Tympanic membrane surface motions in forward and reverse middle ear transmissions

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Characterization of Tympanic Membrane (TM) surface motions with forward and reverse stimulation is important to understanding how the TM transduces acoustical and mechanical energy in both directions. In this paper, stroboscopic opto-electronic holography is used to quantify motions of the entire TM surface induced by forward sound and reverse mechanical stimulation in human cadaveric ears from 0.25 to 18.4 kHz. The forward sound stimulus was coupled to an anatomically realistic artificial ear canal that allowed optical access to the entire TM surface, and the reverse mechanical stimulus was applied to the body of the incus by a piezo-electric stimulator. The results show clear differences in TM surface motions evoked by the two stimuli. In the forward case, TM motion is dominated by standing-wave-like modal motions that are consistent with a relatively uniform sound-pressure load over the entire TM surface. With reverse mechanical stimulation, the TM surface shows more traveling waves, consistent with a localized mechanical drive applied to the manubrium embedded in the TM. With both stimuli, the manubrium moves less than the rest of the TM, consistent with the TM acting like a compliant membrane rather than a stiff diaphragm, and also consistent with catenary behavior due to the TM's curved shape.

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I. INTRODUCTION

Tympanic Membrane (TM) surface motions are involved in the transduction of sound energy into ossicular motion that is then transferred to the inner ear. Previous measurements of TM surface motions induced by ear-canal sound stimulation (forward sound transmission) showed frequency dependent surface motion patterns, described as simple, complex, and ordered motions at low, middle, and high frequencies, respectively (Rosowski *et al.*, 2009). A phenomenological model demonstrated that at higher frequencies, these TM motion patterns are consistent with the combination of larger amplitude low-order (low spatial frequency) standing-wave-like modal motions and smaller amplitude higher-order (high spatial frequency) traveling-wave-like motions (Cheng *et al.*, 2013), where the traveling-wave-like motions may be associated with damping within the TM (De Greef *et al.*, 2014). These measurements and modeling results led us to suggest a *modal motion theory of TM sound transmission*, where acoustic energy is mainly coupled to the middle-ear ossicular chain through low-order modal motion components on the TM surface (Cheng *et al.*,

2013). This theory is consistent with the relatively uniform sound pressure distribution observed over the entire TM surface at frequencies up to about 15 kHz (Stinson, 1985; Ravicz *et al.*, 2014; Cheng *et al.*, 2015), where the uniform sound pressure is the source of the low-order standing-wave-like modal motions of the TM. The contribution of high-order traveling-wave-like TM motion components to middle-ear function is still under debate (Puria and Allen, 1998; Parent and Allen, 2010; de La Rochefoucauld and Olson, 2010; Goll and Dalhoff, 2011; Cheng *et al.*, 2013).

Reverse middle ear transmission has been studied by multiple researchers who describe the reverse flow of sound energy from inside the cochlea to the external ear as oto-acoustic emissions (OAE) (Magnan *et al.*, 1997; Puria, 2003; Voss and Shera, 2004; Dong and Olson, 2006; Dalhoff *et al.*, 2011). Measurements of the sound pressures inside both the ear canal and cochlea have been used to define the forward middle-ear pressure gain and reverse middle-ear pressure loss, and these sound pressures have been combined with measurements of stapes velocity to define forward and reverse middle-ear impedances. These previous studies in different species (guinea pig from Magnan *et al.*, 1997, human from Puria, 2003, and gerbil from Dong and Olson, 2006) suggest a transmission “loss” in the reverse direction of ~30 dB compared to a gain in the forward direction of ~20 dB, where an ideal transformer would produce an equal loss and gain (Shera and Zweig, 1991). While the difference in magnitude between the reverse loss and forward gain can result from different loading conditions on the middle ear in the two different directions (the relatively high impedance

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cochlear load in forward sound stimulation vs the low-impedance ear-canal load in reverse stimulation), it has been hypothesized that the larger magnitude reverse-direction transmission loss arises from the eardrum itself, which, when driven by the ossicles, may vibrate in a manner different from forward transmission (Dong and Olson, 2006). This hypothesis has not been tested due to lack of data to describe TM motions during reverse transmission. To our knowledge, no existing measurements quantify human TM surface displacement during reverse stimulation.

In this study, we measured TM surface motions in human cadaveric ears during forward stimulation by ear-canal sound pressures, and reverse stimulation by mechanical stimulation of the ossicles. Both measurements were made in each ear, one after the other, which allowed direct comparison of the TM surface motions induced by the two different stimuli, and reduced the influence of individual differences on measurement variability. Such measurements can be used to test numerical middle ear models, such as circuit (O'Connor and Puria, 2008) or Finite Element models of the ear (Gan *et al.*, 2004), and can also help in the design of tissue-engineered TM-like materials (Kozin *et al.*, 2016).

II. METHODS AND ANALYSES

A. Preparation of human temporal bones

Seven ($N=7$) de-identified fresh human temporal bones (TBs) without history of pathology were used in this study. The ages of the donors varied between 44 and 79 years old. The preparation of the TB included (1) removal of the bony external ear canal to expose the majority of the TM surface for holographic motion measurement; (2) opening the facial recess to access the middle-ear cavity and check the normality of the middle-ear ossicles. The recess remained open during the experiment to prevent pressure build up inside the middle-ear cavity, which may cause an increase in the low-frequency response and a shift of the middle-ear resonance frequency to lower frequencies (Guinan and Peake, 1967; Ravicz *et al.*, 1992; Maftoon *et al.*, 2014); (3) opening the eptitympanum (attic) to place a mechanical stimulator against the incus body for reverse stimulation of the TM (the stimulator was removed and the attic opening was covered during forward sound stimulation); (4) painting the TM lateral surface with a thin layer of ZnO suspended in saline (60 mg/cc) to increase TM reflectivity for better holographic measurements (the effect of such painting on TM motion is small; Rosowski *et al.*, 2009; Cheng *et al.*, 2013); (5) attaching a brass rod tightly to the petrous bone inferior to the TM surface and roughly perpendicular to the TM annulus plane (the rod was held by a three-dimensional manipulator: MM33D1L, World Precision Instruments, Germany) that enabled adjustment of the position of the TB in front of the holographic system (details of the holographic system can be found in Cheng *et al.*, 2010); (6) coupling of an artificial ear canal to the prepared TB to mimic the natural ear canal. Details of the artificial ear canal are described in previous publications (Ravicz *et al.*, 2014; Cheng *et al.*, 2015) that demonstrate large similarities between sound transmission in

the artificial and natural ear canals. The artificial ear canal remained in place and open for the reverse mechanical stimulation measurements.

B. Forward Sound and Reverse Mechanical Stimulation

We used two different stimulation methods to induce vibrations of the TM (Fig. 1). In forward sound stimulation, continuous sinusoids from 18 to 21 selected frequencies between 0.25 and 18.4 kHz were generated by a stimulus generator (AFG 3102, Tektronix, Beaverton, OR), amplified (D45, Crown D45, Elkhart, IN) and then coupled to the sound source (CF1, Tucker-Davis Technologies, Alachua, FL) to produce continuous tones of levels between 80 and 120 dB sound pressure level (SPL) that were delivered to the lateral surface of the TM by way of the artificial ear canal. The sound stimuli entered the artificial ear canal by way of a side tube, such that the distal opening of the canal remained open during measurements.

In reverse mechanical stimulation, the same continuous sinusoids were coupled to a small piezoelectric stack with a stainless steel rod (diameter 1 mm) glued to the center of the stack. The tip of the rod was brought into contact with the body of the incus through the open epitympanum of the temporal bone. The mechanical stiffness of the stimulator (including the rod) was very high to ensure a load-independent transmission of the stimulator displacement to the ossicles. The displacement of the incus and coupled malleus induced displacement of the TM through the connection between the TM and the manubrium of the malleus.

C. Holographic measurements of TM surface motion and umbo displacement

Sinusoidal forward (sound) and reverse (mechanical) stimuli induced motions of the TM that were quantified at over 100 000 points on its surface by our stroboscopic

FIG. 1. A schematic drawing of the experimental setup that pictures the middle ear of the temporal bone, the placement of the artificial ear canal, and the holographic measurement via the transparent glass window in the canal. In forward sound stimulation, tones are delivered to the lateral surface of the TM through a side tube near the artificial ear canal opening. In reverse mechanical stimulation, a small piezoelectric stack is used to drive the body of incus through the open epitympanum of the bone. A probe microphone is inserted through the opening end of the artificial ear canal to monitor sound pressure levels near the TM annulus during the experiment.

holography technique. The details of stroboscopic holographic measurements of the TM sinusoidal displacement magnitude and phase can be found in [Cheng et al. \(2010\)](#) and [Cheng et al. \(2013\)](#). The stimulus levels were varied to induce vibrations of the TM within the dynamic measurement range of the holographic system between 10 nm and up to 10 μ m. Stimuli that are too small will induce displacements that are smaller than the 10 nm minimum measurable displacement, while stimuli that are too large will produce holographic fringes with a spatial density that is too high to be resolved by the camera. In these studies, typical low-frequency sound and mechanical stimuli produced displacement amplitudes less than a few hundred nanometers. The results of these procedures were sets of two-dimensional (2D) maps of the magnitude and angle of the displacement at over 100 000 points on the TM surface for each stimulus frequency and level. All the measured displacements were in the direction of the sensitivity vector, which was nearly perpendicular to the camera surface ([Hernández-Montes et al., 2009](#); [Flores-Moreno et al., 2011](#); [Khaleghi et al., 2013](#)), and were well approximated by motions perpendicular to the tympanic ring.

Ear-canal sound pressure was measured in both forward and reverse stimulation with a pre-calibrated 20 mm long probe-microphone (EK3027, Knowles, Itasca, IL) inserted along the longitudinal axis of the artificial ear canal and positioned near the annulus of the TM to avoid blocking the view of the TM seen by the holography camera. The probe location was monitored using images captured by the camera. The sound pressures produced by reverse stimulation is the subject of [Ravicz et al. \(2018\)](#).

The umbo displacement, χ_{umbo} , was extracted from holograms using the averaged motion of a 10×10 square pixels at the center of the manubrial spoon ([Cheng et al., 2013](#)). For comparison with other data sets, the umbo displacement magnitude was normalized by the sound pressure magnitude monitored near the TM annulus in forward stimulation, or by the voltage magnitude applied to the piezoelectric stimulator in reverse stimulation. An error in our recording system did not allow comparisons of the phases of the holographically measured displacements and analog measurements of the microphone or stimulator. However, we are able to compare accurately displacement phases within individual holographic measurements, and could normalize the magnitude and phase of the displacement at each point on the TM by the displacement of the umbo (see [Cheng et al., 2015](#) for more explanation).

D. Image registration to facilitate data comparison

As it was not possible to make complete displacement measurements with both forward and reverse stimulations without moving the specimen, the angle and distance between the camera and the tympanic ring varied somewhat between forward and reverse stimulation. The small differences (less than a few degrees in angle and a few mm in distance) in position resulted in differences in the size and shape of the TM's projection on the camera frame. To quantitatively compare holograms driven by the two stimulators

in the same specimen, image registration was performed to normalize the shape and position of the TM.

First the differences in TM shape from the forward and reverse holographic images were normalized by projective transforms in which we assumed the ideal situation of a pin-hole camera and a planar object. Similar to the method described in [Cheng et al. \(2015\)](#), the outline of the TM was identified on phase maps produced by low-frequency (typically 500 Hz) stimulation [Fig. 3(A)]: at this frequency, the entire surface of the TM moves in phase and is readily distinguishable from the non-moving bone at the image edges. The outline was approximated by hand and then optimized using a process called "active contour" ([Chan and Vese, 2001](#)). The manubrium and umbo were outlined on phase maps produced by high frequency stimuli [typically 10 kHz, e.g., Figs. 3(C) and 3(D)]: at these frequencies, the umbo and the manubrium move out of phase with the rest of the TM ([Cheng et al., 2013](#)), and their outline is readily distinguishable from the rest of the TM surface. The umbos were centered in each image and the manubria aligned at 12 o'clock by mapping their location in log-polar coordinates and registering them using phase-only correlation ([Guignard et al., 2014](#)).

Finally, landmarks were created at the intersection of the TM's boundary and ten uniformly distributed lines crossing at the umbo. The projective transform that best warped the landmarks in forward stimulation to match the landmarks in reverse stimulation was calculated using least-squares optimization ([Goshtasby, 1988](#)). The holograms were registered using the resulting projective transforms. The registered TM surface motion maps from various samples and experiment setups have the umbo located at the center and the long axis of the manubrium aligned to 12 o'clock (see Fig. 3).

E. One-dimensional projections of displacements on the TM surface

To aid comparison of TM motions induced by forward and reverse stimulations, the motion along specific diameters of the nearly circular TMs were extracted from the 2D surface maps of the magnitude and phase of TM displacements normalized by umbo displacement. Two diameters were extracted: diameter one is a line that includes the manubrium superior-inferiorly, and diameter two is a line perpendicular to diameter one running across the umbo anterior-posteriorly (see cartoons in Fig. 4). Displacement magnitude and phase along the two diameters were compared between forward and reverse stimulations.

F. Computation of "effective area" of TM motion

Stroboscopic holography measures displacement amplitude and relative phase over the entire TM surface, which allows us to define the relationship between umbo motion and TM surface motion in terms of an "effective area" (A_e), that can be estimated during both forward and reverse stimulation.

The 2D maps of the magnitude and phase of TM surface displacement at any one frequency allow us to compute the

complex volume displacement of the TM, X_{TM} , as the complex average of the displacements at each TM surface point multiplied by the area of the TM. The effective area (computed for either forward or reverse stimulation) is the ratio of the volume displacement to the displacement at the umbo, χ_{umbo} ,

$$A_e = X_{TM} / \chi_{umbo}. \quad (1)$$

Note, A_e has the units of an area.

If the TM acted like a rigid plate (which we know is not true), then A_e would equal the surface area of the TM. In another case, if the TM motion is complex with different magnitudes and phases at different locations (which is what happens at high frequency), then TM displacements in different regions might partially cancel out and A_e could be smaller than the area of the TM. In a third case, if the displacement of the umbo is less than the average displacement of the TM, A_e will be larger than the area of the TM. A_e has previously been estimated from acoustic measurements such as middle ear admittance (e.g., Fig. 21 of [Lynch et al., 1994](#)) or modeling [Eq. (6) of [Shera and Zweig, 1991](#)]. We will compare this “effective area” across a broad frequency range during the two stimulus paradigms.

G. Analyses of the spatial distribution of the phase of motion and complex displacement on the TM surface

In order to compare the contribution of modal standing waves and traveling waves to the motions of the TM in forward and reverse stimulations, we analyzed the distribution of the magnitude and phase of the motion at each of the $\sim 100\,000$ points on the TM in each ear in forward and reverse stimulations using multiple methods. Some of these comparisons were fairly simple, where, we looked at (1) the average phase (relative to the umbo) across the TM surface at different frequencies and compared their mean and variance ($N=7$) between forward and reverse stimulations (as shown in Fig. 6), and (2) the distribution of phase relative to the umbo on the TM surface, summarized as the fraction of TM area either in-phase (within ± 0.125 cycle), a half-cycle out-of-phase (between -0.5 and -0.375 cycle or 0.375 and 0.5 cycle), or in quadrature phase (in-between phase, as shown in Fig. 7).

More complicated analyses were also performed to quantitatively compare the in-phase and more complex displacements on the TM surface in both forward and reverse stimulation.

(1) We investigated motions of all individual TM points using Argand diagrams ([Pedoe, 1988](#)). In these diagrams, the umbo-normalized motion at each individual TM location is represented by a point on the complex (real and imaginary) plane (Fig. 8). The distance from the origin to the point is the displacement magnitude and the angle between a line connecting the point to the origin and the real axis is the phase of the displacement of the corresponding location. When the TM motion is that of a standing wave, the displacements at all locations on the TM vary in magnitude, but are either in-phase or a half-cycle out-of-phase with one another, such that all the points on the Argand diagram are

collinear (i.e., well fit by a single straight line) [e.g., Figs. 8(A) and 8(B)]. In such a condition the vectors of the displacement of all TM points can be aligned to the real axis (phases of either 0 or π radians) by adding a single phase value to all of the measured phases, and the matrix describing the angle shifted displacements of all TM points will only contain real numbers. In contrast, when the TM motion is consistent with a traveling wave, the phases of the TM displacements vary across the entire phase domain and the points describing these motions on the Argand diagram project around the origin in all directions and are *not* collinear. In such a scattered condition, no single phase angle change exists that rotates all the points describing displacements of all the TM points to a purely real matrix, and the motions can only be described using complex numbers.

As the characteristics of the motion vary from standing wave to traveling wave, the distribution of points on the Argand diagram vary from collinear to completely scattered in the complex plane. We use this observation to compare the contribution of standing and traveling waves in forward and reverse stimulation. Note that we first normalize the displacement in each bone at each frequency in each stimulus mode by the maximum displacement of the TM so that all points in the Argand diagram fall within a unit circle.

We also used rose diagrams ([Curtis, 2007](#)), also called polar bar plots or angle histograms, to investigate the distribution of magnitudes and phases across the TM surface. In these diagrams, the distribution of the displacement phases of all individual TM points is plotted in a polar angular histogram with a bin size of 20° (Fig. 9). In such diagrams, a large narrow projection means that the phase values of a large majority of the measured points are located in a single angle bin. The percentage of the points located in each angular bin is quantified by the radii of intermediate circles. While the basic rose angle histogram shows the distribution of angles of displacement, it does NOT separate the data in terms of the magnitude of motion, and noise measurements that contain all angles result in a circular cloud around the origin. To help identify the contribution of noise, we turn each radial bin into a histogram of displacement magnitude using color coding (Fig. 9). The radial histograms are colored according to their magnitude relative to peak magnitude and the number of occurrences of each magnitude in each polar phase bin. For example, in Fig. 9(A), a large majority of the TM locations move with a phase relative to the umbo between 0 and 20 degrees: 10% of the locations with that angle have a magnitude near the maximum magnitude on the TM surface (coded in red), $\sim 20\%$ have magnitudes of 0.4 to 0.5 of the maximum, coded in cyan, and more than 50% of the points have magnitudes less than 0.25 of the maximum (coded in blue to deep blue).

Although Argand and rose diagrams provide quantitative methods to characterize the TM waves, they do not provide a metric to concretely compare motions between forward and reverse stimulations. For such a comparison, we used the Modal Phase Collinearity (MPC) metric ([Pappa and Elliott, 1993](#)) to quantitatively compare motions on the TM surface.

Let $\chi(\omega) = \chi_r + j\chi_i$ be a complex one-dimensional vector that describes the displacement at the 100 000 plus points on the TM surface at frequency ω , where χ_r and χ_i are vectors of real numbers that describe the real and imaginary components of the displacement vector and j is the imaginary unit. The variances (S_{rr} and S_{ii}) and covariance (S_{ri}) of the real and imaginary components of the displacement vector are

$$\begin{aligned} S_{rr} &= \chi_r^T \chi_r, \\ S_{ii} &= \chi_i^T \chi_i, \\ S_{ri} &= \chi_r^T \chi_i, \end{aligned} \quad (2)$$

where superscript T describes the transposition of a vector. Each S value, the product of a one-dimensional vector and a transposition of such a vector, is a single real number. The covariance matrix is defined as

$$\begin{bmatrix} S_{rr} & S_{ri} \\ S_{ri} & S_{ii} \end{bmatrix}. \quad (3)$$

The eigenvalues of the covariance matrix are

$$\lambda_{1,2} = \frac{S_{rr} + S_{ii}}{2} \pm S_{ri} \sqrt{\left(\frac{S_{ii} - S_{rr}}{2S_{ri}}\right)^2 + 1}. \quad (4)$$

MPC is then defined at frequency ω as

$$MPC(\omega) = \left(\frac{\lambda_1 - \lambda_2}{\lambda_1 + \lambda_2}\right)^2. \quad (5)$$

MPC equals 1 when all TM points are in phase or half-cycle out of phase with each other (consistent with a standing wave, and equivalent to a collinear Argand diagram), and equals zero when the phases of the TM points are uniformly distributed in the complex plane (consistent with a cloud of points centered at 0, as a result of purely traveling waves that cover multiple wave lengths). Note that we defined MPC at a specific frequency in contrast to the original modal definition of Pappa and Elliott (1993). MPC provides a single numeric index to describe the mathematical complexity of the motion.

H. Location and amplitude of the maximal displacement

In order to compare the location and magnitude of the motion maxima as a function of frequency and stimulus type, we used the following method to isolate loci of maximal displacement amplitude at each frequency in each bone in the two different stimulus conditions. We used a 5×5 moving window to filter the TM 2D holographic magnitude maps, first using a median filter and then using a Gaussian filter. We then used the running max-min filter proposed by Lemire (2006) to find global maxima in the filtered magnitude maps. Because the number of spatial features increases with frequency and the spatial span of these features decreases with frequency, our implementation uses a

frequency-varying window size for the max-min filter. For frequencies below 1 kHz, we used a constant square window of the size of 20% of the captured hologram (e.g., 200×200 for a 1000×1000 pixel hologram). For higher frequencies, we used piecewise linear interpolation to vary the window size from 20% at 1 kHz to 15%, 10%, 6%, and 5% as the frequency of excitation increased above 2, 5, 9, and 17 kHz, respectively.

III. RESULTS

A. Umbo displacement from forward and reverse stimulation

Umbo displacement magnitudes normalized by ear canal pressure in forward sound stimulation are plotted against stimulus frequency in Fig. 2(A) for all seven bones. The results are compared with Laser Doppler Vibrometry (LDV) measured mean umbo displacement from Gan *et al.* (2004). The umbo displacement in four of our bones agree relatively well with Gan *et al.* between 2 and 8 kHz, but have lower (by a factor of 3) displacement magnitudes at lower frequencies. The other three bones (TB1, 13, and 14) have displacement magnitudes that are an order of magnitude lower than the other four at all frequencies. The consequence of this difference in umbo motion between the two populations is a point of further discussion, though one significant methodological difference between our measurements and those of Gan *et al.* is the use of a semi-open sound stimulus system coupled with the open middle-ear air space; this arrangement allows the possibility of significant stimulator-derived sound pressure in the middle-ear cavity, especially at low frequencies where absorption of sound is low and the long wavelengths could lead to a decreased sound-pressure difference across the TM. Nevertheless, our umbo displacements follow the general trend of published umbo displacement frequency relationship, i.e., relatively flat at low frequencies below 1 kHz, and decreases as frequency increases. We could not find many published results above 10 kHz to compare with ours. We also noticed that there is an increase of umbo displacement around 15 kHz, similar to what we have seen in our earlier studies (Cheng *et al.*, 2015). We think this may be related to pressure variations across the TM surface above 15 kHz (Stinson, 1985; Ravicz *et al.*, 2014) that result in differences between the sound pressure we measured near the tympanic ring (Cheng *et al.*, 2015) and the sound pressure at the umbo. The relative roughness of our results is due to sparse frequency sampling: only 15–25 frequencies are measured between 0.2 and 18 kHz, and the lack of averaging of our individual data curves (the Gan *et al.*, 2004 data are the mean from measurements in ten temporal bones).

Umbo displacement magnitudes normalized by the voltage to the piezo-stimulator during reverse mechanical stimulation are plotted vs stimulus frequency in Fig. 2(B). The umbo displacement relative to stimulus voltage is generally flat across a broad frequency range, as expected when the ossicles are driven mechanically by a frequency-independent piezo-stimulator. The stimulator vibration changes linearly with the driving voltage. Some of the variations with

frequency may be caused by compliant connections that allow relative motion between the incus and malleus (Willi *et al.*, 2002; Dobrev *et al.*, 2016) as well as relative motion in the manubrium–TM connection (Graham *et al.*, 1978; Gulya and Schuknecht, 1995; De Greef *et al.*, 2016). Note that the two specimens with the largest reverse driven motions at low frequencies (TB13 and 14) exhibited small sound-driven umbo displacements [Fig. 2(A)]. Umbo displacement varies linearly with the stimulus voltage level in both cases.

B. Two-dimensional TM surface motion maps with forward and reverse stimulation

Maps of the magnitude (upper panels) and phase (lower panels) of the TM surface in a representative temporal bone (TB7, 71 year old male right ear) with forward (left columns) and reverse (right columns) stimulation are compared in Fig. 3, at four stimulus frequencies: Fig. 3(A) 784 Hz, Fig. 3(B) 3970 Hz, Fig. 3(C) 7304 Hz, and Fig. 3(D) 15 784 Hz. The TM annulus and manubrium are outlined in white. All data are normalized by the displacement at the umbo and the magnitudes are displayed as dB re umbo displacement.¹

We see clear differences in the TM motion between forward and reverse stimulation in this bone (and the others): in their spatial displacement patterns as well as absolute values (relative to the umbo).

(1) At frequencies below 1000 Hz, TM motions are consistent with low-order modal motions: there are only a few local displacement maxima, and the phase distribution is simple. The location and magnitude of the surface displacements differ between forward and reverse stimulation. In Fig. 3(A) at 784 Hz, we see one large local maximum in forward stimulation positioned on the posterior side of the TM next to the manubrium, but in reverse stimulation, we see two large maxima, one on either side of the manubrium. The maximum displacement level (relative to the umbo) in reverse stimulation is 10 dB higher than in forward stimulation (see color bar). The entire TM moves in phase in forward stimulation, but in reverse stimulation the TM is clearly separated into two anti-phasic motion regions (separated by the cyan-colored dotted line).

(2) With stimuli between 2000 and 10 000 Hz, TM surface motion is more complicated with multiple local displacement peaks arranged around the manubrium in both forward and reverse stimulations. Again, the locations and magnitudes of the maxima differ with stimulus type.

For instance, at 3970 Hz [Fig. 3(B)], the largest motion magnitudes appear on the anterior side of the TM in forward stimulation, and on the posterior side in reverse stimulation. The displacement phases show relatively in-phase motion over a majority of the TM in forward stimulation, but there is a near 0.5 cycle difference between two halves of the TM in reverse stimulation.

At 7304 Hz, the areas with larger motion magnitude appear in the anterior region of the TM in forward stimulation, where they are distributed between 2 and 3 concentric half rings. In reverse stimulation, the ring like patterns are less clear and the largest motions appear in the inferior part of the TM. The manubrium moves out of phase with much

(A) Forward

(B) Reverse

FIG. 2. Normalized umbo displacements relative to ear canal pressures from all seven temporal bones quantified in this study through holography, in (A) forward sound stimulation; (B) reverse mechanical stimulation. Only the results of displacement magnitude are shown in this plot.

of the TM in both stimulation cases; however, the manubrium motion tends to lag (a more negative phase) much of the TM in forward stimulation, but leads (more positive phase) much of the TM in reverse stimulation.

(3) Above 10 kHz, the TM moves in a relatively ordered modal pattern with many ring-like displacement peaks surrounding the manubrium in both forward and reverse stimulation. The umbo generally moves less than the rest of the TM in both stimulations. The manubrium moves out of phase with the rest of TM in forward stimulation, while in reverse stimulation, the anterior side of the TM moves relatively out of phase with the posterior side of the TM and the manubrium moves in phase with much of the anterior side of the TM.

FIG. 3. Comparisons of TM surface motions from one of the human temporal bones (TB7) quantified by stroboscopic holography between forward and reverse stimulations, at four different frequencies: (A) 784 Hz, (B) 3970 Hz, (C) 7304 Hz, and (D) 15784 Hz. TM motions induced by forward sound stimulation are shown in the left column, and TM motions by reverse mechanical stimulation are shown in the right column. The top panel of each plot shows the magnitude ratio relative to the umbo motion in dB, and bottom panels show the phase ratio relative to the umbo motion in cycles. Displacement values are coded in colors as shown in color bar to the right. The TM annulus (solid lines) and the manubrium (dashed lines) are outlined in white.

As visible in the supplementary material,¹ there are differences in the TM motions produced by forward and reverse stimulation in the seven bones we measured. For example, the anti-phasic motion pattern between the two halves of the TM in reverse stimulation at low-frequencies is clearly seen in TBs 1, 3, 6, and 7, but is not so clear in TBs 5, 13, and 14. Some of these differences may be related to individual differences in anatomy, as well as differences in the placement of the piezo-stimulator on the incus in reverse stimulation.

C. Displacement along TM diameters in forward and reverse stimulation

We now compare the surface motions across frequency and stimulus using two orthogonal one-dimensional

projections along diameters across the TM surface (Cheng *et al.*, 2013). Examples of such comparisons in TB7 are shown in Fig. 4, at the same frequencies used in Fig. 3. The two diameters are illustrated in cartoon insets: one running along the manubrium from superior to inferior, and the other running perpendicular to the manubrium from anterior to posterior. The two diameters intersect at the umbo. Within each plot, motion from forward stimulation is in black solid line, and motion from reverse stimulation is in gray dotted line. The top panel shows displacement magnitudes, and the bottom panel shows phases (both relative to the umbo). The umbo is located at $x = 0$ and a positive x is towards the inferior or posterior.

At 784 Hz [Fig. 4(A)], in forward sound stimulation, the phase of the displacements along the two diameters is nearly

FIG. 4. Comparisons of measured TM motion along two diameters across the TM surface with the two stimulations (forward in black solid and reverse in gray dotted lines) from the same bone (TB7) as in Fig. 3 and at the same four frequencies: (A) 784 Hz, (B) 3970 Hz, (C) 7304 Hz, and (D) 15784 Hz. The two schematic drawings at the top panel of (A) show two diameters (dotted lines) along which the displacements are plotted. The top panel of each plot shows displacement magnitude ratios (relative to the umbo) in dB, and the bottom panel shows phase (relative to the umbo) in cycles. The x axis represents the distance from the umbo ($x = 0$, marked by the vertical dotted line) along the two diameters. The horizontal dotted lines mark magnitudes of 0 dB and angles of 0 cycles.

constant except for a region of half-cycle phase difference in the inferior of the TM almost near the edge of the TM (black solid lines in phase plots). In reverse mechanical stimulation, clear half-cycle phase variations appear at locations mid-way along the two diameters (two on the diameter along the manubrium, and one on the diameter perpendicular to the manubrium). Each of these half-cycle phase changes is associated with a minimum in displacement magnitude, as is consistent with standing-wave motion.

As the frequency increases [Figs. 4(B)–4(D)], we see more complicated motion patterns along the two diameters in both stimulus conditions: there is an increase in the number of displacement magnitude peaks and valleys, as well as the complexity of the number and type of spatial phase transitions. The displacement patterns produced by the two stimulus conditions are generally different: the locations and absolute values of the peaks and valleys in magnitude differ

and significant stimulus-dependent variations in phase with space are observed at higher frequencies. Some of the phase variations observed are step-like quarter and half-cycle changes that occur rapidly in space and are consistent with standing waves, such as in the inferior and posterior diameters in forward stimulation at 3970 Hz. Other phase changes appear as slow glides, in which the phase slowly changes over a half or more cycle, and are consistent with traveling waves, such as in the posterior diameter during reverse stimulation at the three higher frequencies (glide-like gray dotted lines). In general, we see more step-like variations in phase with position in forward stimulation, and more slow, glide-like changes in reverse stimulation. Furthermore, the glides in reverse stimulation generally (but not always) describe a more negative phase as distance increases from the umbo as is consistent with a wave progressing from the umbo to the periphery of the TM.

At the highest frequencies of stimulation, the displacement phases in response to forward stimulation show small cyclic variations around a near constant value, which is consistent with the combination of a small high-spatial frequency traveling component combined with a larger low-spatial frequency standing-wave-like modal pattern. In the same frequency range, reverse stimulation produces a series of step-like quarter- or half-cycle phase changes.

D. Effective areas from forward and reverse stimulations

As described in the methods, the effective area, A_e , of the TM is a simple frequency-dependent metric that integrates the complex motion across the TM surface and compares it to the motion of the umbo. A_e calculated from Eq. (1) in forward and reverse stimulations are plotted for each TB in Fig. 5. Figure 5(A) shows A_e computed from seven bones (thin lines with different symbols) in forward stimulation, as well as the mean of six bones (thick gray line). The top panel shows the magnitude and the bottom panel shows the phase. The results from TB5 (open square thin line) were excluded from the mean due to TB5's large divergence from the rest of the bones. The A_e computed for reverse stimulation for all seven bones are plotted in Fig. 5(B) (magnitude in top panel and phase in bottom panel), with the mean (thick gray line) from six bones (TB 5 is excluded again).

The effective area magnitude in forward stimulation is relatively stable below about 4 kHz with a value around 50 mm², and then fluctuates at higher frequencies; A_e phase in forward stimulation stays at zero up to about 4 kHz, and then slowly increases with stimulus frequency, reaching a positive half cycle near 18 kHz (a sudden step in phase of nearly a cycle in TB13 is suggestive of a phase-unwrapping error in that data set). The magnitude of A_e in reverse stimulation shows similar frequency variation pattern, i.e., stable below ~4 kHz, then fluctuates at high frequency, although the value of A_e magnitude in reverse stimulation is about 30 mm², a little more than half the value in forward stimulation. A_e phase in reverse stimulation is about zero till ~4 kHz, then tends to decrease as frequency increases.

To better view the differences in A_e between forward and reverse stimulations, we plotted the mean (in lines) and the standard deviation (in shadow) of A_e from six bones with both types of stimulations in Fig. 5(C). One can see clear differences in A_e between the two stimulation methods. The A_e magnitude in reverse stimulation is generally 20 mm² lower than that in forward stimulation. The difference between the mean magnitudes is generally larger than one standard deviation (SD), which with this small data set ($N=6$) suggests a significant statistical difference at $p < 0.05$.

The A_e of ~50 mm² in forward stimulation is close to the surface area of the human TM (8 mm diameter), suggesting at low frequencies, the entire TM is moving roughly in phase in forward stimulation. The fluctuations in A_e at higher frequency suggest the presence of more complicated motions. One possibility is an increase in the out-of-phase modal motions with frequency (Tonndorf and Khanna, 1972;

Shaw and Stinson, 1983); however, such an increase should lead to cancellation of in-phase motions and an overall decrease in A_e with frequency. The data of Fig. 5(A) show an increase in A_e and are not consistent with the phase-cancellation hypothesis, but are consistent with our observations that at higher frequency, the TM still moves relatively in phase with small phase variations over the TM surface (Cheng et al., 2013). The A_e phase in forward stimulation is almost zero below 3 kHz, consistent with the whole TM and the umbo moving in phase at these frequencies. At higher frequencies, the phase increases with frequency, as the averaged TM surface motion leads the umbo motion.

In reverse stimulation, the smaller mean effective area magnitude (30 mm²) is consistent with the more localized stimulation of the TM that results from ossicular motion, and the cancellation of the out-of-phase TM surface motions observed at low frequencies (e.g., Fig. 3). The mean A_e phase shows similar zero phase value below 4 kHz, but then decreases as frequency increases where the mean TM surface motions lags the umbo motion. Such a lag is consistent with the TM motion following the stimulus-induced motion of the umbo and manubrium.

E. Does the TM move in-phase or out-of-phase with the Umbo?

The effective area is the ratio of the complex volume displacement of the TM surface to the umbo displacement, and we saw clear differences in its phase angle between forward and reverse stimulation, particularly with high stimulus frequencies. The results indicate significant sections of the TM move with phase different from the umbo at frequencies above 4 kHz (Fig. 5 suggests the TM leads with forward stimulation and lags with reverse stimulation). However, the effective area calculation scales the contribution of each TM location to the complex volume displacement by the magnitude of displacement at that location, and the phase of the effective area is, therefore, not a good estimate of the average phase of the motion on the TM surface. To overcome this magnitude scaling, we compute the average phase angle (relative to the umbo) $\overline{\theta}_\chi$ of the TM surface independent of the magnitude. In order to avoid the complication of how phase cycles across the surface, we compute $\overline{\theta}_\chi$ as the angle of the mean of a set of complex numbers of magnitude one and phase equal to the measured phase relative to the umbo, which we produce by dividing the complex displacement at each point by its magnitude. Specifically, for the n points on the TM surface

$$\overline{\theta}_\chi = \text{angle} \left(\frac{1}{n} \sum_{k=1}^n \frac{\chi_k}{|\chi_k|} \right). \quad (6)$$

The $\overline{\theta}_\chi$ values computed at each frequency and for each of the seven TBs for the two stimulus conditions are illustrated in Fig. 6, where Fig. 6(A) shows the results in forward stimulation, and Fig. 6(B) shows the results with reverse stimulation. The mean and SD from all seven bones are compared in Fig. 6(C).

FIG. 5. Comparisons of effective areas of the TM computed in forward and reverse stimulations from seven temporal bones. (A) Effective area in forward stimulation; (B) effective area in reverse stimulation; (C) comparison of mean effective areas between forward (in black) and reverse (in gray) stimulation and their standard deviations.

In forward stimulation at frequencies less than 1 kHz, $\overline{\theta}_\chi$ is near zero and relatively stable in all seven specimens [Fig. 6(A)]. Between 1 and 4 kHz, we see more variability in $\overline{\theta}_\chi$, which varies between -0.1 and $+0.3$ cycles among the seven ears. Above 4 kHz, the mean forward-driven $\overline{\theta}_\chi$ becomes

more positive with increasing frequency, consistent with the umbo lagging the motion of the TM surface. With reverse stimulation, the $\overline{\theta}_\chi$ is more variable, with phase steps of more than a half-cycle occurring in some specimens [Fig. 6(B)], though the mean of the seven specimens is an angle

FIG. 6. Displacement phase relative to the umbo averaged over the TM surface in seven temporal bones. (A) Forward stimulation. (B) Reverse stimulation. (C) Comparison of the mean and standard deviation of the TM surface motion phase relative to the umbo between two stimulations (forward in solid lines with open circles, and reverse in dashed lines with filled circles). In all plots, a thin dotted horizontal line marks the 0 phase value.

near 0 zero at frequencies below 5 kHz, with generally more negative values at higher frequencies [Fig. 6(C)] consistent with the TM surface lagging the umbo.

A two-tailed Student's t -test of whether $\overline{\theta_z}$ measured during forward stimulation in the seven ears at 20 frequencies differed from zero was highly significant with $p < 0.00001$, while the angle value in reverse stimulation was not statistically different from zero ($p = 0.2536$). Similar tests looking at only frequencies either below or above 8000 Hz produced similar low probabilities that the forward driven phase angles were zero ($p < 0.0001$), while the reverse-driven mean phase angles were not significantly different from zero.

F. What fraction of the phases are consistent with either standing waves or traveling waves?

We now investigate the distribution of umbo-normalized phase values on the TM surface. The phase

angles measured at each TM location were split into three bins: Those nearly “in-phase” with the umbo ($-0.125 \text{ cycles} \leq \varphi_k \leq +0.125 \text{ cycles}$), those nearly a half-cycle out-of-phase with the umbo ($0.375 \leq \varphi_k \leq 0.5 \text{ cycles}$ and $-0.375 \geq \varphi_k \geq -0.5 \text{ cycles}$), and phases with “other” values. The fraction of the TM surface with phase values in each category was computed for each TB, for each frequency and each stimulus condition. Figure 7 contains plots of the mean and standard deviation of the fractions in the seven bones for each frequency and stimulus.

Figure 7(A) illustrates that about 80% or more of the surface points of the seven TMs move in-phase with the umbo with forward stimulation at frequencies less than 1 kHz. As the stimulus frequency increases, there is a monotonic decrease in the in-phase fraction, which stays around 25% at frequencies above 8 kHz. The in-phase fraction of the TM surface in reverse stimulation follows a similar trend in frequency, but is smaller than in forward stimulation. A paired Student's t -test (over all frequencies and individuals)

FIG. 7. Fraction of TM surface motion (A) in-phase, (B) half-a-cycle-out-of-phase, and (C) quadrature phase with the umbo motion. Mean and standard deviation of the fraction of the TM area in forward (solid-lines and open circles) and reverse (dashed lines and filled circles) are compared across a wide frequency range between 100 and 20 000 Hz. The range indicators describe + and - one standard deviation.

suggests the fraction of TM that moves in-phase with the umbo is significantly higher in the forward case than in reverse case at frequencies below 8 kHz ($p < 0.00001$), but not significantly different above 8 kHz ($p = 0.4439$).

Both forward and reverse stimulations induce a small fraction (generally less than 20%) of the TM moving a half-cycle out-of-phase with the umbo [Fig. 7(B)] across the measured frequency range. Counter to the in-phase results, the out-of-phase fraction is generally larger in reverse stimulation. Similar paired t -tests suggest reverse stimulation induces a significantly higher fraction of half-cycle out-of-phase motion than forward stimulation below 8 kHz ($p < 0.00001$), and above 8 kHz ($p = 0.01442$).

The fraction of other (quadrature) phase relative to the umbo [Fig. 7(C)] in forward stimulation is very small ($< 5\%$) below 1 kHz, and increases up to about 50% at frequencies near 10 kHz. The fraction of other phase in reverse stimulation follows a similar trend, but has a significantly higher fraction ($\sim 20\%$) below 3 kHz ($p < 0.005$).

Figure 7 suggests a significant fraction of the TM is moving in-phase with the umbo below 8 kHz in both forward and reverse stimulations, only a small fraction is moving out-of-phase with the umbo in both cases, and there is also a moderate fraction moving in quadrature phase. Moreover, forward stimulation tends to produce more in-phase motion than reverse stimulation, particular at low frequencies, and reverse stimulation shows a statistically significant larger fraction of out-of-phase motions on the TM surface, as is consistent with our surface-map observations in reverse stimulation. The quadrature-phase fraction increases from near 0 to 50% with frequency in both stimulations, with more in-quadrature-phase motions at low frequency with reverse stimulation, as would be predicted for an increased amount of traveling wave motion.

G. Comparisons of TM motion phase using complex-vector analysis

In this section, we use the analyses introduced in Sec. II G to try to classify and quantify the presence of modal and

FIG. 8. Argand diagrams of the TM surface motion at all measured TM surface points from TB7 in forward (A and C) and reverse (B and D) stimulations, at two selected frequencies (784 and 15 784 Hz).

traveling-wave like motions on the TM surface. Figure 8 shows Argand diagrams of the displacement at all TM surface points in forward and reverse stimulation at two frequencies in TB7. Panels A and B in this figure show the motion in the complex plane at 784 Hz, comparable to Fig. 3(A). At this frequency in forward stimulation [Fig. 8(A)], all TM points move almost in phase with one another, and therefore the collection of near 100 000 lines defined by the origin and the magnitude and phase of each measurement point are almost collinear on the Argand diagram consistent with a standing wave on the TM. The roughly single direction (along the positive real and imaginary axes) from the origin to all magnitude points is consistent with the mostly in-phase behavior described in Figs. 3(A) and 7(A). Reverse mechanical stimulation at this frequency [Fig. 8(B)] is also consistent with standing-wave behavior with another almost collinear representation on the Argand diagram of Fig. 8(B). However, there is an indication of a node with some points of zero magnitude and other points moving a half-cycle out-of-phase from the others, as is consistent with the reverse stimulation map in Fig. 3(A). Also note the presence of a

small number of TM points with small magnitudes and intermediate phases in both Figs. 8(A) and 8(B).

As described in Sec. II G, the presence of spatially graded phase differences in the displacements cause an increase in non-collinear plotted points on the Argand diagram. For example with forward stimulation at 15 784 Hz [Fig. 8(C)], the phase angles on the TM surface are significantly more varied than they are at 784 Hz, though the diagram shows that most of the TM points with considerable motion magnitude are moving within 90° phase of each other (they cover a region equivalent to one quadrant of the real and imaginary plane), consistent with the presence of smaller magnitude travelling waves in addition to larger modal motion on the TM (Cheng *et al.*, 2013). The motion at 15 784 Hz is more complicated in reverse mechanical stimulation [Fig. 8(D)]: the points occur at all phase angles on the complex plane, though again there is clear collinearity as a significant fraction of the points have phases that fall between $310 \pm 20^\circ$ and $130 \pm 20^\circ$. See supplementary material.¹

Although Argand diagrams are useful in visualizing overall motion characteristics, the overlapping variations in

FIG. 9. (Color online) Modified rose map plots of TM surface motions at all measurement points from TB7 in forward and reverse stimulations at four frequencies. (A) and (B) 784 Hz; (C) and (D) 3970 Hz; (E) and (F) 7304 Hz; (G) and (H) 15784 Hz. The circles describe contours of the fraction of the TM area with specific values of phase and magnitude relative to the umbo. The colors code the magnitude relative to the maximum ratio of point and umbo displacement. The extent of the colors within each phase range codes the fraction of points within a specific magnitude range in that phase range.

magnitude and angle of more than 100 000 points make it hard to quantify the density of the point distributions in these diagrams. Figure 9 shows angle and magnitude histograms of TM displacement in the variant of rose diagrams described in Sec. II G. The four frequencies shown in this figure contain the data in the motion maps of Fig. 3. Figure 9(A) illustrates that in forward stimulation at 784 Hz in TB7,

82% of the surface points move with a phase relative to the umbo of between 0 and 20°, and that about 20% of those points have a magnitude of at least 40% of the peak surface magnitude (coded in cyan, yellow, and red). Figure 9(D) illustrates that of the surface displacements measured in TB 7 with 3970 Hz in reverse stimulation, 14% of all surface points have phase angles that fall within the 260° to 280° phase angle bin, but a small number of points with near maximum displacements (coded in red) have phase angles from 320° to 40°. For the four frequencies shown in Fig. 9, reverse stimulation causes wider phase angle distributions, as is consistent with decreased collinearity and more traveling-wave like behavior than forward stimulation at the same frequency. See supplementary material.¹

The *MPC* index, also introduced in Sec. II G, enables us to express each rose diagram into one number and facilitates comparisons between forward and reverse stimulations. Figure 10(A) shows *MPCs* for all measured frequencies in TB7. At frequencies below 1 kHz, *MPCs* are very close to one indicating near-perfect standing-wave-like modal motion in both forward and reverse stimulations equivalent to a collinear scattering of points on an Argand and rose diagram. At higher frequencies, because of the existence of traveling-wave like phase gradients between TM points, the calculated *MPCs* get smaller in both forward and reverse stimulation. In this bone, the *MPC* is generally smaller in reverse stimulation pointing to less in-phase and out-of-phase motions and more mathematically complex (traveling-wave-like) motions than in forward stimulation.

In our measurements, we saw significant individual variations in *MPC*. *MPCs* computed for the other 6 TBs are included in the supplementary material¹ and are summarized in Fig. 10(B) that plots the median and range of the *MPC* measured in 20 frequency bands (described in Table I) that each contain measurements in 5–7 TBs. (We use bands because the set of stimulus frequencies varied slightly within the different experiments.) The salient features of Fig. 10(B) are (1) regardless of stimulation type, the *MPC* are near 1 at frequencies of 1 kHz or less, (2) the *MPC* are generally smaller than 0.3 at frequencies above 1 kHz, (3) there is significant inter-individual variation in *MPC* at frequencies above 1 kHz, and (4) the median *MPC* observed in forward stimulation is generally but not always larger than the median *MPC* in reverse stimulation. This last statement is supported by non-parametric and parametric statistical analyses comparing the 137 (seven individuals at 18–20 different frequencies) pairs of *MPC* computations. A Wilcoxon Matched Pairs test comparing the paired forward and reverse *MPCs* yields a significant difference between the two with an estimated probability that they come from the same population of $p=0.00045$, while a non-parametric sign test demonstrates a significance of $p=0.00151$. A paired Student's *t*-test yields a probability that the two score sets come from the same population of $p=0.00164$.

How is the variability in the *MPC* affected by the observed variability in umbo motion in the test population? Figure 10(C) illustrates a similar plotting of the data from the subset of four TBs with larger low-frequency umbo displacements [Fig. 2(A)]. This subset shows a similar

FIG. 10. (A) Comparison of *MPC* index in TB7 at 20 frequencies between forward and reverse stimulations. (B) Median *MPC* correlations in forward and reverse stimulations from all seven bones. (C) Median *MPC* correlations in forward and reverse stimulations from reduced number of bones ($N = 4$).

frequency dependence of the median *MPC* as the full set of seven TBs, but generally has a smaller range of values, where the difference is a decrease in the number of higher *MPC* values at frequencies above 1 kHz. The reduced data set still shows a propensity for larger *MPC* values with

forward stimulation that is also supported by statistical tests: a Wilcoxon Matched Pairs tests suggests a significant difference with $p = 0.001\ 25$, the sign-test yields a significance of $p = 0.005\ 19$, and a paired t -test suggests a difference of significance $p = 0.021\ 28$.

TABLE I. Surface displacement maxima re umbo displacement.

Freq (kHz)	Count	Forward					Reverse				
		Mean	Stdev	Min	Max	Median	Mean	Stdev	Min	Max	Median
0.2–0.245	6	17.1	23.9	2.9	64.9	7.0	9.0	10.1	1.7	26.3	4.0
0.49–0.5	7	19.9	32.4	5.3	93.1	6.1	34.7	72.4	2.0	198.3	5.9
0.78–0.8	7	19.0	28.3	4.2	82.3	7.5	60.5	142.0	2.0	382.3	4.9
1.0–1.08	7	24.2	38.0	4.4	109.9	12.0	14.9	20.2	2.6	58.7	6.5
1.9–2.0	7	32.0	35.8	7.4	110.0	19.7	20.3	15.7	2.0	49.2	15.9
2.9–3.0	7	15.4	7.6	8.5	26.2	12.0	9.9	8.7	2.0	28.2	6.7
3.9–4.0	7	9.3	2.5	6.1	13.8	9.6	21.4	27.3	2.6	82.5	13.8
5.0	7	9.7	3.5	5.0	15.8	9.5	23.0	30.6	1.9	90.6	13.4
6.0–6.3	7	9.7	3.0	5.4	13.9	10.8	36.2	62.8	3.2	177.9	17.7
7.0–7.3	7	10.3	3.9	6.4	16.9	10.3	13.1	7.7	6.5	26.9	10.2
8.0–8.6	7	11.8	5.2	5.3	19.0	12.2	17.2	22.5	4.4	67.5	10.4
9.0–9.3	7	13.6	8.3	8.9	32.2	10.0	44.5	62.5	3.0	141.2	9.6
10.0–10.8	7	22.3	35.3	6.4	102.1	10.0	42.0	45.1	2.3	99.0	9.6
11.0–11.7	7	15.7	18.4	5.7	57.0	9.3	43.4	47.8	2.0	111.1	12.6
12.0–12.6	7	16.3	18.4	5.4	57.4	9.5	24.6	22.6	2.2	64.3	18.9
13.0–13.6	7	16.3	13.1	8.5	45.4	11.4	19.6	19.2	2.0	53.3	15.2
14.0–14.7	7	15.4	7.2	7.0	28.2	14.7	59.9	87.9	2.9	249.1	29.1
15.0–15.8	7	13.3	7.4	5.1	24.1	12.6	28.6	30.4	2.4	87.8	15.3
16.0–17.1	6	19.1	13.3	8.9	40.4	12.9	30.4	26.1	2.7	61.4	24.8
18.0–18.5	5	15.4	4.0	6.0	21.2	16.3	23.4	21.6	6.1	47.6	10.1

H. Location and relative amplitude of maximal displacements on the TM surface

Quantification of full-field surface motion of the TM across a broad frequency range allows us to describe whether the location and magnitude of the maximum displacement on the TM surface varies with frequency and stimulus type. Such descriptions can help our understanding of how the TM couples acoustic energy into mechanical vibration of the middle ear, and vice versa.

The locations of maximum displacements at 17 frequencies (0.2–18 kHz) on each of seven bones are identified and plotted in Figs. 11(A)–11(C) for forward stimulation, and Figs. 11(D)–11(F) for reverse stimulation. The plot panels divide the stimulus frequencies into three groups (low: 0.2–1 kHz; middle: 2–5 kHz; and high: 6–18 kHz). In each panel, a large circle represents the TM surface, a gray line at 12 o'clock represents the manubrium, and the superior-inferior and anterior-posterior orientations of the TM are labeled. Different symbols and colors are used to describe the stimulus frequency, and the plotted locations define the location of the magnitude maxima for each temporal bone at each frequency.

When we look at the location of magnitude maxima produced by forward stimuli of 1 kHz and less [Fig. 11(A)], we see that a large majority of the maxima are in the posterior half of the TM, and that within any single TB, many of the peak locations are independent of frequency, yielding locations marked by multiple frequency symbols. Furthermore, three TBs (6, 7, and 13) have a maxima at nearly the same posterior-inferior location (see the cluster of points at about -1 mm (x -coordinate) and $+3$ mm (y) relative to the umbo) at all four low frequencies.

In the middle frequency grouping (above 1 and below 6 kHz) with forward stimulation [Fig. 11(B)], the locations

of the maxima vary more with frequency, but are still mostly confined to the posterior half of the TM. In the high-frequency grouping with forward stimulation, the locations of the maxima are more evenly scattered around the umbo, but the radial distance from the umbo to each location maxima is relatively constant at about 2.5 mm, whereas the radial location of the maxima was more varied at lower frequencies.

The locations of the magnitude maxima seen in reverse stimulation [Figs. 11(D)–11(F)] are more varied and are more evenly distributed about the TM surface at all frequencies. Little overlap is seen in the location of the displacement maxima within a TB or particular frequency ranges. Again, there is a tendency for the magnitude maxima to occur at locations about half-way between the umbo and the tympanic ring, with only a few maxima at the umbo or near the ring.

The magnitude of the displacement maxima normalized by the umbo displacement is quite variable across frequency and the different specimens with a magnitude ratio ranging from near 3 to over 100 in forward stimulation and from 1.7 to nearly 400 in reverse stimulation (Table I). The maxima are not well correlated with frequency (a Pearson-Product correlation of 0.06 for forward stimulation and 0.07 for reverse). Analysis of variance (ANOVA) comparisons of the 136 measurements in each of the two stimulus-type populations describe a significant difference ($p < 0.006$) between the maxima observed with forward and reverse stimulation, where the mean magnitudes measured in the two cases are 16.2 and 29.0, respectively. Restricting the comparison to frequencies of 8000 Hz and below yield non-significant differences ($p = 0.245$), while restricting the testing to frequencies of 9 kHz and above yield a higher significance to the difference ($p < 0.0024$) and mean maxima values of 16.4 and 35.6 in forward and reverse stimulation, respectively.

FIG. 11. (Color online) Maps of the location of the maximum displacement magnitude in each of the seven bones across three frequency ranges in forward [(A), (B), and (C)] and reverse [(D), (E), and (F)] stimulations. In Forward stimulation, the location of the maximum is nearly identical in three bones (6, 7, and 13) at all four low frequencies. The other four bones show similar Forward stimulation maxima in at least three of the four low frequencies, but the location differs between the bones.

IV. DISCUSSION

We report and compare measurements of TM surface motion induced by sinusoidal acoustic (forward) and mechanical (reverse) stimulations in human temporal bones, a preparation that is a standard for investigating principles of human middle-ear acoustics and mechanics (Goode *et al.*, 1993; Rosowski *et al.*, 2008). Our earlier work pointed out the presence of frequency-dependent displacement patterns that had features in common with modal (standing-wave-like) and traveling-wave-like motions. Here, we expand on these descriptions and use them to quantify differences in the response to forward (acoustic) and reverse (mechanical) stimulation of the TM.

A. Comparison of forward and reverse driven TM motions

A central question we address is “are the motions of the TM surface relative to the umbo the same in forward and reverse stimulation?” Our results (Figs. 3–7) and analyses (Figs. 8–11) suggest TM motions induced by the two different stimulation mechanisms are different in many ways. In forward stimulation, we see more in-phase motions of the TM surface, with sudden step-like phase changes between

different locations on the TM surface. While in reverse stimulation, we see more traveling-wave-like phase-glides on the TM surface and clear anti-phasic motions between sections of the TM surface with low-frequency stimulation. The presence of wave travel that appears to progress away from the umbo in reverse stimulation is consistent with the TM being driven by the spatially restricted motion of the ossicles rather than the relatively uniform sound pressure load of acoustic stimulation.

We quantitatively compared the average magnitude and phase of the TM motions produced by the two stimulations by computing the effective area (Fig. 5), averaged surface motion phase relative to umbo (Fig. 6), and fraction of TM surface in- and out-of phase with umbo (Fig. 7). These analyses are all consistent with differences in the surface motion of the TM induced by the two stimulation mechanisms. (1) The magnitude of the effective areas in reverse stimulation is about 60% of what we see with forward stimulation (Fig. 5). While the effective area in both stimulations suggest in-phase motion of the TM surface and umbo at frequencies less than 4 kHz, at higher frequencies, the TM surface motion phase leads the umbo in forward stimulation and lags in reverse stimulation (Fig. 5). The differences in the phase of motion relative to the umbo in the two stimulus modes are supported

by our measurements of the average phase of motion (Fig. 6), which demonstrate larger variations in the average surface phase in reverse stimulation. These differences in average phase are supported by the computations of surface fractions with different phase behavior, where in reverse stimulation we see large fractions of the surface with “out-of-phase” and “in-quadrature-phase” behavior.

In order to compare more quantitatively the fraction of standing and traveling waves on the TM surface in the two stimulation types, we introduced several complex-vector analyses that are presented in Figs. 8–10 (and in the supplementary material¹). These analyses use graphical and statistical tools to view the magnitude and phase of motion in large sized datasets, and reduce the more than 100 000 measurements over the TM surface into single plots or a small number of values.

An example is the *MPC* index which quantifies the degree of variability in the displacement phase of all of the points on the TM surface and separates standing-wave-like modal motions (which are well fit by lines on the complex plane in the Argand plots and show as regions of preferred phase and anti-phase in the rose diagrams) with an *MPC* of ~ 1 , from traveling-wave dominated motions which contain all phases (which plot as non-directional point clouds in the Argand plots and as a large spread of phases values in the rose plots) with an *MPC* near 0. [Another factor in relating the *MPC* value to the Argand and rose diagrams is the magnitude of the displacements, as coded in color in our modified rose diagrams. For example, in Fig. 9(D), approximately 25% of the surface has an angle between 260° and 300° , but the *MPC* is only 0.3 in Fig. 10(A). The low *MPC* comes out because the largest magnitude displacements take up only a few % of the TM surface and occur in a band between -20 and $+80^\circ$.]

Figures 10(B) and 10(C) demonstrate that the *MPC* correlation is near 1 in both forward and reverse stimulation with frequencies of less than 1 kHz. With higher frequency stimulation the *MPC* is smaller and is also highly variable between individual TBs, often showing ranges of values greater than 50% within the seven TBs. This variability is reduced if we remove the three TBs with smaller sound-driven umbo velocities [Fig. 2(A)]. However, with either the complete ($n=7$) or displacement restricted ($n=4$) populations, our statistical analyses conclude the *MPC* in forward stimulation is larger than in reverse stimulation, consistent with the notion that there is a larger contribution of modal-standing waves to the measured displacements with forward stimulation. The data also suggest that in forward (but not reverse) stimulation the *MPC* at frequencies above 12 kHz is larger than at frequencies between 2 and 12 kHz.

We also described differences in the location and magnitude of the peak displacements on the TM surface in the two stimulus conditions (Fig. 11 and Table I). With forward stimulation at frequencies less than 5 kHz, the location of the maxima displacement was generally in the posterior half of the TM, and at frequencies less than 1 kHz, the location of the maxima varied from ear to ear but was generally independent of the stimulus frequency. At frequencies above 5 kHz in forward stimulation or at any frequency in reverse

stimulation, the maximal displacement could be found in any quadrant on the TM, though there was a tendency for the maxima to occur near the midpoint of radii drawn between the umbo and the TM rim. This is consistent with Milazzo *et al.* (2017) who report maximal TM motions at the TM’s radial midpoints when sounds enter the ear canal. We observed large variations in the magnitude of the maximum displacement measured during both forward and reverse stimulation; however, in both cases the TM surface motions were generally larger than the umbo displacement. At frequencies above 10 kHz, the umbo normalized displacements along the TM surface were generally greater in reverse stimulation than in forward stimulation. In summary, we see significant differences between forward and reverse stimulation in nearly all of our descriptive and quantitative measurements of TM motion patterns.

The differences we see in TM motion produced by forward and reverse motion are consistent with the Dong and Olson (2006) hypothesis that differences in the relationship between TM surface and ossicular motions contribute to differences observed in the forward sound-pressure gain and reverse sound-pressure loss measured in gerbil ears. However, whether these differences break the expected reciprocal action of the middle ear and TM—as described by Shera and Zweig (1991)—is not all that clear. Reciprocity in an acousto-mechanical system function depends on highly-specific measurements of sound transfer, which are not met by normal measurements of forward and reverse middle-ear gain. The primary complication in using such measurements to test reciprocity are the big differences in the load on the middle ear in the two stimulus paradigms: in forward sound stimulation, the sound stimulus is working against the high-impedance of the middle and inner ear, while in reverse mechanical stimulation, the driving force is working against the low-impedance of the air inside the external ear canal. The response of the TM can be different when it is acts against these different loadings.

B. Is there evidence for the cancellation of TM waves and zero average motion?

Several authors have suggested that the cancellation of in- and out-of-phase modal motions on the TM increases with the frequency of stimulation, which leads to a high-frequency decrease in TM-sound reception and conduction (Tonndorf and Khanna, 1971; Shaw and Stinson, 1983; Fletcher, 1992). Our data do show a difference in the effective area between forward (50 mm^2) and reverse (30 mm^2) sound stimulation, which is consistent with the presence of more cancellation of in- and out-of-phase areas in reverse stimulation [Fig. 7(C)]. However, we also present data that are inconsistent with cancellation limiting high-frequency TM motion: (1) perfect cancellation of the volume displacement of the TM will lead to effective areas of 0, yet the magnitude of the effective areas we compute (Fig. 5) are nearly constant over a broad frequency range, and if anything, the effective area during forward transmission increases with increasing frequency. (2) The fraction of the TM area that moves out-of-phase with the umbo is generally small

(<25%), and is generally less than the in-phase fraction. Therefore, while our data demonstrate the presence of in-phase and out-of-phase motions on the TM surface, the imbalance between these two and the presence of motions of other phases do not lead to significant cancellation of TM volume displacement as suggested by older studies.

C. Do either modal or traveling waves dominate?

In our previous work (Cheng *et al.*, 2013) we described TM surface motions in response to forward stimulation as a combination of standing waves and traveling waves, where the standing-wave amplitudes are generally larger than those of the traveling waves. We now show that in reverse stimulation, TM motion is also dominated by standing-wave-like modal motions at frequencies below 2 kHz (from Figs. 3, 4, 8, and 10); however, we also demonstrate an increased presence of traveling waves as frequency increases (Figs. 4 and 7–10). The traveling waves in reverse stimulation with phases that increase with distance from the umbo are consistent with the spread of the localized motion of the ossicles to the surrounding TM area. In summary, below 2 kHz, TM motions in forward and reverse stimulation are primarily modal like motions. At higher frequencies in forward stimulation, TM motion is consistent with a combination of lower magnitude traveling waves and larger magnitude modal waves; while in reverse stimulation, TM motions are consistent with a larger contribution of traveling waves.

D. Effect of reverse stimulation on sound pressures in the ear canal

In our experiments, we also monitored the sound pressure distribution over the TM surface (within 1 mm distance from the TM surface) during forward (Ravicz *et al.*, 2014; Cheng *et al.*, 2015) and reverse stimulation. The later measurements are being prepared for publication.

V. CONCLUSIONS

(1) TM motions are different between forward and reverse stimulations: we observe dominant standing-wave modal motions in both forward and reverse stimulation at frequencies below 3 kHz ($MPC > 0.8$), though the phase analyses and Argand displays suggest a greater incidence of standing-wave nodes (half-cycle-out-of-phase behavior) in forward stimulation, suggesting a major role of the standing-wave-like modal motion of the TM for sound transmission in this frequency range. At frequencies above 4 kHz, there is an increased contribution of traveling waves ($MPC < 0.5$) with both stimuli. While those data at higher frequencies show large inter-individual variability, the contribution of standing waves appears greater with forward stimulation where the MPC index is significantly higher. This difference is most apparent at the highest frequencies (>14 kHz). The differences in TM motion may be associated with contrast between the more uniform excitation of the TM surface in forward sound stimulation (Cheng *et al.*, 2015)

compared to the local excitation of the TM produced by reverse mechanical stimulation.

- (2) We describe a series of analyses including image registration (to facilitate comparison across different data-sets), and complex vector analyses (Argand diagrams, Rose diagrams, and the MPC index) to help differentiate the complex motions on the TM surface. Our results provide by far the most detailed descriptions of TM motions in both forward and reverse middle ear transmission processes. These results can be used to refine many existing modeling studies of the TM to better understand TM mechanics. The analysis tools developed in this study may also have the potential for clinical applications to provide quantitative metrics to assist in interpretation and differentiation of complex TM motions among normal and pathological ears.
- (3) The relatively small percentage of out-of-phase motion regions we observe and the near frequency-independence of the effective area of the TM are inconsistent with modal motion-based theories that suggest a high-frequency limit to hearing based on the cancellation of in- and out-of-phase regions on the TM surface (Tonndorf and Khanna, 1972; Shaw and Stinson, 1983).
- (4) The differences we see between forward- and reverse-driven TM surface motions are consistent with the hypothesis that such differences are related to measured differences in forward and reverse-driven middle-ear gains (Dong and Olson, 2006). However, the measurements we make cannot be used to test the proposed reciprocal action of the TM and middle ear (Shera and Zweig, 1991).

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¹See supplementary material at <https://doi.org/10.1121/1.5087134> for maps from all seven bones at selected frequencies, Argand diagrams at all other measured frequencies in TB7, Rose diagrams at four measured frequencies in all seven TBs, MPC s computed for the other 6 TBs, and for additional results of all samples.

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