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Impedances of the inner and middle ear estimated from intracochlear sound pressures in normal human temporal bones

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Abstract

For almost a decade, we have measured intracochlear sound pressures evoked by air conducted (AC) sound presented to the ear canal in many fresh human cadaveric specimens. Similar measurements were also obtained during round window (RW) mechanical stimulation in multiple specimens. In the present study, we use our accumulated data of intracochlear pressures and simultaneous velocity measurements of the stapes or RW to determine acoustic impedances of the cochlear partition, RW, and the leakage paths from scala vestibuli and scala tympani, as well as the reverse middle ear impedance. With these impedances, we develop a computational lumped-element model of the normal ear that illuminates fundamental mechanisms of sound transmission.

To calculate the impedances for our model, we use data that passes strict inclusion criteria of: (a) normal middle-ear transfer function defined as the ratio of stapes velocity to ear-canal sound pressure, (b) no evidence of air within the inner ear, and (c) tight control of the pressure sensor sensitivity. After this strict screening, updated normal means, as well as individual representative data, of ossicular velocities and intracochlear pressures for AC and RW stimulation are used to calculate impedances. This work demonstrates the existence and the value of physiological acoustic leak impedances that can sometimes contribute significantly to sound transmission for some stimulation modalities. This model allows understanding of human sound transmission mechanisms for various sound stimulation methods such as AC, RW, and bone conduction, as well as sound transmission related to otoacoustic emissions.

Keywords

impedance modeling; intracochlear pressure

1. INTRODUCTION

Passive macro-mechanics in fresh cadaveric human temporal bones are similar to the living, as is evidenced by similarities in measurements of sound-induced stapes vibration in live ears and fresh cadaveric specimens (Chien et al., 2009). “Passive macro-mechanics” of the cochlea refers to the gross mechanical properties of the inner ear. These do not include the active mechanical processes within the cochlear partition of live ears. For example, the inner-ear sound pressures in scala vestibuli (P_{SV}) and scala tympani (P_{ST}) measured close to the surrounding bone (not the partition near the traveling wave), quantifies the human *cochlear input pressure drive* ($P_{SV} - P_{ST}$), the complex differential pressure across the cochlea partition at the cochlear base that is dominated by fast wave sound pressure and starts the traveling wave along the cochlear partition (Olson, 1998). The cochlear input pressure drive has been shown to have the same frequency response as sensory potentials (cochlear microphonic) measured at the same location in animals (Dancer and Franke, 1980; Lynch et al., 1982). Furthermore, the effects of middle and inner ear lesions (e.g. ossicular discontinuity and superior canal dehiscence) on the cochlear input drive in temporal bones are similar to clinical findings for hearing in live humans (Nakajima et al., 2009; Niesten et al., 2015; Pisano et al., 2012).

Measurements of intracochlear sound pressures and ossicular motions quantify important mechano-acoustic properties of the ear. Knowledge of the impedances of the middle and inner ear are necessary to understand the intricacies of sound transmission through the inner ear (Elliott et al., 2016; Nakajima et al., 2009; Stieger et al., 2013). Our pressure measurement techniques combined with velocity measurements of the stapes and round window are valuable in determining the sound transmission mechanisms that dominate during various forms of inner-ear stimulation (e.g. air conduction (AC), bone conduction (BC), round window (RW) stimulation, soft tissue stimulation, etc.).

Previously, we showed that the paths of sound-related volume velocity through the inner ear differ between ear-canal AC and actuator-driven RW stimulation (Stieger et al., 2013). For AC stimulation, evidence supports the two-window hypothesis: the input to the inner ear – the volume velocity produced by stapes motion (U_{stap}) at the oval window (OW) – and the output of volume velocity from the inner ear via the compliant RW (U_{RW}) are approximately equal (Kringelbotn, 1995; Stenfelt et al., 2004a). Therefore, in AC, other potential sound paths, such as vestibular and cochlear aqueducts, contribute little to sound transmission and have insignificant volume velocity sound flow.

Different from AC, RW stimulation results in inner-ear volume velocities that do not well conform to the two-window hypothesis (Stenfelt et al., 2004a; Stieger et al., 2013), where the volume velocity elicited by the RW actuator flowing into scala vestibuli does not all flow through the oval window, but splits, such that a significant fraction flows through a leakage path on the vestibular side of the cochlear partition (likely the vestibular aqueduct and/or neurovascular channels) (Dancer and Franke, 1980; Stieger et al., 2013; Tonndorf, 1972). A physical factor that contributes to this leak with RW stimulation is that the volume velocity elicited by stimulation faces an impedance at the OW (the reverse middle-ear impedance)

that is similar in magnitude to the high impedance of the scala vestibuli leakage path (Stieger et al., 2013).

The major goal of the present study is to determine the values of the impedances that influence sound transmission within the inner ear. As a prerequisite for this task, we determine a “standard” set of sound-pressure transfer functions for “normal” human temporal bones – those without history of ear disease and with normal middle and inner ear macro-mechanics. From our accumulated measurements of intracochlear sound pressures and ossicular velocities during normal air conduction (AC) and round window (RW) stimulation, we implement strict inclusion criteria to describe the intracochlear sound pressure characteristics in normal ears. This set of standards, expressed as transfer functions, is useful for a) comparisons to past and future experiments, b) validation of computational models of the ear, and c) improving our understanding of the mechanism of sound transmission within the inner ear.

Using this data, we focus on the impedances that most influence the transmission of sound: the differential impedance across the partition measured at the base of the cochlea (Z_{Diff} , which includes the influence of the helicotrema), the RW impedance (Z_{RW}), the reverse middle-ear impedance from the cochlea looking out towards the middle ear (Z_{ME}^{-}), the leakage impedance of the SV to the exterior of the otic capsule (Z_{IKSV}), and the leakage impedance of the ST and RW (Z_{IKSTRW}) to the exterior of the otic capsule. We use a combination of AC and RW stimulation results to determine these impedances. Based on these results we develop a lumped-element model that can help us understand more complex sound transmission mechanisms, such as bone- or soft-tissue-conducted sounds (Perez et al., 2016; Stenfelt, 2016; Stenfelt and Goode, 2005). This model can also impact our understanding of inner-ear sound transmission in pathological and perturbed states, where the flow of volume velocity through the inner ear is altered by changes in the relevant impedances or by the introduction of new volume velocity paths (e.g. superior canal dehiscence).

2. METHODS

A total of 37 fresh human cadaveric temporal bones provide normative data. Pressure data from 22 specimens were already published including AC stimulation data from Nakajima et al. 2009, Stieger et al. 2013, Pisano et al. 2012, and Niesten et al. 2015. The RW stimulation data came from Stieger et al. 2013. In the aforementioned studies, except for Nakajima et al. 2009, there was a computational error such that the reported intracochlear pressures were 7 dB lower than the actual level; this error is now corrected. The methods for the present study were detailed in previous publications (Nakajima et al., 2010, 2009; Stieger et al., 2013). Therefore, only brief descriptions are given here.

2.1 Temporal Bone Preparation

The temporal bones were harvested within 24 hours of death with surrounding dura kept intact, and used either fresh or after freezing and thawing. Inspection of the ear with a surgical microscope was normal with no noticeable pathology. The major difference between fresh and previously frozen is that fresh bones rarely showed evidence of air in the

inner ear, while several of the thawed bones did (Ravicz et al., 2000). Prior to specimen preparation, the fresh and thawed specimens were stored at 4°C in 0.9% normal saline. A mastoidectomy was performed to widely open the facial recess, and the stapedial tendon was usually removed to allow access to the area surrounding the oval window. In the RW stimulated ears, the bony overhang around the perimeter of the RW was reduced to facilitate the coupling of the actuator to the RW membrane.

2.2 AC and RW Stimulation

For AC stimulation, a loudspeaker (either Radio Shack 40–1377 or Beyer Dynamic DT48) was coupled to the bony ear canal. Pure tones of 77 ms length at 74 logarithmically-spaced frequencies between 0.1 and 10 kHz were presented and responses averaged 25 or 50 times. The sound pressure within the ear canal (P_{EC}) was recorded with a probe microphone (ER-7C, Etymotic) with the tip located 1–2 mm from the umbo. The stimulus sound pressures were generally between 50 and 120 dB SPL.

For RW stimulation we used a piezoelectric actuator firmly coupled to a transparent-glass rod (1 mm diameter). In 5 specimens the tip of the rod was coupled to the RW membrane directly or with an interfacing disk (1.5 mm diameter) punched out of a soft contact lens. The glass rod was brought into contact with the RW membrane and pushed towards the inner ear in small increments until the stapes velocity and intracochlear pressure measurements stopped increasing in magnitude (Maier et al., 2013; Schraven et al., 2012). The RW stimulator was driven at the same frequencies as for AC stimulation. The magnitude of the stimulus displacement was generally between 55 nm and 85 nm.

2.3 Pressure and Velocity Measurements

Intracochlear sound pressure measurements were performed with micro fiber-optic pressure sensors (Olson, 1998). Cochleostomies slightly larger than the sensor diameter (167–200 μm) were drilled by hand while the cochlea was immersed in saline to prevent air from entering the cochlea. The sensors were inserted into scala vestibuli near the OW and scala tympani near the RW. The depth of insertion was approximately 100–200 μm from the otic bone-fluid interface. While maintaining saline around the sensors, the gaps between the sensors and the bone were sealed with dental impression material (Jeltrate, L.D. Caulk Co.). In later experiments, a layer of dental cement (Durelon, 3M Corp) was overlaid on the dried Jeltrate and surrounding bone to firmly fix the sensor to the promontory.

We measured intracochlear sound pressures close to the otic bone to maximize measurement of the fast-wave component of intracochlear sound pressure (distant from the cochlear partition), and minimize the “physiologically vulnerable” slow-wave components produced by the motion of the cochlear partition. Therefore, the pressures we measured are not vulnerable to the physiological condition of the sensory mechanism in the living ear, but are related to the mechanisms of gross macro-mechanical sound transmission, which is similar in living and fresh cadaveric specimens.

Simultaneous with the pressure measurements in the cochlea and ear canal, velocities of the stapes (posterior crus), round-window membrane, actuator or cochlear promontory were measured with a laser Doppler vibrometer (Polytec CLV), using reflective tape (0.1–0.2

mm²) on the vibrating surface. To measure the velocity of the stapes (V_{stap}), the laser was aligned along the plane defined by the anterior and posterior crus and as close to orthogonal to the stapes footplate as possible to maximize sensitivity to the piston-like motion of the stapes and to minimize sensitivity to rocking motions. To measure the velocity of the RW (V_{RW}), the laser beam was positioned orthogonal to the plane of the RW membrane and at its center. The velocity of the promontory was measured during AC and RW stimulation to determine the level of artifact motion of the entire temporal bone. Actuator velocity (V_{act}) was measured at the side of the glass rod with an angle of 20 to 30 degrees relative to the direction of the actuator motion.

Data were analyzed using software coded in Matlab. All pressure and velocity measurements with a signal-to-noise ratio (SNR) below 10 dB were excluded. Geometric averages and standard deviations (computed in the log domain) were used to describe the mean data and variation.

2.4 Criteria Set for Normal Ears and Accuracy of Measurements

Experimental data were only included in this study if three criteria were fulfilled for each specimen: 1) normal stapes velocity to ear-canal sound pressure transfer function; 2) no evidence of inner-ear air or fluid leak; 3) consistency (within 2 dB) of the pressure-sensor sensitivity throughout the experiment.

2.4.1 Stapes Velocity to Ear-Canal Sound Pressure Transfer Function—The velocity of the stapes normalized to the sound pressure in the ear canal (V_{stap}/P_{EC}), was used as a measure of the normality of the ears' responses to sound and compared to the normal magnitude range reported by Rosowski et al., 2007 (Fig. 1A). Experiments that fell outside the normal range (gray shaded area) below 2 kHz were excluded. The 2 kHz limit was chosen because the motion of the stapes becomes complex (not a simple piston-like motion) above this range (Chien et al., 2006; Hato et al., 2003; Heiland et al., 1999; Sim et al., 2010), and the one-dimensional laser measurement can vary greatly depending on the three-dimensional direction of the motion.

2.4.2 Tests for air within the cochlea—We tested for the presence of air in the cochlea using two tests. First, we used the observation that during AC stimulation, the motion of the incompressible fluid within the inner ear produces a half-cycle phase difference between the velocities of the stapes and RW (V_{stap}/V_{RW}) at frequencies below 500 Hz (Kringelbotn, 1995; Stenfelt et al., 2004a, 2004b) (above 500 Hz, the mode of RW velocities can become complex). If air enters the inner ear, the inner-ear contents become compressible and the low-frequency phase difference varies from 0.5 cycles. This half cycle relationship was checked before and after the sensors were inserted and sealed in place. Second, we made certain that the phases of V_{stap} and V_{RW} relative to the stimulus sound pressure were unchanged (within 0.02 cycles) before and after pressure sensor insertions. Fig. 1B plots the phase of V_{stap}/V_{RW} with the sensors in place for all 37 temporal bones. Only experiments that exhibited phase differences between -0.48 and 0.52 cycles (corresponding to $\pm 7.2^\circ$) at frequencies less than 500 Hz were included in this study.

2.4.3 Consistency of sensor sensitivity—To ensure accuracy of our inner-ear pressure measurements, we checked the sensitivity of our pressure sensors to determine if their calibrations remained within 2 dB of the initial measurement during the experiment. In earlier studies, we did this by comparing the calibrations of the sensors before inner-ear insertions, and after removal of the sensors at the end of the entire experiment. In later studies, we adopted a different method described as follows:

At the beginning of the experiment we calibrated the sensors outside the ear with a fluid-filled shaker in the manner described previously (Nakajima et al., 2009; Stieger et al., 2013), and then measured the AC stimulus-generated sound pressures within the inner ear after sealing the sensors with Jeltrate® – a flexible quick-setting gel used for dental impressions. The sensors were then removed and recalibrated outside the ear. If the new calibrations were within 2 dB of the originals, these initial measurements in scala vestibuli and scala tympani were considered reliable and accurate and used as comparators for subsequent measurements. The sensors were reinserted and secured using much firmer dental cement that prevented the removal of the intact sensor and did away with the possibility of retesting sensor sensitivity. Repeated new measurements of AC induced sound pressures were compared to the initial measurements to test for consistency of sensor sensitivity and specimen preparation throughout the experiment. Frequency-independent changes in the magnitude (and stable phase) of the AC pressure response that remained relatively stable were considered to indicate slow changes in sensor sensitivity and were used to correct later measurements. Changes from the initial measurements that were complex (frequency dependent magnitude or phase changes) were considered indicators of sensor failure or uncontrolled changes in the preparation.

2.4.4 Summary of inclusion for this study—A summary of the experiments using the inclusion criteria is shown in Table 1. Eighteen out of the 37 experiments passed our strict criteria. Also noted in Table 1 are reasons for the exclusion, which included the failure to perform one or more of the inclusion tests, abnormal stapes-velocity transfer function, abnormal ear structure, air in the inner ear or fluid leak (failed half-cycle phase test), and unstable sensor sensitivity.

2.5 Impedance Modeling

Based on the functional anatomy, the structures, impedances and volume velocity paths relevant to inner-ear sound transmission are presented in block diagrams in Fig. 2. AC stimulation is presented in Fig. 2A and RW stimulation in Fig. 2B. The acoustic impedances are calculated based on experimental results.

The blocks include: Z_{lksv} which accounts for any leakage or compressibility on the vestibular side of the cochlear partition, Z_{Diff} which accounts for both the cochlear partition and the helicotrema (Dallos, 1970; Dancer and Franke, 1980; Lynch et al., 1982) (the pressure across this block is the differential pressure across the cochlear partition), Z_{lkst} which accounts for any leakage or compressibility on the scala tympani side of the cochlear partition, Z_{RW} is the impedance of the RW, Z_{ME} is the impedance of the middle ear looking out from the cochlea via RW stimulation, and Z_{lkstRW} which accounts for Z_{lkst} as well as

leakage near the RW-actuator interface during RW stimulation. Associated with these impedances are P_{SV} which is the sound pressure in the scala vestibuli near the stapes, and P_{ST} which is the sound pressure in the scala tympani near the round window. There are also volume velocities that flow through each impedance block. In AC stimulation (2A) the stimulus volume velocity U_{stap} is estimated as the product of the measured stapes velocity and the area of the stapes footplate. In RW stimulation (2B) the stimulus volume velocity U_{act} is estimated as the product of the stimulator actuator velocity and the area in contact with the round window. Z_{ME} is not required to specify AC stimulation, and Z_{RW} is not required to specify RW stimulation. Detailed calculation of the five impedances from the measured sound pressures and stimulus velocities are explained in the results.

The choice of element values to model the impedances was performed using a least squares fit to both the magnitude and phase of the experimentally-derived impedance calculations. The equations used to calculate the Total Error and obtain a good fit of the data to the model are further explained in Appendix A.

3. RESULTS

3.1 Air Conduction Stimulation

The intracochlear sound pressures (P_{SV} and P_{ST}) were measured simultaneously with sound pressures in the ear canal (P_{EC}) and stapes velocity (V_{stap}). As shown in Fig. 3, P_{SV} is higher than P_{ST} in magnitude for AC stimulation regardless of its reference (referenced to P_{EC} or V_{stap}) for a wide frequency range, except for the lowest and highest frequencies. P_{ST} is generally lower in magnitude due to its proximity to the high compliance (low impedance) RW membrane (Lynch et al., 1982; Nakajima et al., 2009; Nedzelitsky, 1980). As shown in Fig. 3A, P_{SV}/P_{EC} peaks in magnitude around 700 Hz on average, but the frequency and the prominence of the peak varies among individuals. The phase is between 0 and 0.25 periods at low frequencies and decreases with increased frequency at a steady rate as it crosses zero near 700 Hz (the same location as the peak in the magnitude). Fig. 3B shows that P_{ST}/P_{EC} dips in magnitude at about 600 Hz on average, but this dip ranges from 400–1000 Hz for the individual experiments. The phase starts at 0 periods, increases slightly from about 400–1000 Hz, and then decreases steadily as frequency increases.

Because referencing the intracochlear pressure measurements to P_{EC} includes the effect of the middle-ear impedance, we plot intracochlear pressures referenced to V_{stap} to obtain transfer functions related to the input at the cochlea. P_{SV}/V_{stap} , plotted in Fig. 3C has a magnitude that is generally flat over the measured frequency range with a shallow dip at lower frequencies (200–400 Hz) that is more notable in individual experiments. The phase at the lowest frequency is negative but steadily increases and plateaus slightly above 0 periods between 1000 and 4000 Hz. P_{ST}/V_{stap} (Fig. 3D) dips in magnitude between 400–1000 Hz. The average smooths the sharp valleys of the individual magnitude measurements (which occur at different frequencies). The phase transitions from around –0.25 periods to almost 0.25 periods over the 100 – 6000 Hz range. This transition is steep in the individual experiments and occurs at frequencies from 400–1000 Hz, also varying across ears similarly to the magnitude valleys. The low-frequency magnitudes (below the valley) vary considerably, but maintain a –20 dB per decade slope across ears, while the phases are

generally consistent at these low frequencies. This pattern is consistent with the dominance of a RW compliance at low frequencies but with the value of the RW compliance varying across ears.

3.2 Round Window Stimulation

During RW stimulation, the intracochlear sound pressures (P_{SV} and P_{ST}) were measured simultaneously with the actuator velocity (V_{act}). These data are seen in Fig. 4. P_{SV}/V_{act} and P_{ST}/V_{act} are approximately equal during RW stimulation in both magnitude and phase. The magnitudes are high at low frequencies, decrease steadily up to 1–2 kHz, then level off. The phase of both P_{SV}/V_{act} and P_{ST}/V_{act} starts at about -0.25 periods at 100 Hz, increases to 0 periods around 1000 to 2000 Hz, and increase further at higher frequencies. The individual pressures in RW stimulation are less smooth compared to the AC stimulation case.

3.3 Impedance Calculations

In both AC and RW stimulation, volume velocity at the oval window was calculated as $U_{stap} = V_{stap} * A_{stap}$ where $A_{stap} = 3.22 \text{ mm}^2$ is the nominal area of the stapes footplate, consistent with the estimates of von Békésy and Aibara (Aibara et al., 2001; Georg von Békésy and Ernest Glen Wever, 1960). In order to compute Z_{Diff} and Z_{RW} , we use AC stimulation measurements of U_{stap} , P_{SV} , and P_{ST} along with the assumption that $U_{stap} \approx U_{Diff} \approx U_{RW}$, as would be the case if $Z_{lksv} \gg (Z_{Diff} + Z_{RW})$ and $Z_{lkst} \gg Z_{RW}$ in Fig. 2A. We also assume that the cochlear walls are rigid and the cochlear fluid is incompressible (Kringelbotn, 1995; Sim et al., 2012; Stenfelt et al., 2004a). With these assumptions:

$$Z_{Diff} = \frac{P_{SV} - P_{ST}}{U_{Diff}} \approx \frac{P_{SV} - P_{ST}}{U_{stap}}, \text{ and} \quad \text{Eqn 1}$$

$$Z_{RW} = \frac{P_{ST}}{U_{RW}} \approx \frac{P_{ST}}{U_{stap}} \quad \text{Eqn 2}$$

As shown in Fig. 5A, Z_{Diff} magnitude and phase is fairly flat across frequency, but the phase at low frequencies is consistently above zero periods for all experiments. In Fig. 5B, the magnitude of Z_{RW} at low frequencies (below 400–700 Hz) starts high and decreases at around 24dB/decade, with a corresponding phase of around -0.25 periods. At frequencies between 700 and 7000 Hz, Z_{RW} increases in magnitude by around 22dB/decade and with a constant mean phase of about 0.15 periods.

Measuring intracochlear sound pressures and stapes volume velocity during RW stimulation (U_{stap} in Fig. 2B) allows the determination of the impedance of the middle ear driven in reverse (Z_{ME} in Fig. 2B, which includes the effects of the stapes, other ossicles, middle-ear ligaments, TM and ear canal). The reverse middle ear impedance is simply related to P_{SV} and U_{stap} measured during RW stimulation:

$$Z_{ME'} = \frac{P_{SV}}{U'_{stap}} \quad \text{Eqn 3}$$

To compute Z_{lkSV} we assume Z_{Diff} has the same value for AC and RW stimulation. Then we calculate the volume velocity U'_{Diff} (across Z_{Diff}) during RW stimulation using the measured intracochlear sound pressures:

$$U'_{Diff} = \frac{P_{ST} - P_{SV}}{Z_{Diff}} \quad \text{Eqn 4}$$

The model of Fig 2B then specifies the leakage volume velocity during RW stimulation U'_{lkSV} to equal the difference between U'_{Diff} and U'_{stap} :

$$U'_{lkSV} = U'_{Diff} - U'_{stap} \quad \text{Eqn 5}$$

and the impedance Z_{lkSV} is:

$$Z_{lkSV} = \frac{P_{SV}}{U'_{lkSV}} \quad \text{Eqn 6}$$

Computations of the volume velocity and impedance of the ST leakage path were complicated by possible differences between the volume velocity produced by the round window stimulation and U_{RW} . Such a difference could result from the difference in area between the smaller RW actuator and the RW itself. This area difference would allow some of the actuator volume velocity to leak around the actuator and out the uncoupled RW area. Because of this uncertainty we use the RW stimulation methods to estimate the impedance of a *combination* of the ST and RW leakage path (Z_{lkSTRW}). The volume velocity of the actuator (U_{act}) is calculated by multiplying the velocity of the actuator times the diameter of the rod (1 mm) touching the RW membrane. We first compute the leakage volume velocity and then solve for the impedance:

$$U'_{lkSTRW} = U_{act} - U'_{Diff} \quad \text{Eqn 7}$$

$$Z_{lkSTRW} = \frac{P_{ST}}{U'_{lkSTRW}} \quad \text{Eqn 8}$$

The three impedances calculations using the RW stimulation data are also illustrated in Fig. 5 (C, D, E). $Z_{ME'}$, the impedance looking out of the cochlea through the middle ear (Fig. 5C) has a high impedance magnitude and phase of -0.25 periods at low frequencies. At higher frequencies, the $Z_{ME'}$ magnitude starts to flatten out with frequency and the phase approaches 0.25 periods. Also plotted in Fig. 5C is the $Z_{ME'}$ estimated by Puria et al., 2003

(Puria, 2003). The Puria estimate is about 7 dB lower in magnitude than our mean results with RW stimulation.

The SV leakage impedance Z_{lkSV} from Eqn. 6 (Fig. 5D) is similar or even slightly lower in magnitude to Z_{ME} , with a less intense decline across frequency. The phase is 0 periods at low frequencies and slowly increases to almost 0.25 periods.

The combination of leakage at the ST and around the RW actuator during RW stimulation, Z_{lkSTRW} , (Fig. 5E) is nearly an order of magnitude lower than Z_{lkSV} across all frequencies. The phase starts at -0.25 periods and increases steadily to 0 periods at high frequencies.

3.4 Computational Modeling of Impedances

We modeled the five computed impedances with basic circuit components (i.e. resistance, conductance, and inductance) using simple component combinations based on anatomical considerations with element values fitted to the experimental data using least squares techniques (Fig. 6). At frequencies above a few kHz, mean magnitude and phase are influenced by large variations in the individual measurements. Furthermore, the stapes motion at frequencies above 2 kHz becomes less piston-like and incorporates a rocking motion that is not measured well by our one point LDV measurement (Hato et al., 2003; Heiland et al., 1999; Sim et al., 2010). Therefore we focused our analysis and modeling to the frequency range between 100 – 2000 Hz. Separate sets of element values (Table 2) were fit to the average data and to two individual experiments for each impedance that were selected because their magnitudes fell just outside the standard deviations in Fig. 5. The two individual experiments for each impedance are described in Table 2 as “Experiment Hi” and “Experiment Lo” in order to model the extremes of the impedance magnitude range across ears; the individual experiment numbers are listed in brackets on each figure legend. Table 3 lists the root mean square error of the difference between the model and fitted data at frequencies below 2 kHz. This Total Error is the combined error of the model and measured magnitudes and phases (described in Appendix A).

3.4.1 Differential Impedance (Z_{Diff})—The magnitude of Z_{Diff} (Fig. 6A) is relatively independent of frequency with a phase near zero, as is consistent with a simple resistance. However, the phase at low frequencies is consistently (for all experiments, Fig. 5A) greater than zero, which can be modeled with the addition of a parallel inductor that can be attributed to the helicotrema, where the resistor represents the wave impedance of the cochlear partition and surrounding fluid (Lynch et al., 1982). The influence of the inductor (and helicotrema) is to shunt volume velocity around the partition resistance at low frequencies. The combined total error for the fit of the Z_{Diff} model to the average data was lower (0.094) than the fits to the individual data, and was the second lowest error for all the model fits. The individual data has approximately double the total error as compared to the average.

3.4.2 Round Window Impedance (Z_{RW})—The magnitude and phase of Z_{RW} (Fig. 6B) at frequencies below 400–700 Hz is well modeled with a capacitor, analogous to the acoustical compliance of the RW membrane. The magnitude of Z_{RW} at frequencies of 700 Hz to 2 kHz is well modeled by the addition of a series inductor and resistor – an acoustic

mass and resistance. Due to large difference between individual experiments, two additional representative experiments are modeled ([116] and [189] in Fig. 6B). The model fits the experimental data very well up to 1 kHz, and reasonably well up to 2 kHz (the total error is lower than 0.17). However, a simple series combination of the three elements does not match the average Z_{RW} phase, which is lower than 0.25 periods phase above 1 kHz. To account for this lower phase, a model in which the mass and resistance change with frequency is necessary. We chose an iterated Foster network of resistors and inductors (N=6 branches), as described in Nakajima et al. (2009), to better fit the average phase data. Using a Foster network model for the individual data did not improve the fit to the data; therefore the simpler RLC circuit was used for the individual plots.

3.4.3 Reverse Middle Ear Impedance ($Z_{ME'}$)— $Z_{ME'}$ (Fig. 6C) at low frequencies has an impedance magnitude that decreases with increasing frequency and a phase of -0.25 periods, suggesting a compliance related to the acoustic compliance of the annular ligament surrounding the oval window as well as compliant characteristics of the middle-ear chain including the tympanic membrane. At higher frequencies the magnitude becomes more constant with frequency and the phase approaches 0.25 periods – evidence of a series inductor and resistor. From the perspective of the vestibule the inductance is probably related to the mass of the middle-ear ossicles and tympanic membrane. The resistor may reflect losses in the middle ear. The circuit models the experimental data well at low frequencies. Notice that the value of $C_{ME'}$ is an order of a magnitude smaller than that of C_{RW} for the three models in Table 2, such that the magnitude of the middle ear impedance at low frequencies is an order of magnitude greater than the magnitude of the RW impedance. The average and Experiment Hi have errors of 0.114 and 0.086 respectively. Experiment Lo has a higher total error (0.300) due to additional frequency dependences in the magnitude and phase data between 500 and 2000 Hz.

3.4.4 Scala Vestibuli Leakage Impedance (Z_{IKSV})—The SV leakage impedance (Fig. 6D) has a magnitude that is generally flat but sometimes decreases above a kHz, and a phase that increases from 0 to 0.25 periods as frequency increases. Assuming the leak was similar to an open tube, we chose to fit this with the series combination of a resistor and inductor. The best-fit model is Experiment Hi with a total error of 0.128. Experiment Lo has the highest total error of all impedance fits (0.430) because the magnitude decreases at high frequencies while the phase increases, behavior that is inconsistent with a series combination of a resistor and inductor. For similar reasons, the fit to the mean data produce a relatively high error of 0.182.

3.4.5 Scala Tympani and Round Window Leakage Impedance (Z_{IKSTRW})—The ST and RW leakage impedance (Fig. 6E) has a low-frequency magnitude that decreases with frequency and flattens out above 1 kHz; the phase increases with frequency from -0.25 to 0 periods. We modeled this impedance with a resistor and capacitor in series, where the capacitor may represent some of the leakage around the round window stimulator and the resistance models the impedance of a narrow tube. Experiment Hi is fit with the lowest error of the three models at 0.148. The fit to the average and Experiment Lo yields total errors of 0.149 and 0.217 respectively.

4. DISCUSSION

In this paper we present the data and best-fit models that describe the mechano-acoustic measurements of human temporal bone specimens without noticeable mechano-acoustic pathologies. To obtain our most reliable estimates of the normal case, we improved our experimental techniques and implemented strict inclusion criteria to represent healthy specimens and accurate intracochlear pressure measurements. The criteria include normal anatomy, normal ossicular velocity with respect to AC input sound pressure (similar to Rosowski et al. 2007), no evidence of air in the inner ear (checked by measurements described above), and high repeatability of our pressure sensor sensitivity. Implementing these criteria decreased the measurement variability within our population. We then used selected results to compute and model the impedances of structures within and surrounding the inner ear. These analyses quantify how sound is transmitted within the normal inner ear during AC and other forms of cochlear stimulation. The description of middle-ear function based on our selected measurements is valuable for our computational models as well as other analyses (e.g. Puria et al. 2003, Elliott et al. 2016, Stenfelt 2015) requiring accurate estimates of sound transmission in the human ear.

Our population of ‘normal’ measurements included velocity and pressure data that were similar but not identical across ears. This variability may be related to differences in anatomy and mechanical properties of middle-ear and inner-ear structures. While the average of the experiments provides a simple way to compare our data to pre-existing and future data, averaging inevitably smooths the frequency responses, and thus does not represent the frequency variations seen in the responses of individual ears. For some data types, there are considerable variations in the frequency-dependence seen across ears, resulting in an average that is not representative of individual ears. Therefore, we also model the results from individual ears (Fig. 6).

4.1 Impedance Calculations and Modeling

Z_{Diff} represents the differential impedance of the cochlear partition and scala fluids including the helicotrema measured at the base of the cochlea (Figs. 2 & 5A). The magnitude of Z_{Diff} is generally independent of frequency, and has a relatively small standard deviation across ears of about ± 5 dB (a logarithmic standard deviation of a factor of 1.6). The phase is slightly above 0 (0.1 ± 0.05 periods) at low frequencies. The components used to model Z_{Diff} (Fig. 6A) are the same as Elliott et al. 2016 and has a parallel orientation as similar to the model of Lynch et al. 1982. The model resistance accounts for the distributed partition and scala impedance (Zwislocki, 1963), while the parallel inductor can be attributed to the helicotrema (Dallos, 1970). (Note, Z_{Diff} differs from previous reports of Z_C , the “cochlear impedance,” in that $Z_C = Z_{Diff} + Z_{RW}$.) Despite limiting our model fit to data from 100 to 2000 Hz, the model matches the data well up to 7000 Hz.

Z_{RW} represents the impedance of the round window and the contributions of the fluids entrained by its motion (Figs. 2 & 5B). During AC stimulation, we assume any volume velocity leakage out of ST (though Z_{IKST}) is insignificant because Z_{IKST} is greater in magnitude than the combination of $Z_{RW} + Z_{Diff}$ (consistent with the two-window hypothesis). Z_{RW} has a similar frequency response shape across ears, but at low frequencies

the magnitude varies moderately across ears (a standard deviation of 6 to 7 dB), and all experimental data demonstrate the characteristics of a capacitor below 400 Hz (with a phase angle of -0.25 to -0.18 in Fig. 5B). We attribute this compliant behavior to the RW membrane's flexibility, where the variations may be related to variations in the membrane's thickness, size and shape across ears, consistent with our observation of significant variety in the RW anatomy across ears. At frequencies above 1000 Hz the magnitude of Z_{RW} is less variable (a logarithmic standard deviation of a factor of 1.5 equivalent to 3–4 dB), which suggests the mass term (which we associate with the effective mass of fluid entrained with the RW membrane at high frequencies) is more similar across ears.

In this study we fit our models to the data at frequencies of 2 kHz and below (resulting in deviation between model and data for high frequencies). The models chosen to describe the average and individual Z_{RW} data do reasonably well up to 2 kHz, but at higher frequencies, the phase data is generally limited below 0.13 periods while the model goes to 0.25 periods. This difference could be due to the complex motion of the stapes above 2 kHz – the addition of complex modes produces less smooth data and could produce some downward shift in the phase data. The four individual data are modeled in a similar manner (RLC) as in Elliott et al. 2016. Above 1 kHz, the model phase does not perfectly fit the data in both Elliott et al. 2016 and this present study.

Our Z_{RW} element model for the average data is similar to the model used by Nakajima et al. 2009 (Fig. 6B). The Foster form iterated network of the resistor and inductor leads to frequency dependence in the network resistance and inductance, and represents a distributed system. Thus, similar to the data, the phase above 1 kHz in the model is flat at about 0.13 periods instead of the 0.25 periods (as in a simple RLC); this high frequency phase was closely modeled in Nakajima et al., 2009. However, the average data is not a good representation for any individual experiment as the sharp magnitude valleys and steep phase transitions are lost in averaging the data. While capturing the average well, the Foster network was not able to fit the magnitude peaking and steep phase change relative to frequency of the individual data.

Z_{ME}^* is the reverse impedance load of the middle ear (the load affected by the oval window annular ligament, ossicles, middle-ear cavity, tympanic membrane, and ear canal) measured during sound transmission from the inner ear to the ear canal that results from RW stimulation (Fig. 5C). Variations in reverse middle ear impedance Z_{ME}^* magnitudes are largest at frequencies less than 800 Hz (standard deviations of ± 10 dB). However, the phase is consistent across experiments with a value of -0.25 periods at the lowest frequencies, implying compliant behavior due to the flexible components of the middle ear (e.g. OW, ossicles, tympanic membrane, etc.), moving towards 0 as frequency increases. At mid-to-high frequencies, the variation in magnitude is smaller, but the variation in phase is increased. Puria 2003 also estimated Z_{ME}^* by stimulating the scala tympani with a hydrophone (Puria, 2003). His Z_{ME}^* estimated is about 7 dB lower in magnitude than our results. The cause of this discrepancy could be due to different measurement techniques. Puria 2003 used a hydrophone to drive the middle ear in reverse, while we used stimulation of the round window. Puria 2003 also found that comparison of no occlusion and different volumes of air with occlusion did not change the reverse middle-ear impedance Z_{ME}^* . In our

setup we had a large volume of air between speaker and ear canal. We found, similar to Puria 2003, that Z_{ME} remained stable whether the speaker was connected or removed (open system) during RW stimulation. We modeled Z_{ME} with a compliance, mass, and resistance in series (Fig. 6C). Elliott et al. 2016 also estimated the impedances described above using a combination of data (our early Nakajima et al. 2009 data and Puria et al. 2003 data) with a similar lumped-element model. Despite limiting our model from 100 Hz to 2 kHz, the model fits well up to 10 kHz for the average and Hi Experiment.

Z_{lksV} represents the combination of sound leakage paths between the scala vestibuli and the exterior of the otic capsule in our temporal bone preparation (Fig. 5D). These could include the vestibular aqueduct, and any vascular and neural channels that penetrate the bone around the vestibule and scala vestibuli (Georg von Békésy and Ernest Glen Wever, 1960; Otto F. Ranke, 1953). The standard deviation within our estimates of Z_{lksV} is about ± 6 –7 dB. To fit the phase response, we model the SV leakage impedance with a resistor and inductor (Fig. 6D), similar to the model of Elliott et al., 2016. As seen in Fig. 6D, there is a reasonable match between a simple RL circuit model and both the averaged data and experiment Hi data below 2 kHz. Many of the discrepancies happen above 2 kHz (though with experiment Lo discrepancies happen below 2 kHz) where the single-point laser measurements made are less reliable due to the addition of complex motion of the stapes. It is also possible that calculation of the leakage impedance for that ear was unusually affected by compounding of errors from the pressure sensor sensitivity calibrations. The variability of Z_{lksV} across experiments suggests significant anatomical differences across ears (e.g. in the dimensions of the vestibular aqueduct (Elliott et al., 2016; Saliba et al., 2012)), but may also reflect its computational dependence on a difference between two volume velocities of similar magnitude (Eqn. 5).

Z_{lksTRW} (Fig. 5E) is the leakage path of the scala tympani and round window during RW stimulation. The dominant leakage path from the ST is likely due to the incomplete coupling between the interface of the actuator and the RW membrane (e.g. volume velocity leakage where the actuator does not directly touch the RW membrane) and the cochlear aqueduct. We model the ST and RW leakage impedance with a resistor and capacitor (Fig. 6E). This is different than other models that represent just Z_{lksT} (RLC circuit from Stenfelt et al. 2016 or RL circuit in Elliot et al. 2016). The capacitor element is used to model the low frequency phase, and may be needed to explain any volume velocity leaks in the areas of the RW that surround the areas directly coupled to the actuator. To separate the contribution of imperfect actuator coupling, we need to better define the actual volume velocity of the RW that is induced by mechanical RW stimulation. An alternative method is to determine Z_{lksT} by measuring stapes velocity and intracochlear pressures in the normal condition and then with the immobilization of the RW membrane during AC stimulation. To specifically determine the impedance of the cochlear aqueduct, one could also experimentally block the cochlear aqueduct. Anatomical measurements of the vestibular and cochlear aqueducts could also provide estimates of their impedances, as we performed for cat in Rosowski et al., 2017.

Our measurements and models demonstrate that some of the acoustical properties of inner-ear and middle-ear structures (embodied in the acoustic-impedance elements of our model) can be very similar across ears, while other structures vary across individuals. The model

and defined parameters are powerful tools to understand complex sound transmission mechanisms, the effects of pathologies that change inner-ear impedances such as superior canal dehiscence, and consequences of implants that changes impedances surrounding the inner ear such as cochlear and vestibular implants. Various computational models from simple lumped-element model as used here to more complex 3-D models, such as finite element models, can also benefit from our measurements and models which describe the impedances and other transfer functions important in characterizing sound transmission in the human ear.

4.2 Errors and Variability in Estimating SV Leakage Impedance

To compute Z_{lkSV} , assumptions are made and multiple equations are used. Every pressure calculation (particularly difference calculations) has some error associated with the solution; and the need for multiple calculations can compound any error made in the pressure measurements. Although the error in the intracochlear sound pressure measurement was kept to a minimum (e.g. less than 2 dB shift from the start to the end of the experiment), accumulation of those small errors in the calculations can make significant errors in the final result. Small errors in the measured volume velocity of the stapes and volume-velocity calculated from differential pressure could in particular contribute to errors in the leakage impedance estimates (Eqn 4 & 5). Fig. 7 illustrates the ratio of U_{stap} and U_{Diff} during RW stimulation. If we have accurately defined the leak in the SV, the differential volume velocity U_{Diff} should be larger than the stapes volume velocity U_{stap} (a ratio of less than 1 in Fig. 7), and this is generally the case; most experiments remain below 1 (dashed line) for frequencies up to 2 kHz, as seen by the thick black line representing the average. The model chosen for Z_{lkSV} fits reasonably well up to 2 kHz (Fig. 6D), but could use improvement. Future experiments will focus on improvements in the quantification of round-window volume velocity, which will decrease the dependence on assumptions of equal volume velocity during air conduction stimulation.

4.3 Two-window Hypothesis

In this study, a major assumption made for AC stimulation is the two-window hypothesis, where significant volume velocity flows only through the round and oval windows. In order to determine if this approximation is appropriate, we compare the averaged calculated impedances and standard deviation of Z_{lkSV} and Z_{Diff} in Fig. 8. If the two-window hypothesis holds during AC stimulation, differential pressure impedance, Z_{Diff} , should be considerably lower in magnitude than the leakage impedance, Z_{lkSV} . If the impedance of Z_{lkSV} is lower than or approximates Z_{Diff} at any frequency, then there is likely some significant volume velocity flow exiting through the Z_{lkSV} during AC stimulation. Up to 500 Hz the average Z_{lkSV} is at least four times (average ten times) the magnitude of Z_{Diff} but this difference falls to a factor less than two by 2kHz.

The above finding is not contradictory to the work of Stenfelt et al. (2004a). The general conclusion of that past work is that the two-window hypothesis holds during AC from experiments showing similar volume velocities for OW and RW (Fig. 5 of Stenfelt et al. 2004a). However, close inspection of this data also shows frequency-dependent deviation between oval and RW volume velocities (Fig. 6 of Stenfelt et al. 2004a). At higher

frequencies the deviation between individual experiments is greater (4 dB, factor of 1.6) than that at low frequencies (<2dB, factor of 1.3) and there are more instances of the ratio growing and shrinking across higher frequencies. Furthermore, the individual ratio of the RW to OW volume velocity for each experiment are between 0 to -4dB below 500Hz indicating the RW volume velocity is less than the OW volume velocity. Therefore, there is variability across ears and in some ears there is a visible volume velocity loss between the OW to the RW, as shown in Stenfelt et al. 2004a, consistent with what we show in our present study. However, given that the volume velocity losses are small, the two-window hypothesis generally holds well for AC stimulation, especially at low frequencies.

5. CONCLUSIONS

In this study of fresh cadaveric normal ears we provide a carefully selected set of simultaneous measurements of intracochlear pressures in SV and ST, near the otic capsule at the base of the cochlea. These pressures are normalized with stapes velocity during AC and RW stimulation and ear canal pressure during AC stimulation.

From these measurements, component acoustical impedances are calculated and fit to simple lumped element models: The differential impedance, Z_{Diff} , is represented by a resistance due to distributed partition and scala impedance and a parallel fluid mass, due to the helicotrema. The impedance through the RW, Z_{RW} , has compliant behavior due to the flexibility of the RW membrane. A mass and resistor in series can generally simulate the individual data well for frequencies below 2 kHz. However, in the average data the iterated network of a mass and resistance leads to a frequency dependent network to represent a distributed system, consistent with less than 1/4 cycle phase at higher frequencies. The reverse middle ear impedance, Z_{ME} , contains a mass to account for the OW, annular ligament, ossicles, TM, and middle ear cavity. Its compliance is likely dominated by the flexibility of OW owing to the annular ligament, and the entire middle-ear chain. The leakage in the SV, Z_{lkSV} , is represented by a resistor and inductor and is a combination of leakage between SV and exterior of the otic capsule. It is likely the vestibular aqueduct or small channels that innervate the SV. The leakage in the ST and RW, Z_{lkSTRW} , is represented by a resistor and capacitor and is perhaps the cochlear aqueduct. The compliance is likely due to volume velocity leaks at the RW surrounding the actuator-RW interface.

The simple lumped-element models help us understand complex sound transmission mechanisms, effects of pathologies that change inner-ear impedances, and the consequences of implants that change impedances surrounding the inner ear. Finally, we showed that individual measurements can be fitted to this model, which allows us to study the large variations in different specimens.

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Appendix A

The error between the model and experimental data was calculated using a least squares technique as outlined below.

We define:

$x_{m,\nu}$ as the complex result of the model at the ν^{th} frequency,

$x_{e,\nu}$ as the complex result of the experiment (expt) at the ν^{th} frequency, and

T_ν as the complex ratio of these complex numbers:

$$T_\nu = \frac{x_{e,\nu}}{x_{m,\nu}}.$$

This ratio can be written as

$$T_\nu = \text{Re}\{T_\nu\} + j\text{Im}\{T_\nu\}$$

or

$$T_\nu = r_\nu e^{j\theta_\nu},$$

where $r_\nu = \frac{|x_{e,\nu}|}{|x_{m,\nu}|}$ and $\theta_\nu = \text{phase of experiment} - \text{phase of model}$ (in radians).

We want T_ν to be as close to one as possible across frequency points ν such that the model well fits the experimental data. In particular, we'd like both the log magnitude and phase of the model to match the experimental results. To accomplish this, we seek to minimize the root mean square of $\log_{10}(T_\nu)$ across points ν as follows:

Taking the base 10 logarithm of the above equation:

$$\begin{aligned}\log_{10}(T_\nu) &= \log_{10}(r_\nu) + \log_{10}(e^{j\theta_\nu}) \\ &= \log_{10}(r_\nu) + j\theta_\nu \log_{10}(e),\end{aligned}$$

we find the model that minimizes the root mean square (RMS) of $\log_{10}(T_\nu)$ across frequencies ν , where:

$$RMS(\log_{10}(T_{\nu})) = \sqrt{\frac{1}{N} \sum_{\nu=1}^N ((\log_{10}(r_{\nu}))^2 + (\log_{10}(e))^2 * (\theta_{\nu})^2)}$$

$$= Total \ Error = \sqrt{\frac{1}{N} \sum_{\nu=1}^N ((Error_{mag})^2 + (\log_{10}(e))^2 * (Error_{phase})^2)}$$

where

$$Error_{mag}^2 = \frac{1}{N} \sum_{\nu=1}^N (\log_{10}(Model_{mag}) - \log_{10}(Expt_{mag}))^2$$

and

$$Error_{phase}^2 = \frac{1}{N} \sum_{\nu=1}^N (Model_{phase} - Expt_{phase})^2.$$

Note that the error is based on ratios and is dimensionless. The model parameters were systematically adjusted to produce the lowest possible *Total Error* over the 100 to 2000 Hz frequency range. We also use the *Total Error* to compare the fits of all the models (Table 3).

Abbreviations:

Note: italics represent a complex variable with magnitude and phase or real and imaginary parts.

AC	air conduction
RW	round window
OW	oval window
SV	scala vestibuli
ST	scala tympani
<i>P_{EC}</i>	sound pressure in the ear canal
<i>P_{ST}</i>	sound pressure in the scala tympani
<i>P_{SV}</i>	sound pressure in the scala vestibuli
<i>V_{act}</i>	velocity of the actuator on the RW
<i>Z_{Diff}</i>	differential impedance across the partition including the helicotrema
<i>Z_{RW}</i>	RW impedance
<i>Z_{ME}</i>	middle ear impedance from the cochlea looking out

Z_{lkSV}	leakage impedance of the SV and exterior of the otic capsule
Z_{lkSTRW}	leakage impedance of the ST and RW
U_{stap}	volume velocity of stapes during AC stimulation
U_{Diff}	volume velocity across the partition
U_{RW}	volume velocity of RW during AC stimulation
U'_{stap}	volume velocity of stapes during RW stimulation
U_{lkSV} and U'_{lkSV}	volume velocity through the SV leakage for AC and RW stimulation
U_{lkST}	volume velocity through the ST leakage for AC stimulation
U'_{lkSTRW}	volume velocity through the ST and RW leakage for RW stimulation
U_{act}	volume velocity entering the cochlea during RW stimulation with actuator

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Fig. 1: Inclusion criteria (striped gray area) compared to measurements in 37 temporal bones. A) Comparison of air-conducted middle ear transfer function (magnitude of $V_{\text{Stap}}/P_{\text{EC}}$) against the range (gray area) set by Rosowski et al. (2007). B) The difference in phase between the velocity of the stapes and RW (phase of $V_{\text{Stap}}/V_{\text{RW}}$) is plotted against frequency. Only experiments with data that fell within the striped gray areas at frequencies <2000 Hz in A and <500 Hz in B were used in this study.

Fig. 2.

A) AC and B) RW stimulation impedance models. The path of the volume velocity changes based on the stimulation type. The impedances of our models do not change their values from AC to RW stimulation. A) For AC, the volume velocity enters through the stapes, across the cochlear partition (including the helicotrema) and out the RW. The AC model assumes the two-window hypothesis, and assumes the volume velocities through the leakage paths are negligible. B) For BC, the volume velocity enters through the RW via a mechanical stimulus and passes through the cochlear partition or a leakage area in the ST. If it passes through Z_{Diff} the volume velocity splits out into the leakage in the SV or middle ear. The leakage in the ST, Z_{LkST} , is not determined in this paper, but a combination of ST leakage and the leakage at the RW-actuator interface during RW stimulation, Z_{LkSTRW} , is estimated.

Fig. 3:
The magnitude and phase frequency responses of the intracochlear sound pressures referenced to P_{EC} (A, B) or V_{stap} (C, D), measured in 18 normal ears (colored lines). The mean is plotted as a thick black line and the standard deviation as the gray fill.

Fig. 4:

The intracochlear sound pressures measured in five ears with RW stimulation (colored lines). The pressures are referenced to the velocity of the actuator V_{act} . The mean is plotted as a thick black line and the standard deviation as the gray fill.

Fig. 5:

Impedance Magnitude and Phase Frequency Response Plots. The acoustic impedances were calculated for the A) differential across the partition (at the base which includes the influence of the helicotrema) Z_{Diff} , B) round window Z_{RW} , C) reverse middle ear $Z_{ME'}$, D) leakage in the scala vestibuli Z_{ikSV} , and E) leakage in the scala tympani and RW Z_{ikSTRW} . Individual experiments are plotted in light blue lines, the geometric mean in black lines, & the standard deviation in a gray fill and a noise floor estimate in light green fill. Results from Puria 2003 are also plotted in C. Only data with SNR of at least 10dB are plotted.

Fig. 6:

Impedance plots and models. For experimentally obtained impedances, the average is in thick black lines. The “Experimental Hi” and “Experimental Lo” are representative magnitude extremes of the total range of each impedance measured (Note, each “Experimental Hi” and “Experimental Lo” differ in experiment number, as listed in brackets); they are plotted in thin solid lines. Our model was fit to the three experimental curves up to 2 kHz, plotted with dotted and dashed thick lines. The gray high-frequency (>2 kHz) area indicates the region where the data is not used for model fitting. A) Z_{Diff} B) The average Z_{RW} data is best fit with the black circuit. The individual data are best fit with the red circuit. Because of the large variability in experiments, two additional experiments are modeled. C) Z_{ME} D) Z_{IkSV} E) Z_{IkSTRW} . Only data with SNR of at least 10dB are plotted.

Fig. 7: Ratio of volume velocities through the stapes oval window to the differential volume velocity (velocity across the cochlear partition and helicotrema), computed during round window stimulation. The ratio should have a magnitude lower than 1 (dashed line); almost all are below this level for frequencies up to 1kHz. Data are only plotted if the SNR of the U_{stap} measurement is at least 10dB.

Fig. 8:

Average and standard deviations of the differential and SV leakage impedances. The leakage impedance, Z_{lkSV} , is on average greater in magnitude than Z_{Diff} up to about 2 kHz, where they start becoming comparable. The standard deviations are indicated by dashed lines for Z_{Diff} and shading for Z_{lkSV} .

Table 1:

Summary of experiments. (Experiments that were halted early due to different issues are not listed here).

Experiment Number	Status
39, 104, 116, 119, 124, 131, 165, 172, 178, 187, 189, 190, 199, 207, 209, 210, 212	Included for impedance calculation
106	AC stimulation included for impedance calculation. RW stimulation excluded due to inefficient coupling
36, 37, 71, 76, 79, 92	Excluded. Cannot ensure proper seal of pressure sensors
38, 41, 112, 125, 127, 160, 162, 174, 211	Excluded. Abnormal middle ear transfer function or anatomy
40, 41, 115, 162, 211	Excluded. Failure of half-cycle test
108, 118	Sensor calibration varied by more than 2 dB

Table 2:

Circuit values for the acoustic impedance models. R = resistor, C = capacitor, L = inductor. In the average Z_{RW} , RW parameters R and L are iterated for N = 6. Experiment Hi and Lo represent the range of impedance variability across ears. For the individual Z_{RW} , RLC are in series. For experiment 116: R = 2.04×10^9 , L = 1.77×10^6 , and C = 4.13×10^{-14} . For experiment 189: R = 4.19×10^9 , L = 1.36×10^6 , and C = 1.80×10^{-14} .

Impedance	Orientation	Parameter	SI Units	Average	Experiment Hi	Experiment Lo
Z_{Diff}	Parallel	R_{Diff}	N s m ⁻⁵	3.04×10^{10}	Exp 199 5.18×10^{11}	Exp 172 1.58×10^{10}
		L_{Diff}	N s ² m ⁻⁵	6.46×10^7	1.66×10^8	1.34×10^7
Z_{RW}	Foster Network / Series	R_{RW}	N s m ⁻⁵	5.00×10^7	Exp 212 6.33×10^9	Exp 119 6.32×10^8
		L_{RW}	N s ² m ⁻⁵	7.30×10^5	1.24×10^6	1.47×10^6
		C_{RW}	N ⁻¹ m ⁵	3.59×10^{-14}	1.38×10^{-14}	7.62×10^{-14}
$Z_{\text{ME}'}$	Series	$R_{\text{ME}'}$	N s m ⁻⁵	4.76×10^{10}	Exp 127 8.40×10^{10}	Exp 119 2.74×10^{10}
		$L_{\text{ME}'}$	N s ² m ⁻⁵	7.78×10^5	8.60×10^5	8.68×10^5
		$C_{\text{ME}'}$	N ⁻¹ m ⁵	2.56×10^{-15}	1.01×10^{-15}	1.13×10^{-14}
Z_{IKSV}	Series	R_{IKSV}	N s m ⁻⁵	9.80×10^{10}	Exp 127 4.30×10^{10}	Exp 104 1.18×10^{10}
		L_{IKSV}	N s ² m ⁻⁵	5.00×10^6	4.70×10^6	2.00×10^6
Z_{IKSTRW}	Series	R_{IKSTRW}	N s m ⁻⁵	4.10×10^9	Exp 127 2.71×10^9	Exp 119 4.19×10^9
		C_{IKSTRW}	N ⁻¹ m ⁵	7.49×10^{-14}	5.00×10^{-14}	3.04×10^{-13}

Table 3:

Root mean square total error between model and experimental data including log magnitude and phase error up to 2kHz. The smaller the number, the better the model fits to the experimental data.

	Z_{Diff}	Z_{RW}	Z_{ME}	Z_{IKSV}	Z_{IKSTRW}
Average	0.094	0.052	0.114	0.182	0.149
Experiment Hi	0.176	0.164	0.086	0.128	0.148
Experiment Lo	0.186	0.159	0.300	0.430	0.217
[116]		0.118			
[189]		0.070			