Otoacoustic Emission Through Waves on Reissner's Membrane

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Abstract. Otoacoustic emissions are a striking manifestation of mechanical activity within the cochlea. Recent experimental work has stirred a controversy concerning how these mechanical signals propagate outward to the middle ear, from which they are emitted as airborne sounds. Here we show that Reissner's membrane, an elastic structure inside the inner ear, can sustain wave propagation and can therefore transmit otoacoustic emissions from inside the cochlea to the middle ear. We first develop a theoretical description for wave propagation on the parallel basilar and Reissner's membranes. We then describe experimental measurement of the predicted Reissner's membrane wave and its role in distortion-product otoacoustic emissions.

INTRODUCTION

Otoacoustic emissions are a hallmark of the active process in the cochlea and are employed clinically to evaluate hearing in newborns. As an important instance, the cochlea's nonlinear response creates the cubic distortion frequencies $2f_1 - f_2$ and $2f_2 - f_1$ that are produced by stimulation at two close frequencies f_1 and f_2. These distortion tones are then emitted back into the ear canal. How a distortion produced inside the cochlea travels back to the middle ear, however, remains unclear.

Signal propagation into the cochlea involves a wave on the elastic basilar membrane. Stimulation at a single frequency elicits a wave that peaks at a frequency-dependent position, and the membrane's vibration near the peak varies nonlinearly with the applied sound pressure. Distortion is therefore thought to be generated near the peaks of the traveling waves that are elicited by the primary stimulus frequencies f_1 and f_2 [3, 11, 15, 16].

Most theoretical work has assumed that the backward propagation of a distortion tone occurs through a reverse wave on the basilar membrane. Recent experiments that have attempted to measure the reverse wave by laser-scanning interferometry, however, have identified only forward-travelling waves [5, 6, 14]. This result may arise either from masking of the reverse wave by a reflected, forward-traveling wave or because the distortion signal is transmitted to the middle ear through a different mechanism [4-6, 10, 12, 14].

Here we discuss theoretical and experimental evidence that a distortion tone can propagate back to the middle ear through a wave on Reissner's membrane, a second elastic structure in the inner ear that lies in parallel to the basilar membrane. More details can be found in a previous publication [13].

THEORY OF WAVE PROPAGATION ON THE PARALLEL REISSNER'S AND BASILAR MEMBRANES

Reissner's membrane and the basilar membrane delineate three fluid-filled chambers within the cochlea, namely the scala vestibuli, scala media, and scala tympani (Fig. 1A). The basilar membrane supports the organ of Corti with the mechanosensitive hair cells exposed to the scala media. Displacement of the basilar membrane deflects the hair bundles of the hair cells, thus initiating mechanotransduction. This process is aided by an enhanced potential as well as a K^+-rich solution, endolymph, within the scala media. Reissner's membrane separates the specialized scala media from the scala vestibuli. Because Reissner's membrane is, at least near the base, significantly floppier than the basilar membrane, and because its deflection does not serve a physiological purpose, it has commonly been ignored in the study of cochlear hydrodynamics.

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The fluid dynamics of a cochlea can be aptly represented by a two-dimensional section of an uncoiled cochlea (Fig. 1B). Denote by x the longitudinal and by z the vertical coordinate perpendicular to the membranes. For simplicity we assume that all three chambers have the same height h. The hydrodynamics follows from Laplace equations for the pressure in the scala vestibuli, scala media, and scala tympani, which we denote by p_1, p_2, p_3, respectively:

$$\Delta p_1 = 0, \Delta p_2 = 0, \Delta p_3 = 0. \tag{1}$$

We have thereby approximated the fluid as incompressible and the flow as laminar. The vertical fluid velocity must vanish at the upper and lower surfaces of the cochlea, which yields the boundary conditions

$$\partial_z p_1|_{z=3h} = \partial_z p_3|_{z=0}. \tag{2}$$

The membrane's responses yield further boundary conditions. A pressure difference across Reissner's membrane evokes a certain vertical velocity V_{RM} and a pressure across the basilar membrane produces a membrane velocity V_{BM}. The ratio of the membrane velocity to the pressure difference can depend on the frequency of stimulation. We consider a wave of angular frequency ω and denote the specific acoustic impedance of Reissner's membrane at that frequency by Z_{RM} and that of the basilar membrane by Z_{BM}. These impedances relate the pressure differences to the membrane velocities:

$$\begin{aligned} (p_2 - p_1)|_{z=2h} &= Z_{\mathrm{RM}} V_{\mathrm{RM}}; \\ (p_3 - p_2)|_{z=h} &= Z_{\mathrm{BM}} V_{\mathrm{BM}}. \end{aligned} \tag{3}$$

The membrane velocity can be obtained from the derivative of the pressure at each membrane:

$$\begin{aligned} V_{\mathrm{RM}} &= \frac{i}{\rho\omega} \partial_z p_1|_{z=2h} = \frac{i}{\rho\omega} \partial_z p_2|_{z=2h}; \\ V_{\mathrm{BM}} &= \frac{i}{\rho\omega} \partial_z p_2|_{z=h} = \frac{i}{\rho\omega} \partial_z p_3|_{z=h}, \end{aligned} \tag{4}$$

in which r is the fluid's density.

The impedance of the basilar membrane varies spatially: its stiffness decreases from base to apex whereas the organ of Corti grows in size, causing an increasing mass. The local wavelength of a wave as well as the wave's amplitude can thus vary spatially:

$$\begin{aligned} V_{\mathrm{RM}}(x) &= \tilde{V}_{\mathrm{RM}}(x) \exp\left[i\omega t - i \int_0^x dx' k(x')\right] + c.c.; \\ V_{\mathrm{BM}}(x) &= \tilde{V}_{\mathrm{BM}}(x) \exp\left[i\omega t - i \int_0^x dx' k(x')\right] + c.c., \end{aligned} \tag{5}$$

in which "*c.c.*" denotes a complex conjugate.

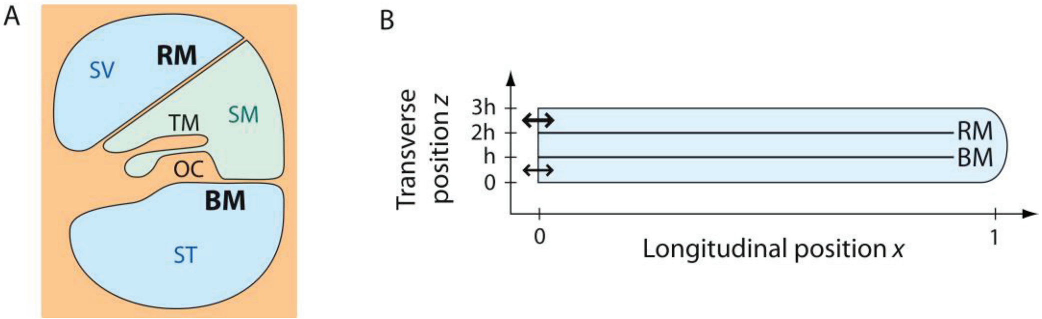

FIGURE 1. [Color version of figure available online] Structure of the inner ear. (A) A transverse section of the cochlea shows the scala vestibuli (SV), scala media (SM), and scala tympani (ST) that are separated by Reissner's membrane (RM) and the basilar membrane (BM). The basilar membrane supports the organ of Corti (OC) and the overlying tectorial membrane (TM). (B) A two-dimensional model for the cochlea in which all three chambers have an equal height h.

These equations describe a wave traveling on both membranes with a local wave vector $k(x)$ and complex local amplitudes $\tilde{V}_{\mathrm{RM}}(x)$ and $\tilde{V}_{\mathrm{BM}}(x)$. Analysis of Eqs. (1) together with the boundary conditions, Eqs. (2) and (3), shows that the local wave vector $k(x)$ obeys the dispersion relation

$$\left\{\frac{ik(x)Z_{\mathrm{RM}}}{\rho\omega}\sinh[k(x)h]-2\cosh[k(x)h]\right\}\left\{\frac{ik(x)Z_{\mathrm{BM}}(x)}{\rho\omega}\sinh[k(x)h]-2\cosh[k(x)h]\right\}=1. \tag{6}$$

Details on the involved computations can be found in the previous publication [13].

An analysis of the dispersion relation (6) shows that two distinct types of waves emerge. These two waves take particularly simple forms for frequencies above 1 kHz that we will consider in the following analysis.

One wave that emerges is the well-known basilar-membrane wave. This wave mode has a large wavelength that exceeds the height of the channels and hence evokes comparable fluid motion throughout a vertical section of the cochlea, with a comparable motion of Reissner's membrane. Because the impedance of the basilar membrane in the basal region of the cochlea greatly exceeds that of Reissner's membrane, the impedance of the latter structure has only a marginal influence on the wavelength.

The second wave mode that emerges has a small wavelength, less than the height of the chambers, and propagates predominantly on Reissner's membrane. Because the penetration depth for a surface wave is proportional to the wavelength, this wave mode causes fluid motion in only a thin layer around Reissner's membrane and is therefore determined by the material properties of this membrane alone. Further analysis shows that the impedance of Reissner's membrane stems from surface tension. The wavelength l of the ensuing Reissner's membrane wave accordingly decreases with frequency according to the power law $\lambda \sim f^{-2/3}$ characteristic of a capillary wave.

EXPERIMENTS AND DISTORTION PRODUCTS

We have tested the above idea of short waves on Reissner's membrane by measuring the membrane's motion with a scanning laser interferometer. For these experiments we employed *in vivo* and *in vitro* preparations of cochleas from the gerbil, guinea pig, and chinchilla. We made an opening 1-2 mm in diameter in the cochlear bone near the apex to gain access to Reissner's membrane through the scala vestibuli. We then stimulated either the intact middle ear or Reissner's membrane itself at different frequencies and scanned along the midline of Reissner's membrane.

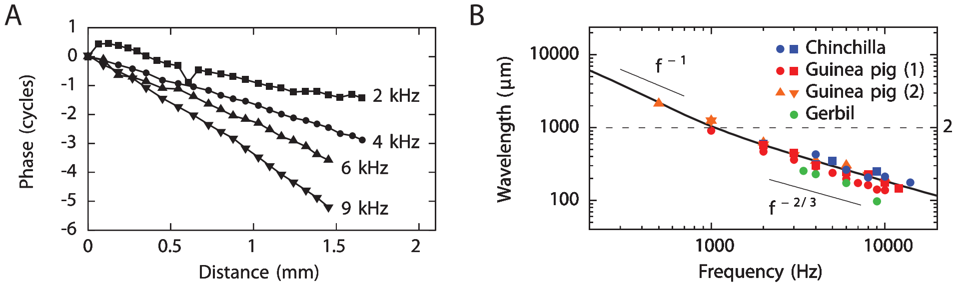

FIGURE 2. [Color version of figure available online] Experimental measurement of waves on Reissner's membrane. (A) The phase of the vibration decreases linearly with distance from the basal edge of the artificial opening in the scala vestibuli. (B) The wavelength l scales as $\lambda \sim f^{-2/3}$ for frequencies above 1 kHz. The measurements from chinchillas and those marked (1) from guinea pigs were performed *in vivo*; the experiments on gerbils and those marked (2) from guinea pigs employed *in vitro* preparations.

For each frequency these measurements show a progressive decline in phase as the measurement position is moved apical, evidencing traveling waves (Fig. 2A). The wavelength can be obtained from the slope of the phase. We find that the wavelength decreases with increasing frequency in the expected manner, namely as $\lambda \sim f^{-2/3}$ (Fig. 2B). Furthermore, the dispersion relation allows us to compute the surface tension of Reissner's membrane in the different species, yielding results in accord with previously reported values [13].

The Reissner's membrane wave can be evoked by nonlinear distortion on the basilar membrane, a process that can be described mathematically through the formalism of inhomogeneous differential equations, Green's functions, and the Born approximation [13]. The description reveals that the nonlinearity on the basilar membrane couples through the fluid to Reissner's membrane and there generates two waves, one that travels basally and one that moves apically. The basally propagating wave then evokes a pressure signal at the oval window and hence in the middle ear.

We have tested whether distortion on the basilar membrane can indeed generate a Reissner's membrane wave. To this end we developed an *in vivo* preparation of the chinchilla's cochlea that we opened near the apex to observe Reissner's membrane. We then stimulated the middle ear at two close frequencies f_1 and f_2. The two signals were generated separately and delivered through independent loudspeakers to avoid the production of distortion before the cochlea. Measuring disturbances of Reissner's membrane by interferometry, we observed a signal at the distortion frequency. Scanning along the midline of Reissner's membrane confirmed that the phase of the distortion signal changed systematically with position [13]. The wavelength agreed with that predicted for the Reissner's membrane wave and thus confirmed that the signal traveled as wave on that membrane.

DISCUSSION

An understanding of the backward propagation of otoacoustic emissions is complicated by the finding that distortion-product otoacoustic emissions contain two components that differ in their behavior when the primary frequencies f_1 and f_2 are changed proportionally such that f_2/f_1 remains constant [1, 8, 9]. In such an experiment, one component exhibits a phase change relative to the primary frequencies that increases as the primary frequencies are raised; the other component maintains an approximately constant phase.

It has been suggested previously that the two components of distortion-product otoacoustic emissions are generated in distinct ways. First, the generation of distortion by the basilar membrane's nonlinearity within the cochlea can elicit both a backward- and a forward-propagating wave on the basilar membrane [2, 17]. One component of a distortion-product otoacoustic emission can therefore result from the backward-traveling wave. Basilar-membrane mechanics is thought to exhibit an approximate scale invariance such that the traveling wave elicited by a pure tone travels the same number of cycles (two or three) from the base to its peak, independent of the tone's frequency. In agreement with one of the experimentally observed components, this component exhibits a constant-phase behavior that is independent of the primary frequencies. Second, the forward-traveling wave produced by distortion may be reflected near its resonance position and then travel basally [7, 17-19]. Reflection may arise from inhomogeneities in the basilar membrane that act as scatterers.

Our results show that otoacoustic emissions can emerge from the cochlea through a distinct type of wave that propagates on Reissner's membrane. This mechanism can explain the phase-varying component of distortion-product otoacoustic emissions. Indeed, because the Reissner's membrane wave does not display the scale invariance of the basilar-membrane wave, a signal propagating backward to the ear canal through a wave on Reissner's membrane has a phase that varies with the primary frequencies. Our computations show that increasing the primary frequencies at a constant ratio leads to a greater phase delay of the emission. This occurs since the wavelength of the Reissner's membrane wave becomes shorter for higher frequencies, such that a higher-frequency distortion tone requires more cycles to reach the stapes. The phase delay matches that of the phase-varying component of distortion-product otoacoustic emissions [13].

We have focused on frequencies above 1 kHz for three reasons: cochlear mechanics is best understood in the basal region, distortion-product otoacoustic emissions can be most easily measured above 1 kHz, and the two wave modes are readily interpretable as a basilar-membrane wave and a Reissner's membrane wave. In the future it will be interesting to investigate frequencies below 1 kHz. This endeavor will require better measurements of low-frequency otoacoustic emissions and may improve our understanding of active mechanics at the cochlear apex.

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COMMENTS AND DISCUSSION

Paul Fahey: It was a pleasure to revisit this result and re-read your reference 13. I am impressed with the scholarship, the physics and the results. I find the explanation for the Knight and Kemp "place-fixed" results physically compelling. Is there any hope of measuring 2f2-f1 and the third harmonics of the primaries on Reissner's? For these signals would you also expect to see a forward traveling wave on Reissner's? Paul Fahey

Tobias Reichenbach [reply to Paul Fahey]: Thank you very much for your comment. I am glad to read that you like the work. As you say, the mechanism that we propose is physically very compelling. I am certain that one can measure not only 2f1-f2, as we did, but also 2f2-f1 and the third harmonics of f1 and f2. Those signals should also propagate from the generation region on Reissner's membrane, both as forward- and as backward-traveling waves. We have focused on 2f1-f2 because it was the strongest of the distortion products. However, with longer averaging or otherwise more precise measuring, the other distortion products should be measurable as well. Determining the relative strength of 2f1-f2 versus 2f2-f1 would be particularly interesting in that it would further clarify the contribution of the "place-fixed" (long-delay) component in both types of DPOAEs.