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

Christopher Bergevin1
Edward J. Walsh2
JoAnn McGeer3
Christopher A. Shera3

1 Columbia University
2 Boys Town National Research Hospital
3 Harvard Medical School, Eaton-Peabody Lab

Background

Tigers 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 mechanics and audition. Tigers, whose BM extends some 36-39 mm in length [Uehlevold 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 that arise from the ear in response to a tone. SFOAEs 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).

Correlations between BM length and SFOAE delay have been noted [Shera et al., 2010]. Because measured BM “signal-front delays” appear similar across mammalian cochlea [Ruggiero & 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 cats 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 5 different tigers (Panthera tigris) with different BMs [e.g., Rasmussen & Amar, 2004], and a range of ages from 3-10 years.

Tigers were immobilized by exo-veterinarians using a combination of ketamine (2-4 mg/kg IV) and medetomidine (0.05 mg/kg IV) delivered by blow dart, along with midazolam (0.1 mg/kg IV). BM measurements were obtained immediately after intubation. Anesthesia was maintained by an intravenous infusion of ketamine and midazolam given at the rate of 30mg/h. A 10 mm catheter was inserted into the jugular vein to administer bolus doses of ketamine and midazolam. Anesthesia was induced with Ketamine (10 mg/kg IV) and Xylazine (0.5 mg/kg IV). One hour after induction, the animal was transported to the SFOAE lab at the university.

A comparison of the hearing sensitivities of the tiger to those of humans and domestic cats was conducted using pure-tone audiometry. The audiograms were obtained with a DT-2 audiometer using 10 dB steps from 125 Hz to 10 kHz.

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 confounded to the magnitudes only: Phase-gradient delays appeared insensitive to age and probe type.

Results

Probe calibration in the canal was unexpectedly straightforward. 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 extracted across tigers. SFOAEs were readily observable in all tigers, though magnitudes were smaller in older individuals (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 (τsp) [ms] and number of stimulus periods (NSF). While the two measures are equivalent, NSF is a dimensionless quantity useful when comparing delays with quantities such as the quality factor (Q) commonly used to report tuning bandwidths.

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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.

Discussion

The generally smaller SFOAE levels in tigers compared to domestic cats may arise, in part, from their significantly larger ear-channel 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.

References

[West, 1985] & Greenwood, 1991. Anatomical differences in the basilar membrane of the domestic cat and guinea pig ear from Shera & Guinan (1985). Chicken, frog and guinea pig data from Berger (1987). Deafness due to central nervous system function performed by Lepley et al. (2007). Detailed data on SFOAEs following these studies have been included. The legend gives approximate BM lengths for each species. Notice the absence of curves representing the frequency range in the second amplification prototype, which is too high.

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Figure 2 - Tiger SFOAEs (magnitude) measured at 40 dB SPL. Data are from 9 ears from 5 different tigers. Dashed brown curves show 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 line in the magnitude plot represents the 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 3 - Tiger SFOAE phase gradient delays computed from the phases shown in Fig. 2. Only points whose corresponding magnitude data at least 10 dB above the noise floor are shown [Shera & Bergevin, in preparation].

Figure 4 - Cross-species comparison of SFOAE phase gradient delays. All data were measured at 40 dB SPL, using similar stimulus paradigm and back-up custom cards controlled by software. Experiments were performed in SFOAE delay magnitude and phase. The legend gives approximate BM lengths for each species. Notice the absence of curves representing the frequency range in the second amplification prototype, which is too high.

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