Reply to “On Cochlear Impedances and the Miscomputation of Power Gain” by Shera et al. *J. Assoc. Re. Otolaryngol.*

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ABSTRACT

Using a scanning laser interferometer, we recently measured the volume velocity of the basilar membrane vibration in the sensitive gerbil cochlea and estimated that the cochlear power gain is ~100 at low sound pressure levels (Ren et al., *Nat Commun* 2:216–223, 2011a). We thank Shera et al. for recognizing the technical challenges of our experiments and appreciating the beauty of our data in their comment (Shera et al., *J Assoc Res Otolaryngol* (in press), 2011). These authors argue that our analysis is inappropriate, invalidating our conclusion; moreover, they suggest that our finding of a power gain of >1 could arise from a passive structure or cochlea. While our analysis and interpretation remain to be verified, they are justified according to commonly accepted assumptions and theories in cochlear mechanics. Here, we also show that the mathematical demonstration of a power gain of >1 in a passive cochlea by Shera et al. is inconsistent with our data, which show that the volume velocity and power gain decrease and become <1 as the sound level increases.

Keywords: Cochlea, basilar membrane vibration, cochlear amplifier, laser interferometer, traveling wave

Shera et al. (2011) criticized our study for not measuring impedance of the cochlear partition, or

pressure across the partition, to quantify the cochlear power gain. Although the cochlear power can be quantified as the product of velocity and pressure, neither the volume velocity nor distributed pressure have been measured previously. To determine whether the cochlea generates power to amplify soft sounds, numerous studies have been conducted using different approaches. For example, de Boer and Nuttall (1999) calculated the organ of Corti impedance by coupling frequency-response data to a cochlear model. In their analysis, the frequency response of the basilar membrane measured at a single location was converted into a spatial response using the cochlear map. Negative resistance of the cochlear partition was detected at a location basal to the response peak. To confirm this important finding, Olson (2001) quantified the organ of Corti resistance by directly measuring intracochlear pressure. She found that the pressure near the basilar membrane was as tuned and nonlinear as the basilar membrane vibration, which resulted in a relatively untuned and linear impedance of the organ of Corti. Since the result could not decisively determine whether the cochlea generates power, Olson suggested that negative resistance might be better measured via a more detailed map of the scala tympani pressure using a smaller pressure sensor. Due to technical challenges, detailed mapping of the intracochlear pressure near the cochlear partition remains to be conducted at the time this letter was written.

By developing a scanning laser interferometer, we measured the volume velocity of the basilar membrane vibration, and, by using commonly accepted assumptions in cochlear mechanics, estimated the relevant power. Most cochlear mathematical models

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(Peterson and Bogert 1950; Zweig 1976; Zwislocki 1953) present the cochlear traveling wave using a series of independent sections along the cochlea and assume that acoustic energy is transmitted through the cochlear fluid (Wever et al. 1954). In one-dimensional cochlear models, it is assumed that the basilar membrane vibrates uniformly over the entire width of the cochlear partition (Puria and Steele 2008) and that cochlear fluid moves in a longitudinal direction (de Boer 1996). This assumption, however, is contradicted by the physical requirement that the fluid must also move up and down with the basilar membrane. To avoid the paradox, it is further assumed that the vertical and longitudinal components of the fluid velocity change over the height of the cochlear duct. When longitudinal coupling in the organ of Corti is neglected, the traveling wave could be presented as a series of independent oscillators along the cochlear partition. In fact, the constant organ of Corti mass and frequency-dependent effective mass of the cochlear fluid were used to calculate the active force of the organ of Corti complex (Olson 2004). Olson also demonstrated two types of intracochlear pressure waves: one near the basilar membrane related to the traveling wave, and the other uniformly distributed in the entire cochlea associated with compression wave (Olson 2004). Since each section of the cochlear partition and nearby fluid vibrates in the transverse direction, which cannot transmit energy in the longitudinal direction, the compression wave in the cochlear fluid likely is responsible for the longitudinal power transmission. Based on this assumption, sound power in the cochlear fluid can be estimated using fluid velocity and impedance, and cochlear power gain can be estimated as the ratio of power in the fluid near the stapes to that at the best-frequency location.

Since the speed of sound (c) is related to impedance, c in the cochlear fluid near the stapes can be calculated from the cochlear input impedance (Z_c). Based on measured Z_c in cat (Lynch et al. 1982) and human (Aibara et al. 2001), Puria and Steele (2008) found that the speed of sound in the cochlear fluid near the stapes is ~15 times lower than the speed of sound in water, which is consistent with the speed of the cochlear slow wave. As the authors pointed out, it is the flexibility of the cochlear partition that slows the wave speed. Thus, the slow sound speed is dominated likely by the slow transverse component of the fluid velocity and may not necessarily exclude the existence of a fast longitudinal component.

Shera et al. also argue that our power measurements have incorrect dimensions. Because of the dispersive nature of the cochlear traveling wave (Lighthill 1981), volume velocity must be measured in a defined time or area that allows comparison

between the measurement near the stapes and that at the best-frequency location. We measured the volume velocity over a half-wavelength area centered at the best-frequency location. We chose a half-wavelength area rather than a random length because the vibration over a half-wavelength area is in phase and the volume displacement over this area can be compared to that at the stapes. The sound energy passing through the in-phase-vibration area in 1 s (I_{bf}) was calculated according to $I_{bf} = (V_{bfV})^2 \rho c$, where V_{bfV} is the volume velocity ($V_{bfV} = 2f\pi V_{bf+}$, f , and V_{bf+} are frequency and the volume displacement), ρ is the density of the cochlear fluid and c is the speed of sound in water. Shera et al. are correct that in the standard equation $I = \rho c V^2$, I is the acoustic intensity (time-averaged power per unit area), and V is the point velocity. V was replaced by the volume velocity V_{bfV} in our analysis because the volume velocity over a half-wavelength area at the best-frequency place is comparable to the stapes volume velocity. This results in a dimension of power $\times$ area ($[\text{power}][\text{area}] = (ML^2/T^3)L^2$, where M , L , and T represent the dimensions of mass, length, and time) as Shera et al. pointed out. Since I_{bf} in our analysis is the energy passing through the in-phase-vibration area in 1 s, the above dimension should be divided by L^2 and multiplied by T , resulting in a dimension of energy ($[\text{energy}] = ML^2/T^2$). Therefore, I_{bf} is in joules, a unit of energy.

Another criticism by Shera et al. is about the area over which we measured the basilar membrane volume velocity. It is true that the total instantaneous volume displacement of the basilar membrane, integrated along the cochlear length, should be equal to the volume displacement of the stapes when the compressibility of the cochlear fluid and the fluid flow through the helicotrema are negligible. Shera et al. argue that this integrated displacement, measured as the stapes volume displacement in our experiment, must be smaller than the volume displacement over a half-wavelength area centered at the best-frequency location. Therefore, our finding of the cochlear power gain of >1 can exist in a passive cochlea. Although the volume displacement at a given half-wavelength region can be canceled by that at adjacent areas as shown by Fig. 1C (Ren et al. 2011a), whether the integrated volume displacement along the cochlear length is smaller than that over a half-wavelength area centered at the best-frequency location remains to be demonstrated. Our data show that the volume-velocity gain decreases with the stimulus level from >10 at 10 dB SPL to <1 at 80 and 90 dB SPL (red solid line in Fig. 5D). Therefore, our experiment result is not consistent with the argument by Shera et al.

One may find that that the gains in Fig. 5D (Ren et al. 2011a) apparently are a function of the length of the cochlear partition used for the volume displace-

ment or velocity measurement. The gain increases from unity to ~ 100 at 10 dB SPL as the length for integrating volume velocity decreases from the entire cochlear length to the minimum, i.e., the single point. Since the peak response at the best-frequency location results from the cochlear amplifier, the volume velocity obtained from the entire cochlear length provides no specific information on the cochlear amplifier. Both the single-point velocity and the volume velocity over a half-wavelength area centered at the best-frequency location can be used to study the cochlear amplification. The single-point data has revealed the remarkable sensitivity, sharp tuning, and compressive nonlinearity of the cochlear partition vibration (Cooper and Rhode 1992; Nuttall et al. 1991; Ren 2002; Rhode 1971; Ruggero and Rich 1991; Russell and Nilsen 1997), which are the experimental basis of the cochlear-amplifier theory. The single-point velocity data provide limited or no information, however, on the power associated with the cochlear partition vibration. To calculate power near the best-frequency location, we measured the volume velocity of the cochlear partition vibration. Since the cochlear amplifier locates at a small region basal to the best-frequency location (de Boer and Nuttall 1999; Ren et al. 2011b), we measured the stapes volume velocity as the input and the volume velocity centered at the best-frequency location as the output to determine the volume-velocity gain. The volume velocity measured from a region smaller or larger than the half-wavelength area cannot be used to calculate the volume-velocity gain because they are not comparable to the stapes volume velocity.

To demonstrate that our finding of the cochlear power gain (G_c) of >1 can exist in a completely passive structure, Shera et al. computed G_c using a one-dimensional cochlear model (Zweig 1976) and showed G_c is >1 under passive conditions. According to $G_c = (G_{vol})^2$, a G_c of >20 in their Fig. 1 indicates a volume-velocity gain (G_{vol}) of >4.47 . This is not consistent with our data which show that both G_{vol} and G_c are <1 at 80 and 90 dB SPL (blue and red lines in Fig. 5D, Ren et al. 2011a), a passive cochlear condition (Robles and Ruggero 2001).

Shera et al. also compared the cochlear volume-velocity gain to that in passive acoustic transformers or in the middle ear (Puria 2003) and argued that the volume-velocity gain cannot be used to estimate the power gain. However, when the volume velocity is measured at different locations in the same media with identical impedances, the volume-velocity gain can indeed be used to estimate the power gain. Neither an acoustic transformer nor the middle ear is comparable to the cochlea because they provide impedance matching between two media; by contrast, the basilar membranes at the base and at the best-

frequency location are in the same cochlear fluid. The cochlear amplifier gain has been estimated from nonlinear compression of the basilar membrane vibration measured from a single location (Robles and Ruggero 2001). Figure 5D in our paper shows that both the volume-velocity and power gain decrease with the sound level as much as >20 and >40 dB, respectively. The compression of >40 dB of the power gain is consistent with the result that the cochlear power gain is >100 at low sound levels, where the cochlear amplifier may dominate the cochlear mechanical response.

The volume velocity can also be used to study cochlear mechanisms using alternative analyses. Dong and Olson (2008) demonstrated ~ 20 -dB nonlinear compression of intracochlear pressure measured from a single location near the basilar membrane. If this pressure data can be used as an estimate of the averaged pressure over the in-phase-vibration area and the ~ 20 -dB compression is considered as the cochlear pressure gain, the volume-velocity gain of ~ 10 shown by our data indicates a power gain of ~ 100 . Thus, our method apparently reliably indicates the cochlear amplifier gain.

In summary, although our analysis remains to be further verified, our experimental data demonstrate that the volume-velocity gain is ~ 100 times smaller than the point velocity gain measured from a single cochlear location. These results extend our view of cochlear mechanical response from a single point into a more realistic two-dimensional area on the cochlear partition. Hopefully, ongoing discussions of these new data will facilitate greater understanding of hearing mechanisms.

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