FEATURED ARTICLE

Middle Ear Biomechanics: Smooth Sailing

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Introduction

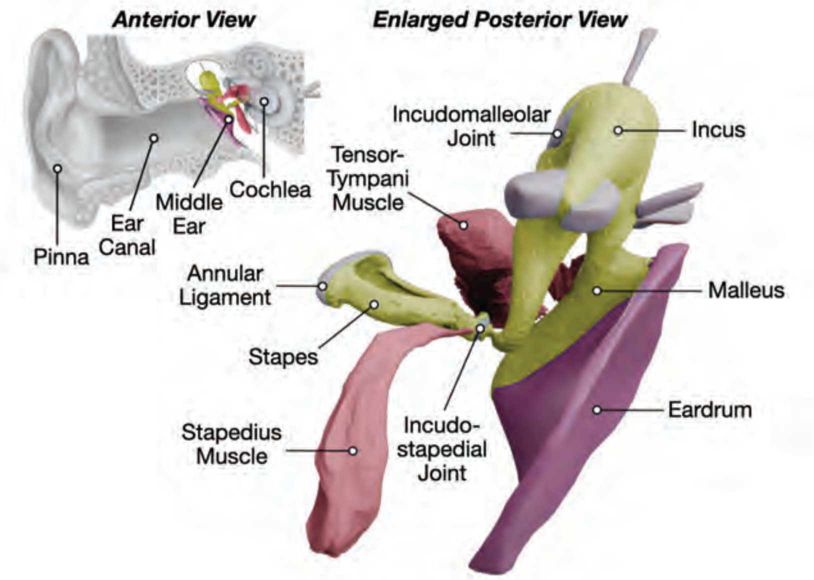
The ability to hear is vital and profound, enabling spoken communication and the emotional power of music, among many other experiences. Two ears allow us to localize sounds, alerting us to potential dangers both day and night. Furthermore, the production and perception of sound requires little energy.

Sound is diffracted by the external part of the ear, the pinna, then passes through the ear canal and vibrates the middle ear (**Figure 1**; see **Multimedia1** at acousticstoday.org/puriamm). Although the sensing itself occurs inside the snail-shaped cochlea of the inner ear deep within the skull, the middle ear is tasked with efficiently transmitting sound from the low-density, highly compressible air in the ear canal to the high-density nearly incompressible fluid in the cochlea (Brownell, 2017). Vibrations of the middle ear apparatus are necessary for sensitive hearing, so damage due to trauma or progressive disease processes, which can often be treated through surgery, reduces the efficiency and frequency range of the middle ear.

The Passage of Sound

From far away, the passage of sound through a healthy middle ear appears straightforward and unsurprising; it happens so faithfully and efficiently under normal

Figure 1. *Anatomy of the human middle ear as reconstructed from micro computed tomography imaging. Key structures are labeled, except for suspensory ligaments that are shown in* ***gray****. For context, the anterior view shows the interconnection between the pinna, ear canal, middle ear, and cochlea. A three-dimensional representation of the middle ear that can be rotated and examined can be found at* ***Multimedia1*** *at acousticstoday.org/puriamm. Figure was generated by Andrew Tubelli of the OtoBiomechanics Group at the Eaton-Peabody Laboratories (EPL).*



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circumstances that the underlying complexities of the process can easily slip by unnoticed. Contemplating the middle ear is like watching a sailboat from the shore where, despite any rough seas, headwinds, or obstacles, all we typically notice is a craft gliding gently along. But from the perspective of being on deck, we see that the boat is constantly responding to changing conditions; it can move up and down and side to side as well as forward, the sails can move wildly as well as billow, the boom can swing violently from one side to the other as well as stay in one place, and so on. In a similar way, the middle ear manages to smoothly transmit airborne sounds to the fluid-filled cochlea in a consistent manner and for a wide range of frequencies, albeit with some transit time involved. However, when we zoom in and measure motions of the eardrum and the chain of three small bones (called the ossicles) using modern holographic and laser Doppler methods, we see that middle ear structures often appear to move chaotically and in directions that at first glance might seem to be off course.

Much like the sailboat, the mammalian middle ear has evolved to have a diverse range of forms, sizes, and specializations. In fact, evolutionary biologists regard the mammalian middle ear as a particularly beautiful example of the repurposing of body parts without disrupting an animal's survival needs, based on the idea that the unique design of the ossicles evolved from upper and lower jaw bones in reptiles (Gould, 2010). Reptiles, amphibians, and most fishes do not hear frequencies above 5 kHz, whereas the upper limit of hearing in birds is 8–12 kHz. Mammals, in contrast, have upper limits ranging from 10 kHz (elephants) to 85 kHz (laboratory mice) and even higher for echolocating animals (Heffner and Heffner, 2016). High-frequency hearing likely evolved in mammals as a means to localize sound (Heffner and Heffner, 2016).

Continuing with the boat analogy, where a smooth ride is important for a pleasant experience, the magnitude of middle ear sound transmission varies relatively smoothly as the frequency of an input tone is varied. Although it has been a challenge to understand exactly how the thin eardrum and three middle ear ossicles joined by flexible joints can accomplish this feat so well, advances in imaging, vibrometry, and computational methods during the past two decades have revealed much about this fascinating biological system.

Journey Through the Middle Ear: An Overview

Our journey begins by recognizing that middle ear sound transmission in mammals is fairly smooth, in that its amplitude does not vary much with frequency, and it also does not limit hearing because the middle ear typically has a wider bandwidth than the cochlea. Next, we observe that it takes a fair amount of time for sound to travel through the middle ear, which is surprising for a wideband system. We then see that much of this middle ear delay is due to the spatially varying mechanical properties of the eardrum, that the motion of the eardrum surface is far from smooth, especially at higher frequencies, and that the shapes of the malleus and eardrum are related in interesting ways.

We then visit the question of whether the three-ossicle middle ear found only in mammals might have any functional advantages over the single-ossicle systems found in birds and lizards, such as providing protection to the cochlea or supporting the action of the two middle ear muscles. We explore how studies involving mathematical models complement experimental studies to enhance our understanding of middle ear structure–function relationships. Finally, we touch on how middle ear research straddles comparative, developmental, clinical, and surgical fields and has inspired a new class of hearing aid that directly vibrates middle ear structures. By the conclusion of this journey, we hope it is clear why the middle ear provides a rich environment for interdisciplinary research and collaboration.

Wideband Sound Transmission

Sound diffracted by the pinna in a direction-dependent way passes through the ear canal and vibrates the flexible cone-shaped eardrum. This in turn vibrates a chain of three small bones, the ossicles, called the malleus (attached to the eardrum), incus, and stapes (in archaic books they may be called the hammer, anvil, and stirrup). The ossicles are housed in an air-filled space, the middle ear cavity, and are suspended in place by ligaments. The ossicles are connected by two fluid-filled flexible joints and have two muscles attached to them. The footplate of the stapes, whose area is typically more than an order of magnitude smaller than that of the eardrum, completes the transmission as it moves in and out of the cochlear entrance (**Figure 1**; see **Multimedia2** at acousticstoday.org/puriamm).

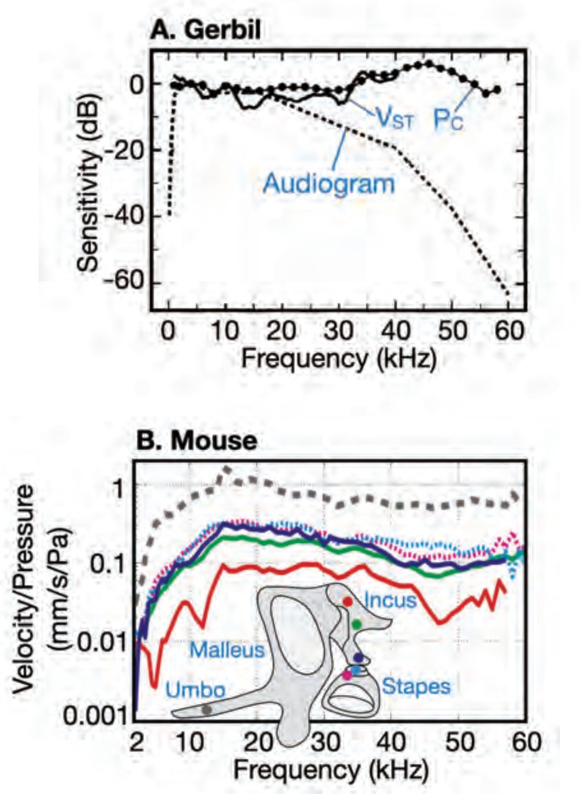


Figure 2. *Middle ear sound transmission in two high-frequency-hearing animals.* ***A:*** *comparison in gerbil of middle ear transmission, represented by stapes velocity (V_{ST};* ***solid line****) and cochlear pressure (P_C;* ***dotted line****) plotted versus hearing sensitivity, represented by an audiogram (****dashed line****). The audiogram has a narrower frequency bandwidth than V_{ST} or P_C, suggesting that hearing is limited by the cochlea rather than by the middle ear. Figure adapted from Ruggero and Temchin, 2002.* ***B:*** *middle ear transmission magnitudes in an individual mouse ear over the 2- to 60-kHz range, represented as ratios of ossicular chain velocity and ear canal pressure. The various lines represent different locations measured on the ossicles, as indicated by dots with matching colors (****inset****). Figure adapted from Dong et al., 2013, with permission.*

The middle ear transmits sound over a broad frequency range that varies by species. Generally, animals with smaller heads can hear higher frequencies because only the shorter wavelengths of these sounds can vary enough between their two ears to assist in sound localization, a significant advantage for predator avoidance. It is now generally accepted that the bandwidth of hearing is limited by the capabilities of the cochlea, not by those of the middle ear (**Figure 2**; Ruggero and Temchin, 2002).

Remarkably, sound transmission through the middle ear varies relatively smoothly with frequency across a wide frequency range. This appears to hold true for large mammals like elephants, all the way down to small mammals like gerbils (**Figure 2A**) or mice (**Figure 2B**) that can hear up to 85 kHz. This smooth wideband transmission through the middle ear involves a significant amount of delay.

Middle Ear Modeling and Delay

Sound takes a surprisingly long time to pass through the middle ear. For humans and domestic cats, the delay is approximately 100 μs, which corresponds to the amount of time needed for sound to travel through a 3.4-cm-long air-filled tube (Puria and Allen, 1998). This delay is remarkable considering that the largest structural dimension in the middle ear, the eardrum diameter, is significantly smaller than this hypothetical tube length. Models composed of a few coupled second-order resonances representing different parts of the middle ear were not able to capture the observed delays and could not realistically represent the full frequency bandwidth of the middle ear.

This led to the idea of representing the eardrum and ossicles as two coupled transmission lines (Puria and Allen, 1998). Inherent in the behavior of a transmission line is a propagation delay through the system, with little loss. Incorporating transmission lines into circuit models led to a better description of measurements at both low and high frequencies and also captured the observed delays in the middle ear.

That there is significant delay as a surface wave travels from the eardrum periphery toward the attached malleus handle is supported by several direct measurements in gerbils (de La Rochefoucauld et al., 2010), humans (Cheng et al., 2013), and, more recently, mice (Dong et al., 2013). Waves traveling around the eardrum circumference have also been observed (Cheng et al., 2013). Although it remains unclear what functional role, if any, middle ear delay plays in hearing, a potential scenario is described in ***A Possible Connection Between Hearing and Seeing***.

An explanation of transmission delay through the eardrum first requires delving into its material composition. The mammalian eardrum is unique among vertebrates in having a composite structure with distinct radial and circumferential

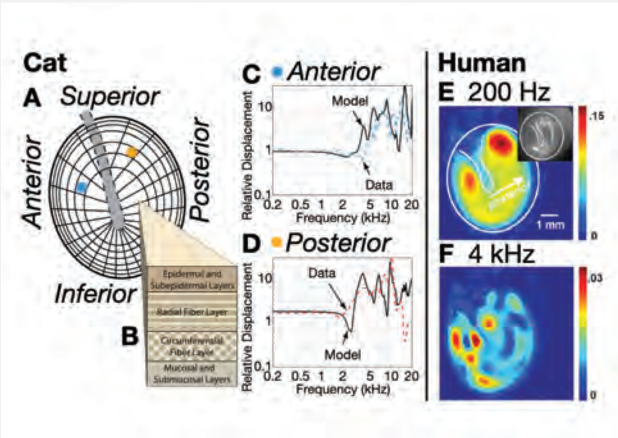


Figure 3. *Eardrum structure and motion. The arrangement of radial and circumferential collagen fibers throughout the eardrum (**A**) and its multilayered construction (**B**) is depicted. Displacements of the cat eardrum relative to malleus motion as a function of frequency for a single point on the anterior (**C**) and posterior (**D**) sides of the eardrum are shown.* ***Blue and red dashed lines*** *indicate a measurement;* ***black lines*** *are model calculations (Fay et al., 2006). Spatial vibration patterns are measured on the surface of a human eardrum (**E, inset**) in response to a 200-Hz tone (**E**) and a 4-kHz tone (**F**), showing multiple modes (Cheng et al., 2013). Colors indicate the displacement magnitude normalized by ear canal pressure in micrometers per pascal.*

collagen-fiber layers (**Figure 3A**) sandwiched between subepidermal and submucosal layers (**Figure 3B**). Modeling this ultrastructure has been challenging because it is difficult to know how to ascribe material properties to the layers of this complex structure. Most early finite-element models treated the eardrum as an isotropic material, with the same properties in the circumferential and radial directions. However, dynamic motion measurements combined with constitutive modeling and composite shell modeling suggest that the material properties of the two fiber layers are very different, such that an orthotropic eardrum with different properties in those two directions is more representative of the physiology (Fay et al., 2006; O'Connor et al., 2017). Now that we know that delay is involved in eardrum transduction, what does eardrum motion look like and how does it relate to this observed delay?

Discordant Eardrum Modes

Experiments have shown that eardrum motions vary sharply in amplitude above a few kilohertz for individual points on the eardrum (**Figure 3**, **C** and **D**) and across the entire eardrum surface for fixed frequencies (**Figure 3**, **E** and **F**). Despite the seemingly chaotic motions of nearby points on the eardrum surface (see **Multimedia2** at acousticstoday.org/puriamm for links to animations of the human eardrum), the motion of the malleus has been shown to be wideband and relatively smooth. This is somewhat akin to a sail on a sailboat moving in a variety of ways on its surface but nonetheless managing to propel the mast, and hence the boat, smoothly forward.

A plausible explanation for this is that all of these modes of vibration are summed together along the length of the relatively rigid malleus handle that attaches to the eardrum. Using one of the earliest finite-element models of the eardrum, Funnell et al. (1987) showed that regardless of the complex vibration patterns of the eardrum surface, the overall sound transmission through the middle ear has smooth frequency characteristics.

Summing It All Together

Why are multiple large-amplitude eardrum modes present in the first place, and do they serve a functional purpose? This remained a mystery for many decades until modeling studies found that the multiple seemingly discordant resonances without significant energy dissipation on the eardrum are summed together at the malleus to produce greater sound transmission to the cochlea at high frequencies, resulting in greater overall hearing sensitivity but with a smooth response (Fay et al., 2006).

That discordant eardrum motions are integrated by the malleus, thus resulting in smooth but delayed middle ear transmission, has been experimentally verified through a series of cleverly designed measurements (Milazzo et al., 2017). Using a pressure-click stimulus in the gerbil ear canal, various locations on the eardrum were shown to have filtered bandlimited responses, but the click reappeared with fidelity in the motion of the malleus after some delay. When simple mathematical models of strings of different lengths, each of which reproduces a bandlimited response to a click akin to the motions on the eardrum surface, are combined, the result is similar to the original click but with a delay. These modeling studies suggest that it is the radial collagen fibers that are mistuned (think of them as strings with different lengths) and are critical for high-frequency sound transmission through the middle ear.

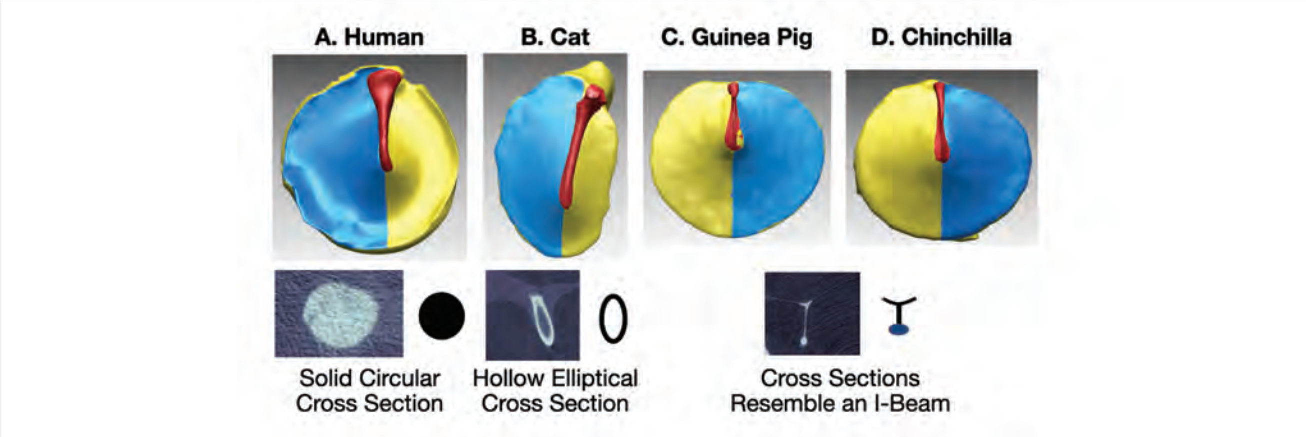


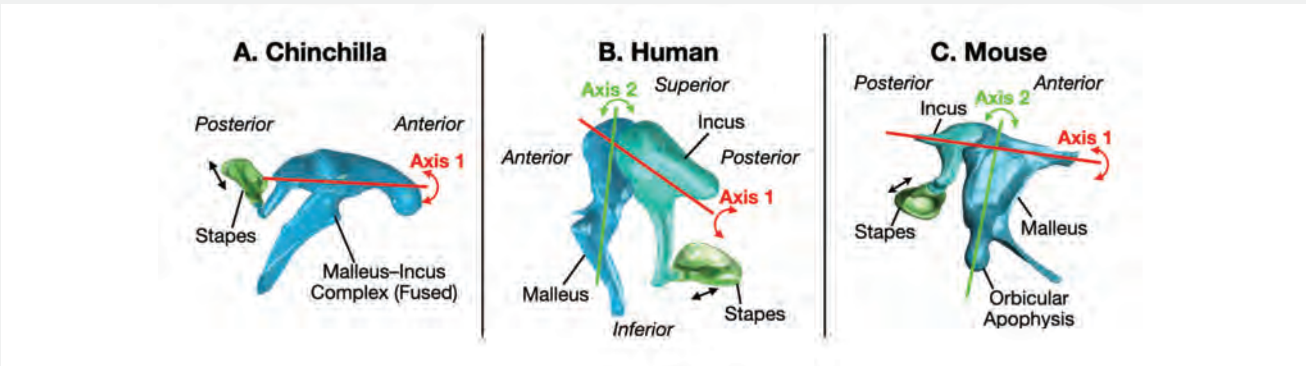
Figure 4. ***Top row:*** *comparison of the anterior (**yellow**) vs. posterior (**blue**) eardrum areas divided by the malleus (**red**) for human (**A**), cat (**B**), guinea pig (**C**), and chinchilla (**D**). The anterior-to-posterior area ratios are 1.6, 1.9, 1.1, and 1.0, respectively.* ***Bottom row:*** *comparison of malleus cross sections from micro computed tomography imaging, with round cross sections for human and cat and I beam-like cross sections for guinea pig and chinchilla. Adapted from Puria and Steele, 2010, with permission.*

The circumferential collagen fibers may be needed to strengthen the eardrum and maintain its curvature. In addition, modeling studies have shown that the circumferential fibers are needed for good low-frequency transmission (Fay et al., 2006). The output of the eardrum comes together at the malleus handle, which in our sailboat analogy is like the mast. But although boat masts are often designed to have rounded cross sections, like the human and cat malleus handles, this is not always the case.

Eardrum Symmetry and Malleus Shape

In the human and cat, the malleus divides the eardrum into unequal sections (**Figure 4**, **A** and **B**, respectively). What's more, the human malleus has a circular, mostly solid cross section (**Figure 4A**), and the cat malleus has an elliptical, fluid-filled cross section (**Figure 4B**), which makes it lighter than if it were all bone. Both of these rounded cross sections appear to be well-suited to rocking or twisting motions with respect to the long axis of the malleus handle. Such motions could be promoted by the larger area on one

Figure 5. ***A:*** *rocking motion of the fused malleus–incus complex in chinchilla with respect to an anterior–posterior axis (Axis 1).* ***B:*** *rocking motion of the human malleus–incus complex about Axis 1 dominates at low frequencies. At higher frequencies, eardrum asymmetry could cause rotation of the malleus about Axis 2 to minimize the moment of inertia, while the flexible joint between the malleus and incus could still allow the incus to rotate with respect to Axis 1.* ***C:*** *for the mouse, Axis 1 dominates for low frequencies, whereas Axis 2 is thought to dominate for high frequencies.* ***A*** *and* ***B*** *adapted from Puria and Steele, 2010, with permission;* ***C*** *generated by Hamid Motallebzadeh of the OtoBiomechanics Group at EPL.*



side of the malleus as well as anterior–posterior differences in the radial-fiber lengths and material properties of the eardrum (Puria and Steele, 2010).

In the guinea pig and chinchilla, on the other hand, the malleus divides the eardrum right down the center (**Figure 4**, **C** and **D**, respectively) and has a cross section that distinctly resembles an I beam along most of its length. This cross section appears to be better suited for transverse motion but not for twisting or rotation of the malleus handle. Although motions of the ossicles along all three dimensions have been reported for the cat and human, a systematic study of the relationships between these diverse malleus morphologies and their three-dimensional motions remains lacking. Regardless of the type of malleus motion, it must be efficiently and smoothly transmitted to the incus and stapes.

Ossicular Axes of Rotation

Malleus motion is transferred to the incus and then the stapes, which, in turn, induces smoothly varying fluid pressure in the cochlea (**Figure 2A**). There are several rotations of the ossicles that take place to make this happen. In various species, an anterior–posterior axis passing through the center of mass of the malleus–incus complex (Axis 1, shown in **Figure 5A** for chinchilla; **Figure 5B** for human; **Figure 5C** for mouse) supports rocking motions that provide a small amount of leverage due to the handle of the malleus being longer than that of the incus (see **Multimedia2** at acousticstoday.org/puriamm for links to animations of the human eardrum and ossicles from a finite-element model).

As previously mentioned, the round cross section of the malleus handle and asymmetrical eardrum attachment in human and cat could also support rotations with respect to another axis oriented along the superior–inferior direction (Axis 2, shown in **Figure 5B** for human). Calculations of the moments of inertia of the malleus in all three perpendicular directions indicate a value that is much smaller for rotations around Axis 2 than for rotations around the two other axes. This suggests a preferred rotation around this lower-inertia inferior–superior axis for higher frequencies because the joint connecting the malleus to the incus is likely to be more flexible at higher frequencies, thus permitting more of this motion.

The anatomy of the mouse malleus–incus complex (**Figure 5C**) is similar in many microtype high-frequency-hearing mammals such as bats and mice that have a bony protuberance called the orbicular apophysis (Mason 2013). These animals also use Axis 1 at low frequencies but are thought to switch to Axis 2 at higher frequencies, which is orthogonal to Axis 1 and passes through the orbicular apophysis. However, the evidence for these different axes of rotation in mouse, based on one-dimensional vibration measurements at several locations (Dong et al., 2013), is not strong. Bending of the malleus and incus at higher frequencies, rather than just translations or rotations of the bones as rigid bodies, is likely to play an important role in sound transmission.

Now that we have examined the biomechanics of the eardrum and ossicular chain, we return to the question of what evolutionary pressures may have led to the repurposing of jaw bones and their accompanying joints into a flexible three-ossicle linkage between the eardrum and cochlea in mammals.

Why Three Ossicles?

The mammalian middle ear is unique among vertebrates in having three ossicles with two intervening flexible joints and two dedicated muscles. What might be some advantages of this unusual design in comparison to the single-ossicle middle ear of birds and lizards? As mentioned previously, the malleus-to-incus length ratio, averaging close to a factor of two across mammals, provides some leverage to facilitate the air-to-fluid impedance-matching function of the middle ear. Although this can be considered one functional advantage of having three ossicles, it provides a relatively small benefit when compared with the stiletto heel-like force multiplication provided by the eardrum-to-footplate area ratio. The area ratio is approximately a factor of 20 among a range of mammals, but this cannot be claimed as a mammalian advantage because birds and lizards have similar area ratios. Thus, most of the impedance matching of the middle ear is achieved by the area ratio and not the ossicular lever ratio. So, what other functional advantages might this three-piece flexible design provide?

Safety Engineering

The late surgeon and researcher at the Stanford Otolaryngology Department and Palo Alto VA Hospital Richard Goode (1935–2019) often quipped "The designer of the middle ear must have been a safety engineer." By this, he meant that the flexibility of the two joints between the three ossicles affords some degree of protection to the cochlea. This has indeed been shown to be the case. In everyday life, our middle ears cushion the effects of very large and sudden pressure changes, such as when we cough or sneeze. Also, when there is a large difference in static pressure between the middle ear cavity and the environment, the flexible ossicular chain and eardrum are able to expand outward or squeeze together until pressure equalization can occur, thus reducing the amount of stress exerted on the cochlea, which might otherwise receive damage to its delicate hair cells (Brownell, 2017).

Impulsive Sounds

It is known that sudden impulsive sounds tend to cause far more damage to the cochlear hair cells than sounds with the same energy spread out over time. It was recently shown that flexibility of the malleus–incus joint might provide a protective means of spreading out the energy of impulsive sounds over time as they travel toward the cochlea (Gottlieb et al., 2018). Experimental measurements with impulsive stimuli showed that the shape of the impulse reaching the cochlea becomes higher in amplitude and more sharply focused in time after the malleus–incus joint is fused. This suggests that the normal flexible joint disperses the energy over time, thus broadening the impulse and lowering its peak amplitude.

Two Muscles, Two Joints

Another potential advantage of this design could be the need for independent activity by the two middle ear muscles. These are the tensor tympani muscle, which attaches to the malleus handle and pulls it inward, and the stapedius muscle, which attaches to the head of the stapes and pulls it to the side (**Figure 1**). Recent evidence for the evolutionary coadaptation of the two muscles and joints comes from the observation that rodents like the guinea pig and chinchilla that have a fused malleus–incus joint also have a reduced or complete lack of stapedius muscle function (Mason, 2013). The fused malleus–incus joint and relatively large middle ear cavities of these animals may be important for improving low-frequency hearing.

The stapedius muscle has been studied extensively, and it is generally agreed that it forms part of an acoustic reflex arc that operates with a latency of about 20 ms, after which point it is able to attenuate sounds below a few kilohertz. This reflex arc is thought to help protect the cochlea against loud, long-duration sounds. However, its onset is too slow to protect against sudden impulsive sounds, such as a gunshot, that can be very damaging to the cochlea.

The function of the tensor tympani muscle is not well-established. Contractions of the tensor tympani muscle are elicited by tactile stimulation of facial areas, a puff of air against the eyes, and during speaking. Many subjects can voluntarily contract their tensor tympani muscles and perhaps also their stapedius muscles.

A Possible Connection Between Hearing and Seeing

Recently, an intriguing new idea has been posited for the role of the tensor tympani muscles. It was shown that when people move their eyes to one side, pressure waves of opposite polarities can be measured in the two ear canals, with the polarities reversing when the eyes move to the other side (Gruters et al., 2018). One interpretation of this is that the pressure waves are produced by the left eardrum being pulled inward by the tensor tympani muscle and the right eardrum relaxing outward as the eyes move to the right and vice versa as the eyes move to the left. Because a tense eardrum is thought to reduce transmission time through the middle ear, it is possible that linking eardrum tension to eye movement could allow the interaural time difference cues used for sound localization (Heffner and Heffner, 2016) to be adjusted as the eyes move, such that the brain perceives a shift in the location of the sound in accord with the new visual field, even though the ears themselves have not moved. One can speculate that this might be one of the reasons for the existence of substantial delay in the middle ear to begin with. Many of the middle ear biomechanics concepts we have encountered above have found their way into several application areas that are now discussed.

The Breadth and Depth of Middle Ear Biomechanics

The middle ear apparatus comes into play in several areas spanning scientific, surgical, and technological fields. Many aspects of middle ear research have not been covered here, but review articles can be found elsewhere (e.g, Puria et al., 2013), including ongoing work on developmental biology (Anthwal et al., 2013), evolutionary biology (Manley, 2010), and comparative anatomy (Rosowski, 2013). Much of the present treatment relates to hearing via air conduction through the middle ear. Sound can also reach the cochlea via bone-conduction pathways, in which the middle ear also plays an important role (Stenfelt, 2013).

Otologists often perform surgery to restore function in damaged or diseased middle ears, such as patching a damaged eardrum, replacing an eroded incus with a prosthesis, or bypassing a stapes immobilized by otosclerotic bone growth with a prosthesis inserted into a hole in the footplate (Merchant and Rosowski, 2013). Before surgery can be performed, however, a proper diagnosis has to be made. The noninvasive diagnosis of middle ear pathologies is an important area of clinical research, particularly in the case of newborns because they cannot participate in standard clinical tests (Keefe et al., 2012). Surgery is more common in patients with middle ear pathologies. For patients with cochlear damage, a clinician will typically prescribe an acoustic hearing aid to provide amplified sound. However, a number of groups have been developing implantable hearing aids that amplify sound by mechanically vibrating the ossicles. A major advantage of these devices is reduced feedback, which allows greater amplification and wider bandwidth. Although these new devices cost more than traditional acoustic hearing aids, they can enable improved sound quality and better hearing in noisy environments (Puria, 2013). A nonimplantable alternative has also been developed that contacts the eardrum from the ear canal side and mechanically vibrates the malleus (Puria, 2013).

Conclusions

Like a trusty sailboat with a seasoned captain, the mammalian middle ear is able to navigate through a sea of complexity to provide a smooth and graceful experience of the environment. And much as a small, nimble craft must adapt to the perils of seafaring in different ways than a larger, more robust ship, the middle ear too has evolved in clever ways to suit the needs of different species. Although a multitude of vibration modes on the eardrum and many varied motions of the ossicles are involved in this voyage, the middle ear reveals none of these secrets until we get on board and examine it using modern measurement tools and computational approaches. Finally, by straddling the worlds of acoustics, mechanics, materials science, fluid mechanics, biology, medicine, computational modeling, and technology, the middle ear provides an ideal playground for an interdisciplinary crew of adventure-seeking collaborative researchers.

Acknowledgments

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