smell adapt rapidly. Slowly adapting receptors monitor stimuli associated with pain, body position, and the chemical composition of the blood.

Types of Sensory Receptors

Both structural and functional characteristics of sensory receptors can be used to group them into different classes (Table 12.1). Structurally, the simplest are *free nerve endings*,

Table 12.1 Classification of Sensory Receptors

Basis of Classification	Description
Structure	
Free nerve endings	Bare dendrites are associated with pain, thermal, tickle, itch, and some touch sensations.
Encapsulated nerve endings	Dendrites enclosed in a connective tissue capsule, such as a corpuscle of touch.
Separate cells	Receptor cell synapses with first-order neuron; located in the retina of the eye (photoreceptors), inner ear (hair cells), and taste buds of the tongue (gustatory receptor cells).
Function	
Mechanoreceptors	Detect mechanical pressure; provide sensations of touch, pressure, vibration, proprioception, and hearing and equilibrium; also monitor stretching of blood vessels and internal organs.
Thermoreceptors	Detect changes in temperature.
Nociceptors	Respond to painful stimuli resulting from physical or chemical damage to tissue.
Photoreceptors	Detect light that strikes the retina of the eye.
Chemoreceptors	Detect chemicals in mouth (taste), nose (smell), and body fluids.
Osmoreceptors	Sense the osmotic pressure of body fluids.

which are bare dendrites that lack any structural specializations at their ends that can be seen under a light microscope (Figure 12.1). Receptors for pain, thermal, tickle, itch, and some touch sensations are free nerve endings. Receptors for other somatic and visceral 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, for example, hair cells in the inner ear.

Another way to group sensory receptors is functionally—according to the type of stimulus they detect. Most stimuli are in the form of mechanical energy, such as sound waves or pressure changes; electromagnetic energy, such as light or heat; or chemical energy, such as in a molecule of glucose.

- *Mechanoreceptors* are sensitive to mechanical stimuli such as the deformation, stretching, or bending of cells. Mechanoreceptors provide sensations of touch, pressure, vibration, proprioception, and hearing and equilibrium. They also monitor the stretching of blood vessels and internal organs.
- *Thermoreceptors* detect changes in temperature.
- *Nociceptors* respond to painful stimuli resulting from physical or chemical damage to tissue.
- *Photoreceptors* detect light that strikes the retina of the eye.
- *Chemoreceptors* detect chemicals in the mouth (taste), nose (smell), and body fluids.
- *Osmoreceptors* detect the osmotic pressure of body fluids.

CHECKPOINT

1. Which senses are "special senses"?
2. How is a sensation different from a perception?

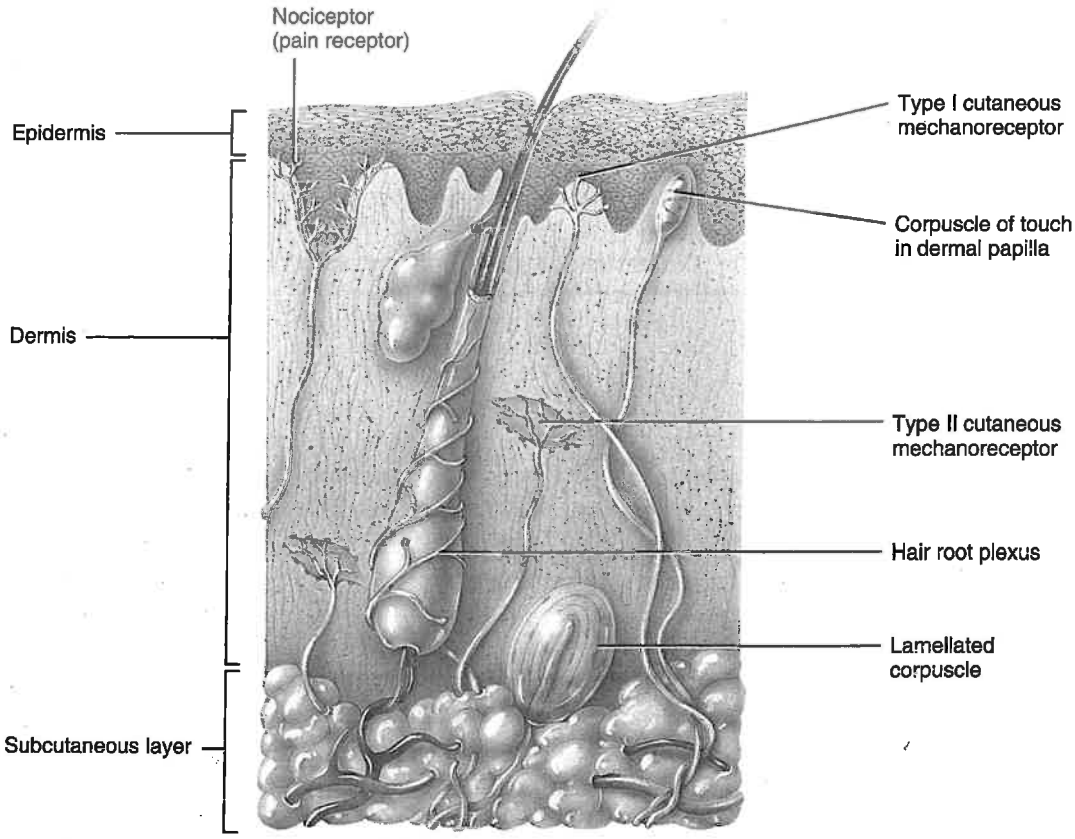
SOMATIC SENSES

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 in the skin, mucous membranes, muscles, tendons, and

Figure 12.1 Structure and location of sensory receptors in the skin and subcutaneous layer.

The somatic sensations of touch, pressure, vibration, warmth, cold, and pain arise from sensory receptors in the skin, subcutaneous layer, and mucous membranes.



Which receptors are especially abundant in the fingertips, palms, and soles?

joints. The sensory receptors for somatic sensations are distributed unevenly. Some parts of the body surface are densely populated with receptors, and other parts contain only a few. The areas with the largest numbers of sensory receptors are the tip of the tongue, the lips, and the fingertips.

Tactile Sensations

The ***tactile sensations*** (TAK-tīl; *tact-* = touch) are touch, pressure, vibration, 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 (Table 12.1). 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. There are two types of rapidly adapting touch receptors. ***Corpuscles of touch***, or ***Meissner corpuscles*** (MĪS-ner), are located in the dermal papillae of hairless skin. Each corpuscle is an egg-shaped mass of dendrites enclosed by a capsule of connective tissue. They are abundant in the fingertips, hands, eyelids, tip of the tongue, lips, nipples, soles, clitoris, and tip of the penis. ***Hair root plexuses*** consist of free nerve endings wrapped around hair follicles in hairy skin. Hair root plexuses detect movements on the surface of the skin that disturb hairs. For example, an insect landing on a hair causes movement of the hair shaft that stimulates the free nerve endings.

There are also two types of slowly adapting touch receptors. ***Type I cutaneous mechanoreceptors***, also known as ***Merkel discs***, are saucer-shaped, flattened free nerve endings that make contact with Merkel cells of the stratum basale; they are plentiful in the fingertips, hands, lips, and external genitalia. ***Type II cutaneous mechanoreceptors***, or ***Ruffini corpuscles***, are 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*** (pa-SIN-ē-an), ***corpuscles*** 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.

Sensations of ***vibration*** result from rapidly repetitive sensory signals from tactile receptors. The receptors for vibration sensations are corpuscles of touch and lamellated corpuscles. Corpuscles of touch can detect lower-frequency vibrations; lamellated corpuscles detect higher-frequency vibrations.

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 nerve 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.

> Patients who have had a limb amputated may still experience sensations such as itching, pressure, tingling, or pain as if the limb were still there. This phenomenon is called **phantom limb sensation.** One explanation for phantom limb sensations is that the cerebral cortex interprets impulses arising in the proximal portions of sensory neurons that previously carried impulses from the limb as coming from the nonexistent (phantom) limb. Another explanation for phantom limb sensations is that neurons in the brain that previously received sensory impulses from the missing limb are still active, giving rise to false sensory perceptions.

Thermal Sensations

Thermoreceptors are free nerve endings. Two distinct ***thermal sensations***—coldness and warmth—are mediated by different receptors. Temperatures between 10° and 40°C (50–105°F) activate *cold receptors*, which are located in the epidermis. *Warm receptors* are located in the dermis and are activated by temperatures between 32° and 48°C (90–118°F). Cold and warm receptors both adapt rapidly at the onset of a stimulus but continue to generate nerve impulses more slowly throughout a prolonged stimulus. Temperatures below 10°C and above 48°C stimulate mainly nociceptors, rather than thermoreceptors, producing painful sensations.

Pain Sensations

The sensory receptors for pain, called ***nociceptors*** (nō′-sē-SEP-tors; *noci-* = harmful), are free nerve endings (Figure 12.1). Nociceptors 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. Pain may persist even after a pain-producing stimulus is removed because pain-causing chemicals linger and because nociceptors exhibit very little adaptation. The lack of adaptation of nociceptors serves a protective function: If there were adaptation to painful stimuli, irreparable tissue damage could result.

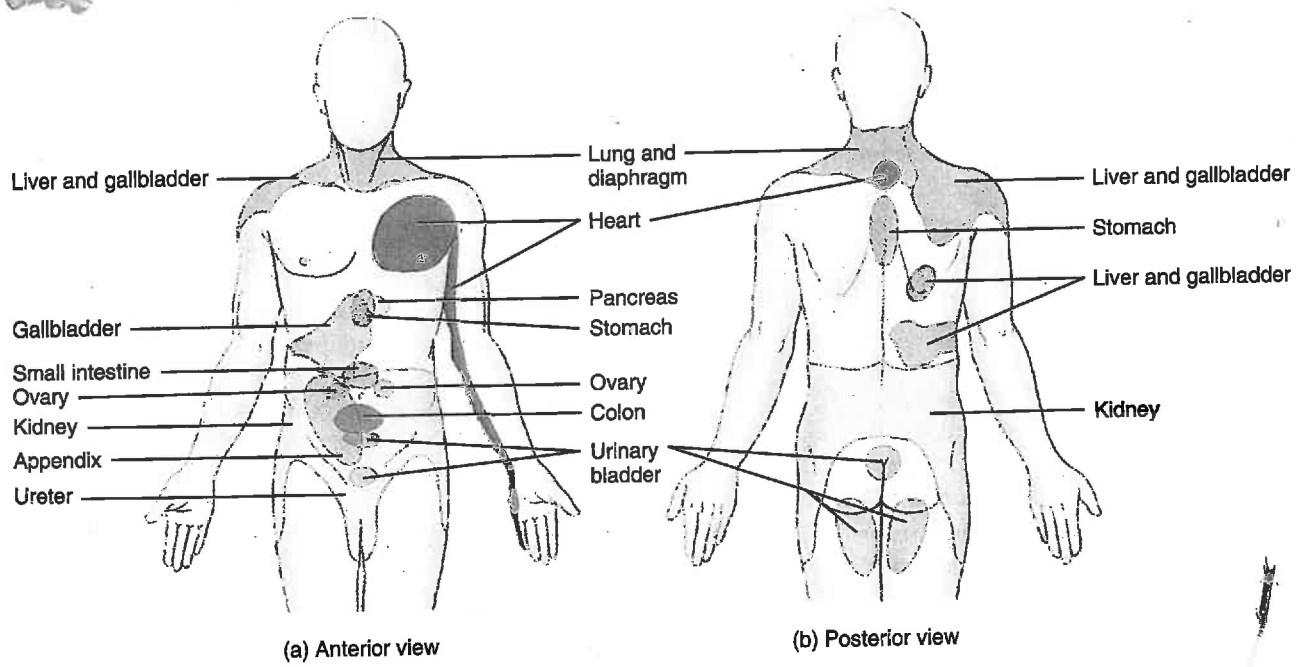
There are two types of pain: fast and slow. The perception of ***fast pain*** occurs very rapidly, usually within 0.1 second after a stimulus is applied. This type of pain is also known as acute, sharp, or pricking pain. The pain felt from a needle puncture or knife cut to the skin are examples of fast pain. Fast pain is not felt in deeper tissues of the body. The perception of ***slow pain*** begins a second or more after a stimulus is applied. It then gradually increases in intensity over a period of several seconds or minutes. This type of pain, which may be excruciating, is also referred to as chronic, burning, aching, or throbbing pain. Slow pain can occur both in the skin and in deeper tissues or internal organs. An example is the pain associated with a toothache.

Fast pain is very precisely localized to the stimulated area. For example, if someone pricks you with a pin, you know exactly which part of your body was stimulated. Somatic slow pain is well localized but more diffuse (involves large areas); it usually appears to come from a larger area of the skin. In many instances of visceral pain, the pain is felt in or just deep to the skin that overlies the stimulated organ, or in a surface area far from the stimulated organ. This phenomenon is called ***referred pain*** (Figure 12.2). In general, the visceral organ involved and the area in which the pain is referred are served by the same segment of the spinal cord. For example, sensory neurons from the heart, the skin over the heart, and the skin along the medial aspect of the left arm enter spinal cord segments T1 to T5. Thus, the pain of a heart attack typically is felt in the skin over the heart and along the left arm.

Some pain sensations occur out of proportion to minor damage or persist chronically for no obvious reason. In such cases, **analgesia** (*an-* = without; *-algesia* = pain) or pain relief is needed. Analgesic drugs such as aspirin and ibuprofen (for example, Advil®) block formation of some chemicals that stimulate nociceptors. Local anesthetics, such as Novocaine®, 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.

Figure 12.2 Distribution of referred pain. The colored parts of the diagrams indicate skin areas to which visceral pain is referred.

Nociceptors are present in almost every tissue of the body.



Which visceral organ has the broadest area for referred pain?

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.

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 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 help 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?*

Proprioceptive Sensations

Proprioceptive sensations (prō-prē-ō-SEP-tive; *proprio-* = one's own) allow us to know where our head and limbs are located and how they are moving even if we are not looking at them, so that we can walk, type, or dress without using our eyes. ***Kinesthesia*** (kin'-es-THĒ-zē-a; *kin-* = motion; *-esthesia* = perception) is the perception of body movements. Proprioceptive sensations arise in receptors termed ***proprioceptors***. Proprioceptors are located in skeletal muscles (muscle spindles), in tendons (tendon organs), in and around synovial joints (joint kinesthetic receptors), and in the inner ear (hair cells). Those proprioceptors embedded in muscles, tendons, and synovial joints inform us of the degree to which muscles are contracted, the amount of tension on tendons, and the positions of joints. Hair cells of the inner ear monitor the orientation of the head relative to the ground and head position during movements. Proprioceptive sensations also allow us to estimate the weight of objects and determine the muscular effort necessary to perform a task. For example, as you pick up a bag you quickly realize whether it contains popcorn

or books, and you then exert the correct amount of effort needed to lift it.

Nerve impulses for conscious proprioception pass along sensory tracts in the spinal cord and brain stem and are relayed to the primary somatosensory area (postcentral gyrus) in the parietal lobe of the cerebral cortex (see Figure 10.13 on page 259). Proprioceptive impulses also pass to the cerebellum, where they contribute to the cerebellum's role in coordinating skilled movements. Because proprioceptors adapt slowly and only slightly, the brain continually receives nerve impulses related to the position of different body parts and makes adjustments to ensure coordination.

CHECKPOINT

3. Why is it beneficial to your well-being that nociceptors and proprioceptors exhibit very little adaptation?
4. Which somatic sensory receptors detect touch sensations?
5. What is referred pain, and how is it useful in diagnosing internal disorders?

SPECIAL SENSES

Receptors for the special senses—smell, taste, sight, hearing, and equilibrium—are housed in complex sensory organs such as the eyes and ears. Like the general senses, the special senses allow us to detect changes in our environment. ***Ophthalmology*** (of′-thal-MOL-ō-jē; *ophthalmo-* = eye; *-logy* = study of) is the science that deals with the eye and its disorders. The other special senses are, in large part, the concern of ***otorhinolaryngology*** (ō′-tō-rī′-nō-lar′-in-GOL-ō-jē; *oto-* = ear; *rhino-* = nose; *laryngo-* = larynx), the science that deals with the ears, nose, and throat and their disorders.

OLFACTION: SENSE OF SMELL

OBJECTIVE • Describe the receptors for olfaction and the olfactory pathway to the brain.

The nose contains 10–100 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 12.3a) and consists of three types of cells: olfactory receptors, supporting cells, and basal stem cells (Figure 12.3b). ***Olfactory receptors*** are the first-order neurons of the olfactory pathway. 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 inhaled chemicals. Chemicals that have an odor and can therefore stimulate the olfactory hairs are called ***odorants***. The axons of olfactory receptors extend from the olfactory epithelium to the olfactory bulb. ***Supporting cells*** are columnar epithelial cells of the mucous membrane lining the nose. They 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*** are stem cells located 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. ***Olfactory glands*** produce mucus that 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 the existence of hundreds of primary odors. Our ability to recognize about 10,000 different odors 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 an electrical signal that triggers one or more nerve impulses. 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.

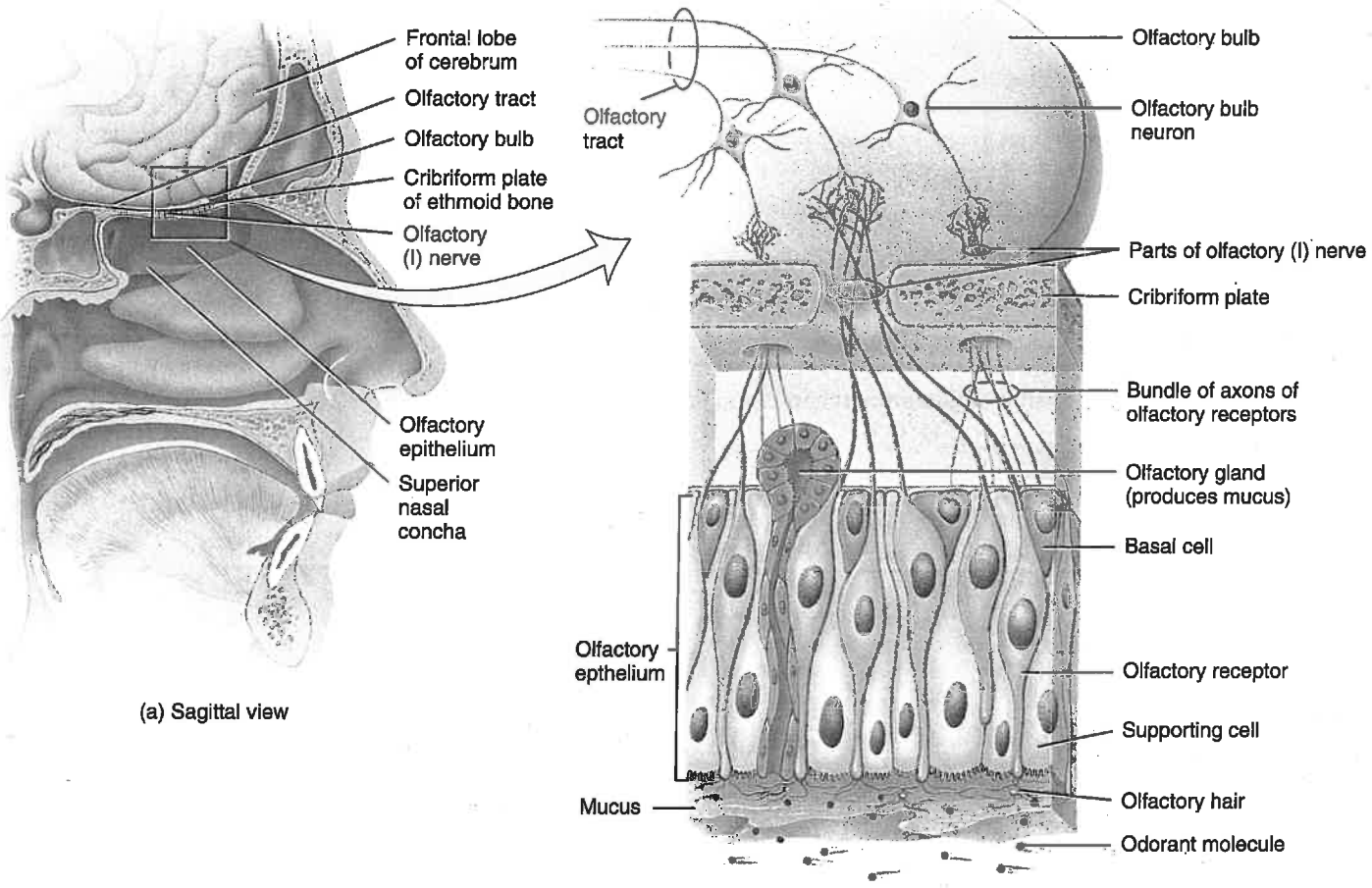
The Olfactory Pathway

On each side of the nose, about 40 bundles of the slender, unmyelinated axons of olfactory receptors extend through about 20 holes in the cribriform plate of the ethmoid bone (Figure 12.3b). These bundles of axons collectively form the right and left ***olfactory (I) nerves***. The olfactory nerves terminate in the brain in paired masses of gray matter called the ***olfactory bulbs***, which are located below the frontal lobes of the cerebrum. Within the olfactory bulbs, the axon terminals of olfactory receptors—the first-order neurons—form synapses with the dendrites and cell bodies of second-order neurons in the olfactory pathway.

The axons of the neurons extending from the olfactory bulb form the ***olfactory tract***. Some of the axons of the olfactory tract project to the *primary olfactory area* in the temporal lobe of the cerebral cortex (see Figure 10.13 on page 259),

Figure 12.3 Olfactory epithelium and olfactory receptors. (a) Location of olfactory epithelium in the nasal cavity. (b) Anatomy of olfactory receptors, whose axons extend through the cribriform plate to the olfactory bulb.

The olfactory epithelium consists of olfactory receptors, supporting cells, and basal cells.



(a) Sagittal view

(b) Enlarged aspect of olfactory receptors

What is the function of basal stem cells?

where conscious awareness of smell begins. Other axons of the olfactory tract project to the limbic system and hypothalamus; these connections account for emotional and memory-evoked responses to odors. Examples include sexual excitement upon smelling a certain perfume or nausea upon smelling a food that once made you violently ill.

Hyposmia (hī-POZ-mē-a, *hypo-* = below; *-osmia* = smell, odor), a reduced ability to smell, affects half of those over age 65 and 75% of those over age 80. With aging the sense of smell deteriorates. Hyposmia also can be caused by neurological changes, such as a head injury, Alzheimer disease, or Parkinson disease; certain drugs, such as antihistamines, analgesics, or steroids; and the damaging effects of smoking.

■ **CHECKPOINT**

6. What functions are carried out by the three types of cells in the olfactory epithelium?
7. Define the following terms: olfactory nerve, olfactory bulb, and olfactory tract.

GUSTATION: SENSE OF TASTE

OBJECTIVE • **Describe the receptors for gustation and the gustatory pathway to the brain.**

Taste or ***gustation*** (gus-TĀ-shun; *gust-* = taste) is much simpler than olfaction because only five primary tastes can be distinguished: *sour*, *sweet*, *bitter*, *salty*, and *umami* (ū-MAM-ē).

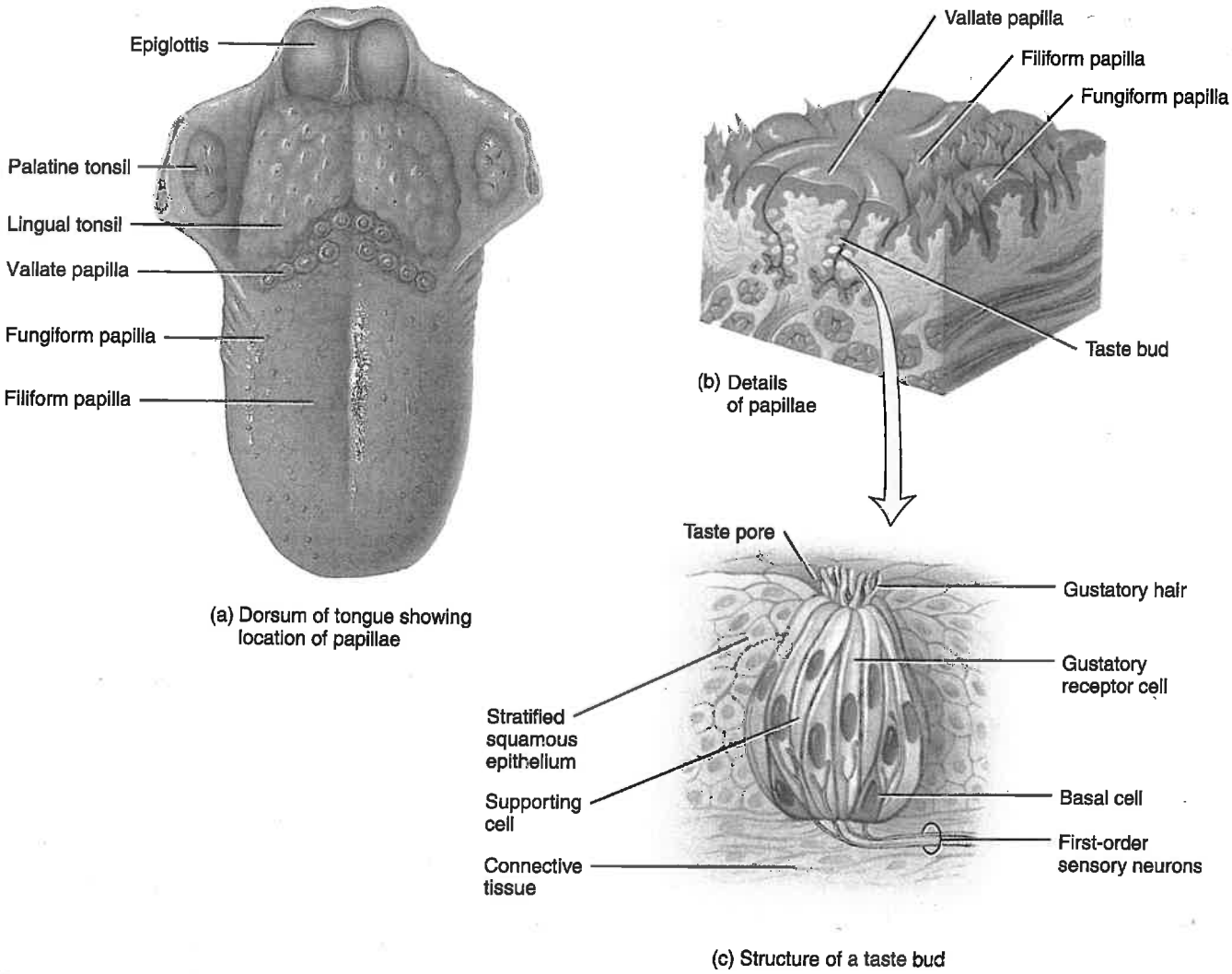
The umami taste is described as "meaty" or "savory." All other flavors, such as chocolate, pepper, and coffee, are combinations of the five primary tastes, plus the accompanying olfactory and tactile (touch) sensations. Odors from food can pass upward from the mouth into the nasal cavity, where they stimulate olfactory receptors. Because olfaction is much more sensitive than taste, a given concentration of a food substance may stimulate the olfactory system thousands of times more strongly than it stimulates the gustatory system. When you have a cold or are suffering from allergies and cannot taste your food, it is actually olfaction that is blocked, not taste.

Structure of Taste Buds

The receptors for taste sensations are located in the ***taste buds*** (Figure 12.4). Most of the nearly 10,000 taste buds of a young adult are on the tongue, but some are also found on the roof of the mouth, pharynx (throat), and epiglottis (cartilage lid over the voice box). The number of taste buds declines with age. Taste buds are found in elevations on the tongue called ***papillae*** (pa-PIL-ē; singular is *papilla*), which provide a rough texture to the upper surface of the tongue (Figure 12.4 a,b). *Vallate papillae* (VAL-āt = wall-like) form an inverted V-shaped row at the back of the tongue; *Fungiform papillae* (FUN-ji-form = mushroomlike) are

Figure 12.4 The relationship of gustatory receptors in taste buds to tongue papillae.

Gustatory (taste) receptor cells are located in taste buds.



In order, from the tongue to the brain, what structures form the gustatory pathway?

mushroom-shaped elevations scattered over the entire surface of the tongue. In addition, the entire surface of the tongue has *filiform papillae* (FIL-i-form = threadlike), which contain touch receptors but no 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 12.4c). The ***supporting cells*** surround about 50 ***gustatory receptor cells***. A single, long ***gustatory hair*** projects from each gustatory receptor cell to the external surface through the ***taste pore***, an opening in the taste bud. ***Basal cells*** are stem cells that produce supporting cells, which then develop into gustatory receptor cells that have a life span of about 10 days. The gustatory receptor cells are separate receptor cells. They do not have an axon (like olfactory receptors) but rather synapse with dendrites of the first-order sensory neurons of the gustatory pathway.

Stimulation of Gustatory Receptors

Chemicals that stimulate gustatory receptor cells are known as ***tastants***. Once a tastant is dissolved in saliva, it can enter taste pores and make contact with the plasma membrane of the gustatory hairs. The result is an electrical signal that stimulates release of neurotransmitter molecules from the gustatory receptor cell. Nerve impulses are triggered when these neurotransmitter molecules bind to their receptors on the dendrites of the first-order 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 five primary tastes. Complete adaptation (loss of sensitivity) to a specific taste can occur in 1 to 5 minutes of continuous stimulation.

If all tastants cause release of neurotransmitter from many gustatory receptor cells, why do foods taste different? The answer to this question is thought to lie in the patterns of nerve impulses in groups of first-order taste neurons that synapse with the gustatory receptor cells. Different tastes arise from activation of different groups of taste neurons. In addition, although each individual gustatory receptor cell responds to more than one of the five primary tastes, it may respond more strongly to some tastants than to others.

The Gustatory Pathway

Three cranial nerves contain axons of first-order gustatory neurons that innervate the taste buds. The facial (VII) nerve and glossopharyngeal (IX) nerve serve the tongue; the vagus (X) nerve serves the throat and epiglottis. From taste buds, impulses propagate along these cranial nerves to the medulla oblongata. From the medulla, some axons carrying taste signals project to the limbic system and the hypothalamus, and others project to the thalamus. Taste signals that project from the thalamus to the *primary gustatory area* in the parietal lobe of the cerebral cortex (see Figure 10.13 on page 259) give rise to the conscious perception of taste.

Probably because of taste projections to the hypothalamus and limbic system, there is a strong link between taste and pleasant or unpleasant emotions. Sweet foods evoke reactions of pleasure while bitter ones cause expressions of disgust, even in newborn babies. This phenomenon is the basis for **taste aversion**, in which people and animals quickly learn to avoid a food if it upsets the digestive system. Because the drugs and radiation treatments used to combat cancer often cause nausea and gastrointestinal upset regardless of what foods are consumed, cancer patients may lose their appetite because they develop taste aversions for most foods.

■ CHECKPOINT

8. How do olfactory receptors and gustatory receptor cells differ in structure and function?
9. Compare the olfactory and gustatory pathways.

VISION

OBJECTIVES • **Describe the accessory structures of the eye, the layers of the eyeball, the lens, the interior of the eyeball, image formation, and binocular vision.**

• **Describe the receptors for vision and the visual pathway to the brain.**

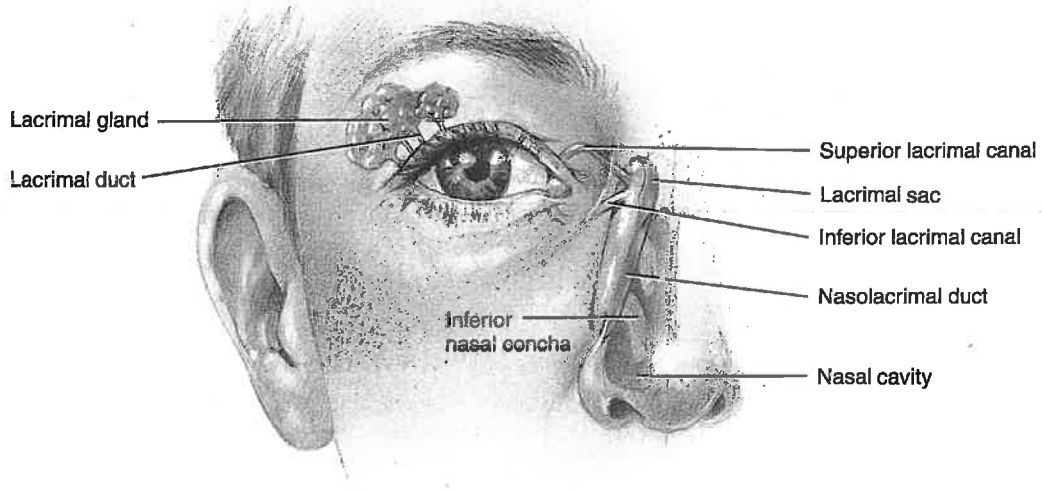
More than half the sensory receptors in the human body are located in the eyes, and a large part of the cerebral cortex is devoted to processing visual information. In this section of the chapter, we examine the accessory structures of the eye, the eyeball itself, the formation of visual images, the physiology of vision, and the visual pathway from the eye to the brain.

Accessory Structures of the Eye

The ***accessory structures*** of the eye are the eyebrows, eyelashes, eyelids, extrinsic muscles that move the eyeballs, and lacrimal (tear-producing) apparatus. The ***eyebrows*** and ***eyelashes*** help protect the eyeballs from foreign objects, perspiration, and direct rays of the sun (Figure 12.5). 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). Six extrinsic eye muscles cooperate to move each eyeball right, left, up, down, and diagonally: the *superior rectus*, *inferior rectus*, *lateral rectus*, *medial rectus*, *superior oblique*, and *inferior*

Figure 12.5 Accessory structures of the eye.

Accessory structures of the eye are the eyebrows, eyelashes, eyelids, extrinsic eye muscles, and the lacrimal apparatus.



What are the functions of tears?

oblique. Neurons in the brain stem and cerebellum coordinate and synchronize the movements of the eyes.

The ***lacrimal apparatus*** (*lacrima* = tear) is a group of glands, ducts, canals, and sacs that produce and drain ***lacrimal fluid*** or ***tears*** (Figure 12.5). The right and left ***lacrimal glands*** are each about the size and shape of an almond. They secrete 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.

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. Only humans express emotions, both happiness and sadness, by ***crying***. 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. This is how crying produces a runny nose.

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 12.6).

Fibrous Tunic

The ***fibrous tunic*** is the outer coat of the eyeball. It consists of an anterior cornea and a posterior sclera. The ***cornea*** (KOR-nē-a) is a transparent fibrous coat that covers the colored iris. Because it is curved, the cornea helps focus light rays onto the retina. The ***sclera*** (SKLER-a = hard), the "white" of the eye, is a coat of dense connective tissue that covers all of the entire eyeball except the cornea. The sclera gives shape to the eyeball, makes it more rigid, and protects its inner parts. An epithelial layer called the ***conjunctiva*** (kon-junk-TĪ-va) covers the sclera but not the cornea and lines the inner surface of the eyelids.

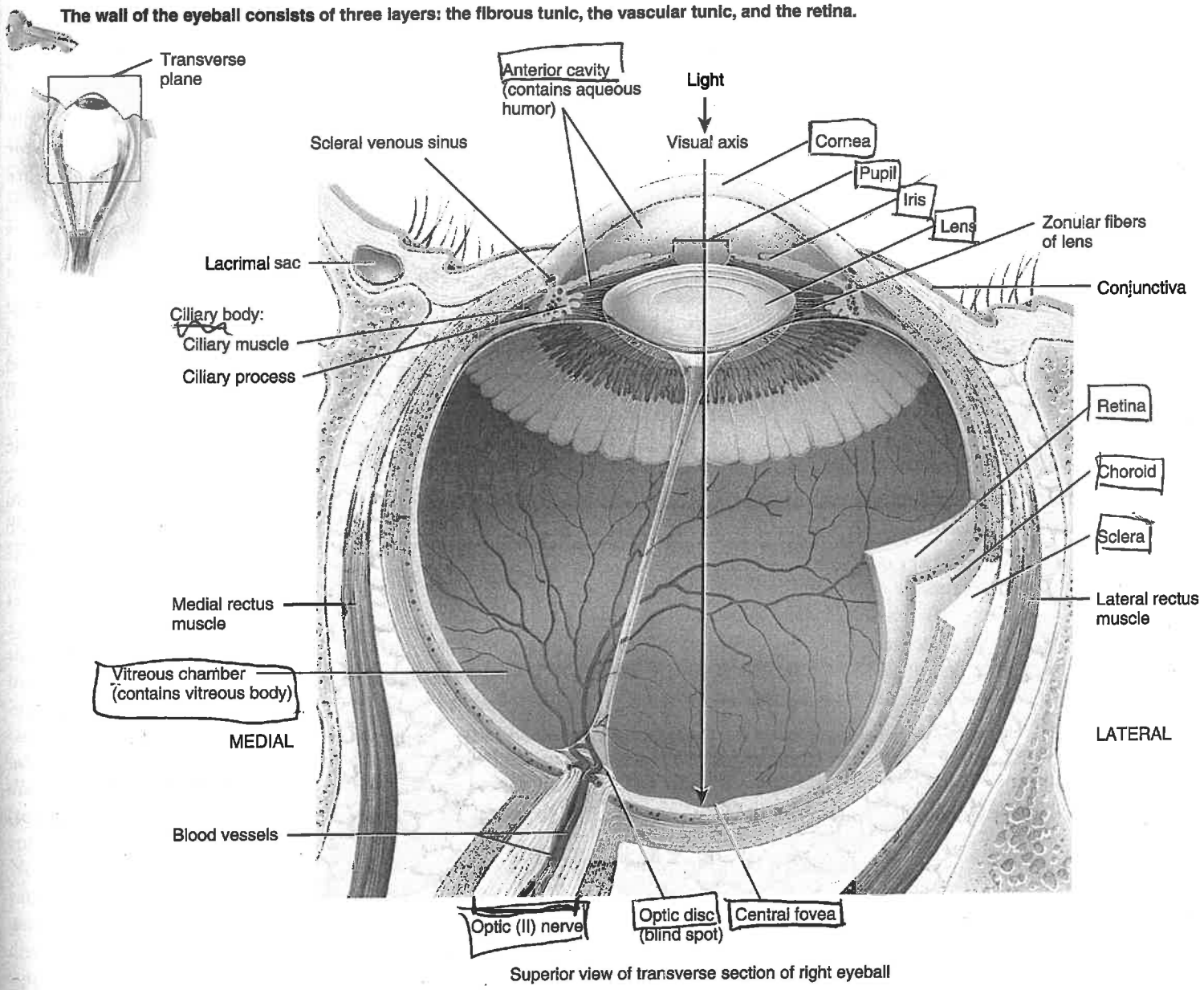
Vascular Tunic

The ***vascular tunic*** is the middle layer of the eyeball and is composed of the choroid, ciliary body, and iris. The ***choroid*** (KŌ-royd) is a thin membrane that lines most of the internal surface of the sclera. It contains many blood vessels that help nourish the retina. The choroid also contains melanocytes that produce the pigment melanin, which causes this layer to appear dark brown in color. Melanin in the choroid 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.

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 fluid called aqueous humor, and the *ciliary muscle*, a smooth muscle that alters the shape of the lens for viewing objects up close or at a distance. The ***lens***, a transparent structure that focuses light rays onto the retina, is

Figure 12.6 Structure of the eyeball.

The wall of the eyeball consists of three layers: the fibrous tunic, the vascular tunic, and the retina.



Superior view of transverse section of right eyeball

What are the components of the fibrous tunic and vascular tunic?

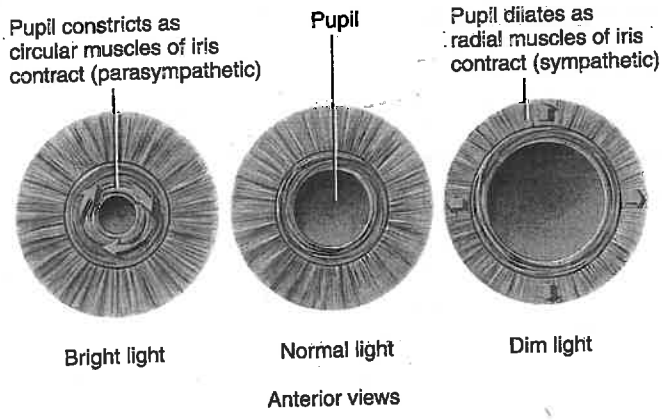
constructed of many layers of elastic protein fibers. *Zonular fibers* attach the lens to the ciliary muscle and hold the lens in position.

The ***iris*** (= colored circle) is the colored part of the eyeball. It includes both circular and radial smooth muscle fibers. The hole in the center of the iris, through which light enters the eyeball, is the ***pupil*** (Figure 12.7). The smooth muscle of the iris regulates the amount of light passing through the lens. When the eye is stimulated by bright light, the parasympathetic division of the autonomic nervous system (ANS) causes contraction of the circular muscles of the iris, which decreases the size of the pupil (constriction). When the eye must adjust to dim light, the sympathetic division of the ANS causes the radial muscles to contract, which increases the size of the pupil (dilation).

Using an **ophthalmoscope**, (of-THAL-mō-skōp; *ophthalmos-* = eye, *-skopeo* = to examine), an observer can peer through the pupil and see 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.

Figure 12.7 Responses of the pupil to light of varying brightness.

Contraction of the circular muscles causes constriction of the pupil; contraction of the radial muscles causes dilation of the pupil.



Which division of the autonomic nervous system causes pupillary constriction? Which causes pupillary dilation?

Retina

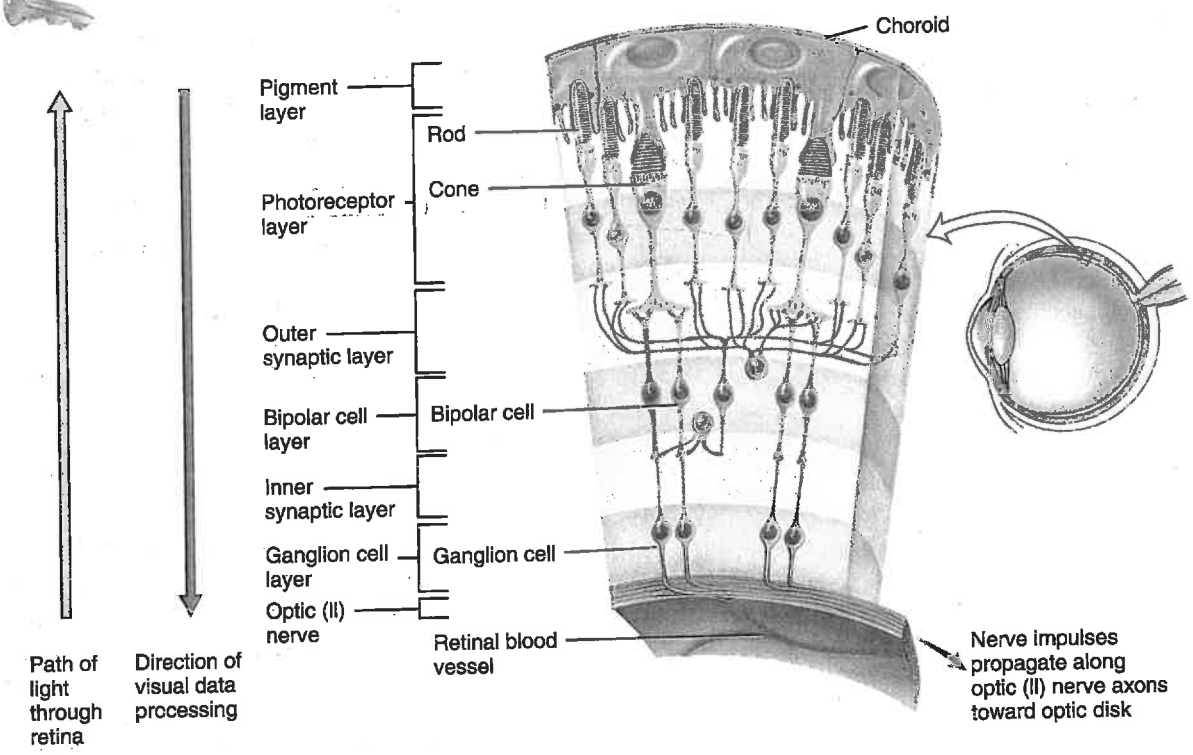
The third and inner coat of the eyeball, the ***retina***, lines the posterior three-quarters of the eyeball and is the beginning of the visual pathway (Figure 12.8). Two layers comprise the retina: the neural layer and the pigmented layer. The ***neural layer*** of the retina is a multilayered outgrowth of the brain. Three distinct layers of retinal neurons—the ***photoreceptor layer***, the ***bipolar cell layer***, and the ***ganglion cell layer***—are separated by two zones, the outer and inner synaptic layers, where synaptic contacts are made. Note that light passes through the ganglion and bipolar cell layers and both synaptic layers before it reaches the photoreceptor layer.

The *pigmented layer* of the retina is a sheet of melanin-containing epithelial cells located between the choroid and the neural part of the retina. The melanin in the pigmented layer of the retina, like in the choroid, also helps to absorb stray light rays.

Photoreceptors are specialized cells that begin the process by which light rays are ultimately converted to nerve impulses. There are two types of photoreceptors: rods and cones. ***Rods*** allow us to see shades of gray in dim light, such as moonlight. Brighter lights stimulate the ***cones***, giving rise to highly acute, color vision. Three types of cones are present

Figure 12.8 Microscopic structure of the retina. The downward blue arrow at left indicates the direction of the signals passing through the neural layer of the retina. Eventually, nerve impulses arise in ganglion cells and propagate along their axons, which make up the optic (II) nerve.

In the retina, visual signals pass from photoreceptors to bipolar cells to ganglion cells.



What are the two types of photoreceptors, and how do their functions differ?

in the retina: (1) *blue cones*, which are sensitive to blue light, (2) *green cones*, which are sensitive to green light; and (3) *red cones*, which are sensitive to red light. Color vision results from the stimulation of various combinations of these three types of cones. 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. 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-ū-la LOO-tē-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. Between 6 and 600 rods synapse with a single bipolar cell in the outer synaptic layer; a cone usually synapses with just one bipolar cell. The convergence of many rods onto a single bipolar cell increases the light sensitivity of rod vision but slightly blurs the image that is perceived. Cone vision, although less sensitive, has higher acuity because of the one-to-one synapses between cones and their bipolar cells. The axons of the ganglion cells extend posteriorly to a small area of the retina called the ***optic disc (blind spot)***, where they all exit as the optic (II) nerve (see Figure 12.6). Because the optic disc contains no rods or cones, we cannot see an image that strikes the blind spot. Normally, you are not aware of having a blind spot, but you can easily demonstrate its presence. Cover your left eye and gaze directly at the cross below. Then increase or decrease the distance between the book and your eye. At some point, the square will disappear as its image falls on the blind spot.

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*** (Ā-kwē-us HŪ-mor; *aqua* = water), a watery fluid similar to cerebrospinal fluid. Blood capillaries of the ciliary processes of the ciliary body secrete aqueous humor into the anterior cavity. It then drains into the *scleral venous sinus (canal of Schlemm)*, an opening where the sclera and cornea meet (see Figure 12.6), 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. Normally, aqueous humor is completely replaced about every 90 minutes.

Behind the lens is the second, and larger, cavity of the eyeball, the ***vitreous chamber***. It contains a clear, jellylike substance called the ***vitreous body***, which forms during embryonic life and is not replaced thereafter. This substance helps prevent the eyeball from collapsing and holds the retina flush against the choroid.

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 summarizes the structures of 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 or narrowing 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 12.9a on page 299). About 75% of the total refraction of light occurs at the cornea. Then, the lens of the eye further refracts the light rays so that they come into exact focus on the retina.

Images focused on the retina are inverted (upside down) (Figure 12.9b, 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 12.9b). However, light rays from objects closer than 6 meters are divergent rather than parallel (Figure 12.9c). The rays must be refracted more if they are to be focused on the retina. This

Table 12.2 Summary of the Structures of the Eyeball and Their Functions

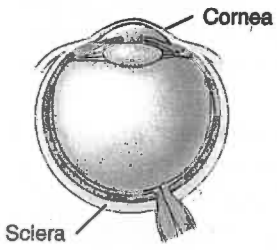
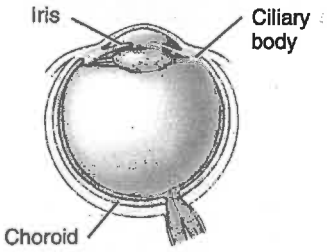
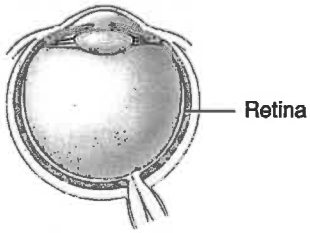
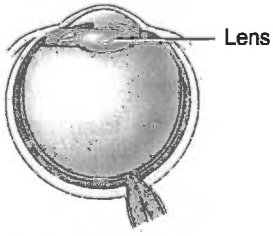
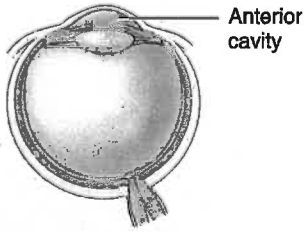
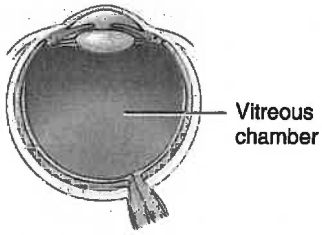
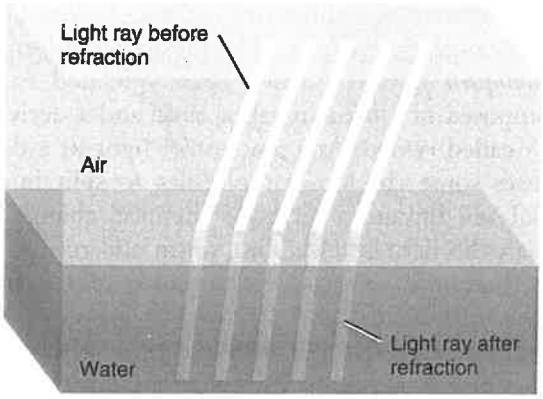
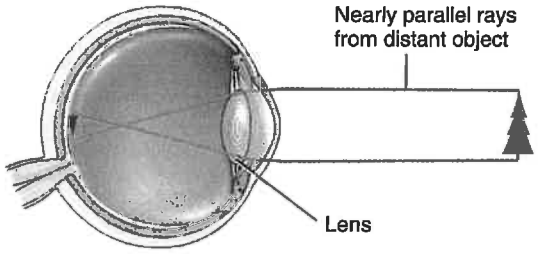
Structure	Function
Fibrous tunic 	***Cornea:*** Admits and refracts (bends) light. ***Sclera:*** Provides shape and protects inner parts.
Vascular tunic 	***Iris:*** Regulates the amount of light that enters eyeball. ***Ciliary body:*** Secretes aqueous humor and alters the shape of the lens for near or far vision (accommodation). ***Choroid:*** Provides blood supply and absorbs scattered light.
Retina 	Receives light and converts it into nerve impulses. Provides output to brain via axons of ganglion cells, which form the optic (II) nerve.
Lens 	Refracts light.
Anterior cavity 	Contains aqueous humor that helps maintain the shape of the eyeball and supplies oxygen and nutrients to the lens and cornea.
Vitreous chamber 	Contains the vitreous body, which helps maintain the shape of eyeball and keeps the retina attached to the choroid.

Figure 12.9 Refraction of light rays and accommodation.

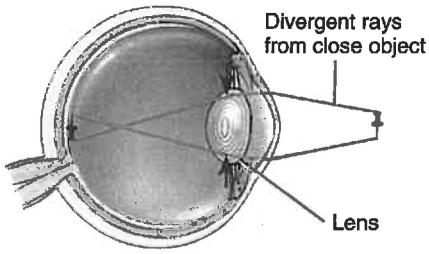
Refraction is the bending of light rays.



(a) Refraction of light rays



(b) Viewing distant object



(c) Accommodation

What changes occur during accommodation for near vision?

additional refraction is accomplished by changes in the shape of the lens.

Accommodation

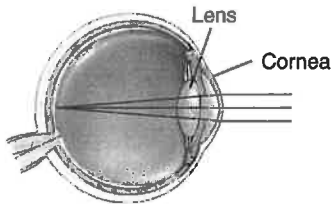
A surface that curves outward, like the surface of a ball, is said to be *convex*. The convex surface of a lens refracts incoming light rays toward each other, so that they eventually intersect. The lens of the eye is convex on both its anterior and posterior surfaces, and its ability to refract light increases as its curvature becomes greater. When the eye is focusing on a close object, the lens becomes more convex and refracts the light rays more. This increase in the curvature of the lens for near vision is called ***accommodation*** (Figure 12.9c).

When you are viewing distant objects, the ciliary muscle of the ciliary body is relaxed and the lens is fairly flat because it is stretched in all directions by taut zonular fibers. 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.

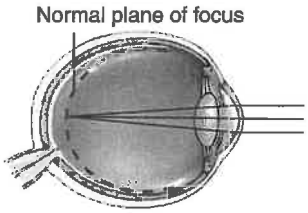
The normal eye, known as an ***emmetropic eye*** (em′-e-TROP-ik), can sufficiently refract light rays from an object 6 m (20 ft) away so that a clear image is focused on the retina (Figure 12.10a). Many people, however, lack this ability

Figure 12.10 Normal and abnormal refraction in the eyeball. (a) In the normal (emmetropic) eye, light rays from an object are bent sufficiently by the cornea and lens to focus on the central fovea. (b) In the nearsighted (myopic) eye, the image is focused in front of the retina. (c) Correction is by use of a concave lens that diverges entering light rays so that they have to travel further through the eyeball. (d) In the farsighted (hyperopic) eye, the image is focused behind the retina. (e) Correction is by a convex lens that causes entering light rays to converge.

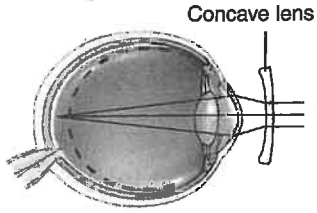
In uncorrected myopia, distant objects can't be seen clearly; in uncorrected hyperopia, nearby objects can't be seen clearly.



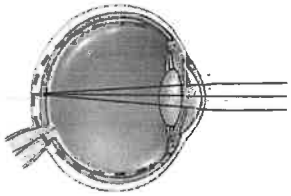
(a) Normal (emmetropic) eye



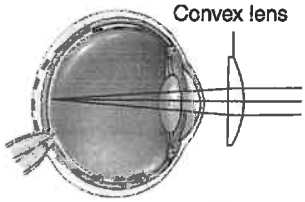
(b) Nearsighted (myopic) eye, uncorrected



(c) Nearsighted (myopic) eye, corrected



(d) Farsighted (hyperopic) eye, uncorrected



(e) Farsighted (hyperopic) eye, corrected

What is presbyopia?

because of refraction abnormalities. Among these abnormalities are ***myopia*** (mī-Ō-pē-a), or nearsightedness, which occurs when the eyeball is too long relative to the focusing power of the cornea and lens. Myopic individuals can see nearby objects clearly, but not distant objects. In ***hyperopia*** (hī-per-Ō-pē-a) or farsightedness, also known as ***hypermetropia*** (hī′-per-me-TRŌ-pē-a), the eyeball length is short relative to the focusing power of the cornea and lens. Hyperopic individuals can see distant objects clearly, but not nearby objects. Figure 12.10b–e illustrates these conditions and shows how they are corrected. Another refraction abnormality is ***astigmatism*** (a-STIG-ma-tizm), in which either the cornea or the lens has an irregular curvature.

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 close vision, such as reading. This condition is called **presbyopia** (prez′-bē-Ō-pē-a; *presby-* = old; *-opia* = pertaining to the eye or vision).

Constriction of the Pupil

Constriction of the pupil is a narrowing of the diameter of the hole through which light enters the eye due to contraction 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 only one 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*. 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 as fast as rhodopsin is split apart. Rods usually are nonfunctional in daylight, however, because rhodopsin is split apart faster than it can be reformed. 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 in each of the three types of cones. The cone photopigments reform much more quickly than the rod photopigment.

The complete 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. Prolonged vitamin A deficiency and the resulting below-normal amount of rhodopsin may cause **night blindness**, an inability to see well at low light levels. An individual with an absence or deficiency of one of the three types of cones from the retina cannot distinguish some colors from others and is said to be **colorblind**. In the most common type, *red–green color blindness*, either red cones or green cones are missing. Thus, the person cannot distinguish between red and green. The inheritance of color blindness is illustrated in Figure 24.12 on page 606.

The Visual Pathway

After stimulation by light, the rods and cones trigger electrical signals in bipolar cells. Bipolar cells transmit both excitatory and inhibitory signals to ganglion cells. The ganglion cells become depolarized and generate nerve impulses. The axons of the ganglion cells exit the eyeball as the ***optic (II) nerve*** (Figure 12.11) and extend posteriorly to the ***optic chiasm*** (KĪ-azm = a crossover, as in the letter X). In the optic chiasm, about half of the axons from each eye cross to the opposite side of the brain. After passing the optic chiasm, the axons, now part of the ***optic tract***, terminate in the thalamus. Here they synapse with neurons whose axons project to the