



Research Paper

A sum of simple and complex motions on the eardrum and manubrium in gerbil

Ombeline de La Rochefoucauld^{a,*}, Elizabeth S. Olson^b^a Department of Otolaryngology, Head and Neck Surgery of Columbia University, 630 West 168th Street, New York, NY 10032, USA^b Departments of Otolaryngology, Head and Neck Surgery and Biomedical Engineering, Columbia University, 630 West 168th Street, New York, NY 10032, USA

ARTICLE INFO

Article history:

Received 1 July 2009

Received in revised form 29 September 2009

Accepted 26 October 2009

Available online 28 October 2009

Keywords:

Motion

Manubrium

Tympanic membrane

Gerbil

Middle ear

ABSTRACT

Based on comparisons of ear canal and scala vestibuli pressures the gerbil middle ear transmits sound with a gain of ~25 dB that is almost flat from 2 to 40 kHz, and with a delay-like phase corresponding to a 25–30 μ s delay. How the middle ear is able to transmit sound with such high temporal and amplitude fidelity is not known, and is particularly mysterious given the complex motion the ossicles and tympanic membrane (TM) are known to undergo. To explore this question, we looked at the velocities of the manubrium and along a line on the TM. The TM motion was complex, and could be approximated as the combination of a wave-like motion and an in-and-out piston-like motion. The manubrium underwent bending at some stimulus frequencies and therefore its motion was not like a rigid body. It had a complex motion with frequency fine structure that seemed likely to be derived from resonances on the drum-like TM.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

In the gerbil ear the relationship between intracochlear pressure at the stapes and pressure within the ear canal is simple: there is a gain of ~25 dB, and a delay-like phase amounting to ~25–30 μ s. The high frequency limit of this simple behavior is at least 40 kHz but hard to set precisely due to pressure variations in the ear canal at high frequencies (Ravicz et al., 2007). The low frequency limit is about 1–2 kHz with an open bulla (Dong and Olson, 2006; Olson, 1998; Ravicz et al., 1996). Roughly similar behavior is observed in some other mammals, for example cat (Puria and Allen, 1998) and chinchilla (Slama et al., 2008). The flat transmission amplitude is perplexing because above a few kHz the motion of the mammalian ossicles and tympanic membrane are known to be quite complex; similarly, it is not clear what middle ear components are responsible for the delay. We undertook a study to observe tympanic membrane (TM) and ossicular motion along what we considered the likely transmission path through the middle ear. Only motion in one direction was measured; this is not a study of 3-D motion. The present work discusses results along the manubrium and in a line part way across the TM from the umbo. The frequency structure observed on the TM could be seen either as traveling waves or modal patterns as discussed by Decraemer et al. (1989), Khanna and Tonndorf (1972), and Puria and Allen

(1998) or more recently by Rosowski et al. (in press). The manubrium bent in response to sound stimuli as has been reported previously in cat (Decraemer and Khanna, 1994; Decraemer et al., 1991). The frequency dependence of the manubrium motion showed regular peaks and valleys in frequency, with the spacing between adjacent peaks/valleys decreasing with increasing frequency, as is predicted for the modal frequencies of a drum-head. This behavior is likely due to the (drum-like) TM forcing the manubrium motion. The TM motion was complex, and could be approximated as a sum of a wave motion (with waves traveling at a speed of ~11 m/s) and an in-and-out, quasi-piston motion. The delays of the wave-like motion are much longer (~180 μ s considering the 2 mm gerbil TM radius) than the observed ~25–30 μ s middle ear delay.

2. Materials and methods

2.1. Animal preparation

Experiments were performed on 10 gerbils (Exp#41-42-43-44-45-46-47-49-50-59): four a few hours post mortem (Exp#42-44-46-50) and six alive (Exp#41-43-45-47-49-59). Data were also collected post mortem for four of the six live experiments (Exp#41-43-47-49). The care and use of animals were approved by the Institutional Animal Care and Use Committee of Columbia University. Most of the animal preparation has been described previously (de La Rochefoucauld et al., 2008). The main difference is in the ear canal (EC) entrance, which was enlarged in this project to view the entire manubrium, the umbo and part of the TM as illustrated in Fig. 1A. The TM is composed of two parts. Pars tensa appears relatively “tense” and is the major component of the tympanic

Abbreviations: TM, tympanic membrane; EC, ear canal; PF, pars flaccida; LPM, lateral process of the malleus

* Corresponding author. Tel.: +1 212 305 3993.

E-mail addresses: odelarochefoucauld@gmail.com, ombelinerossier@yahoo.fr (O. de La Rochefoucauld), eao2004@columbia.edu (E.S. Olson).

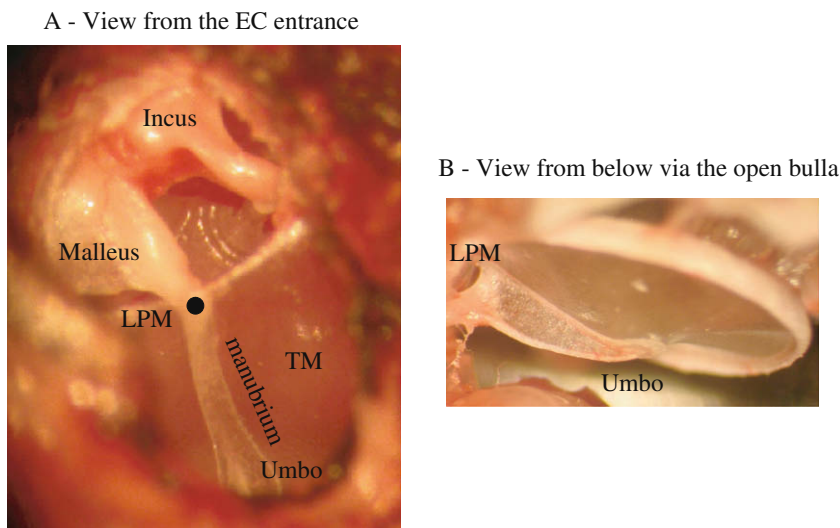


Fig. 1. (A) View of the middle ear from the enlarged EC entrance. The pars flaccida has been removed from its position just above the malleus and incus. The pars tensa of the tympanic membrane (TM), the umbo, the lateral process of the malleus (LPM), the malleus, the incus and the head of the stapes are visible with this approach. The manubrium extends from the LPM to the umbo. (B) Side view of the manubrium to illustrate the shape of the manubrium. The gerbil manubrium is ~2–2.5 mm from LPM to umbo edge.

membrane, whereas pars flaccida (PF) is a small circular region that appears “flaccid” (Teoh et al., 1997). The velocity of pars tensa was measured. The PF was opened widely using a small hook and was left open for most of the experiments (PF was sealed using saran wrap for Exp#43). The bulla was left open (Exp#41–45–47–49–50) except for Exp#43 (the bulla hole was sealed with clay) and for Exp#59 (the bulla was not opened at all). These variations did not much affect the qualitative results presented in this paper. Fig. 1B represents the view of the manubrium, the blade-shaped part of the malleus that is connected to the TM, as seen from the side through the open bulla. Viewed through the ear canal as in Fig. 1A, the manubrium is narrow at the lateral process of the malleus (LPM) and widens at the umbo (the distal tip of the malleus), where it takes a spoon-like shape. We expect the blade-shaped part of the manubrium to resist bending, whereas the spoon-shaped part appears more flexible.

2.2. Experimental set-up

The same data acquisition system as described previously was used during these experiments (de La Rochefoucauld et al., 2008). Measurements were performed under open-field stimulation using a Sony earphone (diameter ~ 1 cm) positioned ~1.5 cm from the EC entrance and oriented toward it so that the main sound path was through the EC. Either a $\frac{1}{4}$ " Brüel & Kjær microphone or a $\frac{1}{2}$ " Brüel & Kjær microphone with probe tube was used to calibrate the sound field ~1 cm from the EC entrance (and 0.5 cm from the speaker). Frequency sweeps from 250 Hz to 50 kHz were applied at a level of 80 or 90 dB SPL at the microphone. Velocity was measured without reflecting beads using the confocal microscope/heterodyne laser interferometer developed by Khanna and colleagues (de La Rochefoucauld et al., 2008; Khanna et al., 1996). The sound system was mounted on the same post as the animal. The velocity was measured at many points (with x, y, z coordinates recorded) on the TM and along the manubrium from the umbo to the LPM. The laser's axis of measurement was along the line of view illustrated in Fig. 1A.

3. Experimental results

3.1. The tympanic membrane motion

Results presented in Figs. 2 and 3 are from one experiment (Exp#45) and are representative. The velocity was measured at

the umbo and on the TM. These data were recorded 30–80 min post mortem. The bulla and PF were open. The sound pressure level was set to 80 dB SPL at the microphone.

Fig. 2 shows the velocity amplitude (A) and phase (B and C) compared to the velocity measured at the center of the umbo (R#43). TM responses were measured along a line in the anterior region of the TM as illustrated by the positions of the dots in Fig. 2. The measurement locations were up to a distance 650 μ m from the umbo center, about a third of the ~2 mm radius of the gerbil TM (Nummela, 1995; Ravicz et al., 1996). All points located on the umbo (thick lines) moved in phase, with about the same amplitude. The TM velocity amplitude varied much more and could be up to four times greater or less than the umbo motion depending on the location and frequency. Phase responses when unwrapped extended over 5 cycles (Fig. 2B) and the “raw” phase responses are included in Fig. 2C. The unwrapped phase responses had a cascade-like shape, they were either ~ in phase with the umbo or delay-like (rapidly decreasing with frequency) depending on the frequency regions. For example, the relative phase between the umbo and a point far on the TM (R#58) was ~0 up to 8 kHz, delay-like from 8 to 20 kHz, at ~–4 cycles from 20 to 38 kHz, delay-like from 38 to 42 kHz and at ~–5 cycles above. When the phase responses were not delay-like, they were ~ proportional to a full number of cycles. This observation suggests that the TM is characterized by a combination of a quasi-piston-like motion (the TM and the umbo are in phase, they move together with all locations approximately in phase) and a slow traveling wave motion. (Note that in a standing wave, half cycle phase jumps would result, not the full cycle phase jumps we observed. The full cycle jumps call for a piston-like component of motion.) This combination of motions is illustrated by a simple conceptual model presented in Section 4.

From the measured velocity amplitude (A) and phase (θ) at several locations, we can determine the displacement $d(x, f) = (A/(2\pi f)) \cos(2\pi f t + \theta)$ as a function of position, at fixed frequency and different times in the cycle (t). In Fig. 3 the same experimental data as in Fig. 2 (Exp#45) are plotted as displacement versus position at six times in the cycle. Results at six frequencies are shown. Points on the umbo are represented using thicker symbols (R#43–50). The umbo moved as a rigid unit that either simply translated (displacements similar all along the umbo) or translated and rotated (producing a “tilting” of the umbo). In either case, the displacements along

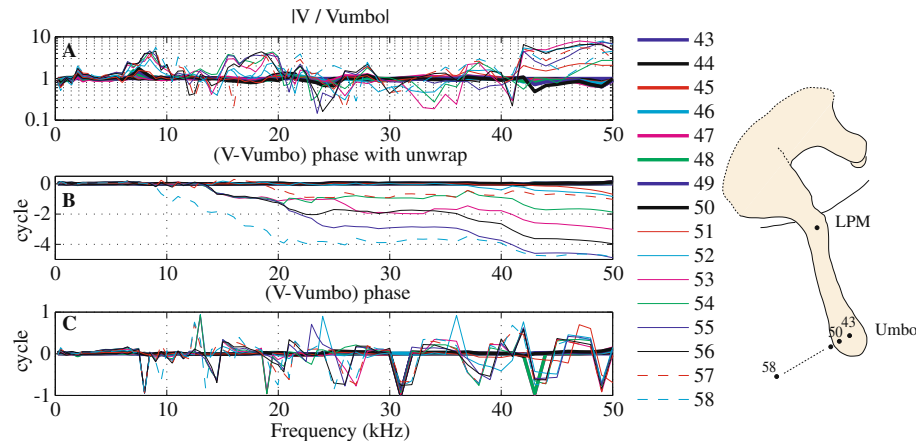


Fig. 2. The diagram illustrates the recording positions following a line from the center of the umbo (R#43) to a point at $\sim 650 \mu\text{m}$ on the anterior section of the tympanic membrane (R#58). Each number corresponds to one recording position: from R#43 to 50 on the umbo (thick lines) and from R#51 to 58 on the TM (thin lines). (A) Velocity amplitude compared to umbo velocity (R#43). (B) Velocity phase relative to the umbo (R#43). (C) Same as (B) but the phase was not unwrapped. (Exp#45, 30–80 min post mortem, PF and Bulla open, 80 dB SPL at the microphone.)

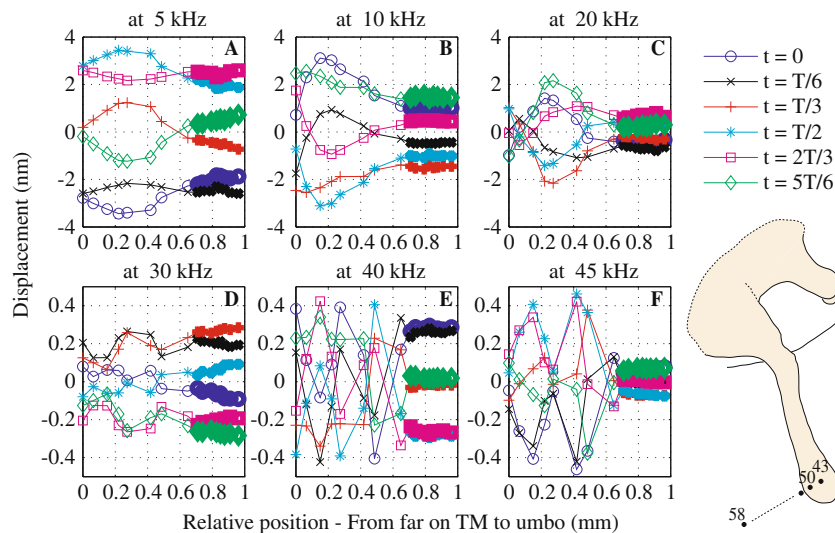


Fig. 3. Displacement as a function of position (from far on the TM to the umbo) at six times ($t = 0, T/6, 2T/6, 3T/6, 4T/6$ and $5T/6$). Each panel (A–F) corresponds to one frequency, respectively: 5, 10, 20, 30, 40 and 45 kHz. Thicker lines correspond to positions on the umbo (R#43–50) and thin lines to positions on the TM for a total distance of $650 \mu\text{m}$ on the TM (R#51–58). The diagram on the right illustrates the recording positions. Each number corresponds to one recording position. (Exp#45, 30–80 min post mortem, PF and Bulla open, 80 dB SPL at the microphone.)

the umbo were well-described by a straight line segment. The TM in contrast did change shape. It moved in-and-out with the umbo, with a wave-like motion superimposed. This is most apparent 30 kHz and below (Fig. 3A–D). Even if all the points look $\sim$ in phase at 30 kHz in Fig. 2B, when plotted as displacement versus position (Fig. 3D) we can clearly see the superposition of the two motions. At 5 kHz, the TM displacement described half a wavelength over a distance of $\sim 0.56 \text{ mm}$. At 30 kHz, there was one wavelength over $\sim 0.45 \text{ mm}$ and at 45 kHz, there were two wavelengths over $\sim 0.6 \text{ mm}$. From these curves, we calculated a wave speed on the TM (wavelength $\times$ frequency) of $\sim 11 \text{ m/s}$. The wave-like motion of the eardrum is well known from studies in human temporal bone (Cheng et al., 2009; Tonndorf and Khanna, 1972) and cat (Decraemer et al., 1989, 1999; Khanna and Tonndorf, 1972). The cat data were analyzed for wave speed, with results ranging from 10 to 100 m/s (Fay et al., 2005; Puria and Allen, 1998). A recent analysis of wave speed in cat, chinchilla and human (Rosowski et al., in press) found values that ranged from 25 to 60 m/s.

To summarize our TM measurements in gerbil, it appears that under sound stimulation the tympanic membrane undergoes a complex motion with the superposition of an in-and-out quasi-piston-like motion and a slow traveling wave.

3.2. Motion of the manubrium

Velocity was measured along the manubrium from the umbo to the LPM. Fig. 4 presents results from one experiment (Exp#59) and is a representative case. Fig. 4A shows the relative velocity along the manubrium compared to the umbo distal edge velocity (R#20). There was a gradual decrease of the amplitude as the measurement position moved from the umbo to the LPM (R#27) with the amplitude of the LPM velocity being approximately half that of the umbo. Above 18 kHz, the response contained fine structure, with dips and peaks at fixed frequencies that became more pronounced as the location moved away from the umbo (minima in the amplitude responses at 24, 36, 42 and 48 kHz illustrated by

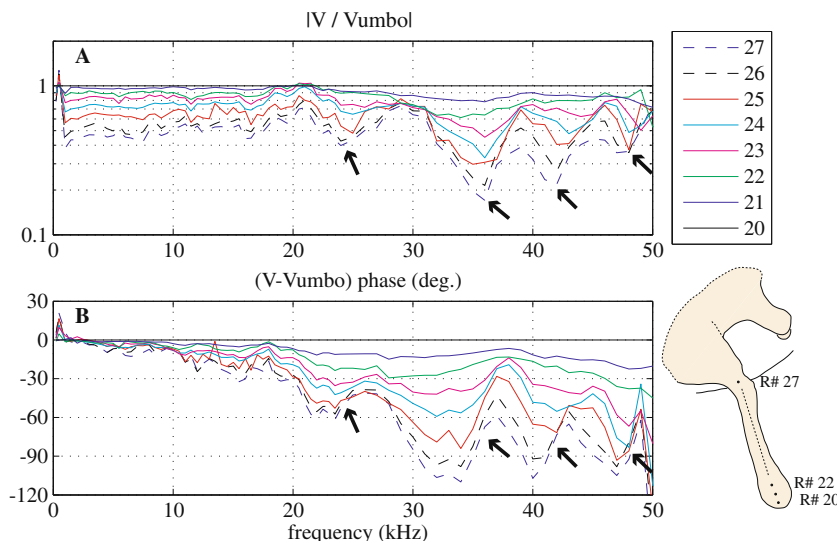


Fig. 4. (A) Velocity amplitude measured along the manubrium relative to the velocity amplitude measured at the edge of the umbo (R#20). (B) Velocity phase relative to the umbo velocity phase. The diagram on the right illustrates the positions where the measurements were taken from R#20 (at the umbo edge) to R#27 (at the LPM). R#22 was at the center of the umbo. Each number corresponds to one recording position. The arrows show the frequencies of minimum amplitude and corresponding steepest phase. Exp#59: Alive, Bulla closed, PF open, 80 dB SPL.

the arrows in Fig. 4A). (Note that the results are normalized to those at the umbo, so its response appears perfectly flat by definition.) A feature of the results is that the frequencies of the peaks and valleys did not depend on the measurement location. Fig. 4B shows the velocity phase measured along the manubrium relative to the umbo velocity phase. From 1 to 18 kHz, the phase responses were delay-like, with an increasing delay as the distance from the umbo increased. Above 18 kHz, the phase responses, like the amplitude responses, contained fine structure that became more pronounced as the distance from the umbo increased (with minima in the phase responses at 22.5, 33, 40 and 47 kHz). The peaks and valleys of the amplitude response occurred at frequencies where the phase had its steepest slopes (arrows in Fig. 4B). The frequency spacing between the dips became smaller as the frequency increased.

In Fig. 5 the frequency responses presented in Fig. 4 are plotted as displacement versus position along the manubrium at fixed fre-

quencies and at four times in the cycle. From Figs. 4 and 5, it appears that the manubrium moved as a rigid body from 0.2 to 13.5 kHz (all the points at one instant appear to belong to the same straight line) and moved with slight bending motion at higher frequencies (20.5–50 kHz). The flattened anatomy of the umbo (Fig. 1B) makes it seem more flexible than the blade-like portion of the manubrium, and in fact the bending was more marked at the umbo (bold portions of lines especially at 25 and 30 kHz).

Responses in cat were similar in displaying fine structure in amplitude and phase (Decraemer et al., 1990) but also showed differences. In particular, the systematically increasing delay with distance from the umbo towards the LPM that we observed was not apparent (Decraemer et al., 1991) and in the same study, the measured velocity at the LPM appeared bigger than at the umbo above 12 kHz (which we do not see). The bending motion of the manubrium tip has been reported in cat (Decraemer and Khanna, 1994; Decraemer et al., 1991). Finite element model calculations

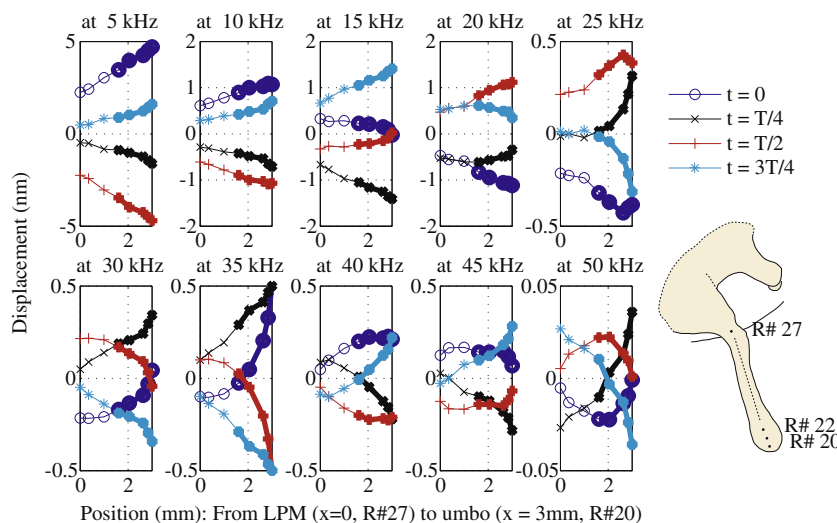


Fig. 5. Displacement as a function of position along the manubrium at 10 frequencies (5, 10, 15, 20, 25, 30, 35, 40, 45 and 50 kHz) at four times ($t = 0, T/4, T/2$ and $3T/4$). The diagram on the right illustrates the relative measurement positions: R#20–27 with R#27 at the LPM ($x = 0$), R#22 at the umbo center ($x = 2.63$ mm) and R#20, at the umbo edge ($x = 3$ mm). Filled symbols correspond to points on the umbo (R#20–24). The Y-scale differs to illustrate the bending. Exp#59: Alive, Bulla closed, PF open, 80 dB SPL.

(Funnell et al., 1992) predicted this bending motion and suggested that even at low frequencies the bending may be present.

In summary, the gerbil manubrium did not move as a rigid body. Its tip, the umbo, is relatively flexible which allows relatively more bending. The umbo moved before the LPM with an amplitude $\sim$ two times bigger. At higher frequencies, the phase and amplitude responses contained fine structure, with peaks and dips at fixed frequencies independent of the measurement position. Amplitude extrema roughly corresponded to regions where the phase changed most rapidly.

3.3. TM, umbo and LPM velocity

Fig. 6 presents the amplitude responses measured at one position on the TM, at the umbo and at the LPM under the same open-field sound stimulation for two experiments: Exp#45 in Fig. 6A (umbo and TM data are part of Figs. 2 and 3) and Exp#59 in Fig. 6B (LPM and umbo are part of Figs. 4 and 5). For both animals, the umbo and the LPM had similar frequency responses with smaller amplitude at the LPM. The TM frequency response had many peaks. Some of them were present in the malleus response (at 3, 22, 35, 37.5, 43 and 47 kHz, Fig. 6B), but overall the manubrium response is smoother than that of the TM. Similar observations were made in cat. Decraemer et al. (1989) found that the displacement frequency responses measured at points on the TM exhibited sharp variations in amplitude, especially at high frequencies. By comparison, the frequency response measured at the umbo was relatively smooth. Funnell et al. (Fig. 7 in (Funnell et al., 1987)) suggested that a spatial integration was performed over the eardrum.

4. Discussion

4.1. How to understand the tympanic membrane motion

To understand the experimental responses of Fig. 2B, we constructed a simple conceptual model in which a slow traveling wave and a piston-like motion were superimposed. Results are presented in Fig. 7. As a first approximation, the amplitude of the traveling wave was set to one at all frequencies (dashed thin line,

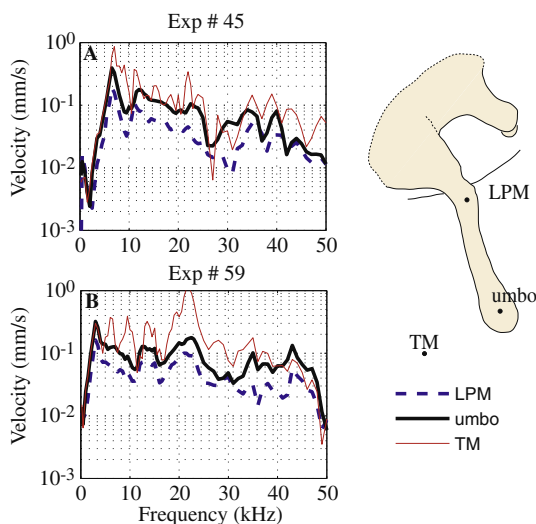


Fig. 6. Velocity measured at the LPM (blue dashed thick line), at the umbo (black thick line) and on the TM (red thin line) for Exp#45 R#17–43–58 (A) and Exp#59 R#27–22–40 (B). Exp#45 R#43–58 were part of Figs. 2 and 3 and Exp#59 R#27–22 of Figs. 4 and 5.

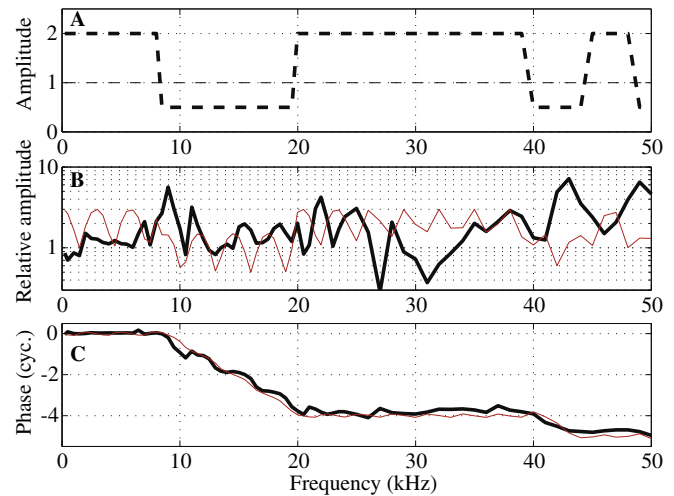


Fig. 7. Combination of a piston motion (of amplitude b) and a slow traveling wave (with velocity $c = 2$ m/s): $S = b(\omega, x) + e^{-i\omega x/c}$. x is the distance between the recording position on the TM and the umbo. (A) Amplitude of the model's traveling wave was set to one (thin dashed line) while the piston amplitude was either 0.5 or 2 depending on the frequency (thick dashed line). Magnitude (B) and phase (C) of the resulting model response and experimental data. Results (thin red line) are compared to experimental results (thick black line) from one location, Exp#45 run # 58 ($x = 687 \mu\text{m}$). (Data from several locations are in Fig. 2.)

Fig. 7A), while the amplitude of the piston-like motion was frequency dependent and was either equal to 0.5 or 2 (dashed thick line, Fig. 7A). The superposition of these two motions is shown in Fig. 7B for the amplitude and Fig. 7C for the phase (thin lines). The resulting phase is determined by the dominant response in the frequency region of interest: where the piston-motion dominates, the phase is flat; where the traveling wave dominates, the phase response is delay-like. Thick lines correspond to experimental results from one position on the TM, which serves as an example. (Data as in Fig. 2, Exp#45 R#58.) This simple simulation was helpful to understand a basic mechanism for the cascade-like phase observations, with full-cycle steps. The important components are a wave-like response summed with a piston-like response. A multi-component wave summed with the piston-like motion is likely needed to reproduce the amplitude patterns in Fig. 3, but the simple simulation conveys the basic idea.

The wavelength estimates from Fig. 3 indicated a TM wave speed of ~ 11 m/s. With a 2 mm radius this speed corresponds to a delay (measured from the outer edge of the TM) of $180 \mu\text{s}$, much longer than the observed 25–30 μs middle ear transmission delay. (In a manuscript in preparation we show that the ossicular delay in gerbil is substantial and the TM contribution to the middle ear delay is in fact less than 25 μs , emphasizing the seemingly overly long duration from the TM traveling waves.) That the TM waves appear to be overly slow has been noted by others (Rosowski et al., in press). These observations suggest that the simpler quasi-piston-like component of the TM motion is more important than the slow wave motion for sound transmission. In support of the idea that the wave-like motion of the TM is not significant for sound transmission, in (Aarnisalo et al., 2009) the application of cartilage on the TM surface changed the local motion response of the TM but not the overall sound transmission (the stapes velocity stayed $\sim$ the same). Similarly, Kachroo et al. (2004) found that the middle ear transmission delay (from EC to scala vestibuli) was very robust to TM modifications (for example, layer of epoxy to increase stiffness).

However, several modeling studies have concluded that the TM waves are important for sound transmission (O'Connor et al., 2008;

Parent and Allen, 2007; Puria and Allen, 1998), and a conceptualization of the piston-like motion as “important” for sound transmission and the wave motion as “unimportant” might be incorrect, even if evidence points that way. The flexible TM with drum-like geometry will of necessity break up into wave patterns. On the other hand, the stimulating pressure is known to be uniform across the TM up to frequencies of 70 kHz (Ravicz et al., 2007), which would drive a piston-like, in-and-out motion. So it is easy to understand how these two motions would arise. In the model of Parent and Allen (2007) mechanical TM waves are launched all along the TM, and travel inward to the umbo. As long as the pressure at the TM was fairly spatially uniform a sum of piston-like and wave-like motion would result. In an earlier version of the model (Puria and Allen, 1998) the TM wave was thought to be launched from a relatively flexible region near the annulus and travel inward; in this case, the piston-like motion would not be expected, and only traveling waves would be observed on the TM. Both these models were fairly abstract. A more concrete computer model that demonstrated realistic wave-like behavior on the TM also showed reasonable delays (Fay et al., 2006). In that model the resulting sound transmission through the middle ear was interpreted as a summation of many TM waves. The substantial piston-like motion of the TM observed in the present study was not explicitly noted in the output of any of these models, but it might be present, and our observations are a touch point for future model validation. In a finite element model of the cat middle ear, the sum of wave-like and piston-like motion is apparent. A simulation can be seen at <http://audilab.bmed.mcgill.ca/AudiLab/eardrum.html> (Funnell et al., 1997).

4.2. The fine structure seen on the manubrium can be attributed to the manubrium being driven by a drum-like structure

In addition to the overall location-dependent change in amplitude (smaller at the LPM than the umbo) the frequency response data of Fig. 4 are characterized by (i) location independent fine structure in amplitude (ii) corresponding ripples in phase and (iii) decreasing spacing between adjacent amplitude peaks as the frequency increases. Observations (i) and (ii) indicate a bounded structure, with preferred, “fitting” wavelengths – and thus frequencies – causing the frequency specific ripples. The third observation suggests the spacing that is known to exist between modes of a drum-head. For example, in a circular membrane with fixed boundary conditions, the mode frequencies are given by $\omega_{mn} = (c/a)j_{mn}$ with a the membrane radius and j_{mn} the n th root of the Bessel function J_m (Hall, 1993). The spacing between the resonant frequencies decreases as the frequency increases ($f_{m1}/f_0 = [1, 1.59, 2.14, 2.65, \dots]$), which is roughly what we observed along the manubrium. In this interpretation, the dominant modal motion of the drum-like TM is transmitted to the manubrium and the manubrium fine structure has to do with modes on the TM. The observed overall phase accumulation along the manubrium in Fig. 4 corresponds to about 3–4 μ s, which is of the right size to contribute to the ~25–30 μ s delay of middle ear transmission. Whether this delay is based more in the TM forcing on the manubrium, or the physical properties of the manubrium and its attachments, is not known. We saw above that the TM moves with the sum of a piston-like and a wave-like motion. In an upcoming paper we will report on the phase delay between the ear canal pressure and umbo motion, and further discuss this interesting question.

In conclusion, observations on the TM and the manubrium in gerbil showed complex motion with frequency fine structure and bending motion. Simple simulations were used to understand the observations, leading to the observations that (i) the TM motion can be thought of as a combination of in-and-out, quasi-piston-like motion and wave-like motion and (ii) that the fine structure of the

manubrium motion might be attributable to resonances on the drum-like TM. In that case the manubrium fine structure might be useful to explore the TM's dominant modes because the frequency structure (location of peaks and valleys) is more stable on the manubrium than it is on the TM itself. The observed character of TM motion prompted us to question whether the slow traveling waves on the TM are significant for sound transmission; we hope that our results will be explored with physics-based models of TM mechanics in order to resolve this question.

Acknowledgments

This work was supported by the NIH/NIDCD (DC003130) and the Emil Capita Foundation. We thank Wei Dong for comments on the manuscript and the Hearing Research reviewers, Jont Allen and John Rosowski, for their help in improving the manuscript.

Appendix A. What is the cochlear condition? What is the termination? J. Allen

Most of the experiments were performed in vivo or few hours post mortem. The cochlea was intact and in normal condition. The stability of the preparation was checked by repeats of the velocity at different locations (umbo, stapes). A good repeat of the velocity implies no significant change in the cochlear condition.

Appendix B. How do you explain that the phase responses contain full cycle transitions, rather than the half cycle transitions present in standing wave patterns? M. Ravicz

We were surprised to see steps of a full cycle in the relative phase responses instead of the typical standing wave pattern with steps of half cycle; this is what led us to the conclusion that there is a piston-like component of the motion.

Appendix C. Comments from S. Puria and J. Rosowski

Sunil Puria suggested that maybe this TM motion was a characteristic of small mammals. But John Rosowski argued that in their human temporal bones (Aarnisalo et al., 2009; Cheng et al., 2009), they measured similar responses.

References

- Aarnisalo, A.A., Cheng, J.T., Ravicz, M.E., Furlong, C., Merchant, S.N., Rosowski, J.J., 2009. The effects of ossicular chain pathology and cartilage placement on the tympanic membrane to the motion of the tympanic membrane evaluated with time-averaged holography. *Middle-Ear Mechanics in Research and Otolaryngology*, Stanford University, CA, USA, June 24–28.
- Cheng, J.T., Aarnisalo, A.A., Harrington, E., Hernandez-Montes, M.D.S., Furlong, C., Merchant, S.N., Rosowski, J.J., 2009. Stroboscopic holography measurement of motion of human tympanic membrane: a preliminary study. *Middle-Ear Mechanics in Research and Otolaryngology*, Stanford University, CA, USA, June 24–28.
- de La Rochefoucauld, O., Decraemer, W.F., Khanna, S.M., Olson, E.S., 2008. Simultaneous measurements of ossicular velocity and intracochlear pressure leading to the cochlear input impedance in gerbil. *Journal of the Association for Research in Otolaryngology* 9, 161–177.
- Decraemer, W.F., Khanna, S.M., 1994. Modelling the malleus vibration as a rigid body motion with one rotational and one translational degree of freedom. *Hearing Research* 72, 1–18.
- Decraemer, W.F., Khanna, S.M., Funnell, W.R., 1989. Interferometric measurement of the amplitude and phase of tympanic membrane vibrations in cat. *Hearing Research* 38, 1–17.
- Decraemer, W.F., Khanna, S.M., Funnell, W.R., 1990. Heterodyne interferometer measurements of the frequency response of the manubrium tip in cat. *Hearing Research* 47, 205–217.
- Decraemer, W.F., Khanna, S.M., Funnell, W.R., 1991. Malleus vibration mode changes with frequency. *Hearing Research* 54, 305–318.
- Decraemer, W.F., Khanna, S.M., Funnell, W.R., 1999. Vibrations at a fine grid of points on the cat tympanic membrane measured with a heterodyne interferometer. In: *EOS/SPIE International Symposia on Industrial Lasers and*

- Inspection, Conference on Biomedical Laser and Metrology and Applications, Munchen, Germany.
- Dong, W., Olson, E.S., 2006. Middle ear forward and reverse transmission in gerbil. *Journal of Neurophysiology* 95, 2951–2961.
- Fay, J., Puria, S., Decraemer, W.F., Steele, C., 2005. Three approaches for estimating the elastic modulus of the tympanic membrane. *Journal of Biomechanics* 38, 1807–1815.
- Fay, J.P., Puria, S., Steele, C.R., 2006. The discordant eardrum. *Proceedings of the National Academy of Sciences of the United States of America* 103, 19743–19748.
- Funnell, W.R., Decraemer, W.F., Khanna, S.M., 1987. On the damped frequency response of a finite-element model of the cat eardrum. *The Journal of the Acoustical Society of America* 81, 1851–1859.
- Funnell, W.R., Khanna, S.M., Decraemer, W.F., 1992. On the degree of rigidity of the manubrium in a finite-element model of the cat eardrum. *The Journal of the Acoustical Society of America* 91, 2082–2090.
- Funnell, W.R., Decraemer, W.F., Khanna, S.M., 1997. Damped vibration patterns on a finite-element model of the cat eardrum. In: 20th ARO Midwinter Meeting (Association for Research in Otolaryngology), St. Petersburg, FL, USA.
- Hall, D.E., 1993. *Basic Acoustics*. Krieger Publishing Company, Malabar, Florida.
- Kachroo, P., Chakradeo, V., Fayad, J., Dong, W., Olson, E.S., 2004. Sound transmission through the middle ear in-vivo in human and gerbil: measurements of scala vestibuli and ear canal pressure. In: 27th ARO Midwinter Meeting (Association for Research in Otolaryngology), Daytona Beach, FL, USA.
- Khanna, S.M., Tonndorf, J., 1972. Tympanic membrane vibrations in cats studied by time-averaged holography. *The Journal of the Acoustical Society of America* 51, 1904–1920.
- Khanna, S.M., Koester, C.J., Willemin, J.F., Dandliker, R., Rosskoth, H., 1996. A noninvasive optical system for the study of the function of inner ear in living animals. *SPIE* 2732, 64–81.
- Nummela, S., 1995. Scaling of the mammalian middle ear. *Hearing Research* 85, 18–30.
- O'Connor, K.N., Tam, M., Blevins, N.H., Puria, S., 2008. Tympanic membrane collagen fibers: a key to high-frequency sound conduction. *The Laryngoscope* 118, 483–490.
- Olson, E.S., 1998. Observing middle and inner ear mechanics with novel intracochlear pressure sensors. *The Journal of the Acoustical Society of America* 103, 3445–3463.
- Parent, P., Allen, J.B., 2007. Wave model of the cat tympanic membrane. *The Journal of the Acoustical Society of America* 122, 918–931.
- Puria, S., Allen, J.B., 1998. Measurements and model of the cat middle ear: evidence of tympanic membrane acoustic delay. *The Journal of the Acoustical Society of America* 104, 3463–3481.
- Ravicz, M.E., Rosowski, J.J., Voigt, H.F., 1996. Sound-power collection by the auditory periphery of the mongolian gerbil *Meriones unguiculatus*. II. External-ear radiation impedance and power collection. *The Journal of the Acoustical Society of America* 99, 3044–3063.
- Ravicz, M.E., Olson, E.S., Rosowski, J.J., 2007. Sound pressure distribution and power flow within the gerbil ear canal from 100 Hz to 80 kHz. *The Journal of the Acoustical Society of America* 122, 2154–2173.
- Rosowski, J.J., Cheng, J.T., Ravicz, M.E., Hulli, N., Hernandez-Montes, M., Harrington, E., Furlong, C., in press. Computer-assisted time-averaged holograms of the motion of the surface of the mammalian tympanic membrane with sound stimuli of 0.4–25 kHz. 253, 83–96.
- Slama, M., Ravicz, M.E., Nakajima, H., Dong, W., Rosowski, J.J., 2008. In: Measurements of Middle-Ear Pressure Gain and Cochlear Input Impedance in the Chinchilla 29th ARO Midwinter Meeting (Association for Research in Otolaryngology), Phoenix, AZ, USA.
- Teoh, S.W., Flandermeyer, D.T., Rosowski, J.J., 1997. Effects of pars flaccida on sound conduction in ears of Mongolian gerbil: acoustic and anatomical measurements. *Hearing Research* 106, 39–65.
- Tonndorf, J., Khanna, S.M., 1972. Tympanic-membrane vibrations in human cadaver ears studied by time-averaged holography. *The Journal of the Acoustical Society of America* 52, 1221–1233.