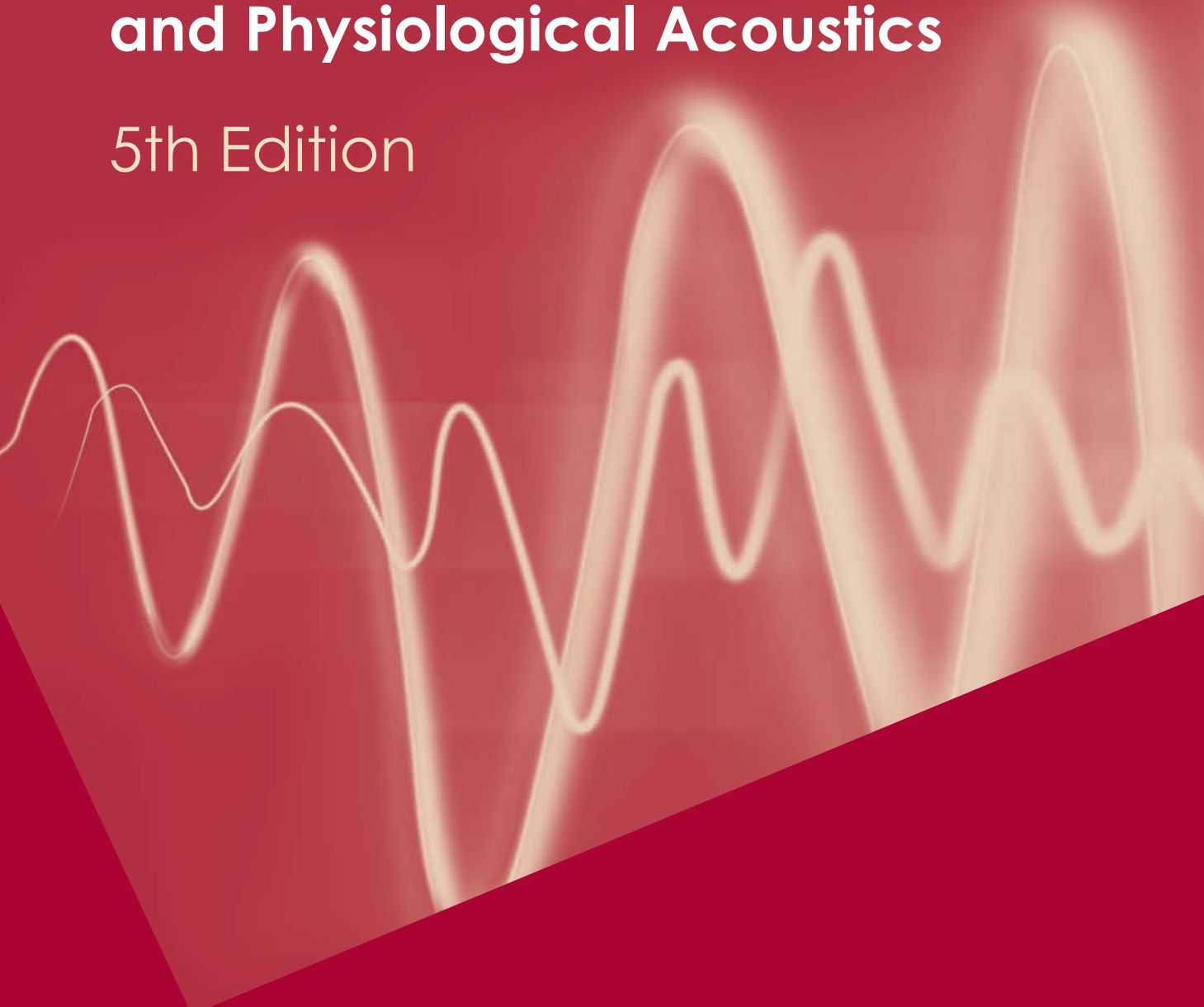


# Hearing

## An Introduction to Psychological and Physiological Acoustics

5th Edition



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Stanley A Gelfand

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# Hearing: An Introduction to Psychological and Physiological Acoustics

5th Edition

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A CIP record for this book is available from the British Library.  
Library of Congress Cataloging-in-Publication Data

Data available on application

ISBN-13: 978-1-4200-8865-6 (Hardcover)

Orders in the rest of the world

Informa Healthcare  
Sheepen Place  
Colchester  
Essex CO3 3LP  
UK

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Typeset by Aptara<sup>®</sup>, Inc.  
Printed and bound in Great Britain by CPI, Antony Rowe, Chippenham, Wiltshire

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## 2 Anatomy

### GROSS ANATOMY AND OVERVIEW

The auditory system comprises the ears and their connections to and within the central nervous system. From the standpoint of physical layout, the auditory system may be divided into the outer, middle, and inner ears; the auditory nerve; and the central auditory pathways. This section provides a very brief and simplified overview of the auditory system, in the hope that a brief glance at the forest will help the student avoid being blinded by the trees. Before proceeding, those not familiar with anatomical terminology should review the pictures in Fig. 2.1 and the definitions in Table 2.1, which summarize some of the terms used to describe the orientation of anatomical structures and the relationships among them.

The major divisions of the ear are shown in Fig. 2.2, and their relative positions within the head are given in Fig. 2.3. The **outer ear** is made up of the pinna (auricle) and ear canal (external auditory meatus). The eardrum (tympanic membrane) separates the outer and middle ears and is generally considered to be part of the latter. The **middle ear** also includes the tympanic (middle ear) cavity; the ossicular chain with its associated muscles, tendons, and ligaments; and the eustachian (auditory) tube. The **inner ear** begins at the oval window. It includes the sensory organs of hearing (the cochlea) and of balance (the semicircular canals, utricle, and saccule). While the balance system is certainly important, the concern here is hearing, and accordingly the balance apparatus is mentioned only insofar as it is directly associated with the auditory system.

The inner ear, beyond the oval window, is composed of the vestibule, the cochlea, and the vestibular apparatus. A membranous duct is continuous throughout these. In the cochlea, it separates the perilymph-filled scala vestibuli and scala tympani above and below from the endolymph-filled scala media between them. The scala media contains the organ of Corti, whose hair cells are the sensory receptors for hearing. When stimulated, the hair cells initiate activity in the auditory nerve fibers with which they are in contact. The **auditory nerve** leaves the inner ear through the internal auditory canal (internal auditory meatus), enters the brain at the angle of the pons and cerebellum, and terminates in the brainstem at the cochlear nuclei. We are now in the central auditory system.

### TEMPORAL BONE

The ear is contained within the **temporal bone**. Knowledge of the major landmarks of this bone is thus important in understanding the anatomy and spatial orientation of the ear. The right and left temporal bones are two of the 22 bones that make up the skull. Eight of these bones (including the two temporal bones) contribute to the cranium, and the remaining 14 bones

form the facial skeleton. Figure 2.4 gives a lateral (side) view of the skull, emphasizing the temporal bone. The temporal bone forms the inferior portion of the side of the skull. It is bordered by the mandible, zygomatic parietal, sphenoid, and occipital bones. The temporal bone itself is divided into five anatomical divisions: the squamous, mastoid, petrous, and tympanic portions, and the anteroinferiorly protruding styloid process. These parts of the temporal bone, as well as its major landmarks, are shown in Fig. 2.5.

The **squamous portion** is the fan-shaped part of the temporal bone. It is quite thin, often to the point of being translucent. Its inferior surface forms the roof and part of the posterior wall of the ear canal. The **zygomatic process** protrudes forward from the squamous portion to meet the zygomatic bone. The fan-shaped squamous plate is also in contact with the sphenoid bone anteriorly and with the parietal bone superiorly and posteriorly. The mandible attaches to the temporal bone just anterior to the ear canal, near the base of the zygomatic process, forming the **temporomandibular joint**.

The **mastoid portion** lies behind and below the squamous and forms the posterior aspect of the temporal bone. The mastoid portion attaches to the parietal bone superiorly and to the occipital bone posteriorly. It projects downward to form the **mastoid process**, which appears as a somewhat cone-shaped extension below the base of the skull. The mastoid process contains interconnecting air cells of variable size, shape, and number. Continuous with these air cells is a cavity known as the **tympanic antrum**, which lies anterosuperior to the mastoid process. The antrum also connects with the **epitympanic recess (attic)** of the middle ear via the **aditus ad antrum**. The antrum is bordered inferiorly by the mastoid process, superiorly by the thin bony plate called the **tegmen tympani**, medially by the wall of the lateral **semicircular canal**, and laterally by the squamous part.

The **tympanic portion** of the temporal bone forms the floor as well as the anterior and inferoposterior walls of the ear canal. It is bordered superiorly by the squamous and petrous portions and by the mastoid process posteriorly. The lower part of the tympanic portion partially covers the **styloid process**, which is a thin, cylinder-like anteroinferior projection from the base of the temporal bone. The styloid process, which varies in length from as little as 5 mm to as much as 50 mm, is generally considered to be a separate portion of the temporal bone. Although it does not contribute to the hearing mechanism, per se, the styloid process is important as a connecting point for several muscles involved in speech production.

The **petrous portion** houses the sensory organs of hearing and balance and contains the **internal auditory canal**. It is medially directed and is fused at its base to the tympanic and squamous portions. The mastoid lies posterior to the petrous portion, and in fact develops from it postnatally. The details

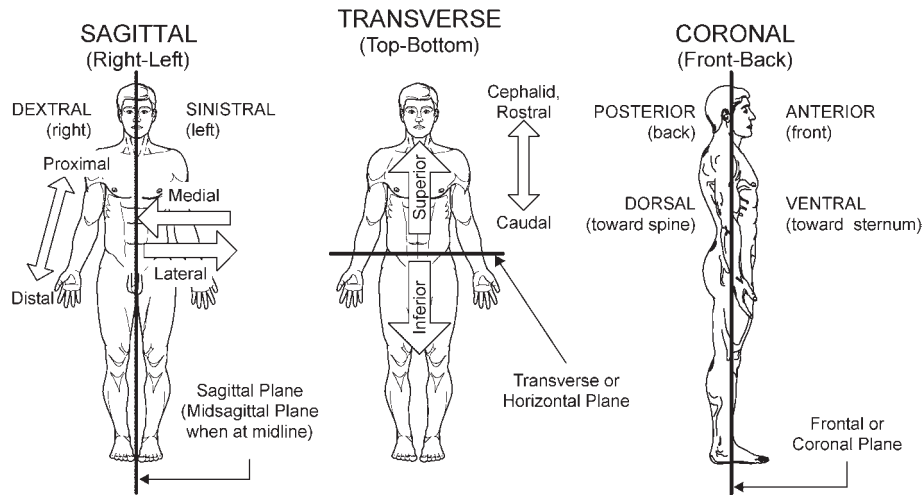


Figure 2.1 Commonly used anatomical orientations and directions. Source: From Gelfand (2001), *Essentials of Audiology, Second Edition*, by permission of Thieme Medical Publishers.

of the petrous portion are equivalent to those of the inner ear, discussed below.

## OUTER AND MIDDLE EAR

### Pinna

The **pinna (auricle)** is the external appendage of the ear. It is an irregularly shaped ovoid of highly variable size, which folds over

the side of the head posteriorly, superiorly, and inferiorly. It is basically composed of skin-covered elastic cartilage, although it contains some grossly undifferentiated muscles that are of a completely vestigial nature in humans. The pinna has a number of extrinsic muscles as well, which are also essentially vestigial in humans.

The landmarks of the pinna are shown in Fig. 2.6. Most of its perimeter is demarcated by a ridge-like rim called the **helix**.

Table 2.1 Summary of Commonly Used Terms Describing Anatomical Planes, Orientations, and Directions

| Term              | Definition                                                                 |
|-------------------|----------------------------------------------------------------------------|
| Anterior          | Front                                                                      |
| Caudal            | Toward the tail                                                            |
| Cephalad          | Toward the head                                                            |
| Contralateral     | Opposite side of the body                                                  |
| Coronal plane     | Vertical plane separating the structure into front and back; frontal plane |
| Cranial           | Toward the head                                                            |
| Dextral           | Right                                                                      |
| Distal            | Away or further from a reference point (e.g., midline of the body)         |
| Dorsal            | Toward the spine (posterior in humans)                                     |
| Homolateral       | Same side of the body                                                      |
| Inferior          | Below                                                                      |
| Ipsilateral       | Same side of the body                                                      |
| Lateral           | Away from the midline (toward the side)                                    |
| Medial            | Toward the midline                                                         |
| Midsagittal plane | Sagittal plane at the midline                                              |
| Posterior         | Back                                                                       |
| Proximal          | Toward, closer to a reference point (e.g., midline of the body)            |
| Rostral           | Toward the head (toward the beak)                                          |
| Sagittal plane    | Vertical plane separating the structure into right and left                |
| Sinistrall        | Left                                                                       |
| Superior          | Above                                                                      |
| Transverse plane  | Horizontal plane separating the structure into top and bottom; axial plane |
| Ventral           | Toward the sternum (anterior in humans)                                    |

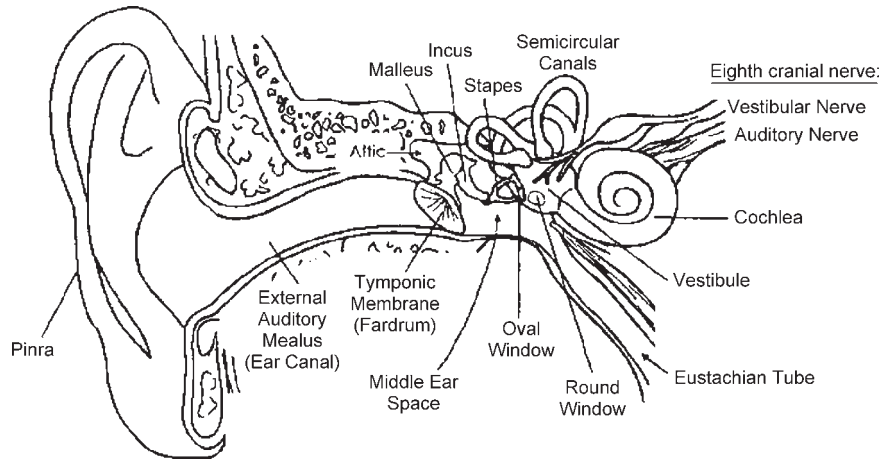


Figure 2.2 Cross-sectional view of the human ear.

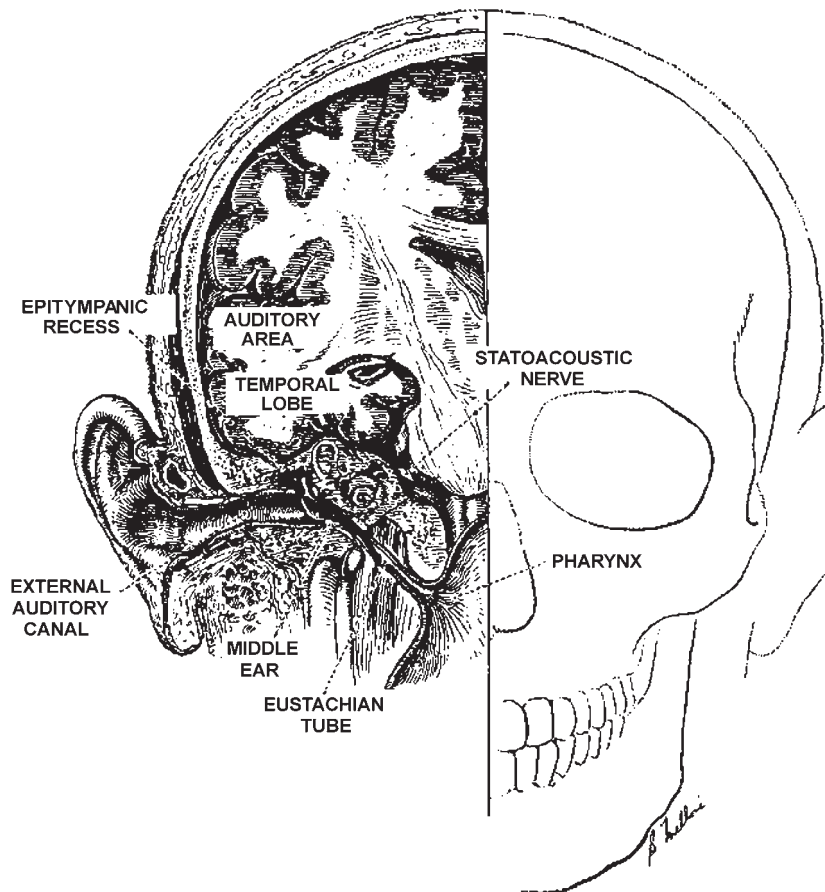


Figure 2.3 Structures of the ear in relation to the head. Source: Courtesy of Abbott Laboratories.

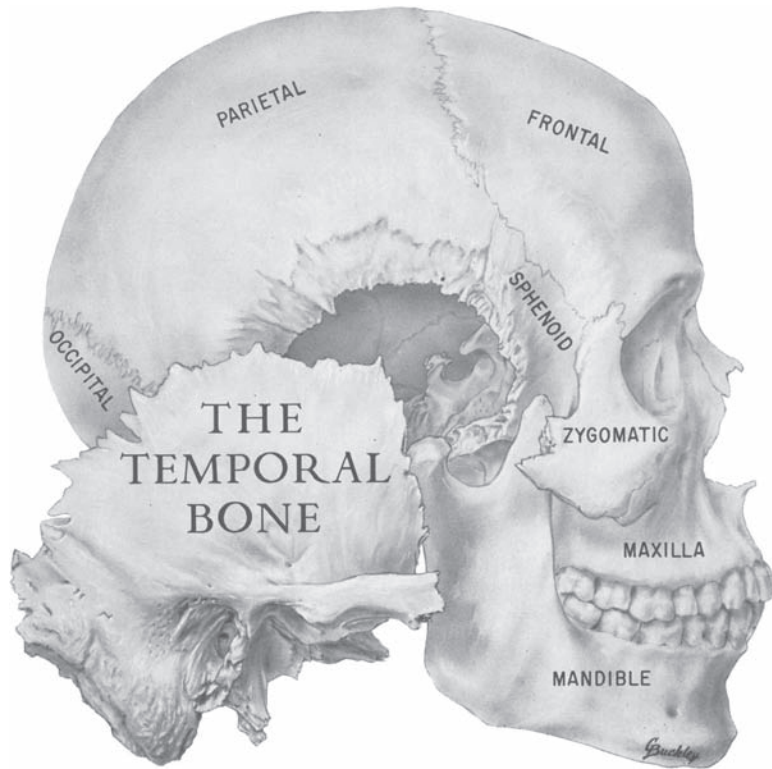


Figure 2.4 Lateral view of the skull emphasizing the position of the temporal bone. Source: From Anson and Donaldson (1967). *The Surgical Anatomy of the Temporal Bone and Ear*, Copyright © 1967 by W.B. Saunders, with permission.

If we first follow the helix posteriorly from the top of the ear, we see that it curves widely back and down to end in the **earlobe (lobule)** at the bottom of the pinna. Unlike the rest of the pinna, the lobe does not have any cartilage. Starting again from the apex of the helix, we see that it proceeds anteriorly and downward, and then turns posteriorly in a rather sharp angle to form the **crus of the helix**, which is an almost horizontal shelf at about the center of the pinna. The **scaphoid fossa** is a depression lying between the posterior portion of the helix posteriorly and a ridge called the **antihelix** anteriorly.

The **antihelix** is a ridge that runs essentially parallel to the posterior helix. Its upper end bifurcates to form two crura, a rather wide **superoposterior crus** and a narrower **anterior crus**, which ends under the angle where the helix curves backward. A triangular depression is thus formed by the two crura of the antihelix and the anterior part of the helix, and is called the **triangular fossa**. From the crura, the antihelix curves downward and then forward, and ends in a mound-like widening, the **antitragus**. Opposite and anterior to the antitragus is a backward-folding ridge called the **tragus**. The inferoanterior acute angle formed by the tragus and antitragus is called the **intertragal incisure**. The tragus, the antitragus, and the crus of the helix border a relatively large and cup-shaped depression called the **concha**. Sebaceous glands are present in the skin of

the concha as well as in the ear canal. At the bottom of the concha, protected by the tragus, is the entrance to the ear canal.

#### Ear Canal

The **ear canal (external auditory meatus)** leads from the concha to the eardrum and varies in both size and shape. The outer portion of the canal, about one-third of its length, is cartilaginous; the remaining two-thirds is **bony**. The canal is by no means straight; rather it is quite irregular in its course. It takes on a somewhat S-shaped form medially. It curves first anterosuperiorly, then posterosuperiorly, and finally anteroinferiorly. It is for this reason that the pinna must be pulled up and back in order for one to see the eardrum.

The ear canal has a diameter of about 0.7 cm at its entrance, with an average horizontal diameter of 0.65 cm and a mean vertical diameter of 0.9 cm (Wever and Lawrence, 1954). As would be expected from its irregular course, the length of the canal is not uniform. Instead, it is approximately 2.6 cm long posterosuperiorly and about 3.1 cm long inferoanteriorly (Donaldson and Miller, 1973). Also contributing to the greater length of the lower part of the ear canal is the oblique orientation of the eardrum as it sits in its **annulus** at the end of the canal.

The canal is lined with tight-fitting skin that is thicker in the cartilaginous segment than in the bony part. **Ceruminous (wax)**

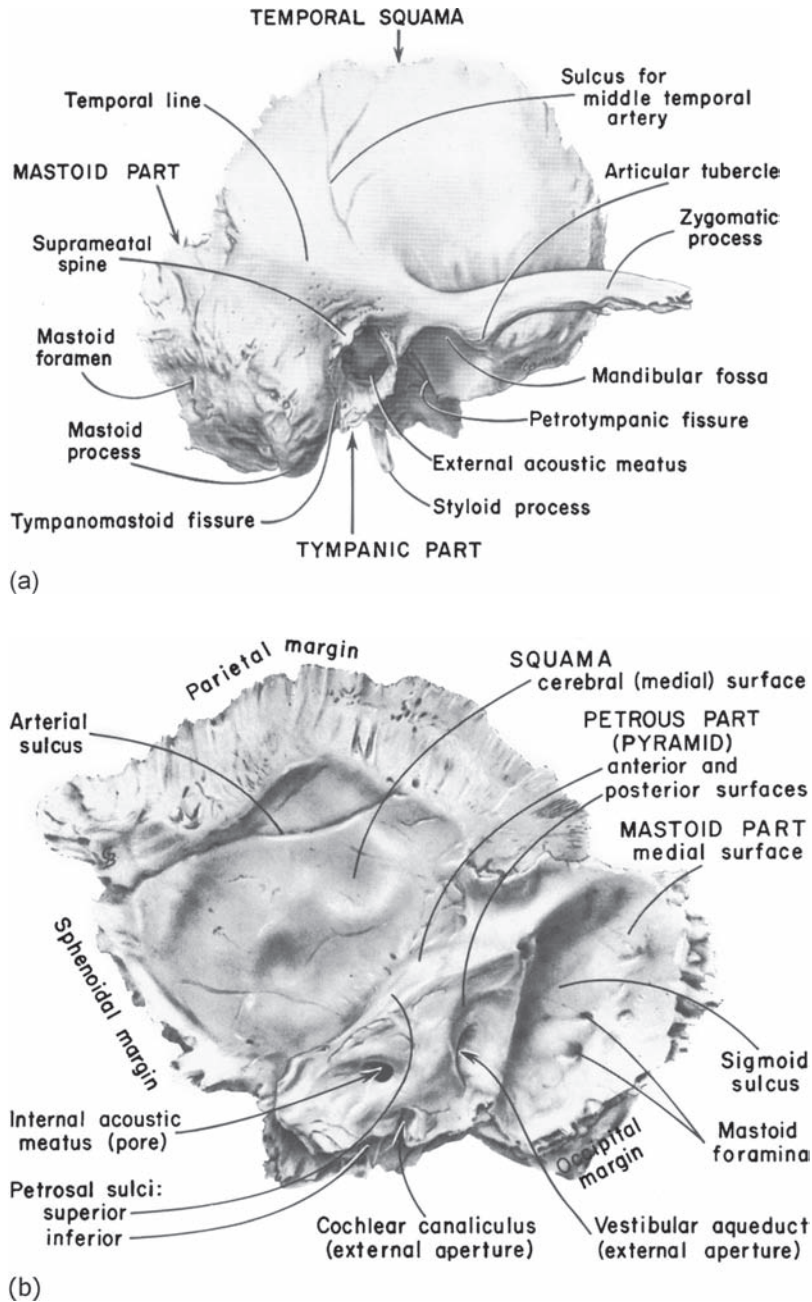


Figure 2.5 Lateral (a) and medial (b) aspects of view of the temporal bone. Source: From Anson and Donaldson (1967). *The Surgical Anatomy of the Temporal Bone and Ear*, Copyright © 1967 by W.B. Saunders, with permission.

and **sebaceous (oil) glands** are plentiful in the cartilaginous segment and are also found on the posterior and superior walls of the bony canal. The wax and oil lubricate the canal and help to keep it free of debris and foreign objects. Tiny hairs similarly contribute to the protection of the ear from invasion.

#### Eardrum

The canal terminates at the **eardrum (tympanic membrane)**, which tilts laterally at the top, so as to sit in its annulus at an angle of about  $55^\circ$  to the ear canal (see Fig. 2.1). The membrane is quite thin and translucent, with an average thickness of approximately

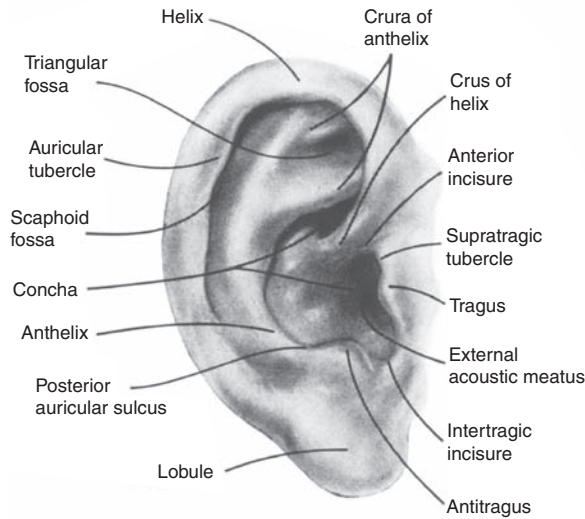


Figure 2.6 Landmarks of the pinna. Source: From Anson and Donaldson (1967). *The Surgical Anatomy of the Temporal Bone and Ear*, Copyright © 1967 by W.B. Saunders, with permission.

0.074 mm (Donaldson and Miller, 1973). It is elliptical in shape, with a vertical diameter of about 0.9 to 1.0 cm and a horizontal cross section of approximately 0.8 to 0.9 cm. The eardrum is concave outward, and the peak of this broad cone is known as the **umbo**. This inward displacement is associated with the drum's attachment to the **manubrium** of the **malleus**, the tip of which corresponds to the umbo (Fig. 2.7). In contact with the drum, the malleus continues upward in a direction corresponding to the 1-o'clock position in the right ear and the 11-o'clock position in the left. The **malleal prominence** of the malleus is formed by the lateral process of the malleus, from which run the **malleal folds**, which divide the drum into the **pars flaccida** above and the **pars tensa** below.

The eardrum is made up of four layers. The outermost layer is continuous with the skin of the ear canal, and the most medial layer is continuous with the mucous membrane of the middle ear. The pars flaccida is composed solely of these two layers. The pars tensa has two additional layers: a layer of radial fibers just medial to the skin layer, and a layer of nonradial fibers between the radial and mucous membrane layers.

### Tympanic Cavity

The **middle ear cavity** or **tympanum** may be thought of schematically as a six-sided box or room. The lateral wall is the eardrum, and opposite to it the promontory of the basal cochlear turn forms the medial wall. Figure 2.8 shows such a schematic conceptualization of the right middle ear. The view is as though the lateral wall of the room (the eardrum, shown with the malleus attached to it) had been folded downward to reveal its contents. The front of the head would be toward the right in the drawing and the back of the head would be toward the left.

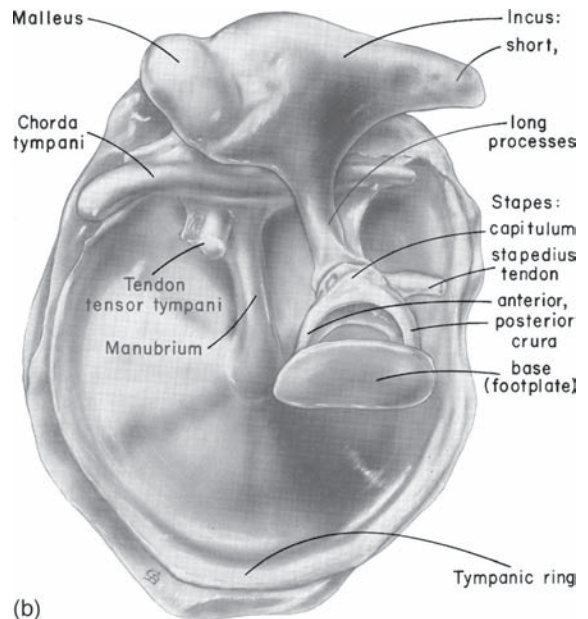
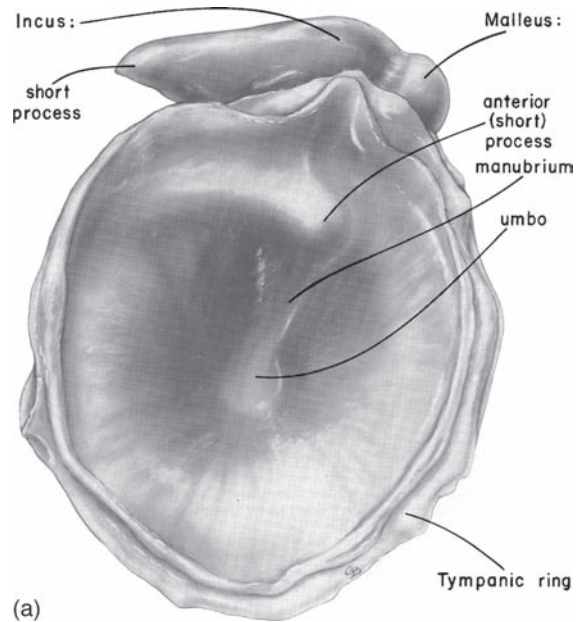


Figure 2.7 Lateral (a) and medial (b) aspects of the tympanic membrane and its connections to the ossicular chain. Source: From Anson and Donaldson (1967). *The Surgical Anatomy of the Temporal Bone and Ear*, Copyright © 1967 by W.B. Saunders, with permission.)

The roof of the middle ear is formed by the **tegmen tympani**, which separates the middle ear from the middle cranial fossa above. The floor of the tympanum separates it from the jugular bulb. In the anterior wall is the opening to the **eustachian tube**, and above it the canal for the tensor tympani muscle. The canal

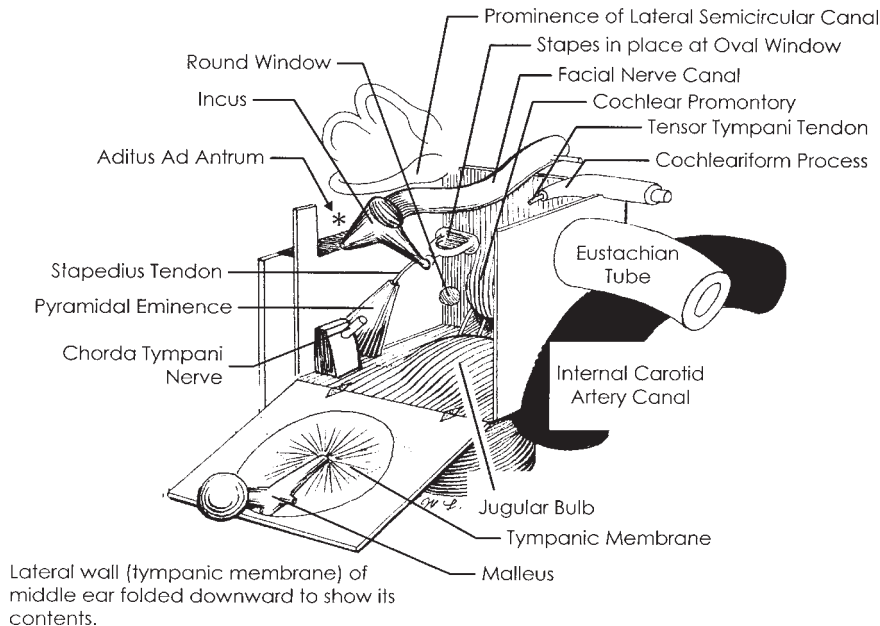


Figure 2.8 Schematic representation of the middle ear as though it were a room with its lateral wall (including the tympanic membrane with the malleus attached) folded downward. Source: Adapted from Proctor (1989), *Surgical Anatomy of the Temporal Bone*, by permission of Thieme Medical Publishers.

of the internal carotid artery lies behind the anterior wall, posteroinferior to the tubal opening. The posterior wall contains the **aditus ad antrum**, through which the upper portion of the middle ear called the **epitympanic recess or attic** communicates with the **mastoid antrum**. The posterior wall also contains the **fossa incudis**, a recess that receives the short process of the incus, and the **pyramidal eminence**, which houses the **stapedial muscle**. The **stapedial tendon** exits from the pyramidal prominence at its apex.

Returning to the medial wall, we see that the **oval window** is located posterosuperiorly to the **promontory**, while the **round window** is posteroinferior to the latter. Superior to the oval window lies the **facial canal prominence** with the **cochleariform process** on its anterior aspect. The **tendon** of the **tensor tympani muscle** bends around the cochleariform process to proceed laterally to the malleus.

The **eustachian tube**, also known as the **auditory tube**, serves to equalize the air pressure on both sides of the eardrum as well as allow for drainage of the middle ear by serving as a portal into the nasopharynx. Its principal features are highlighted in relation to the structures of the ear in Fig. 2.9. From its opening in the middle ear, the eustachian tube courses medially, downward at an angle of approximately  $45^\circ$ , and forward to exit into the nasopharynx via a prominence called the **torus tubarius**. The overall length of the tube is about 3.5 cm. The lateral first third of the eustachian tube beginning at the middle ear is surrounded by bone, whereas the remainder is enclosed within an incomplete ring of hook-shaped elastic cartilage, as illustrated in Fig. 2.9. The meeting of the **bony and cartilaginous portions** is called

the **isthmus**. At this point, the lumen of the tube may be as little as 1.0 to 1.5 mm compared to a diameter of about 3.0 to 6.0 mm at its opening into the middle ear. The cartilaginous part of the eustachian tube is normally closed (Fig. 2.10a), and it opens reflexively by action of the **tensor palatini muscle**, which

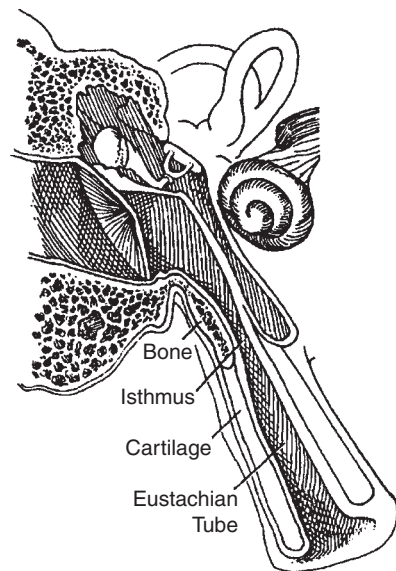


Figure 2.9 Orientation of the eustachian tube with respect to the ear. Source: Adapted from Hughes (1985), *Textbook of Otolaryngology*, by permission of Thieme Medical Publishers.

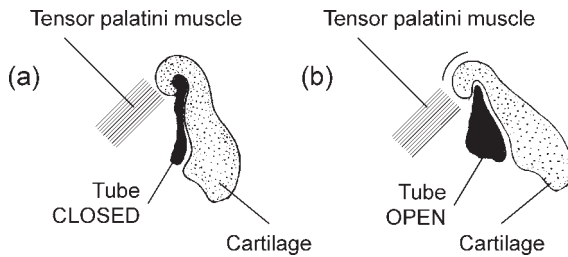


Figure 2.10 (a) Cross-section of the hook-shaped cartilage in the normally closed state of the tube. (b) Opening of the tube by action of the tensor palatini muscles, which uncurls the hook-shaped cartilage. Source: Adapted from Gelfand (2001), *Essentials of Audiology, Second Edition*, by permission of Thieme Medical Publishers.

uncurls the normally hook-shaped cartilages (Fig. 2.10b) in response to swallowing, yawning, sneezing, or shouting.

### Ossicular Chain

Sound energy impinging upon the eardrum is conducted to the inner ear by way of the ossicles, which are the smallest bones in the body. There are three ossicles in each ear, the **malleus, incus, and stapes**; they are collectively referred to as the **ossicular chain**. Schematic illustrations of these bones are shown with the ossicular chain in place in Fig. 2.11. (Different and somewhat more life-like perspectives of the ossicles may also

be seen in Fig. 2.7.) Instead of being attached to the other bones of the skull, the ossicular chain is *suspended* in the middle ear by a series of ligaments, by the tendons of the two intratympanic muscles, and by the attachments of the malleus to the eardrum and of the stapes to the oval window.

The malleus is commonly called the hammer, although it more closely resembles a mace. It is the largest of the ossicles, being about 8 to 9 mm long and weighing approximately 25 mg. The head of the malleus is located in the epitympanic space, to which it is connected by its superior ligament. Laterally, the **manubrium** (handle) is embedded between the mucous membrane and fibrous layers of the eardrum. The anterior process of the malleus projects anteriorly from the top of the manubrium just below the neck. It attaches to the tympanic notch by its anterior ligament, which forms the axis of malleolar movement. The malleus is connected to the tensor tympani muscle via a tendon, which inserts at the top of the manubrium.

The **incus** bears a closer resemblance to a tooth with two roots than to the more commonly associated anvil. It weighs approximately 30 mg and has a length of about 5 mm along its short process and about 7 mm along its long process. Its body is connected to the posteromedial aspect of the malleolar head within the epitympanic recess. The connection is by a saddle joint, which was originally thought to move by a cog-like mechanism when the malleus was displaced (Helmholtz, 1868). However, subsequent research demonstrated that these

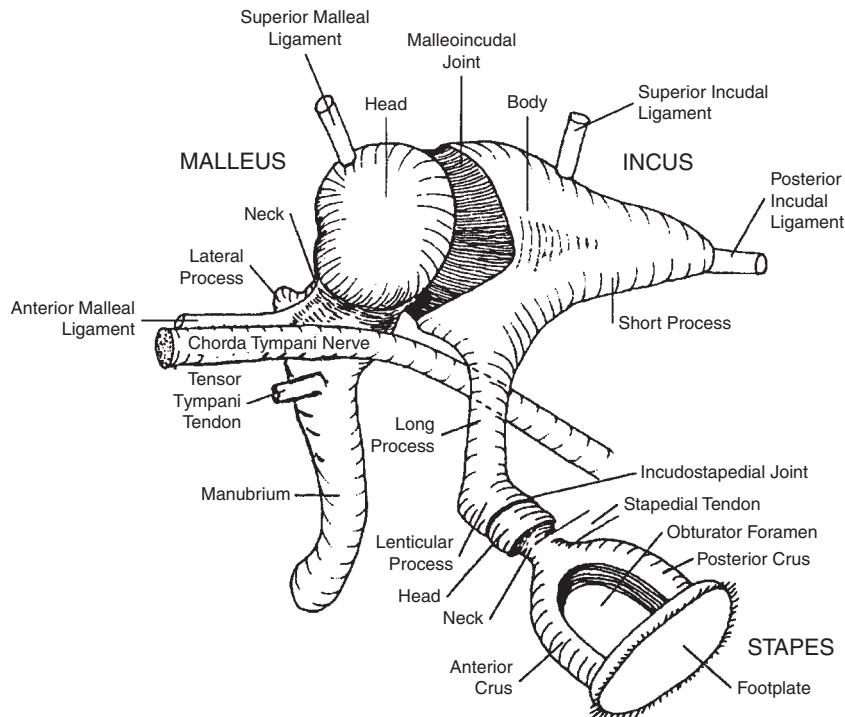


Figure 2.11 Schematic representation of the ossicular chain. Source: Adapted from Tos (1995), *Manual of Middle Ear Surgery, Vol 2*, by permission of Thieme Medical Publishers.

two bones move as a unit rather than relative to one another (Wever and Lawrence, 1954). The short process of the incus connects via its posterior ligaments to the fossa incudis on the posterior wall of the tympanic cavity. Its long process runs inferiorly, parallel to the manubrium. The end of the long process then bends medially to articulate with the head of the stapes in a true ball-and-socket joint.

The **stapes** (stirrup) is the smallest of the ossicles. It is about 3.5 mm high, and the footplate is about 3 mm long by 1.4 mm wide. It weighs on the order of 3 to 4 mg. The head of the stapes connects to the footplate via two crura. The anterior crus is straighter, thinner, and shorter than the posterior crus. The **footplate**, which encases the very fine stapedial membrane, is attached to the oval window by the annular ligament. The stapedius tendon inserts on the posterior surface of the neck of the stapes and connects the bone to the stapedius muscle.

### Intratympanic Muscles

The middle ear contains two muscles, the tensor tympani and the stapedius (Figs. 2.7 and 2.8). The **stapedius muscle** is the smallest muscle in the body, with an average length of 6.3 mm and a mean cross-sectional area of 4.9 mm<sup>2</sup> (Wever and Lawrence, 1954). This muscle is completely encased within the pyramidal eminence on the posterior wall of the tympanic cavity and takes origin from the wall of its own canal. Its tendon exits through the apex of the pyramid and courses horizontally to insert on the posterior aspect of the neck of the stapes. Contraction of the stapedius muscle thus pulls the stapes posteriorly. The stapedius is innervated by the stapedial branch of the **seventh cranial (facial) nerve**.

The **tensor tympani muscle** has an average length of 25 mm and a mean cross-sectional area of approximately 5.85 mm<sup>2</sup> (Wever and Lawrence, 1954). The tensor tympani occupies an *osseous semicanal* on the anterior wall of the tympanum, just superior to the eustachian tube, from which it is separated by a thin bony shelf. The muscle takes origin from the cartilage of the auditory tube, from the walls of its own canal, and from the part of the sphenoid bone adjacent to the canal. Emerging from the canal, the tendon of the tensor tympani hooks around the **cochleariform process**, and inserts on the top of the manubrium of the malleus. Contraction of the tensor tympani thus pulls the malleus anteromedially, at a right angle to the uninterrupted motion of the ossicles. The tensor tympani muscle is innervated by the tensor tympani branch of the otic ganglion of the **fifth cranial (trigeminal) nerve**.

Both intratympanic muscles are completely encased within bony canals and attach to the ossicular chain by way of their respective tendons. Bekesy (1936) pointed out that this situation reduces the effects that muscular contractions might have upon the transmission of sound through the middle ear system. Contraction of either muscle increases the stiffness of the ossicular chain as well as of the eardrum. The stapedius muscle pulls posteriorly whereas the tensor tympani pulls anteromedially so that they might initially be thought to be antagonists.

However, the effect of these muscles is to lessen the amount of energy conducted by the ossicular chain, and they thus function as synergists with respect to hearing.

Of particular interest in this context is the **acoustic reflex**, which is the response of the intratympanic muscles to intense sound stimulation. It is generally accepted that the acoustic reflex *in humans* is due mainly, if not exclusively, to contraction of the *stapedius* muscle. In contrast, auditory activation of the tensor tympani muscle in humans occurs only for extremely intense sounds, as part of a *startle* response. The acoustic reflex arc is described in the context of the auditory pathways later in this chapter.

## INNER EAR

### Osseous and Membranous Labyrinths

The inner ear structures are contained within a system of spaces and canals, the **osseous** or **bony labyrinth**, in the petrous portion of the temporal bone. As shown in Fig. 2.12, these spaces and canals are grossly divided into three sections: the vestibule, the cochlea, and the semicircular canals. The oval window accepts the footplate of stapes and opens medially into the **vestibule**, which is about 4 mm in diameter and is somewhat ovoid in shape. The snail-shaped **cochlea** lies anterior and slightly inferior to the vestibule and is approximately 5 mm high and 9 mm in diameter at its base. Posterior to the vestibule are the three **semicircular canals**, lying at right angles to one another, each about 1 mm in diameter. The general shape of the bony labyrinth is followed by the enclosed **membranous labyrinth**, which contains the *end organs* of hearing and balance. The membranous labyrinth and its principal structures are illustrated in Fig. 2.13.

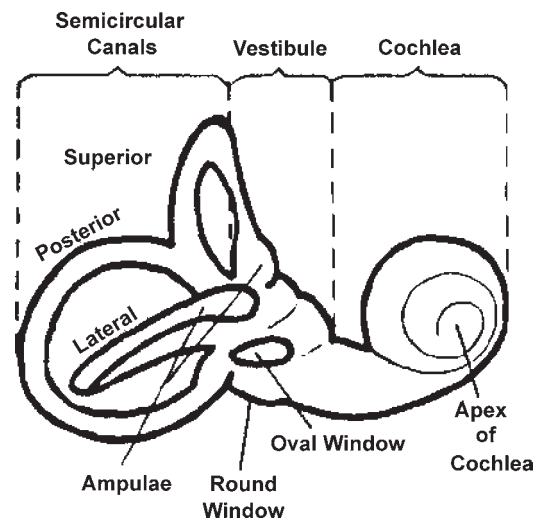


Figure 2.12 The osseous (bony) labyrinth.

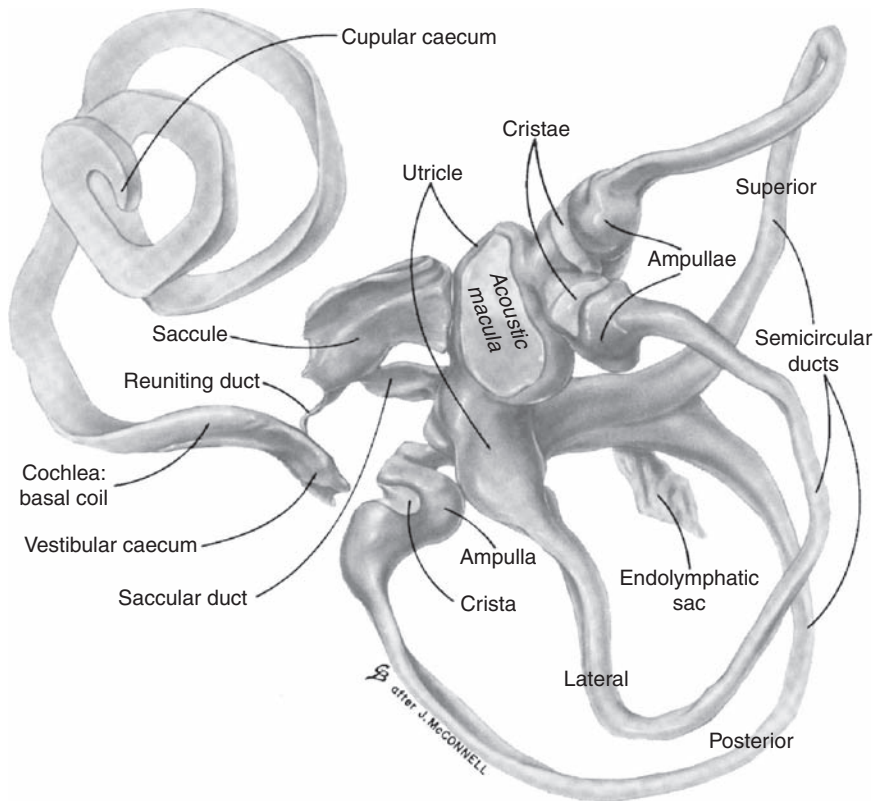


Figure 2.13 The membranous labyrinth. Source: From Donaldson and Miller (1973), *Anatomy of the ear*, in *Otolaryngology*, Vol. 1, Paparella and Schurnick (eds.), Copyright © 1973 by W.B. Saunders (with permission).

### Inner Ear Fluids

The spaces between the bony walls of the osseous labyrinth and the membranous labyrinth are filled with a fluid called **perilymph** or **perilymphatic fluid**, and the membranous labyrinth itself is mostly filled with **endolymph** or **endolymphatic fluid**.<sup>1</sup> Because they are located outside of any cells, perilymph and endolymph are referred to as **extracellular fluids**. In contrast, fluids contained within cells are called **intracellular fluids**. Smith Lowry, and Wu (1954) found that perilymph is chemically similar to other extracellular fluids (e.g., cerebrospinal fluid and blood serum) in the sense that it has a very high concentration of sodium and a very low concentration of potassium. Oddly, they found that endolymph has just the opposite concentrations—it is high in potassium but low in sodium. In fact, endolymph has the distinction of being the only extracellular fluid in the body with this characteristic. Subsequent research has not only confirmed the different compositions of perilymph and endolymph, but has also richly expanded our knowledge about their composition and properties, relation-

ships to other fluids and structures, as well as their roles in the cochlea.

The spaces within the organ of Corti itself are filled with perilymph-like fluid that diffuses across the basilar membrane from the scala tympani.<sup>2</sup> As a result, the cochlear hair cells and other structures within the organ of Corti are bathed in a sodium-rich fluid (Slepecky, 1996; Wangemann and Schacht, 1996). Tight junctions among the cells forming the reticular lamina (discussed below) isolate the endolymph above from the organ of Corti below.

The origins of perilymph and endolymph have been the subject of controversy. Perilymph appears to be a derivative of the cerebrospinal fluid and/or the cochlear blood supply, and several lines of evidence have suggested that endolymph components may be derived from perilymph rather than from the blood. Overall, modern experiments disproved early ideas that these fluids are secreted at one site and flow longitudinally to another location, replacing them with the concept that the compositions of the inner ear fluids are maintained locally within the

<sup>1</sup> A third inner ear fluid called **intrastrial fluid** is found in the stria vascularis (see, e.g., Wangemann and Schacht, 1996).

<sup>2</sup> It was previously thought that the organ of Corti contained a distinct sodium-rich fluid called "cortilymph."

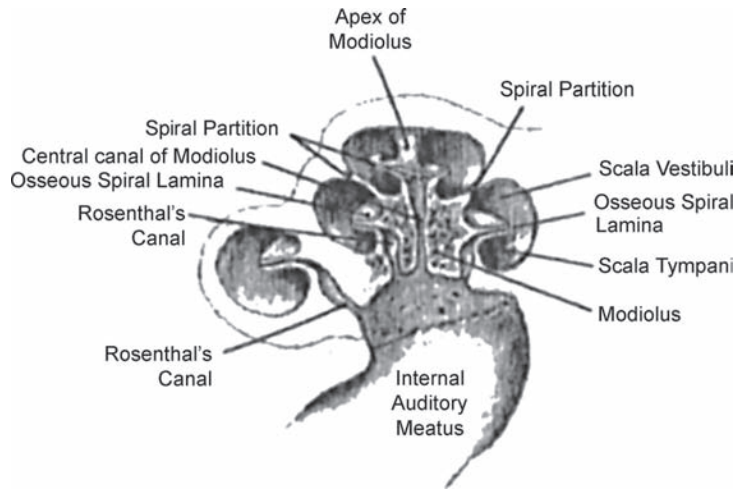


Figure 2.14 The modiolus. Source: Adapted from Proctor (1989), *Surgical Anatomy of the Ear and Temporal Bone*, by permission of Thieme Medical Publishers.

cochlea (e.g., Ohyama et al., 1998; Salt, 2001; Salt et al., 1986). Informative reviews are provided by Wangemann and Schacht (1996), Salt (2001), and Rask-Andersen, Schrott-Fisher, Pfaller, and Glueckert (2006).

The **cochlear aqueduct** leads from the vicinity of the round window in the scala tympani to the subarachnoid space medial to the dura of the cranium. Although the aqueduct leads from the perilymph-filled scala to the cerebrospinal fluid-filled subarachnoid space, it is not patent in many humans. Thus, it is doubtful that there is any real interchange between these two fluid systems. The **endolymphatic duct** leads from the membranous labyrinth within the vestibule to the **endolymphatic sac**. The sac is located partially between the layers of the dura in the posterior cranial fossa and partly in a niche in the posterior aspect of the petrous portion of the temporal bone.

### Vestibular Organs

Returning to the structures of the inner ear, the vestibule contains two **vestibular** or **balance organs**, which are concerned with linear acceleration and gravity effects. These organs are the **utricle and saccule**. The **semicircular canals**, located behind the vestibule, widen anteriorly into five sac-like structures, which open into the somewhat elongated utricle. These widenings are the **ampullae**, and they contain the sensory receptors for rotational acceleration. (The interested reader is referred to any of the fine books listed in the References section for a detailed discussion of the balance system.) The most important connection between the areas of hearing and balance is the **ductus reuniens**, which joins the membranous labyrinth between the cochlea and the utricle.

### Cochlea

The **cochlea** is the part of the inner ear concerned with hearing. An extensive albeit rather advanced review of cochlear anatomy

and physiology may be found in Dallos, Popper, and Fay (1996). The human cochlea is about 35 mm long and forms a somewhat cone-shaped spiral with about  $2\frac{3}{4}$  turns. It is widest at the base, where the diameter is approximately 9 mm, and tapers toward the apex. It is about 5 mm high. The **modiolus** is the core, which forms the axis of the cochlear spiral, as illustrated in Fig. 2.14. Through the modiolus course the auditory nerve and the blood vessels that supply the cochlea. The osseous spiral lamina is a bony ramp-like shelf that goes up the cochlea around the modiolus much like the spiral staircase of a lighthouse, as illustrated in Fig. 2.15. Notice how the basilar membrane is attached to the osseous spiral lamina medially, as it proceeds up the cochlea. Figure 2.16 illustrates how the osseous spiral lamina

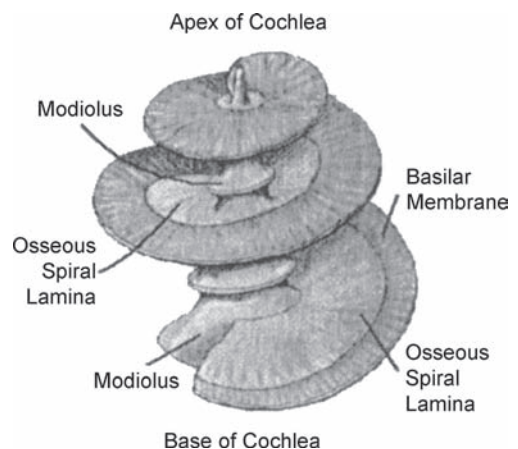


Figure 2.15 The osseous spiral lamina coils around the modiolus like the spiral staircase of a lighthouse. Notice how the basilar membrane is attached to osseous spiral lamina. Source: Adapted from Proctor (1989), *Surgical Anatomy of the Ear and Temporal Bone*, by permission of Thieme Medical Publishers.

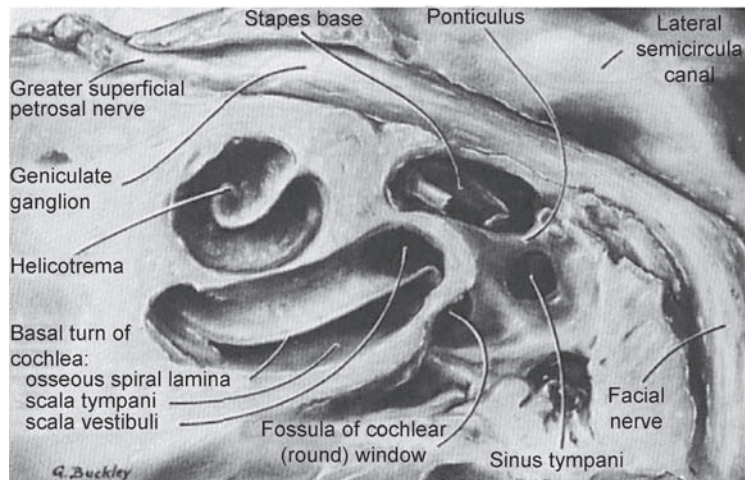


Figure 2.16 The osseous spiral lamina, scala vestibuli, scala tympani, and helicotrema. Source: From Anson and Donaldson (1967), *The Surgical Anatomy of the Temporal Bone and Ear*, Copyright © 1967, by W.B. Saunders with permission.

separates the scala vestibuli above from the scala tympani below. It also shows the orientation of the helicotrema at the apical turn, and the relationship between the round window and the scala tympani at the base of the cochlea.

It is easier to visualize the cochlea by imagining that the spiral has been uncoiled, as in Fig. 2.17. In this figure, the base of the cochlea is shown at the left and the apex at the right. We see three chambers: the **scala media**, **scala vestibuli**, and **scala tympani**. The scala media is self-contained and separates the other two. The scalae vestibuli and tympani, on the other hand, communicate with one another at the apex of the cochlea, through an opening called the **helicotrema**. The scala media is enclosed within the membranous labyrinth and contains endolymph, while the other two contain perilymph. The scala vestibuli is in contact with the stapes at the oval window, while the scala tympani has a membrane-covered contact with the middle ear at the round window. The scala media is separated from the scala vestibuli above by **Reissner's membrane**,

and from the scala tympani below by the **basilar membrane**. Reissner's membrane is only two cells thick and separates perilymph above from endolymph below without influencing the mechanical properties of the cochlea. In contrast, the basilar membrane plays a major role in cochlear functioning. Bekesy (1960/1989) reported that the basilar membrane is approximately 32 mm long, and that it tapers from about 0.5 mm wide at the apex to about 0.1 mm wide near the stapes at its base. Figures 2.15 and 2.17 illustrate how the basilar membrane gets progressively wider going from the base to the apex. Furthermore, it is thicker at the base than at the apex. Central to its role in cochlear functioning, the basilar membrane is stiffest at its base and becomes progressively less stiff toward the apex (Bekesy, 1960/1989).

The structures and orientation of the **scala media** are shown schematically in Fig. 2.18. The scala media is attached medially to the osseous spiral lamina, just described, and laterally to the outer wall of the cochlea by a fibrous connective tissue

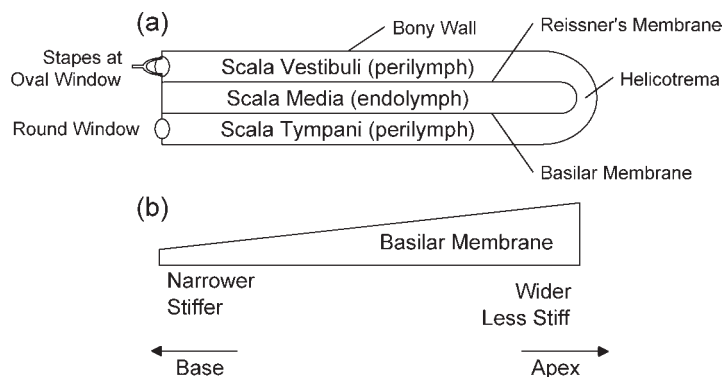


Figure 2.17 Schematic representations of the uncoiled cochlea. (a) Side view showing the three chambers. (b) Top view looking down on the basilar membrane (cochlear partition).

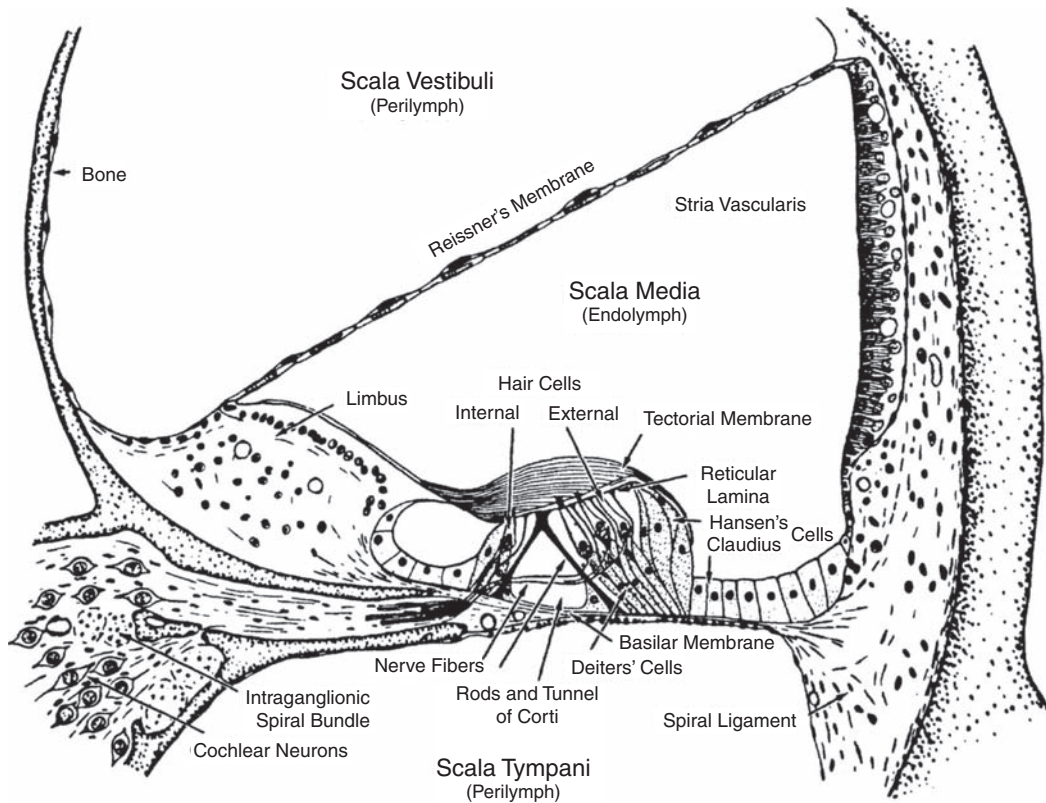


Figure 2.18 Cross-section of the organ of Corti. Source: From Davis (1962), with permission.

called the **spiral ligament**. Looking first at the osseous spiral lamina (toward the left in the figure), we see that this bony shelf is actually composed of two plates, separated by a space through which fibers of the auditory nerve pass. These fibers enter via openings called the **habenula perforata**. Resting on the osseous spiral lamina is a thickened band of periosteum, the **limbus**. Reissner's membrane extends from the top of the inner aspect of the limbus to the outer wall of the canal. The side of the limbus facing the organ of Corti is concave outward. The **tectorial membrane** is attached to the limbus at the upper lip of this concave part, forming a space called the **internal spiral sulcus**. The basilar membrane extends from the lower lip of the limbus to the spiral ligament at the outer wall of the duct. The spiral ligament itself has been described in considerable detail (Henson et al., 1984; Morera et al., 1980; Takahashi and Kimura, 1970); it is involved in the metabolic activities of the inner ear in addition to its role as a crucial supporting structure.

The basilar membrane has two sections. The inner section extends from the osseous spiral lamina to the outer pillars and is relatively thin. The remainder is thicker and extends to the spiral ligament. These two sections are called the **zona arcuata** and the **zona pectinata**, respectively. Sitting on the basilar membrane is the end organ of hearing—the organ of Corti. The width,

thickness, and orientation of the basilar membrane and the organ of Corti on it vary along the course of the cochlear duct (Lim, 1980).

The **organ of Corti** runs longitudinally along the basilar membrane. Grossly, it is made up of a single row of **inner hair cells (IHCs)**, three rows of **outer hair cells (OHCs)** (though as many as four or five rows have been reported in the apical turn), the **pillar cells** forming the **tunnel of Corti**, and various **supporting cells** (see Slepecky, 1996, for a detailed review). The tunnel pillars contribute considerably to the rigidity of the zona arcuata of the basilar membrane (Miller, 1985).

This tunnel separates the IHCs from the OHCs. Each of the approximately 3500 IHCs is supported by a **phalangeal cell** that holds the rounded base of the IHC as in a cup. There are about 12,000 OHCs, shaped like test tubes, which are supported by **Deiters' cells**. The closeup drawing of the organ of Corti in Fig. 2.19 shows that the IHCs are surrounded by supporting cells. In contrast, the OHCs are attached to the Deiters' cells below and the reticular lamina above, but their sides are not in contact with other cells.

Between the inner and outer hair cells are the tilted and rather conspicuous pillars (rods) of Corti, which come together at their tops to enclose the triangular tunnel of Corti. Fibers of

## TECTORIAL MEMBRANE

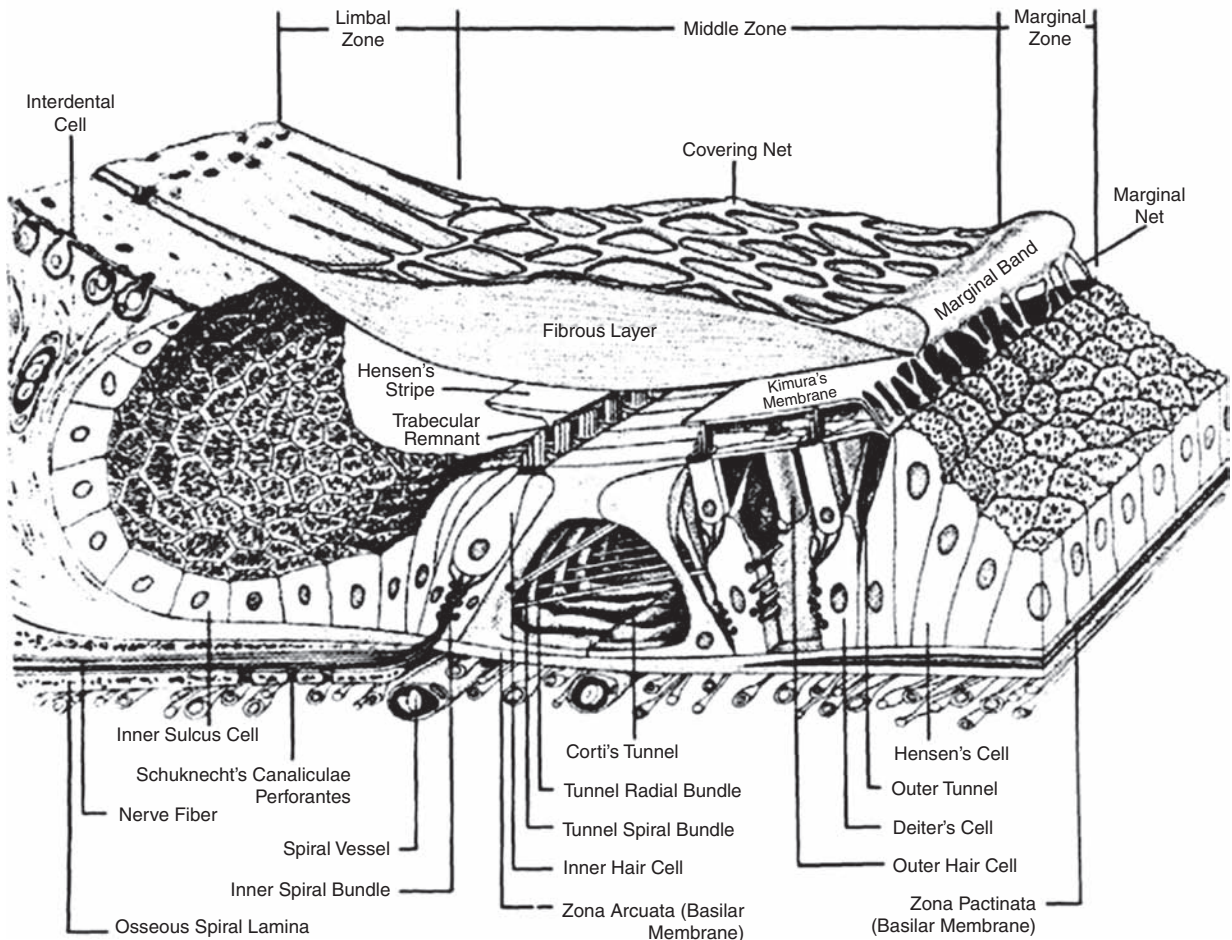


Figure 2.19 Schematic drawing of the organ of Corti and the tectorial membrane. The inner hair cells are surrounded by supporting cells. The outer hair cells attach to the Deiters' cells below and the reticular lamina above, but their lateral aspects do not make contact with other cells. Source: From Lim (1980) with permission of *J Acoust Soc Am*.

the eighth cranial (auditory) nerve traverse the tunnel to contact the OHCs. Just lateral to Deiters' cells are several rows of tall, supporting cells called **Hensen's cells**. Lateral to these are the columnar **Claudian cells**, which continue laterally to the spiral ligament and the stria vascularis.

The **reticular lamina** is made up of the tops of the hair cells (cuticular plates; see below) along with the upward-extending processes of the phalangeal and Deiters' cells. *Tight junctions* between the apical parts of these cells provide a barrier that isolates the endolymph-filled portions of the scala media from the structures and spaces of the organ of Corti. The distinctive surface pattern of the reticular lamina is shown in Fig. 2.20. The pillar cells maintain a strong structural attachment between the reticular lamina above and the basilar membrane below, and thus the reticular lamina provides a source of support for the

hair cells at their upper surfaces. This relationship is exemplified in Fig. 2.21, showing the OHCs and Deiters' cells in the reticular lamina, as well as the stereocilia of the hair cells protruding through the lamina.

The **tectorial membrane** (Fig. 2.19) extends from its medial connection to the upper lip of the limbus, courses over the hair cells, and then connects laterally to the Hensen's (and perhaps to the most lateral Deiters') cells by a border or marginal net. Its connection to the limbus is a strong and robust one; however, the attachment of the tectorial membrane to the Hensen's cells is quite fragile. The undersurface of the main body of the tectorial membrane (fibrous layer) is marked by Hensen's stripe located above the inner hair cells. Informative reviews of the tectorial membrane are provided by Steel (1983, 1985) and Lim (1986a).

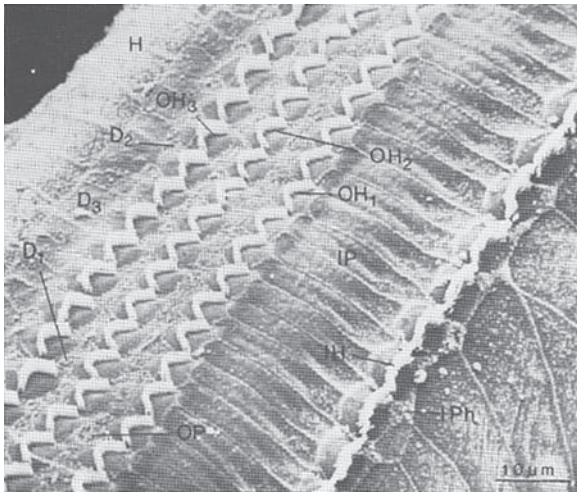


**Figure 2.20** The upper surface of the organ of Corti (chinchilla) showing the stereocilia of the inner and outer hair cells protruding through the reticular lamina. The outside aspect (toward the spiral ligament) is at the left, and the medial side (toward the modiolus) is at the right. Landmarks indicated are the Hensen's cells (H), three rows of Deiters' cells ( $D_1$ ,  $D_2$ ,  $D_3$ ), and outer hair cells ( $OH_1$ ,  $OH_2$ ,  $OH_3$ ), outer (OP) and inner (IP) pillar cells, inner hair cells (UH), and inner phalangeal cells (UPh). *Source:* From *Hearing Research* 22, Lim (Functional structure of the organ of Corti: a review, 117–146, © 1986) with kind permission from Elsevier Science Publishers-NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.

The tectorial membrane is frequently described as being ribbon-like in appearance, although Fig. 2.19 shows that this is really not the case. Instead, the tectorial membrane has a gelatinous consistency containing various proteins, mainly collagen II, which is arranged in fibers going across the tectorial

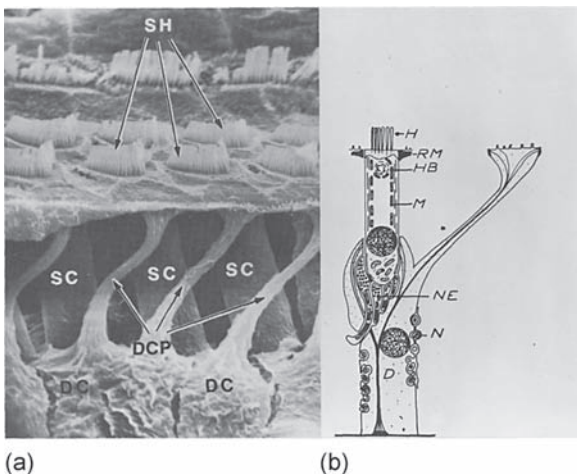


**Figure 2.21** Scanning electron micrograph (a) and schematic diagram (b) of Deiters' cells, outer hair cells, and the reticular lamina. *Abbreviations:* DC, Deiters' cell; DCP, phalange of Deiters' cell; SC, sensory (outer hair) cell; SH, sensory hairs (stereocilia). *Source:* From Engstrom and Wersall (1958) by permission of Academic Press.

membrane (Thalmann et al., 1987, 1993). Notice also that it is topped by a covering net. The collagen II provides the tectorial membrane with tensile strength (Zwislocki et al., 1988). The collagen fibers in the part of the tectorial membrane overlying the OHCs become increasingly tightly packed going from the apex toward the base of the cochlea, and its stiffness changes going up the length of the cochlea from stiffest at the base to least stiff at the apex (Gueta et al., 2006, 2007).

The **stria vascularis** contains a rich network of capillaries and is attached to the spiral ligament on the lateral wall of the scala media. Structurally, the stria vascularis is composed of three layers having characteristic cell types (e.g., Slepecky, 1996). The hexagonal **marginal cells** face into the scala media. Next are irregular **intermediate cells**, which have projections into the marginal layer. Finally, there are rather flat **basal cells**, which are in contact with the spiral ligament. The stria vascularis maintains the electrochemical characteristics of the endolymph, and in particular is viewed as the source of its high concentration of potassium as well as the endocochlear potential discussed in Chapter 4 (see Wangemann and Schacht, 1996, for an in-depth discussion).

The **blood supply** to the cochlea is well described (see, e.g., Axelsson and Ryan, 2001; Slepecky, 1996). It follows a course of successive arterial branches, going from the **basilar artery** to the **anterior inferior cerebellar artery**, to the **labyrinthine (internal auditory) artery**, to the **common cochlear artery**, and finally to the **spiral modiolar artery**. As its name implies, the spiral modiolar artery follows a corkscrew-like course up the modiolus from the base to the apex of the cochlea, as shown in Fig. 2.22a. The distribution of the blood supply to the structures in the cochlear duct is illustrated in Fig. 2.22b. Notice that the system involves one branch supplying the spiral ligament above the point of attachment of Reissner's membrane, the capillary network within the stria vascularis, and the spiral prominence, as well as a second branch feeding the limbus and a plexus under the basilar membrane. Venous drainage of the cochlea is into the internal auditory vein.

### Hair Cells

There are roughly 12,000 **outer hair cells (OHC)** and 3500 **inner hair cells (IHC)** in each ear, averaging (with considerable variability among people) about 86 IHCs and 343 OHCs per millimeter of cochlear length (Ulehlova et al., 1987; Wright, 1981; Wright et al., 1987).

The inner and outer hair cells were shown in relation to the cross-section of the organ of Corti in Fig. 2.17. A closer look at these cells is provided in Fig. 2.23. The hair cells are so-named because of the presence of cilia on their upper surfaces. Notice in Fig. 2.23 that the upper surface of each hair cell contains a thickening called the **cuticular plate**, which is topped by three rows of **stereocilia**, as well as a noncuticular area that contains the **basal body** of a rudimentary **kinocilium**.

The structures and interrelationships of the cuticular plate and stereocilia have been described by many researchers

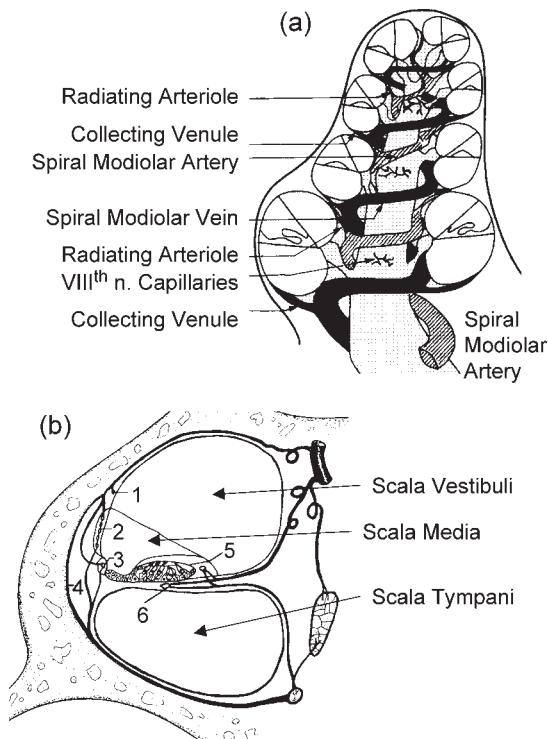
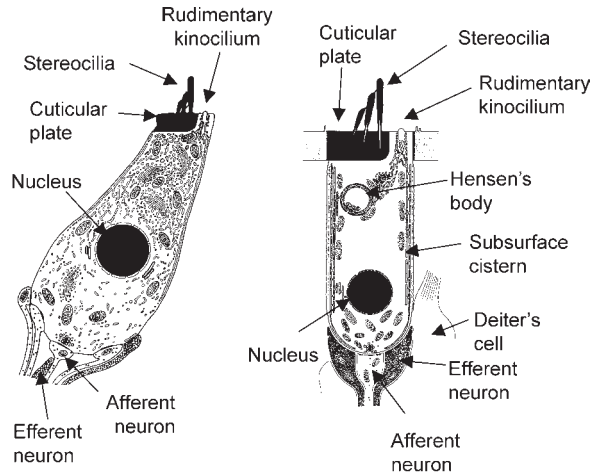


**Figure 2.22** Cochlear blood supply: (a) Modiolar view emphasizing the spiral modiolar artery (crosshatched) and the spiral modiolar vein (black). *Source:* Adapted from Axelsson A and Ryan AF (2001), with permission. (b) Cross-sectional view of the cochlear duct emphasizing distribution of blood supply to the spiral ligament above Reissner's membrane (1), stria vascularis (2), spiral prominence (3), limbus (5), and (6) basilar membrane. Also shown are terminal branches to collecting venules (4). *Source:* Adapted from Lawrence (1973), *Inner ear physiology*, in *Otolaryngology*, Vol. 1, Paparella and Schumrick (eds.), Copyright © 1973 by W.B. Saunders with permission.

(e.g., Crawford and Fettiplace, 1985; Flock and Cheung, 1977; Flock et al., 1981; Hirokawa and Tilney, 1982; Tilney et al., 1980; Tilney and Tilney, 1986). The stereocilia are composed of bundles of actin filaments and are encased in plasma membranes. The actin filaments are extensively cross-linked, and the cuticular plate into which the stereocilia rootlets are planted is similarly made up of a mosaic of cross-linked actin filaments. The filaments of the stereocilia rootlets extend into the cuticular plate, where fine cross bridges also interconnect the rootlet and cuticular plate filaments.

The stereocilia are arranged in a W-shaped pattern on the OHCs and a very wide "U" or "W" shape on the IHCs, as shown in Fig. 2.20. The base of the "W" faces away from the modiolus (or toward the outer wall of the duct). The stereocilia themselves taper toward the base. When the stereocilia are displaced, they remain stiff, bending at the tapered base in response to physical stimulation (Flock et al., 1977; Flock and Strelhoff, 1984; Strelhoff and Flock, 1984).



**(a) Inner Hair Cell**

**(b) Outer Hair Cell**

**Figure 2.23** Schematic representation of (a) an inner hair cell and (b) an outer hair cell (see text). *Source:* Used with permission from Lim DJ (1986b), *Effects of noise and ototoxic drugs at the cellular level in the cochlea: A review*. *Am J Otolaryngol* 7, 73–99.

Figure 2.24 shows closeup views of the stereocilia bundles from all three rows of OHCs and also for IHCs. The figure highlights the tapering of stereocilia heights from row to row on each hair cell, with the tallest row toward the outer wall of the duct (or away from the modiolus). At least the tallest stereocilia of the OHCs are firmly attached to the undersurface of the tectorial membrane; however, the IHC stereocilia are not attached to Hensen's stripe, or their attachment is tenuous if it does exist (see, e.g., Slepecky, 1996; Steel, 1983, 1985).

The height (length) of the stereocilia increases going from the base (high-frequency end) to the apex (low-frequency end) of the cochlea in many species (Fettiplace and Fuchs, 1999; Lim, 1986b; Saunders et al., 1985; Tilney and Saunders, 1983; Weiss et al., 1976; Wright, 1984). In humans, Wright (1984) found that the longest IHC stereocilia increased linearly from about 4 to 5  $\mu\text{m}$  near the base to about 7 to 8  $\mu\text{m}$  near the apex. The length of the OHC stereocilia also increased with distance up the cochlear duct, although there was more variability and the relationship was not linear.

A particularly interesting aspect of the hair cell stereocilia may be seen in Fig. 2.23. Looking back to this figure, one may notice that the stereocilia are joined by tiny lines. These lines represent filaments that serve as cross-links among the stereocilia. These cross-links occur in both inner and outer hair cells (Flock et al., 1977; Flock and Strelhoff, 1984; Furness and Hackney, 1986; Osborne et al., 1988; Pickles et al., 1984; Rhys Evans et al., 1985; Strelhoff and Flock, 1984; Vollrath, Kwan, and Corey, 2007). Different types of cross-links occur between the stereocilia of both inner and outer hair cells and are variously named according to their locations and configurations (Figs. 2.25–2.28). Thus, **shaft connectors** go between the main

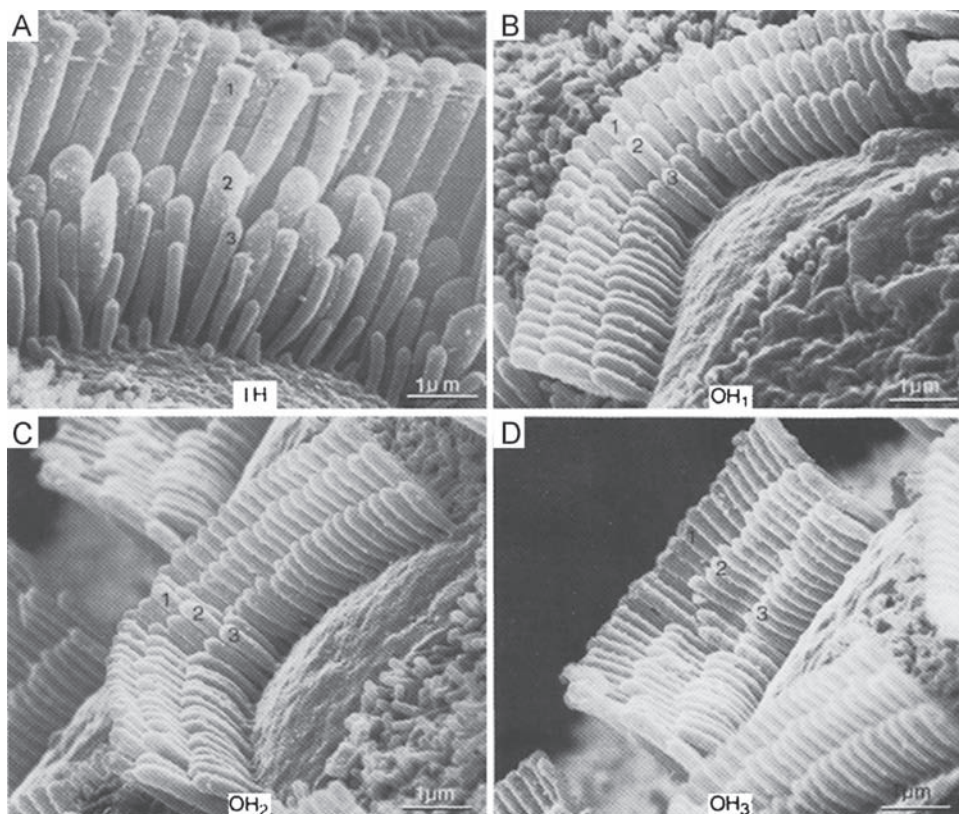


Figure 2.24 Close-up views of the stereocilia bundles of inner (a) and outer (b-d) hair cells demonstrating the decreasing cilia heights from row to row (numbered 1 to 3). Source: From *Hearing Research* 22, Lim (Functional structure of the organ of Corti: A review, 117–146, © 1986) with kind permission from Elsevier Science Publishers-NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.

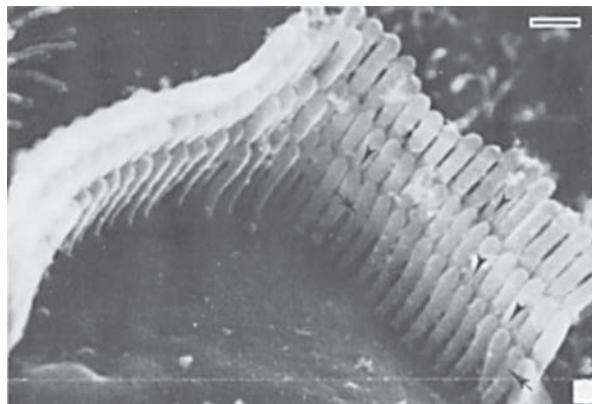


Figure 2.25 Side-to-side (arrows) and tip-links (tip-to-side) cross-links on OHCs. Source: From *Hearing Research* 21, Furness and Hackney (High-resolution scanning-electron microscopy of stereocilia using the osmium-thiocarbohydrazide coating technique, © 1986) with kind permission from Elsevier Science Publishers-NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.

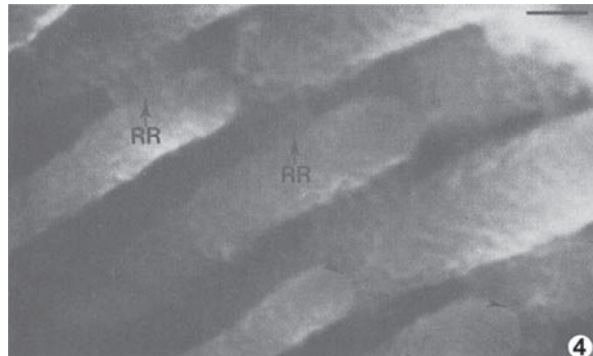


Figure 2.26 Row-to-row cross-links (RR) on OHCs. Source: From *Hearing Research* 21, Furness and Hackney (High-resolution scanning-electron microscopy of stereocilia using the osmium-thiocarbohydrazide coating technique, © 1986) with kind permission from Elsevier Science Publishers-NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.

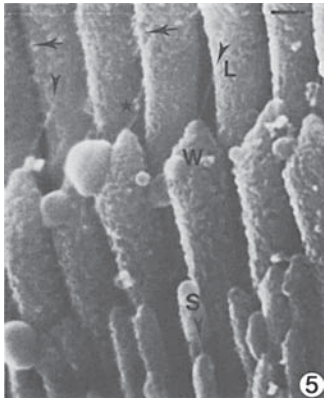


**Figure 2.27** Inner hair cell stereocilia showing examples of side-to-side cross links (arrows) and tip-links (arrowheads), which may be relatively long (L) or short (S). *Source:* From *Hearing Research* 21, Furness and Hackney (High-resolution scanning-electron microscopy of stereocilia using the osmium-thiocarbohydrazide coating technique, 1986) with kind permission from Elsevier Science Publishers-NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.

shafts of the stereocilia; **ankle connectors** are links between the tapered bottoms of the stereocilia; **side-to-side cross-links** join stereocilia that are juxtaposed within the same row; **row-to-row cross-links** go from stereocilia in one row to adjacent ones in the next row.<sup>3</sup> Finally, **tip links** (also known as **tip-to-side** or **upward-pointing cross-links**) go from the tips of stereocilia in a shorter row upward to the sides of the stereocilia in the adjacent taller row and plays a central role in the functioning of the hair cells. As we shall see in Chapter 4, bending of the stereocilia toward the outer wall of the duct stretches these tip links, which in turn open mechanoelectrical transduction pores at the tops of the shorter stereocilia, triggering the hair cell's response (Fettiplace and Hackney, 2006; Vollrath et al., 2007; Beurg et al., 2009).

The structures of the hair cells and their orientation in the organ of Corti reflect their function as sensory receptors, which transduce the mechanical signal carried to them into electrochemical activity. Yet, the contrasting structures and associations of the inner and outer hair cells reflect functional differences between them. Even a casual look at Fig. 2.23 reveals that the test tube-shaped OHCs are very different from the flask-shaped IHCs. Many of these characteristics are associated with the unique property of OHC **electromotility**, their ability to contract and expand, which is central to the active cochlear processes discussed in Chapter 4. For example, OHCs contain **contractile proteins** (e.g., actin, fibrin, myosin, tropomyosin, tubulin) in their cell bodies and cell membranes, stereocilia,

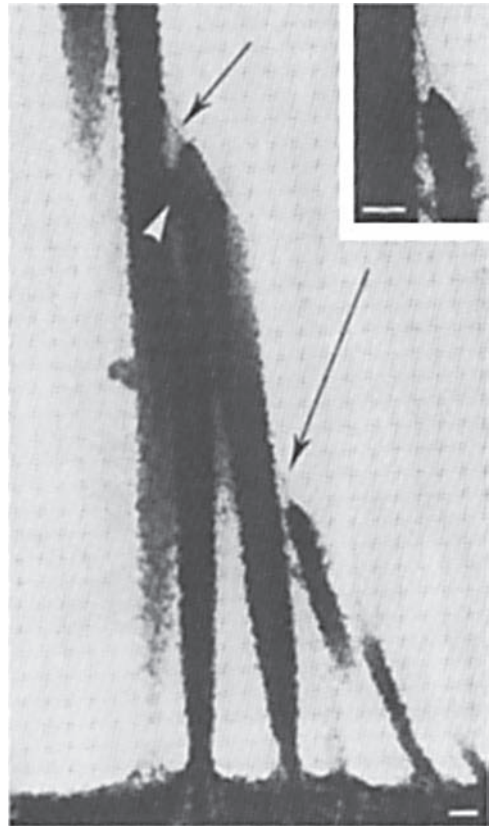


**Figure 2.28** Tip-links (arrows) on an outer hair cell. The white arrowhead shows a row-to-row link. *Inset:* close-up of a tip-link. *Source:* From *Hearing Research* 15, Pickles, Comis, and Osborne (Cross links between stereocilia in the guinea pig organ of Corti, and their possible relation to sensory transduction, 103–112, © 1984) with kind permission from Elsevier Science Publishers-NL Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.

and cuticular plates (e.g., Flock, 1980; Flock et al., 1982, 1986; Slepecky, 1996; Slepecky et al., 1988). A more apparent difference pertains to the arrangement of their intracellular structures. Notice that the intracellular structures are distributed throughout the IHC, which is the typical arrangement. In contrast, the nucleus and many organelles in the OHC tend to be concentrated toward the bottom and top of the cell, leaving the cytoplasm between these areas relatively free of cellular structures (Brownell, 1990).

The lateral walls of the OHCs are particularly interesting. They are composed of three layers, as illustrated in Fig. 2.29 (e.g., Brownell and Popel, 1998; Dallos, 1992; Holley, 1996; Slepecky, 1996). The outside layer is the cell's **plasma membrane**, and the inside layer comprises the **subsurface cisternae**. Between them is the **cortical lattice**, which is a matrix composed of parallel rows of actin filaments going circumferentially around the tube-shaped cell, with spectrin cross-links between them. The actin filaments appear to be attached to the outer surface

<sup>3</sup> Horizontal top connectors going between the apical ends of the cilia have been described in the mouse cochlea (Goodyear, Marcotti, Kros, and Richardson, 2005).

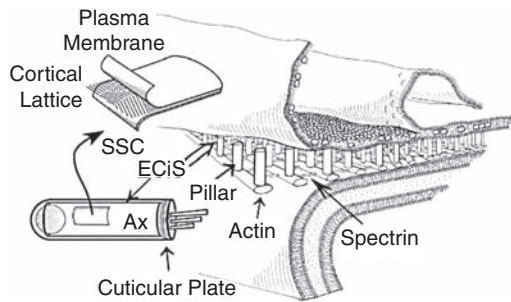


Figure 2.29 The lateral wall of the outer hair cell is composed of the subsurface cisternae on the inside, the plasma membrane on the outside, and a filamentous matrix between them (see text). *Abbreviations:* Ax, axial core of the hair cell; ECIS, extra-cisternal space; SSC, subsurface cisternae. *Source:* Adapted from Brownell and Popel (1998), *Electrical and mechanical anatomy of the outer hair cell*, in *Psychophysical and Physiological Advances in Hearing*, Palmer et al. (eds.), copyright © 1998 by Whurr, with permission.

of the subsurface cisternae, and they are attached to the plasma membrane by **pillars**. The actin filaments are slanted at about  $15^\circ$  (instead of horizontal) so that they go around the cell in the form of a helix (Fig. 2.30). The OHC's cytoplasm provides positive hydrostatic pressure (turgor) within the cell, and its test tube-like shape is maintained by the tension of the matrix of structures in its lateral walls (Fig. 2.30).

## INNERVATION

The sensory hair cells of the cochlea interact with the nervous system by way of the **auditory (cochlear) branch** of the **eighth cranial (vestibulocochlear or statoacoustic) nerve**. The auditory nerve was probably first described in the 1500s by Falloppia. However, its structure and connections have become well defined only during the 20th century. A com-

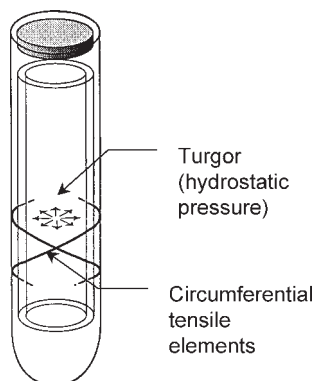


Figure 2.30 Schematic illustration of the hydrostatic pressure (or turgor) of the cytoplasm of an OHC and the matrix of circumferential tensile elements of its lateral walls. *Source:* Adapted from Brownell (1990), with permission.

prehensive discussion of the auditory nerve, its relationship to the cochlea, and its central projections are provided by Ryugo (1992).

There are approximately 30,000 neurons in the human auditory nerve, and approximately 50,000 or more cochlear neurons in the cat (Engstrom and Wersall, 1958; Furness and Hackney, 1986). These neurons are primarily afferents, which carry sensory information up from the hair cells, but they also include efferents, which descend from the brainstem to the cochlea. The efferent fibers of the auditory nerve represent the terminal portion of the **olivocochlear bundle**, described later in this chapter. The cell bodies of the afferent auditory neurons constitute the spiral ganglia, residing in Rosenthal's canal in the modiolus. These neurons may be myelinated or unmyelinated before exiting through the habenula perforata, but all auditory nerve fibers are unmyelinated once they enter the organ of Corti. Figure 2.31 shows how the auditory nerve and spiral ganglia relate to a cross section of the cochlear duct.

Most sensory neurons are bipolar, so called because the cell body is located part way along the axon, as illustrated in Fig. 2.32. Auditory neurons are of this general type. More specifically, the cells of the spiral ganglia are composed of at least two distinctive types. Spoendlin (1969, 1971, 1978) demonstrated that approximately 95% of these cells are *relatively large, myelinated, bipolar* neurons. Spoendlin classified these cells as type I auditory neurons. In contrast, he found that roughly 5% of the spiral ganglion cells were *relatively small, unmyelinated*, and tended to be *pseudo-monopolar* in structure. These spiral ganglion cells were classified as type II auditory neurons. These two types of auditory neurons are illustrated in the lower left hand portion in Fig. 2.33.

Upon exiting the habenula perforata into the organ of Corti, the now unmyelinated neural fibers follow different routes to distribute themselves asymmetrically between the inner and outer hair cells, as shown schematically in Figs. 2.33 and 2.34. About 95% of these fibers are inner radial fibers, which course directly out to innervate the *inner* hair cells. The remaining 5%, consist of 2500 to 3000 outer spiral fibers that cross the tunnel of Corti as *basal fibers*, and then turn to follow a route of about 0.6 mm toward the base as the *outer spiral bundle*. These outer spiral fibers then make their way up between the Deiters' cells to synapse with the *outer* hair cells.

Innervation patterns are very different for inner and outer hair cells. Each inner hair cell receives a fairly large number of radial fibers. Each IHC in the cat cochlea receives an exclusive supply of 10 to 30 afferent fibers, with fewer toward the apex and more toward the base (Liberman, Dodds, and Pierce, 1990; Spoendlin, 1978). In contrast, outer spiral bundle gives off collaterals so that each neural fiber innervates several outer hair cells (up to 10 toward the base, and about 10–20 toward the apex), and each OHC receives collaterals from roughly 10 neurons. In humans, IHCs receive about 10 afferents throughout the cochlea, and some fibers branch at their ends to synapse with two or three IHCs instead of to just one (Nadol, 1983a).

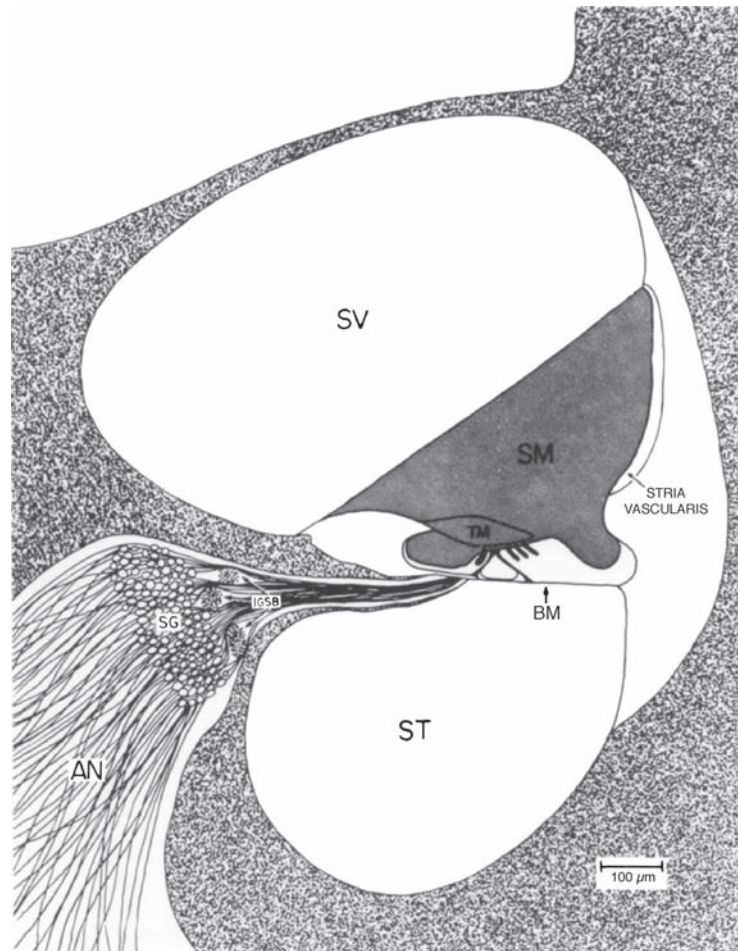


Figure 2.31 Relationship of the auditory nerve to a cross-section of the cochlear duct (cat). Abbreviations: AN, auditory nerve; SG, spiral ganglion; IGSB, intraganglionic spiral bundle primarily composed of efferents; TM, tectorial membrane; BM, basilar membrane; SV, SM, ST, scalae vestibuli, media, and tympani, respectively. Source: From *Hearing Research* 22, Kiang, Liberman, Sewell, and Guinan (Single unit clues to cochlear mechanisms, 171–182, © 1984) with kind permission from Elsevier Science Publishers-NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.

Human OHCs typically receive 4 to 6 afferent fibers (Nadol, 1983b).

Liberman (1982) traced the courses of single auditory neurons by marking them with horseradish peroxidase (HRP). All of the type I auditory neurons he labeled with intracellular injections of HRP could be traced to radial fibers going to IHCs. Kiang et al. (1982) injected HRP into the auditory nerve within

the internal auditory canal. They were then able to trace the courses of 50 radial and 11 outer spiral fibers. Their HRP labeling studies confirmed earlier conjectures by Spoendlin (1971, 1978) that the large caliber (over 2  $\mu\text{m}$ ), bipolar type I cells continue as radial fibers in the organ of Corti; and that the small caliber (under 1  $\mu\text{m}$ ), pseudomonopolar type II cells correspond to the outer spiral fibers (see Figs. 2.32 and 2.33).

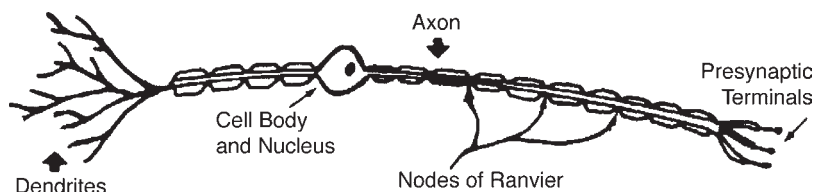


Figure 2.32 Schematic drawing of a typical bipolar sensory neuron.

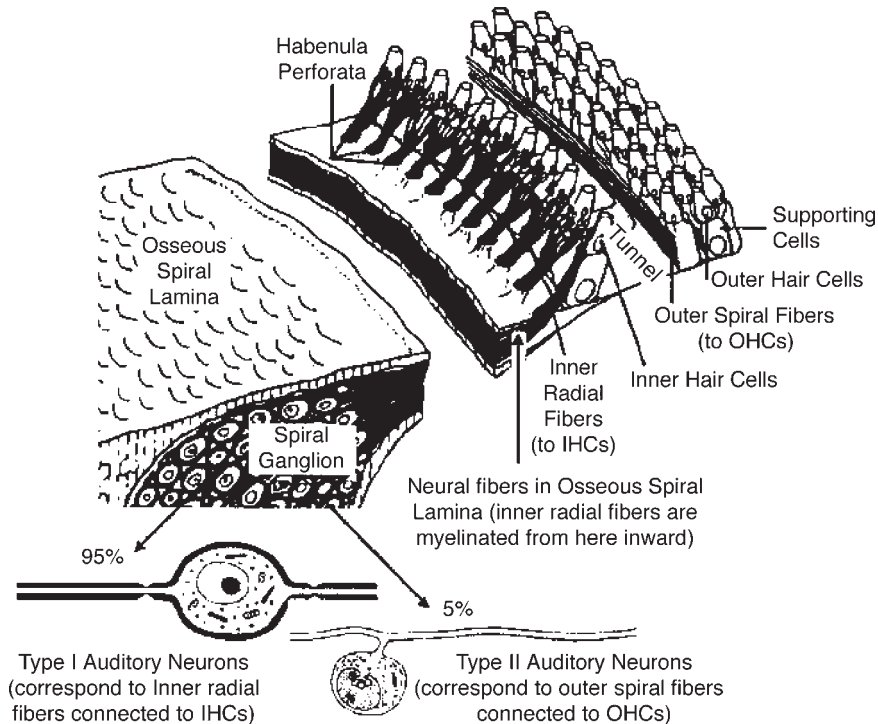


**Figure 2.33** The afferent innervation of the organ of Corti. Notice how Type I auditory neurons in the spiral ganglion continue in the organ of Corti as inner radial fibers to inner hair cells, and Type II auditory neurons continue as outer spiral fibers to outer hair cells. Examples of Type I and Type II neurons are illustrated in the lower left-hand section of the drawing. *Source:* Adapted from drawings by Spoendlin H. The afferent innervation of the cochlea, in *Electrical Activity of the Auditory Nervous System*, R.F. Naunton and C. Fernandez (eds.), Copyright © 1978 by Academic Press, with permission.

As illustrated in Fig. 2.35, Liberman and Simmons (1985) demonstrated that a given inner hair cell makes contact with three types of radial fibers, differing in terms of their average diameters, cellular characteristics, and spontaneous firing rates (see Chap. 5). Moreover, these three types of radial fibers attach to the IHC at characteristic locations. The thickest fibers (having the highest spontaneous rates) always attach on the surface of the IHC, which is toward the OHCs. The thinnest and medium thickness fibers (having low and medium spontaneous rates, respectively) attach to the IHC on the surface facing toward the modiolus.

### **Efferent Innervation of the Hair Cells**

Other kinds of neurons are also found in the organ of Corti. Figures 2.34 and 2.36 show that two different types of fibers can be identified with respect to their nerve endings (Engstrom, 1958; Smith and Sjostrand, 1961). One group of cells has smaller nonvesiculated endings. These are afferent (ascending sensory) neurons.

The second group of cells has larger vesiculated endings and is derived from the **efferent** (descending) neurons of the **olivo-cochlear bundle** (see below). The vesiculated endings contain *acetylcholine*. Various studies found degeneration of these vesiculated units when parts of the descending olivocochlear bundle

were cut (Smith and Rasmussen, 1963; Spoendlin and Gacek, 1963). However, no degeneration was found to occur for the nonvesiculated afferent neurons. The endings of the efferent fibers are in direct contact with the OHCs, whereas they terminate on the afferent neural fibers of the IHCs rather than on these sensor cells themselves (Fig. 2.36). This suggests that the efferents act directly upon the OHCs (presynaptically), but that they act upon the associated afferent fibers of the IHCs (postsynaptically). The density of efferent fibers is substantially greater for the OHCs than for the IHCs. Furthermore, there is greater efferent innervation for the OHCs at the base of the cochlea than at the apex, and this innervation of the OHCs also tapers from the first row through the third.

### **CENTRAL AUDITORY PATHWAYS**

The auditory (or cochlear) nerve appears as a twisted trunk—its core is made up of fibers derived from the apex of the cochlea, and its outer layers come from more basal regions. The nerve leaves the inner ear via the internal auditory meatus and enters the brainstem at the lateral aspect of the lower pons. We are now in the **central auditory nervous system**, or the **central auditory pathways**, the major aspects of which are outlined in

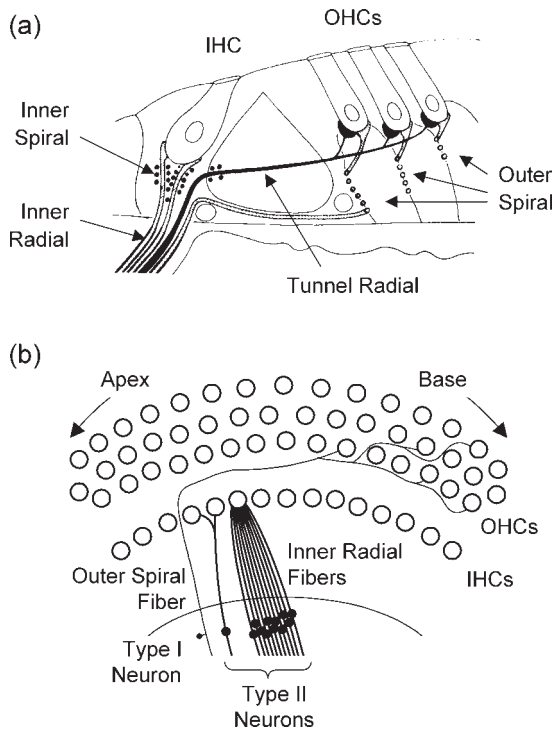


Figure 2.34 (a) Afferent and efferent innervation of the organ of Corti. Source: Adapted from Spoendlin (1975) with permission. Efferent fibers are shown in black. (b) Arrangement of Type I and Type II afferent auditory nerve fibers to inner and outer hair cells [based on findings of Spoendlin (1975) and Nadol (1983a)].

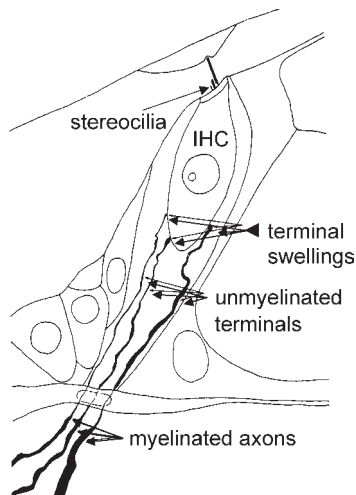


Figure 2.35 The thickest radial fibers attach to the IHC surface facing the OHCs, whereas the thinnest and medium thickness fibers attach on the surface toward the modiolus. Source: From Liberman and Simmons (1985), with permission of *J Acoust Soc Am*.

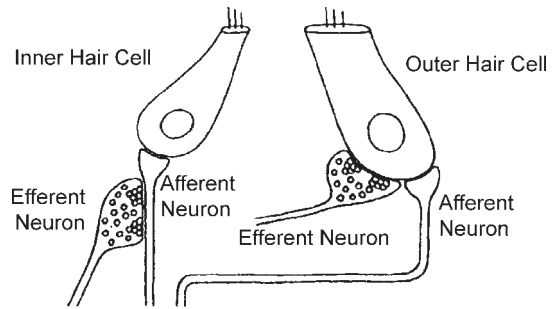


Figure 2.36 Relationship between afferent and efferent neural fibers and the inner and outer hair cells. Source: Adapted from Spoendlin (1975), with permission.

this section. Although not addressed here, interested students will find a summary of the neurotransmitters associated with the auditory system in Table 2.2. In addition, many sources are available to those wishing to pursue a more detailed coverage of the anatomy and physiology of the auditory pathways (e.g., Ehret and Romand, 1997; Møller, 2000; Musiek and Baran, 2007; Popper and Fay, 1992; Webster, Popper and Fay, 1992; Altschuler, Bobbin, Clopton, and Hoffman, 1991; Winer, 1992).

### Afferent Pathways

The major aspects of the ascending central auditory pathways are shown schematically in Fig. 2.37. The fibers of the auditory nerve constitute the first-order neurons of the ascending central auditory pathways. The number of nerve fibers associated with the auditory system increases dramatically going from the auditory nerve to the cortex. For example, the rhesus monkey has roughly 30,000 cells in its auditory nerve, compared to approximately 10 million at the auditory cortex (Chow, 1951).

Upon entering the brainstem, the auditory nerve fibers synapse with cells in the **cochlear nuclei**, constituting the first level of way stations in the central auditory nervous system. Comprehensive discussions of the cochlear nuclei and their synaptic connections may be found in Cant (1992) and Ryugo (1992). The cochlear nuclei are composed of three main sections: the **anterior ventral cochlear nucleus (AVCN)**, the **posterior ventral cochlear nucleus (PVCN)**, and the **dorsal cochlear nucleus (DCN)**. The incoming type I auditory neurons (originating from the inner hair cells) bifurcate into ascending branches to the AVCN and descending branches to the PVCN and DCN. [Type II auditory neurons also project to the cochlear nuclei, following paths parallel to the type I fibers, but they terminate in different cellular regions (Leak-Jones and Snyder, 1982; Ruggero et al., 1982; Ryugo, 1992).] Auditory neurons arising from the more basal (higher frequency) areas of the cochlea terminate in the dorsomedial parts of the cochlear nuclei, and fibers from the more apical (lower frequency) parts of the cochlea go to the ventrolateral parts of these nuclei. Frequency-place relationships extend throughout the central

Table 2.2 Likely/Possible Neurotransmitters in the Auditory Nervous System

| Location                     | Neurotransmitter(s)                                                                     | Reference examples                                                         |
|------------------------------|-----------------------------------------------------------------------------------------|----------------------------------------------------------------------------|
| Auditory nerve               | Aspartate, glutamate                                                                    | Wenthold (1978), Romand and Avan (1997)                                    |
| Cochlear nucleus             | Ach, aspartate, GABA, glutamate, glycine                                                | Godfrey et al. (1990), Wenthold et al. (1993), Romand and Avan (1997)      |
| Superior olivary complex     | Aspartate (in MSO), GABA, glutamate (in MSO), glutamate decarboxylase, glycine (in LSO) | Wenthold (1991), Helfert and Aschoff (1997)                                |
| Lateral lemniscus            | GABA, glycine                                                                           | Helfert and Aschoff (1997)                                                 |
| Inferior colliculus          | GABA, glutamate decarboxylase, glycine                                                  | Faingold et al. (1989), Wynne et al. (1995)                                |
| Medial geniculate            | GABA, glutamate                                                                         | Li et al. (1995), Schwartz et al. (2000)                                   |
| Auditory cortex              | Ach, GABA, glutamate, noradrenoline, serotonin                                          | Metherate and Ashe (1995), Metherate and Hsieh (2003)                      |
| Medial olivocochlear bundle  | Ach, CGRP, GABA                                                                         | Sahley et al. (1997)                                                       |
| Lateral olivocochlear bundle | Ach, CGRP, dopamine, dynorphin, enkephalin, GABA, urocortin                             | Fex and Altschuler (1981), Sahley et al. (1997), Gil-Loyzaga et al. (2000) |

*Abbreviations:* Ach, acetylcholine; CGRP, calcitonin gene-related peptide; GABA,  $\gamma$ -aminobutyric acid; LSO, lateral superior olive; MSO, medial superior olive.

auditory nervous system and are covered in the discussion of *tonotopic organization* in Chapter 6.

Second-order neurons arise from the cochlear nuclei to proceed up the auditory pathways. Some fibers ascend ipsilaterally, but most cross the midline and ascend along the contralateral pathway. The **ventral acoustic stria** arises from the AVCN, forming the **trapezoid body**. The fibers of the trapezoid body *decussate* [cross to the opposite side to synapse with the nuclei of the contralateral superior olivary complex (SOC) or to ascend

in the lateral lemniscus]. Other fibers of the trapezoid body terminate at the SOC on the ipsilateral side and at the trapezoid nuclei. The PVCN gives rise to the **intermediate acoustic stria** (of Held), which contralateralizes to ascend in the lateral lemniscus of the opposite side. The **dorsal acoustic stria** (of Monakow) is made up of fibers projecting from the DCN, which cross to the opposite side and ascend in the contralateral lateral lemniscus.

The **superior olivary complex** constitutes the next way station in the auditory pathway and is distinguished as the first (lowest) level that receives information originating from both sides of the head (*bilateral representation*). The SOC is made up of the **medial superior olive (MSO)**, the **lateral superior olive (LSO)**, and the **medial nucleus of the trapezoid body (MNTB)**, as well as rather diffuse accumulations of cell bodies known as the **periolivary nuclei** (Helfert and Aschoff, 1997; Moore, 1987, 2000; Schwartz, 1992). Each MSO receives bilateral inputs from the right and left AVCNs, and then projects to the ipsilateral inferior colliculus via the lateral lemniscus on its own side. The LSO also receives inputs directly from the AVCN on the same side as well as from the opposite AVCN via the ipsilateral MNTB. In turn, the LSO projects bilaterally to the inferior colliculi via the lateral lemnisci on both sides. As just implied, the MNTB receives its input from the opposite AVCN and then projects to the LSO on its own side. Although similar to the SOC of lower mammals, the human SOC has a relatively smaller LSO, more prominent periolivary cell groups, and the TB does not appear to be organized into a identifiable nucleus (Moore, 2000).

The **lateral lemniscus (LL)** is the pathway from the lower nuclei of the auditory pathway just described to the level of the inferior colliculus and has been described in some detail (e.g., Brunso-Bechtold, Thompson, and Masterton, 1981; Ferraro and Minckler, 1977a; Glendenning, Brunso-Bechtold, Thompson, and Masterton, 1981; Helfert and Aschoff, 1997; Moore, 1987; Schwartz, 1992). Each lateral lemniscus includes neural

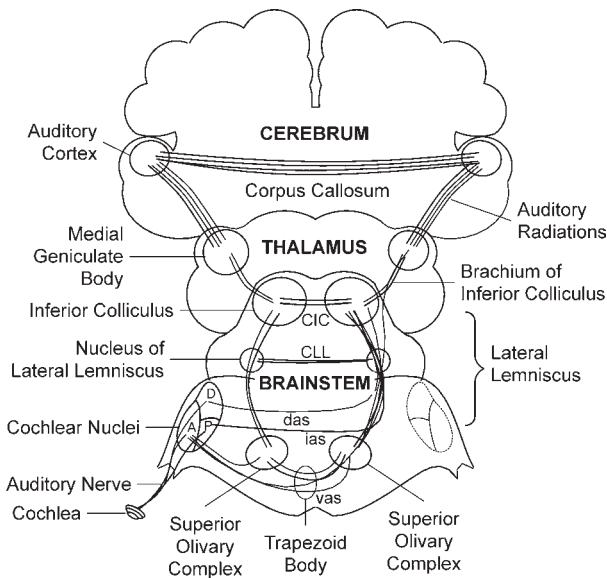


Figure 2.37 Schematic representation of the major aspects of the ascending central auditory pathways. *Abbreviations:* A, anterior ventral cochlear nucleus; P, posterior ventral cochlear nucleus; D, dorsal cochlear nucleus; CIC, commissure of the inferior colliculus; CLL, commissure of the lateral lemniscus; das, dorsal acoustic stria; ias, intermediate acoustic stria; vas, ventral acoustic stria.

fibers originating from the cochlear nuclei and superior olivary complexes on both sides, as well as fibers arising from the nuclei of the LL itself. The LL principally includes a **ventral nucleus (VNLL)** and a **dorsal nucleus (DNLL)**, which have typically been described, although an intermediate nucleus has also been described. However, Ferraro and Minckler (1977a) reported that the nuclei of the human LL are somewhat dispersed into scattered cell clusters among the lemniscal fibers, and that a clear-cut demarcation between them could not be found. Communication between the lateral lemnisci of the two sides occurs via the **commissural fibers of Probst**.

The majority of the ascending fibers from the LL project to the **inferior colliculi (IC)**, which are large nuclei on the right and left sides of the midbrain (see, e.g., Ehret and Romand, 1997; Oliver and Huerta, 1992; Oliver and Morest, 1984). The divisions of the IC have been variously described based on different anatomical and physiological methods (e.g., Morest and Oliver, 1984; Rockel and Jones, 1973a, 1973b). The **central nucleus** of the IC is the principal way station for auditory signals arising from the LL, while its **dorsal cortex** and **pericentral** and **external (lateral) nuclei** interact with the central nucleus as well as being involved in many interconnections with other neural systems. Hence, the IC plays a role in multisensory integration. Communication between the inferior colliculi of the two sides occurs via the **commissure of the inferior colliculus**. The auditory pathway continues from the IC to the medial geniculate body (MGB) of the thalamus by way of the **brachium of the inferior colliculus**, which also includes ascending fibers that bypass the IC (Ferraro and Minckler, 1977b). See Oliver and Huerta (1992) for a comprehensive review of the anatomy of the inferior colliculus.

The **medial geniculate body** is the highest subcortical way station of the auditory pathway, which has been described in great detail by Winer (1984, 1985, 1991, 1992). Unlike other way stations along the ascending auditory pathway, all fibers reaching the MGB will synapse here. Moreover, the right and left MGBs are not connected by commissural pathways. Each MGB is composed of **ventral, dorsal, and medial divisions**, which are relatively similar in humans and other mammals. The ventral division receives auditory signals from the central nucleus of the IC (and nonauditory inputs from the reticular nucleus of the thalamus and the ventrolateral medullary nucleus). It projects mainly to the primary auditory cortex, as well as to some other cortical auditory areas. The dorsal division receives auditory signals from the IC and nonauditory information from a variety of brainstem and thalamic inputs and projects mainly to the auditory association cortex as well as to a wide variety of other cortical sites. The medial division receives a wide range of both auditory inputs (from the IC, periolivary nuclei of the SOC, and the ventral nucleus of the LL) and multisensory nonauditory inputs (from the spinal cord, superior colliculus, vestibular nuclei, and spinal cord), and projects to diverse areas of the cortex, including the somatosensory and prefrontal cortices. The **auditory (geniculocortical or thalamocortical)**

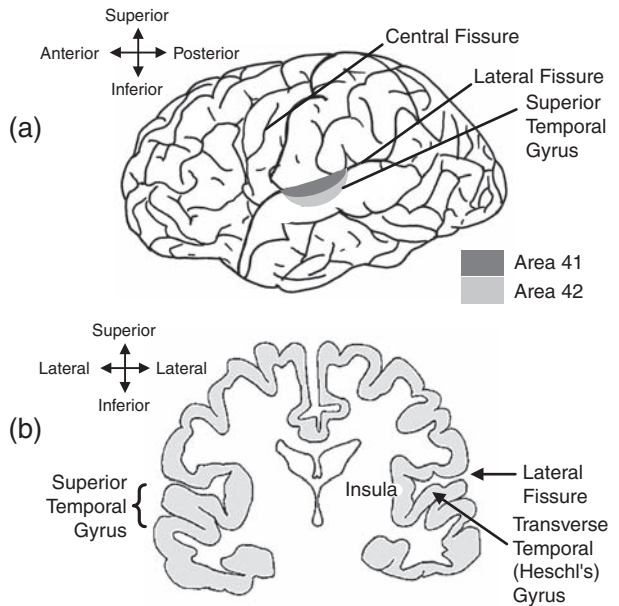


Figure 2.38 Lateral (a) and coronal (b) representations of the human brain illustrating the locations of the primary and secondary auditory areas.

**radiations** project ipsilaterally from the MGB to the **auditory cortex**, which is located in the temporal lobe.

The **auditory cortex** occupies a band of tissue along the superior border of the temporal lobe just below the **lateral (Sylvian) fissure**, largely involving the **transverse temporal (Heschl's) gyrus** and the posterior two-thirds of the **superior temporal gyrus** (Fig. 2.38). The traditional view of the auditory cortex distinguishes between the primary auditory and auditory association cortices. The **primary auditory cortex (konioncortex)**, or **area AI**, mainly involves Heschl's gyrus located within the lateral fissure, and roughly corresponds to **area 41** in the classic Brodmann classification system. Area AI is largely surrounded by the **auditory association cortex (parakonioncortex)**, or **area AII**, which is mainly situated on parts of the posterior transverse and superior temporal gyri, more-or-less corresponding to Brodmann **area 42**. A more precise description of the auditory cortex is still evolving, with current descriptions of the anatomy expressed in terms of **core** regions and secondary **belt** regions (e.g., Galaburda and Sanides, 1980; Hackett, Preuss, and Kaas, 2001; Rivier and Clark, 1997; Wallace, Johnson, and Palmer, 2002). For example, Wallace et al. (2002) integrated their findings with those of Rivier and Clark (1997) to delineate the anatomical regions in the human auditory cortex illustrated in Fig. 2.39. The figure identifies two core regions surrounded by six belt regions. The **core regions** are (filled with dots in the figure) include (a) the primary auditory area (**AI**) involving the posteromedial two-thirds of Heschl's gyrus, and (b) a narrow lateroposterior area (**LP**) adjacent to it and abutting Heschl's sulcus. The surrounding **belt regions** (filled with lines

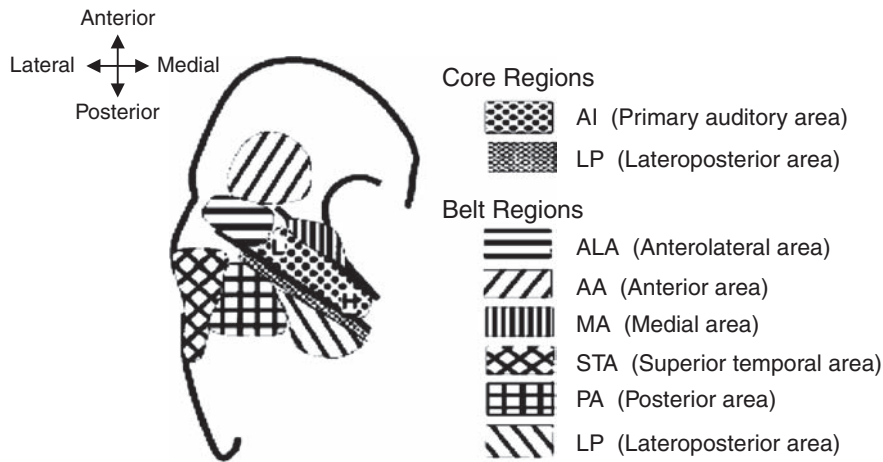


Figure 2.39 The core and belt regions of the human auditory cortex based on the combined findings of Rivier and Clarke (1997) and Wallace et al. (2002). Dots represent core regions; lines and cross-hatching represent belt regions. *Abbreviations:* AI, primary auditory area; LP, lateroposterior area; ALA, anterolateral area; AA, anterior area; MA, medial area; LA, lateral area (lateral to LP); PA, posterior area; STA, superior temporal area; L, responsive to low frequencies; H, responsive to high frequencies. *Source:* From Wallace et al. (2002), *Histochemical identification of cortical areas, Experimental Brain Research, Vol 143, p. 506, Fig. 6A, ©2002, used with kind permission of Springer Science+Business Media.*

and cross-hatching in the figure) include the (a) anterolateral (ALA) area on the posterior third of Heschl's gyrus, (b) anterior area (AA) anterior to area AI, (c) medial area (MA) anteromedial to AI, (d) lateral area (LA) lateral to LP, (e) posterior area (PA) posterior to LP, and (f) a superior temporal area (STA).

The fiber connections between the medial geniculate body and auditory cortex have been described based on findings in various animals and humans (e.g., Diamond et al., 1958; Mesulam and Pandya, 1973; Niimi and Matsuoaka, 1979; Ravizza and Belmore, 1978; Rose and Woolsey, 1949, 1958; Winer et al., 1977). The principal connections are from the ventral division of the MGB to area AI; however, there are also connections from other parts of the MGB to many of the areas that respond to auditory stimulation, such as areas AII and Ep, among others.

As suggested in the previous paragraph, areas AI and AII are by no means the only cortical locations that respond to sound. Additional cortical auditory areas have been known for some time (e.g., Reale and Imig, 1980; Rose, 1949; Rose and Woolsey, 1958), and are discussed further in Chapter 6. Communication between right and left auditory cortices occurs via the **corpus callosum** (e.g., Karol and Pandya, 1971; Musiek and Baran, 2007; Pandya et al., 1969).

In contrast to the principal afferent auditory pathway from the cochlea to the primary auditory cortex (AI), as in Fig. 2.37, those involving more diverse connections and leading to other areas have been identified as the **nonclassical (adjunct) auditory pathways** (see, Aitkin, 1986; Ehret and Romand, 1997; Møller, 2000). This include the **diffuse system** from IC to the dorsal division of the MGB, and then to auditory association cortex (AII); and the **polysensory system**, which goes from the IC (including visual and somatosensory inputs) to the medial division of the MGB, and then projecting to sites such as

the anterior auditory field of the cortex, the thalamic reticular nucleus, and the limbic system.

### Acoustic Reflex Arc

The **acoustic reflex** was mentioned earlier in this chapter and is addressed in some detail in Chapter 3. The **acoustic reflex arc** has been described in detail (Borg, 1973; Lyons, 1978) and is shown schematically in Fig. 2.40. The afferent (sensory) leg of the reflex arc is the **auditory nerve**, and the efferent (motor) legs are the **seventh cranial (facial) nerve** to the stapedius muscle and the **fifth cranial (trigeminal) nerve** to the tensor tympani. We will trace the pathways for just the **stapedius reflex**, which constitutes the acoustic reflex in humans (see Chap. 3).

The afferent leg of the reflex goes from the stimulated cochlea via the auditory nerve to the ipsilateral VCN. From

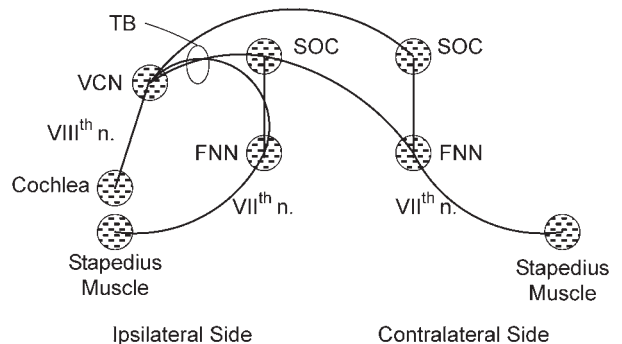


Figure 2.40 Schematic diagram of the crossed and uncrossed acoustic (stapedius) reflex pathways. *Abbreviations:* FNN, facial nerve nucleus; SOC, superior olivary complex; TB, trapezoid body; VCN, ventral cochlear nucleus.

there, second-order neurons pass through the trapezoid body leading to two uncrossed and two crossed pathways. One of the **uncrossed pathways** goes from the VCN to the facial nerve nucleus, from which motor neurons go to the stapedius muscle on the same side. The other uncrossed pathway goes from the VCN to the ipsilateral SOC, from which third-order neurons go to the facial nerve nucleus. From there, motor neurons proceed to the ipsilateral stapedius muscle.

One of the **crossed pathways** goes from the ipsilateral VCN to the ipsilateral SOC, from which third-order neurons cross the midline to the facial nerve nucleus on the opposite side. From there, the facial nerve goes to the stapedius muscle on the side opposite the stimulated ear. The other crossed pathway goes from the ipsilateral VCN to the contralateral SOC, and then to the facial nerve nucleus on that side (opposite to the stimulated cochlea). The facial nerve then proceeds to the stapedius muscle contralateral to the stimulated cochlea.

### Efferent Pathways

As described above, descending efferent fibers enter the inner ear and make contact with the OHCs directly and with the IHCs indirectly via synapses with their associated afferent fibers. These fibers are the cochlear terminations of the **olivocochlear bundle (OCB)**. The OCB is sometimes referred to as *Rasmussen's bundle* because it was originally characterized in 1946 by Rasmussen. Since then, the OCB has been described in considerable detail (e.g., DeVenecia, Liberman, Guinan, and Brown, 2005; Guinan, 1996, 2006; Guinan et al., 1983, 1984; Liberman and Brown, 1986; Luk et al., 1974; Robertson, 1985; Strutz and Spatz, 1980; Warr, 1978, 1992).

The general organization of the olivocochlear pathway system is depicted in Fig. 2.41. It is made up of neurons derived from the regions of the **medial superior olive (MSO)** and the **lateral superior olive (LSO)** on both sides. The neurons of the OCB enter the inner ear along with the vestibular branch of the auditory nerve, and then enter the cochlea to distribute themselves to the inner and outer hair cells.

Figure 2.40 shows that we are really dealing with two efferent systems rather than one. The **lateral olivocochlear (LOC) system**, or **uncrossed olivocochlear bundle (UOCB)**, is made up of efferent fibers derived from the vicinity of the lateral superior olive. These unmyelinated, small diameter fibers project to the ipsilateral cochlea, where they synapse with the afferents of the inner hair cells. A comparably small number of myelinated fibers from the ipsilateral medial superior olive go to outer hair cells on the same side.

The **medial olivocochlear (MOC) system** or **crossed olivocochlear bundle (COCB)** involves large-diameter, myelinated neurons originating from the vicinity of the medial superior olive. These cross the midline of the brainstem at the level of the fourth ventricle and eventually terminate directly upon the outer hair cells on the opposite side. (A few unmyelinated fibers from the lateral superior olivary area also cross the midline, going to the contralateral inner hair cells.)

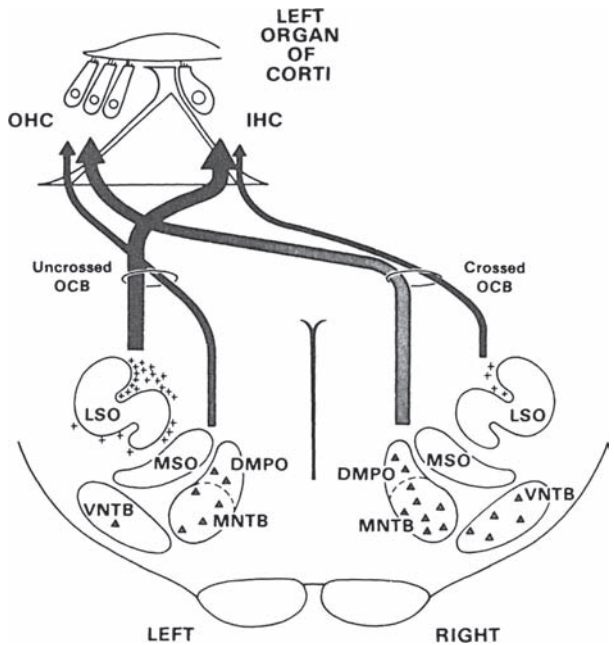


Figure 2.41 Schematic representation of the crossed and uncrossed olivocochlear bundles. As suggested by the wider lines, the crossed OCB goes mainly from the MSO to the contralateral OHCs, and the uncrossed OCB goes mainly from the LSO to the ipsilateral IHCs. *Abbreviations:* OCB, olivocochlear bundle; LSO, lateral superior olive; MSO, medial superior olive; DMPO, dorsal periolivary nucleus; MNTB, medial nucleus of trapezoid body; VNTB, ventral nucleus of trapezoid body; triangles, large OCB neurons; crosses, small OCB neurons. *Source:* Adapted from Warr (1978), *The Olivocochlear bundle: Its origins and terminations in the cat*, in *Evoked Electrical Activity in the Auditory Nervous System*, R.E. Naunton and C. Fernandez (eds.), Copyright © 1978 by Academic Press.

In addition to the olivocochlear systems, other efferent connections have been demonstrated coming from the inferior colliculus, the nuclei of the lateral lemniscus, and possibly the cerebellum (e.g., Harrison and Howe, 1974; Huffman and Henson, 1990; Rasmussen, 1967), as well as descending fibers that may also provide cortical feedback and/or control over lower centers including, for example, corticofugal pathways to the inferior colliculus and to the medial geniculate (e.g., Anderson et al., 1980; Diamond et al., 1969; Oliver and Huerta, 1992; Rockel and Jones, 1973a, 1973b; Winer, 1992; Winer et al., 1977).

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