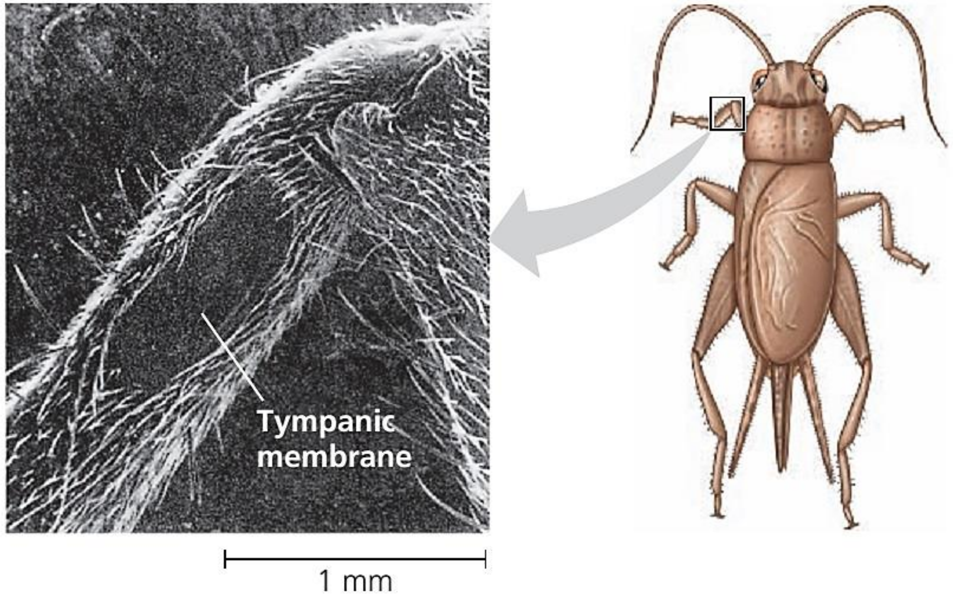
In hearing and equilibrium, mechanoreceptors detect moving fluid or settling particles

For most animals, the sense of hearing is closely related to the sense of balance, the perception of body equilibrium. For both senses, mechanoreceptor cells produce receptor potentials in response to deflection of cell-surface structures by settling particles or moving fluid.

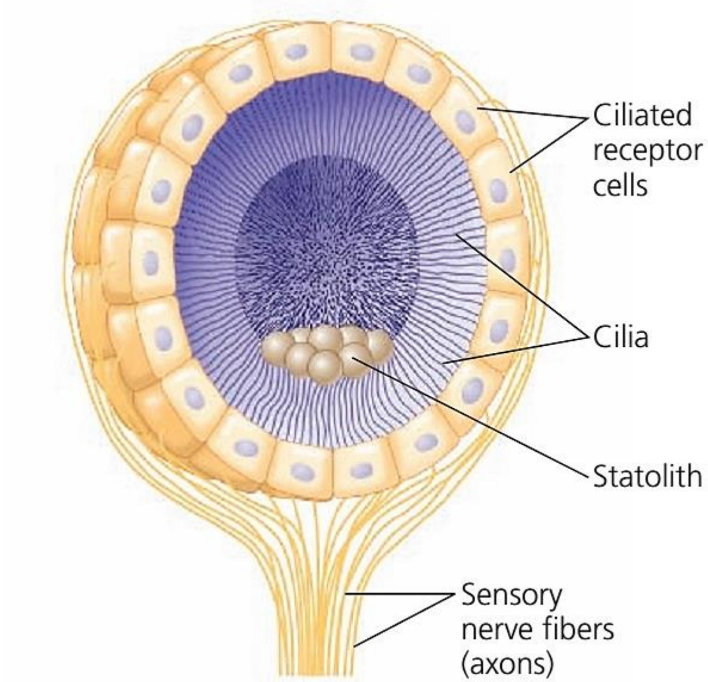
Sensing of Gravity and Sound in Invertebrates

To sense gravity and maintain equilibrium, most invertebrates rely on mechanoreceptors located in organs called **statocysts**. In a typical statocyst, **statoliths**, granules formed by grains of sand or other dense materials, sit freely in a chamber lined with ciliated cells. Each time an animal repositions itself, the statoliths resettle, stimulating mechanoreceptors at the low point in the chamber.

Many (perhaps most) insects have body hairs that vibrate in response to sound waves. Many insects also detect sound by means of vibration sensitive organs, which consist in some species of a tympanic membrane (eardrum) stretched over an internal air chamber. Cockroaches lack such a tympanic membrane, but instead have vibration-sensitive organs that sense air movement, such as that caused by a descending human foot.



▼ Figure 50.9 An insect's "ear"—on its leg. The tympanic membrane, visible in this SEM of a cricket's front leg, vibrates in response to sound waves. The vibrations stimulate mechanoreceptors attached to the inside of the tympanic membrane.



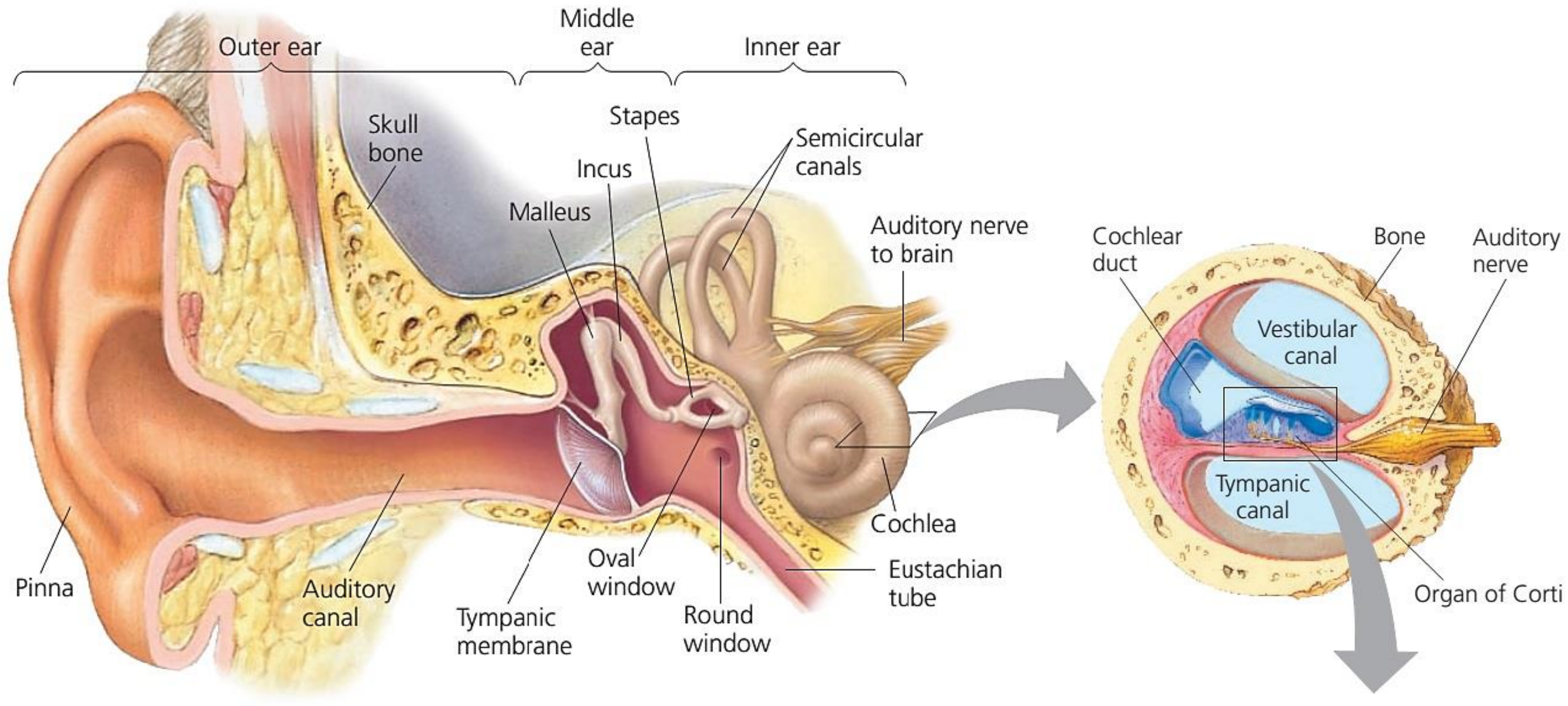
▼ Figure 50.8 The statocyst of an invertebrate. The settling of granules called statoliths to the low point in the chamber bends cilia on receptor cells in that location, providing the brain with information about the orientation of the body with respect to gravity.

Hearing and Equilibrium in Mammals

In mammals, as in most other terrestrial vertebrates, the sensory organs for hearing and equilibrium are closely associated.

1 Overview of Ear Structure

The **outer ear** consists of the external pinna and the auditory canal, which collect sound waves and channel them to the **tympanic membrane** (eardrum), a thin tissue that separates the outer ear from the **middle ear**. In the middle ear, three small bones—the malleus (hammer), incus (anvil), and stapes (stirrup)—transmit vibrations to the **oval window**, which is a membrane beneath the stapes. The middle ear also opens into the **Eustachian tube**, a passage that connects to the pharynx and equalizes pressure between the middle ear and the atmosphere. The **inner ear** consists of fluid-filled chambers, including the **semicircular canals**, which function in equilibrium, and the coiled **cochlea** (from the Latin meaning "snail"), a bony chamber that is involved in hearing.

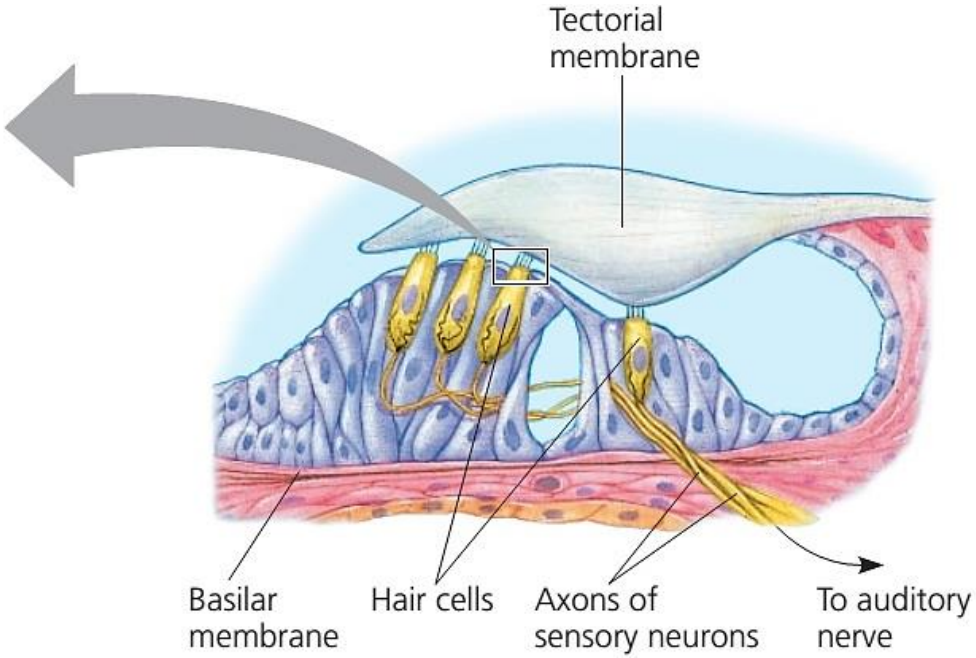


2 The Cochlea

The cochlea, shown here in cross section, has two large canals—an upper vestibular canal and a lower tympanic canal—separated by a smaller cochlear duct. Both canals are filled with fluid.

3 The Organ of Corti

The floor of the cochlear duct, the basilar membrane, is the base of the **organ of Corti**, which contains the mechanoreceptors of the ear—hair cells with bundles of rod-shaped "hairs" projecting into the cochlear duct. Many of the hairs are attached to the tectorial membrane, which hangs over the organ of Corti like an awning.



▲ Bundled hairs projecting from a single mammalian hair cell (SEM). Two shorter rows of hairs lie behind the tall hairs in the foreground.

4 Hair Cell

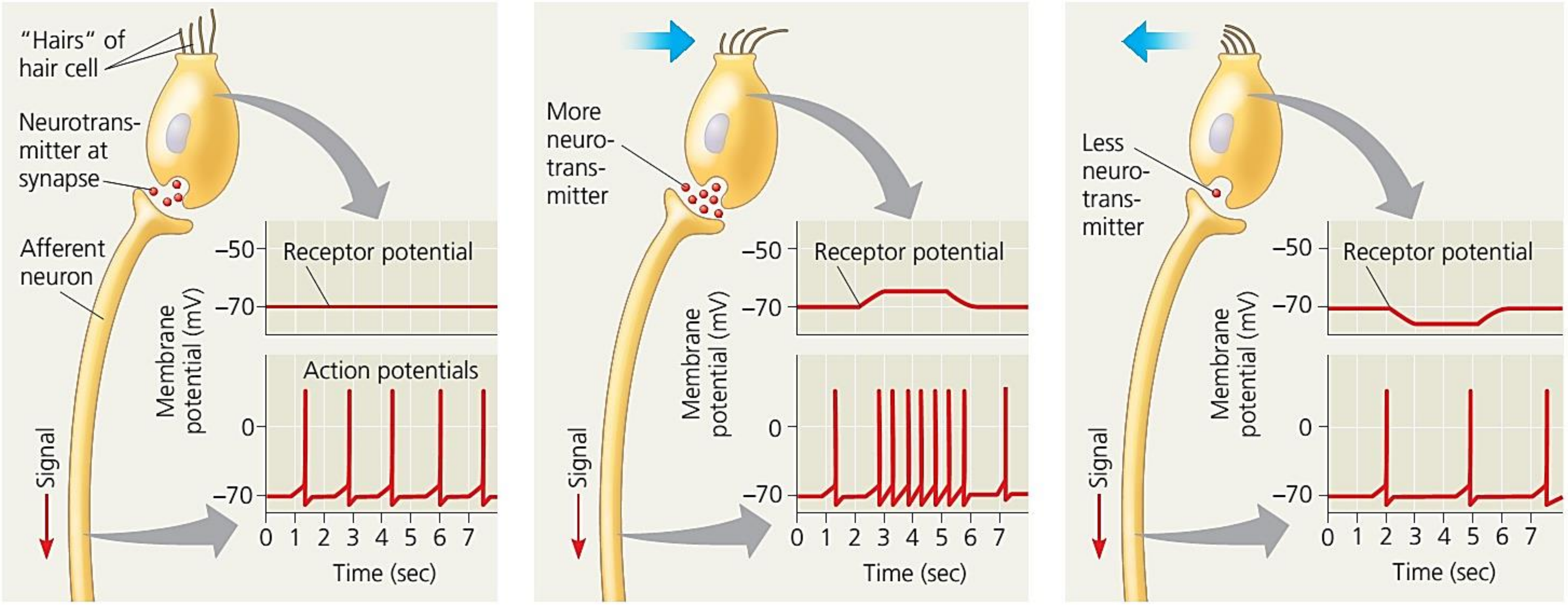
Within the bundle of hairs projecting from each hair cell lies a core of actin filaments. Vibration of the basilar membrane in response to sound raises and lowers the hair cells, bending the hairs against the surrounding fluid and the tectorial membrane. Displacing the hairs causes a change in the membrane potential of the hair cell.

Hearing:

Vibrating objects, such as a plucked guitar string or the vocal cords of a person who is speaking, create pressure waves in the surrounding air. In hearing, the ear transduces this mechanical stimulus (pressure waves) into nerve impulses that the brain perceives as sound. To hear music, speech, or other sounds in our environment, we rely on hair cells, sensory cells with hairlike projections that detect motion. Before vibration waves reach hair cells, they are amplified and transformed by accessory structures. The first steps involve structures in the ear that convert the vibrations of moving air to pressure waves in fluid. Moving air that reaches the outer ear causes the tympanic membrane to vibrate. The three bones of the middle ear transmit these vibrations to the oval window, a membrane on the cochlea's surface. When one of those bones, the stapes, vibrates against the oval window, it creates pressure waves in the fluid inside the cochlea.

Upon entering the vestibular canal, fluid pressure waves push down on the cochlear duct and basilar membrane. In response, the basilar membrane and attached hair cells vibrate up and down. The hairs projecting from the hair cells are deflected by the fixed tectorial membrane, which lies above. With each vibration, the hairs bend first in one direction and then the other, causing ion channels in the hair cells to open or close. Bending in one direction depolarizes hair cells, increasing neurotransmitter release and the frequency of action potentials directed to the brain along the auditory nerve. Bending the hairs in the other direction hyperpolarizes hair cells, reducing neurotransmitter release and the frequency of auditory nerve sensations.

▼ **Figure 50.11 Sensory reception by hair cells.** In hearing or balance, each hair cell forms a synapse with an afferent neuron that conducts action potentials to the CNS. Bending of the hairs of the hair cell in one direction depolarizes the cell. Depolarization increases release of excitatory neurotransmitter, resulting in more frequent action potentials in the afferent neuron. Bending the hairs in the other direction decreases neurotransmitter release, reducing action potential frequency in the afferent neuron.



(a) No bending of hairs

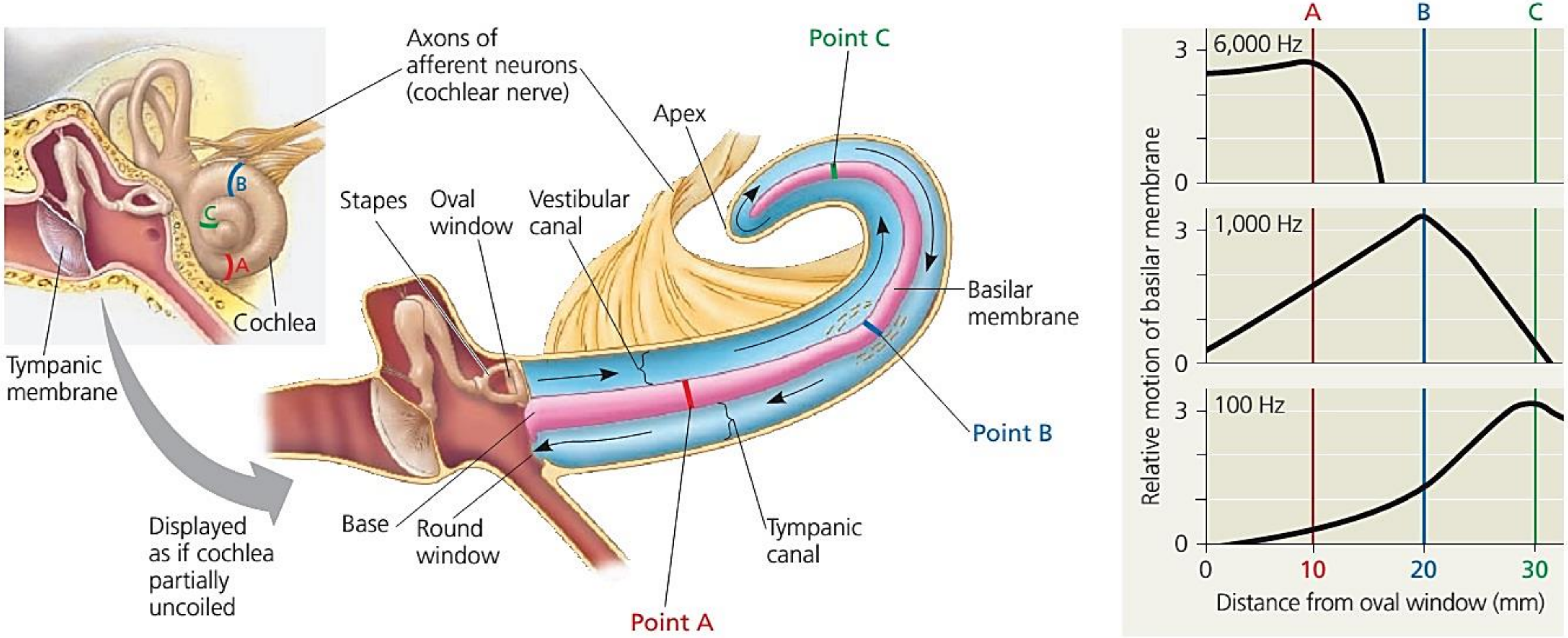
(b) Bending of hairs in one direction

(c) Bending of hairs in other direction

The ear captures information about two important sound variables: **volume** and **pitch**. Volume (loudness) is determined by the amplitude, or height, of the sound wave. A large amplitude wave causes more vigorous vibration of the basilar membrane, greater bending of the hairs on hair cells, and more action potentials in the afferent neurons that transmit information to the brain. Pitch is determined by a sound wave's frequency, the number of vibrations per unit time. The detection of sound wave frequency takes place in the cochlea and relies on the asymmetric structure of that organ.

The cochlea can distinguish pitch because the basilar membrane is not uniform along its length: It is relatively narrow and stiff near the oval window and wider and more flexible at the apex at the base of the cochlea. Each region of the basilar membrane is tuned to a different vibration frequency. Furthermore, each region is connected by axons to a different location in the cerebral cortex. Consequently, when a sound wave causes vibration of a particular region of the basilar membrane, nerve impulses are transduced to a specific site in our cortex and we perceive sound of a particular pitch.

▼ Figure 50.12 Sensory transduction in the cochlea.



(a) Vibrations of the stapes against the oval window produce pressure waves (black arrows) in the fluid (perilymph; blue) of the cochlea. (For purposes of illustration, the cochlea on the right is drawn partially uncoiled.) The waves travel to the apex via the vestibular canal and back towards the base via the tympanic canal. The energy in the waves causes the basilar membrane (pink) to vibrate, stimulating hair cells (not shown). Because the basilar membrane varies in stiffness along its length, each point along the membrane vibrates maximally in response to waves of a particular frequency.

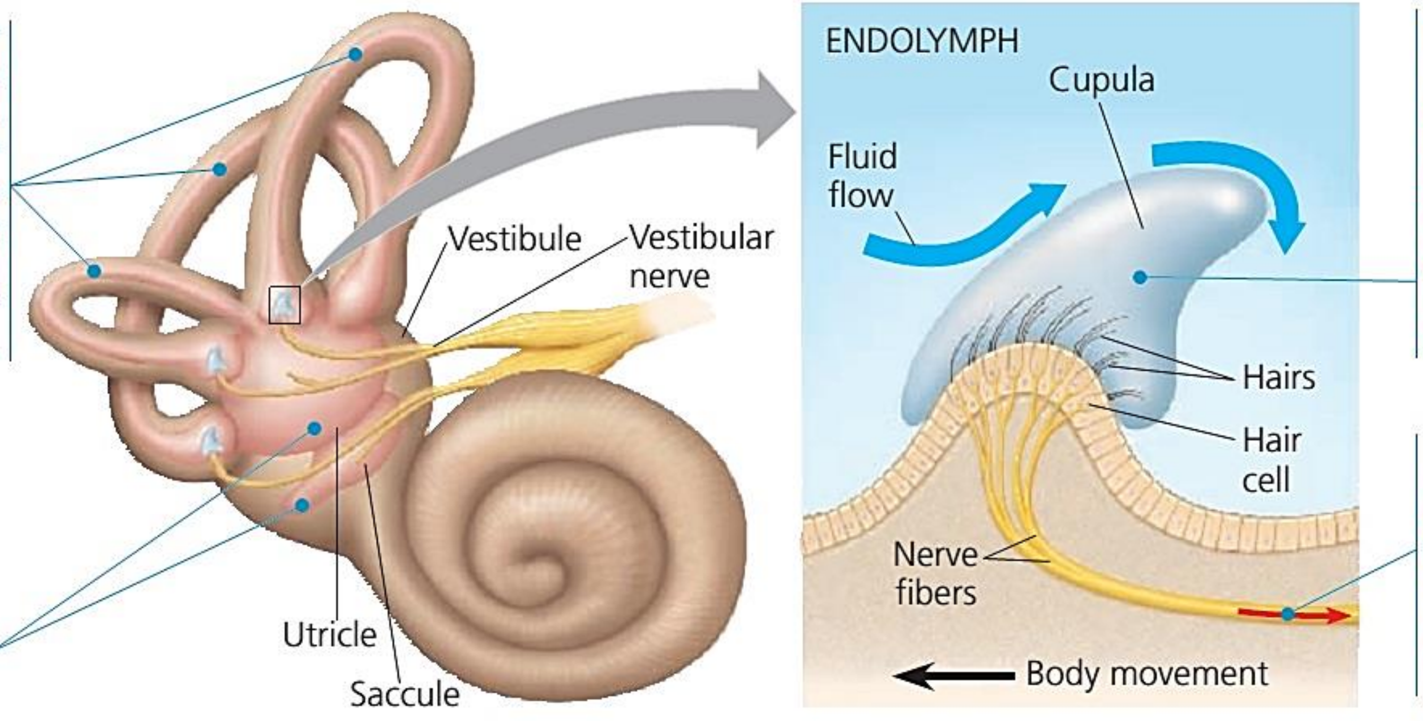
(b) These graphs show the patterns of vibration along the basilar membrane for three different frequencies, high (top), medium (middle), and low (bottom). The higher the frequency, the closer the vibration to the oval window.

Equilibrium

Sensory information travels through the nervous system as action potentials. A sensory receptor that is also a neuron Several organs in the inner ear of humans and most other mammals detect body movement, position, and equilibrium. For example, the chambers called the **utricle** and **saccule** allow us to perceive position with respect to gravity as well as linear movement.

Situated in a vestibule behind the oval window, each of these chambers contains hair cells that project into a gelatinous material. Embedded in this gel are small calcium carbonate particles called **otoliths** (“ear stones”). When you tilt your head, the otoliths shift position, contacting a different set of hairs protruding into the gel. The hair cell receptors transform this deflection into a change in neurotransmitter output. This alters the activity of afferent neurons, signaling the brain that your head is at an angle. The otoliths are also responsible for your ability to perceive acceleration, such as when a stationary car in which you are sitting moves forward.

▼ Figure 50.13 Organs of equilibrium in the inner ear.



The semicircular canals, arranged in three spatial planes, detect angular movements of the head. The swelling at the base of each canal contains a cluster of hair cells.

The utricle and saccule tell the brain which way is up and inform it of the body‘s position or linear acceleration.

The hairs of the hair cells project into a gelatinous cap called the cupula. When the head starts or stops rotating, the fluid (endolymph) in the semicircular canals presses against the cupula, bending the hairs.

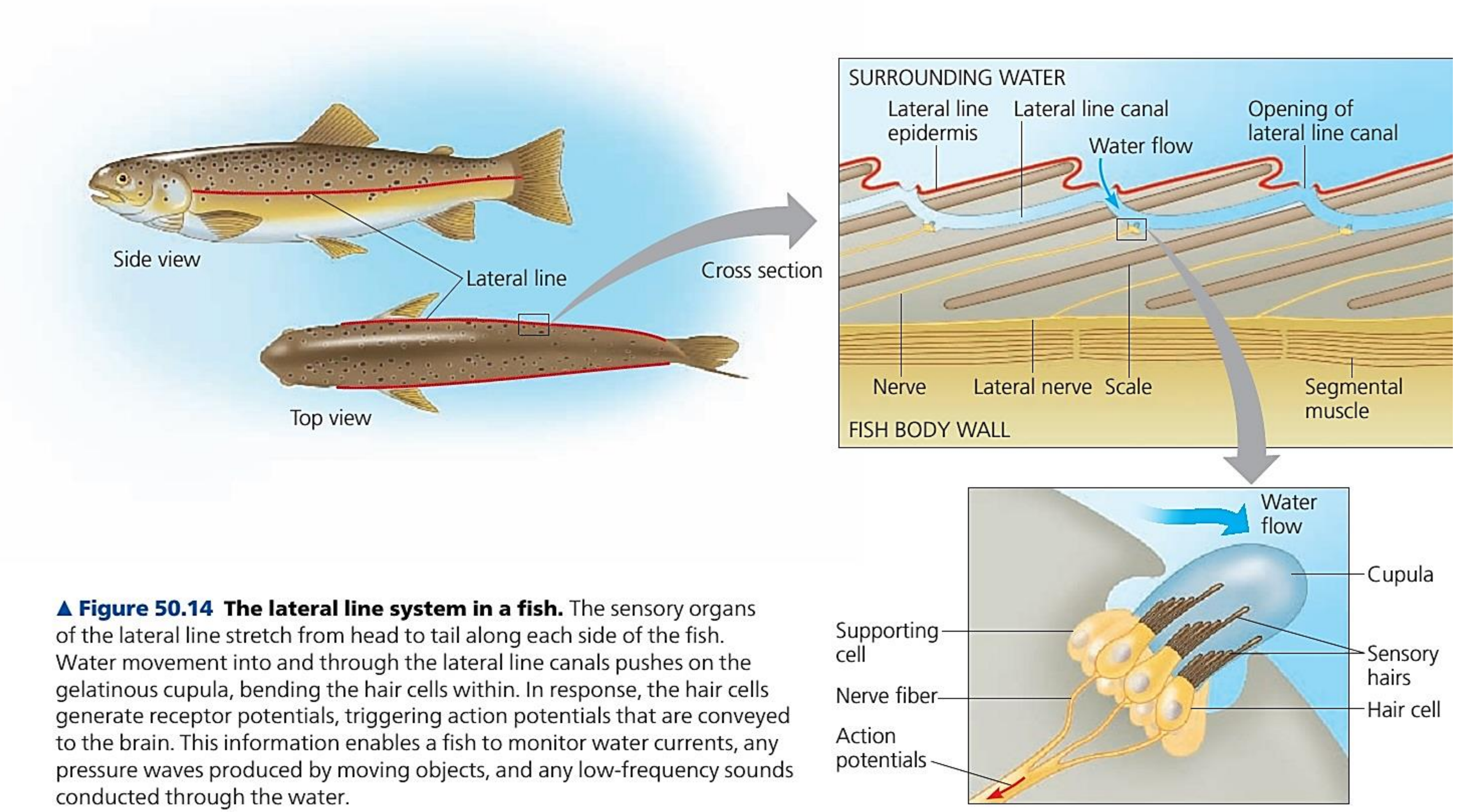
Bending of the hairs increases the frequency of action potentials in afferent neurons in direct proportion to the amount of rotational acceleration.

Hearing and Equilibrium in Other Vertebrates

Fishes rely on several systems for detecting movement and vibrations in their aquatic environment. One system involves a pair of inner ears that contain otoliths and hair cells. Unlike the ears of mammals, these ears have no eardrum, cochlea, or opening to the outside of the body. Instead, the vibrations of the water caused by sound waves are conducted to the inner ear through the skeleton of the head. Some fishes also have a series of bones that conduct vibrations from the swim bladder to the inner ear.

Most fishes and aquatic amphibians are able to detect low frequency waves by means of a **lateral line system** along each side of their body. As in our semicircular canals, receptors are formed from a cluster of hair cells whose hairs are embedded in a cupula. Water entering the lateral line system through numerous pores bends the cupula, leading to depolarization of the hair cells and production of action potentials. In this way, the fish perceives its movement through water or the direction and velocity of water currents flowing over its body. The lateral line system also detects water movements or vibrations generated by prey, predators, and other moving objects.

In the ear of a frog or toad, sound vibrations in the air are conducted to the inner ear by a tympanic membrane on the body surface and a single middle ear bone. The same is true in birds and other reptiles, although they, like mammals, have a cochlea.



▲ **Figure 50.14** **The lateral line system in a fish.** The sensory organs of the lateral line stretch from head to tail along each side of the fish. Water movement into and through the lateral line canals pushes on the gelatinous cupula, bending the hair cells within. In response, the hair cells generate receptor potentials, triggering action potentials that are conveyed to the brain. This information enables a fish to monitor water currents, any pressure waves produced by moving objects, and any low-frequency sounds conducted through the water.