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The Mechanisms Underlying Multiple Lobes in SOAE Suppression Tuning Curves in a Transmission Line Model of the Cochlea

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Abstract. Spontaneous otoacoustic emissions (SOAE) can be suppressed by presenting an acoustical stimulus. For stimuli with frequencies close to the SOAE frequency, the SOAE either show a beating pattern or are heavily suppressed while the spectral energy of the stimulus increases. This effect indicates that the self-sustained oscillations in the cochlea underlying SOAE are entrained by the oscillation evoked by the stimulus. The level required to entrain SOAE needs to be higher for a larger spectral distance between SOAE and stimulus compared to a smaller spectral distance, leading to a V-shaped tuning curve. When these tuning curves are measured over a broad frequency range spanning several octaves, additional lobes of suppression can be found with a spectral distance of about half an octave. It has been proposed that SOAEs are generated by a standing wave pattern in the cochlea that arises by interference of multiple reflections between the best place and the oval window [1]. It has further been hypothesized that the additional side lobes in the SOAE suppression tuning curves are the result of interaction of the stimulus with the nodes and antinodes of the standing wave pattern underlying the SOAE [4]. In the present study, a nonlinear and active transmission line model of the cochlea is used to investigate this hypothesis. The model is able to produce SOAEs with plausible characteristics and further shows the suggested standing wave pattern. This approach hence makes it possible to disentangle contributions of entrainment and compression of the forward-traveling wave to the SOAE suppression tuning curves.

INTRODUCTION

Spontaneous otoacoustic emissions (SOAE) are low-intensity sound signals generated in the inner ear of many species, including some mammals. The presence of this signal in the absence of any stimulation is an indicator for the existence of an active process in the inner ear, leading to spontaneous, self-sustained oscillations. SOAE can be suppressed, i.e. reduced in amplitude, by the presence of an external stimulus. The level required for the external stimulus to suppress the SOAE depends on the spectral distance from the SOAE. High levels are required for larger distances, and low levels for small distances. At a given level, the amount of suppression decreases with increasing spectral distance between suppressor and SOAE. At spectral distances of around 0.5 and 1 octave, additional suppression can occur [4]. Since the SOAE is defined and measured as a signal in the ear canal, multiple mechanisms could be underlying the reduction in SOAE level. For suppressors close in frequency, entrainment effects between the self-sustained activity underlying the SOAE and the evoked oscillation by the stimulus have been discussed [3, 5]. This mechanism can, however, not account for the increased suppression at spectral distances of 0.5 or 1 octave. In the present study, a one-dimensional active and nonlinear model of the cochlea, able to simulate SOAEs, was used to investigate SOAE suppression and the contributions of suppression and mechanical biasing of the cochlear amplifier.

METHODS

Transmission Line Model of the Cochlea

A nonlinear and active TLM with 1000 segments that included roughness of the cochlea was used to simulate SOAE (all parameters taken from [3]):

$$p_j = m\ddot{x}_j + d_j(\dot{x}_j)\dot{x}_j + s_j \left[x_j + c_j(\dot{x}_j)\dot{x}_j(t)|_{t-\tau} \right]$$

p_j	pressure at j-th oscillator
m	effective mass of j-th oscillator
x_j	displacement of j-th oscillator
$d_j(\dot{x}_j)$	nonlinear damping coefficient
s_j	linear spring constant of j-th element
$c_j(\dot{x}_j)$	nonlinear feedback stiffness term
τ	feedback time delay

The model equations were solved in the time domain at a rate of 400 kHz using a modified 4th order Runge-Kutta method.

Simulations

Spontaneous otoacoustic emissions were simulated by evaluating the spontaneous, self-sustained activity of the model in the simulated ear canal. The ear canal pressure was simulated for a duration of 1 second and weighted with a Hann window of 1 s duration. Thereafter, the Fast Fourier Transform was applied to obtain the SOAE spectrum. A spectral peak was identified and used as a reference frequency for the SOAE suppression simulations. To identify the frequencies corresponding to a node or antinode in the standing wave pattern of the simulated cochlea, the temporal wave form of each segment was band pass filtered using an 8-th order Butterworth filter with a bandwidth of 80 Hz centred at the SOAE frequency. To simulate SOAE suppression, the model was stimulated with a pure tone of a frequency corresponding to the mechanical tuning of the segment coinciding either to a node or an antinode on the standing wave pattern. The stimulus had an overall duration of 2 s and was multiplied with an on- and offset raised-cosine ramp of 10 ms duration. The simulated ear canal pressure and the velocity of each segment were saved for each integration time step for later analysis.

RESULTS

Figure 1 shows A) the simulated SOAE spectrum, B) the corresponding cochleogram, and C) the bandpass filtered cochleogram, filtered around the centre frequency of the SOAE component at 2413 Hz. Panel B illustrates the complex dynamics of the self-sustained oscillations of the BM. The band pass filtered cochleogram (panel C) shows an alternating pattern of velocity minima (blue) and maxima (red) of varied length for the basal segments, clearly showing a standing wave pattern. Closer to the segment tuned to the SOAE frequency of 2413 Hz, a forward traveling wave can be observed. Figure 2 shows the synchronization across a broad frequency- and level range (1.5 octaves and 40 dB, respectively). Close to the SOAE frequency, the main lobe of suppression is V-shaped, as observed in previous studies. The side lobe is aligned with an antinode in the standing wave pattern, separated from the main lobe by a region of facilitation coinciding with a node in the standing wave pattern. Multiple additional sidelobes are present at more remote frequencies, but with much lower suppression. Panels A-C in Figure 3 show the maximum velocity of each segment in the BP filtered cochleogram over the simulation period (BM velocity profiles) in the cases of a suppressor frequency either coinciding with an antinode (3250 Hz, panel A), a node close to the SOAE frequency (3690 Hz, panel B) or a node further away from the SOAE frequency (5230 Hz, panel C). Arrows indicate the mechanical best place of the suppressor frequency. The velocity profiles were normalized to the maximum of the BP filtered cochleogram in the absence of a suppressor. In all cases, an almost constant suppression of the SOAE frequency component was found across all segments basal to that tuned to the SFOAE frequency. The amount of suppression decreased with increased spectral distance between suppressor and SOAE, and was highest for the condition with the suppressor in the antinode (A).

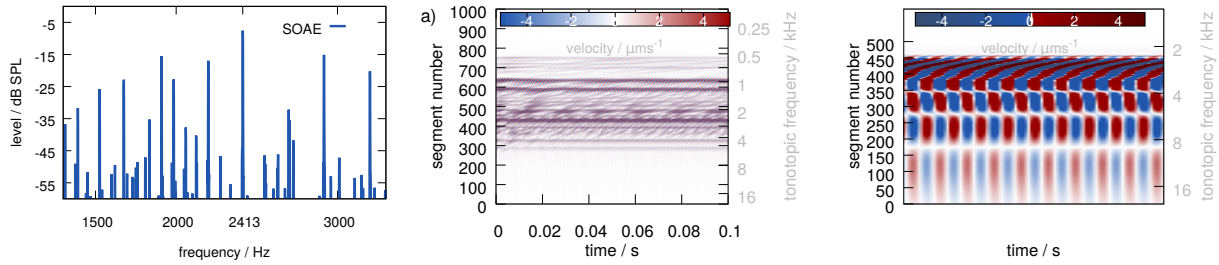


FIGURE 1. Simulated SOAE spectrum (A), cochleogram of the self-sustained activity underlying SOAE (B) and cochleogram from B) band pass filtered around the SOAE frequency of 2413 Hz.

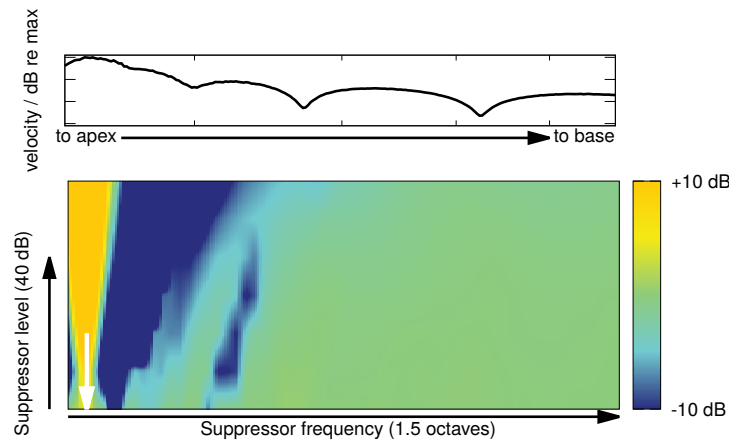


FIGURE 2. Velocity profile (top) and suppression tuning map (bottom). The regions of suppression and facilitation align with the pattern of the velocity profile.

The amount of suppression in each segment is shown in Figure 4 for each of the conditions. The suppression was rather constant at basal segments, with some deviations at segments coinciding with a node in the SOAE velocity profile. For the suppressor placed in an antinode, the largest suppression was found for a segment basal to the suppressor's best place. For the other two suppressors, the largest suppression was limited to a very small group of segments, located basally to the suppressor's best place. For the highest suppressor levels, the suppression was around 10 dB for the suppressor frequency corresponding to an antinode, and almost absent for the suppressor frequency corresponding to the more basal node. Besides the narrow regions deviating, most segments show a rather constant suppression in all cases.

DISCUSSION

For suppressor frequencies close to the SOAE frequency, the energy at the SOAE frequency is entrained to the energy of the suppressor frequency, consistent with previous findings [3]. This mechanism seems, however, not feasible for larger spectral distances. The velocity profiles show a rather constant suppression of the SOAE frequency at segments basal to the SOAE best place, indicating a constant decrease of amplitude, possibly due to a decrease in amplification along the basal path of the traveling wave. The fact that the suppression was largest for the spectrally close suppressor and smallest for the spectrally farthest suppressor indicates a relation between suppression strength and spectral distance, as also observed in the tips of SOAE tuning curves [4]. Since the suppression was, however, constant across basal segments, a different mechanism than entrainment seems to cause the reduction in SOAE amplitude. Entrainment would only affect segments close to the SOAE and the effect would be smaller for more remote segments [3].

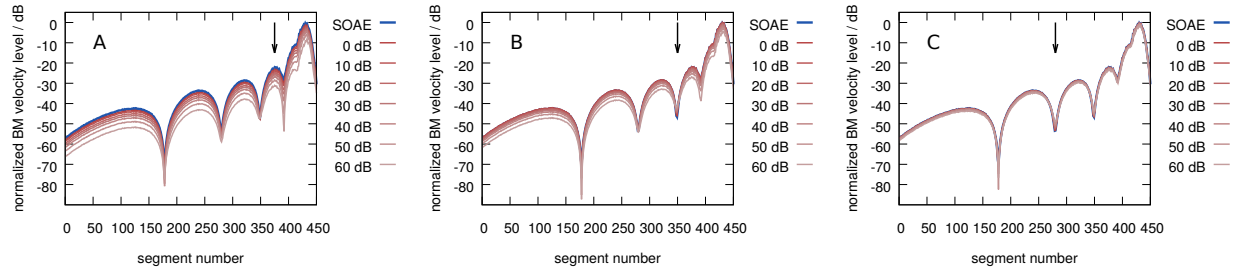


FIGURE 3. Velocity profiles of the band pass filtered cochleograms for the three different suppressor conditions: Antinode (A), node close (B) and node far (C).

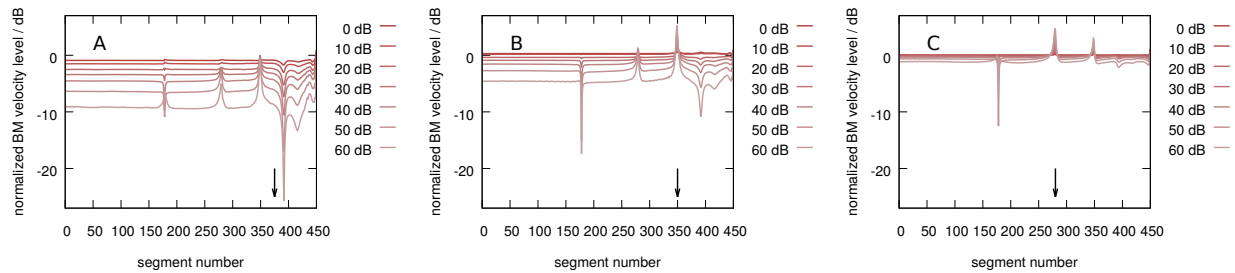


FIGURE 4. Same as Fig. 3, but showing suppression relative to the absence of a suppressor.

A possible mechanism might be an offset in the operating point of the cochlear amplifier at basal sites by the basal tail of the traveling wave envelope. Such an offset would reduce the amount of amplification provided to the reflected forward traveling wave at the SOAE frequency, consequently reducing the amount of reflected energy and hence reducing the net amplitude of the standing wave pattern. A more detailed analysis is, however, required to rule out any effects of entrainment at larger spectral distances between suppressor and SOAE. Only one difference in the suppression could be found for a suppressor frequency coinciding with an antinode compared to the suppressor frequency coinciding with a node: The largest suppression was found for a small peak apically to the best place of the suppressor frequency, while for the two suppressors coinciding with the nodes, the maximum suppression was located basally. The simulations show that two mechanisms potentially contribute to SOAE suppression: entrainment for suppressors close in frequency, and tonic suppression for all segments basally to the best place of the SOAE frequency. Since the basal tail of the excitation patterns is, however, rather broad in comparison to the pattern of nodes and antinodes, the direct link between the standing wave pattern and the suppression side lobes remains to be clarified.

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COMMENTS & QUESTIONS

[*Online Forum*]

Christopher Shera: The first sentence of the Discussion says that for “suppressor frequencies close to the SOAE frequency, the energy at the SOAE frequency is entrained...”. Can you demonstrate this? How do you know that the energy of the SOAE is entrained rather than suppressed? Are there criteria for distinguishing these effects?

Author: This is a very interesting point which we hopefully can discuss. I have been discussing this with some people already, and depending on the metric these two are hard to separate. I think though that close (in frequency) to the SOAE, the energy of the SOAE is entrained by the oscillation due to the suppressor (in agreement with data on OAEs and perceptual evaluation, done by Glenis and coauthors - I’ll find the reference). We can also see this in the dynamics of the simulated cochlea AND (in agreement with the data) in the simulated ear canal pressure where the amplitude of the SOAE shows interesting dynamics which is in line with entrainment of limit cycle oscillators (as demonstrated analytically by Talmadge et al and others). We also have a manuscript in preparation (with quite some patina on it I have to admit), but I hope this would provide some model-based support for this.

Christopher Shera (cont.): The third sentence of the Discussion says the “rather constant suppression” in the basal regions indicates “a constant decrease of amplification along the basal path of traveling wave”. If I understand the analysis, though, you are quantifying the component of the response at the SOAE frequency and not the amount of amplification. If so, doesn’t the constant suppression simply indicate a constant decrease in the response? Some extra step seems necessary to tie this to the amount of amplification.

Author: True and thanks for the comment. I have been trying to quantify the amplification, but I did not find a good way. My initial idea was to get a “normalized” measure of the active process (negative damping + delayed feedback stiffness in this case) and see where we are. But I would appreciate some discussions on this. So far the quantification is more phenomenological in nature.

Christopher Shera (cont.): Likewise, if you remove the roughness and play the 2413 Hz as an external tone (with level adjusted to produce the same peak BM velocity), how are the results similar and/or different?

Author: Some preliminary simulations indicate that you indeed get a very similar pattern of suppression when using a low-intensity probe tone instead of looking at a suppressor - but without facilitation. These results indicate that the oscillation to be suppressed/entrained does not need to be a self-sustained limit cycle oscillator. However, a driven, nonlinear and active oscillator shows the same properties when embedded into the system. After discussions at MOH, we will look into ‘Arnold tongues’, but not for a single, but rather a number of coupled oscillators to see if the entrainment frequencies found for a coupled oscillator in a transmission line can be accounted for by purely entrainment. In order to look at facilitation, we will look at the interaction of entrainment (Arnold tongues) and the reorganization of the oscillators into frequency plateaus to see if this explains the regions of facilitation.

Yi-Wen Liu: I am also interested in seeing a discussion on how to distinguish entrainment from suppression. I imagine that entrainment means the SOAE gets “merged” or “sucked in” by the stimulus tone when their frequencies are close by. Has there been a study on the threshold of the stimulus level required to entrain an SOAE component?

Author: There are experimental data from [6], showing SOAE suppression tuning curves, both in the ear canal and perceptually. We are trying to map out the suppression tuning pattern over a broad frequency range and then apply

methods from nonlinear dynamics to see if/how much entrainment is present. Visually, this is rather simple since a suppression will leave the waveform more or less harmonic, while entrainment (if not fully entrained) will have cases where the entrainment flips in and out, leading to very interesting waveforms that are far from harmonic. There are some treatments of single, forced oscillators, but AFAIK not much on coupled ones, leave alone as many as 1000 with such a large gradient of parameters.

Yi-Wen Liu (cont.): Regarding Fig. 2A, when SOAE is suppressed by a frequency corresponding to the nearest antinode, would SOAE completely disappear when the suppressor level goes higher than 60 dB?

Author: The spectral amplitude will be rather small, yes.

Yi-Wen Liu (cont.): Regarding the model itself, I am particularly interested in knowing how changing the feedback delay parameter τ in the equation affects SOAE – it appears that this delay implies that the nonlinearity is not instantaneous. Could you get SOAE while setting τ equals zero?

Author: The feedback delay is a very sensitive parameter. Not matching this properly will lead to instabilities (of the kind diverging response). Since the parameters are fitted purely empirically, I can not provide a stability map or similar. The approach of [7] is a bit more systematic in that respect. I will try to map this numerically and then see which mechanisms to focus on in more detail.

[Post-Talk Q&A]

Glenis Long: I see similar patterns in suppression tuning curves, but the patterns vanish with Aspirin. The SOAE is still present although reduced in level, but there is no enhancement and no tail in the tuning curve.

Author: The small effect of enhancement in the range of 1-2 dB might be hidden in the measurement noise.

Glenis Long (cont.): The SOAEs in the measurements I saw were rather stable, and changes were easily measurable. Further, in the Discussion of the paper that reported these measurements, there is mention of the distinction of entrainment (close to the SOAE frequency) and suppression. This study, however, seems to have combined these two aspects.

Author: The term “suppression” is probably often used as a description of the phenomenon, but the underlying mechanisms might differ. There are differences between the reduced energy observed in the frequency domain for a SOAE going in and out of entrainment versus a constant reduction in the envelope of an essentially harmonic oscillation.

Marcel van der Heijden: Can you elaborate on your comment about absence (or presence) of a traveling wave in lizards?

Author: In this type of model, where standing waves are the underlying mechanism of the simulated SOAEs, a traveling wave is essential. *(Note, the conversation continued for a short while but was not transcribed. Although, the statement from the author about the absence of traveling waves in lizards was questioned.)*

Christopher Bergevin: Regarding your comment about the absence of traveling waves in lizards, there is some evidence for wave propagation in lizard ears, which might differ from the traveling wave in mammals. I can discuss further during the workshop, if interested.

Marcel van der Heijden: Can you elaborate on the suppression mechanism in the model? Specifically, is the energy injection into the traveling wave being suppressed, or is suppression due to a reduction in the reflection or the propagation mechanism? Further, could this be distinguished in the model?

Author: Most likely (and potentially necessary), the mechanism is a reduction in the cumulative gain due to the distributive nature (as mentioned by Marcel van der Heijden) along the propagation of the wave, as proposed by others.