GLOBAL EDITION

Foundations of Behavioral Neuroscience

TENTH EDITION

Neil R. Carlson
Melissa Birkett

Foundations of Behavioral Neuroscience

Tenth Edition

Global Edition

Neil R. Carlson
University of Massachusetts, Amherst

Melissa Birkett
Southern Oregon University

Pearson

Harlow, England • London • New York • Boston • San Francisco • Toronto • Sydney • Dubai • Singapore • Hong Kong
Tokyo • Seoul • Taipei • New Delhi • Cape Town • Sao Paulo • Mexico City • Madrid • Amsterdam • Munich • Paris • Milan

Evidence suggests that neural circuits used to process music are already present in newborn infants. A functional-imaging study by Perani et al. (2010) found that one- to three-day-old infants showed changes in brain activity (primarily in the right hemisphere) when music they were hearing changed key. Brain activity also altered when babies heard dissonant music, which adults find unpleasant.

Module Review Audition

Thought Question

Have you ever heard an accessible pedestrian signal at a cross walk that sounds like a chirp, intended to help people with visual impairments safely cross streets? Many of these signals have been replaced because they were not optimally effective and can be difficult to interpret. New recommendations include a rapid ticking or beeping sound and/or a speech message saying the walk sign is on to help people cross streets more safely. What aspects of complex sounds—spatial location or timbre, loudness or pitch perception—could be used to improve these systems even more and why?

Vestibular System

The functions of the vestibular system include balance, maintaining the head in an upright position, and adjusting eye movement to compensate for head movements. This section describes the vestibular system of the inner ear and the vestibular pathway in the brain.

Anatomy of the Vestibular System

LO 7.10 Identify the structures of the vestibular system.

The vestibular system has two components: the vestibular sacs and the semicircular canals. They represent the second and third components of the *labyrinths* of the inner ear. (We just studied the first component, the cochlea.) The **vestibular sacs** respond to the force of gravity and inform the brain about the head's orientation. The **semicircular canals** respond to angular acceleration—changes in the rotation of the head—but not to steady rotation. They also respond (but rather weakly) to changes in position or to linear acceleration. Typically, we are not directly aware of the information received from the vestibular system; however, certain low-frequency stimulation of the vestibular sacs can produce nausea, and stimulating the semicircular canals can produce dizziness and rhythmic eye movements *(nystagmus)*.

Figure 7.14 shows the labyrinths of the inner ear, which include the cochlea, the semicircular canals, and the two vestibular sacs: the **utricle** ("little pouch") and the **saccule** ("little sack"). The semicircular canals approximate the three major planes of the head: sagittal, transverse, and horizontal. Receptors in each canal respond maximally to angular acceleration in one plane. The semicircular canal consists of a membranous canal floating within a bony one; the membranous canal contains a fluid called *endolymph.* An enlargement called the **ampulla** contains the organ in which the sensory receptors reside. The sensory receptors are hair cells similar to those found in the cochlea. Their cilia are embedded in a gelatinous mass called the **cupula**, which blocks part of the ampulla. Rotating the head causes fluid in the semicircular canals to rotate in the opposite direction, which pushes against the cupula, triggering action potentials in the hair cells located there.

The vestibular sacs (the utricle and the saccule) work very differently. These organs are roughly circular, and each contains a patch of receptive tissue. The receptive tissue is located on the "floor" of the utricle and on the "wall" of the saccule when the head is in an upright position. The receptive tissue, like that of the semicircular canals and cochlea, contains hair cells. The cilia of these receptors are embedded in an overlying gelatinous mass, which contains something rather unusual: *otoconia,* which are small crystals of calcium carbonate (see Figure 7.15). The weight of the crystals causes the gelatinous mass to shift in position as the orientation of the head changes. In this way, movement produces a shearing force on the cilia of the receptive hair cells.

vestibular sac One of a set of two receptor organs in each inner ear that detect changes in the tilt of the head.

semicircular canal One of the three ringlike structures of the vestibular apparatus that detect changes in head rotation.

utricle (*you trih kul*) One of the vestibular sacs.

saccule (*sak yule*) One of the vestibular sacs.

ampulla (*am pull uh*) An enlargement in a semicircular canal; contains the cupula and the crista.

cupula (*kew pew luh*) A gelatinous mass found in the ampulla of the semicircular canals; moves in response to the flow of the fluid in the canals.

Figure 7.14 Receptive Organ of the Semicircular Canals

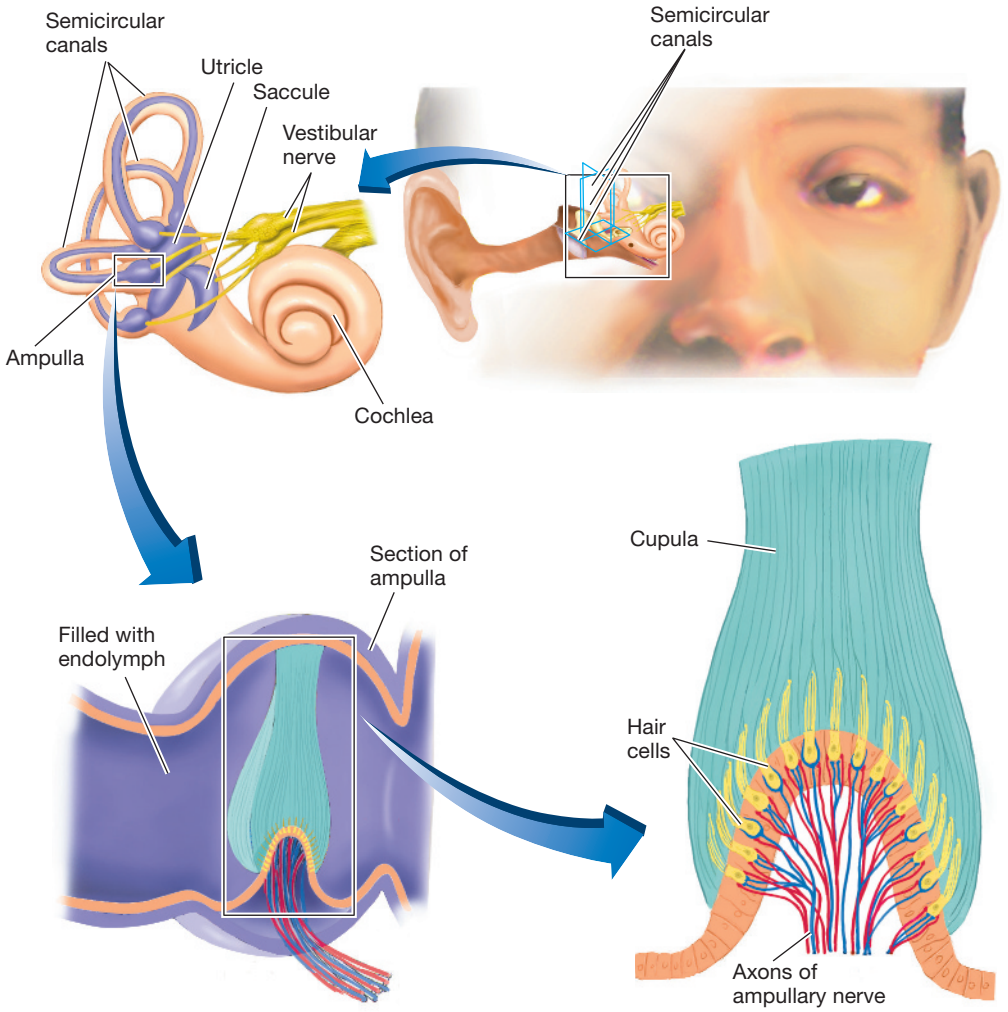
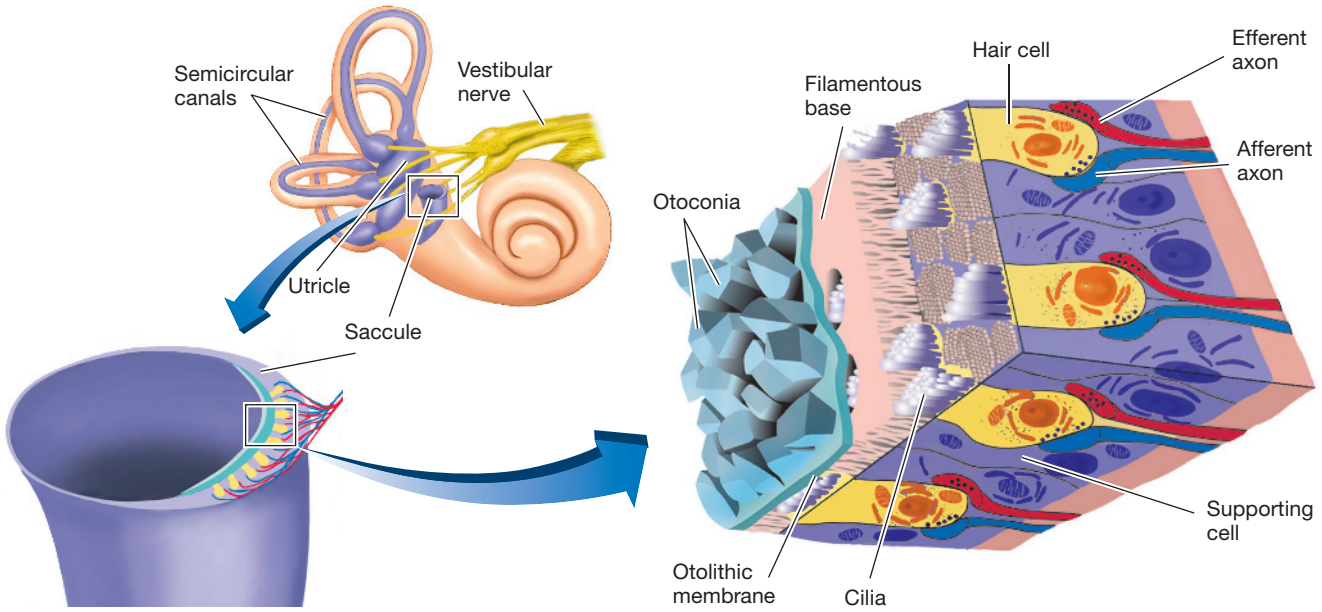


Figure 7.15 Receptive Tissue of the Vestibular Sacs: The Utricle and the Saccule



The Vestibular Pathway

LO 7.11 Outline the vestibular pathway.

The vestibular and cochlear nerves constitute the two branches of the eighth cranial nerve (auditory nerve). The bipolar cell bodies that give rise to the afferent axons of the vestibular nerve (a branch of the eighth cranial nerve) are located in the **vestibular ganglion**, which appears as a nodule on the vestibular nerve.

Most of the axons of the vestibular nerve synapse within the vestibular nuclei in the medulla, but some axons travel directly to the cerebellum. Neurons of the vestibular nuclei send their axons to the cerebellum, spinal cord, medulla, pons, and cortex. Most researchers believe that the cortical projections are responsible for feelings of dizziness. The activity of projections to the lower brain stem can produce the nausea and vomiting that accompany motion sickness. Projections to brain stem nuclei controlling neck muscles are involved in maintaining an upright position of the head and in producing eye movements to compensate for sudden head movements, like when we are running. Without this compensatory mechanism, our vision of the world would become a blur whenever we walked or ran.

Module Review Vestibular System

Thought Question

Persistent dizziness has a lifetime prevalence of approximately 25 percent and represents a significant risk factor for falls among older adults. Select one structure involved in vestibular perception and explain how damage or dysfunction in this structure could contribute to the experience of dizziness (even if the exact pathways are not yet known).

Somatosenses

The somatosenses provide information about what is happening on the surface of our body and inside it. The **cutaneous senses** (skin senses) are the most studied of the somatosenses and include several submodalities commonly referred to as *touch*. **Proprioception** and **kinesthesia** provide information about body position and movement. We will describe the contribution of sensory receptors in the skin to these perceptual systems in this section. The muscle receptors and their role in feedback from limb position and movement are discussed in this section and in Chapter 8. The **organic senses** arise from receptors in and around the internal organs. (See Table 7.2.)

The Stimuli

LO 7.12 Provide examples of stimuli that activate receptors for the somatosenses.

The cutaneous senses respond to several different types of stimuli: pressure, vibration, heating, cooling, and events that cause tissue damage (and hence, pain). Feelings of pressure are caused by mechanical deformation of the skin. Vibration occurs when we move our fingers across a rough surface. We use vibration sensitivity to judge an object's roughness. Sensations of warmth and coolness are produced by objects that raise or lower skin temperature. Sensations of pain can be caused by many different types of stimuli, especially those that cause at least some tissue damage.

vestibular ganglion A nodule on the vestibular nerve that contains the cell bodies of the bipolar neurons that convey vestibular information to the brain.

cutaneous sense (*kew tane ee us*) One of the somatosenses; includes sensitivity to stimuli that involve the skin.

proprioception Perception of the body's position and posture.

kinesthesia Perception of the body's own movements.

organic sense A sense modality that arises from receptors located within the inner organs of the body.

Table 7.2 Somatosenses

Somatosense	Function
Cutaneous Senses	Provide information from the surface of the body.
Proprioception	Provide information about location of the body in space.
Kinesthesia	Provide information about movement of the body through space.
Organic Senses	Provide information from in and around internal organs.

One source of kinesthesia is the stretch receptors found in skeletal muscles that report changes in muscle length to the central nervous system. Receptors within joints between adjacent bones respond to the magnitude and direction of limb movement. However, the most important source of kinesthetic feedback appears to come from receptors that respond to changes in the stretching of the skin during movements of the joints or of the muscles themselves, such as those in the face (Johansson and Flanagan, 2009). We are not consciously aware of information from muscle length detectors, located within the muscles, but this information is used to control movement. These receptors will be discussed separately in Chapter 8.

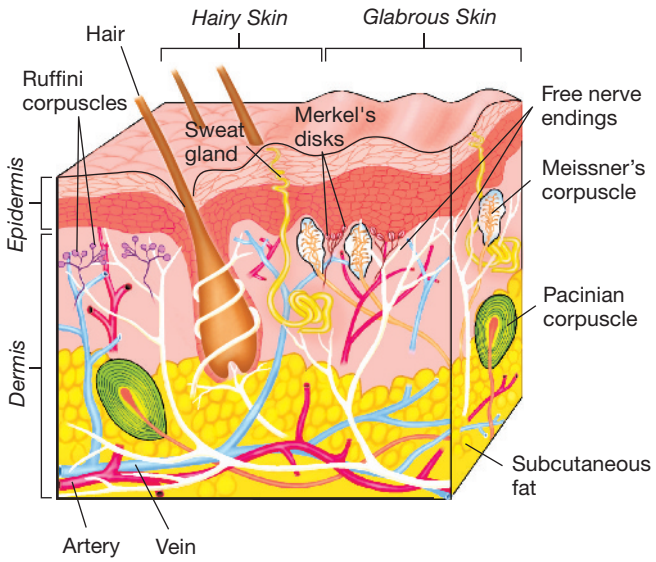
Anatomy of the Skin and Its Receptive Organs

LO 7.13 Describe the anatomy and somatosensory receptors of the skin.

The skin is a complex and vital organ of the body—one that we often take for granted. We cannot survive without it; extensive skin burns are fatal. Our cells, which must be bathed by a warm fluid, are protected from the hostile environment by the skin's outer layers. The skin participates in thermoregulation by producing sweat to cool the body, or by restricting its circulation of blood to conserve heat. Its appearance varies widely across the body, from mucous membrane to hairy skin to the smooth, hairless skin of the palms and the soles of the feet, which is known as **glabrous skin**. Skin consists of subcutaneous tissue, dermis, and epidermis and contains various receptors scattered throughout these layers. Glabrous skin contains a dense, complex mixture of receptors, which reflects the fact that we use the palms of our hands and the inside surfaces of our fingers to actively explore the environment. In contrast, the rest of our body most often contacts the environment passively when other things come into contact with it.

Figure 7.16 shows the appearance of free nerve endings and the four types of encapsulated somatosensory receptors, also known as mechanoreceptors: **Merkel's disks**, **Ruffini corpuscles**, **Meissner's corpuscles**, and **Pacinian corpuscles**. The locations and functions of these receptors are listed in Table 7.3.

Figure 7.16 Cutaneous Receptors



glabrous skin (*glab russ*) Skin that does not contain hair; found on the palms and the soles of the feet.

Merkel's disk A touch-sensitive cutaneous receptor, important for detection of form and roughness, especially by fingertips.

Ruffini corpuscle A touch-sensitive cutaneous receptor, important in detecting stretching or static force against the skin, important in proprioception.

Meissner's corpuscle A touch-sensitive cutaneous receptor, important in detecting edge contours or Braille-like stimuli, especially by fingertips.

Pacinian corpuscle (*pa chin ee un*) A vibration-sensitive cutaneous receptor, important in detecting vibration from an object being held.

Perception of Cutaneous Stimulation

LO 7.14 Describe receptors involved in the perception of touch, temperature, pain, and itch.

The three most important qualities of cutaneous stimulation are touch, temperature, and pain. These qualities, along with itch, are described in the sections that follow.

TOUCH Stimuli that cause vibration in the skin or changes in pressure against it (*tactile* stimuli) are detected by **mechanoreceptors**—the encapsulated receptors shown in Figure 7.16 and some types of free nerve endings. Movement of the dendrites located in the mechanoreceptors cause ion channels to open, and the flow of ions into or out of the dendrite causes a change in the membrane potential.

Most information about tactile stimulation is precisely localized—that is, we can perceive the location on our skin where we are being touched. However, a case study by Olausson et al. (2002) discovered a new category of tactile sensation. Read the case study below to learn more about a unique example of cutaneous stimulation.

Watch

MECHANORECEPTORS

Table 7.3 Categories of Cutaneous Receptors

Size and Nature of Receptive Field	Identity of Receptor	Location of Receptor	Function of Receptor
Small, sharp borders	Merkel's disks	Hairy and glabrous skin	Detection of form and roughness, especially by fingertips
Large, diffuse borders	Ruffini corpuscles	Hairy and glabrous skin	Detection of static force against skin; skin stretching; proprioception
Small, sharp borders	Meissner's corpuscles	Glabrous skin	Detection of edge contours; Braille-like stimuli, especially by fingertips
Large, diffuse borders	Pacinian corpuscles	Hairy and glabrous skin	Detection of vibration; information from end of elongated object being held, such as tool

Patient G.L., a 54-year-old woman, lost the ability to perceive tickle but retained the ability to perceive temperature, pain, and itch (Olausson et al., 2002,). When the hairy skin on her forearm or the back of her hand was stroked with a soft brush, she reported a faint, pleasant sensation. However, she could not determine the direction of the stroking or its precise location. An fMRI analysis showed that this stimulation activated the insular cortex, a region associated with emotional responses and sensations from internal organs. The somatosensory cortex was not activated. When regions of hairy skin of control subjects were stimulated this way, fMRI showed activation of the primary and secondary somatosensory cortex as well as the insular cortex because the stimulation activated both large and small axons. The glabrous skin on the palm of the hand is served only by large-diameter, myelinated axons. When this region was stroked with a brush, G.L. reported no sensation at all, presumably because of the absence of small, unmyelinated axons.

Our cutaneous senses are often used to analyze shapes and textures of stimulus objects that are moving with respect to the surface of the skin. Sometimes, the object itself moves, but more often, we do the moving ourselves. If an object is placed in your palm and you are asked to keep your hand still, you will have a great deal of difficulty recognizing the object by touch alone. If you are then allowed to move your hand, you will manipulate the object, letting its surface slide across your palm and the pads of your fingers. You will be able to describe the object's three-dimensional shape, hardness, texture, slipperiness, and so on. In order to describe it, your motor system must cooperate, and you need kinesthetic sensation from your muscles and joints, in addition to the cutaneous information. Our somatosenses work dynamically with the motor system to provide useful information about the nature of objects that come into contact with our skin.

TEMPERATURE There are two categories of free nerve-ending thermal receptors: those that respond to warmth and those that respond to coolness. Cold sensors in the skin are located just beneath the epidermis, and warmth sensors are located more deeply in the skin. We can detect thermal stimuli over a very wide range of temperatures, from less than 8° C (noxious cold) to over 52° C (noxious heat). At present we know of six mammalian thermoreceptors that help us detect this wide range of temperatures (Bandell et al., 2007; Romanovsky, 2007).

mechanoreceptor A sensory neuron that responds to mechanical stimuli: for example, those that produce pressure, stretch, or vibration of the skin or stretch of muscles or tendons.

Some of the thermal receptors respond to particular chemicals as well as to changes in temperature. For example, one receptor helps detect coolness, such as peppermint or menthol. These chemicals provide a cooling sensation because they bind with and stimulate the receptor and produce neural activity that the brain interprets as coolness. Chemicals can also bind with receptors to produce the sensation of heat.

Figure 7.17 Feeling the Heat

Free nerve ending nociceptors respond to capsaicin, which accounts for the heat we feel when eating peppery foods.

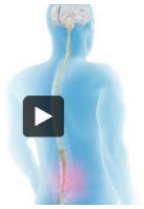
Lisa F. Young/Shutterstock

PAIN Pain perception, like thermoreception, is accomplished by the networks of free nerve endings in the skin. There appear to be at least three types of pain receptors (usually referred to as *nociceptors*, or "detectors of noxious stimuli"). High-threshold mechanoreceptors are free nerve endings that respond to intense pressure, which might be caused by something striking, stretching, or pinching the skin. A second type of free nerve ending appears to respond to extremes of heat, to acids, and to the presence of *capsaicin*, the active ingredient in chile peppers that make them feel "hot" (Kress and Zeilhofer, 1999) (Figure 7.17). Mice lacking the pain receptor sensitive to capsaicin showed less sensitivity to painful high-temperature stimuli and would drink water to which capsaicin had been added (Caterina et al., 2000). The mice responded normally to other noxious mechanical stimuli. Presumably, these receptors are responsible for pain produced by burning of the skin and to changes in the acid/base balance within the skin. These receptors are responsible for the irritating effect of chemicals such as ammonia on the mucous membranes of the nose (Dhaka et al., 2009). These receptors also appear to play a role in regulation of body temperature. In addition, Ghilardi et al. (2005) found that a drug that blocks TRPV1 receptors reduced pain in patients with bone cancer, which is apparently caused by the production of acid by the tumors.

Another type of pain receptor is found in the cilia of auditory and vestibular hair cells. This type of receptor is sensitive to pungent irritants found in mustard oil, wintergreen oil, horseradish, and garlic and to a variety of environmental irritants, including those found in vehicle exhaust and tear gas (Bautista et al., 2006; Nilius et al., 2007). The primary function of this receptor appears to provide information about the presence of chemicals that produce inflammation.

Another noxious sensation, itch (or, more formally, *pruritus*) is caused by skin irritation and has an interesting relationship with pain. Scratching reduces itching because pain suppresses itching (and, ironically, itching reduces pain). Histamine and other chemicals released by skin irritation and allergic reactions are important sources of itching. Experiments have shown that painful stimuli such as heat and electrical shock can reduce sensations of itch produced by an injection of histamine into the skin, even when the painful stimuli are applied up to 10 cm from the site of irritation (Nilsson et al., 1997; Ward et al., 1996). Little is known about the receptors that are responsible for the sensation of itch, but at least two different types of neurons transmit itch-related information to the CNS (Johanek et al., 2007).

Watch
PAIN PROCESSING



The Somatosensory Pathways

LO 7.15 Describe the pathway for somatosensory processing from nerves to subcortical and cortical structures.

The somatosensory pathways relay information about somatosensation from the receptors, through subcortical structures to the primary and secondary somatosensory cortex, enabling somatosensory perception.

NERVES AND SUBCORTICAL PROCESSING Somatosensory axons from the skin, muscles, or internal organs enter the central nervous system via spinal nerves. Those located in the face and head primarily enter through the trigeminal nerve (fifth cranial nerve). The cell bodies of the unipolar neurons are located in the dorsal root ganglia and cranial nerve ganglia. Axons that convey precisely localized information, such as fine touch, ascend through the *dorsal columns* in the white matter of the spinal cord to nuclei in the lower medulla. From there, axons cross the brain and ascend through the *medial lemniscus* to the *ventral posterior nuclei of the thalamus,* the relay nuclei for somatosensation. Axons from the thalamus project to the primary somatosensory cortex, which in turn sends axons to the secondary somatosensory cortex. In contrast, axons that convey poorly localized information, such as pain or temperature, form synapses with other neurons as soon as they enter the spinal cord. The axons of these neurons cross to the other side of the spinal cord and ascend through the *spinothalamic tract* to the ventral posterior nuclei of the thalamus. (See Figure 7.18.)

Damage to the visual association cortex can cause visual agnosia, and damage to the auditory association cortex can cause auditory agnosia. Similarly, damage to the somatosensory association cortex can cause tactile agnosia.

Patient E.C., a woman with left parietal lobe damage, was unable to recognize common objects by touch. For example, she identified a pine cone as a brush, a ribbon as a rubber band, and a snail shell as a bottle cap. The deficit was not due to a simple loss of tactile sensitivity; the patient was still sensitive to light touch and to warm and cold objects, and she could easily discriminate objects by their size, weight, and roughness (Reed, Caselli, and Farah 1996).

Perception of Pain

LO 7.16 Describe why pain is experienced, and the three components of pain.

Pain is a curious phenomenon. It is more than a mere sensation and it can be defined only by some sort of withdrawal reaction or, in humans, by verbal report. Pain can be modified by opiates, by hypnosis, by the administration of placebos, by emotions, and even by other forms of stimulation, such as acupuncture. Here we explore the physiological bases of pain.

WHY DO WE EXPERIENCE PAIN? Although it may seem counterintuitive, pain in most cases serves a constructive role. For example, inflammation, which often accompanies injuries to skin or muscle, greatly increases sensitivity of the inflamed region to painful