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## Species differences in low-level otoacoustic emissions may be explained by 'hot regions' in the cochlea

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Otoacoustic emissions evoked by low-level transients and single tones appear to excite the same emission mechanism, a concept formulated by Kemp and others not long after his discovery of the phenomenon. Kalluri and Shera have demonstrated in humans a remarkable quantitative match between the spectra of emissions evoked by clicks and tones at near-threshold levels. Our evidence from humans is consistent with this finding. But where the emissions originate inside the cochlea remains uncertain. We have studied emissions evoked by single tones (SFOAE) measured using a variant of the suppression method of Kemp and Chum. In humans, typical moderate-level (50-70 dB SPL) tones most readily suppress SFOAE evoked by lower-level tones when the suppressor is near the frequency of the evoking tone, suggesting that most of the emission originates near the peak of mechanical activity induced by the evoking tone. However, in small laboratory animals, including chinchillas, Mongolian gerbils and mice, emission components originating basal to the peak appear to be relatively larger than in humans. These findings suggest that hair cells contribute components of emissions based on local basilar membrane displacements and exhibit phase cancellation similar to the cochlear microphonic.

## 1 Introduction

Stimulus frequency otoacoustic emissions (SFOAE) are tones emitted by the ear in response to a stimulus tone at the same frequency as the stimulus tone. They are characterized by a delay that generally declines with increasing frequency. This feature immediately suggests that the origin of the emission is near the peak of the traveling wave of the evoking tone. But it has been pointed out that, in a cochlea that exhibit “shift invariance” the delay of the emission should be close to zero [i.e., 1]. The theory of coherent linear reflection filtering (CRF) has been introduced as a way to “break” shift invariance so that the underlying cochlear delays become manifest [1, 2]. In the CRF formulation, contributions to the ear canal SFOAE originate predominantly from the peak region because the conditions for optimal reflection are only met there. Contributions from other regions tend to cancel.

Evidence from our studies in chinchillas has suggested that the delays of SFOAEs predicted by the CRF theory, somewhat less than twice the group delay at the CF place of the probe tone, are significantly larger than those observed experimentally, particularly for probe frequencies below about 4 kHz [3]. Interpreting otoacoustic emissions measured in chinchillas has the advantage that basilar membrane responses to tones have been studied extensively in this species [4].

In this contribution I will present evidence to test the prediction of the CRF theory that contributions to SFOAE from the peak region dominate contributions from other regions of the probe’s excitation function. Our measurements strongly suggest that the region of significant contribution to the ear canal signal is larger than expected, extending substantially in the region basal to the peak. Apparent species differences in SFOAE behavior appear to be resolved by considering in each species the frequency of the probe tone relative to the frequency region that generally produces the largest otoacoustic emissions. This evidence suggests that the cochlea of each mammalian species contains not simply a range of frequencies that produce the strongest emissions, but that the structure of the cochlea and active cochlear mechanics combine to create a “hot region” that contributes disproportionately to the otoacoustic emissions measured in the ear canal.

## 2 Methods

The method used to extract the SFOAE from the stimulus was a variant of the suppression technique introduced by Kemp and Chum [5, see also 1, 3, 6, 7]. Figure 1 depicts a crude representation of a conceptualized distribution in cochlear space of SFOAE generators representing the contributions of individual hair cells. Also shown are postulated profiles of effective suppression by the stimulus tones used to remove the emission so that the stimulus pressure can be estimated.

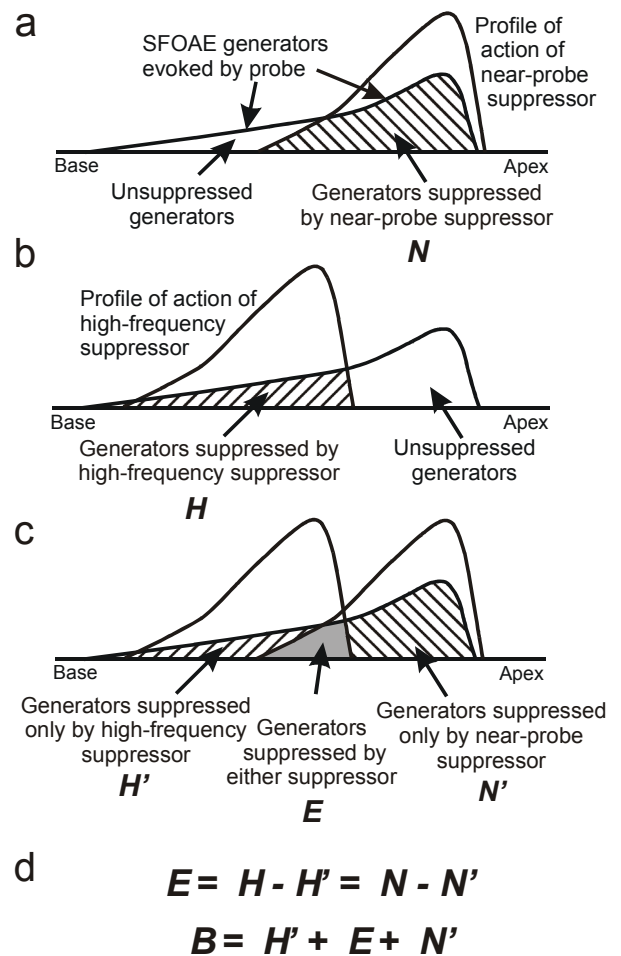


Fig.1 Suppression method. Hypothetical distribution of SFOAE generators and the proposed regional action of suppressors of differing

frequencies. (a) Conventional suppressor near the probe frequency reveals generators in the peak region ( $\mathbf{N}$ ), but may fail to reveal emission components basal to the effective region of suppression. (b) A suppressor higher than the probe frequency demonstrates more basal generators ( $\mathbf{H}$ ). (c) Simultaneous presentation of both suppressors reveals a more accurate measure of the whole emission ( $\mathbf{B}$ ), composed of those generators revealed only by the near-probe suppressor ( $\mathbf{N}'$ ), those revealed only by the high-frequency suppressor ( $\mathbf{H}'$ ) and those revealed by either suppressor ( $\mathbf{E}$ ). (d) Equations used to calculate the SFOAE components  $\mathbf{E}$  and  $\mathbf{B}$ .

Vector subtraction of the response to the probe tone presented alone and the probe's response in the presence of the suppressor yields the estimate of the emission. The emission is estimated accurately only when the suppressor completely eliminates its contribution to the total sound pressure in the ear canal. Kalluri and Shera [7] have formalized the errors due to incomplete suppression.

Figure 1 identifies subpopulations of SFOAE generators that are removed using a suppressor either near the probe frequency or appreciably higher. It is important to note that the region of effective suppression is more restricted than the excitation pattern of the suppressor because the amplitude of its displacement must be large enough at a given cochlear location to drive the nonlinear hair cell transducer into saturation. Depending on the level of the suppressor, even a low-level probe tone may generate components of the emission from cochlear regions not effectively suppressed and thus not demonstrated by the suppression method [8]. The figure legend identifies and defines subcomponents of the emission that are either measured directly or calculated from the measured emissions. The emissions defined as the change in probe response introduced by either the near-probe or above-probe suppressors alone or when presented simultaneously are straightforward.

The subcomponents represented in Fig. 1c require some explanation. Each emission measurement requires a pair of stimulus presentations: one in which the emission component of interest is present and the second in which it has been eliminated with a suppressor. The vector component  $\mathbf{H}'$ , the population of generators that is suppressed by the higher-frequency suppressor, is measured using the probe + near-probe suppressor condition as one of the two stimuli. The near-probe suppressor removes the subpopulation of emission generators  $\mathbf{N}$ , but leaves unsuppressed the subpopulation of interest ( $\mathbf{H}'$ ) and can be considered the "control" condition. The second stimulus presentation includes both suppressors with the probe tone, which removes both  $\mathbf{N}$  and  $\mathbf{H}'$ . Vector subtraction yields  $\mathbf{H}'$ . The same procedure is used to measure component  $\mathbf{N}'$ , substituting the higher-frequency suppressor for the near-probe suppressor in the control condition. The only component that can not be measured directly using a pair of stimulus presentations is the subpopulation of emission generators that are removed by either suppressor tone when paired with the probe-alone condition  $\mathbf{E}$ . This last component is of interest because its presence can be used to evaluate the hypothesis that the two suppressors act via different and independent mechanisms [9].

All animal procedures were approved by the Animal Care and Use Committee of Northwestern University. All

experiments with human subjects were approved by the Institutional Review Board of Northwestern University.

### 3 Results

#### 3.1 SFOAE levels and group delay depend on the suppressor frequency

Extensive recordings of SFOAEs in chinchillas consistently reveal smaller emission levels for 30 dB SPL probe tones lower than about 2.5 kHz when using a 55 dB SPL suppressor near the frequency of the probe than for suppressors displaced slightly more than one octave above the probe frequency. The reverse is true for probe frequencies above 2.5 kHz. The data shown as the dotted curves in Fig 2 were the average ( $N=24$ ) SFOAE level (Fig. 2a) and group delay (Fig. 2b) are reproduced from a previous publication [3]. The individual data and solid average curves were measured using the high frequency suppressor. The slope of the emission phase with frequency, measured as the group delay, is considerably steeper for the near-probe suppressor (Fig. 2b, dotted line) than for the high frequency suppressor (Fig. 2b, solid line).

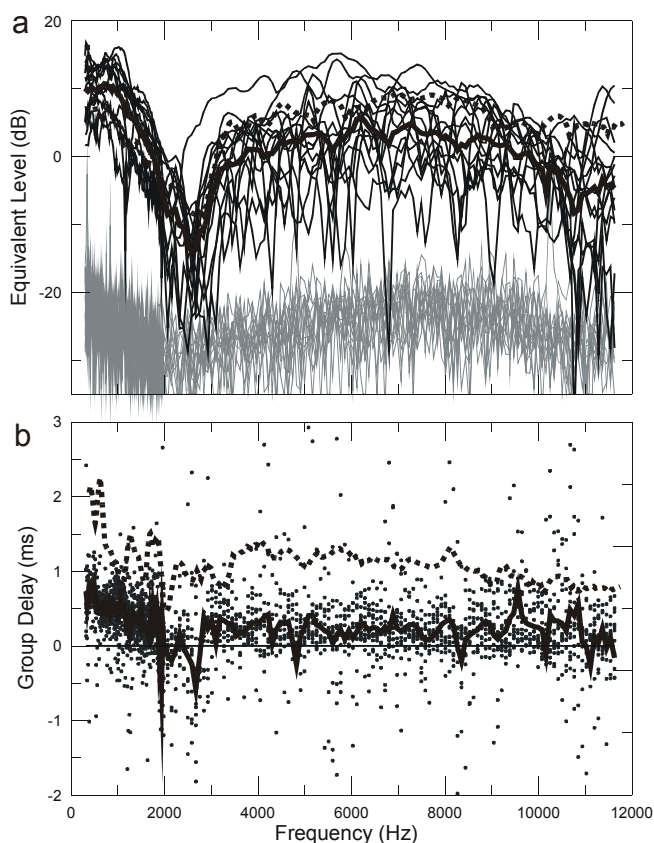


Fig.2 Suppressor frequency affects SFOAE level and delay. SFOAEs measured in chinchillas with a suppressor near the frequency of the probe tone (dotted lines represent averages reported previously [3] or 2.1 times the probe frequency.

The relative levels of SFOAE revealed by the two suppressors reverses near 2.5 kHz.

Under these stimulus conditions it is unlikely that the suppressor tone affects the sensitivity of the cochlea to the probe tone in the region of the peak displacement of the

probe tone. The excitation pattern of the suppressor is sharply curtailed apical to its place in the cochlea and thus does not cause two tone suppression of the probe tone at its place. Despite the expected absence of a significant effect on the peak of probe activity, the suppressor slightly more than an octave above the probe frequency demonstrates a large SFOAE, which in many animals exceeds that demonstrated by a suppressor near the probe frequency. Based on fundamental principles of cochlear mechanics, the unavoidable conclusion is that the primary region of action of the higher-frequency suppressor is near its own place, basal to the place of the probe and where the amplitude of displacement of the probe tone induced vibration is much smaller than at the peak.

This result might be partly explained by the rapid phase shift with distance for the probe response near the peak, compared with the shallower spatial phase slope basal to the peak. This would be analogous to the relative weighting of basal turn hair cells to the cochlear microphonic, compared to those near the peak of a tone with a frequency well below the basal turn CF range [10]. Consistent with this interpretation, the SFOAE demonstrated by the displaced suppressor exhibits a much shallower phase slope than that of a near-probe suppressor (Fig 2b), implying a much shorter delay as would be expected from a more basal origin in the long wave region of the probe tone's excitation function. This relative weighting of basal vs peak generators of the CM is opposite to the prediction of the CRF theory for SFOAE.

### 3.2 Components of SFOAE characterized using the dual suppressor method in three species demonstrate qualitative similarity

For each probe frequency, the probe was presented either alone, or in combination with one or both suppressors. There was a particular frequency where the relative dominance of the SFOAE components changed in each of the three species for which results are presented in Fig. 3. Components likely to originate basal the peak in the probe response (*E* and *H'*) were larger than or comparable to the component presumably localized closer to the peak region (*N'*) for frequencies lower than the break frequency (Fig. 3a-c). Break frequencies were approximately 12 kHz for mice (Fig. 3a), 3.5 kHz for chinchillas (Fig. 3b) and 1 kHz for humans (Fig. 3c). The more basal components in the example from a chinchilla persist to relatively high frequencies above the break frequency compared with the mouse and human data. But this is a variable finding, even in chinchillas, so further study is needed. But whether the contribution from basal generators is small enough to be ignored also varies from animal to animal, even within a species.

The spectral periodicities in emission levels, readily apparent in components *N* and *N'* are related to differing SFOAE delays in each species. The longest SFOAE group delays range from 10-15 ms in humans, about 1.5 kHz in chinchillas and about 0.75 ms in mice. The largest emission levels are generally similar for probe levels of 30 dB SPL in mice and chinchillas and 40 dB SPL in humans.

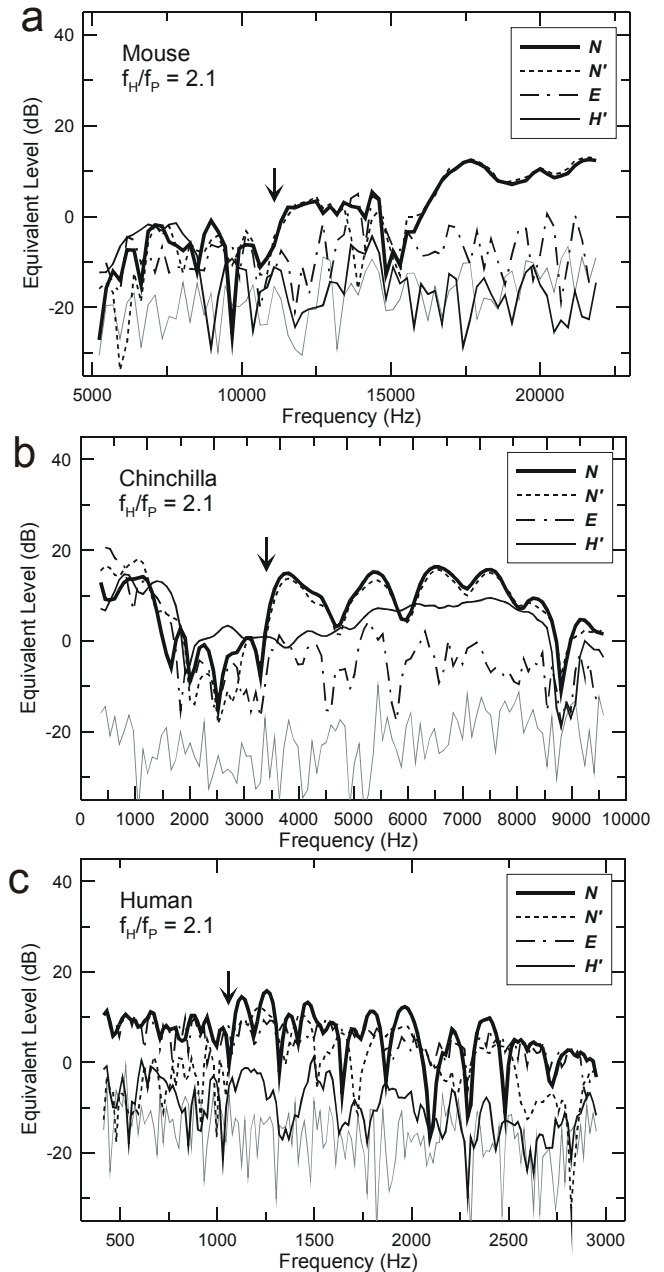


Fig.3 Components of SFOAE in three species. The emissions were measured using probe levels of 30 dB in mice (a) and chinchillas (b) and 40 dB SPL in humans (c). The level of the near-probe suppressor was 55 dB SPL and that of the higher-frequency suppressor was 65 dB SPL. All three species demonstrate a break point (arrows) where lower probe frequencies exhibit relatively large contributions from generators inferred to be basal to the peak and where higher probe frequencies exhibit relatively larger contributions from generators interpreted to originate near the peak.

## 4 Conclusion

In each species studied the relative dominance of the peak region compared to more basal generators shifted near the low-frequency boundary where spontaneous otoacoustic emissions (SOAE) and the largest SFOAEs are routinely measured. Spontaneous otoacoustic emissions are most commonly detected in humans between about 500 Hz and 6 kHz, while those in chinchillas are most common in the range of 5 to 16 kHz [11]. We have recently reported evidence of proto-spontaneous emissions in mice in the

frequency range where the largest SFOAEs are detected in this species, about 15 to 25 kHz. [12]. The fact that the minimum spacing between SOAEs can be predicted using a model that incorporates the SFOAE delay measurements strongly suggests that the two phenomena are products of the same mechanism [13]. Spontaneous emissions are strong evidence of especially high cochlear amplifier gain in which the cochlea becomes unstable. The results presented here suggest that whatever combination of passive structural features and active mechanics of the cochlea give rise to the SOAE phenomenon also enhance basal contributions of SFOAEs when the probe tone is below the CF range of the “hot region”. This is surprising, given that the concept that a tuned resonance on the basilar membrane can become unstable with high gain is generally when the driving stimulus is at the frequency of the resonant peak, not well below it.

These results also suggest that the prediction of the current form of the CRF theory that the peak region of the probe tones response contributes overwhelmingly to SFOAE is not valid, at least for probe tones below the frequency range of the “hot region”. This may well be the explanation of the short latency component of SFOAEs that is the subject of Dr. Shera’s presentation in this session. Regardless, this appears to be fertile ground for some good active cochlear mechanical modeling because, at least for this author, intuition fails nearly completely.

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