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<td>Chan, Wei Xuan; Kim, Namkeun; Yoon, Yong-Jin</td>
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Empirical and biophysical estimations of human cochlea’s psychophysical tuning curve sharpness

Wei Xuan Chan, Namkeun Kim, and Yong-Jin Yoon

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Empirical and biophysical estimations of human cochlea’s psychophysical tuning curve sharpness

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Despite the advances in cochlear research, the estimation of auditory nerve fiber frequency tuning of human cochlea is mostly based on psychophysical measurements. Although efforts had been made to estimate human frequency tuning sharpness from various physiological measurements which are less species dependent such as the compound action potential and stimulus-frequency otoacoustic emission delay, conclusions on the relative frequency tuning sharpness compared with that of other mammals vary. We simulated the biophysical human cochlea’s tuning curve based on physiological measurements of human cochlea and compared the human frequency tuning sharpness with results from empirical methods as well as experimental data of other mammalian cochleae. The compound action potential are more accurate at frequencies below 3 kHz while the stimulus frequency-otoacoustic emission delay are more accurate at frequencies above 1 kHz regions. The results from mechanical cochlear models, with support from conclusions of the other two empirical methodologies, suggest that the human frequency tuning sharpness at frequencies below 1 kHz is similar to common laboratory mammals but is exceptionally sharp at higher frequencies. © 2016 Author(s). All article content, except where otherwise noted, is licensed under a Creative Commons Attribution 3.0 Unported License.

The mammalian cochlea resembles a system of band-pass filters and transducers that convert amplitude-based acoustic vibrations from the stapes into frequency-based electro-chemical signals at the nerve fibers of inner hair cells. The band-pass filters are arranged tonotopically, from high characteristic frequency (CF) regions at the base, to low CF regions near the apex. The frequency tuning sharpness, Q, is given by the quotient of the CF and the bandwidth, and describes the system performance. The bandwidth is determined from the auditory nerve fiber (ANF) tuning curves (TCs). Although the ANF TCs may be measured experimentally using animals,¹ it is impossible to obtain these directly from humans because measurement of the ANF response of a single nerve fiber requires an invasive in vivo process. However, there have been several approaches used to quantify the human ANF frequency tuning sharpness (FTS).

The earliest research focused on recordings of human behavioral responses to acoustic input,² in particular the relationship between the ANF TCs and the psychophysical TCs. Although there has been much progress using this method,³ ⁵ it is still based on the assumptions that psychophysical auditory frequency selectivity is similar to ANF frequency selectivity⁶ and that the psychological transformation function involved in signal transformation from acoustic to psychophysical measurements (see Fig. 1) is independent of the frequency of the acoustic input signal.⁷ Comparisons of

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psychophysical and physiological measurements in guinea pigs support such assumptions; however, there is no supporting evidence in the case of humans, due largely to difficulties in obtaining physiological measurements.

There are several methods for estimating ANF TCs based on non-invasive physiological measurements without assuming a relationship between the physiological and psychophysical responses. The first measures the compound action potential (CAP) using masking procedures. The relationship between the $Q$ of ANF TCs and that of the CAP TCs can be obtained by comparing several species for which both ANF TCs and CAP TCs can be measured. Verschooten et al. used an FM CAP procedure, and Ruggero et al. used an SM CAP method. Verschooten et al.’s work did not provide any species-invariant parameter or function (see Fig. 5 in Ref. 9); however, Ruggero et al. estimated the range of human ANF tuning with three rapidly varying first-order SMCAP-to-ANF $Q$-value transform functions, which were derived using ANF and SM CAP measurements of gerbils, rats, mice, guinea pigs, and chinchillas. Shera et al. developed a method of calculating ANF FTCS using the delay of stimulus-frequency otoacoustic emission (SFOAE). Rapidly varying functions to transform the SFOAE delay to ANF $Q$-values have been obtained from ANF and SFOAE measurements of cats, guinea pigs and chinchillas. Ruggero et al. concluded that the human cochlear tuning sharpness is similar to those of these mammals and to that of squirrels, monkeys and cats. However, Shera et al.’s results revealed sharper cochlear frequency tuning in humans and macaque monkeys compared with cats, guinea pigs and chinchillas, which is inconsistent with the work by Ruggero et al.

Both Ruggero et al. and Shera et al. measured the ANF responses indirectly using unknown transformation functions. These attempts at defining a species-invariant rapidly varying function to describe the transform between the CAP- and the SFOAE-ANF $Q$-value require several species to provide reliable data. Figures 2(a) and 2(b) show the variation of the transformation functions obtained for different species obtained by Ruggero et al. and Shera et al., respectively. Ruggero et al.’s method was more accurate at lower frequencies, where the $Q_{10}$ of the SM CAP TC was small (see Fig. 2(a)). The estimates quickly diverge when the $Q_{10}$ of the SM CAP TC exceeds 3.5. Furthermore, the transforms were assumed to be frequency-independent, which limits the accuracy of the CAP method to low frequencies, where $Q_{10} < 3.5$. Shera et al.’s method may be considered reasonably accurate at high frequencies where the CF is located close to the stapes; however, estimates of the tuning ratio (Shera et al.’s species-invariant parameter) had a large error margin below the CF transition for different species (see Fig. 2(b)). Note that the CF transition for humans is $\sim 1$ kHz; therefore, these estimates are limited to frequencies above 1 kHz.

Yoon et al. described a process to determine human ANF TCs using a three-dimensional (3D) model of the human cochlea based on physiological measurements. Narayan et al. reported matching of the response between the ANFTC and the isovelosity FTC of the basilar membrane (BM) in chinchillas, which indicates that only a minimal transformation is required from the mechanical BM vibration to the auditory nerve excitation, supporting the use of the BM isoveloc-
the iso-response is similar to that used in ANF TC measurements, and does not exaggerate the frequency tuning sharpness compared with iso-input procedures.\textsuperscript{15,16} However, the assumption of a constant gain in the linear regions (where displacement of the BM is small) is poor in the compressive regions (i.e., at frequencies far from the CF), where displacement of the BM is large (see Fig. 7 in Ref. 17).

Here we investigate the methods to calculate human ANF TCs using mechanical models of the BM isovelocity FTC, together with Ruggero et al.’s estimates of the SM CAP and Shera et al.’s SFOAEs. The results obtained from the mechanical model support Ruggero et al.’s findings of unexceptional human cochlear tuning sharpness at low frequencies,\textsuperscript{10} and corroborate Shera et al.’s work on SFOAE, giving exceptionally sharp frequency tuning of the human cochlea at high frequencies.\textsuperscript{7,11} The findings from all three approaches provide useful conclusions on the relative FTS of the human cochlea in different frequency regions.

A general 3D push-pull mechanism (see Fig. 4) is assumed with a two-box cochlear model as shown in Figure 3, which was developed by Yoon et al.\textsuperscript{13,19,20} and is based on the two-dimensional model of Geisler et al.\textsuperscript{21} and the 3D model of Steele et al.\textsuperscript{22} This active push-pull mechanism provides good agreement with various experimental data for gerbils, chinchillas and cats.\textsuperscript{13,19}

The solution process includes integrating the fluid pressure over the cross-section of the BM to obtain the relationship between the volume flow and pressure using a Fourier series expansion. By balancing the forces per unit length in the two-box model (see Fig. 3), we can see that $F(n, \omega) = 0$, where $n$ is the wavenumber, and $\omega$ is the frequency. This gives the eikonal equation,

$$F_{BM} - 2F_{BM}^f - F_{BM}^C = 0$$

$$F_{BM} = \frac{2b}{\pi} [1 - \rho_p \omega^2 h + D_x \omega^4 + 2D_{xy} (\frac{\pi}{b})^2 n^2]$$
FIG. 3. Schematic diagram of the cochlear box model. The Cartesian coordinates (x, y, z) represent the distance from the stapes, the distance across the scala width and the height above the partition, respectively. (a) An overview, (b) front view, (c) top view, and (d) side view of the cochlear model. The box is filled with a viscous fluid with properties similar to water. The partition has an elastic portion, representing the basilar membrane. The input acoustic signal is via a piston at the end (i.e., the stapes), and the round window connected to the lower fluid region consists of a thin membrane giving essentially a zero pressure condition.

\[
+ D_{yy} \left( \frac{\pi b}{D} \right)^4 - \frac{2b}{\pi} \rho \rho_0 \omega^2
\]

(2)

\[
F_{BM}^F = \rho_f \omega^2 bh_f
\]

(3)

where \( F_{BM} \) is the total force on the BM and includes the dynamic fictitious force, \( F_{BM}^F \) is the sum of the viscous fluid forces on the top and bottom of the BM (see Fig. 3), and \( F_{BM}^C \) is the force on the outer hair cells (OHCs), which acts through the Deiters rod (see Fig. 4). The BM width, b, and thickness, h, are extracted from Figure 2 in Yoon et al.’s work, \(^{13}\) \( h_f \) is the effective thickness of fluid layer (see Lim et al.’s work\(^ {17}\)) and the other constants are shown in Table I.

The force acting on the BM at the point indicated in Figure 4(b) is related to the OHC (pushing) force by the coefficient \( \alpha_1 \) and the phalangal (pulling) force by the coefficient \( \alpha_2 \):

FIG. 4. (a) Overview of the Organ of Corti showing the positions of various cells. (b) Schematic diagram showing the tilt of the OHCs based on SEM images. \(^ {18}\) The OHCs provide active amplification of the traveling wave. The walls of the OHCs are piezoelectric, so a downward pressure on the basilar membrane at a distance x results in shear in the stereocilia, and leads to the opening of ion channels, resulting in a change in the intracellular electrical potential. This expands the cell, leading to a downward force on the basilar membrane at \( x + \Delta x_1 \) via the Deiters rod at the lower end of the cell, as well as an upward force at \( x - \Delta x_2 + \Delta x_1 \) via the phalangeal process, connected to the upper end of the cell.
TABLE I. Material properties used in the cochlear model.

<table>
<thead>
<tr>
<th>Region</th>
<th>Symbol</th>
<th>Description</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basilar Membrane</td>
<td>$\rho_P$</td>
<td>Density of the BM plate</td>
<td>$1.0 \times 10^3$ kg/m$^3$</td>
</tr>
<tr>
<td></td>
<td>$E_{11}$</td>
<td>Longitudinal Young’s Modulus</td>
<td>$1.0 \times 10^{-3}$ GPa</td>
</tr>
<tr>
<td></td>
<td>$E_{22}$</td>
<td>Radial Young’s Modulus</td>
<td>1.0 GPa</td>
</tr>
<tr>
<td></td>
<td>$E_{12}$</td>
<td>Coupling Young’s Modulus</td>
<td>0.0 GPa</td>
</tr>
<tr>
<td></td>
<td>$\nu$</td>
<td>Poisson’s ratio</td>
<td>0.5</td>
</tr>
<tr>
<td>Scala fluid</td>
<td>$\rho_f$</td>
<td>Density of fluid</td>
<td>$1.0 \times 10^7$ kg/m$^3$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fluid viscosity</td>
<td>$0.7 \times 10^{-3}$ Pa·s</td>
</tr>
</tbody>
</table>

This is due to the linearity of the motion of the OHC and the small-signal transduction assumption.\(^{17}\) The net push and pull forces must be equal due to the small vertical resistance of the reticular lamina and of the tectorial membrane; therefore, $\alpha_1 = \alpha_2 = \alpha$, and $F_{BM}$ can be expressed as

$$F_{BM} = \frac{2F^f_{BM}}{1 - \alpha e^{-in\Delta x_1} + \alpha e^{-in(\Delta x_2 - \Delta x_1)}}$$

(5)

For any given harmonic frequency $\omega$, the eikonal equation can be solved to yield the wave number $n$ using a Newton-Raphson iterative process for each cross-section along the cochlear duct. Once $n$ is determined, the ratio of the velocity of the BM, $V_{BM}$, to that of the stapes, $V_{ST}$, is obtained using the transport equation, where

$$\int \nabla^2 \varphi dV = 0$$

(6)

and

$$\frac{\delta^2}{\delta x^2} \int_{A(x)} \varphi dA - \int \varphi_z |_{z=0} dy = 0$$

(7)

where $V$ is a small section volume, $A$ is the cross-sectional area and $\varphi$ is the fluid scalar potential derived by applying the wall and non-slip boundary conditions to the linearized Naiver-Stokes equation.\(^{17}\) The solution to Equation (7) is obtained with WKB asymptotic method to accommodate the changing wavenumber along the BM.

The threshold velocities of the BM (which cannot be measured directly using existing experimental approaches) can then be calculated by matching with the FM psychophysical-tuning threshold. The input sound pressure level (SPL) and coefficients $\alpha$ for a given model are then computed for the other frequencies, such that the threshold velocities of the BM are conserved at the CF. The resulting ensembles of input SPLs are then reported as the BM isovelocity tuning curves (i.e., iso-response) for the respective CF.

Parameters are available for the human cochlear model\(^{13}\) to describe the BM and scala fluid (see Table I), as well as the dimensions of the human cochlea (see Table II), which were taken from

\begin{table}[h]
\centering
\begin{tabular}{|c|c|c|}
\hline
Region & Symbol & Description & Value \\
\hline
Length of cochlea (mm) & & & 35 \\
Stapes footplate area (mm$^3$) & & & 3.21 \\
Length of outer hair cell ($\mu$m) & & & 25-65 (from stapes to apex) \\
Fiber volume fraction (%) & & & 3-0.6 (from stapes to apex) \\
\hline
\end{tabular}
\end{table}
TABLE III. Human push-pull gains for various input SPLs at the ear canal.\textsuperscript{13}

<table>
<thead>
<tr>
<th>Input sound pressure at ear canal (dB SPL)</th>
<th>Human</th>
</tr>
</thead>
<tbody>
<tr>
<td>70-90</td>
<td>–</td>
</tr>
<tr>
<td>60-70</td>
<td>0.07</td>
</tr>
<tr>
<td>50-60</td>
<td>0.09</td>
</tr>
<tr>
<td>0-50</td>
<td>0.11</td>
</tr>
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</table>

Bekesy’s anatomical measurements\textsuperscript{23} and Voldrich’s anatomical observations.\textsuperscript{24} The data listed in Table III are for chinchilla’s and cat’s models which show the greatest similarity with available experimental data for humans.\textsuperscript{13} The variation of the width and thickness of the BM, as well as the length of the cochlea, were extracted from Wever’s measurements\textsuperscript{25} (see Fig. 2 in Ref. 13). The cross-sectional area of the scala vestibuli and scala tympani along the length of the BM was taken from Thorne et al.’s magnetic resonance images (see Fig. 8 in Ref. 26).

Figure 5 shows a CF map of the human cochlear model, as well as experimentally measured data from cochlear-microphonic recordings. The two datasets show excellent agreement; however, the relative magnitude of velocity and phase of the BM (see Figs. 6(a) and 6(b)) reveal that the response of the model deviates slightly from the experimental measurements. A roll-off is observed around $2\pi$ for all mammalian cochlea;\textsuperscript{20} thus, the lack of agreement in phase between theoretical and experimental results shown in Figure 6(b) after the CF may be due to measurement errors. Another possible cause is the assumption that the gain (see Table III) depends only on the input SPL. In the cochlea, the gain is constant in the linear regions where displacement of the BM is small; however, it decreases in compressive regions where displacement of the BM increases (see Fig. 4 in Ref. 17). For this reason, the relative velocity of the human model remains in the range of the experimental data from Stenfelt and Gundersen for low BM velocities, but exceeds the maximum velocity near the CF where the BM velocity is high.

Figure 7 shows a comparison of estimates of the ANF TCs at 25.4 mm, 18.2 mm and 9 mm from the stapes using the human cochlear model with Moore’s iso-response forward-masking psychophysical tuning measurements.\textsuperscript{30} By matching the threshold SPL from the psychophysical experiments with the model, the threshold BM velocities at 0.5 kHz, 2 kHz and 7.5 kHz were found to be 100 $\mu$m/s, 160 $\mu$m/s and 330 $\mu$m/s respectively.

FIG. 5. Characteristic frequency (CF) as a function of position along the human cochlea based on 3D cochlear modeling data and cochlear-microphonic recording measurements.\textsuperscript{27}
The bandwidth, $Q_{10}$, of the tuning curves in Table IV were calculated as follows:

$$Q_{10} = \frac{\text{center frequency}}{10\text{-dB bandwidth}}$$

(8)

The gain of the OHCs was assumed to be linear, and therefore the resulting iso-velocity TC may only be considered accurate for sufficiently small input SPLs so that the cochlear response is linear. Lopez-Poveda et al.\textsuperscript{16} used pure tone iso-level TC (see Fig. 1 in Ref. 16) to show that the chinchilla cochlea only exhibits compressive characteristics for an SPL $\geq 50$ dB. Therefore, the $Q_{10}$ value extracted from the iso-velocity tuning curve shown in Figure 7 may be considered a good estimate of the human cochlear FTS and free from significant errors due to the compressive characteristics of the cochlea response.

Another possible source of error is the use of psychophysical thresholding (i.e., non-physiological measurements) in determining the BM threshold velocity. However, the only assumption is that there are no psychological processes involved in the tuning threshold measurements. This assumption is reasonable due to the single frequency, the small acoustic input signal and the simple nerve fiber response of the measurements. Moreover, the process of determining such thresholds is less complicated than measuring the tuning curve.

Both Ruggero et al. and Shera et al. used empirical transformation functions to calculate the Q-values of human cochlear ANF TCs based on physiological measurement data\textsuperscript{7,9–12} using population trends for different species to develop empirical formulations. However, we must acknowledge
the broad range of the tuning sharpness that has been reported for cochleae within a single-species population. As shown in Figure 8 in Ref. 11 (Shera et al.’s work) and Figure 4(b) in Ref. 10 (Ruggero et al.’s data), there are a range of Q-values, SFOAE delay and SM CAP within cats, guinea pigs and chinchillas for each CF. For example, the value of $Q_{ERB}$ for cats calculated using ANFTCs at 1 kHz was in the range between 1 and 9. Such a wide range of values for the cochlea of one species draws into question the reliability of regression between population trends for two variables. Work employing empirical transformation functions for Q-values should consider the transformation function for the cochlea of a given species to establish evidence of a relationship between proposed physiological tuning measurements and ANF TC Q-values.

The SM CAP empirical transformation function is relatively accurate at low frequencies. Ruggero et al. concluded that the $Q_{10}$ value of human ANF tuning at low frequencies is similar to that of other mammals (see Table IV). At higher frequencies, we rely on the conclusions from the SFOAE empirical transformation function. Although there are no available $Q_{10}$ data from SFOAE empirical transformation functions, Shera et al. found exceptionally high human tuning sharpness compared with other mammals at high frequencies.

The findings of both Ruggero et al. and Shera et al. (at their respective frequencies with higher accuracies) support the conclusion from an analysis of the sharpness of the theoretical human ANF TCs (see Fig. 7); the sharpness of the human cochlea is comparable to that of other mammals at low frequencies (i.e., ∼0.5 kHz), but is sharper at frequencies above the human transition CF (i.e., >1 kHz).

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