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Investigating the Effect of Change in Cochlear Micromechanics and Activity Levels on Stimulus Frequency Otoacoustic Emissions Phase-gradient Delay

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Abstract. Stimulus frequency otoacoustic emissions (SFOAEs), which are sounds emitted by the cochlea at the frequency of the stimulus, have been used as a noninvasive measure of cochlear function. The gradient of the SFOAE phases characterizes the latency of emission and is associated with the frequency selectivity and sharpness of tuning of the mammalian cochlea. However, whether the phase-gradient delay of SFOAE can be used as a indicator of cochlear tuning and sensitivity reliably when the properties of the cochlea change remains unclear. The objective of this study is to address this question by varying cochlear model activity, tectorial membrane (TM) properties and organ of Corti (OoC) micromechanical properties to change cochlear tuning. In this work, a three-dimensional gerbil cochlear model that couples mechanical, electrical and acoustic domains with cochlear roughness has been used. The roughness is implemented on outer hair cells (OHCs) force acting on the basilar membrane (BM). Parameters that control the activity levels, TM longitudinal coupling and OoC impedance are varied. The results show that changes in sharpness of tuning due to reduction in cochlear activity and TM longitudinal coupling can be detected by using SFOAE phase-gradient delay. However, changes in cochlear tuning due to changes in OoC impedance are not necessarily reflected by corresponding changes in SFOAE phase-gradient delay.

INTRODUCTION

Otoacoustic emissions (OAEs) are sounds generated inside of cochlea, which are caused by the active feedback by outer hair cells (OHCs) and can be measured at the ear canal (EC). OAEs have been used as a simple, efficient and noninvasive measure of cochlear function in both research and clinical practice [1]. Based on coherent reflection theory, a linear reflection mechanism due to impedance perturbations gives rise to reflection OAEs [2, 3]. Rapidly rotating phase has been found to be one of the key characteristics of reflection OAEs [3]. This study focuses on one type of reflection OAEs called stimulus frequency OAEs (SFOAEs), which are sounds emitted by the cochlea at the frequency of the external stimulus. The gradient of the SFOAE phase characterizes the latency of emission and is associated with frequency selectivity and sharpness of tuning of the mammalian cochlea. The phase-gradient delay of SFOAEs has been proposed to estimate the quality factor of the basilar membrane (BM) response [4, 5]. A more recent study has found the tuning ratio (ratio of tuning sharpness to SFOAE phase-gradient delay expressed in periods) to be approximately invariant among cat, guinea pig, and chinchilla, opening the possibility of determining cochlear tuning from SFOAE phase-gradient delay [6]. However, whether the phase-gradient delay of SFOAE can be used as an indicator of cochlear tuning and sensitivity reliably when the properties of the cochlea change remains unclear. The objective of this study is to address this question by varying cochlear model activity levels, tectorial membrane (TM) properties and organ of corti (OoC) impedance that can affect the cochlear tuning and sensitivity. Varying TM properties in the case study is inspired by studies that have shown that changing tectorial membrane (TM) longitudinal coupling affects cochlear tuning [7, 8, 9], spontaneous OAEs (SOAEs) [10] and SFOAEs [11].

METHOD

In this work, a three-dimensional gerbil cochlear model that couples mechanical, electrical and acoustic domains with cochlear roughness is used, which has been described in detail in previous works [12, 13]. The parameters of the baseline model can be found in [12]. The smooth version of this cochlear model has been calibrated based on in vivo recent experiments, with both mechanical and electrical data. In order to simulate reflection OAEs, cochlear roughness on the OHCs electromechanical coupling coefficient (which relates the electromotile force applied on the

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BM to the transmembrane potential) is introduced as in our previous work [13]. ΔR is the standard deviation of the perturbations from the smooth case that quantifies the roughness. A random number seed (RNS) is used in the model to initialize the random number generator, which enables the possibility of simulating a family of various roughness profiles using different RNS values, which mimics the measurement of OAEs in multiple cochleae. $\Delta R = 0.1\%$ has been used throughout this work for the rough models. As in Ref. [13], calculation of the SFOAE is based on the reflection component in EC pressure, which is the vector difference between the steady-state pure tone response of the model with roughness and without roughness (smooth model).

To get the phase-gradient delay of SFOAE at 20 kHz, two methods are implemented. The first method (phase-fitting method) applies a quadratic regression to the phase of SFOAE between 10 kHz to 30 kHz to extract the trend line of the phase. The slope of the quadratic fit at stimulus frequency $f = 20$ kHz is used to determine the SFOAE phase-gradient delay (τ_{SFOAE}), and the equivalent number of stimulus periods, $N_{\mathrm{SFOAE}}(f) = \tau_{\mathrm{SFOAE}}(f) \cdot f$. The second method implements the peak-picking algorithm [14], which considers only those values of $N_{\mathrm{SFOAE}}(f)$ that occur near frequencies corresponding to peaks in SFOAE level. Here the peak-picking selection includes the peak itself and two points on either side of the peak. The peak-picked phase-gradient delays of SFOAE are then smoothed with a LOESS fit to find the value at $f = 20$ kHz. The theory of reflection emissions implies that τ_{SFOAE} is around twice the phase-gradient delay of BM response (τ_{BM}) evaluated at the location where CF is equal to the stimulus frequency [15]. To facilitate the comparison between BM and SFOAE phase-gradient delay, normalized values $\frac{1}{2}N_{\mathrm{SFOAE}}$ and $N_{\mathrm{BM}} = \tau_{\mathrm{BM}} \cdot \mathrm{CF}$ are analyzed in the RESULTS section. To compare the cochlear tuning sharpness, parameter-free measure $Q_{\mathrm{ERB}}(f_{\mathrm{CF}}) = f_{\mathrm{CF}}/\mathrm{ERB}(f_{\mathrm{CF}})$ is computed [16]. Here, $\mathrm{ERB}(f_{\mathrm{CF}})$ is the equivalent rectangular bandwidth at the local characteristic frequency, f_{CF}.

Three model parameters that can change cochlear tuning have been varied. The first parameter is activity level (α_{ActLev}), which is defined as a factor constant that scales the saturating mechano-electrical transduction (MET) conductance G_{hb}^{max} from the baseline value used in [12]. Activity level of 1 corresponds to a fully active model, and 0 corresponds to a passive model. In this study, the activity level is varied between 0.4 to 1. The second parameter is TM longitudinal coupling ratio (R_{TMLC}) that scales the value of longitudinal stiffness and viscosity of the TM [9] from its baseline value [12]. The range of interest for R_{TMLC} is between 0.5 and 1 here, where 1 corresponds to the normal cochlea and a value of 0.5 is representative of the TM coupling observed in mutant mice with reduced longitudinal coupling [7]. The third model parameter that has been varied is OoC impedance ratio (R_{OOC}). It is a factor constant that scales the stiffness of OHCs, reticular lamina (RL) and hair bundles (HBs), as well as the bending stiffness, mass and damping of TM from the corresponding baseline values [12]. $R_{\mathrm{OOC}} = 1$ corresponds to the baseline model which was calibrated based on the vivo data. In addition, the state-space formulation of the model is ran in frequency domain and the linear stability of each case considered has been checked [17, 18].

RESULTS

Change in BM responses and SFOAE due to reduction in cochlear activity level

Figure 1 shows the effect of change in activity levels on BM responses to 20 dB SPL pure tones and SFOAE. Decreasing the activity levels broadens the tuning of the responses of the BM velocity and decreases their sensitivity (panel a). The sharpness of tuning, indicated by Q_{ERB}, decreases as the activity level decreases (panel f). The slope of the phase of V_{BM} (panel d) decreases near the best frequency (BF) when the activity levels decreases. The model predicts the fine structure of SFOAE, including the relatively broad peaks separated by deep notches in the amplitude plot (panel b). The SFOAE level tends to decrease as the activity level decreases, and the deep notches in the fine structure shift from high frequencies to lower frequencies. In parallel with the changes in SFOAE amplitude and fine structure, the slope of the SFOAE phase becomes shallower at lower activity levels, indicating a shortening of the phase-gradient delay. Panel c compares $\frac{1}{2}N_{\mathrm{SFOAE}}$ obtained by two different methods to N_{BM} for various activity levels. Variance of the normalized SFOAE phase-gradient delay exists between different RNS values; however, at the population level, by taking the average of those individual values $\left(\frac{1}{2}\bar{N}_{\mathrm{SFOAE}}\right)$, N_{SFOAE} remains approximately equal to twice N_{BM} as the activity level is reduced. Comparing panels c and f shows that the changes in $\bar{N}_{\mathrm{SFOAE}}$ and Q_{ERB} are correlated.

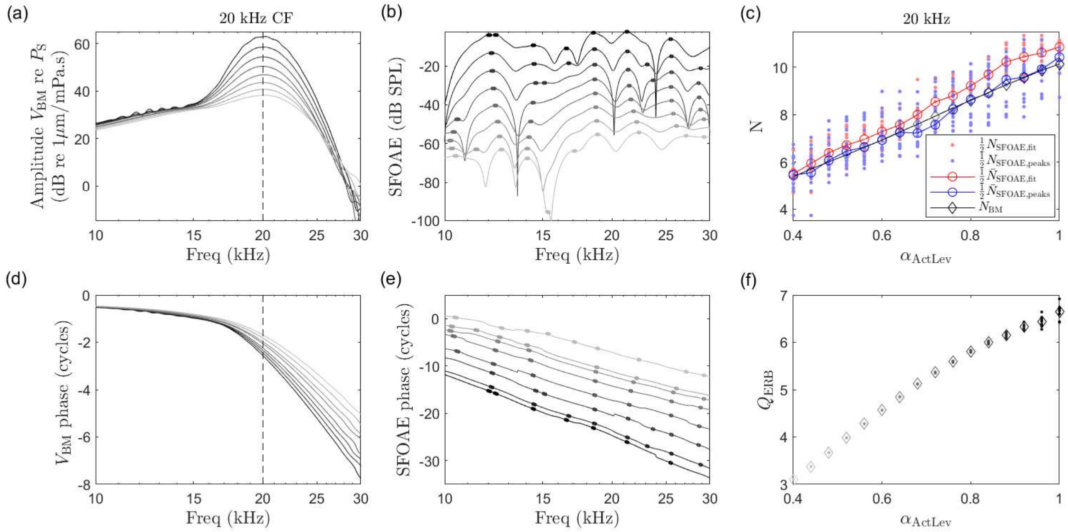

FIGURE 1: Effect of change in activity levels on BM responses and SFOAE with roughness parameter $\Delta R = 0.001$. Amplitude (a) and phase (d) of BM velocity response to a pure tone of 20 dB SPL for various reduced activity levels (from 100% to 40% activity level with respect to baseline). Amplitude (b) and phase (e) of SFOAE with reduced activity levels. Dots mark data points used in peak-picking algorithm to determine the phase-gradient delay values. All intracochlear responses are at the location tuned to 20 kHz, i.e., the 20 kHz best place (BP). The roughness parameter is set to be $\Delta R = 0.1\%$. Only RNS$= 0$ case is shown here among 10 different random seed numbers. Phases are offset by integer numbers of cycles to distinguish them in panel e. (c) Normalized phase-gradient delay with respect to activity levels, α_{ActLev} at 20 kHz. Dots indicate normalized SFOAE phase-gradient delays obtained by phase-fitting method (red) and peak-picking method (blue) for RNS$= 0-9$; circles represents the mean values of normalized SFOAE phase-gradient delays obtained by phase-fitting method (red) and peak-picking method (blue) among 10 different random seed numbers; black diamonds show the normalized phase-gradient delays of BM response. (f) Tuning sharpness of BM response as a function of activity levels at 20 kHz. Dots represent the individual values of $Q_{\text{ERB}}(20\text{ kHz})$ for RNS$= 0-9$; diamond markers represent the mean values of $Q_{\text{ERB}}(20\text{ kHz})$ among 10 different seed numbers. The color gradient is corresponding to change in activity levels: from black to light gray reflects the baseline case ($\alpha_{\text{ActLev}} = 1$) to lowest reduced activity level case ($\alpha_{\text{ActLev}} = 0.4$) accordingly.

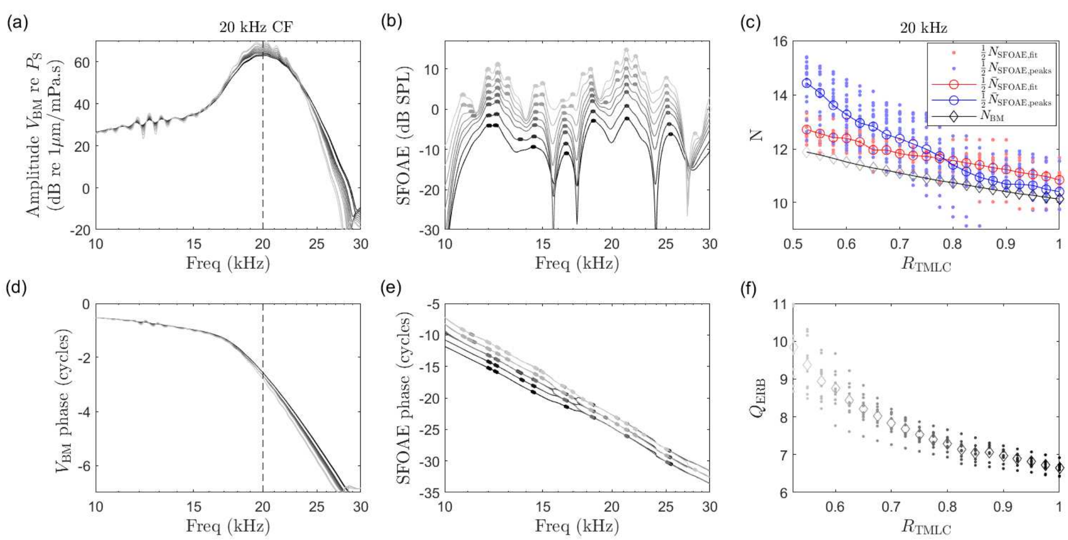

FIGURE 2: Same as Figure 1 but for the effect of change in TM longitudinal coupling.

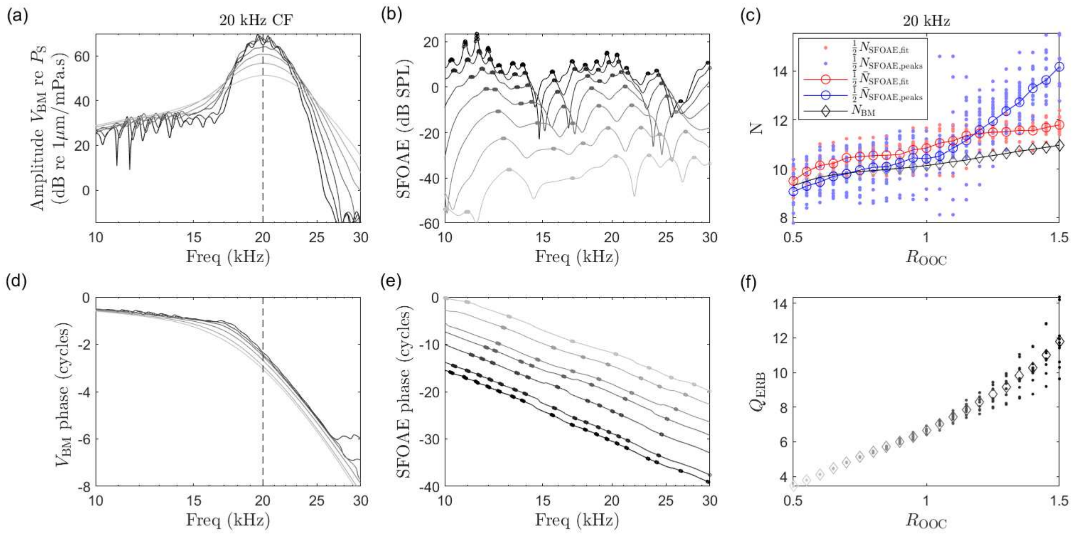

FIGURE 3: Same as Figure 1 but for the effect of change in OoC impedance.

Change in BM responses and SFOAE due to reduction in TM longitudinal coupling

Figure 2 shows the effect of changes in TM longitudinal coupling on BM responses and SFOAE. Response of the BM velocity (panel a) at the CF increases as the R_{TMLC} decreases; the bandwidth of the responses becomes slightly narrower as discussed in [9]. As a consequence, the sharpness of the tuning increases as the TM longitudinal coupling decreases (panel f). The slope of the phase of V_{BM} (panel d) steepens slightly near the BF when R_{TMLC} decreases. The SFOAE level grows as R_{TMLC} decreases, and more peaks are formed in the fine structure and the deep notches become less pronounced. The phase-gradient delay increases since the slope of the SFOAE phases becomes slightly steeper when TM longitudinal coupling is weaker. As shown in panel c, $\frac{1}{2}\bar{N}_{\mathrm{SFOAE}}$ decreases as R_{TMLC} increases. Even though the values of $\frac{1}{2}\bar{N}_{\mathrm{SFOAE,fit}}$ obtained from phase-fitting method are biased (higher than N_{BM}), the trend of $\frac{1}{2}\bar{N}_{\mathrm{SFOAE,fit}}$ is more consistent with the change in N_{BM} as compared to the trend of $\frac{1}{2}\bar{N}_{\mathrm{SFOAE,peaks}}$ when TM longitudinal coupling varies. The peak-picking method correctly determines the phase-gradient delay value at specific frequency (i.e., 20 kHz) when R_{TMLC} is close to 1; however, it starts to overestimate the phase gradient delay when the SFOAE responses have more peaks caused by multiple internal reflections [14] as R_{TMLC} decreases.

Change in BM responses and SFOAE due to variation in OoC impedance

The effect of change in OoC impedance on BM responses and SFOAE is demonstrated in Figure 3. Panel a shows that decreasing the OoC impedance reduces the peak values and expands the bandwidth of BM velocity responses. Subsequently, the tuning sharpness drops as the OoC impedance decreases as shown in panel f. There exists a shift in the BM velocity phases as OoC impedance changes; however, the slope of the phase barely changes as the traveling wave approaching BF when the OoC impedance varies. The SFOAE level tends to decrease as the OoC impedance decreases, and the fine structure becomes less prominent with less pronounced peaks. The SFOAE phase-gradient delay changes slightly since the slope of the SFOAE phases hardly decreases as the OoC impedance decreases. Panel c compares the change in $\frac{1}{2}\bar{N}_{\mathrm{SFOAE}}$ obtained by two different methods and N_{BM} as R_{OOC} varies. N_{BM} grows as R_{OOC} increases with almost a constant rate; on the other hand, the relationship between $\frac{1}{2}\bar{N}_{\mathrm{SFOAE,fit}}$ obtained from phase-fitting method and R_{OOC} is monotonic with a varying rate. The slope of $\frac{1}{2}\bar{N}_{\mathrm{SFOAE,fit}}$ turns to almost zero as the R_{OOC} varies around 0.75 and 1.25. In terms of phase-gradient delays obtained by peak-picking method, $\frac{1}{2}\bar{N}_{\mathrm{SFOAE,peaks}}$ follows the trend of N_{BM} when $R_{\mathrm{OOC}} < 1$ (when SFOAE has less prominent fine structures with less pronounced peaks), being unable to reflect the change in OoC impedance well when the impedance values are smaller than the baseline value. When the SFOAE responses include more prominent fine structures with more peaks as R_{OOC} increases

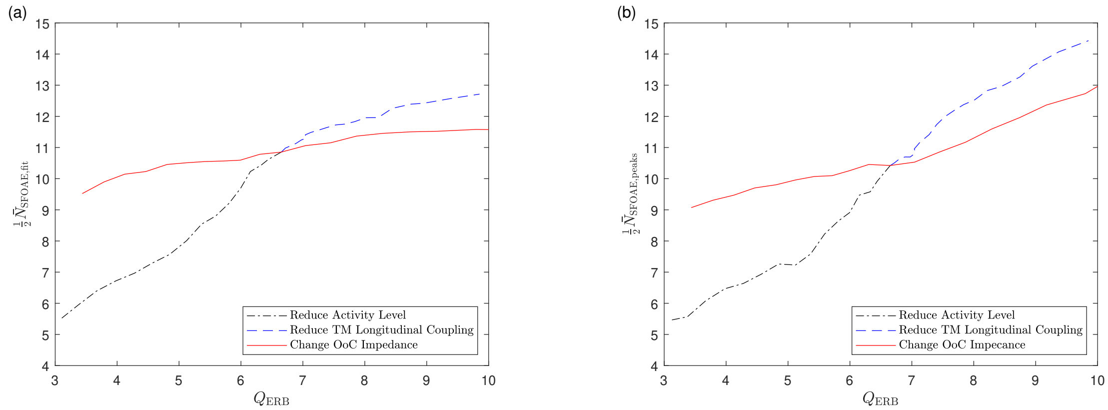

FIGURE 4: Comparison of normalized phase-gradient delay of SFOAE as a function of quality factor of the response between three considered scenarios based on (a) phase-fitting method, (b) peak-picking method.

($R_{\mathrm{OOC}} > 1$), $\frac{1}{2}\bar{N}_{\mathrm{SFOAE,peaks}}$ deviates from N_{BM}, not reflecting the BM phase-gradient delay correctly. Since the change in $\frac{1}{2}\bar{N}_{\mathrm{SFOAE}}$ can be hard to notice at a certain range where the R_{OOC} varies, the phase-gradient delay of SFOAE cannot indicate the change in OoC impedance as well as the BM phase-gradient delay.

SFOAE phase-gradient delay can detect changes in tuning sharpness due to reduction in cochlear activity level, decrease in TM longitudinal coupling, but not necessarily variation in OoC impedance

Figure 4 compares the normalized phase-gradient delay of SFOAE with respect to Q_{ERB} of the BM responses based on phase-fitting method (a) and peak-picking method (b) to evaluate whether SFOAE phase-gradient delay can detect change of cochlear tuning. As shown in both panel a and b, there exists a strong positive correlation between $\frac{1}{2}\bar{N}_{\mathrm{SFOAE}}$ and Q_{ERB} for the sharpness change due to reduction in cochlear activity and TM longitudinal coupling. However, the positive correlation between $\frac{1}{2}\bar{N}_{\mathrm{SFOAE}}$ and Q_{ERB} for the varied OoC impedance case is much weaker compared to the previous two cases ($\frac{1}{2}\bar{N}_{\mathrm{SFOAE}}$ varies only by around 20% when Q_{ERB} varies nearly by 300% in Fig. 4a for example), indicated by the shallower slope among all Q_{ERB} values shown in panel a, and when $Q_{\mathrm{ERB}} < 6.5$ in panel b. Both methods confirm that changes in tuning sharpness due to reduction in cochlear activity and decrease in TM longitudinal coupling can be detected by measuring the changes in SFOAE phase-gradient delays. However, changes in the tuning sharpness due to variation in OoC impedance are not necessarily reflected by changes in SFOAE phase-gradient delays, especially when the OoC impedance decreases from baseline value.

DISCUSSION

This work utilizes a physiologically-based model of gerbil cochlea to investigate the influence of changes in OoC micromechanics and activity levels on SFOAE phase-gradient delay. Two different methods are used to obtain the phase-gradient delay of SFOAE at specific stimulus frequency. The phase-fitting method provides better trend of the phase-gradient delay, including models that have sharp peaks in SFOAE. However, this does not compute the physical meaningful phase-gradient delay, i.e., the red curve is significantly above the black curve in panel c in Figs.$1-3$. The peak-picking method is better at getting the correct phase-gradient delay when the SFOAE peaks are not too sharp.

Both methods lead to a similar conclusion. At the individual levels, SFOAE phase-gradient delay cannot be used to indicate the cochlear tuning and sensitivity since there is no clear correlation between N_{SFOAE} and Q_{ERB} of the BM response for different RNS values. At the population level, the results show that changes in cochlear tuning due to variations in cochlear activity and TM longitudinal coupling can be detected by using average SFOAE phase-gradient delay among various RNS values. However, changes in cochlear tuning as a result of changes in OoC impedance are

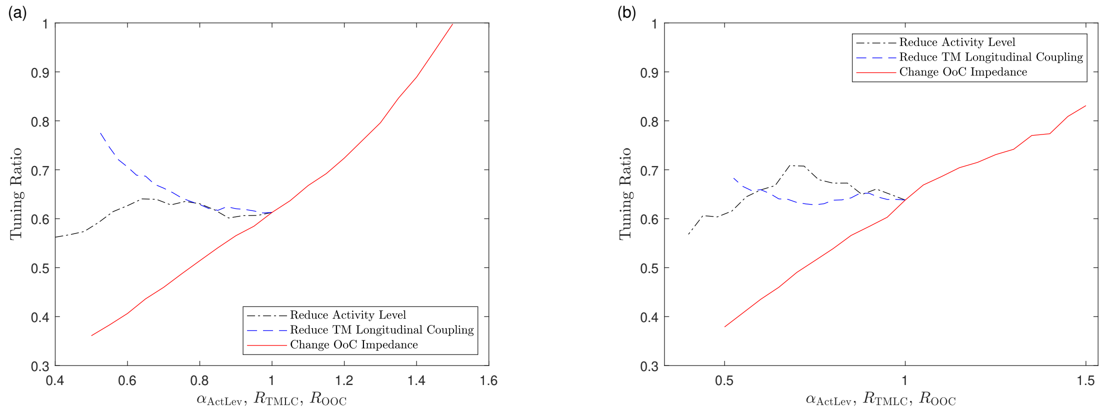

FIGURE 5: Comparison of tuning ratio with respect to variables that control the three considered parameters according to (a) phase-fitting method, (b) peak-picking method.

not necessarily reflected by corresponding changes in mean SFOAE phase-gradient delay. When R_{OOC} is varied, the shape of BM responses varies, such that it affects the relation between Q_{ERB} and N_{BM}, as well as the relation between Q_{ERB} and N_{SFOAE} since N_{SFOAE} and N_{BM} are correlated. This implies that changes in cochlear micromechanics (such as varying OoC impedance) can affect the tuning ratio [6], which is the ratio of tuning sharpness to SFOAE phase-gradient delay in periods (i.e., $Q_{\text{ERB}}/\frac{1}{2}\bar{N}_{\text{SFOAE}}$). Figure 5 compares the tuning ratio with respect to variables that control activity level, TM longitudinal coupling and OoC impedance respectively using (a) phase-fitting method and (b) peak-picking method. The possibility that the tuning ratio may change significantly needs to be kept in mind when SFOAE phase-gradient delays are used to estimate cochlear tuning in multiple species, or in animals with altered properties (such as transgenic mice with altered TM expressions [11]).

An alternative method to estimate cochlear tuning using SFOAE is by measuring the quality factor of SFOAE suppression tuning curves (SFOAE-STC) [19]. Future work might explore the influence of cochlear micromechanics and activity levels on SFOAE-STC.

ACKNOWLEDGMENTS

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COMMENTS AND QUESTIONS

[*Online Forum*]

Pawel. B: Thank you for an interesting article in a field that I do not know well. After reading, I started to wonder if there are any other parameters in the model, besides the three that were considered (activity level, TM longitudinal coupling ratio, and OoC impedance ratio), that could affect the stimulus frequency otoacoustic emissions. If so, what are these parameters - can they have a significant impact on the results? My second question is related to the number of variables analyzed in your paper. If we study the influence of one of the selected parameters, then the other two have to be established at some levels - how was it done in your model?

Author: Besides the three parameters that were considered in this paper, the sound pressure level (SPL) of external stimulus can also affect the SFOAEs. It has been suggested that SFOAE phase-gradient delay decreases as the SPL is increased [13]. In this paper, we have only considered responses to a pure tone at 20 dB SPL that we obtained by simulating the model in frequency domain. Simulations in time domain are necessary to evaluate the effect of SPLs. The smooth version of our cochlear model (baseline model) has been previously calibrated based on in vivo measurements [12, 13]. All the parameters for the baseline model can be found in [12]. When we study the influence of one of the select parameters, the other two parameters are kept the same as the baseline model.

Karolina Charaziak: Nice paper! I was wondering about the reverse OAE travel in your model. In your model $N_{\mathrm{OAE}} = 2*N_{\mathrm{BM}}$. In experimental data the OAE delay is typically less than twice the BM delay. Can the model be adjusted to account for that?

Author: One potential way to adjust the model is applying spatially low-pass filtering on the roughness profile with cut-off wavelength larger than half of the wavelength of BM response at the best place. In this way, the reflected wavelet will be significantly reduced, and the phase-gradient delay of SFOAE will decrease.

Vaclav Vencovsky: Dear authors. I think the paper is clearly and very well written. It provides an important information how the cochlear amplifier gain, coupling along TM and OoC impedance affect group delay estimated from SFOAE phase. Very nice and important work, thank you for it. I suggest to add into Figs. 4 and 5 data for N_{BM} estimated from the cochlear filters. This would show how the parameters affect group delay and tuning ratio without errors due to group delay estimation from the SFOAE phase. It is very obvious from the data that the model gain affects N_{BM} and estimated N_{SFOAE} are not much different from N_{BM}, which is a good results, however, in Fig. 2(c) and Fig. 3(c), the difference between N_{BM} and N_{SFOAE} is in some cases large. The authors stated that the reason for departure between N_{BM} and N_{SFOAE} are multiple internal reflections, whose effect probably gets stronger as R_{TMLC} goes down from 1 to 0.5 or as R_{OOC} goes up from 1 to 1.5. Do I understand it correctly that if we used some form of time-frequency filtering (e.g. wavelets in Shera and Bergevin (2012) or Moleti et al. (2012), the agreement between N_{SFOAE} and N_{BM} would be better? Did you mean it in your conclusive sentence: "The possibility that the tuning ratio may change significantly needs to be kept in mind when SFOAE phase-gradient delays are used to estimate cochlear tuning in multiple species, or in animals with altered properties (such as transgenic mice with altered TM expressions [11])" or would you suggest something else? Otherwise, I think that for Rooc < 1, the agreement between N_{BM} and N_{SFOAE} is very nice and the tuning ratio changes a lot, which is interesting result. I was struggling to find information on the probe level used to simulate SFOAEs. Would be good to state it in the figure captions. Sorry if I overlooked it.

Author: Thanks for the suggestions about Figs. 4 and 5. However, we think that since this paper focuses on whether the change in phase-gradient delays of SFOAEs (N_{SFOAE}) can predict the change of cochlear tuning (Q_{ERB}), it is better not to show N_{BM} to complicate the figures and create distractions from the conclusion. In terms of getting more accurate N_{SFOAE} values, we totally agree that some form of time-frequency filtering will need to be applied to reduce multiple internal reflections and get better agreement between N_{SFOAE} and N_{BM}. For the conclusion part, we believe that even after applying time-frequency filtering to get more accurate N_{SFOAE}, the tuning ratio will still change significantly in the case of changing OoC impedance. Last but not the least, pure tone at 20 dB SPL was used to simulate SFOAEs, and this information has been added in the main text.

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