Chapter 3
Comparative Middle Ear Structure and Function in Vertebrates

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3.1 Introduction

This chapter is an attempt to provide a brief review comparing middle ear structure and function in the vertebrate line. A vast amount of information on this topic is readily available in the literature. Hundreds of relevant scientific papers, book chapters, and books on comparative hearing that have been published within the last 170 years, and a significant fraction of the earliest papers contain information on structure as well as data and intuitions on function. There are also extensive reviews of this topic that, more often than not, concentrate on selected vertebrate classes (e.g., Rosowski 1994; Lewis and Narins 1999; Saunders et al. 2000; Mason 2007). This chapter heavily references those earlier reviews, while touching on a fraction of the information contained in those more detailed works. The interested reader should use this chapter as a gateway to those more fundamental chapters and research papers.

The chapter starts with a discussion of the unique issues associated with the coupling of environmental sound to the inner-ear sensory organs and the different adaptations used to help overcome these issues in different vertebrate classes. Following in the footsteps of some of the extensive reviews of this topic, notably

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Henson (1974), a broad definition of "middle ear" is used that includes any anatomical mechanisms that assist the coupling of sound from the external environment to the sensory mechanisms within the inner ear.

3.2 Sound Stimulation of the Inner Ears of Vertebrates

3.2.1 What Is Sound?

Sound is a time-varying physical disturbance in pressure, velocity, density, and temperature within a medium that propagates in space, where the medium can be a fluid (such as air or water) or a solid (Wever and Lawrence 1954; Beranek 1993). Owing to differences in compressibility, these physical disturbances travel faster in water than in air, and faster still in materials with even lower compressibility such as compacted earth and rock and metal (Kinsler et al. 1982).

3.2.2 Sound Reception Within Vertebrate Inner Ears

The basic anatomical specialization used by vertebrates for sound reception is the hair cell (Wever 1974; Coffin et al. 2004). Sound stimulation produces a motion of the ciliary bundle at the apex of these cells relative to their cell body. Collections of hair cells are grouped in multiple sensory organs within the inner ear of vertebrates, including the ampullae of the semicircular canals, the utricle, the saccule, the lagena (all of which may also be sensitive to more constant inertial and rotary stimulation), as well as papillary organs that appear to be more specialized for sensitivity to sound (Wever 1974; Lewis and Narins 1999; Gleich and Manley 2000).

The hair cell organs that are most receptive to sound vary within the different vertebrate orders. In individual species within the orders of fish, the auditory organs include the utricle, saccule, and lagena (Popper and Fay 1999). In Amphibia the hearing organs include several specialized papillary organs (Feng et al. 1975; Wever 1985) and the saccule, which responds to vibratory stimuli at low sound frequencies (Narins and Lewis 1984; Christensen-Dalsgaard and Narins 1993). The hearing organ in reptiles and birds is the basilar papilla (Wever 1978; Miller 1980; Smith 1985), whereas in mammals the hearing organ is the cochlea (Slepecky 1996). Associated with these different organs are different specializations for producing the relative motions of the ciliary bundles that stimulate the hair cells. These specializations vary greatly between the different vertebrate orders and suborders. The next section of this chapter describes these specializations more or less along phylogenetic lines, starting with fish and ending with the ears of mammals.

3.3 Specializations for Conducting Sound to the Inner Ear

3.3.1 Fish Without a Specialized Sound-Conduction Apparatus

The multiple vertebrate classes that include the cartilaginous and bony fish exhibit a great complexity of hearing specializations including significant differences in the structure of the inner ear and the inner-ear hair cell organs that are most sensitive to sound. The least specialized of this collection of species have relatively poor hearing (Popper and Fay 1999, 2011). In these nonspecialized ears, the mechanisms for sensing sound are differences in inertia that induce relative motions between the hair cell body and those structures that determine the motions of the ciliary bundles as the entire body of the fish moves back and forth within the surrounding water that has been set into vibration by a sound source. Generally the inertial structure that determines the motion of the ciliary bundle is a macular membrane that sits on the tips of the bundle (Popper and Fay 1999, 2011). As the body of the fish is set into motion, the hair cells and the macula move with a different magnitude and phase, producing the relative motion of the ciliary tips and cell bodies necessary for sensory stimulation of the hair cells underneath the macula. Because the sound-induced displacements of fluid particles fall off more quickly with distance from a sound source than the sound pressures associated with these motions (Kinsler et al. 1982; Kalmijn 1988, 1989), this dependence on the motion of the surrounding fluid results in an ear whose sensitivity falls off faster with distance than an ear that is directly sensitive to sound pressure.

One outcome of this relatively simple mechanism for stimulating auditory hair cells is that populations of hair cells with specific orientations of their hair bundles relative to the body axes will respond in a direction selective manner to sound-induced displacement of these macula organs (Fay 1984; Fay and Edds-Walton 1997). The introduction of directional cues by the mechanisms that couple sound to the inner ear is a common theme throughout vertebrates.

3.3.2 Fish: Ears with Close Connections to a Swim Bladder

While fish with unspecialized sound-conductive systems are sensitive to sound, the range of sound frequencies and levels that elicit an auditory response are generally restricted to relatively intense sounds of frequencies below 1,000 Hz (Popper and Fay 1999). Multiple lines of bony fish have independently developed various specializations that enhance the frequency and level ranges of the sounds that can stimulate the auditory sensors. The basic anatomical feature that is common across these specializations is an association of a gas-filled swim bladder with the ear (Popper and Fay 1999, 2011), where the primary function of the swim bladder is to help fishes maintain the proper buoyancy within their aquatic environment.

A swim bladder is essentially a bubble of gas held within a sack within the fish's body. When subjected to an alternating sound pressure, the gas in the bladder is alternately squeezed and rarified resulting in time-varying displacements of the walls of the bladder. The displacements of the bladder walls produce displacements of the surrounding fluids and body tissues that are larger than the sound-induced displacements that would have occurred if there were no compressible bladder (Popper et al. 2003; Popper and Schilt 2008). Additional specializations, such as the development of chains of bone to connect better the displacements of the swim bladder with the fluid-filled inner ears, or the close approximation of the bladder or air pockets within the bladder to the inner ear, are apparent in varied fish species (Henson 1974; Popper and Fay 1999).

3.3.3 Amphibians: The Transition to Land

As the early vertebrates first moved to land, their ears were poorly designed for the reception of airborne sound. Although the fish with specialized conductive apparatuses used their swim bladders to increase the inner-ear fluid displacements associated with small sound pressures, these mechanisms were less effective when the stimulus was airborne sound, which is not efficiently conducted through the body walls. The basis of the problem is the impedance mismatch between air and the body tissues. Only a small fraction of the sound energy available in air borne sound enters the body's tissues, while the rest is reflected away. The loss in sound energy in these circumstances is on the order of 30 dB (Wever and Lawrence 1954; Dallos 1973). Several different improvements in inner-ear sound conduction occur in amphibians to increase the displacements of inner-ear fluid produced by sound. The various specializations in structure in the amphibian ear are well described in other reviews (Wever 1985; Lewis and Narins 1999; Mason 2007).

One improvement is the change in the location of the air pocket from inside the body to a position between the surface of the skull and the bony inner ear. This change permitted more efficient compression of the pocket by airborne sound as well as improved coupling to the inner ear. While apparent in several of the suborders in Amphibia, this structural alteration may have already occurred in the some of the lobe-finned fishes that are thought to be the evolutionary precursors of terrestrial vertebrates. For example, in Latimeria (e.g., *Latimeria chalumnae*), a modern example of the lobe-finned fishes, there is a spiracular pouch associated with the gills between the surface of the head and the bone covering the inner ear that may be air filled (Fritzsch 1992).

A second improvement was the development of a tympanic membrane on the lateral surface of the air space that is coupled by an ossicular chain to the inner ear. An important part in the development of such a "tympano-ossicular" middle ear is the presence of a window in the bone surrounding the inner ear that allows direct coupling of the inner-ear fluids and the mobile ossicular element bound in the window by a flexible ligament. (Following the common practice this window will

be referred to as the "oval window," a name that comes from human anatomy. In reality the window is more round than oval in many nonhuman terrestrial vertebrates.) The combination of a large tympanic membrane and a small oval window is the basis for a hydromechanical transformer that better couples airborne sound energy to the inner-ear fluids. Such a transformation brings a new problem. In fish ears with conductive specializations, the swim bladder acts to increase the sound-induced displacements of fluid near the inner ear structures so as to produce significant relative displacements between the ciliary bundles and the hair-cell bodies. The tympano-ossicular system, however, actually decreases the sound-induced displacements presented to the inner ear while increasing the sound pressure at the oval window.

To take advantage of the increased sound pressures produced at the entrance of the inner ear by the tympano-ossicular system, the third improvement was the development of inner-ear specializations in the lymph-filled periotic (around the ear) pathways that connect motions of the ossicle to the sense organs (Lewis and Narins 1999). Three distinct and separate specializations can be seen in amphibians. The common effect of these specializations is to increase the displacement of fluid within the inner ear by taking advantage of the increased sound pressures produced by the tympano-ossicular system (Wever 1985; Mason 2007).

3.3.3.1 Specializations in the Periotic Lymphatic Spaces of Amphibians

For an increase in sound pressure at the oval window interface of the tympano-ossicular system and the inner ear to induce significant displacements within the relatively incompressible lymphs of the inner ear, there must be some compliant or compressible "window" on the other side of the hair-cell sensors where the sound pressure is smaller in magnitude. In such a system, the displacement of the inner-ear lymphs is directly related to the sound pressure difference between the two windows. Three different types of pressure-difference mechanism are observed in amphibians.

Caecilians (limbless borrowing amphibians) have a "re-entrant" inner-ear fluid system (Wever 1985), in which the ossicular "footplate" (the flat end of the ossicle in the oval window) is sealed within a perilymph filled space that is connected to both the proximal input to the inner ear (on the medial surface of the footplate) and the distal "output" of the system via a fluid path that ends at the lateral surface of the footplate. The hearing sense organs of the amphibian inner ear are located between the input and the output pathways to and from the inner ear. Inward motions of the footplate simultaneously produce a positive pressure on the medial surface of the footplate and a negative pressure on the lateral surface. This pressure difference between the two sides of the footplate allows a wave of fluid displacement to progress from the medial surface of the footplate to stimulate the receptors. The wave then circles through the "re-entrant" lymphatic pathway to the lateral surface of the moving footplate.

In some urodeles (salamanders and newts) the second window for lymphatic displacements is a connection between the inner-ear lymphatic spaces and the fluid spaces with the brain case (Wever 1985; Mason 2007). The relatively large size of the brain case (compared to the small volume of the inner ear) and the small but nonzero compressibility of body fluids and tissues within the brain, allows a fluid displacement wave produced by motion of the footplate to be relieved by small compressions of the fluid and tissues within the brain. (A similar path for fluid displacement has been suggested in some pathologic human ears due to abnormal fluid pathways between the inner ear and the brain [Songer and Rosowski 2007; Merchant and Rosowski 2008]). It has also been suggested that some fraction of the sound-related displacements is conducted through the brain to the contralateral ear, where the displacements induce opposite motions of the contralateral footplate (Wever 1985). This idea has not been tested extensively, and any compressions within the brain would act to reduce such coupling.

The anurans (frogs and toads) display a third mechanism for increased lymphatic displacements that result from sound pressure at the entrance to the inner ear, which is identical to the specialization seen in most reptiles and in birds and mammals. In these species a second membrane-covered window exists between the inner ear and the air-filled middle ear (Wever 1985; Mason 2007). This "round window" allows ready motion of the cochlear lymphs in response to a difference between the relatively high sound pressure within the lymphs at the oval window and the low sound pressure within the middle ear air space around the round window. Placement of the inner-ear sensing organs astride the fluid path provides efficient stimulation of the sensors (Lewis and Narins 1999; Purgue and Narins 2000a, b).

3.3.3.2   Variations in the Structure of the Middle Ear in Amphibia

The middle ear system of frogs and toads is similar to that in many amniotes. The distinguishing features of such a system include (1) a relatively thin sound receptive membrane (the tympanic membrane [TM]) placed laterally on the skull, possibly at the medial termination of an ear canal; (2) a compressible air-filled cavity behind the TM that allows the TM to move in and out when there is a difference between the sound pressure on the TM's outer surface and the sound pressure within the cavity; and (3) an ossicular system consisting of bony and cartilaginous rods and connecting levers that couple the motions of the TM to the inner ear. The footplate is the distal end of the ossicular system and is sealed in the oval window by a flexible ligament. The area of the footplate is small relative to the TM, and the combination of the hydraulic advantage of the difference in area between the TM and the footplate, and any mechanical advantages derived from potential ossicular-lever mechanisms are the source of the transformer action of the tympano-ossicular middle ear (Wever and Lawrence 1954; Dallos 1973; Rosowski 2010).

Although many anurans exhibit the tympano-ossicular middle ear described in the preceding text, individual anuran species and the non-anuran amphibians show significant variations in middle ear anatomy, including the lack of a specialized

tympanic membrane, or the lack of an air-filled middle ear cavity (Wever 1985; Mason 2007). On the other hand, most amphibian middle ears contain an operculum, a bony structure not found in amniote (reptile, bird, and mammal) middle ears. This small rounded bone sits in the oval window alongside the ossicular footplate in many amphibians. The operculum often interdigitates with the footplate, and appears to be loosely held in place by muscles. The function of the operculum is controversial. Wever (1979, 1985) ascribed an auditory feedback control mechanism to the anuran operculum, where contractions and relaxations of opercular supporting muscles and a muscle attached to the footplate either inhibited or allowed large sound-induced motions of the footplate. Hetherington (1994) argued against such a protective mechanism and instead suggests the operculum has a role in the conduction of extratympanic sounds and vibrations to the inner ear.

3.3.3.3 Extratympanic Sound Conduction in Amphibians

It has been well established that sound can cause significant vibration of the skin of frogs, especially when the skin covers the respiratory air spaces (e.g., the lungs and the buccal cavity) (Narins et al. 1988; Ehret et al. 1990). Although the sound-induced displacements of these regions tend to be smaller than the vibration of the TM, the vibration of these larger surfaces can lead to significant volume displacements of the air cavities in the thorax and pharynx. It has been demonstrated that some fraction of these volume displacements is coupled to the middle ear via the normally open bony "Eustachian-tube" orifice that couples the middle ear air spaces to the pharynx (Narins et al. 1988). Further, the coupling of the bilateral middle ears to the pharynx allows sounds that displace the TM on one side of the head to propagate across the head to the contralateral middle ear (Aertsen et al. 1986). How all of these air paths for sound conduction interact when the whole body is immersed in a sound field is not completely understood. However, there is considerable evidence that these multiple sound pathways to the middle ear impart directionality to the ear that is used in the localization of sound sources (Feng and Shofner 1981; Gerhardt and Rheinlaender 1982; Vlaming et al. 1984).

In some anurans (Hetherington 1988, 1992), sound acts on the body wall and sets skeletal components into vibration (especially the broad scapula of the shoulder girdle). These vibrations can be conducted to the inner ear through displacements of the operculum, which is coupled to the scapula by the opercular muscle. The data of Hetherington (1992) suggest that the opercular path of sound conduction is most significant in small frogs. This scapular to opercular path has also been implicated in the conduction of substrate vibrations to the saccule within the inner ear (Hetherington 1985, 1987; Lewis and Narins 1999).

3.3.3.4 Feedback Control of Middle Ear Function

A common feature of the ears of terrestrial vertebrates is the feedback control of middle ear sound conduction via the efferent control of muscles whose actions modify the transduction process (Borg et al. 1984). Two separate control systems have been hypothesized in anurans. As noted previously, Wever (1979, 1985) has presented evidence that muscles attached to the operculum and footplate control the magnitude of sound-induced displacement of these structures, where variations in muscle tension alter the coupling between the footplate and the operculum. Such variations could either increase the motion of the ossicular footplate–operculum complex (Lombard and Straughan 1974) or decrease footplate motion (Wever 1979). Evidence against the reduction in motion hypothesis has been presented by Hetherington (1994), who argues that Wever misidentified the different muscle groups involved and that variations in the tension of the opercular muscle do not modulate sound transmission by the tympano-ossicular system.

Although the use of muscles to modulate the stiffness of the ossicular system is a common theme throughout amniotes, a unique form of control of middle ear sound transmission has been described in a frog that appears specialized for the reception of sound frequencies well above the normal range of amphibians (Gridi-Papp et al. 2008). The torrent frog (*Amolpos tormotus*) lives in rapidly moving streams in China, where the highly turbulent water flow produces significantly loud sounds in the frequency range of hearing of many amphibians. These frogs appear to have the ability to use muscular contractions to seal the normally open bony orifice that couples the middle ear cavity to the pharynx. Closing the tubal orifice increases the stiffness of the air within the middle ear, which reduces the sound-induced motion of the TM and ossicular system at low frequencies, but also moves the middle ear resonance to a higher frequency. The shift in resonance leads to an increase in sensitivity near the new resonance.

3.3.4 The Columellar Ear of Reptiles and Birds

3.3.4.1 The Inner Ears of Reptiles and Birds

The inner ears of reptiles and birds contain a basilar papilla specialized for the sensation of sound energy. Unlike the specialized hearing organs in fish and Amphibia, this organ sits on a basilar membrane, which vibrates when sound is presented to the inner ear (Wever 1978; Miller 1980; Gleich and Manley 2000). The direct vibration of the basilar membrane that supports the hair cells represents a significant adaptation that takes advantage of the trans-inner-ear pressure differences produced by the development of the two-window inner ear. Such a membrane produces an increase in the displacements of the hair cells and their ciliary bundles in response to a sound pressure difference between the two cochlear windows.

There are many publications describing different schema for turning these displacements of the hair cell body into relative motions of the cell and its ciliary bundle (e.g., Wever 1971; Weiss and Leong 1985; Manley et al. 1988).

Even though all reptilian and bird inner ears exhibit a specialized papilla placed on a mobile membrane (Schwartzkopf 1973; Wever 1978; Miller 1980), there is significant variability in the size and form of the papilla, especially in lizards, as well as great variation in the accessory "tectorial" structures that enhance the motion of the ciliary bundles (Wever 1978; Manley 2000). The presence of the round window is another point of variance. The inner ears of lizards, crocodylids, and birds contain a true round window membrane that releases the sound pressure produced in the inner ear by the motion of the ossicular footplate in the oval window, and thereby increase the motions of the lymphs within the inner ear. Snakes, turtles, and the rare amphisbaenids and sphenodon have no round window and seem to rely on the "re-entrant" model of inner-ear lymph displacement described previously (Wever 1978).

3.3.4.2 The Tympano-ossicular Middle Ear in Reptiles and Birds

The middle ears of most reptiles and birds use a single bony ossicle and associated cartilaginous connecting elements to couple sound-induced motions of the tympanic membrane to the oval window of the middle ear (Schwartzkopf 1973; Wever 1978; Saunders et al. 2000). As in anurans, the distal end of the single column-like ossicle (here called the columella) widens out into a flat bony plate that fits into the oval window. (The term *columella* describes the shape of this long and thin ossicle; however, because this bone is believed homologous to the mammalian stirrup-shaped stapes, many authors equate the columella and the stapes.) The area of the columellar footplate is anywhere from 10 to 60 times smaller (Kirikae 1960; Schwartzkopf 1973; Rosowski and Graybeal 1991) than the area of the tympanic membrane, and this ratio of areas is the primary determinant of the transformer function of the reptilian/avian middle ear (Wever 1978; Gummer et al. 1989a; Saunders et al. 2000).

There is a secondary transformer within the reptilian and avian middle ear: The shape of the cartilaginous "extra-columella" (or extra-stapes), which couples the columella to the TM, allows a lever action between the motion of the center of the TM and the motion of the columella that provides a mechanical lever advantage of a factor of 2–3 (Gaudin 1968; Wever 1978; Gummer et al. 1989a). The combination of the mechanical lever and the hydroacoustic transformation of the TM-to-footplate area ratio provide an increase in sound pressure and a decrease in volume displacements at the entrance to the inner ear, relative to the sound stimulus and volume displacement of air lateral to the tympanic membrane (Rosowski et al. 1985; Gummer et al. 1989a, b). This "transformation" of the sound between the TM and inner ear, together with the two inner-ear windows and the basilar membrane, allows more efficient transfer of ear canal sound pressure to the inner ear and increased motions of the stereocilliary bundle (Wever 1978; Manley et al. 1988).

The introduction of a mechanical lever into the middle ear to help transform the impedance of the air in the ear canal and the fluids in the cochlea introduces a problem into the design of the middle ear. The basis for such levers is rotation about a fulcrum, where rotation can lead to significant three-dimensional motions at the ends of the lever. Specifically, in a one-ossicle ear, the lever action produced by the rotation of the extracolumellar cartilage embedded in the TM evokes a combination of a side-to-side and in-and-out motion of the proximal end of the bony columella (e.g., Kirikae 1960; Gaudin 1968). However, the annular ligament constrains the footplate within the oval window and reduces the side-to-side motions of the distal bony columella. This reduction, relative to the side-to-side motions at the proximal end, is made possible by a bending within the cartilaginous extracolumellar. Such bending leads to a reduction in signal transfer through the middle ear that is most prominent with higher frequency sounds (Manley 1972b; Gummer et al. 1989a; see also Manley and Sienknecht, Chap. 2).

There is significant variation in the middle ear air spaces in reptiles and birds (Henson 1974; Wever 1978). Individual turtle and snake species have very small or nonexistent middle ear air spaces (Kirikae 1960; Wever 1978). Most lizards have middle ear air spaces that are not constrained by bony walls; the air spaces are really pockets of the larger pharynx (Wever 1978). The middle ear air spaces of birds and crocodylids are generally surrounded by bone (except of course for the TM); however, a bony-walled air-filled channel connects the binaural air spaces, allowing sound conduction between the middle ears (Wever and Vernon 1957; Hill et al. 1980; Rosowski and Saunders 1980). The potential for each TM to respond to a difference in sound pressures between sounds entering the middle ear from the two sides of the head could again be useful in providing directional cues for the localization of sound sources (Coles and Guppy 1988; Christensen-Dalsgaard and Manley 2005; cf. Moiseff and Konishi 1981).

3.3.4.3 The Columellar Muscle

A few reptiles—the varanids, geckos, and crocodylids (Wever 1978)—and the birds (Henson 1974; Counter and Borg 1979, 1982) exhibit a muscle attached to the bony columella. This muscle appears to be innervated by the facial nerve (cranial nerve VII), and is thought to be homologous to the mammalian stapedius muscle. There has been little work describing the function of this muscle in reptiles, but it has been noted that the reptilian species that possess a columellar muscle are those that phonate. Evidence exists that contraction of this muscle in birds reduces the transfer of low-frequency sound energy to the inner ear (Counter and Borg 1982); however, the evidence that the columellar muscle is activated by external sound is mixed. Sound-induced contractions of the muscle have been looked for but not found in pigeons and chickens, but have been described in a species of owl (Borg et al. 1984). It is known, though, that the avian muscle contracts during phonation and may function to reduce the transfer of self-generated sounds to the inner ear (Counter and Borg 1979).

3.3.5   The Three-Ossicle Ear of Mammals

The ears of mammals have many features in common with birds and reptiles, but there are also significant differences compared to other vertebrates. Variations in mammalian middle ear structure and function are the subjects of many earlier reports and reviews (e.g., Doran 1879; Keen and Grobbelaar 1941; Fleischer 1973).

3.3.5.1   The Inner Ear of Mammals and Its Sensitivity to Sound

The auditory inner ear, or cochlea, of mammals is a highly organized collection of hair cells, and their accessory structures supported on a flexible basilar membrane (Slepecky 1996). As in most reptiles and birds, there are two windows (the oval and the round) in the bone surrounding the inner ear, both of which open to the middle ear. Also as in most reptiles and birds, the footplate at the termination of the mammalian ossicular apparatus is bound in the oval window by a ligament (Guinan and Peake 1967; Bolz and Lim 1972), while the round window is covered by a thin membrane (Wever and Lawrence 1954; Békésy 1960; Paparella et al. 1983).

Some of the best evidence for the sensitivity of the two-windowed inner ear to the difference in sound pressure acting on the windows has been gathered in mammals (Wever and Lawrence 1950, 1954; Voss et al. 1996). These data demonstrate that the cochlear response to simultaneous and direct sound stimulation of the two windows is largest when the sound pressures applied to the windows are of equal magnitude and opposite phase, a condition that leads to the largest fluid displacements within the inner ear. The data also demonstrate a greatly reduced response of the inner ear when the stimuli applied to the two windows are identical in magnitude and phase. This latter demonstration is a strong argument against the possibility that the sensory apparatus within the inner ear responds directly to applied pressure, although some small response to such a stimulus might result if the contents of the cochlea were compressible (Shera and Zweig 1992), or if there were a normal "third window" allowing fluid motion within the inner ear when there was no pressure difference between the oval and round window (Ranke 1953; Békésy 1960; Tonndorf and Tabor 1962).

3.3.5.2   The Three Mammalian Ossicles

The mammalian ossicular chain (Figs. 3.1 and 3.2) is made up of three interconnected bones: the malleus, incus, and stapes (Dahmann 1929; Wever and Lawrence 1954; Henson 1974). These ossicles are coupled by joints and supported by ligaments in a manner that allows rotation of the malleus and incus about their combined center of gravity (Puria and Steele 2010; Lavender et al. 2011). Differences in the lengths of the malleus and incus lever arms provide a transformation of sound energy consistent with an increase in sound pressure inside the
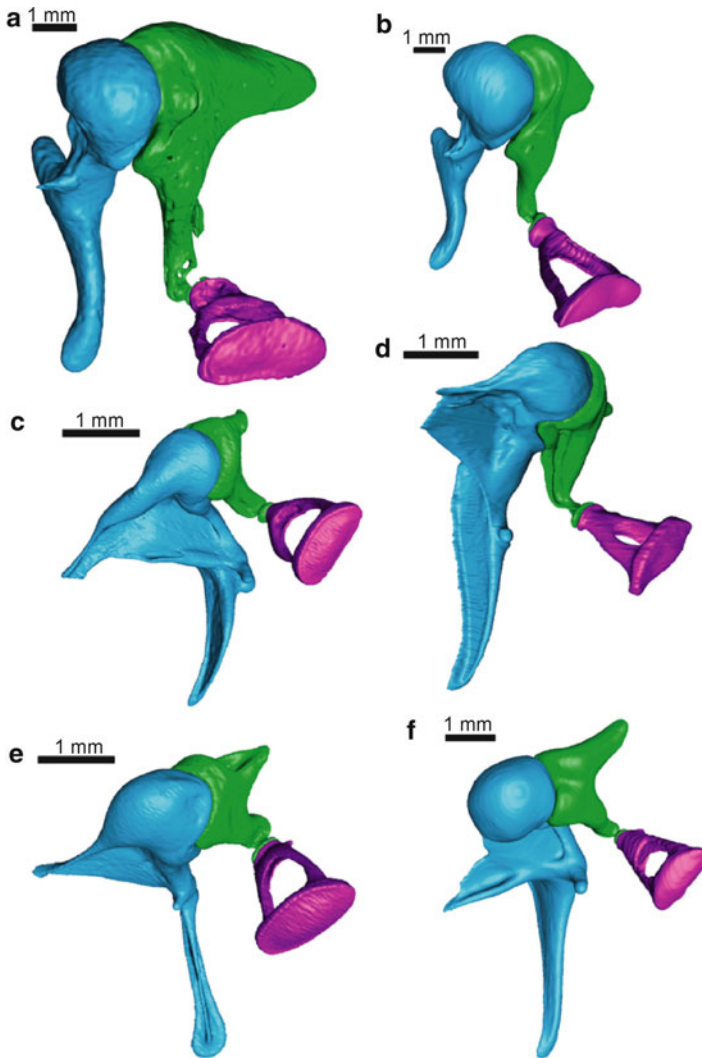
Fig. 3.1 The ossicular chains of five different mammalian species (Modified from Salih et al. 2012). The mallei are in *blue*, the inci in *green*, and the stapes in *magenta*. Each of the chains is viewed from and antero-medial direction. Ossicles from (**a**, **b**) two humans of different age and body size; (**c**) a rat; (**d**) a rabbit *(Oryctolagus cuniculus)*; (**e**) a gerbil *(Meriones unguiculatus)*; and (**f**) a cat. Each of the scales bars is 1 mm in length; the largest ossicles are those from the two humans; the smallest are from the gerbil and rat. Note the large variation in (1) the absolute sizes of the ossicles, (2) the relative sizes of the malleus and incus, (3) the orientation of the malleus and incus lever arms, and (4) the shape of the malleus and incus. The shape of the stapes also varies, but less dramatically
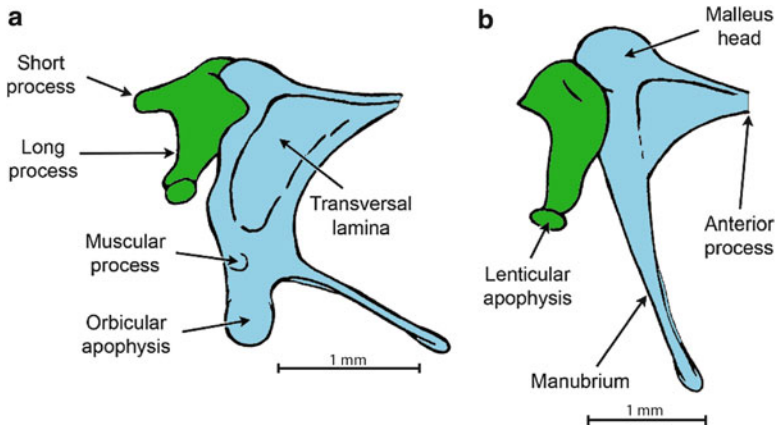
Fig. 3.2 Large variations in mammalian ossicular form (Modified from Lavender et al. 2011). The malleus and incus from two small mammals. The views are of the medial surface of a left ear, with anterior to the right and dorsal to the top. (**a**) A mouse: Note the elongated and widened shape of the malleus neck (including the transversal lamina), with the long process of the incus nearly perpendicular to the manubrium (the handle) of the malleus. This arrangement is consistent with Fleischer's (1973, 1978) categorization of a "microtype" ossicular system. (**b**) A golden hamster (*Mesocricitus auratus*): this ossicular system approaches Fleischer's (1973, 1978) "free-standing" ossicular chain, with the incus long process more parallel to the manubrium—as in human (Fig. 3.1)

cochlea and a decrease in the volume displacement of the stapes (Helmholtz 1868; Wever and Lawrence 1954; Dallos 1973).

Historically, ideas regarding the evolutionary development of the three ossicles have been varied, but it is now generally assumed that the malleus and incus developed from the bones of the jaw of early reptiles in a manner that was independent of the development of the reptilian and avian tympano-ossicular system (Allin and Hopson 1992; Bolt and Lombard 1992; Manley 2010; see also Manley and Sienknecht, Chap. 2). Although many have suggested that the development of the three-ossicle middle ear allows mammals to hear sounds of higher frequency than other terrestrial animals (e.g., Masterton et al. 1969; Manley 2010), the precise mechanism that determines this hypothesized superior ossicular function has not been clearly elucidated. It has been suggested that the rotary lever action inherent in the mammalian three-ossicle chain is responsible for its superior conduction of high-frequency sounds; however, lever actions have been described in the ossicular systems of amphibians (Wever 1985), reptiles (Manley 1972a; Wever 1978), and birds (Gaudin 1968; Saunders and Johnstone 1972; Gummer et al. 1989a). It has also been suggested that flexibility within the cartilaginous components of the reptile and avian ossicular connection is the root of the lower frequency limits of hearing in reptiles and birds (Manley 1972b, 1990), but similar flexibility exists within the joints that connect the mammalian ossicles, and this flexibility can reduce the transfer of high-frequency sound through the middle ear (Zwislocki 1962; Guinan and Peake 1967; Willi et al. 2002). It may be that

the presence of the flexible joints closer to the rotary axis of the mammalian ossicular chain allows tighter ossicular coupling and improved high-frequency sound transfer (Manley 2010), but this theory has not been tested. An alternative hypothesis is that the multiple degrees of freedom allowed by the coupling of separate ossicles by flexible joints allow alterations in the mode of motions of the ossicles, where different modes of motion favor sound transmission in different frequency ranges (Fleischer 1978; Puria and Steele 2010; Lavender et al. 2011).

3.3.5.3 Two Mammalian Middle Ear Muscles

A significant structural difference between the mammalian ossicular chain and the columellar system of reptiles and birds is the presence of two separate middle ear muscles. One of the mammalian middle ear muscles, the stapedius muscle, has a tendinous insertion on the stapes, is innervated by the facial nerve (cranial nerve VII), and is thought homologous to the columellar muscles in birds and some reptiles. Contractions of the stapedius muscle stretch the ligament holding the stapes in the oval window, resulting in a stiffening of the ligament (Bennett 1984; Pang and Peake 1986) and a reduction in the transfer of lower-frequency sounds through the middle ear (Wever and Lawrence 1954; Møller 1964, 1974). The lower frequencies are those at which the transfer of sound through the middle ear is governed by stiffness (Zwislocki 1962; Møller 1965); the muscular contraction increases the stiffness and leads to the reduction in sound transfer. Sounds of frequencies above the region of stiffness control are generally unaffected, but may show small improvements in sound conduction depending on the interaction of the increased ossicular stiffness with the other impedances that govern middle ear sound transmission (Wever and Lawrence 1954; Henson 1970; Borg and Zakrisson 1975).

The second mammalian middle ear muscle is the tensor tympani, which is innervated by the motor branch of the trigeminal nerve (cranial nerve V). The tendon of the tensor tympani is attached to the malleus neck or handle (the manubrium of the malleus), and contraction of the tensor tympani pulls the TM and malleus into the middle ear air space. This contraction stiffens the middle ear by increasing the stiffness of the tympanic membrane (Nuttall 1974). Contraction of the tensor also increases the static pressure within the middle ear by reducing the volume of the middle ear spaces; this result is thought to aid in opening the Eustachian tube (Ingelstedt and Jonson 1966) as reflex contraction of the tensor occurs during swallowing.

Both the stapedius and tensor tympani are known to contract in response to loud sounds, but the stapedius generally responds at lower stimulus levels (Borg et al. 1984; Silman 1984). This sound-induced contraction is part of an acoustic reflex arc that has been suggested to reduce the sensation of loud sounds (Wever and Lawrence 1954; Wever and Vernon 1961; Henson 1965); however, contractions of the middle ear muscles take time to develop, and these muscles would be of little use in protecting the ear from rapidly developing impulsive sounds (see Popelka

and Hunter, Chap. 8). Nonetheless, data suggest that an intact functioning stapedius muscle can reduce the noise exposure of the ears of workers exposed to continuous loud noise (Zakrisson et al. 1980; Borg and Nilsson 1984). Another hypothesized function is that the middle ear muscles may help reduce the masking effects of low-frequency sounds in noisy environments (Borg and Zakrisson 1974; Pang and Guinan 1997). Both muscles also contract before phonation and other activities (Carmel and Starr 1963; Borg and Zakrisson 1975; Borg et al. 1984).

A commonly suggested function of the tensor tympani is that it applies a pretension to the tympano-ossicular system that helps in the conduction of sounds to the inner ear (see Borg et al. 1984). However, there is little evidence for such a function. Measurements of middle ear function have been made in multiple animal species, and the tensor is generally found to be relaxed, except under circumstance of periodic contraction (e.g., Wiggers 1937; Rosowski et al. 2006). Also, stimulation of the tensor tympani in anesthetized animals where the muscle is relaxed produces a stiffening of the TM and a reduction of sound transfer (e.g., Wever and Lawrence 1954; Nuttall 1974). It has also been demonstrated that the sound-induced displacements of the TM and malleus in human cadaveric ears, in which the tensor is relaxed, are very similar to such measurements in live human ears (Rosowski et al. 1990; Goode et al. 1996). Finally, if such a pretension was necessary to better couple the TM and the ossicular chain, then one might expect that the application of a static pressure gradient across the TM might counterbalance the tensor effect and lead to a more compliant TM and poorer sound conduction to the ear. Multiple studies of the effect of static pressure on TM mechanics and middle ear sound conduction (Wever et al. 1948; McPherson et al. 1976; Erlandsson et al. 1980) demonstrate that both TM compliance and middle ear sound transfer are at or near maximum when there is no static pressure difference across the TM. The maximum in TM mobility with zero static pressure is one of the basic tenets of clinical tympanometry (Jerger 1970; Lidén et al. 1970; Margolis and Shanks 1985).

The presence of two middle ear muscles in the mammalian ear suggests a separation of function, which is generally borne out by the higher sensitivity of the stapes muscle contractions to sound, and the contribution of tensor contractions in the Eustachian tube reflex. Such a separation of function is possible in the mammalian ear because of the existence of multiple ossicles separated by ossicular joints (Marquet 1981). In such an arrangement, contractions of the stapes can alter the mechanics of the stapes without inducing large TM motions (Pang and Peake 1986), and contraction of the tensor tympani can pull the TM and malleus into the middle ear cavity without inducing large inward motions of the stapes (Hüttenbrink 1988; Marquet 1981). Of course such a separation of function can be achieved by ossicular systems that have the two muscles on either side of a single flexible ossicular joint, as is functionally the case in many mammals where the joint between the malleus and incus is either very tight or the two ossicles have fused (e.g., Fleischer 1973; Rosowski et al. 1999; Puria and Steele 2010).

3.3.5.4   The Mammalian Tympanic Membrane

Like the TMs of most other vertebrates, the mammalian TM is composed of three distinct layers: an external dermal layer that is continuous with the skin layer of the ear canal, a middle fibrous layer, and an internal layer of mucosal epithelium that is continuous with the epithelial layer that lines the middle ear air spaces (Lim 1968a, b; Funnell and Laszlo 1982; Decraemer and Funnell 2008). The TMs of reptiles and birds have a similar lamellar structure, but the fibrous layer appears less organized in nonmammals (Funnell and Laszlo 1982). The mammalian TM has a tentlike shape with the spine of the tent defined by the manubrium of the malleus, which is more medially placed than the tympanic bone that surrounds much of the TM. This arrangement produces a TM that appears to protrude into the middle ear air spaces. The TMs of birds and reptiles appear more flattened, and the central spine of the tent (defined by the connection of the cartilaginous extracolumellar with the TM) appears to protrude slightly into the ear canal.

Unlike other vertebrates the mammalian TM has two components, the central pars tensa and the more posterior-dorsal pars flaccida (Shrapnell 1832; Funnell and Laszlo 1982; Kohllöffel 1984). As the names imply, the pars tensa is generally stiffer and less deformable than the pars flaccida, whose shape is easily altered by small static pressure differences on either side of the membrane (Decraemer and Dirckx 1998; Dirckx et al. 1998). Indeed the pars flaccida is often assumed to play a role in maintaining equal static pressures on either side of the TM: It is thought to buffer small changes in middle ear volume produced by the absorption or generation of middle ear gas by and from the blood (Hellstrom and Stenfors 1983; Sadé et al. 1996; Decraemer and Dirckx 1998). Further, although only the pars tensa is directly coupled to the ossicular chain, it has been suggested that the pars flaccida, whose motions appear independent of the pars tensa, plays a role in equalizing low-frequency sound pressures across the pars tensa, thereby indirectly reducing the motion of the pars tensa in response to low-frequency sounds (Kohllöffel 1984; Teoh et al. 1997).

The mammalian TM is generally supported by the tympanic bone, which also can form parts of the bony ear canal and the bony wall of the middle ear air spaces. There is a wide variation in the size and extent of the tympanic bone and its support for the TM, which varies from "U-shaped" to nearly circular (van der Klaauw 1931; Keen and Grobbelaar 1941; Henson 1974). In general, the ring of tympanic bone around the TM is more complete in carnivores and primates but also in selected species of other families, including the chinchilla (*Chinchilla laniger*) and the guinea pig (*Cavia procellus*). The ring appears more "U-shaped" in nonplacental mammals and in many small mammals, for example, rats, mice, and shrews (Fleischer 1973, 1978; Henson 1974). The pars flaccida occurs at the edge of the pars tensa that is not bound by the tympanic bone (Henson 1974). The absolute area of the pars tensa varies widely among mammals (Hunt and Korth 1980; Nummela 1995; Coleman and Ross 2004). There is also significant variation in the absolute and relative size of the pars flaccida (Kohllöffel 1984; Vrettakos et al. 1988;
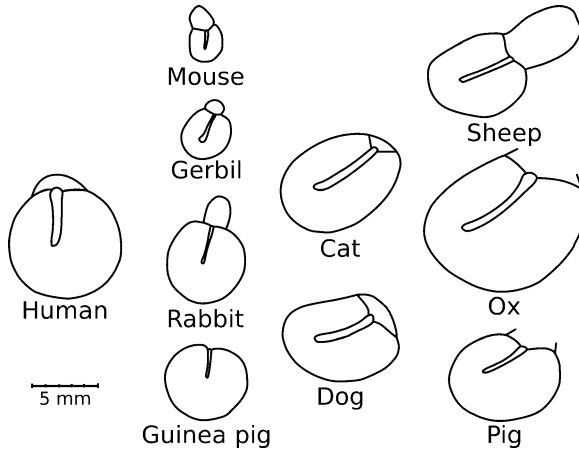
Fig. 3.3 Outlines of the TM from ten mammalian species, including human, cat, dog, mouse, gerbil (*Meriones unguiculatus*), rabbit *(Oryctolagus cuniculus)*, guinea pig (*Cavia procellus*), sheep, ox (*Bos taurus*), and pig (*Sus scrofa*). The *pars tensa* of the TM is attached to the arm of the manubrium (the long thin structure). The *pars flaccida* is not apparent or complete in all of the specimens (Redrawn from Decraemer and Funnell 2008. The mouse TM is after Reijnen and Kuijpers 1971; the cat after Khanna 1970; the sheep after Lim 1968b; the gerbil after Decraemer and Funnell 2008; others after Fumagalli 1949.)

Rosowski et al. 1997); the variation in the relative size of flaccida and tensa has been associated with variation in the low-frequency hearing capabilities of different mammalian species (Kohllöffel 1984; Rosowski et al. 1997) (Fig. 3.3).

3.3.5.5 The Middle Ear Air Spaces

The middle ear air spaces behind the TM of terrestrial vertebrates act as a compressible cushion that allows large sound-induced motions of the TM. The motion of the TM is related to the difference in sound pressures acting on its middle ear and external-ear surfaces, where, in mammals, the sound pressure in the middle ear air spaces is generally related to the acoustic impedance of the air spaces and the inward and outward displacements of the entire TM (Møller 1965; Huang et al. 1997; Ravicz and Rosowski 1997). (As discussed previously, in nonmammalian terrestrial vertebrates, e.g. amphibians, reptiles and birds, there are often other pathways for sound to enter the middle ear, and these other pathways complicate the computation of sound pressure within the middle ear air spaces just medial to the TM.) Motions of both the pars flaccida and tensa contribute to the volume displacement of the TM with sound, and therefore both contribute to the sound pressure within the mammalian middle ear air spaces. Therefore, when the middle ear air spaces are intact, as noted earlier, motions of the pars flaccida indirectly affect the motion of the pars tensa (Kohllöffel 1984; Teoh et al. 1997).

The contribution of the middle ear air spaces to sound-induced motions of the pars tensa and the coupled ossicles depends on the relative impedances of the air spaces and the rest of the middle ear. There is significant variation in the relative and absolute magnitudes of these impedances in different mammalian species (Dallos 1970; Rosowski 1994). In some species (mouse [*Mus musculus*], chinchilla, guinea pig), the impedance of the air spaces (which is inversely related to the air-space volume) dominates the middle ear input impedance and opening the middle ear air spaces to the outside produces large increases in middle ear sound transfer in response to low sound frequencies, whereas in others (e.g., human, cat, kangaroo rat [*Dipodomys merriami*]) the impedance of the TM and the attached ossicles and cochlea is generally larger than the impedance of the middle ear air spaces, and opening the middle ear air spaces produces small changes in middle ear sound transfer (Dallos 1970; Rosowski 1994).

The middle ear air spaces of different species are often broken into several compartments by partial bony partitions (Kampen 1905; Werner 1960; Møller 1965). These partitions include: the incomplete bony septum that separates the middle ear air spaces of cat-like carnivores, feloids, into two compartments connected by a narrow foramen (e.g., Møller 1965; Huang et al. 1997), the bony wall around the facial nerve that nearly separates the human tympanic cavity from the generally larger air volume within the mastoid antrum and air cells (Zwislocki 1962; Molvær et al. 1978; Stepp and Voss 2005), and the many interconnected air spaces of the chinchilla (Browning and Granich 1978) and gerbil (*Meriones unguiculatus*: Lay 1972) middle ear. There is also a wide variation among species in the total volume of air enclosed in the middle ear air spaces (Rosowski 1994); not surprisingly this volume correlates with body size (Huang et al. 1997). However, individual species of similar body size can have significantly different middle ear air volumes: Compare the 0.25-cc air spaces of the guinea pig with the 2.0-cc middle ear air volume of the chinchilla (Rosowski 1994). There is also significant variation in the middle ear air volumes within species; this has been best demonstrated in humans (e.g., Molvær et al. 1978), in whom the total middle ear volume in an adult human ear varies by a factor of 10 among individuals.

The bones of the skull that enclose the middle ear air spaces differ from species to species (Kampen 1905; Werner 1960; Novacek 1977) and include the tympanic, endotympanic, petrous, and the squamous among others. These differences have been used in the past as an indicator of the phylogenetic relationship between different mammalian species (e.g., Hunt 1974; Novacek 1977). This role has been superseded by direct genetic analyses (e.g., Johnson et al. 2006).

In many mammalian species the bones covering the middle ear air spaces form smooth nearly egg-shaped bony protrusions on the posteroventral surface of the skull (van der Klaauw 1931; Keen and Grobbelaar 1941). This protrusion is often called the bulla (e.g., Legouix and Wisner 1955), though in some instances of common use "bulla" is used to refer to the entire middle ear apparatus within the bulla. Not all mammalian species have a smooth egg-shaped bulla surrounding their middle ear; e.g., in many primates (including humans) the middle ear air spaces are

more deeply embedded in the bones of the posterodorsal skull and these species are sometimes said to have no bulla (e.g., Keen and Grobbelaar 1941).

Any discussion of the mammalian middle ear air spaces needs to point out that the spaces remain aerated due to the periodic opening of the Eustachian tube (e.g., Ingelstedt 1976; Elner 1976). In mammals the bilateral Eustachian tubes are supported by cartilage walls and open via muscular contraction and the generation of static pressure differences between the middle ear and the pharynx (Swarts and Rood 1990; Doyle 2000). A similar mechanism must be in place for opening the Eustachian tube in crocodylids and birds, where this tube can simultaneously aerate both of the connected middle ears (Wever and Vernon 1957; Rosowski and Saunders 1980). In lizards and anurans the middle ears are aerated through large open connections to the pharynx. Blockage of the mammalian Eustachian tube via experimental manipulation or pathology leads to replacement of the air with body fluids (e.g., Wiederhold et al. 1978; Doyle et al. 1980; Alper et al. 1997).

3.3.5.6 Correlations Between Mammalian Middle Ear Structure and Hearing Capabilities

Although all mammalian middle ears have some basic features in common, including three ossicles, a TM and air-filled middle ear spaces, there are large differences in the form and size of these components within the order of mammals (Fleischer 1973; Rosowski 1994; Nummela 1995). Differences in size should not be surprising, as the entire body of the smallest mammals (e.g., the dwarf shrew [*Suncus etruscus*] with a body mass of 0.01 kg) would fit into the middle ear air spaces of the largest terrestrial mammals (the African elephant [*Loxodonta africans*] with a body mass of 6,000 kg; Rosowski 1994). It is worthwhile noting that although ear size varies regularly with body size, the relationship is not isometric: the ratio of the body weights between the elephant and shrew above is about 6×10^5:1, while the ratio of the areas of their TMs is about 100:1 (Hunt and Korth 1980). If the TM areas were to scale with body weight, we might expect the two TMs to have a ratio of $(6 \times 10^5)^{2/3}$:1, or 7,100:1. Therefore, in smaller animals the ear is larger relative to body size than it is in larger animals (Nummela 1995). (The use of the 2/3 power in the preceding relationship is a dimensional factor to compensate for comparing the change in body mass—a measure of body volume— with TM area).

It is also known that there are large variations in the hearing capabilities of different mammalian species (Fay 1988; Heffner and Heffner 1992, 2010), and significant correlations have been observed between the frequency range of hearing, body size, and form and size of the middle ear structures across mammals of different species (Heffner and Heffner 1992; Hemilä et al. 1995; Coleman and Colbert 2010). These correlations suggest that species of large body size have larger middle ear structures than species of small body size, are more sensitive to sounds at frequencies below 1 kHz than smaller mammals, and are less sensitive to sounds of frequencies greater than 10 kHz.

There also appears to be significant correlation between some basic structural types of the middle ear and the frequency range of hearing (Rosowski 1992). Fleischer (1973, 1978) separated the middle ears of a large collection of mammals into three groups based on ossicular structure, including (see Fig. 3.2): (1) a "free-standing" ossicular group in which the malleus and incuse are only supported by mobile ligaments, as exemplified by humans, chinchillas, and guinea pigs; (2) a "micro-type" middle ear in which the middle ear structures are small and there is a large bony or firm ligamentous connection between the malleus and the tympanic bone, as exemplified by bats, shrews, marsupials, and many murid rodents, including rats of the genus *Rattus* and mice of the genus *Mus*; (3) an "intermediate" or "transitional" form in which there is a small but firm connection bony between malleus and the tympanic ring, for example, small bony connections between the anterior malleus and the tympanic ring have been described in cats and gerbil (Rosowski et al. 1999). These classes of ossicular structure are associated with differences in hearing capabilities: Ears with free-standing ossicular chains tend be more sensitive to sounds of frequencies below 500 Hz than other ears and less sensitive to sounds above 20 kHz; microtype ears tend be more sensitive to sounds above 10 kHz and less sensitive to sounds below 2 kHz; intermediate ears, however, seem to show high sensitivity to both low and higher sounds (Rosowski 1992). Of course the preceding relationships are complicated by the observations that small animals with small middle ear structures tend to have micro-type ears.

3.3.5.7 Middle Ear Function in Marine Mammals

Marine mammals evolved from mammals that arose on land and then re-entered the sea (Nummela et al. 2007). In doing so they returned to an environment in which the animal was surrounded by a fluid with an acoustic impedance more similar to that of the animal's body and inner ear. In truly aquatic animals, such as cetaceans, the external ear appears vestigial and the pathway by which sound is conducted from the environment to the inner ear is not well defined (Ketten 1994, 2000; Rosowski 1994). Although the ears of cetaceans still maintain the presence of an ossicular chain, their size and structure is much different from that observed in terrestrial mammals (Ketten 1992, 2000; Nummela et al. 1999). Further, the analog of the tympanic membrane is much different in structure from the fairly thin and fragile tympanic membranes of terrestrial mammals (Ketten 1992, 2000). Nonetheless most models of middle-function in cetaceans assume ossicular conduction of sound to the inner ear (Hemilä et al. 1999; Tubelli et al. 2012), and use measurements and estimates of ossicular mass, and stiffness to define sound transmission through these middle ears (Hemilä et al. 2001; Miller et al. 2006; Zosuls et al. 2012). Such models have been used to compute audiograms for different cetaceans (Hemilä et al. 1999, 2001; Tubelli et al. 2012).

3.4 Issues in Comparative Middle Ear Function

3.4.1 The Frequency Dependence of the Middle Ear Mechanism

Comparisons of the frequency dependence of middle ear sound transfer in terrestrial vertebrates with aerated middle ears and ossicular coupling of the TM to the inner ear demonstrate significant differences between columellar and three-ossicle ears (Saunders and Johnstone 1972; Rosowski 2003; Manley 2010): The sound-induced velocity of the columella in frogs, reptiles, and birds is limited in response at sound frequencies greater than 4 or 5 kHz (Manley 1972b; Saunders and Johnstone 1972; Gummer et al. 1989b), whereas the velocity of the stapes in many mammalian species continues at a high level past 10–20 kHz (Saunders and Johnstone 1972; Wilson and Bruns 1983; Ruggero and Temchin 2002; Ravicz et al. 2008). Manley (1972b) suggested that the root of the limitation in high-frequency response in the nonmammalian ossicular system is flexibility in the coupling between the TM and columella that acts as a low-pass filter. As described previously, mammals also have flexible couplings within their ossicular chains that limit the high-frequency response of the middle ear (Zwislocki 1962; Guinan and Peake 1967; Willi et al. 2002), but this limitation occurs above 10 kHz in many mammals (though at lower frequencies in humans: Willi et al. 2002). Whether the rotational lever action of the mammalian ossicular system is better able to transfer high-frequency sound energy from the TM to the inner ear (Manley 2010) needs further study.

3.4.1.1 Are Three Ossicles Better than One?

Although it has been suggested that the three-ossicle mammalian middle ear is inherently superior in the conduction of high-frequency sound to the inner ear, as has been discussed previously, a precise mechanism for this advantage has never been defined, although there are several hypotheses that consider alterations in the mode of motion of the ossicles at higher frequencies (e.g., Fleischer 1978; Puria and Steele 2010). Three-ossicle ears and columellar ears all have nonrigid ossicular components that produce reductions in the high-frequency response of middle ear, and both also contain lever mechanisms to assist in the transformation of sound in air to sound in the inner ear. Indeed, because it is generally thought that the middle ear of mammals developed independently of the columellar ears of birds and reptiles, arguments that one form of middle ear is superior to the other may not be productive. Instead, one might argue that both columellar and three-ossicle middle ears allow the animals they serve to function in the environmental niche to which they have adapted.

As discussed previously, one known difference provided by multiple ossicles is the ability for independent muscular control of the position of the TM-malleus and the stapes. Because of the presence of the ossicular joints, the tensor tympani

can produce significant changes in the static position of the tympanic membrane without producing large displacements of the stapes (Marquet 1981; Hüttenbrink 1988). Similarly, the stapedius muscle can significantly stiffen the stapedial–-vestibular joint (the annular ligament between the stapes footplate and the oval window of the inner ear) without producing large changes in the position of the malleus and tympanic membrane (Pang and Peake 1986). The joints also help isolate the inner ear from sudden changes in air pressure that produce large inward and outward motions of the TM (Hüttenbrink 1988), where the potential hazard to changes in air pressure were increased when the middle ear became enclosed by bone.

Another hypothesis concerning the benefit of three-ossicles in the mammalian ear is the presence of a moment of inertia about the rotational axis of the ossicular chain (e.g., Puria and Steele 2010; Lavender et al. 2011). Coincidence of the rotational axis and the center of gravity of the ossicle will greatly reduce the contribution of ossicular mass to the middle ear function. On the other hand, ossicular specializations that lead to significant differences between the location of the ossicular center of gravity and the rotational axes could enhance the middle ear's response to sounds conducted through the bone by substrate and other vibrations (Bárány 1938; Mason 2003; Puria and Rosowski 2012).

3.4.1.2   The Middle Ear and Audibility

It has long been noted that the middle ear controls which sounds reach the inner ear with enough stimulus power to produce an auditory sensation (e.g., Waetzman and Keibs 1936). Indeed, the concept of middle ear pathology producing a "conductive" hearing loss is built on the concept that sounds must pass through the middle ear before they can be sensed by the inner ear. An academic question that is often asked is, How does the action of the normal middle ear shape the frequency-dependence of hearing? More specifically, does the function of the middle ear define the frequency range to which the entire ear is most sensitive?

The best answer to the question above is "Not entirely." After all, the sensitive range of the inner ear must play some role (e.g., Ruggero and Temchin 2002), and in mammals, the frequency dependence of sound transfer through the external ear also contributes to the transfer of sound from the environment to the cochlea (e.g., Wiener et al. 1966; Shaw 1974). Further, the acousto-mechanical load of the inner ear on the stapes plays a significant role in determining the frequency dependence of the middle ear (e.g., Møller 1965; Allen 1986; Rosowski et al. 2006). Comparisons of middle ear transfer characteristics that are corrected for the action of the external ear do accurately predict the range of best hearing in a number of mammalian species (e.g., Dallos 1973; Rosowski 1991; Puria et al. 1997), but usually do a poorer job of defining the extreme limits of low and high-frequency sensitivity. (One exception is Ravicz et al. (2008), who found a good match between the high-frequency roll off of the audiogram and middle ear transfer function in the gerbil.)

3.4.2 The Role of the TM in Sound Conduction

One of the biggest current questions in the study of the middle ear concerns the precise mechanisms involved in the coupling of sound to the ossicular system by the TM. The complex motion patterns on the surface of the mammalian TM that are induced by sounds of frequencies above a few kHz (Khanna and Tonndorf 1972; Tonndorf and Khanna 1972; Rosowski et al. 2009) have been interpreted in a number of ways. Tonndorf and Khanna (1970) suggested that these complex patterns indicated the breakup of the motion of the TM into multiple out-of-phase modal maxima, which would lead to a reduction of the average motion of the TM and a decrease in the efficacy of middle ear function at higher frequencies (Rosowski et al. 2009). Others (Puria and Allen 1998; Parent and Allen 2007, 2010) have suggested that the conical mammalian TM acts like an acoustic horn that is better matched to the impedance of air at the external edges of the cone, and that sound energy travels from the edges toward the ossicular attachment at the center of the TM. A third hypothesis is that the presence of multiple closely spaced natural frequencies of the TM ensures that the membrane can be set into motion by nearly any sound frequency (Fay et al. 2006). A related but fundamentally different hypothesis is based on observations of a combination of traveling waves on the mammalian TM surface and larger more uniform simple motions of the TM (Cheng et al. 2010; de La Rochefoucauld and Olson 2010; Rosowski et al. 2011). These studies suggest that simple low-order natural response of the TM to sound dominate the motion of the TM, even at high sound frequencies. Which of these hypotheses is most correct has yet to be established. Also, although there are significant differences in the shape and ultrastructure of the TM between mammals and nonmammalian terrestrial vertebrates, there have been no studies of the detailed motion of the TMs of nonmammalian vertebrates. The latter might be useful in evaluating the effect of the significant structural differences.

3.4.3 The Two-Window Hypothesis: Evidence for and Against a Normal "Third Window"

One of the most fundamental hypotheses of middle ear function in terrestrial vertebrates is that the inner ear is sensitive to waves of fluid displacement produced by a difference in sound pressure across the two windows between the inner ear and the middle ear. It is this near instantaneous fluid wave that deforms the hair-cell support or accessory structures tied to the ciliary bundles in amphibians; displaces the basilar membrane in reptiles, birds, and mammals; and is responsible for the launching of the traveling wave in the mammalian cochlea. The two-window hypothesis has been used to explain not only the function of the normal middle ear, but also the effects of middle ear pathology on hearing function and some forms of reconstructive middle ear surgery (e.g., Peake et al. 1992; Rosowski et al. 1995;

Merchant and Rosowski 2010). The evidence for this hypothesis includes (1) experiments in which the window-pressure difference was externally controlled (e.g., Wever and Lawrence 1950; Voss et al. 1996) that demonstrate the largest responses when the stimuli at the two windows are of equal level and opposite phase; (2) observations of near equality between the sound-induced volume displacements of the stapes and round window during stimulation with air-conducted sound (Kringlebotn 1995; Stenfelt et al. 2004); and (3) the positive results of middle ear reconstructive procedures designed to maximize the difference in the sound pressures at two functional cochlear windows (e.g., Shambaugh 1954; Wüllstein 1959; Merchant et al. 1995).

Although the two-window hypothesis can explain much of the inner ear's response to sound conducted via the normal middle ear, and in cases of specific middle ear pathologies—e.g., interruption of the ossicular chain (Peake et al. 1992)—there are inner-ear pathologies that it does not readily explain. One such case is pathological or developmental immobilization of the round window. The two-window hypothesis would predict that round-window immobilization would prevent stimulation of the inner ear by the direct middle ear route; however, while humans with such a disorder demonstrate significant hearing loss, the hearing loss is smaller than expected (e.g., Harrison et al. 1964; Linder et al. 2003; Mansour et al. 2011). Attempts to block the round window in animal experiments also produced hearing losses that are smaller than expected (e.g., Tonndorf and Tabor 1962).

One possible explanation for the failure of round-window immobilization to produce large hearing losses is the presence of either other paths for sound energy to leave the inner ear, or compressible elements for energy storage within the inner ear (Shera and Zweig 1992). These other paths or compressible elements would act like normal "third windows" into the inner ear that would allow a difference in the magnitude of the motion of the round and oval window and allow stimulation of the inner ear when either the stapes or round-window was immobilized (Ranke 1953; Tonndorf and Tabor 1962;). Obvious candidates for such pathways are direct communications between the fluid spaces of the inner ear and the brain cavity, including the cochlear and vestibular aqueducts, the vascular channels to the brain and the interstitial spaces around the neurons innervating the inner ear (Békésy 1960; Tonndorf and Tabor 1962; Rask-Andersen et al. 1977; Nakashima et al. 2000).

3.5   Summary

This chapter summarizes the structural adaptations that help conduct sound energy within the environment to the inner ears of different vertebrate species. It also describes some of the inner-ear adaptations required to sensitize the inner ear in terrestrial vertebrates to sound conducted by the middle ear. One lesson of this chapter is that adaptations within the different parts of the ear do not occur in isolation. Put another way, the efficacy of the varied middle ears of terrestrial

vertebrates is tightly tied to the adaptations to the periotic system of the inner ear in these same species that enabled the different middle ears to produce significant sound-induced fluid motion within the inner ear. This coupling of adaptations in the inner ear and the middle ear also leads to parallelisms in the sensitivity of the inner ear and middle ear to sounds of different frequencies. For example, in common laboratory mice whose inner ear contains neurons tuned to frequencies between 2 and 60 kHz (Taberner and Liberman 2005) the middle ear is very stiff and the velocity of the stapes is small (<0.1 mm-s^{-1}-Pa^{-1}) at frequencies less than 1 kHz but is maintained at high levels out to 30–40 kHz (Saunders and Summers 1982). Another example is the human inner ear, which is thought to contain hair cells tuned to frequencies from near 50 Hz to near 20 kHz (Merchant 2010) and has a highly compliant middle ear that produces stapes velocities greater than 0.1 mm-s^{-1}-Pa^{-1} in response to sound stimulus frequencies as low as 100 Hz but not at frequencies above 10 kHz (Aibara et al. 2001). The similarity between the frequency range of inner-ear sensitivity and the frequency range of effective middle ear sound transfer is a common feature in terrestrial vertebrates and supports the notion that the inner and middle ears of vertebrates adapted in parallel to meet the demands required for species survival.

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