8

BASIC ANATOMY OF THE HEARING SYSTEM

Sumalai Maroonroge
Diana C. Emanuel
Tomasz R. Letowski

Hearing System

Hearing is the sense by which biological systems are aware of the surrounding acoustic environment and perceive sound (see Chapter 11, *Auditory Perception and Cognitive Performance*). It is the primary sense by which various species respond to limited range of physical vibrations in the atmosphere. Human hearing allows for the perception of speech and other acoustic events and for 360° spatial detection and localization of sound sources. However, human hearing is sensitive to a limited range of sound intensities and frequencies and only allows for full 360° of spatial orientation when the listener is not obstructed by any proximal acoustic barriers. Therefore, in order for audio head- and helmet- mounted displays (HMDs) to take full advantage of the wearer's hearing capabilities, HMD designers and the acquisition corps need to have a solid understanding of the anatomy and physiology of human hearing.

The act or process of hearing is called *audition,* and the anatomical structure processing incoming acoustic stimuli is called the *hearing system* or *auditory system*. The human hearing system consists of two ears, located on the left and right sides of the head, the vestibulocochlear nerve, and the central auditory nervous system (CANS) – consisting of auditory centers in the brain and the connecting pathways in the brainstem. Each ear is additionally divided into three functional parts: the outer (external) ear, the middle ear and the inner (internal) ear. The overall anatomical structure of the human ear and its division in three functional parts are shown in Figure 8-1. (A more detailed but more schematic picture of the ear structures is shown in Figure 8-10). The inner ear contains three parts: the vestibule, semicircular canals, and the cochlea and serves as housing for two sensory organs, specifically, the organ of balance and the organ of hearing. The parts of the organ of balance are contained within the vestibule and the semicircular canals. The organ of hearing, the *organ of Corti*, is located in the cochlea. The adjacent locations of the senses of hearing and balance result in some interactions between the sense of hearing and the sense of balance.

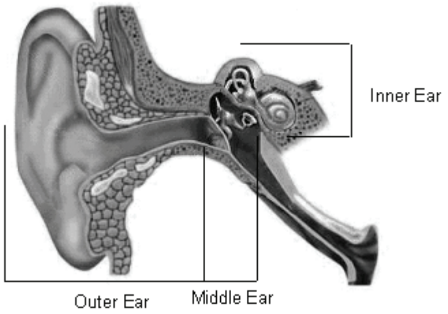

Figure 8-1. Overall structure of the human ear (adapted from http://www.telezdrowie.pl/slysze/english/info.htm).

The structures of the human ear are embedded in the temporal bone of the skull, with only part of the outer ear (the pinna) protruding outside the skull and being visible. The temporal bone is a dense bony structure on either side of the head that forms part of the cranium (cranial vault) around the brain. The *cranium* consist of 8 bones (paired temporal and parietal bones and single frontal, occipital, sphenoid, and ethmoid bones) connected by seams called *sutures.* In addition to the cranium, the skull is comprised of a group of 14 facial bones that make up the facial skeleton. The facial bones include paired nasal, lacrimal, palatine, inferior nasal concha, maxilla, and zygomatic bones; with single mandible and vomer bones. A list of all the main bones of the skull is provided in Table 8-1. The overall structure of the skull and the locations of the main constituent bones of the skull are shown in Figure 8-2. Note that the sphenoid bone appears to be a plate on the side of the skull, but is actually a butterfly-shaped bone that extends the width of the skull from right to left. Only the lateral aspects are visible in the figure.

Table 8-1.
Cranial and facial bones of the human skull
(Henry and Letowski, 2007)

Cranial Bones		Facial Bones	
Single	*Paired*	*Single*	*Paired*
Frontal bone	Parietal bone	Mandible	Maxilla
Occipital bone	Temporal bone	Vomer bone	Palatine bone
Sphenoid bone			Zygomatic bone
Ethmoid bone			Nasal bone
			Lacrimal bone
			(Inferior) nasal concha

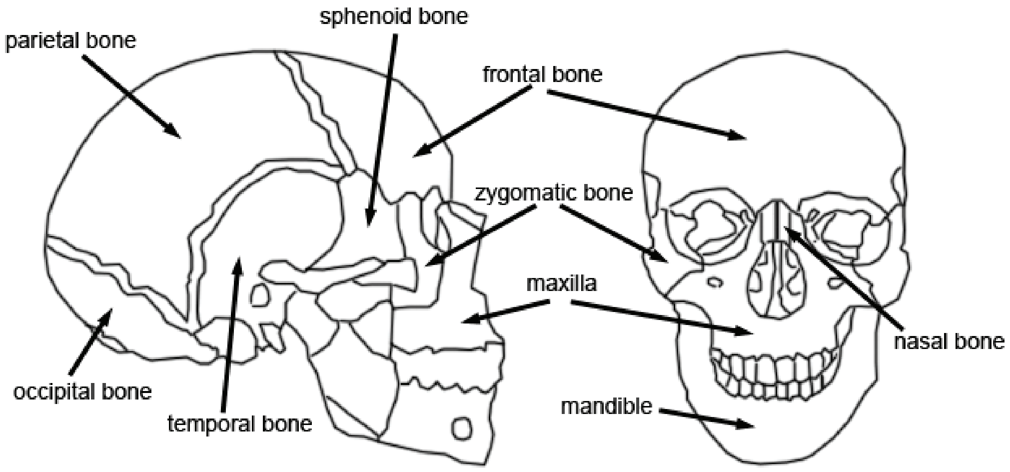

Figure 8-2. Bones of the skull (Howell, Williams and Dix, 1988).

Figure 8-3 shows several important landmarks of the skull for placing bone communication HMDs (see Chapter 5, *Auditory Helmet-Mounted Displays*) including the condyle, mastoid process, forehead, and temple (the bony point above the temple), which are parts of the mandible, temporal bone, frontal bone, and frontal bone again, respectively.

The location of the ear canal in the temporal bone is marked in Figure 8-3 as a small oval in the lower part of the bone. The middle ear and inner ear are located in the petrous portion of the temporal bone, which is a dense core of bone that provides protection for the delicate ear structures. In addition to housing the structures of the ear, the petrous portion of the temporal bone has additional canal, the internal auditory meatus, through which pass the vestibulocochlear (8^{th} cranial) and the facial (7^{th} cranial) nerves. The facial nerve provides sensory and motor innervation to the face.

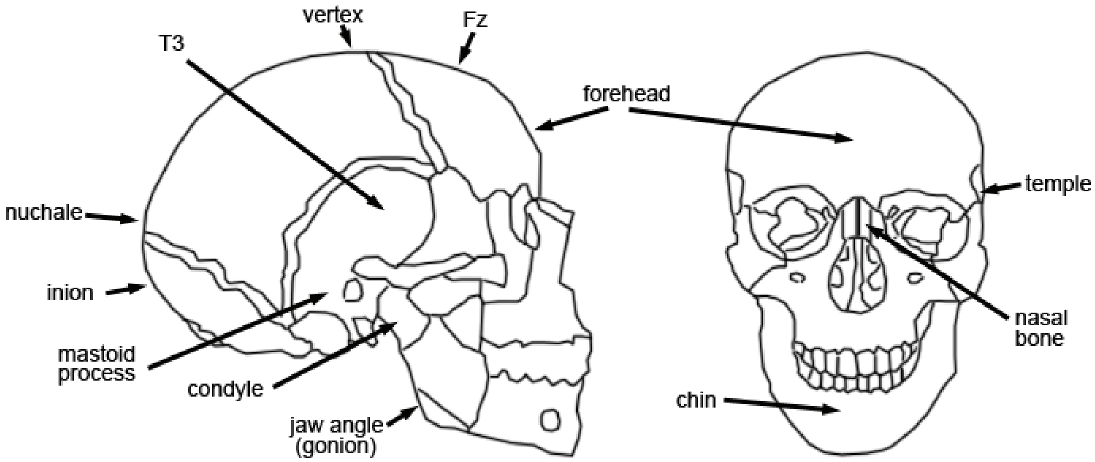

Figure 8-3. Landmark points of the skull used for placing bone conduction vibrators (adapted from (Howell, Williams, and Dix, 1988).

The anterior (front) portion of the temporal bone articulates with the condyle of the mandible, forming the temporomandibular joint (TMJ). The superior (top) portion of the temporal bone is the squamous portion, which is a fan like projection that attaches to the occipital and parietal bones. The posterior (back) portion of the temporal bone is the mastoid portion. The mastoid portion includes a bony protuberance called the mastoid process. The mastoid process is the bony ridge that one can feel on the skull just behind the pinna. The mastoid process is the usual place for attaching bone conduction hearing aids and placing bone conduction vibrators during hearing testing. The condyle, which lies just in front of the visible part of the outer ear, is the very effective location for placing a bone vibrator is speech communication applications (McBride, Tran and Letowski, 2005; 2008).

Outer Ear

The outer ear consists of two major elements: the external flange of the ear (called the pinna) and the ear canal. Both elements are shown in Figure 8-4. The ear canal is terminated by the tympanic membrane (eardrum), which separates the outer ear from the middle ear. The pinna projects from the side of the head at an angle of 25° to 35° (mean value 30°) to the occipital scalp (Glasscock and Shambaugh, 1990; McDonald, 1993; Sclafani and Ranaudo, 2006) and serves as a sound collector. The entrance to the ear canal is located within the pinna, in front of the pinna flap. The ear canal directs sound waves toward the eardrum and protects the eardrum from the external environment (e.g., dust, small flies, and changes in temperature).

Pinna

The pinna (auricle) is an ovoid-shaped structure with an uneven surface filled with numerous grooves and depressions. Humans have two pinnae, one on each side of the head. Similarly to most paired anatomical structures, the two pinnae differ in their specific shape and in their patterns of grooves and pits. In addition, their locations are usually slightly asymmetrical in reference to each other in both vertical and horizontal planes. These differences, together with the fact that acoustic signals are simultaneously received by the two ears, facilitate our ability to localize sounds in space and are responsible for the fact that localization mechanisms are not transferable from one person to another. This is the reason that the Head-Related Transfer Function (see Chapter 11, *Auditory Perception and Cognitive Performance*), of one person cannot be successfully used by another person without some adjustments.

The internal frame of the pinna is composed of a single piece of cartilage that is attached to surrounding tissues and covered with skin. The pinna is innervated by nerve fibers from the great auricular nerve and the auriculotemporal nerve. The blood supply to the pinna is provided by the posterior auricular and superficial temporal arteries. The pinna is connected to the head by ligaments and small muscles. Many species use these muscles to direct the pinna towards incoming sound, but humans lost this ability (although some humans have maintained rudimentary pinna motion ability).

The average length of the pinna is approximately 65 millimeters (mm) (2.6 inches [in]) and the average width is approximately 35 mm (1.4 in). See Table 8-2 for more information about pinnae dimensions. In most adults the width of the pinna is approximately 55% of its length (McDonald, 1993). The main axis of the pinna points upwards with a posterior tilt of 5° to 30° (typical values: 15° to 20°) (McDonald, 1993; Shaw, 1974; Yost and Nielsen, 1977). The highest point or superior aspect (crux) of the pinna is typically even with the brow.

A view of the pinna and its major structures is shown in Figure 8-5. The prominent curved rim is called the helix. The second, internal, ridge is the antihelix, which runs almost parallel to the helix. The helix and antihelix are separated by a narrow curved depression called the scaphoid fossa.

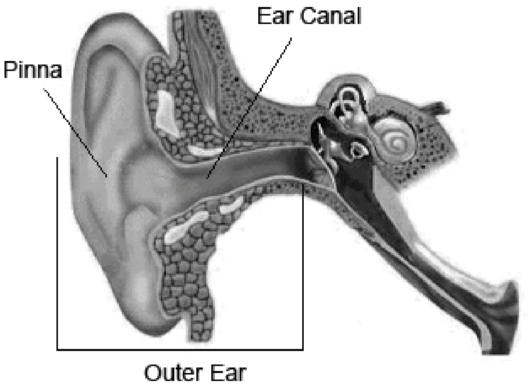

Figure 8-4. The outer ear and its main elements (adapted from http://www.telezdrowie.pl/slysze/english/info.htm).

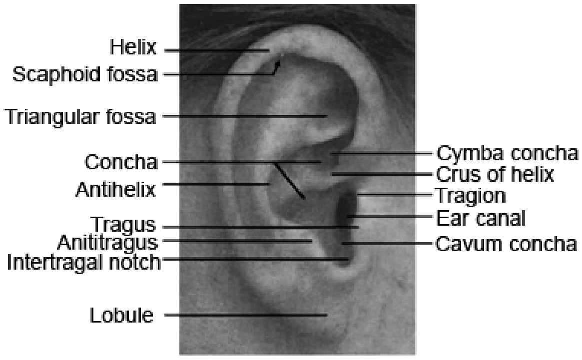

Figure 8-5. The pinna and its major structures (adapted from Rohen and Yokochi, 1983).

The entrance to the ear canal is located in the lower part of the pinna and in the center of the major pinna depression called the concha. The concha is an oval, bowl-like, major depression in the pinna and is divided by the crus of the helix into the cymba concha and cavum concha. The cavum concha surrounds the inlet to the ear canal. The dimensions of the concha vary from person to person but the average diameter of the concha is typically 15 to 20 mm (0.6 to 0.8 in) and its average depth is approximately 13 mm (0.5 in) (Burkhard and Sachs, 1975). The average volume of the concha cavity is approximately 4.0 cm^3 (0.2 in^3) (Teranishi and Shaw, 1968; Zwislocki, 1970; 1971). More detailed information about concha dimension is provided in Table 8-2.

In the front of the entrance to the ear canal, there is a small cartilaginous flap called the tragus. The tragus partially covers the opening of the ear. The notch above the tragus is called the tragion and is frequently used as a point of reference in anatomical measurements. A similar notch located below the tragus and separating the tragus from a second cartilaginous flap, called the antitragus, is the intertragal notch (intertragal incisure). The intertragal notch is used as a reference point for inserting a probe microphone into the ear canal in real-ear measurements (Henry and Letowski, 2007). The distance between the entrance to the ear canal and the intertragal notch is approximately 10 mm (0.4 in) (Hawkins, Alvarez and Houlihan, 1991; Pumford and Sinclair, 2001). At the very bottom of the pinna, below the intertragal notch, there is a large soft flap called the lobule (ear lobe). The lobule does not contain cartilage and is entirely made of fat and skin.

Table 8-2.
Basic average (mean) dimensions of the human ear (pinna).

Dimension	Unit	Male Adult	Female Adult	Source(s)
Ear width (Pinna breath)	mm	37.7 35.5 34.5 29.2 37.0	33.6 33.0	Burkhard and Sachs, 1975 Dreyfus, 1967 Alexander and Laubach, 1968 Algazi et al., 2001 IEC 60318-7, 2009
Ear length (Pinna height)	mm	68.5 63.5 67.0 64.1 66.0	62.4 58.4	Burkhard and Sachs, 1975 Dreyfus, 1967 Alexander and Laubach, 1968 Algazi et al., 2001 IEC 60318-7, 2009
Ear length above tragion	mm	33.0 30.4 30.0	30.7	Burkhard and Sachs, 1975 Dreyfus, 1967 IEC 60318-7, 2009
Ear protrusion distance	mm	22.8 21.0 23.0	20.3	Burkhard and Sachs, 1975 Dreyfus, 1967 IEC 60318-7, 2009
Ear protrusion angle	°	23.3 28.5 20.0	24.9	Burkhard and Sachs, 1975 Algazi et al., 2001 IEC 60318-7, 2009
Ear vertical tilt to the back	°	7.6 24.1 10.0	4.7	Burkhard and Sachs, 1975 Algazi et al., 2001 IEC 60318-7, 2009
Ear vertical tilt to the side	°	3.0 6.0	2.7	Burkhard and Sachs, 1975 IEC 60318-7, 2009
Ear canal offset down	mm	30.3		Algazi et al., 2001
Ear canal offset back	mm	4.6		Algazi et al., 2001
Concha length	mm	27.3 25.9 28.0	25.3	Burkhard and Sachs, 1975 Algazi et al., 2001 IEC 60318-7, 2009
Concha breadth	mm	18.8 15.8 23.0	17.2	Burkhard and Sachs, 1975 Algazi et al., 2001 IEC 60318-7, 2009
Concha depth	mm	12.9 10.2 15.0	12.9	Burkhard and Sachs, 1975 Algazi et al., 2001 IEC 60318-7, 2009
Concha volume	cm^3	4.65	3.94	Burkhard and Sachs, 1975

Note: IEC 60318-7 data refer to a standardized acoustic manikin. See also IEC 60268-7 (2009).

Ear canal

The ear canal (auditory canal; external meatus) is an “S” shaped duct providing an access route for acoustic waves to travel to the tympanic membrane. A general view of the ear canal is shown in Figure 8-4. The outer one third of the ear canal is surrounded by cartilage, whereas the remaining inner two thirds of the canal are surrounded by bone, as the canal enters the temporal bone. The two respective parts of the canal are called the cartilaginous part and the osseous part of the canal. The cartilaginous part is lined with relatively thick layer of skin (0.5 to 1.0 mm [0.02 to 0.04 in] thick) that is continuous with that of the pinnae and contains numerous sebaceous glands, ceruminous (wax) glands, and hair follicles (Lucente, 1995). The cartilaginous part of the ear canal produces cerumen (ear wax), which is comprised of secretions from sebaceous and apocrine glands (Lucente, 1995; Ballachanda, 1995). Cerumen acts to moisturize the skin and, together with hairs, trap dust, debris and other small objects entering the ear canal

The osseous part of the ear canal is covered with relatively thin skin (approximately 0.2 mm [0.01 in] thick) that is continuous with the outer layer of the tympanic membrane (Muller, 2003). There are no hairs or secretion producing glands located in this part of the ear canal (Lucente, 1995). The skin of the ear canal is innervated by the branches of three cranial nerves: the auriculotemporal (mandibular) nerve, the facial nerve, and the vagus nerve.

The outer layer of the skin lining the ear canal and tympanic membrane has lateral migratory properties. The surface cells of the skin move laterally from the tympanic membrane toward the ear canal opening. This property is an active process that enables self-cleaning of the tympanic membrane and the removal of the wax and trapped debris from the inside of the ear canal. The rate of skin cell migration is approximately 100 microns (μm) per day (Muller, 2003).

The average length of an adult ear canal is approximately 25 mm (1.0 in) with a standard deviation of approximately 2 mm (0.2 in) and is approximately 5% longer in males than in females (Alvord and Farmer, 1997; Wever and Lawrence, 1954; Zemlin, 1997; Zwislocki, 1970). The effective acoustic length of the ear canal is approximately 25% larger than its geometrical length due to the "end effect" of the concha and the manner in which the concha is coupled to the ear canal (Teranishi and Shaw, 1968). The canal is oval in shape with an average diameter of 7.0 to 8.0 mm (0.28 to 0.31 in) (Alvord and Farmer, 1997; Békésy, 1932; Zemlin, 1997; Zwislocki, 1970). The shape and cross sectional dimensions of the ear canal change along its length. The oval opening of the canal has average dimensions of 9 mm (0.4 in) by 6.5 mm (0.3 in), and the canal becomes narrower along its length (Shaw, 1974). The cross sectional area of the canal is approximately 0.45 cm^2 (0.07 in^2) at the opening and approximately 0.4 cm^2 (0.06 in^2) in the middle of the canal (Zwislocki, 1970). The final 8 to 10 mm (0.3 to 0.4 in) of the ear canal is slightly tapered and reaches its narrowest point at the isthmus [isthmus (gr.) – passageway], which is located just past the second bend of the ear canal and approximately 4 mm (0.2 in) from the tympanic membrane (Seikel, King, and Drumright, 2000). The tympanic membrane terminates the ear canal at an oblique angle of 45° to 60° in reference to the floor of the canal (Gray, 1918; Stinson and Lawton, 1989; Decraemer, Dirckx and Funnell, 1991; Seikel, King and Drumright, 2000; Sundberg, 2008). This oblique position of the tympanic membrane causes the length of the ear canal to be approximately 6 mm (0.24 in) shorter at its posterior/superior (back/top) portion compared to its anterior/inferior (front/bottom) portion. The cross sectional area of the ear canal in male adults is approximately 10% larger than in female adults (Zwislocki, 1970). The average volume of the canal has a range of approximately 1.0-1.4 cm^3 (0.06 to 0.09 in^3) range (Liu and Chen, 2000; Wever and Lawrence, 1954).

Since the proper selection and fitting of an audio HMD depends on the dimensions of the human head, locations and dimensions of pinnae, and the geometry of the ear canal, the mean values of some of the main dimensions of the pinnae and human head are provided in Tables 8-2 and 8-3, respectively, for reference purposes. The illustration of the extent of each of the main dimensions listed in Table 8-3 is shown in Figure 8-6.

The sources of the values listed in Table 8-3 are large databases or anthropometric studies conducted with large number of participants. For example, the data provided by Burkhard and Sachs (1975) are based on a survey of over 4000 people conducted by Churchill and Truett (1957) and the large set of data accumulated by Dreyfuss (1967). The data for ear dimensions, listed in Table 8-2, are based on a smaller number of measurements compared with data in Table 8-3. These samples include data published by Algazi et al. (2001), which are based on 45 people and data of Burkhard and Sachs (1975) based on 12 male and 12 female adults.

Table 8-3.
Basic average (mean) dimensions of the human head.

Dimension	Unit	Male Adult	Female Adult	Source
Head width (Head breath)	mm	155	147	Burkhard and Sachs, 1975
		152	144	DoD, 2000; IEC 60318-7, 2009
		150		Algazi et al., 2001
		154		ISO 7250-2, 2008
Head length (Head depth)	mm	196	180	Burkhard and Sachs, 1975
		197	187	DoD, 2000
		220		Algazi et al., 2001
		191		IEC 60318-7, 2009
		200	180	ISO 7250-2, 2008
Head height	mm	215		Algazi et al., 2001; IEC 60318-7, 2009
Head height from tragion (point at the notch above tragus)	mm	130	130	Burkhard and Sachs, 1975
Head circumference	mm	570	550	NASA, 1978
		573		Algazi et al., 2001
		576	551	ISO 7250-2, 2008
Menton (chin)-vertex height	mm	232	211	Burkhard and Sachs, 1975
		232	218	DoD, 2000
		224		IEC 60318-7, 2009
Tragion-to-tragion distance (bitragion diameter)	mm	142	135	Burkhard and Sachs, 1975
		145	132	DoD, 2000
		143		IEC 60318-7, 2009
Tragion-to-shoulder distance	mm	188	163	Burkhard and Sachs, 1975
		175		IEC 60318-7, 2009
Tragion-to-wall (behind the head)distance	mm	102	94	Burkhard and Sachs, 1975
		97		IEC 60318-7, 2009
Neck diameter	mm	121	103	Burkhard and Sachs, 1975
		117		Algazi et al., 2001
		113		IEC 60318-7, 2009
Head-torso forward offset	mm	30		Algazi et al., 2001
Shoulder breadth	mm	455	399	Burkhard and Sachs, 1975
		491	431	DoD, 2000
		459		Algazi et al., 2001
		440		IEC 60318-7, 2009
Chest breadth	mm	305	277	Burkhard and Sachs, 1975
		315		Algazi et al., 2001
		282		IEC 60318-7, 2009

Note 1: Burkhard and Sachs (1975) data are median values.
Note 2: Algazi et al. (2001) data are overall means for male and female adults.
Note 3: DOD – U.S. Department of Defense.
Note 4: IEC 60318-7 data refer to a standardized acoustic manikin. See also IEC 60268-7 (2009).
Note 5: ISO 7250-2 data are for the U.S. population

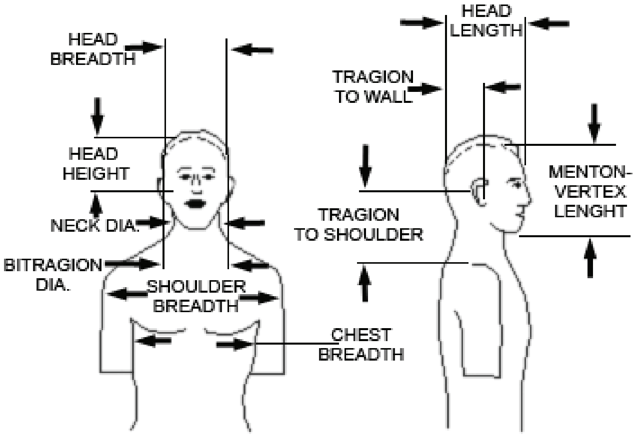

Figure 8-6. Selected anthropometric dimensions of the human head (Burkhard and Sachs, 1975)

Middle Ear

The middle ear is an air-filled cavity called the *tympanic cavity* (tympanum). The walls of the cavity are formed from the temporal bone and the cavity is lined with mucous membrane tissue. The overall volume of the middle ear is approximately 2 cm^3 (0.12 in^3) (Dallos, 1973; Yost and Nielsen, 1977; Zemlin, 1997). The lateral wall of the middle ear contains the tympanic membrane (previously described), and the medial wall is formed by a bony wall that separates the middle ear from the inner ear. This wall contains two membranous windows, called the oval and round windows, which act to anatomically and physiologically connect the middle ear with the inner ear. The air in the middle ear cavity remains just below atmospheric pressure due to the connection between the tympanic cavity and the upper part of throat (nasopharynx) by a narrow duct called the *Eustachian tube* (auditory tube). Within the middle ear cavity are three small bones called the *malleus* (hammer), *incus* (anvil), and *stapes* (stirrup). These bones are collectively called the *ossicles* and form a chain called ossicular chain that connects the tympanic membrane with the oval window. The chain is suspended inside the cavity by middle ear ligaments and two middle ear muscles: the *tensor tympani* and the *stapedius*. The overall structure of the middle ear is shown in the Figure 8-7.

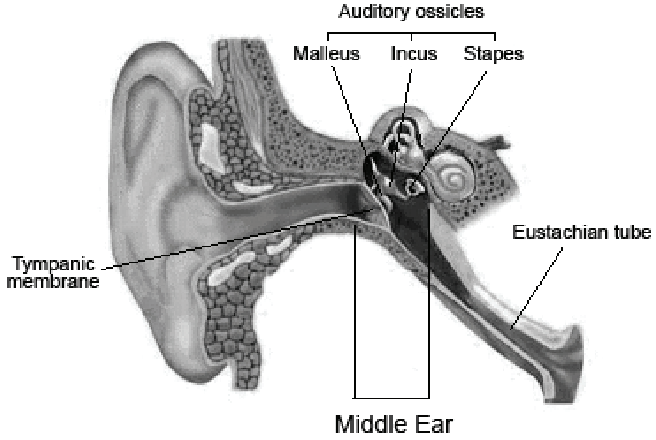

Figure 8-7. The middle ear and its main elements (adapted from http://www.telezdrowie.pl/slysze/english/info.htm).

The tympanic cavity has the shape of a narrow, irregular rectangular box that is narrower in the middle than the edges. A schematic view of the middle ear cavity is shown in Figure 8-8. The largest dimension of the tympanic cavity does not exceed 10 mm (0.4 in). The ossicular chain and middle ear muscles take up most of the space within the cavity. The small empty space above the ossicles is called the *epitympanum recess* (attic). The remaining empty space is referred to as the tympanic *cavity proper*. The superior wall (ceiling) of the tympanic cavity is formed by a thin bone called the *tegmen tympani*, which separates the middle ear from the brain cavity. A small narrow aperture, called the *aditus ad antrum*, located at the top of the posterior (back) wall, connects the middle ear cavity to another small chamber called the *mastoid antrum* (tympanic antrum) that is surrounded by the *mastoid air cells*. The entrance to the Eustachian tube is located in the anterior (front) wall of the middle ear cavity. The oval and round windows of the inner ear form the medial wall of the cavity. The windows are separated by a ridge of bone called the *promontory*. The inferior wall (floor) of the cavity contains the *jugular fossa* that contains the jugular vein. The pulsation of blood in the vein can be a source of ringing noise (tinnitus) in the ear.

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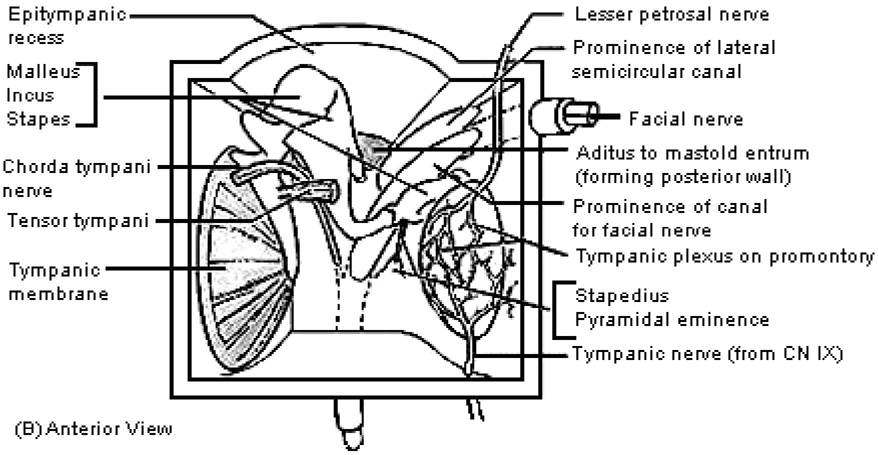

Figure 8-8. A schematic view of the middle ear cavity without the anterior wall (Moore and Dalley, 1999).

The tympanic cavity also contains two middle ear muscles: the tensor tympani muscle and the stapedius muscle. These two muscles are the smallest muscles in the human body, with the tensor tympani being the larger of the two. The tendon of the stapedius muscle emerges from the pyramidal eminence of the posterior (back) wall. The other end of the muscle is connected to the stapes. The *chorda tympani* nerve, a branch of the facial nerve, also emerges from the posterior wall of the cavity. The chorda tympani travels through the middle ear from back to front, joining the lingual nerve and providing taste sensation to part of the tongue. The tendon of the second middle ear muscle, the *tensor tympani*, emerges from the anterior wall of the middle ear and attaches to the malleus bone. A thin plate of anterior bone separates the middle ear from the internal carotid artery (Zemlin, 1997).

Tympanic membrane

The tympanic membrane (eardrum) is a thin, semi-transparent, oval membrane terminating the ear canal. The membrane is shaped like a shallow cone with its tip approximately 1.5 to 2 mm (0.06 to 0.08 in) out towards the middle ear (Alvord and Framer, 1997; Sundberg, 2008). The tip is called the *umbo* and is attached to the tip of *manubrium* ("handle") of the malleus bone (Pickles, 1988). The apex angle of the tympanic membrane is approximately 120° (Fumagalli, 1949). The membrane is attached around most of its circumference to the temporal bone surrounding the ear canal except for the very narrow area called the *notch of Rivinus* (incisura tympanica). The dimensions of the membrane along its two major perpendicular axes are 9 to 10 mm (0.35 to 0.39 in) and 8 to 9 mm (0.31 to 0.35 in) (Gelfand, 1998; Gray, 1918). The total surface area of the tympanic membrane varies from 55 to 90 mm^2 (0.09 to 0.14 in^2) with a mean value of 64 mm^2 (0.10 in^2) (Harris, 1986; Zemlin, 1997). However, due to its conical shape the effective area of the membrane is smaller with a mean value of approximately 55 cm^2 (0.09 in^2) (Seikel, King, and Drumright, 2000; Zemlin, 1997). The membrane is the thinnest at its center and the thickest at its edge. It has an average thickness of approximately 70 µm but can vary from approximately 30 µm to 120 µm (Donaldson and Miller, 1980; Kojo, 1954; Lim, 1970; Wever and Lawrence, 1954). The membrane is composed of four layers of tissue; the outer epithelial layer that is continuous with the skin of the ear canal, two middle fiber layers consisting of radial and concentric fibers and responsible for the stiffness of the membrane, and the inner mucus layer that is continuous with the lining of the middle ear cavity. The external layer of the membrane is innervated by the auriculotemporal nerve. The average mass of the tympanic membrane is approximately 14 milligrams (mg) (0.0005 ounces [oz]) (Lee, 2009; Shennib and Urso, 2000).

The surface of the membrane does not have a uniform stiffness and can be divided into two main regions that differ greatly in their stiffness: a small lax triangular area located at the top of the membrane called the *pars flaccida* (also Shrapnell's membrane) and the much larger and stiffer portion called the *pars tensa.* The function of the pars flaccida is to compensate for small air pressure changes between the middle and outer ear and to allow the tympanic membrane to work like a piston rather than a membrane that is fixed at its circumference (Gray, 1918). Only the pars tensa is involved in the transmission of acoustic energy from the outer ear to the middle ear and therefore the effective area of the tympanic membrane is smaller than the overall area. The modulus of elasticity[1] (Young's modulus) for the tympanic membrane at its center is approximately 0.02-0.03 GPa (Békésy, 1949; Decraemer, Maes, and VanHuyse, 1980).

Ossicular chain

The ossicular chain connects the tympanic membrane with the membrane covering the oval window. The primary purpose of the ossicles and supporting muscles is to transfer sound energy from the tympanic membrane to the inner ear while shielding the inner ear from excessive harmful noise. A diagram of the ossicular chain together with the supporting middle ear muscles is shown in Figure 8-9.

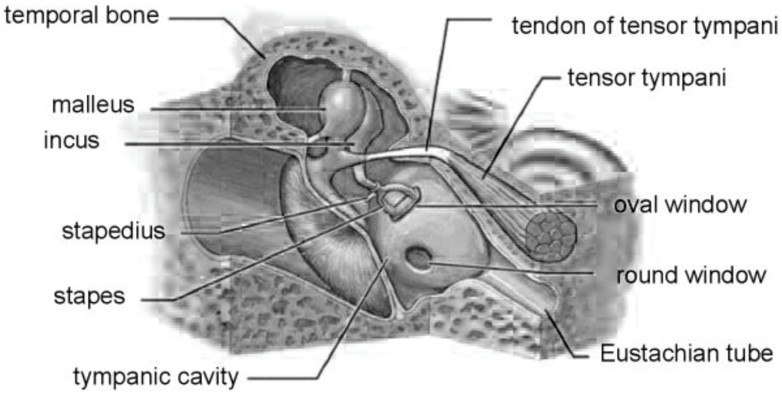

Figure 8-9. The middle ear space and ossicle chain. Petrous part of the temporal bone. (http://www.sfu.ca/ ~saunders/l33098/Ear.f/midear.html).

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[1] The modulus of elasticity (also known as Young's modulus [E]) is a measure of stiffness of an elastic material. The common unit of elasticity is the *Pascal*, a unit of pressure equal to 1 Newton per square meter; the unit *GPa* is a gigapascal; 1 GPa = 145,038 pounds per square inch.

The ossicles are the smallest bones in the human body. The malleus, the largest of the three, is approximately 8 to 9 mm (0.31 to 0.35 in) in length, while the stapes, the smallest human bone, is approximately 3 mm (0.12 in) long (Hall and Mueller, 1997; Wever and Lawrence, 1954). The incus is approximately 5 to 7 mm (0.20 to 0.28 in) long. Their respective weights are approximately 25, 3 and 28 mg (0.00088, 0.00011 and 0.00099 oz) (Yost and Nielsen, 1977). The maleus is the first bone in the ossicular chain and the largest of its three processes, the manubrium (the handle), is firmly attached to the tympanic membrane. They both move in unison. The opposite end of the malleus, called the head, is attached to the second bone in the chain, the incus. The incus consists of a body and two processes. The body of the incus connects to the head of the malleus while the longer of the two projections, the lenticular process, connects with the final bone in the chain, the stapes. The shorter projection is connected by a ligament to the back (posterior) wall of the tympanic cavity. The body of the stapes is divided into four parts: a head, a neck, two arms and the footplate. The footplate and the arms form a characteristic shape of the stirrup. The bottom surface of the footplate is tightly attached to the membrane covering the oval window.

The ossicles move in response to the acoustic pressure impinging on the tympanic membrane and in response to the actions of two middle ear muscles: the tensor tympani muscle and the stapedius muscle. The muscles contractions reduce the level of very intense sounds transmitted to the inner ear. The tensor tympani muscle is attached to the manubrium of malleus (see Figure 8-8) and its contraction pulls the handle of the malleus inward and regulates the tension on the tympanic membrane (Gray, 1918; Rodriguez-Velasquez et al. 1998). The stapedius muscle is connected to the stapes and its contraction pulls the stapes in an inferior and lateral (away from the oval window) direction which reduces the range of motion of the stapes (Djupesland and Zwislocki, 1971; Zwislocki, 2002).

Eustachian tube

The Eustachian tube is a thin tube, which connects the middle ear with the nose and throat (Figure 8-6). The tube is approximately 35 to 45 mm (1.4 to 1.8 in) long and it travels downward and inward from the middle ear to the nasopharynx (upper throat). At its upper end, the tube is narrow and surrounded by bone. Nearer the pharynx it widens and becomes cartilaginous.

The Eustachian tube is normally closed, opening only during swallowing and yawning. It is responsible for maintaining the air pressure within the middle ear at approximately ambient pressure. Similar pressure on both sides of tympanic membrane ensures that the tympanic membrane can vibrate maximally when struck by sound waves arriving from the ear canal.

Inner Ear

The inner ear is the final and the most complex part of the ear. It occupies a small bony cavity called the *bony labyrinth* (osseous labyrinth) that is located directly behind the medial wall of the middle ear. The inner ear consists of three main anatomical elements: the *semicircular canals*, the *vestibule*, and the *cochlea*. The structure and main elements of the inner ear are shown in Figure 8-10.

The bony labyrinth of the inner ear has a volume of approximately 2 cm^3 and is lined by the *membranous labyrinth* that closely follows the shape of the bony labyrinth (Buckingham and Valvassordi, 2001). The blood supply to the membranous labyrinth is provided by various small blood vessels extending from the *labyrinthine artery*.

The space between the bony labyrinth and the membranous labyrinth is filled with incompressible body fluid called *perilymph*. The perilymph is high in sodium but low in potassium resembling in its chemical composition in the blood and the cerebrospinal fluid surrounding the brain. The space inside the membranous labyrinth is filled with another incompressible body fluid called *endolymph*. Endolymph is low in sodium but high in potassium and chemically resembles the intercellular fluid found inside cells in the body. The differences in the chemical composition of the perilymph and endolymph create an electric potential difference that like a battery, sustains the physiological activities of the sensory organs located in the inner ear.

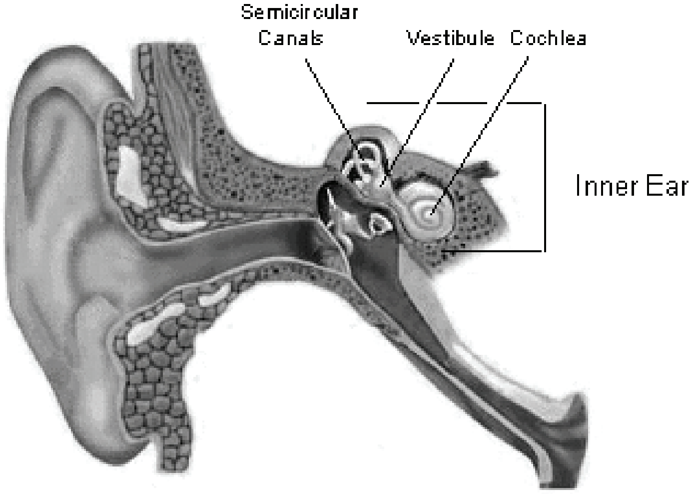

Figure 8-10. The inner ear and its main elements (adapted from [http://www.telezdrowie.pl/ slysze/ english/info.htm).

Functionally, the inner ear consists of two major elements: the *cochlea* and the *vestibular system* (comprising the utricle and saccule of the vestibule and the three semicircular canals). The cochlea contains the organ of hearing (organ of Corti) while the vestibular system contains five balance organs: two maculae (utricular macula and secular macula) and three cristae ampullares (one in each of the three semicircular canals). The cochlea and the semicircular canals are located at the two ends of the inner ear, while the utricle and saccule are parts of the centrally-located vestibule. The oval window is located on the wall of the vestibule and the round window is located at the base of the cochlea. The locations of the windows and the other major parts of the inner ear are shown schematically in Figure 8-11.

Two vary narrow channels; the *vestibular aqueduct* and the *cochlear aqueduct* (not shown in Figure 8-11); connect the inner ear with the cranial cavity surrounding the brain. At their narrowest points, the vestibular aqueduct and the cochlear aqueduct do not normally exceed 0.8 mm (0.03 in) and 0.15 mm (0.006 in) in diameter, respectively. Both aqueducts seem to have little effect on normal ossicular transmission of sound for frequencies above 20 Hertz (Hz) (see, for example, Gopen, Rosowski and Merchant [1997]) and their exact function is still unknown.

Cochlea

The cochlea is a coiled structure that resembles the snail and extends anteriolaterally from the vestibule. Its structural base is the bony *spiral lamina,* which makes 2½ to 2¾ turns around the bony core of the cochlea called the *modiolus*. The external diameter of the cochlea varies from approximately 9 mm (0.35 in) at its base to approximately 5 mm (0.20 in) at its apex (top) and its uncoiled length is 32 to 35 mm (1.25 to 1.38 in). The cochlea is divided along its length into three parallel channels: the *scala vestibuli*, *scala media*, and *scala tympani*. The scala vestibuli and scala tympani are parts of the bony labyrinth whereas the scala media is a part of the membranous labyrinth. The inside of the cochlea is shown in Figure 8-12.

The scala vestibuli and scala tympani are connected at the apex (top) of the cochlea through a small opening called the *helicotrema*. At the base of the cochlea, the scala vestibuli joins the vestibule. The scala vestibule is terminated at its base by the oval window, the *fenestra ovalis,* while scala media terminates at the round window,

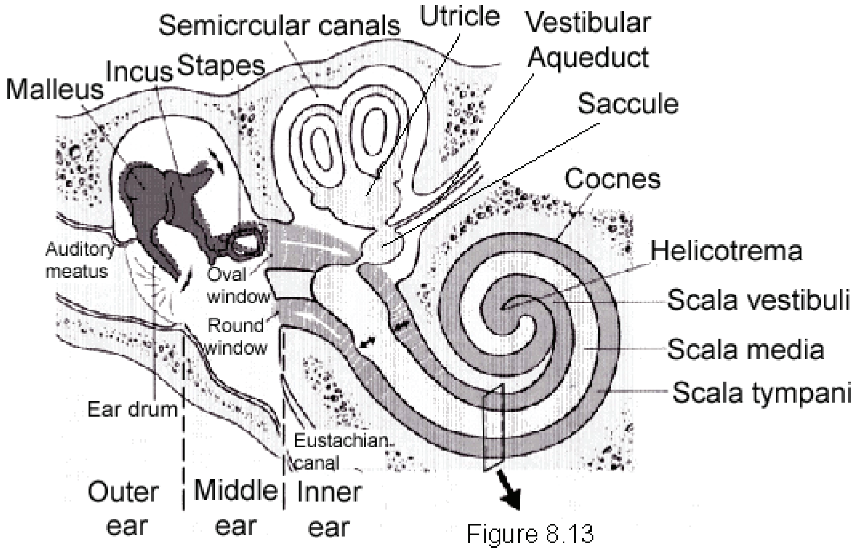

Figure 8-11. A schematic view of the main structures of the inner ear (adapted from Despopoulos and Silbernagl, 1991).

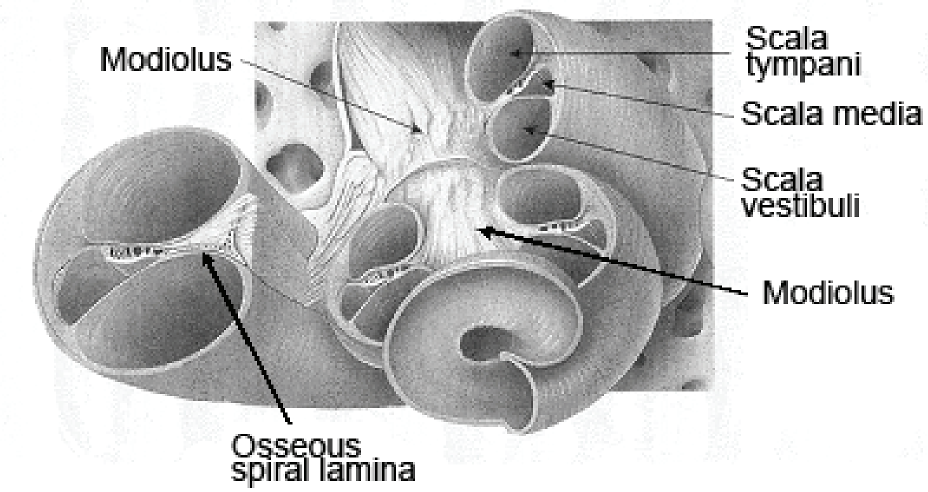

Figure 8-12. View of the cochlea (adapted from Emanuel and Letowski, 2009).

the *fenestra rotunda*. The membrane of the oval window has a surface area of 3.2 to 3.5 mm^2, is completely covered by the footplate of the stapes, and is sealed in the bony opening by the annular ligament. The round window has a surface area of approximately 2 mm^2 and is located inferior and anterior to the oval window in the wall between the middle ear and inner ear and serves as a pressure valve between the two scalae. When an acoustic stimulus causes mechanical vibration of the stapes footplate this movement is translated to the membrane of the oval window. The membrane pushes back and forth on the perilymph of the scala vestibuli and through the helicotrema, the perilymph of the scala tympani. This motion results in alternating outward and inward movement of the membrane of the round window. The membrane bulges outward as the fluid moves from the scala vestibuli to the scala tympani and bulges inward as the fluid moves from the scala tympani to the scala vestibuli.

The central most duct of the cochlea is the membranous scala media (cochlear duct). This duct separates the scala tympani and scala vestibuli. The border between the scala media and the scala vestibuli is *Reissner's membrane* and the border between the scala media and the scala tympani is the *basilar membrane.* Reissner's membrane (vestibular membrane) is attached to the osseous spiral lamina and projects obliquely from it to the outer wall of the cochlea forming a roof of the scala media. Together, the basilar and Reissner membranes would make the scala media into a closed tube if not for the *ductus reunions,* a tiny opening at its base that connects it to the saccule (Figure 8-11). .

The basilar membrane forms the floor of the scala media. The membrane is anchored to the spiral lamina on one end and to the spiral ligament on the other end. When uncoiled, the membrane has an approximate length of 32 to 35 mm (1.25 to 1.38 in), practically the same as the whole cochlea. Blood vessels and nerve fibers supporting the cochlea enter the cochlea through the modiolus and spiral lamina.

The spiral lamina is narrower at the apex of the cochlea and wider at the base. Conversely, the basilar membrane is wider, thicker and more flaccid at the apex and narrower, thinner, and stiffer at the base. These factors affect the vibrational properties of the basilar membrane, which responds to low frequency vibrations at the apex and high frequency vibrations at the base of the cochlea.

The organ of hearing (organ of Corti) is located primarily on the basilar membrane, with a small segment projecting onto the spiral lamina. The organ of Corti is made up of sensory cells (hair cells) and supporting cells. A schematic cross section of the cochlea showing the content of the scala media and the structure of the organ of Corti are shown in Figure 8-13.

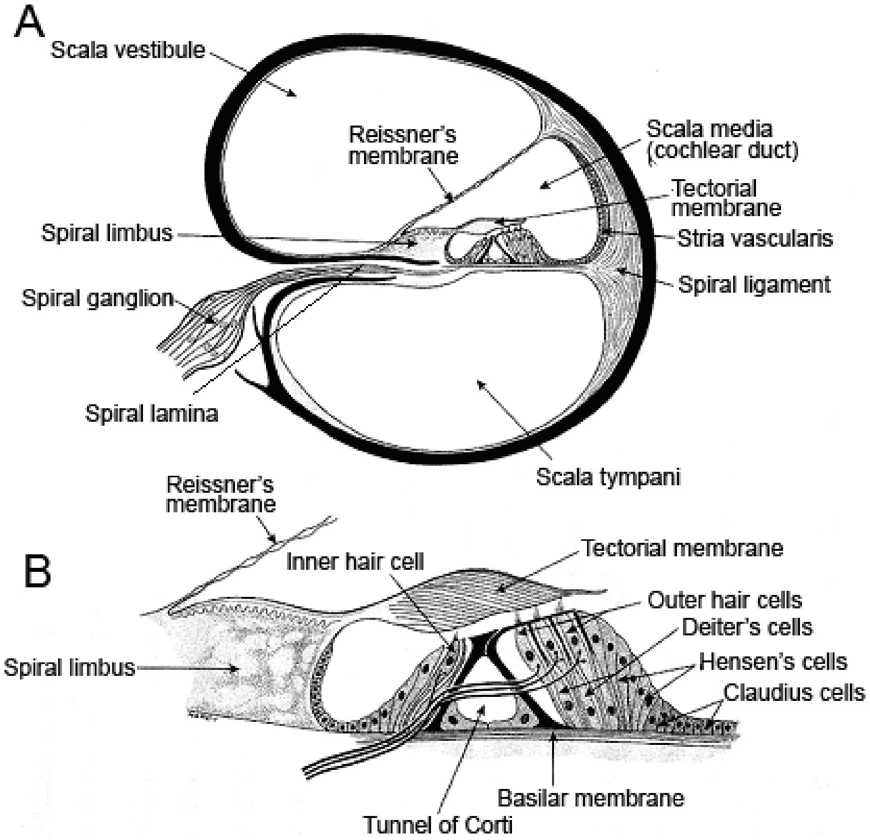

Figure 8-13. Cross section of the cochlea (A) and the structure of the organ of Corti (B) (Emanuel and Letowski, 2009).

Organ of Corti

The organ of Corti converts the mechanical vibrations of the basilar membrane into neural impulses that then travel through the auditory nerve and brainstem to the brain. The organ is composed of sensory cells, called *hair cells*, and several types of supporting cells distributed along the length and width of the basilar membrane. The arrangement of the sensory cells and supporting cells on the basilar membrane is shown in Figure 8-13B. The fibers of the auditory nerves travel from the organ of Corti through a system of small perforations in the spiral lamina collectively called *habenula perforata* that start at the tympanic edge of the spiral lamina and continue further through it. From habenula perforata, nerve fibers travel through a channel in the center of the modiolus (Rosenthal's canal), exit the base of the cochlea, and join vestibular nerve fibers to form the vestibulocochlear nerve.

There are two types of hair cells in the organ of Corti: the inner hair cells (IHCs) and the outer hair cells (OHCs). They are shown in Figure 8-14. Each hair cell has a number of small hair-like projections called *stereocilia* (cilia) extending from the top of the cell. The group of stereocilia at the top of a hair cell is called a *stereocilia bundle*. The stereocilia bundle of each hair cell is organized in several rows forming either a "W" or "V" pattern for OHCs and shallow "U" pattern for IHCs. Stereocilia in each row have graduated heights (like stair steps) and their tips are connected together by thin fibers called *tip links*. Each type of hair cell in the ear is connected to the nervous system by both afferent (ascending) and efferent (descending) nerve endings, but the number and function of these types of connections varies between IHCs and OHCs.

There are altogether approximately 3500 IHCs and approximately 12,000 OHCs distributed along each basilar membrane (thus, each ear contains between 15,000 and 16,000 hair cells). The IHCs are shaped like a flask and form a single row of cells supported by the spiral lamina. The OHCs have a cylindrical shape with a diameter of approximately 9 µm and are organized into three rows located farther away from the spiral lamina. The groups of IHCs and OHCs are separated by two rods (pillars) of Corti, which structurally support the organ of Corti. The inner rod rests on the spiral lamina while the outer rod is attached to the basilar membrane. The rods are attached at their tops and more widely separated at the base, forming a triangular shape called the *tunnel of Corti*. The tunnel is filled with the *cortilymph fluid* that has similar properties to the perilymph fluid found in the bony labyrinth. The tops of the hair cells and supporting cells of the organ of Corti are tightly connected together at their tips to form a continuous layer called the *reticular lamina.* The reticular lamina isolates all of the organ of Corti from the endolymph of the scala media except for stereocilia which project through the reticular lamina into the endolymph.

The OHCs are held in position by the outer rod of Corti on one side and by Deiters cells on the other side. Each Deiters cell holds an OHC at the bottom and through long projections called *phalangeal processes* from above. The middle part of an OHC is not firmly supported and is surrounded by a perilymph-filled space called the *space of Nuel*.

Next to the Deiters cells, moving towards the outer end of the cochlea, there are several groups of supporting cells, called Hensen cells, Claudius cells, outer spiral sulcus cells, and Boettcher cells. Several of these cells are shown in Figure 8-13B. Lateral to these support cells is the *Stria vascularis*, a highly vascular organ attached to the outer surface of the scala media. Stria vascularis recycles potassium and produces endolymph for the scala media, thus maintaining the endocochlear potential (battery) of the inner ear.

The IHCs are structurally supported by the inner rod of Corti on one side and by inner sulcus and pharyngeal cells on the other (Lim, 1986). The inner sulcus cells occupy the region extending from IHCs toward the spiral limbus. The spiral limbus projects from the spiral lamina towards the organ of Corti and provides the attachment point for the *tectorial membrane*. The tectorial membrane is a gelatinous membrane extending above the organ of Corti from the upper surface of the spiral limbus. The largest stereocilia of the OHCs make contact with the tectorial membrane, and this connection is part of the mechanism that leads to the neural responses of the organ of Corti. The basic characteristics of the OHCs and the IHCs are summarized in Table 8-4.

Vestibular system

The vestibular system groups together make up the peripheral organs of balance. The bony structures include three semicircular canals and the vestibule. Within the bony structure, the three semicircular canals contain the three membranous semicircular ducts and the vestibule contains the utricle and saccule. In evolutionary terms, the organs of balance are much older than the organ of hearing, which actually evolved from them (Zemlin, 1997). The arrangement of the components of the vestibular system is shown in Figure 8-11.

Table 8-4.
Summary of the basic characteristics of OHCs and IHCs.

Characteristic	Outer Hair Cells	Inner Hair Cells
Number of hair cells	12,000	3500
Location of hair cells	Further from modiolus	Nearer modiolus
Number of rows	Three to four	One
Shape of hair cells	Cylindrical shape	Flask shape
Number of rows of cilia	6-7 rows per cell	2-4 rows per cell
Stereocilia arrangement	“W” or “V” shape	Shallow “U” shape
Length of stereocilia	Longer and thinner	Shorter and fatter Length of stereocilia increases along the basilar membrane and varies within a single cell
Cell body restriction	Largest cilia contact the tectorial membrane	Cilia are free at the upper end and not in contact with any structure
Motility	Motile	Not motile
Efferent innervation	80% of the efferent fibers terminate directly at the cell bodies of the hair cells Connect to efferent fibers from the medial superior olive Efferent fibers synapse on the base of the hair cell	20% of the efferent fibers synapse with the afferent fibers on the hair cells Connect to efferent fibers from the lateral superior olive Efferent fibers synapse on afferent nerve but not the cell body
Afferent innervation	One afferent fiber supplies multiple hair cells 5% of the afferent fibers supply the hair cells	8-10 afferent fibers supply a single inner hair cell 95% of the afferent fibers supply the hair cells

The three semicircular canals are hoop-shaped structures connected at both ends to the vestibule. One of the ends is almost twice as wide as the other and is called the *ampulla*. The canals are perpendicular to each other and are called the horizontal (lateral), the anterior (superior), and the posterior (inferior) semicircular canal. The horizontal canal is located not exactly horizontally but forms a 30° angle relative to the horizon. The spatial arrangement of the canals is shown in Figure 8-15. Each semicircular canal is sensitive to head motion in the plane of that canal. The canals also form bilateral differential pairs between the ears (e.g., right anterior with left posterior which have their hair cells aligned oppositely). Rotation in one plane will be excitatory to one canal and inhibitory to the other.

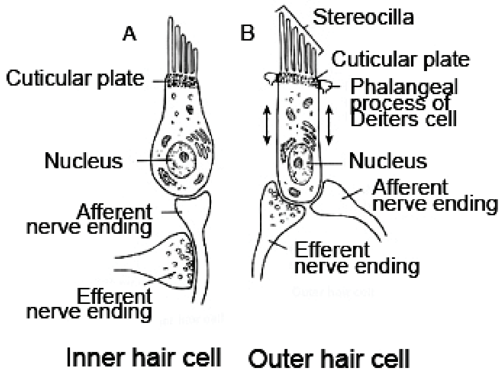

Figure 8-14. Shape and structure of the inner (A) and outer (B) hair cells (Emanuel and Letowski, 2009).

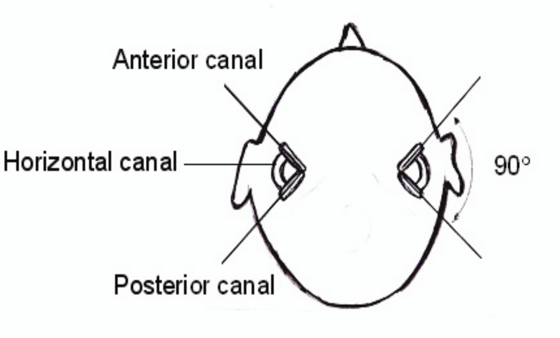

Figure 8-15. Spatial arrangement of the semicircular canals.

The semicircular canals are filled with perilymph and the semicircular ducts are filled with endolymph. The ampulla (bulge) of each canal contains the *crista ampulliaris*, a saddle-shaped, raised section of wall that is populated with the hair cells whose stereocilia respond to angular acceleration. The stereocilia of the semicircular canals are embedded in a gelatinous mass called a *cupula* that is similar in function to the tectorial membrane of the organ of Corti, that is, its motion bends the hair cells, which then creates a neural impulse.

While the sensory organs in the semicircular canals respond to angular accelaration of the head, two other organs of balance, the sense organs within the utricle and the saccule, respond to gravity and linear acceleration in horizontal (utricle) and vertical (saccule) directions. The sense organs within the utricle and saccule are the maculae. They occupy the concave spaces at the bottom of the utricle and the saccule and contain tiny pieces of calcium carbonate, called *otoliths* (ear stones) or otoconia (ear dust), which are embedded into a gelatinous membrane (*otolithic membrane*) into which the stereocilia of the maculae project. Since the otoliths are quite numerous in the otolithic membrane and they are heavier then the surrounding fluid, the membrane gets displaced towards the Earth during head tilting (due to gravity) and away from the source of motion during linear acceleration (due to inertia); thus, head motions are translated by stereocilia deflection into neural impulses.

There are two types of hair cells in the semicircular canals and the vestibule. Type I hair cells are flask-shaped cells while type II hair cells are cylinder-shaped cells. Type I and type II hair cells are very similar in their structure and innervation to the inner hair cells and the outer hair cells of the organ of Corti, respectively. Each hair cell in the semicircular canals has 50 to 100 small stereocilia and a single larger cilium called a *kinocilium,* which only exists in rudimentary form in the hair cells of the cochlea. The stereocilia are arranged by length, with the longest stereocilia located close to the kinocilium, and are all connected by tip links. Movement of the stereocilia hair bundle toward the kinocilium causes a depolarizing (excitatory) sensory response whereas movement away from the kinocilium causes a hyperpolarization (inhibitory) sensory response.

Bone Conduction System

The inner ear receives mechanical vibrations and converts them into neural impulses by the organ of Corti. As such it can be stimulated by sounds transmitted through the system of outer and middle ear <u>or</u> by skull vibrations. The first mode of stimulation is called air conduction, while the second mode is referred to as bone conduction.

The anatomical system responsible for transmitting skull vibrations to the organ of Corti is called the bond conduction system.

The bone conduction system can be stimulated by either sound waves impinging on the human head or by delivering a vibratory signal by means of a mechanical driver (vibrator) coupled to the head. In the former case, the resulting stimulation is approximately 1000 times (60 decibels [dB]) weaker than the simultaneous air conduction stimulation. This is due to the air-bone mismatch when sound tries to enter the bones of the skull (Chapter 9, *Auditory Function*). Vibration of the whole head may also cause distractive interference between vibrations delivered to various parts of the skull. Therefore, such stimulation only has practical meaning in the case of people wearing hearing protectors or with severe conductive hearing loss (Henry and Letowski, 2007). In the case of people wearing audio HMDs (Chapter 5, *Auditory Helmet-Mounted Displays*) or heavily sound-attenuating head gear, even though their air conduction pathways may be completely blocked, they may still hear very intense sounds, such as explosions, jet engine sounds, pile driver impact sounds, etc. due to the stimulation received through bone conduction.

When the vibrations are delivered directly to the head by a mechanical driver, the driver-bone is much smaller than the air-bone mismatch and the person may hear even very weak vibrations of the driver. Thus, this mode of stimulation can be effectively used for speech communication, human-robot interaction, and delivery of tactical signals during military operations.

In order to understand the potential applications and limitations of bone conduction hearing it is necessary to understand the basic elements of the human head and how they interact with one another. The typical weight of the human head is approximately 3.5 kg and the basic dimensions of the male and female heads are given in Table 8-3. The head is a complex structure made of bones, cartilage, several types of soft tissue, and fluids (e.g., cerebrospinal fluid), which differ in their mechanical properties. These different forms of matter transmit sound with different speeds and with various degrees of attenuation. Densities for select components of the head together with their associated speeds of sound transmission are listed in Table 8-5. According to Evans and Lebow (1951) and Sauren and Classens (1993) the average density of the bones of the skull is 1412 kg/m^3, the Young modulus is 6.5 x 10^9 N/m^2, and the Poisson ratio[2] is 0.22. All these values, however, are highly dependent on the amount of water in the bones and other tissue and the boundary conditions. The more dry and less constrained the bone is, the higher the speed of sound through the bone. In addition, solid matter, like the bone, can simultaneously propagate longitudinal, transverse (traveling), and surface waves that have different speeds and can interact with one another.

The bones of the skull are listed in Table 8-1 and their arrangement is shown in Figure 8-2. The manner in which the skull and associated tissue respond to mechanical stimulation depends on the point of stimulation and the frequency of the signal. Two typical driving points described in the literature are the mastoid process and the forehead. The distance from the mastoid process to the cochlea is approximately 30 mm (1.2 in) and is the shortest distance between the cochlea and the head periphery (Tonndorf and Jahn, 1981). The main stimulation pathway from the mastoid process lies wholly within the respective temporal bone, which results in relatively low attenuation of the initial stimulus. In addition, the direction of this stimulation is the same as that of the air conduction pathway, which causes elements of the latter pathway to also become excited by bone stimulation.

The forehead is the relatively flat surface of the frontal bone, which is the largest bone of the skull. It is a fairly symmetrical and deeply extended bone that can easily transfer its vibration to many other bones of the skull. Another effective bone conduction pathway in the skull is from the condyle of the mandible (jaw bone), which is located on the side of the head just in front of the entrance to the ear canal. Stimulation of condyle activates bones and cartilage surrounding the ear canal and tympanic cavity creates a secondary pathway through the air conduction system even more effectively than stimulation at the mastoid process. The most common excitation points for bone conduction communication are shown in Figure 8-3.

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[2] Poisson's ratio is the ratio of the relative contraction strain, or transverse strain (normal to the applied load), divided by the relative extension strain, or axial strain (in the direction of the applied load).

Table 8-5.
Material components of the human head with their densities and corresponding speeds of sound transmission.
(O'Brien and Liu, 2005)

Material	Speed of Sound (m/s)	Density (kg/m^3)
Air	340	1.2
Water	1500	1000
Soft Tissues	1520-1580	980-1010
Lipid-based tissues	1400-1490	920-940
Collagen-based tissues	1600-1700	1020-1100
Blood	1580	1040-1090
Brain – grey	1532-1550	1039
Brain – white		1043
Skull – compact inner and outer tables	2600-3100	1900

Depending on the frequency of stimulation, the skull has several modes of vibration that differ in the phase relationship between the vibrations at different locations on the skull. At low frequencies, e.g. 200 Hz, the skull driven at the forehead location moves as a whole in a back and forth pattern (Bekesy, 1932). This type of vibration is called inertial vibration and its corresponding mode of vibration is called the inertial mode. At higher frequencies, e.g., 800 Hz, the direction of vibration remains the same, but the front and the back of the skull vibrate 180° out-of-phase. Vibration where different parts of the skull vibrate out-of-phase is referred to as compressional vibration. Out-of-phase vibration of the front and back of the head is called the first compressional mode. More complex compressional modes are elicited at even higher frequencies. Vibration patterns for the inertial and first two compressional modes of vibration are illustrated in Figure 8-16. A more detailed discussion of how different points and frequencies of stimulation affect bone conduction hearing is included in Chapter 9, *Auditory Function*.

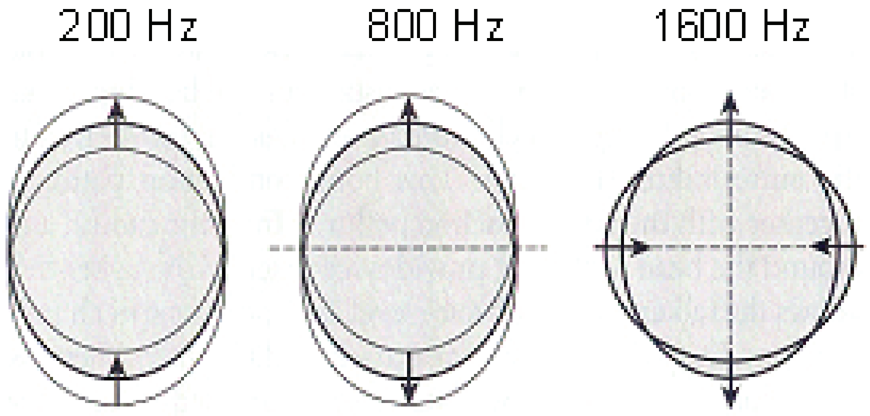

Figure 8-16. Modes of bone vibration at three different frequencies (adapted from Bekesy, 1932).

Vestibulocochlear Nerve

The vestibulocochlear nerve (the VIII cranial nerve) is the nerve connecting the organs of hearing and balance to the brain. It consists of two parts: the *auditory nerve* (cochlear nerve) and the *vestibular nerve*. Sensory signals that produce sensations of sound travel from the ear to the brainstem via the auditory nerve. The ascending neurons of the auditory nerve innervate the hair cells of the organ of Corti, exit the organ of Corti through the habenula perforata, and then form the *spiral ganglion* in the modiolus. The ascending neurons, called the *afferent neurons*, carry information from the sensory cells toward the brain. The descending neurons, called the *efferent neurons*, carry information from the brain to the sensory cells and other cells of the peripheral nervous system.

A neuron consists of a neuron cell and input (dendrites) and output (axon) projections extending from the neuron cell. These projections are called nerve fibers. Depending upon their location and function, neurons may be any length from 1 inch to 4 feet (2.5 cm to 1.2 m) long. Neurons transmit electrochemical signals to and from the brain via their nerve fibers. Upon receiving a signal, one neuron sends information to its adjacent neuron, through a junction called a synapse

The nerve fibers of the auditory nerve originate all along the cochlea, from its apex to its base, and project to the cell bodies of these nerves, which form the spiral ganglion. The fibers extending from the apex follow a straight course and form the core of the spiral ganglion, while the fibers from the base are twisted to form the outside surface of the ganglion. After leaving the cochlea, the auditory nerve joins the vestibular nerve, another bundle of fibers supporting the vestibular system, and they together form a bundle of approximately 30,000 afferent and efferent nerve fibers called the vestibulocochlear nerve. The vestibulocochlear nerve exits the inner ear through the *internal auditory meatus*, approximately 1 cm long channel in the temporal bone, which also houses the facial nerve, and enters the brainstem, where the auditory and vestibular parts of the vestibulocochlear nerve separate and take different pathways through the central nervous system. The structural representation of the vestibulocochlear nerve is shown in Figure 8-17.

The ascending pathways of the vestibulocochlear nerve that support the hair cells of the organ of Corti involve two types of afferent neurons: *inner radial neurons* (type I afferent neurons) and *outer spiral neurons* (type II afferent neurons). The inner radial neurons constitute approximately 95% of the ascending neurons in the cochlea and the outer spiral neurons make up the remaining 5% (Gelfand, 1998). The inner radial neurons, which are myelinated (insulated with a fatty substance) and larger of the two, innervate the IHCs. The innervation pattern is many-to-one and approximately 8 to 10 afferent fibers supply one IHC (Gelfand, 1998). The outer spiral neurons, which are unmyelinated and thinner, innervate the OHCs. The innervation pattern is one-to-many with one neuron making synapse connections with approximately 10 OHCs (Gelfand, 1998).

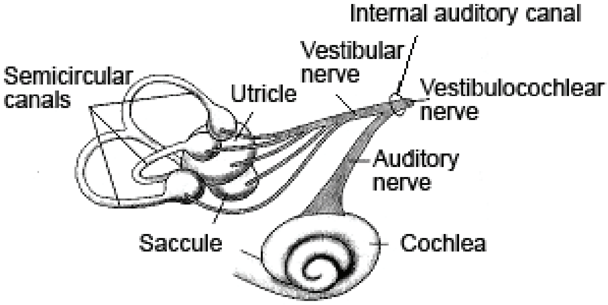

Figure 8-17. General structure of the vestibulocochlear nerve (adapted from Lass and Woodford, 2007).

Similar to the ascending pathways, the descending pathways of the vestibulocochlear nerve also involve two types of efferent neurons. They are the lateral olivocochlear neurons and the medial olivocochlear neurons, both of which descend from the superior olivary complex in the brainstem. The lateral olivocochlear neurons are myelinated and the larger, more numerous of the two, and they synapse with the projections of the afferent neurons connected to the IHCs. They constitute approximately 20% of the efferent neurons in the cochlea. The remaining 80% of efferent neurons in the cochlea are medial olivocochlear neurons (Gelfand, 1998). They are thin and unmyelinated and synapse to the OHCs. The distribution of the efferent fibers on the OHCs heavily favors the base of the cochlea. A schematic view of the innervation pattern for IHCs and OHCs is shown in Figure 8-18.

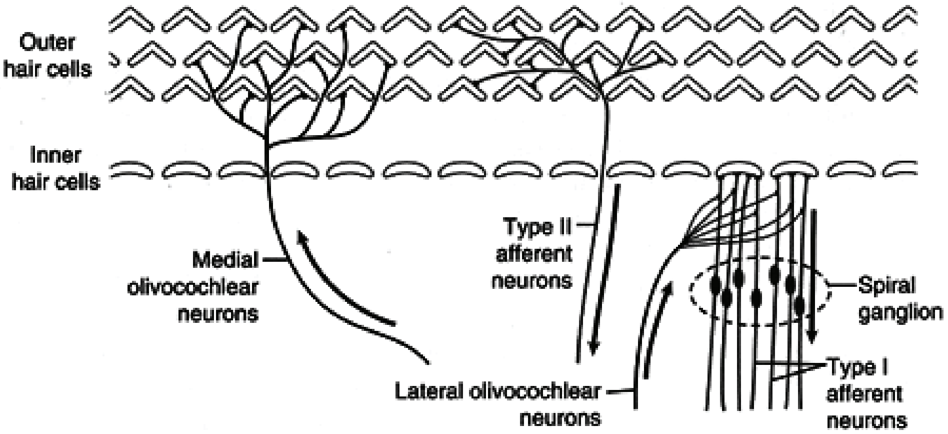

Figure 8-18. The innervation pattern of the hair cells of the organ of Corti (Emanuel and Letowski, 2009).

Central Auditory Nervous System

The central auditory nervous system (CANS) is a system of neural structures and connections within the brain that processes neural impulses transmitted from the vestibulocochlear nerve and converts them into auditory sensations. It is a subsystem of the *central nervous system* (CNS), which includes the entire brain and the spinal cord. The CNS is a dynamic system composed of various types of nerve cells (neurons), which form an extraordinary network of neural connections reaching out from the brain to every part of the body. The human brain is estimated to contain 100 billion (10^{11}) neurons[3] and a quadrillion (10^{15}) synapses[4] (Kimball, 2005). The anatomical organization of the main structural elements of the human brain is shown in Figure 8-19.

The most inferior (lowest) portion of the brain is the *brainstem*. The brainstem is approximately 10 cm long and 2.5 cm wide at the central core (Seikal, King, and Drumright, 2000). It is the superior extension of the spinal cord and the place where the vestibulocochlear nerve enters the brain. The main anatomical elements of the brainstem are the *medulla oblongata*, *pons*, and *midbrain*. The medulla oblongata, pons, and *cerebellum* form the posterior (back) part of the brain called the *hindbrain*. The midbrain is the most superior (top) part of the brainstem and it is connected to and located just below the *forebrain* (*cerebrum*), the largest and the most advanced part of the brain. The main parts of the forebrain are the telencephalon (including the *cerebral hemispheres*, basal nuclei, and medullary center of nerve fibers) and the diencephalons (including the *thalamus*, and *hypothalamus).*

Neural pathways in the CANS consist of various nuclei (groups of cell bodies) and fiber tracts (bundles of nerve fibers) which carry information between and among the nuclei. Each nucleus serves as a relay station for dispatching neural information from one nucleus to the next. The neurons comprising a specific neural pathway travel through several nuclei in the brainstem before reaching the auditory cortex. The nuclei involved in the classical ascending auditory pathway are the cochlear nucleus, superior olivary complex, inferior colliculus, and medial geniculate body. Neural fibers carrying specific information may synapse with nuclei on the same side or

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[3] A *neuron* is a cell specialized to conduct and generate electrical impulses and to carry information from one part of the brain to another.

[4] A *synapse* is the junction between two nerve cells across which a nerve impulse is transmitted.

decussate (cross from one side to the other) and synapse with nuclei on the other side of the brainstem. The pathway that connects the nuclei on the same side of the brainstem is called the *ipsilateral pathway* and the pathway that crosses from one side to the other is called the *contralateral pathway*. A general view of the ascending auditory pathway is shown in Figure 8-20. Note the size of the lateral lemniscus, which is the largest fiber tract in the CANS.

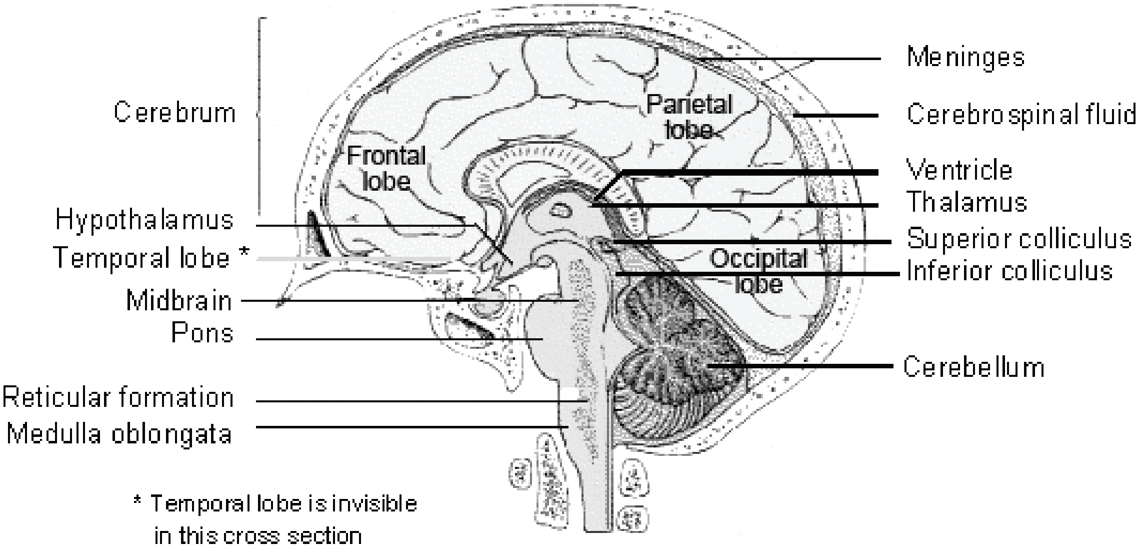

Figure 8-19. Main elements of the human brain (adapted from Kimball, 2005).

The *cochlear nucleus*, which spans the pons and medulla, is the first processing center and relay station of the ascending auditory pathways. The two other major relay stations in the brainstem are the superior olivary complex in the pons and the inferior colliculus in the midbrain. From the cochlear nucleus, the nerve fibers project to the *superior olivary complex* (SOC) or directly to the lateral lemniscus. Approximately 75% of the ascending CANS fibers leaving the cochlear nucleus cross over to the contralateral side of the brain to terminate at the SOC on the opposite side of the brainstem or project to the lateral lemniscus. The remaining 25% of the fibers follow the pathway on the ipsilateral side of the brainstem and terminate at the SOC or the lateral lemniscus (Pickles, 1988). The SOC consists of a cluster of nuclei including the lateral superior olive (LSO), the medial superior olive (MSO), and the ventral nucleus of the trapezoid body (VNTB). The SOC is also the site at which afferent auditory neurons connect with facial nerve, which innervate the stapedius muscle in the middle ear. When a very intense sound traveling via the vestibulocochlear nerve arrives at the cochlear nucleus, the signal is sent to SOC via several different pathways (including ipsilateral and contralateral SOC) to the facial nerve nucleus. From the nucleus the signal travels via the facial nerve to the stapedius muscle, which contracts. Contraction of the stapedius muscle pulls the stapes posteriorly increasing stiffness of the ossicles and tympanic membrane and decreasing the effective level of transmission for loud low frequency sounds (Deutsch and Richards, 1979; Moller, 1965; Stach and Jerger, 1990; Wilber, 1976). In addition, VNTB projects to many cochlear nuclei and forms efferent medial olivocochlear bundle (MOCB) innervating ipsilateral and contralateral OHCs (Guinan, 2006; Warr and Beck, 1996) decreasing gain of the cochlear amplifier (see Chapter 9, *Auditory Function*).

The organization of superior olivary complex and the connecting neural fibers are shown in Figure 8-21. Ascending projections from both cochlear nuclei and both superior olivary complexes travel via the largest fiber tract in the CANS, the lateral lemniscus, to the inferior colliculi (one colliculus on each side), located on the posterior surface of the midbrain. Similar to the decussation seen at earlier levels in the brainstem, the two *inferior colliculi* are connected by fibers that allow crossover of signals from one side of the brainstem to the other. The connections between the two sides of the brainstem, from the SOC to the inferior colliculi, are important for directional hearing. From the inferior colliculi, all fibers ascend to the *medial geniculate body* in the thalamus. The thalamus is located immediately above the midbrain and it directs all sensory information (except smell) to the appropriate area of the cerebrum. The cerebellum, or "little brain," is primarily responsible for coordinating motor commands with sensory inputs in order to control movement and communicates with the brainstem, spinal cord and cortex.

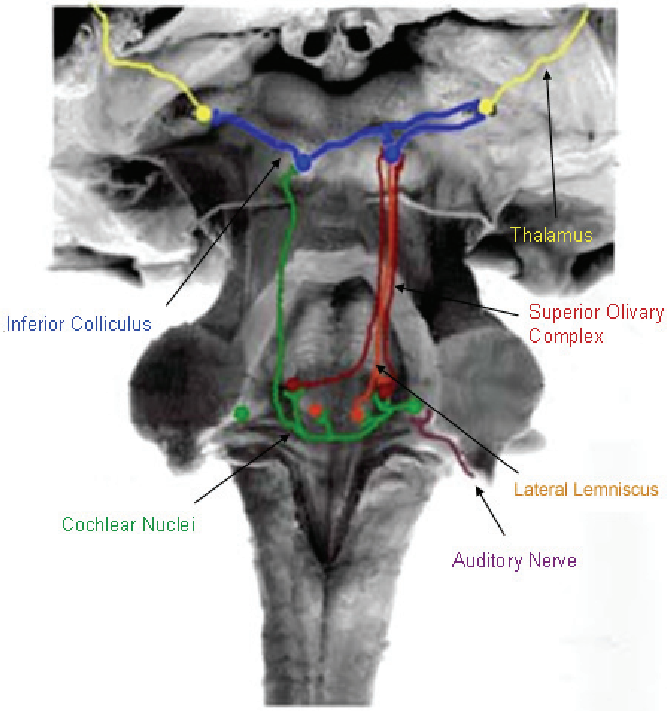

Figure 8-20. Ascending pathway of the central auditory nervous system. Different parts of the auditory pathway are color coded (adapted from http://serous.med.buffalo.edu/hearing/).

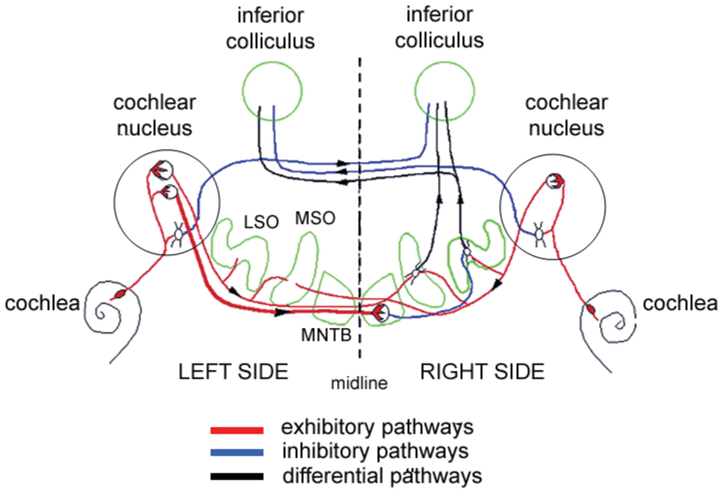

Figure 8-21. Nuclei and pathways of the left and right complex olivary complexes; LSO - lateral superior olivary nucleus, MSO - medial superior olivary nucleus, MNTB – medial nucleus of the trapezoid body (adapted from Johnson, 1997)

The cerebral hemispheres make up the largest portion of the forebrain. There are a number of connections between the medial geniculate body and the cerebral hemispheres, but the main ascending auditory pathway travels from the medial geniculate nucleus to the ipsilateral transverse temporal gyri (Heschl's gyrus) of the cerebrum and then to auditory association areas in other areas of the brain

The outermost segment of the cerebrum is called the cerebral cortex; commonly referred to as the "gray matter." The cortex is 2-6 mm (0.08 to 0.23 in) thick and is made up of the "gray-looking" nerve cell bodies. It is supported from underneath by the "white matter." which consists of the myelinated nerve fibers (axons) connecting various gray matter areas of the brain to each other. The surface of the cortex contains numerous peaks (gyri) and valleys (sulci) that serve to increase the overall area of the cortex. Extremely deep sulci are called fissures. The deepest fissure of the brain, the *longitudinal fissure* divides the cerebrum into two cerebral hemispheres. Cerebral hemispheres are only connected by a narrow structure called the *corpus callosum,* which is the only communication link between the hemispheres.

Each hemisphere is divided into four basic anatomical areas called lobes. They are called the frontal lobe, temporal, parietal, and occipital lobes. The frontal lobe takes up 1/3 of the cortex and is associated with executive functions such as the planning and initiation of motor actions. The parietal lobe is the primary reception area for somatic sensory data, while the occipital lobe is the main visual processing center of the brain (Seikel, King and Drumright, 2000). The main site of auditory and receptive language (Wernicke's area) processing centers is the temporal lobe. The four lobes are additionally divided into smaller functional areas based on the type and organization of neurons occupying these areas. These areas are called Brodmann areas and numbered from 1 to 48. Many of them have also been found to be responsible for specific cortical activities and so are labeled by these activities. For example, auditory activity in the cortex has been found to be concentrated in Brodmann areas 41 and 42, which are called the *primary auditory cortex*, and in area 22, called the *secondary auditory cortex*. Both these regions are located in the posterior (back) part of the *superior temporal gyrus* and descend into the *lateral sulcus* (Sylvain fissure) as the *transverse temporal gyri*, known also as the *Heschl's gyri*. A schematic view of various part of the cortex with a map of the Brodmann areas is shown in Figure 8-22.

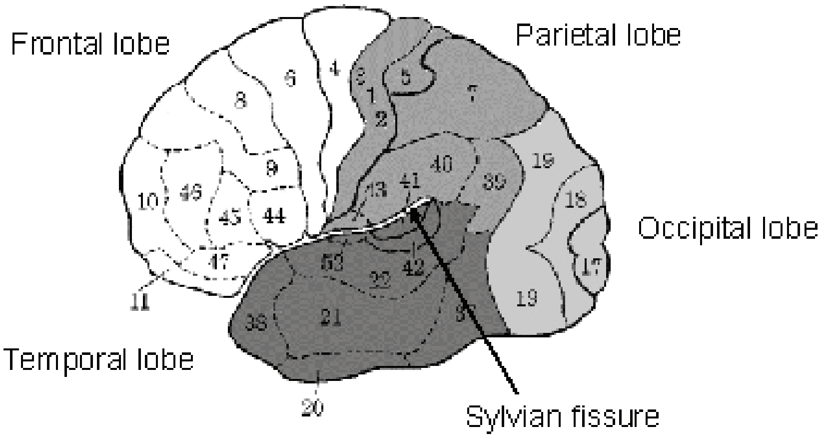

Figure 8-22. Sagittal view of the cerebral cortex and the Brodmann areas (adapted from http://www.umich.edu/ ~cogneuro/jpg/Brodmann.html).

The cortex, and thus the auditory cortex, is organized in six neural layers numbered from I to VI (Emanuel and Letowski, 2009). Auditory information arriving at the thalamus is further relayed to nonpyramidal neurons located in layer IV of the primary auditory cortex. Layers V and VI have efferent connections to the medial geniculate nucleus and the inferior colliculus, respectively. Other layers are involved in motor function (layer II and III) and have connections to other parts of the brain. Through theses connections all information entering the brain creates a synergistic perceptual image of the surrounding environment together with corresponding emotional state created by this image.

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