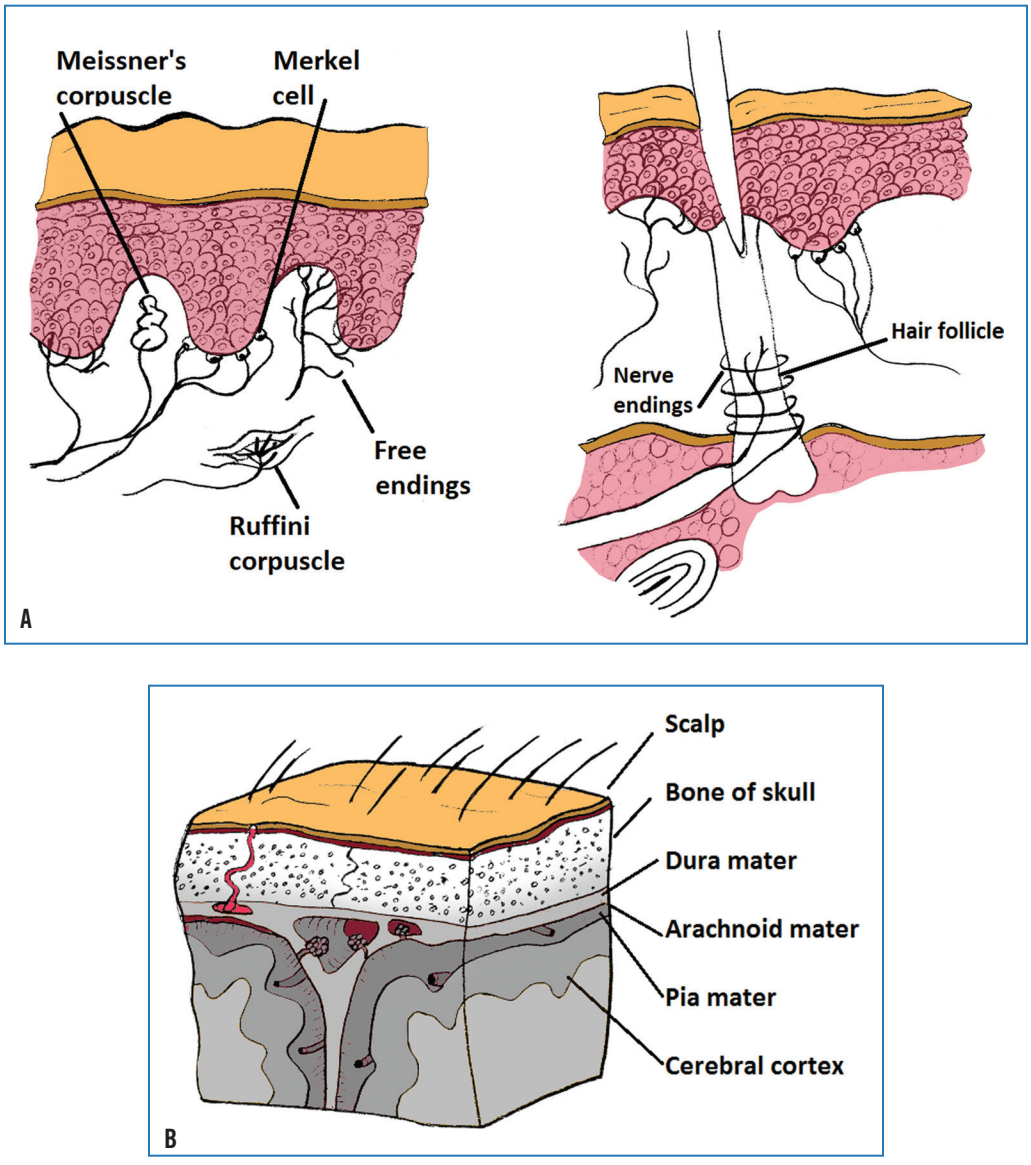

FIGURE 3–2. Receptors within the epidermis. **A.** Meissner's corpuscles, Ruffini's corpuscles, Merkel cells, and free endings. *Source:* Adapted from Brodal (2004). **B.** Receptors *in situ* in epidermis of scalp. *Source:* Adapted from Seikel, Drumright, and King (2016).

the response. Some of these mechanoreceptors also mediate heat and cold or chemical changes in tissue caused by irritation and inflammation. These thermal receptors look the same as pain sensors under magnification but have the added properties of perceiving a range of stimulation. We sense the range of thermal experiences through cool, cold, warm, and hot sensors. Obviously, the painful stimuli are at the ends of the continuum (cold and hot), but the cool and warm sensors prepare us for those extremes so that we can avoid them. In contrast to other mechanoreceptors, nociceptors not only do not adapt to stimuli, but *they become more sensitive to the painful stimulus the longer you maintain it.* You know this from your own experience, of course: walking with a rock in your boot doesn't get easier as you go along! Again, this is an appropriate response by your body, although it can lead to neurophysiological hypersensitization to pain, which increases the effects of these chronic conditions (Møller, 2003).

There is another group of mechanoreceptors that provide us with knowledge of how the joints of our bodies are oriented and moving. There are at least four types of sensors that reside within the joint capsule: some of them sense movement and rate of change of the joint, while others are similar to GTOs, in that they sense stretching of ligaments that bind

the bones together. Studies on humans have revealed that stimulation of the sensors related to joint movement causes a person to perceive that the structure (in this case a finger) has moved. Thus, joint sense serves the subconscious proprioception function that helps us organize our navigation of space, but it also provides conscious knowledge of those movements as well (Dye, Vaupel, & Dye, 1998; Macefield, Gandevia, & Burke, 1990).

We would be remiss if we didn't mention proprioceptive sense. **Proprioception** refers to sensory perception related to the musculoskeletal system. The position sense of joints, tension on muscles, movement of the arms and legs, and so forth are all mediated by sensors within the muscle and skeletal systems. There are minute sensors within the joints, in the fascia, and, of course, in the muscles (muscle spindle) and tendons (Golgi tendon organs) that are informing me of my body "condition" at all times. Most of the sensation is related to stretching of tissue, and these are typically low-threshold sensors. "Silent nociceptors" are a group of pain sensors that mediate homeostasis. These sensors monitor the effluent of tissues that are damaged, such as cytokines released by the mucosa of the stomach in response to an assault on the tissue by bacteria or viruses. These sensors mediate the behaviors we know as "sickness," which serve to slow us down for the healing process (National Research Council. Committee on Recognition and Alleviation of Pain in Laboratory Animals, 2009).

In summary, muscle spindles are the mechanism for providing feedback to the neuromotor system concerning muscle length, tension, motion, and position.

- Muscle spindles run parallel to the intrafusal muscle fibers and provide information concerning change in length of muscle, whereas Golgi tendon organs sense muscle tension.
- Acceleration is sensed by means of nuclear bag fibers, which convey information concerning acceleration. Nuclear chain fibers respond to sustained lengthening.
- A segmental reflex is triggered when a muscle is passively stretched, and this activates the extrafusal muscles, which shorten the muscle.
- Tension of the muscle during contraction is sensed by the Golgi tendon organs, which mediate inhibition of antagonist muscles.
- Receptors transduce internal or external environment information into electrochemical impulses. Information from a receptor is sent to the CNS for processing.

REPRESENTATION OF THE SOMATIC SENSATION IN THE SPINAL CORD

The spinal cord receives sensory information from diverse sources, such as skin receptors for touch, temperature, and pain, as well as sensors in joints and muscles, as we will discuss. For the information to be useful in responding to the environment it has to enter the central nervous system. In our discussion of the muscle spindle response, the muscle spindle communicates with the spinal cord by means of a spinal nerve that enters the spinal cord segment. We also talked about multi-segment reflexes, which span more than one spinal cord segment.

Figure 3–3 shows a dermatome map for the human body. A **dermatome** is defined as an area of skin that is innervated by a single spinal nerve, and it represents the distribution of the cutaneous region served by the nerve (Barr, 1974). Sensory dermatomes are the receptive map for the body. Motor innervation arises from the ventral root of the spi-

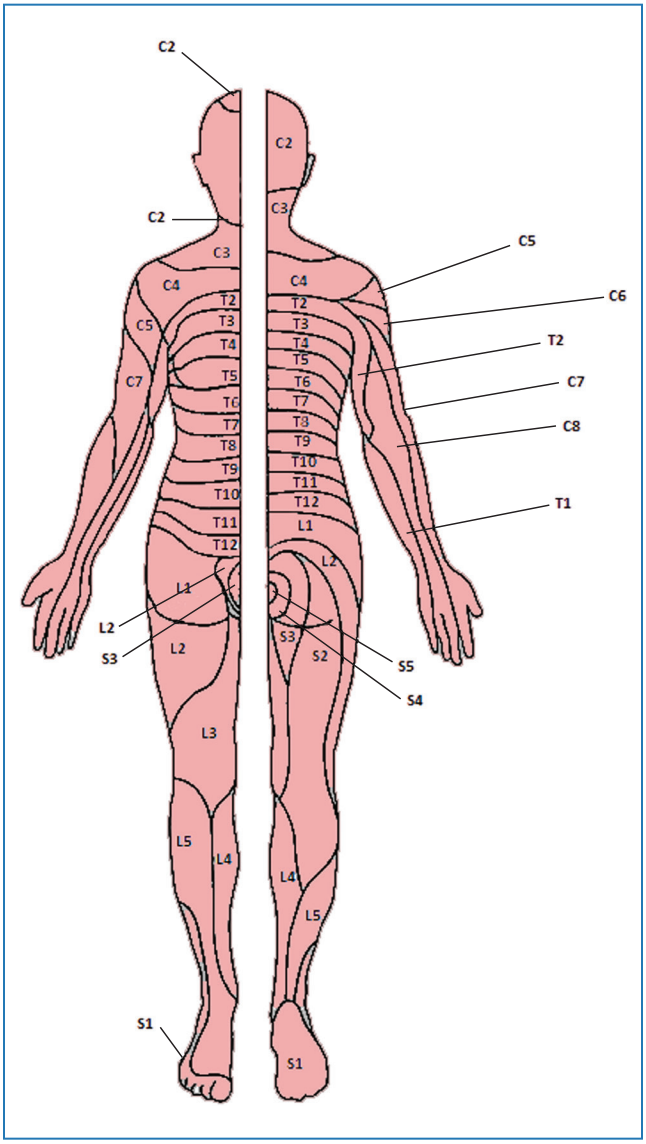

FIGURE 3–3. Dermatomes of the epidermal layer.

nal cord segment, and these nerves serve muscles of the legs, arms, thorax, and abdomen. Typically, efferent nerves combine to create **plexuses** (groups of nerves coming together for a common purpose; Table 3–2), and these plexuses give rise to the motor nerves that activate muscle. For example, cervical nerves C1, C2, C3, and C4 come together to form the cervical plexus, and this plexus gives rise to the phrenic nerve, which innervates the diaphragm. In contrast, the sensory nerves have specific territories or dermatomes that they serve. For instance, you can see that C2 and C3 have a sensory territory that serves the back of the neck and scalp. That is to say, if a mosquito bites you on your neck, the histamine that she introduces into your skin will cause an itch that will be mediated by C2 to the spinal cord. Neurologists can use this information to pinpoint lesions to the afferent nervous system. If, for instance, you have reduced or absent sensation below the level of your knees, the neurologist can infer that there is damage to the sensory component of the spinal cord in the lumbar and sacral regions.

Dermatomes actually overlap, so the correspondence is not as tight as one might guess from looking at the map. Although Herrington performed the first dermatome mapping, on monkeys, in 1898, the human dermatome map was developed through information gained from clinical evaluations of people with spinal cord injuries by Head in the 1920s (Brodal, 2004).

Dermatomes are important tools for the neurologist but also give clues as to site of lesion for the speech-language pathologist. That having been said, we will be much more interested in the cranial nerves that provide input about muscles and structures related to speech. We'll spend a whole chapter on those nerves!

SPECIAL SENSES

While somatic senses serve the broader needs of the body, including proprioception and homeostasis, some special senses have also evolved that are designed to mediate specific stimuli impinging on our bodies. This evolutionary process has taken quite some time, and we humans are the beneficiaries of these eons of development. Our cochlea is echoed in the lateral line organ of fish, and some form of an eye has evolved at least four times in history! Smell is so elemental that it is the only sense that doesn't enter the thalamus of the brain, and taste takes up a sizable portion of the cerebral cortex (the insula). Let's take a moment to examine these senses and a little of their mechanisms. Of course, for us, the sense of hearing is critical, but our work in swallowing as speech-language pathologists means that we need to have some knowledge of taste and olfaction as well.

Visual Sensation

Sensors for the visual system are both elegant and complex (Figure 3–4). Retinal cells of the eye are located in the posterior inner surface of the eye. Myelin is absent in the retinal sensors, which allows the structure of the retina to be essentially translucent (i.e., it allows light through). The paper-thin retina consists of eight layers. The outermost layer contains pigment cells that protect the retinal cells deep to them, as well as provide a bed for the photoreceptors. The photoreceptor layer includes rod and cone cells that are sensitive to light stimulation. The outer nuclear layer contains the nuclei of the photosensors, while the next five layers contain horizontal

TABLE 3–2. Nerve Plexuses of the Spinal Cord

Plexus	Nerve components	Function
Cervical	C1–C4	Motor fibers; innervate muscles of head, neck, and shoulders; interacts with X vagus and XI accessory; gives rise to phrenic nerve of diaphragm
Brachial	C4–C8, T1 and T2	Motor and sensory fibers; thorax, shoulders, arms, hands
Lumbar	L1–L4, T–12	Sensory and motor innervation; sensory innervation of pleurae and peritoneum; motor fibers; interacts with sacral plexus; motor innervation for abdomen, groin, thighs, knees, calves
Sacral	L4–S4	Sensory and motor innervation; interacts with lumbar plexus; gives rise to sciatic nerve; innervation of pelvis, buttocks, genitals, thighs, calves, feet
Coccygeal	S4, S5, coccygeal 1	Coccyx; sensation of skin in coccygeal region

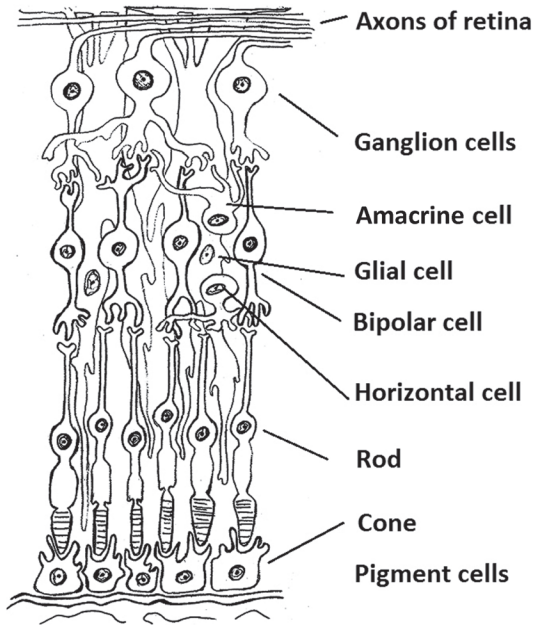

FIGURE 3–4. Layers of the retina. The pigment layer is the most superficial layer, providing protection to the photoreceptors of the second layer. The outer nuclear layer includes cell bodies and axons of photoreceptors, while the outer plexiform, inner nuclear and inner plexiform layers include bipolar, Muller, and glial cells. The ganglion and nerve fiber layers are the beginning stages of the optic nerve.

bipolar cells and interneurons (amacrine cells), whose role is to sharpen the photoreceptor input through inhibition of non-target regions (see the box on Negative Afterimages). The deepest nerve fiber layer includes the axons of the ganglion cell layer, the final processing stage of the retina. The retina is particularly unique in that, despite being a sensory organ, it performs a great deal of pre-processing. By contrast, in the auditory system, that pre-processing primarily occurs in the brainstem.

Negative Afterimages and Feature Detection

Have you ever had the experience of briefly glancing at the sun and then quickly looking away? We all have experienced the blinding flash of that experience, but there's a secret embedded in the recovery process. Even after you look away, you can still see the image of the sun. The photoreceptors of your retina have been overstimulated and fatigued by the intensity of the light, similar to what you experience when you've heard a loud sound (temporary threshold shift). If you pay attention to this image, you'll see it change over time, reflecting the recovery of your visual system.

But there's more to that recovery than "meets the eye." Activation of rods and cones inhibits the spontaneous activity of adjacent neurons, a feature that enhances the image produced by making a stronger output difference between the activated cell and those around it. This is called edge enhancement. You can verify this effect by looking at a page that is solid black on half the page and white on the other: you'll see that the black edge appears even blacker than the field. Perceptual scientists have used these edge-effects to determine that the retinal neurons are actually feature detectors, capable of pre-processing basic visual features of the image being viewed. Hubel and Wiesel earned their Nobel Prize for work with visual neurophysiology, and some of their early work involved feature detection in the frog. They found there were feature detectors in the frog retina that sensed movement in an upwardly vertical direction, downwardly vertical direction, horizontal direction, etc., precisely mirroring the movements a fly would have in the visual field. Remarkably, these detectors were responsive only to one type of stimulus (e.g., upward vertical movement) and not to another stimulus. In fact, movement in that upward vertical dimension inhibited activity in the downward vertical detectors.

What does this have to do with negative afterimage? You can demonstrate the presence of feature detectors easily in your own visual system. Try this experiment. Stand in front of a cluttered shelf of your cupboard, or in front of a bookshelf with a variety of shapes and sizes, and then turn off the lights so it's good and dark. Let your eyes adapt to the dark for several minutes, and then flash your camera at the shelf and watch what happens. You will see the image during the flash instant, for sure, and then you will see it disappear and be replaced by a negative image, which will gradually decay. That negative afterimage is the product of the cells that are normally inhibited when viewing that image, but which were released from inhibition because of fatigue of the primary neurons. Want another example? Watch a blockbuster movie with credits that seem to go on forever. Pay close attention to the credits, without letting your eyes wander away from the screen. When you get to the very end of the credits, the scrolling stops on a final logo, and you will have the impression that the logo is moving in the opposite direction from the credits. You have fatigued feature detectors for movement in the vertical direction, going from top to bottom, and the detectors for the opposite direction are able to respond because of that fatiguing effect. Once you starting looking for the effect, you will see dozens of examples!

Unlike most other receptors, photoreceptors become hyperpolarized when stimulated. That is, they turn off when stimulated, but are depolarized or active in darkness. Another unique characteristic is that they produce a **graded potential** rather than an all-or-none action potential, so we can actually see shades of a color. Activation of retinal cells disinhibits bipolar cells, which produce action potentials that stimulate ganglion cells. We'll return to the visual system when we examine cranial nerves.

Olfactory Sensation

Olfaction refers to the sense of smell, and it is mediated by the first cranial nerve. Olfactory sense utilizes chemoreceptors, which respond to chemicals that impinge on the sensors. Olfaction and gustation are very important for speech-language pathologists because of our work in swallowing disorders. The sense of smell is not as well used in humans as in non-humans, such as dogs or cats, but its basic and important nature can be felt in the evocative nature of smells. The olfactory sense is tied closely to the hippocampus, which is the major memory element of the central nervous system. Smells can evoke memories for which there are no words because those memories were put in place before you had language. Smell is the most basic and oldest of our special senses.

Olfactory sensors are embedded in the olfactory epithelium, in the mucous membrane lining of the superior nasal cavity. The 10 million sensors take up very little space (about 1 cm^3) and undergo constant regeneration (Brodal, 2004).

Gustatory Sensation

Gustation (taste) is a very important process for speech-language pathologists because of its relationship with mastication and deglutition. Taste is what keeps us eating to fulfill our nutritional requirements. Taste receptors (**taste buds**, or **taste cells**) are **chemoreceptors** that are found in the tongue epithelia within **papillae**. Taste pores within the papillae are openings that isolate a tasted substance. The material in the taste pore is held in place by small hair-like fibers called **microvilli**, which project from the taste cell into the **taste pore** (Figure 3–5).

We categorize tastes into five broad categories: sweet, salty, sour, bitter, and umami. The perception of taste arises from activation of taste sensors in varying combinations, so the taste of strawberries differs from that of chocolate because of the combinations of sensors that have been activated. You may have never run across the term *umami*. Umami is a basic "meaty" or protein-like flavor elicited by the spice monosodium glutamate. For over a century, we believed that taste receptors were restricted to zones of the tongue, with sweet tastes being sensed at the tip, salty at the sides in front, and sour at the sides in the back. Bitterness was thought to be sensed on the posterior tongue. The reality is that all the tastes can be sensed all over the tongue.

There are four basic forms that the papillae take. **Filiform papillae** dominate, but they aren't taste sensors at all. They look like small pink or gray threads on the dorsum of the tongue and have mechanoreceptors that give your tongue exquisite tactile sensory ability, permitting fine discrimination of the bolus characteristics. Bright red **fungiform papillae** are found among the filiform papillae on the tip and sides of the tongue. **Foliate papillae** populate the posterior lateral tongue and faucial pillars. A dozen or so **circumvallate** (or **vallate**) papillae are located on the posterior dorsal surface, arrayed in a V-formation.

Taste receptors (also known as taste buds; Figure 3–6) are chemosensors that work with saliva to do their job. Saliva

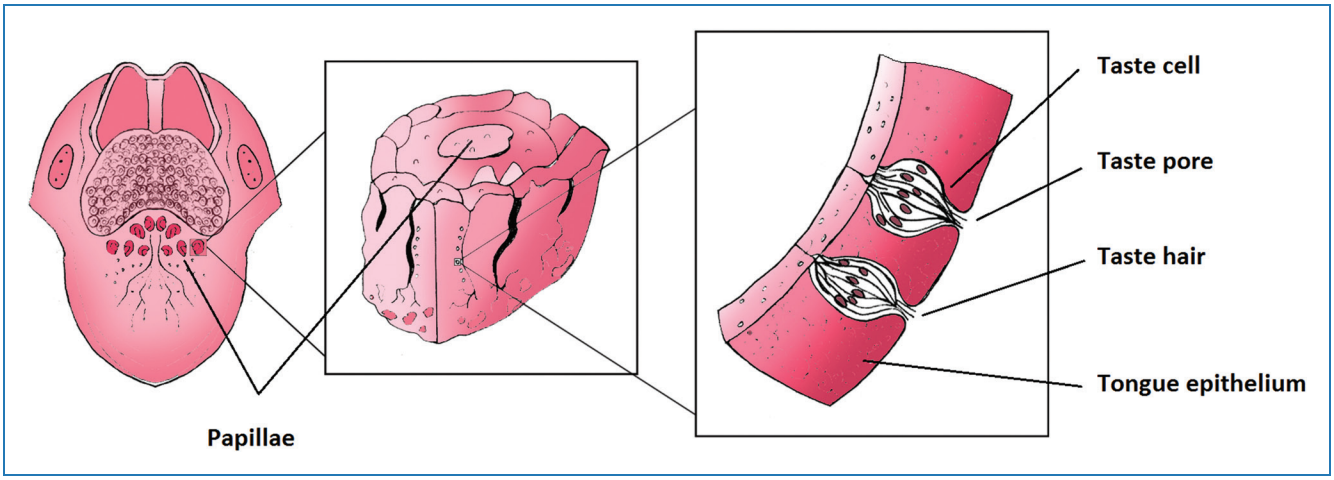

FIGURE 3–5. Taste buds of the tongue. Relationship among tongue, papillae, and taste buds. *Source:* Adapted from Seikel, Drumright, and King (2016).

is made of enzymes that dissolve materials you place in your mouth, putting the food into a format that your sensors can process. The taste buds are found throughout the tongue, but are concentrated on the lateral aspects of the anterior tongue, as well as the tongue dorsum. They are also found in the valleculae, on the velum, and even at the entrance of the larynx. There are even reports of taste sensors deep within the linings of the intestines (Bezencon, le Coutre, & Damak, 2006)!

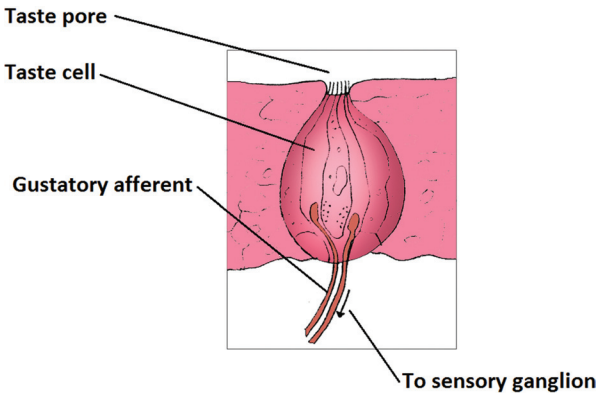

FIGURE 3–6. Fine structure of the taste bud, taste pore, and microvilli.

Auditory Sensation

Of course audition and vestibular function are bedrock processes for our professions. Acoustical information represents a disturbance in air that is translated to movement of the perilymph and, ultimately, endolymph fluids of the cochlea. Acoustic information is a mechanical stimulus that requires a mechanoreceptor, the hair cell. Hair cells have evolved into exquisite systems for sensing minute changes in air pressure, though we should humbly acknowledge that the auditory mechanism arises from the lateral line organ of fish.

There are two basic types of hair cells (Figure 3–7), inner and outer, with different structure and function. The **inner hair cells** are considered to be the primary mechanism for auditory discrimination of frequency, while the **outer hair cells** serve the critical role of sound amplification. There are about 3,500 inner hair cells (IHC) and 12,000 outer hair cells (OHC). Inner hair cells are arrayed in a single row along the basilar membrane, while outer hair cells are in three rows (Pickles, 2012).

Each hair cell has critically important **stereocilia** (also known as **cilia**) on the upper surface. On the IHC there are about 50 cilia, which are arrayed as a flattened "U," and on the OHC, about 150 cilia take the form of a "W." The cilia are very important to the transduction process. The cilia are graduated in length, but are all connected by means of tip links made up of fibrin molecules, which provide a rigid connection between the cilia. The cilia are thinner at the base than at the top, which means they are more prone to

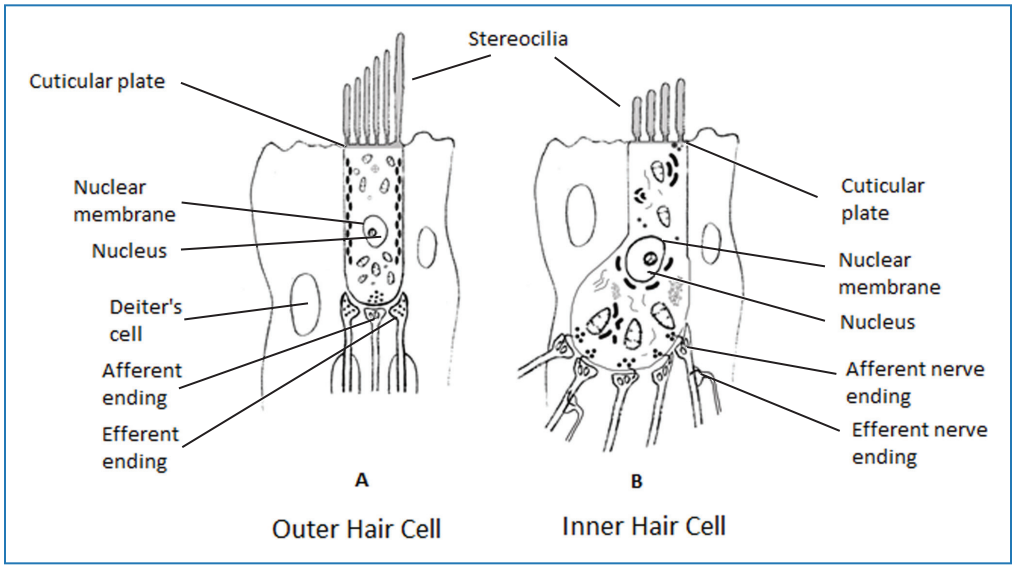

FIGURE 3–7. Hair cells of the cochlea. **A.** Outer hair cell of cochlea. Note that efferent endings of olivocochlear bundle synapse directly with cell body. **B.** Inner hair cell of cochlea. Note that efferent endings of olivocochlear bundle synapse with afferent component rather than cell body.