Using otoacoustic emissions to explore cochlear tuning and tonotopy in the tiger

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Background

➤ Tiger are a critically endangered species, with their numbers estimated to have decreased from ~100,000 to 3,200 free-ranging individuals over the course of the 20th century. Better understanding of their basic physiology (e.g., auditory capabilities) could lead to more effective conservation strategies.

➤ The length of the basilar membrane (BM) has been correlated to important aspects of cochlear function [West, 1985; Greenwood, 1991]. Members of the cat family possess a wide range of BM lengths and, therefore, offer a compelling opportunity to study comparative cochlear mechanics and audition. Tigers, whose BM extends some 36-39 mm in length [Ulehlova et al. 1984; Walsh et al., 2004] – as long or longer than that of humans – present an especially interesting case.

➤ We focus here on stimulus-frequency otoacoustic emission (SFOAEs), which are sounds evoked from the ear in response to a tone. SFOAE delays are related to cochlear tuning and can be used to predict tuning bandwidths [Shera et al., 2002,2010]. Humans have the longest SFOAE delays of any species so far examined (Fig. 1).

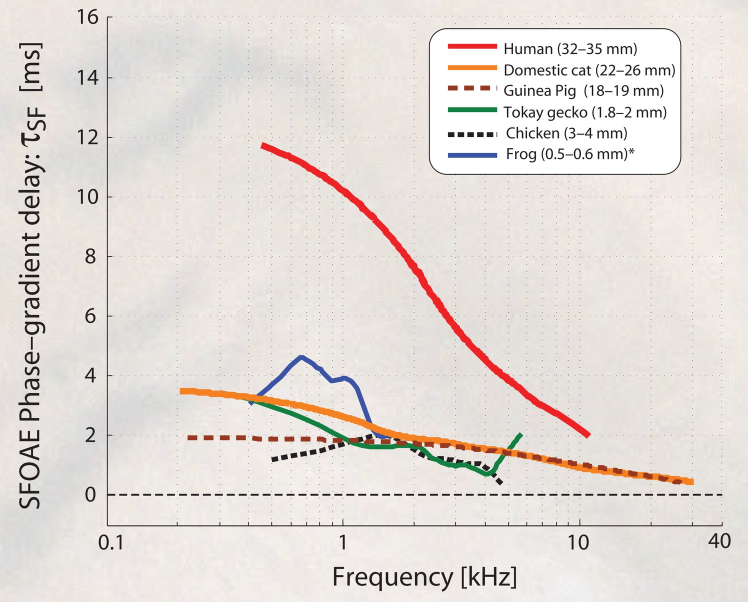


FIGURE 1 - Cross-species comparison of SFOAE phase-gradient delays. All data were measured at 40 dB SPL using similar stimulus paradigm and hardware. Human, cat and guinea pig data are from Shera & Guinan (2003). Chicken, frog & gecko data are from Bergevin et al. (2008). Delays due to ear-canal travel times have been removed. Only data with magnitudes at least 10 dB above the noise floor are included. The legend gives approximate BM lengths for each species. Note that for frog(*) , the length given is of the leopard frog amphibian papilla, which lacks a flexible BM.

➤ Correlations between BM length and SFOAE delay have been noted [Shera et al. 2010]. Because measured BM "signal-front delays" appear similar across mammalian cochleae [Ruggero & Temchin, 2007], including humans, these correlations appear unrelated to BM "travel times".

➤ Because of the broad range of species compared in Fig. 1, it is instructive to compare species in a more phylogenetically-matched context. Comparing responses from domestic cat and tiger provides such an opportunity. SFOAE properties in domestic cats have been well characterized [Guinan,1990; Shera & Guinan, 2003].

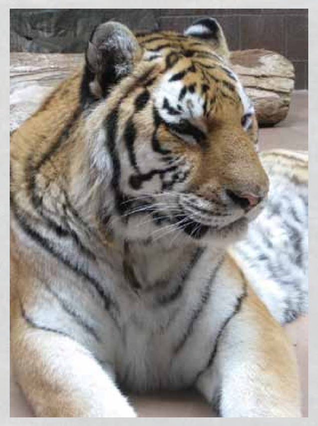
➤ Tigers allow us to further explore the relationship between cochlear morphology (e.g., BM length) and function (e.g., sharpness of tuning, SFOAE delay).

Methods

➤ Measurements were performed at the Henry Doorly Zoo, Omaha Nebraska. Data was collected from 9 ears of 5 different tigers (*Panthera tigris*; two different sub-species, Bengal & Amur, were examined). The tigers were of both sexes and ranged in age from 3–10 years.

➤ Tigers were immobilized by zoo veterinarians using a combination of ketamine (2–4 mg/kg IM) and medetomidine (0.05 mg/kg IM) delivered by blow darts, along with midazolam (0.1 mg/kg IM) as needed. Supplemental doses of ketamine (1 mg/kg IM) were administered as necessary to maintain an immobilized state until intubation. Following induction of anesthesia, the animal was transported to an IAC sound-attenuating chamber at the zoo hospital. After intubation, the inhalation agent sevoflurane mixed with oxygen was used to maintain general anesthesia throughout the measurements. Recording sessions typically lasted 1–3 hours. At the completion of each recording session, animals were returned to the holding cage and monitored until fully recovered from anesthesia.

➤ OAEs were measured simultaneously from both ears using Etymotic ER-10C and ER-10A/ER2 probe systems. Stimuli were generated and recorded digitally using Lynx TWO-A sound cards controlled by custom software.



➤ Stimulus level of Lp = **40 dB SPL** and frequency range of 0.7–13 kHz were used. SFOAE were obtained using a two-tone suppression paradigm (Shera & Guinan, 1999). Suppressor parameters: fs=fp+40 Hz, Ls=Lp+15 dB.

➤ Phase-gradient delays were computed via centered-differences [Shera & Guinan, 2003]. Delays associated with the ear canal length (~0.4 ms, round trip along a 7 cm canal) were subtracted out. Delays are plotted in Fig. 3 both as latencies (τ_{SF}) and as number of stimulus periods (N_{SF}).

➤ Trends (e.g., thick lines in Figs. 3 & 4) were computed using locally-weighted regression (loess). Confidence intervals (95 %) for the trends (e.g., thin lines in Fig. 3) were computed using bootstrap resampling [Shera & Bergevin, in preparation].

Results

➤ Probe calibration in the canal was unexpectedly straight-forward. In contrast to the results of Huang et al. (2000), we found no deep notches indicative of significant canal/tympanic membrane reflection or middle-ear cavity effects. No spontaneous OAEs were observed.

➤ Figure 2 shows the SFOAE magnitudes and phases compiled across tigers. SFOAEs were readily observable in all tigers, though magnitudes were smaller in older individuals (see Fig. 1 caption). Each tiger exhibited a unique/reproducible pattern of magnitude peaks and valleys as the stimulus tone was swept. Magnitudes were smaller by approximately 5-10 dB compared to both human [Bergevin et al., 2008] and domestic cat [Guinan, 1990].

➤ Figure 3 shows the rate of phase accumulation (or the phase-gradient delay). The delays are plotted in two different ways: Latency (τ_{SF}) [ms] and number of stimulus periods (N_{SF}). While the two measures are equivalent, N_{SF} is a dimensionless quantity useful when comparing delays with quantities such as the quality factor (Q) commonly used to report tuning bandwidths.

➤ No significant differences in SFOAE properties were apparent with regard to sex, species, or color (i.e., white vs. orange), though the sample pool is limited. Age-related differences were confined to the magnitudes only: Phase-gradient delays appeared insensitive to age and probe type.

➤ Figure 4 shows a comparison of Nsf trends with those of human and domestic cat. Tiger delays are longer than those of domestic cat over the 4+ octaves examined, but still significantly shorter than human.

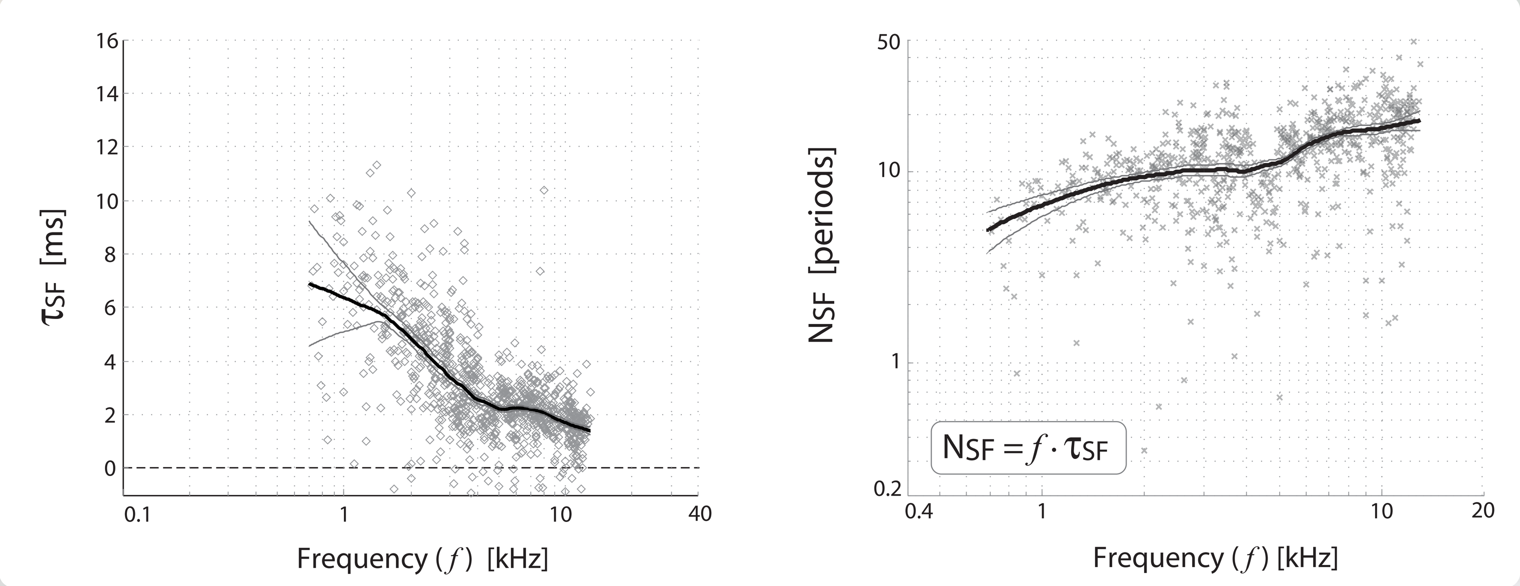


FIGURE 3 - Tiger SFOAE phase-gradient delays computed from the phases shown in Fig. 2 . Only points whose corresponding magnitude was at least 10 dB above the noise floor are shown [Shera & Bergevin, in preparation].

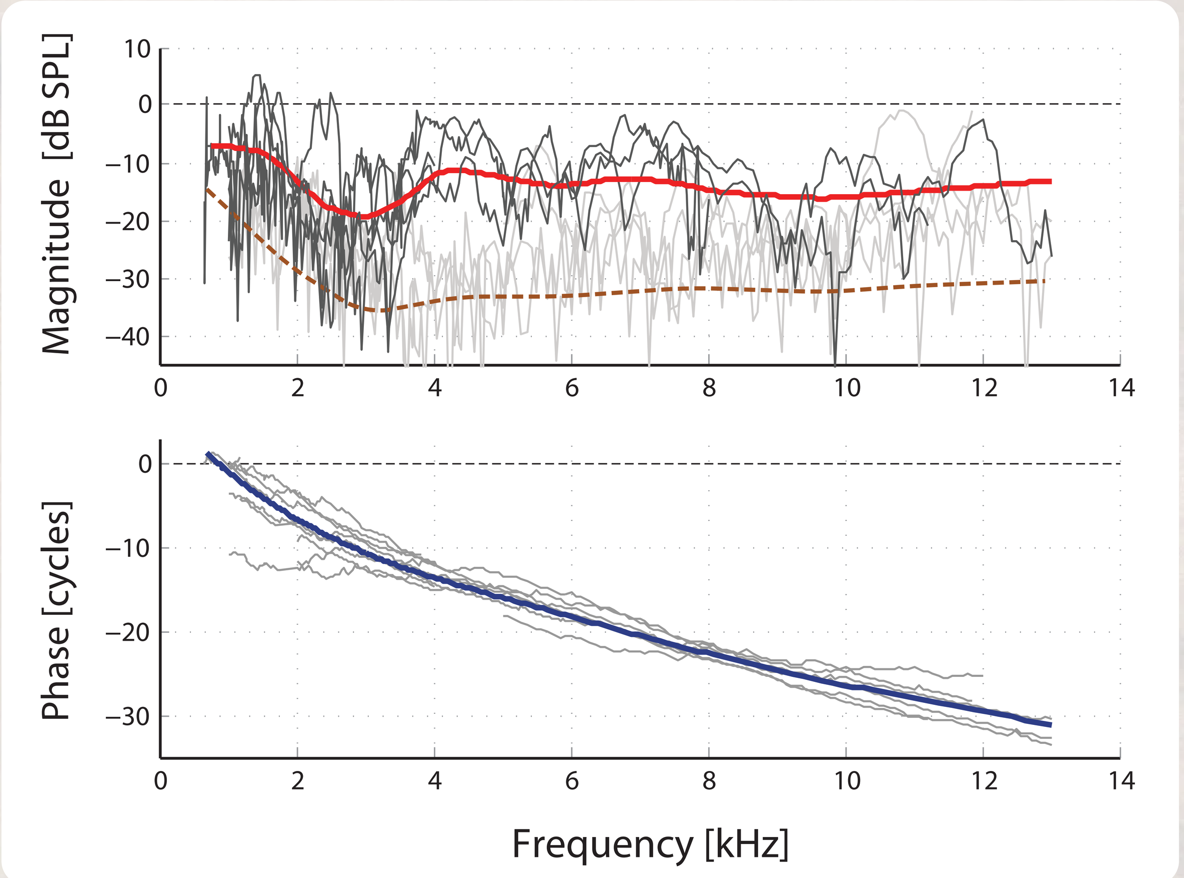


FIGURE 2 - Tiger SFOAEs (magnitude and phase) measured at 40 dB SPL. Data are from 9 ears from 5 different tigers. Dashed brown curve shows the approximate magnitude noise floor. Magnitude data from younger tigers (one 3 year old, two 5 year olds) are indicated by darker shading, older tigers (two 10 year old tigers) are indicated via lighter shading. The solid red curve in the magnitude plot shows the trend for all data that passed a 10 dB SNR threshold, regardless of age. The solid blue curve in the phase indicates the integrated phase-gradient trend. Some phase curves have been offset vertically for clarity.

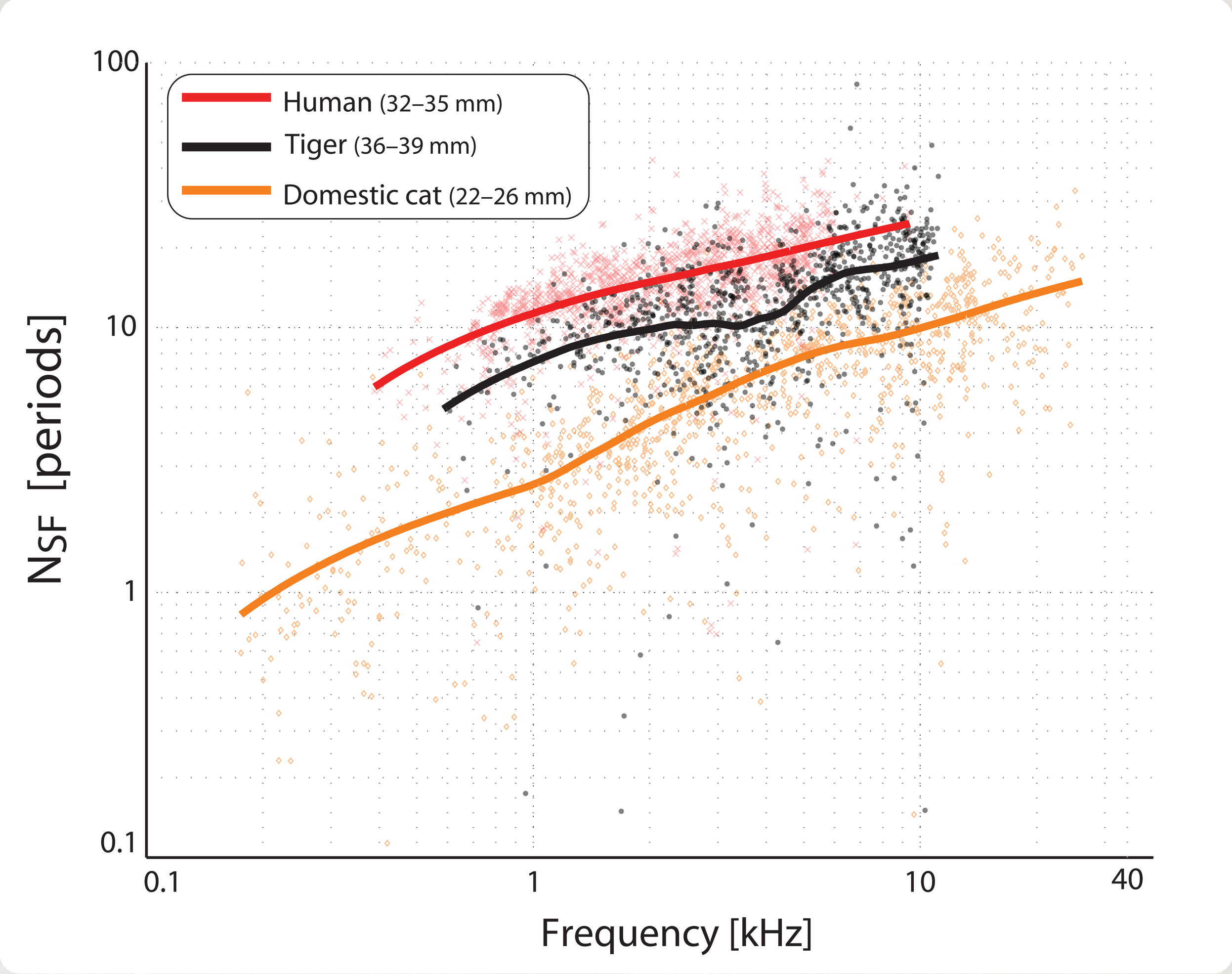


FIGURE 4 - Cross-species comparison of SFOAE phase-gradient delays in stimulus periods (Nsf). Data points and trends are shown for all species. Human and domestic cat data are from Shera & Guinan (2003) and were measured using the same paradigms and stimulus levels (40 dB SPL). The legend gives approximate BM lengths for each species.

Discussion

➤ The generally smaller SFOAE levels in tigers compared to domestic cats may arise, in part, from their significantly larger ear-canal volumes. The lower emission levels in the older individuals (the two 10 year old tigers) suggest mild presbycusis (average captive tiger lifespan is ~15–20 years).

➤ Although tigers have longer BMs, humans have longer SFOAE delays at all frequencies examined (Fig. 4). Thus, BM length by itself cannot account for the variation in SFOAE delay across species (Fig. 1).

➤ Differences in OAE delays between tiger and domestic cat suggest corresponding differences in cochlear tuning/tonotopy:

- In a wide variety of species, longer SFOAE delays correlate with sharper cochlear tuning [Shera et al., 2002, 2010; Bergevin & Shera, 2010].
  ➤ Our data therefore suggest that tigers (with longer SFOAE delays) have sharper tuning than domestic cat.
- In many mammals, the sharpness of cochlear tuning correlates with the slope (mm/octave) of the cochlear tonotopic map, implying that the widths of spatial excitation patterns along the BM are more similar across species than the sharpness of tuning [Shera et al. 2010].
  ➤ Our data therefore suggest that the tiger has a larger tonotopic slope (mm/octave) than domestic cat. Additional support for this suggestion comes from ABR data that indicate a lower high-frequency limit to hearing in tiger [Walsh et al., 2008]

➤ The present results deal only with frequencies $0.6 < f < 13$ kHz. However, further study of tiger auditory sensitivity outside this range (e.g., 0.2-0.5 kHz, >20 kHz) could be useful for developing new conservation strategies. For example, acoustic deterrents at boundaries between human/tiger habitats or along corridors connecting viable 'conservation units' [Wikramanayake et al., 1998] designed to preserve genetic diversity.

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Acknowledgements

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