example, humans have great difficulty noticing a change in the visual world unless their attention is drawn to the spatial location of a change.

7. The activity of neurons in the parietal cortex predicts a monkey's locus of spatial attention as measured by their perceptual thresholds. The parietal cortex sums a number of different signals—motor, visual, cognitive—to create a priority map of the visual field. The motor system uses this map to choose targets for movement. The visual system uses the same map to find the locus of visual attention.
8. Lesions in the parietal cortex cause a neglect of the contralateral visual world.
9. Visual information provided by the parietal cortex enables the motor system to adjust hand grip to match the size of the object to which it reaches before the hand actually lands on the target. By contrast, patients with perceptual deficits caused by lesions in inferior temporal cortex adjust their grip perfectly well even though they cannot describe the nature or size of the object to which they reach perfectly.
10. There are at least four different visual maps in the intraparietal sulcus, each of which corresponds to a particular motor workspace.
11. Neurons in the anterior intraparietal area respond to targets for grasping, respond even when monkeys make grasping movements in total darkness, and project to the grasp region of premotor cortex.
12. Neurons in the ventral intraparietal area respond to objects coming toward the mouth, have tactile receptive fields on the face, and project to the mouth area of premotor cortex.
13. Neurons in the medial intraparietal area have a representation of arm position and respond to targets for reaching.
14. Neurons in the lateral intraparietal area respond to targets for eye movements and objects of visual attention, discharge before eye movements, and have a representation of eye position. Activity of these neurons is modulated by the position of the eyes in the orbit.
15. Neurons in the face region of area 3a in the somatosensory cortex have a representation of the position of the eye in the orbit that arises from the contralateral eye.

Michael E. Goldberg
Robert H. Wurtz

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26

Auditory Processing by the Cochlea

The Ear Has Three Functional Parts

Hearing Commences With the Capture of Sound Energy by the Ear

The Hydrodynamic and Mechanical Apparatus of the Cochlea Delivers Mechanical Stimuli to the Receptor Cells

- The Basilar Membrane Is a Mechanical Analyzer of Sound Frequency
- The Organ of Corti Is the Site of Mechanoelectrical Transduction in the Cochlea

Hair Cells Transform Mechanical Energy Into Neural Signals

- Deflection of the Hair Bundle Initiates Mechanoelectrical Transduction
- Mechanical Force Directly Opens Transduction Channels
- Direct Mechanoelectrical Transduction Is Rapid
- Deafness Genes Provide Components of the Mechanotransduction Machinery

Dynamic Feedback Mechanisms Determine the Sensitivity of the Hair Cells

- Hair Cells Are Tuned to Specific Stimulus Frequencies
- Hair Cells Adapt to Sustained Stimulation
- Sound Energy Is Mechanically Amplified in the Cochlea
- Cochlear Amplification Distorts Acoustic Inputs
- The Hopf Bifurcation Provides a General Principle for Sound Detection

Hair Cells Use Specialized Ribbon Synapses

Auditory Information Flows Initially Through the Cochlear Nerve

- Bipolar Neurons in the Spiral Ganglion Innervate Cochlear Hair Cells
- Cochlear Nerve Fibers Encode Stimulus Frequency and Level

Sensorineural Hearing Loss Is Common but Is Amenable to Treatment

Highlights

Human experience is enriched by the ability to distinguish a remarkable range of sounds—from the intimacy of a whisper to the warmth of a conversation, from the complexity of a symphony to the roar of a stadium. Hearing begins when the sensory cells of the cochlea, the receptor organ of the inner ear, transduce sound energy into electrical signals and forward them to the brain. Our ability to recognize small differences in sounds stems from the cochlea's capacity to distinguish among frequency components, their amplitudes, and their relative timing.

Hearing depends on the remarkable properties of hair cells, the cellular microphones of the inner ear. Hair cells transduce mechanical vibrations elicited by sounds into electrical signals, which are then relayed to the brain for interpretation. The hair cells can measure motions of atomic dimensions and transduce stimuli ranging from static inputs to those at frequencies of tens of kilohertz. Remarkably, hair cells can also serve as mechanical amplifiers that augment auditory sensitivity. Each of the paired cochleae contains approximately 16,000 of these cells. Deterioration of hair cells and their innervation accounts for most of the hearing loss that afflicts about 10% of the population in industrialized countries.

The Ear Has Three Functional Parts

Sound consists of alternating compressions and rarefactions propagated by an elastic medium, the air, at a speed of approximately 340 m/s. This wave of pressure changes carries mechanical energy that stems from the work produced on air by our vocal apparatus or some other sound source. The mechanical energy is captured and transmitted to the receptor organ, where it is transduced into electrical signals suitable for neural analysis. These three tasks are associated with the external ear, the middle ear, and the cochlea of the inner ear, respectively (Figure 26–1).

The most obvious component of the human external ear is the auricle, a prominent fold of cartilage-supported skin. The auricle acts as a reflector to capture sound efficiently and focus it into the external auditory meatus, or ear canal. The ear canal ends at the tympanum, or eardrum, a diaphragm approximately 9 mm in diameter and 50 µm in thickness.

The external ear is not uniformly effective at capturing sound from all directions; the auricle's corrugated surface collects sounds best when they originate at different, but specific, positions with respect to the head. Our capacity to localize sounds in space, especially along the vertical axis, depends critically on these sound-gathering properties. Each auricle has a unique topography; its effect on sound reflections at different frequencies is learned by the brain early in life.

The middle ear is an air-filled pouch connected to the pharynx by the Eustachian tube. Airborne sound traverses the middle ear as vibrations of the auditory ossicles, three tiny bones that are linked together: the malleus (hammer), incus (anvil), and stapes (stirrup; Figure 26–1). A long extension of the malleus is attached to the tympanic membrane; its other extreme makes a ligamentous connection to the incus, which is similarly connected to the stapes. The flattened base of the stapes, the footplate, is seated in an opening—the oval window—in the bony covering of the cochlea. The auditory ossicles are relics of evolution. The stapes was originally a component of the gill support of ancient fish; the malleus and incus were components of the primary jaw joint in reptilian ancestors.

The inner ear includes the auditory sensory organ, the cochlea (Greek *cochlos,* snail), a coiled structure of progressively diminishing diameter wound around a conical bony core (Figure 26–1). In humans, the cochlea is approximately 9 mm across, the size of a chickpea, and is embedded within the temporal bone. The interior of the cochlea consists of three parallel liquid-filled compartments termed *scalae*. In a cross section of the cochlea at any position along its spiral course, the top compartment is the *scala vestibuli* (Figure 26–2). At the broad, basal end of this chamber is the oval window, the opening that is sealed by the footplate of the stapes. The bottom compartment is the *scala tympani;* it too has a basal aperture, the round window, which is closed by

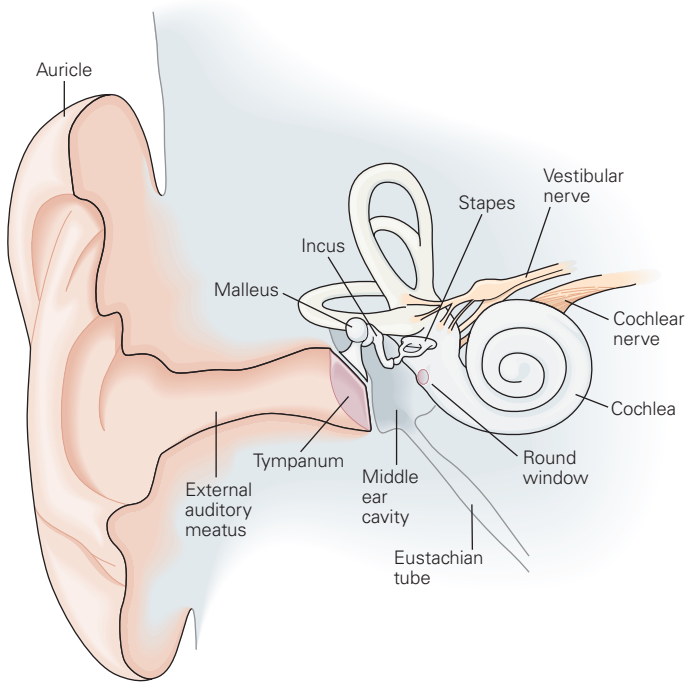


Figure 26–1 The structure of the human ear. The external ear, especially the prominent auricle, focuses sound into the external auditory meatus. Alternating increases and decreases in air pressure vibrate the tympanum. These vibrations are conveyed across the air-filled middle ear by three tiny, linked bones: the malleus, the incus, and the stapes. Vibration of the stapes stimulates the cochlea, the hearing organ of the inner ear.

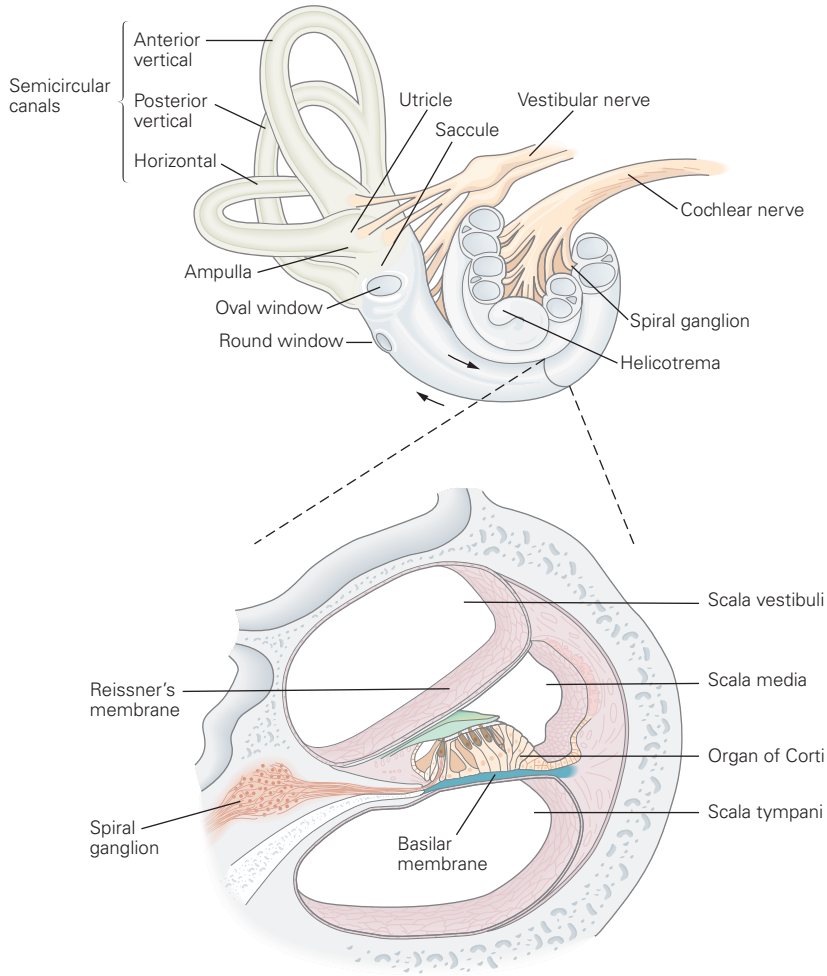


Figure 26–2 The structure of the cochlea. A cross section of the cochlea shows the arrangement of the three liquid-filled ducts or scalae, each of which is approximately 33 mm long. The scala vestibuli and scala tympani communicate through the helicotrema at the apex of the cochlea. At the base, each duct is closed by a sealed aperture. The scala vestibuli is closed by the oval window, against which the stapes pushes in response to sound; the scala tympani is closed by the round window, a thin, flexible membrane. Between these two compartments lies the scala media, an endolymph-filled tube whose epithelial lining includes the 16,000 hair cells in the organ of Corti surmounting the basilar membrane (**blue**). The hair cells are covered by the tectorial membrane (**green**). The cross section in the lower diagram has been rotated so that the cochlear apex is oriented toward the top.

a thin, elastic diaphragm beyond which lies the air of the middle-ear cavity. The two chambers are separated along most of their length by the cochlear partition but communicate with one another at the very tip of the cochlea, through the helicotrema.

The cochlear partition contains the third liquid-filled cavity, the *scala media,* and is delimited by two membranes. The thin Reissner's, or vestibular, membrane divides the scala media from the scala vestibuli. The basilar membrane separates the cochlear partition from the scala tympani and supports the complex sensory structure involved in auditory transduction, the organ of Corti (Figure 26–2).

Hearing Commences With the Capture of Sound Energy by the Ear

Psychophysical experiments have established that we perceive an approximately equal increment in loudness for each 10-fold increase in the magnitude of a sound stimulus. This type of relation is characteristic

of many of our senses and is the basis of the Weber-Fechner law (Chapter 17). A logarithmic scale is therefore useful in relating the magnitude of sound pressure to perceived loudness. Sound pressure corresponds to the sound-evoked modulation of the air pressure with respect to the mean atmospheric pressure; the louder the sound, the larger is the modulation. The sound-pressure level, L, of any sound may be expressed in decibels (dB) as

$$L = 20 \cdot \log_{10}(P / P_{REF}),$$

in which P, the magnitude of the stimulus, is the root-mean-square sound pressure (in units of pascals, abbreviated Pa, or newtons per square meter). For a sinusoidal stimulus, the amplitude exceeds the root-mean-square value by a factor of $\sqrt{2}$. The arbitrary reference level on this scale, 0 dB sound-pressure level (SPL), corresponds to a root-mean-square sound pressure, P_{REF}, of 20 μPa. This level represents the approximate threshold of human hearing at 1 to 4 kHz, the frequency range in which our ears are most sensitive.

Sound consists of very small alternating changes in the local air pressure. The loudest sound tolerable to humans, approximately 120 dB SPL, transiently alters the local atmospheric pressure by only ±0.01%. In contrast, a sound at the threshold level causes a change in the local pressure of much less than one part in a billion. From the faintest sounds that can be detected to sounds so intense that they hurt, the sound pressure increases by one millionfold, which correspond to a trillionfold range in stimulus power. The dynamic range of hearing is enormous.

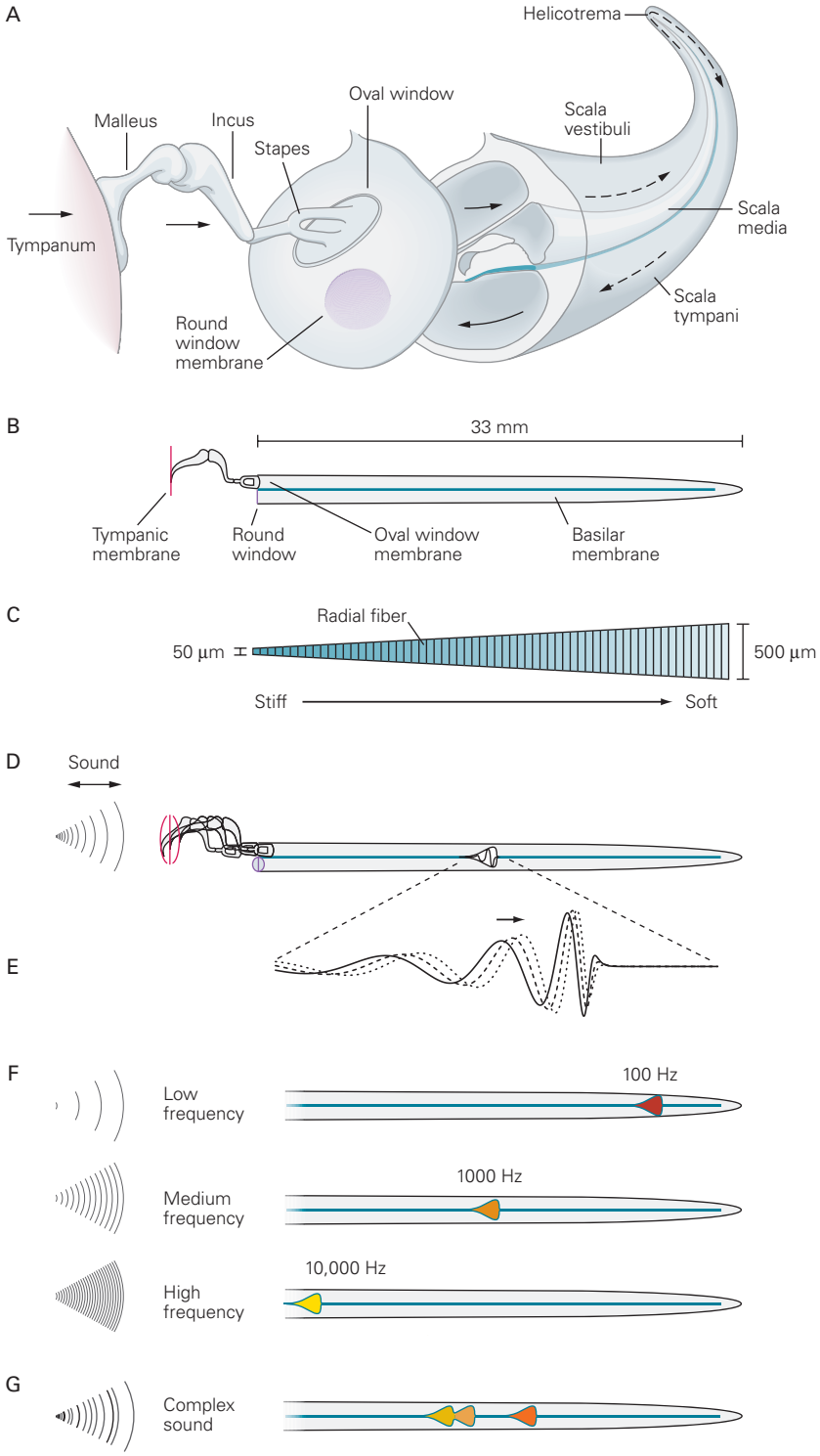
Despite their small magnitude, sound-induced increases and decreases in air pressure move the tympanum inward and outward (Figure 26–3A,B). Near threshold, the amplitude of vibration is in the picometer range, which is comparable to the tympanum's own thermal fluctuations. Even loud sounds elicit vibrations of the tympanum that do not exceed 1 μm in amplitude. The resulting motions of the ossicles are essentially like those of two interconnected levers (the malleus and incus) and a piston (the stapes). The vibration of the incus alternately drives the stapes deeper into the oval window and retracts it, like a piston that pushes and pulls cyclically upon the liquid in the scala vestibuli. In humans, the area of the eardrum is about 20-fold larger than that of the stapes footplate. As a result, pressure changes applied on the liquid of scala vestibuli by the stapes footplate are larger than those pushing and pulling the tympanum. Pressures are further magnified by the lever operating between the malleus and the incus, the incus in humans being only about 70% of the length of the malleus.

The action of the stapes produces pressure changes that propagate through the liquid of the scala vestibuli at the speed of sound in water. Because liquids are virtually incompressible, however, the primary effect of the stapes's motion is to displace the liquid in the scala vestibuli in the one direction that is not restricted by a rigid boundary: toward the elastic cochlear partition (Figure 26–3B). The deflection of the cochlear partition downward increases the pressure in the scala tympani, displacing a liquid mass that causes outward bowing of the round window. Each cycle of a sound stimulus thus evokes a cycle of up-and-down movement of a minuscule volume of liquid in each of the cochlea's three chambers, thus displacing the sensory organ.

By increasing the magnitude of pressure changes by up to 30-fold, the overall effect of the middle ear is to match the low impedance of the air outside the ear to the higher impedance of the cochlear partition, thus ensuring the efficient transfer of sound energy from the first medium to the second. The pressure gain afforded by the middle ear depends on sound frequency, which determines the U-shape tuning curve of auditory threshold.

Changes of the middle ear's normal structure that reduce its displacement amplitudes can lead to *conductive hearing loss*, of which two forms are especially common. First, scar tissue caused by middle-ear infection (*otitis media*) can immobilize the tympanum or ossicles. Second, a proliferation of bone in the ligamentous attachments of the ossicles can reduce their normal freedom of motion. This chronic condition of unknown origin, termed *otosclerosis*, can lead to severe deafness.

A clinician may test for conductive hearing loss by the simple Rinné test. A patient is asked to assess the loudness of a vibrating tuning fork under two conditions: when the tuning fork is held in the air or when it is pressed against the head just behind the ear. For the second stimulus, sound is conducted through bone to the cochlea. If the second stimulus is perceived to be louder, the patient's conductive pathway through the middle ear may be damaged, but the inner ear is likely to be intact. In contrast, if bone conduction is not more efficient than airborne stimulation, the patient may have inner-ear damage, that is, sensorineural hearing loss. The diagnosis of conductive hearing loss is important, because surgical intervention can be highly effective: Removal of scar tissue or reconstitution of the conductive pathway with a prosthesis may restore excellent hearing.


A
Helicotrema
Oval window
Malleus
Incus
Stapes
Scala vestibuli
Scala media
Tympanum
Scala tympani
Round window membrane
B
33 mm
Tympanic membrane
Round window
Oval window membrane
Basilar membrane
C
Radial fiber
50 µm
500 µm
Stiff
Soft
D
Sound
E
F
Low frequency
100 Hz
Medium frequency
1000 Hz
High frequency
10,000 Hz
G
Complex sound

The Hydrodynamic and Mechanical Apparatus of the Cochlea Delivers Mechanical Stimuli to the Receptor Cells

The Basilar Membrane Is a Mechanical Analyzer of Sound Frequency

The continuous variation of the mechanical properties of the basilar membrane along the cochlea's length, approximately 33 mm, is key to the cochlea's operation. The basilar membrane at the base of the human cochlea is less than one-fifth as broad as at the apex. Thus, although the cochlear chambers become progressively smaller from the organ's base toward its apex, the basilar membrane *increases* in width (Figure 26–3C). Moreover, the basilar membrane is relatively thick toward the base of the cochlea but thinner at the apex. Both morphological gradients contribute to a base-to-apex decrease in basilar-membrane stiffness. Radial collagen fibers within the membrane determine most of its elasticity. The basilar membrane may schematically be regarded as a set of weakly coupled radial segments of increasing length along the longitudinal axis of the cochlea, with the shortest segment at the base and the longest segment at the apex, analogous to the multiple strings of a piano.

Stimulation with a pure tone evokes a complex and elegant movement of the basilar membrane. Over one complete cycle of a tone, each affected segment along the basilar membrane undergoes a single cycle of vibration (Figure 26–3D,E). The various segments of the membrane do not, however, oscillate in phase with one another. As first demonstrated by Georg von Békésy using stroboscopic illumination, each segment reaches its maximal amplitude of motion slightly later than its basal neighbor. The normalized sinusoidal movement of the basilar membrane reproduces that of the stapes, but with a time delay that increases with the distance from the cochlear base.

The overall pattern of motion of the membrane is that of a traveling wave that traverses the cochlea from the stiff base toward the floppier apex. As each wave advances toward the apex, the amplitude of vibration grows to a maximum and then declines rapidly. The position at which the traveling wave reaches its maximal amplitude depends on sound frequency. The basilar membrane at the base of the cochlea responds best to the highest audible frequencies—in humans approximately 20 kHz. At the cochlear apex, the membrane responds to frequencies as low as 20 Hz. The intervening frequencies are represented along the basilar

Figure 26–3 (Opposite) Motion of the basilar membrane.

A. An uncoiled cochlea, with its base displaced to show its relation to the scalae, indicates the flow of stimulus energy. Sound vibrates the tympanum, which sets the three ossicles of the middle ear in motion. The piston-like action of the stapes, a bone inserted partially into the elastic oval window, produces oscillatory pressure differences that rapidly propagate along the scala vestibuli and scala tympani. Low-frequency pressure differences are shunted through the helicotrema, where the two ducts communicate.

B. The functional properties of the cochlea are conceptually simplified if the cochlea is viewed as a linear structure with only two liquid-filled compartments separated by the elastic basilar membrane.

C. The basilar membrane, here represented in a surface view, increases in width from approximately 50 μm near the base to 500 μm near the apex of the cochlea. Radial collagen fibers run from the neural to the abneural edge of the membrane. As the result of its morphological gradients, the basilar membrane's mechanical properties vary continuously along its length.

D. The oscillatory stimulation of a sound causes a traveling wave on the basilar membrane, shown here within the envelope of maximal displacement over an entire cycle. The magnitude of movement is grossly exaggerated in the vertical direction; the loudest tolerable sounds move the basilar membrane by only ±150 nm, a scaled distance less than one-hundredth the width of the lines representing the basilar membrane in these figures.

E. An enlargement of the active region in D demonstrates the motion of the basilar membrane in response to stimulation with sound of a single frequency. The continuous curve depicts a traveling wave at one instant; the vertical scale of basilar-membrane deflection is exaggerated about one-millionfold. The **dashed** and **dotted curves** portray the traveling wave at successively later times as it progresses from the cochlear base (*left*) toward the apex (*right*). As the wave approaches the characteristic place for the stimulus frequency, it slows and grows in amplitude. The stimulus energy is then transferred to hair cells at positions within the wave's peak.

F. Each frequency of stimulation excites maximal motion at a particular position along the basilar membrane. Low-frequency sounds produce basilar-membrane motion near the apex, where the membrane is relatively broad and soft. Mid-frequency sounds excite the membrane in its middle. The highest frequencies that we can hear excite the basilar membrane at its narrow, stiff base. The mapping of sound frequency onto the basilar membrane is approximately logarithmic.

G. The basilar membrane performs spectral analysis of complex sounds. In this example, a sound with three prominent frequencies, such as the three formants of a vowel sound, excites basilar-membrane motion in three regions, each of which represents a particular frequency. Hair cells in the corresponding positions transduce the basilar-membrane oscillations into receptor potentials, which in turn excite the nerve fibers that innervate these particular regions.

membrane in a continuous array (Figure 26–3F). In the 19th century, the German physiologist Hermann von Helmholtz was the first to appreciate that the basilar membrane's operation is essentially the inverse of a piano's. The piano synthesizes a complex sound by combining the pure tones produced by numerous vibrating strings; the cochlea, by contrast, deconstructs a complex sound by isolating the component tones at the appropriate segments of the basilar membrane.

For any frequency within the auditory range, there is a characteristic place along the basilar membrane at which the magnitude of vibration is maximal. Although the morphological gradients of the basilar membrane are key to the process, the actual dispersion of a sound's frequency components along the cochlea's longitudinal axis depends on the mechanical properties of the cochlear partition as a whole. In particular, as we shall detail later, the hair cells within the organ of Corti provide active mechanical feedback that sharpens mechanical tuning of the basilar membrane and enhances its sensitivity to sound. The arrangement of vibration frequencies along the basilar membrane is an example of a *tonotopic map.* The relationship between frequency and position along the basilar membrane varies monotonically, but is not linear; the logarithm of the frequency decreases roughly in proportion to the distance from the cochlea's base. The frequencies from 20 kHz to 2 kHz, those between 2 kHz and 200 Hz, and those spanning 200 Hz to 20 Hz are each represented by approximately one-third of the basilar membrane's extent.

Analysis of the response to a complex sound illustrates how the basilar membrane operates in daily life. A vowel sound in human speech, for example, ordinarily comprises three dominant frequency components termed formants. Each frequency component of the stimulus establishes a traveling wave that, to a first approximation, is independent of the waves evoked by the others (Figure 26–3G) and reaches its peak excursion at a point on the basilar membrane appropriate for that frequency component. The basilar membrane thus acts as a mechanical frequency analyzer by distributing the energies associated with the different frequency components of the stimulus to hair cells arrayed along its length. In doing so, the basilar membrane begins the encoding of the frequencies in a sound.

The Organ of Corti Is the Site of Mechanoelectrical Transduction in the Cochlea

The organ of Corti, a ridge of epithelium extending along the basilar membrane, is the receptor organ of the inner ear. Each organ of Corti contains approximately 16,000 hair cells that are innervated by approximately 30,000 *afferent* nerve fibers; these are fibers that carry information into the brain along the eighth cranial nerve. Like the basilar membrane itself, each hair cell is most sensitive to a particular frequency, and these frequencies are logarithmically mapped in descending order from the cochlea's base to its apex. Thus, the information transmitted by these sensory cells to their innervating nerve fibers is also tonotopically organized.

The organ of Corti includes a variety of cells, some of unknown function, but four types have obvious importance. First, there are two types of hair cells. The *inner hair cells* form a single row of approximately 3,500 cells, whereas approximately 12,000 *outer hair cells* lie in three rows farther from the central axis of the cochlear spiral (Figure 26–4). The space between the inner and outer hair cells is delimited and mechanically supported by pillar cells. The outer hair cells are supported at their bases by Deiters's (phalangeal) cells.

A second epithelial ridge adjacent to the organ of Corti, but nearer the cochlea's central axis, gives rise to the tectorial membrane, a gelatinous shelf that covers the organ of Corti (Figure 26–4). The tectorial membrane is anchored at its base, and its tapered distal edge forms a fragile connection with the organ of Corti.

Hair cells are not neurons; they lack both dendrites and axons (Figure 26–5A). A special saline solution, the endolymph that fills scala media, bathes the cell's apical aspect. Tight junctions between hair cells and supporting cells separate this liquid from the standard extracellular fluid, or perilymph, that contacts the basolateral surface of the cell. Immediately below the tight junctions, a desmosomal junction provides a strong mechanical attachment for the hair cell to its neighbors.

The hair bundle, which serves as a receptive antenna for mechanical stimuli, projects from the flattened apical surface of the hair cell. Each bundle comprises a few tens to a few hundred cylindrical processes, the *stereocilia*, arranged in 2 to 10 parallel rows and extending several micrometers from the cell surface. Successive stereocilia across a cell's surface vary monotonically in height; a hair bundle is beveled like the tip of a hypodermic needle (Figure 26–5B). The inner hair-cell bundles of the mammalian cochlea, when viewed from above, have a roughly linear form. Outer hair-cell bundles, in contrast, have a V or W shape (Figure 26–6).

Each stereocilium is a rigid cylinder whose core consists of a fascicle of actin filaments that are heavily cross-linked by the proteins plastin (fimbrin), fascin, and epsin. Cross-linking renders a stereocilium