



## Research Paper

# Tympanic-membrane and malleus–incus-complex co-adaptations for high-frequency hearing in mammals

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## ABSTRACT

The development of the unique capacity for high-frequency hearing in many mammals was due in part to changes in the middle ear, such as the evolution of three distinct middle-ear bones and distinct radial and circumferential collagen fiber layers in the eardrum. Ossicular moment(s) of inertia (MOI) and principal rotational axes, as well as eardrum surface areas, were calculated from micro-CT-based 3-D reconstructions of human, cat, chinchilla, and guinea pig temporal bones. For guinea pig and chinchilla, the fused malleus–incus complex rotates about an anterior–posterior axis, due to the relatively lightweight ossicles and bilateral symmetry of the eardrum. For human and cat, however, the MOI calculated for the unfused malleus are 5–6 times smaller for rotations about an inferior–superior axis than for rotations about the other two orthogonal axes. It is argued that these preferred motions, along with the presence of a mobile malleus–incus joint and asymmetric eardrum, enable efficient high-frequency sound transmission in spite of the relatively large ossicular masses of these species. This work argues that the upper-frequency hearing limit of a given mammalian species can in part be understood in terms of morphological co-adaptations of the eardrum and ossicular chain.

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## 1. Introduction

Mammals are unique among vertebrates in their ability to hear high-frequency sounds. While reptiles, amphibians, and most fish do not hear above 5–7 kHz (Heffner and Heffner, 1998), and birds do not hear above 8–12 kHz (Dooling et al., 2000), mammals have upper-frequency limits of hearing that range from 10 kHz (for the elephant) to 90 kHz (for the wild mouse), and even higher for some species that use echolocation (Heffner and Heffner, 2008).

It is well established that the capacity for high-frequency hearing in mammals provides an important means for localizing sound. While studying the auditory cortex, Masterton et al. (1969) observed that there was an inverse correlation between the head size of an animal and its upper-frequency limit of hearing, and concluded that head size was related to sound-localization ability (Masterton et al., 1969; Heffner and Heffner, 2008). There are three primary types of sound-localization cues: (1) Inter-aural time difference (ITD) cues, which are dominant primarily at low frequencies (typically below 500 Hz), and allow horizontal-plane localization; (2) Inter-aural level difference (ILD) cues, or spectral

difference cues (e.g. due to “head shadow”), which are dominant at higher frequencies, and also enable horizontal-plane localization; and (3) Pinna-diffraction cues, which assist in vertical-plane localization and become important for frequencies above about 5 kHz in human (Shaw, 1966), and above about 8 kHz in cat (Muscant et al., 1990; Young et al., 1996). As the frequency increases, the wavelength becomes shorter, so in order to maintain the ILD cues for smaller heads it becomes necessary to hear higher frequencies. Thus, for both horizontal and vertical-plane localization, the ability to hear beyond 5–10 kHz becomes important – especially for animals with smaller head sizes.

Of the various physical characteristics that distinguish mammals from other vertebrates, several pertain to the biomechanics of hearing. For example, the presence of three distinct middle-ear bones is one of the criteria used for classifying fossilized or living animals as mammals (Masterton et al., 1969; Colbert and Morales, 1991); the presence of distinct radial and circumferential collagen fiber layers of the tympanic membrane (Lim, 1968; Funnell and Laszlo, 1982; Rabbitt and Holmes, 1986; Fay et al., 2006) is also unique to mammals; as are the elongation of the basilar membrane (Manley, 1971) and motility of the organ of Corti outer hair cells, which are responsible for the high sensitivity of the mammalian cochlea (Brownell et al., 1985). These adaptations, in addition to others, serve to endow mammals with their unique capacity for

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high-frequency hearing. While the mechanics of the cochlea and outer hair cells is being studied in a significant number of laboratories, less attention has been paid to the role of the middle-ear structures in mammalian high-frequency hearing, and this is the primary subject of the present work.

It has been known for some time that there is tremendous variability in the size and shape of the middle-ear ossicles across different mammalian species (Doran, 1879; Hemila et al., 1995; Nummela, 1995; Schmelzle et al., 2005), and that the morphometry of the eardrum also varies across species (Funnell and Laszlo, 1982). The mass of the malleus–incus complex is often thought to limit the upper-frequency of hearing (Hemila et al., 1995), but in practice this appears not to be the case (Ruggero and Temchin, 2002). We propose that in small mammals (e.g. guinea pig and chinchilla), with lighter and fused malleus–incus complexes, the prevalent motion of these bones across all frequencies is the classical “hinging” motion about the anterior–posterior axis, as can be inferred from motion measurements on guinea pig ossicles (Manley and Johnstone, 1974). However, in larger mammals (e.g. human and cat), with heavier malleus and incus bones but a flexible malleus–incus joint, we argue that a new “twisting” mode along the inferior–superior axis of the malleus may reduce the effective inertia and thus allow the middle ear to transmit sound at higher frequencies than would be possible otherwise. An asymmetry in the anterior and posterior eardrum areas, which is seen in human and cat but not in guinea pig and chinchilla, is hypothesized to allow pressure in the ear canal to induce such a twisting motion of the malleus. Thus, for a given mammal, anatomical co-adaptations of the tympanic membrane and malleus–incus complex appear to be determining factors of the upper-frequency limit of the middle ear. Preliminary aspects of this work were previously presented (Puria et al., 2007, 2006).

## 2. Materials and methods

### 2.1. Temporal bone preparation

Cadaveric temporal bones from human, cat, chinchilla, and guinea pig were used for the reported morphometry measurements. To facilitate micro-CT scanning, each temporal bone was dissected to fit into as small a bore size as possible while keeping all structures of interest intact. Depending on the specimen, the bore diameter ranged from 20.5 to 39 mm. To prevent the tissue from drying out, each temporal bone was wrapped in cellophane before being placed inside the scanner bore. The human temporal bones were obtained from the Palo Alto VA Hospital, the cat temporal bone came from the Carolina Biological Supply Company ([www.carolina.com](http://www.carolina.com)), the guinea pig temporal bone came from the laboratory of Nik Blevins (MD) at Stanford University, and the chinchilla temporal bone was shipped frozen from Northwestern University by Mario Ruggero (PhD).

### 2.2. Micro-CT imaging

The vivaCT 40 micro-CT scanner (SCANCO Medical AG; [www.scanco.ch](http://www.scanco.ch)), located at the Palo Alto VA Hospital, was used for this study. The scanning parameters and procedures, as well as segmentation and volume reconstruction methods, have been described in two previous publications (Sim et al., 2007; Sim and Puria, 2008).

### 2.3. Determining ossicular moments of inertia (MOI)

It was possible to produce segmentations of the ossicles from the scanned images using automatic contouring techniques, since the

density of the bone was sufficiently high compared to that of the surrounding air and soft tissue (Sim et al., 2007). Stacks of segmented slices were then combined to construct the 3-D volumes of each ossicle. These 3-D volumes were then used to calculate the centers of mass and moments of inertia (MOI) for the malleus, incus, and the combined malleus and incus. For the present study, each bone was assumed to have a uniform density, though in the future more accurate results might be obtained by taking into account the different density of the vascular regions within each bone.

An “inertia matrix” was initially calculated for each ossicle based on the scan reference frame. The inertia matrices were also recalculated using a coordinate system relative to the center of gravity of each given rigid body, such that all off-diagonal terms were zero simultaneously. The principal axes and corresponding three principal MOI were calculated from the eigenvectors and eigenvalues of the inertia matrix for each bone in the human and cat cases, and for the fused malleus–incus and stapes in the chinchilla and guinea pig cases. See (Sim et al., 2007) for calculation details. The MOI calculations were all normalized by density.

### 2.4. Determining eardrum surface areas

To determine the eardrum anterior and posterior surface areas, the 3-D eardrum shapes were reconstructed after performing manual segmentation of eardrum slices. The manubrium was segmented and registered in the same reference frame as the eardrum surface. The segmentation and reconstruction were performed using the vivaCT 40 scanner software, and the resulting data were exported in STL (Standard Tessellation Language) format and then imported into another program called RapidForm (INUS Technology). The axis along the length of the manubrium was used to divide the eardrum into anterior and posterior sides, and RapidForm was used to calculate the eardrum surface area between the manubrium and the tympanic annulus for each side.

## 3. Results

### 3.1. Principal moments of inertia

At frequencies below a few kHz, middle-ear dynamics are limited by the suspensory ligaments and tendon attachments of the ossicles to the surrounding bony walls, which behave approximately as springs with stiffnesses that decrease as frequency increases (Sim and Puria, 2008). At high frequencies, the rotational and translational inertias of the ossicles are thought to be the limiting factors affecting the transmission of sound from the eardrum to the cochlea. A cross-species comparison of ossicular rotational inertias is presented here, to provide a basis for examining the relationship between these inertias and the upper-frequency limit of hearing in each species.

The three-dimensional reconstructions of the guinea pig and chinchilla ossicles are shown in Fig. 1, and those of the human and cat ossicles are shown in Fig. 2. Orthogonal rotational axes, corresponding to the maximum (red), minimum (blue), and intermediate (green) rotational moment(s) of inertia (MOI), are shown passing through the centers of gravity of the stapes and fused malleus–incus complex in Fig. 1, and through the centers of gravity of the stapes and unfused malleus and incus in Fig. 2. For the fused malleus–incus complex of the chinchilla and guinea pig, the axes for the minimum MOI (blue solid lines in Fig. 1) lie along the anterior–posterior direction. The minimum MOI for the chinchilla is around 3–4 times smaller than the intermediate and maximum MOI, and for the guinea pig it is 1.7–2.3 times smaller.

The axis for the minimum MOI of the unfused human malleus lies along the superior–inferior direction, which is perpendicular

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