

Stimulus-Frequency Otoacoustic Emissions As a Probe of Cochlear Tuning in the Common Marmoset

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Background

Given their vocal nature, marmosets have increasingly become a popular model for auditory neuroscience [e.g., Wang 2000, 2007]. As such, there is a desire for more in-depth knowledge about their peripheral function (e.g., sharpness of cochlear tuning).

Basilar membrane length is believed important for many aspects of cochlear function [e.g., West, 1985; Greenwood, 1991]. The marmoset BM is relatively short, only ~15–17 mm [Johnson & Wang, 2009]. Being phylogenetically closer to human and rhesus monkeys than other common laboratory mammals (e.g., cat, chinchilla, gerbil, guinea pig), marmosets present an opportunity for comparative study of morphological and functional differences within primates (bottom of Fig. 1).

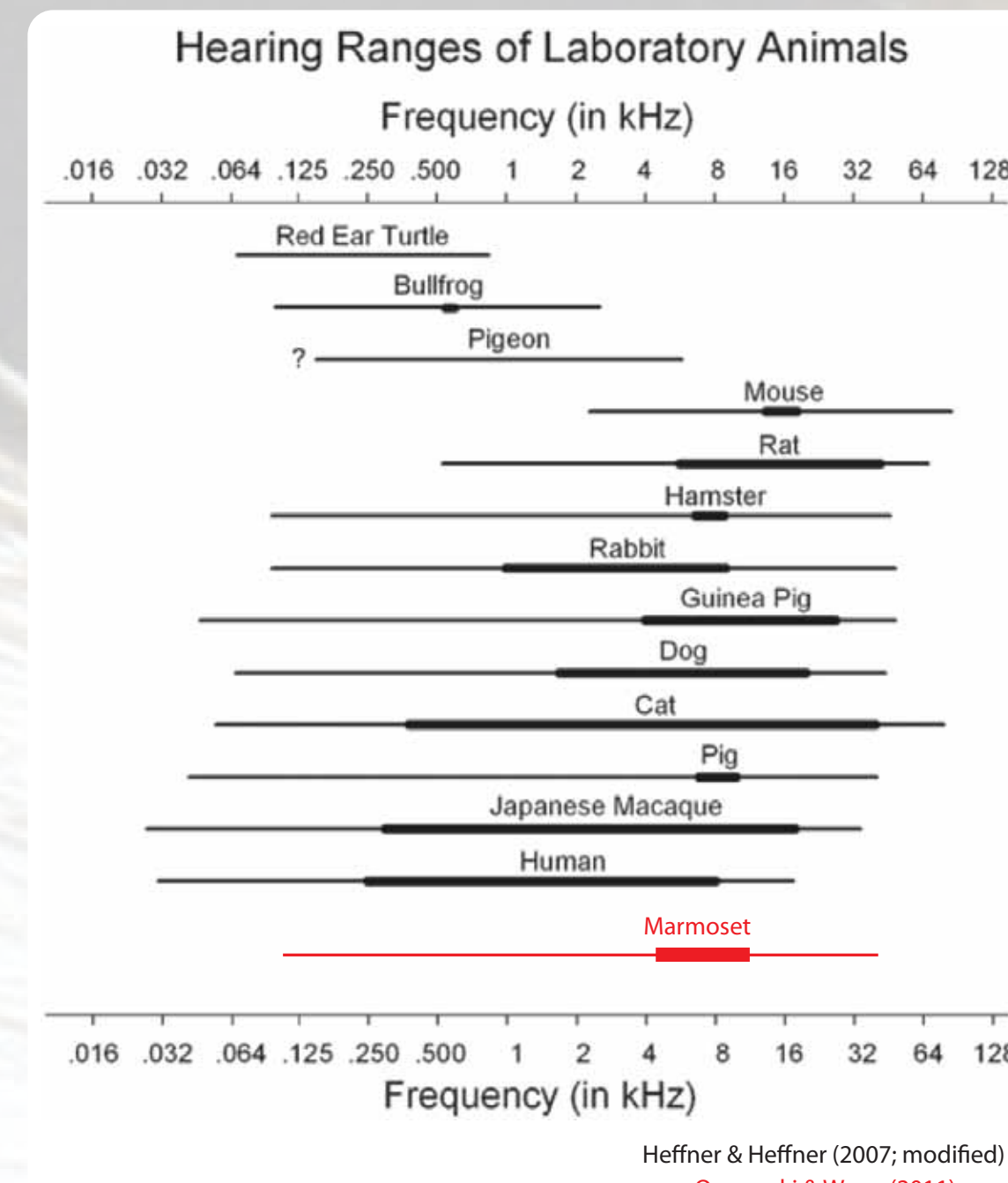


FIGURE 1 - Comparison of approximate audiometric ranges across species, as compiled by Heffner & Heffner (2007). Thin lines indicate the range of sensitivity at or below 60 dB SPL, while the thick line indicates the range at or below 10 dB SPL. The figure is chiefly derived from Heffner & Heffner (2007), modified to include the marmoset [Osmanski & Wang, 2011].

Marmosets use a wide repertoire to communicate (e.g., to warn others) and much of their vocal range is shifted toward higher frequencies, ~5–15 kHz (Fig. 2). The most sensitive region of their audiometric range (Fig. 1) appears to coincide with these frequencies, suggesting a peripheral bias favoring species-specific communication.

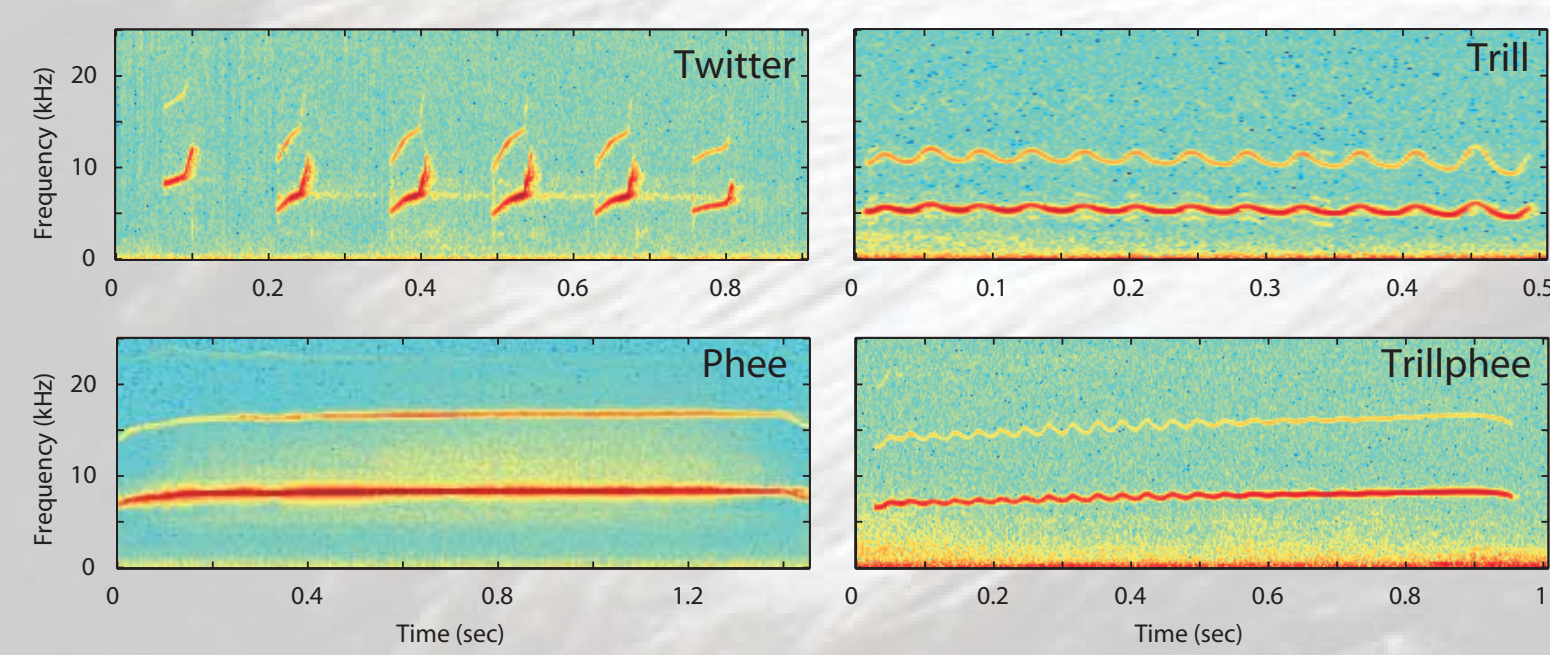


FIGURE 2 - Example spectrograms of marmoset vocalizations. Note that energy appears primarily confined to 5–15 kHz, chiefly 5–10 kHz. The figure is adapted from DiMattina & Wang (2006).

The present study focuses on stimulus-frequency otoacoustic emissions (SFOAEs), which are sounds emitted from the ear in response to a tone. SFOAE delays have been hypothesized to reflect the sharpness of cochlear tuning, as suggested by filter theory [Shera et al. 2002, 2010], and are larger in primates (humans & rhesus monkeys) than in any other species so far examined [Joris et al., submitted].

Given their short BM length, close phylogenetic relationship with other primates, & complex vocal nature, marmosets present an opportunity to explore how morphological differences (e.g., BM length) affect cochlear function. Furthermore, their study can help shed light on how primate peripheral auditory function differs from that of other mammals commonly used in the laboratory (e.g., cat, guinea pig, gerbil & chinchilla).

Methods

Experiments were performed at the Johns Hopkins University. Data were collected from 14 ears of 10 different marmosets (*Callithrix jacchus*). The monkeys were of both sexes and ranged in age from 3–10 years.

Monkeys were immobilized by an injectable anesthetic. Following induction of anesthesia, the animal was placed in a sound-attenuating chamber. Recording sessions typically lasted 0.5–1.5 hours. At the completion of each recording session, animals were 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 $L_p = 40$ 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: $f_s = f_p + 40$ Hz, $L_s = L_p + 15$ dB.

Phase-gradient delays were computed via centered-differences [Shera & Guinan, 2003]. Delays associated with the ear canal length (~0.05 ms, round trip along a 0.8 cm canal) were subtracted out. Delays are plotted in Fig. 4 both as latencies (τ_{SF}) and as number of stimulus periods (N_{SF}).

Trends (e.g., thick lines in Figs. 4 & 5) were computed using locally-weighted regression (loess). Confidence intervals (95 %) for the trends (e.g., thin lines in Fig. 4) were computed using bootstrap resampling [Shera & Bergevin, in preparation].



Results

No spontaneous OAEs were observed, consistent with the findings of Valero et al. (2008).

Figure 3 shows the SFOAE magnitude and phases compiled across monkeys. SFOAEs were readily observable in all animals, each exhibiting a unique/reproducible pattern of magnitude peaks and valleys as the stimulus tone was swept. Magnitudes were smaller by approximately 5–10 dB over the range 1–6 kHz compared to human [Bergevin et al., 2008], domestic cat [Guinan, 1990], and rhesus monkey [Joris et al., submitted].

Figure 4 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}). Although the two measures are equivalent, the latter is a dimensionless quantity useful when comparing delays with quantities such as the quality factor (Q) commonly used to report tuning bandwidths.

Some differences in both magnitude (5–10 dB) and phase-gradient delay (0–0.5 ms) were apparent between probe types (ER-10C vs. 10A) and with age. However, these factors were not systematically examined in the present study, nor independent of one another in the present data set. Thus, the trends shown in Fig. 4 are representative of all monkeys and probes. As such, the present data set cannot address sex differences previously reported for marmoset distortion-product OAEs [Valero et al., 2008].

Figure 5 shows a comparison of N_{SF} trends with those of human, domestic cat, and rhesus monkey. Marmoset delays are longer than those of domestic cat over 3+ octaves from 0.8–8 kHz, but similar above 8 kHz. Marmoset delays are significantly shorter than human and rhesus at all frequencies tested (Fig. 5).

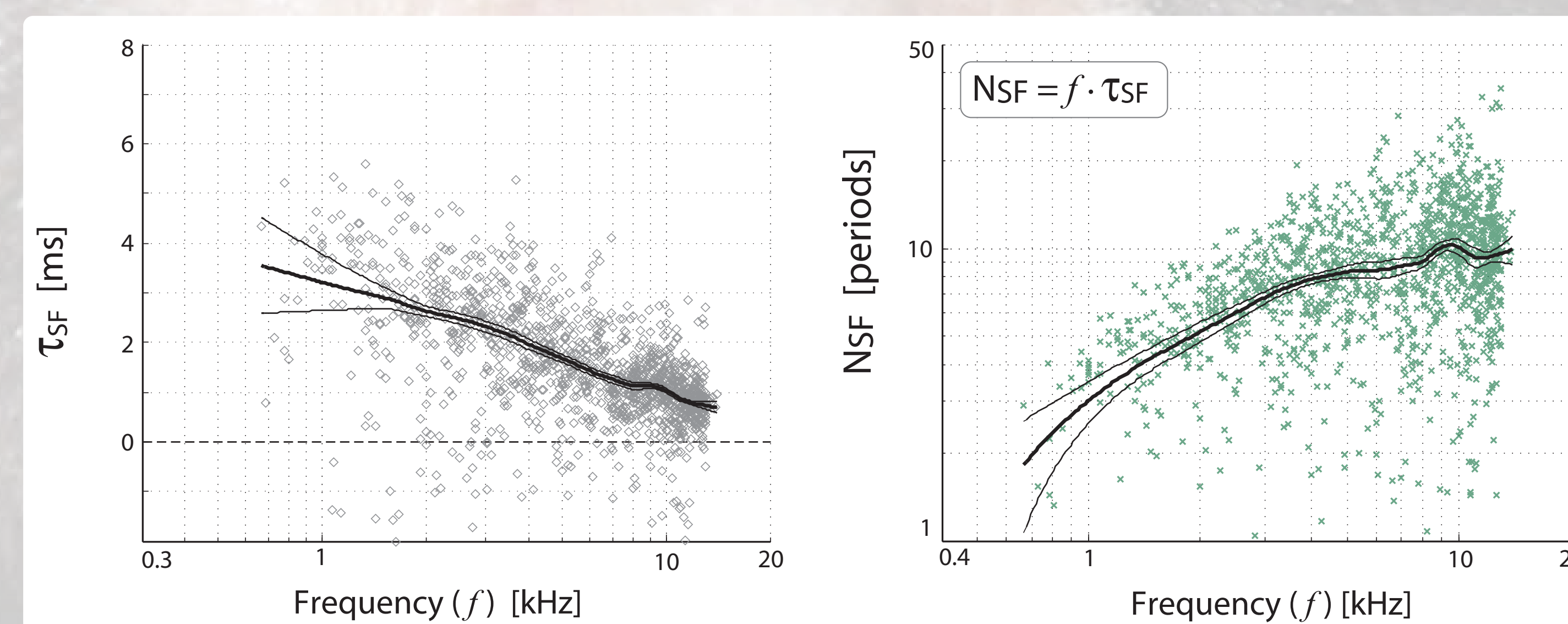


FIGURE 4 - Marmoset SFOAE phase-gradient delays, computed from the phase curves shown in Fig. 3 (i.e., the delay is the slope of the phase vs. frequency curve). Only points whose corresponding magnitude was at least 10 dB above the noise floor are shown [Shera & Bergevin, in preparation].

Discussion

SFOAE delays in marmoset are comparable to or longer than those in domestic cat (Fig. 5). Thus animals with shorter SFOAE delays.

Correlations between SFOAE delay and cochlear tuning established in other animals [Shera et al. 2002, 2010] suggest that marmoset cochlear tuning is comparable to or slightly sharper than in domestic cats.

Correlations between the sharpness of cochlear tuning and the slope (mm/octave) of the cochlear map seen in other mammals [Shera et al., 2010] suggest that the slope of the marmoset map is similar to that of domestic cat. This is consistent with the fact that both the BM length and the frequency range of hearing in marmoset are smaller than in domestic cat (Fig. 1).

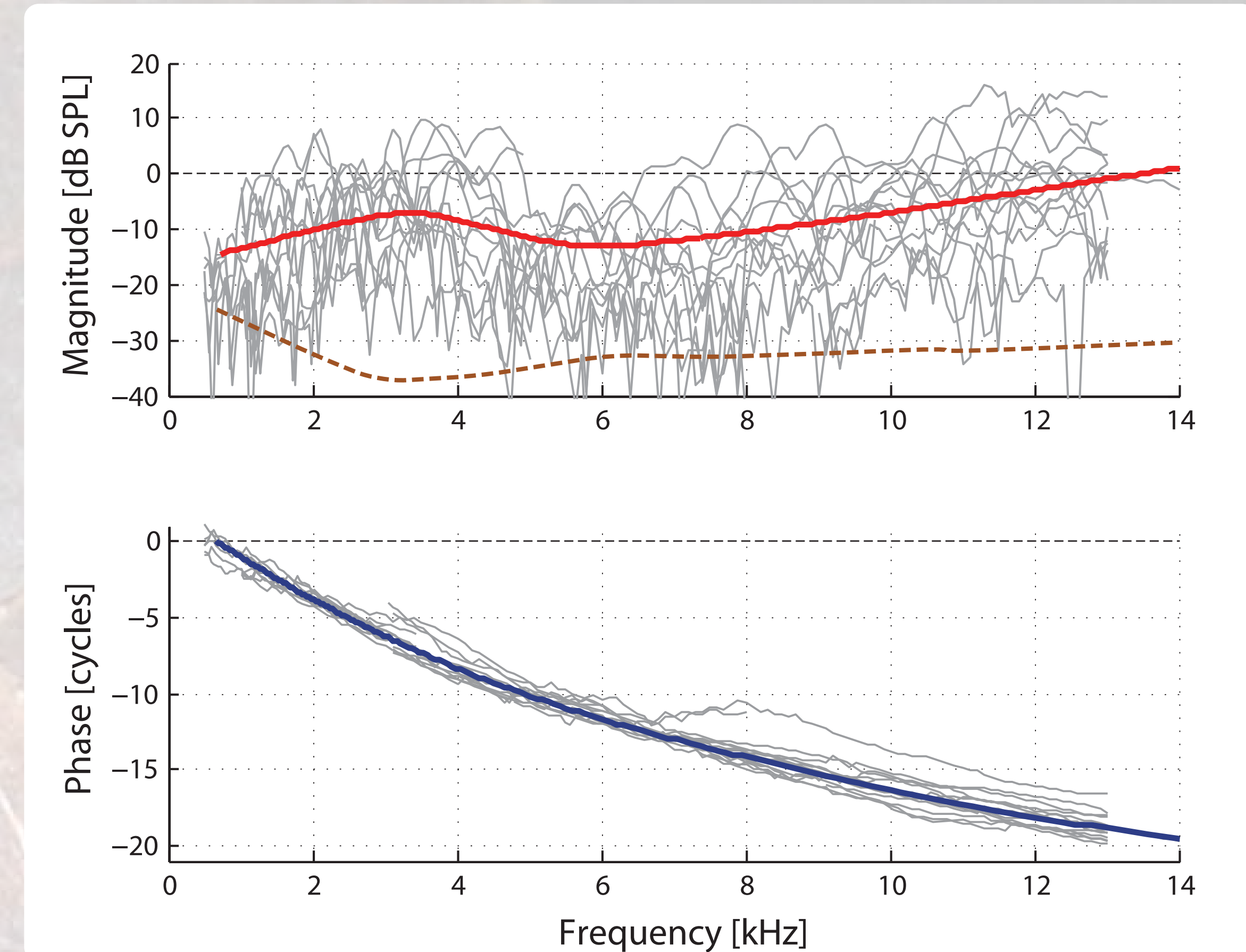


FIGURE 3 - Marmoset SFOAEs (magnitude and phase) measured at 40 dB SPL. Data are from 14 ears from 10 different monkeys. Each grey curve represents a unique ear. Dashed brown curve shows the approximate noise floor. The solid red curve in the magnitude plot shows the trend for all data that passed a 10 dB SNR threshold, regardless of age. The solid blue curve in the phase indicates the integrated phase-gradient trend (from Fig. 4). Some phase curves have been offset vertically for clarity.

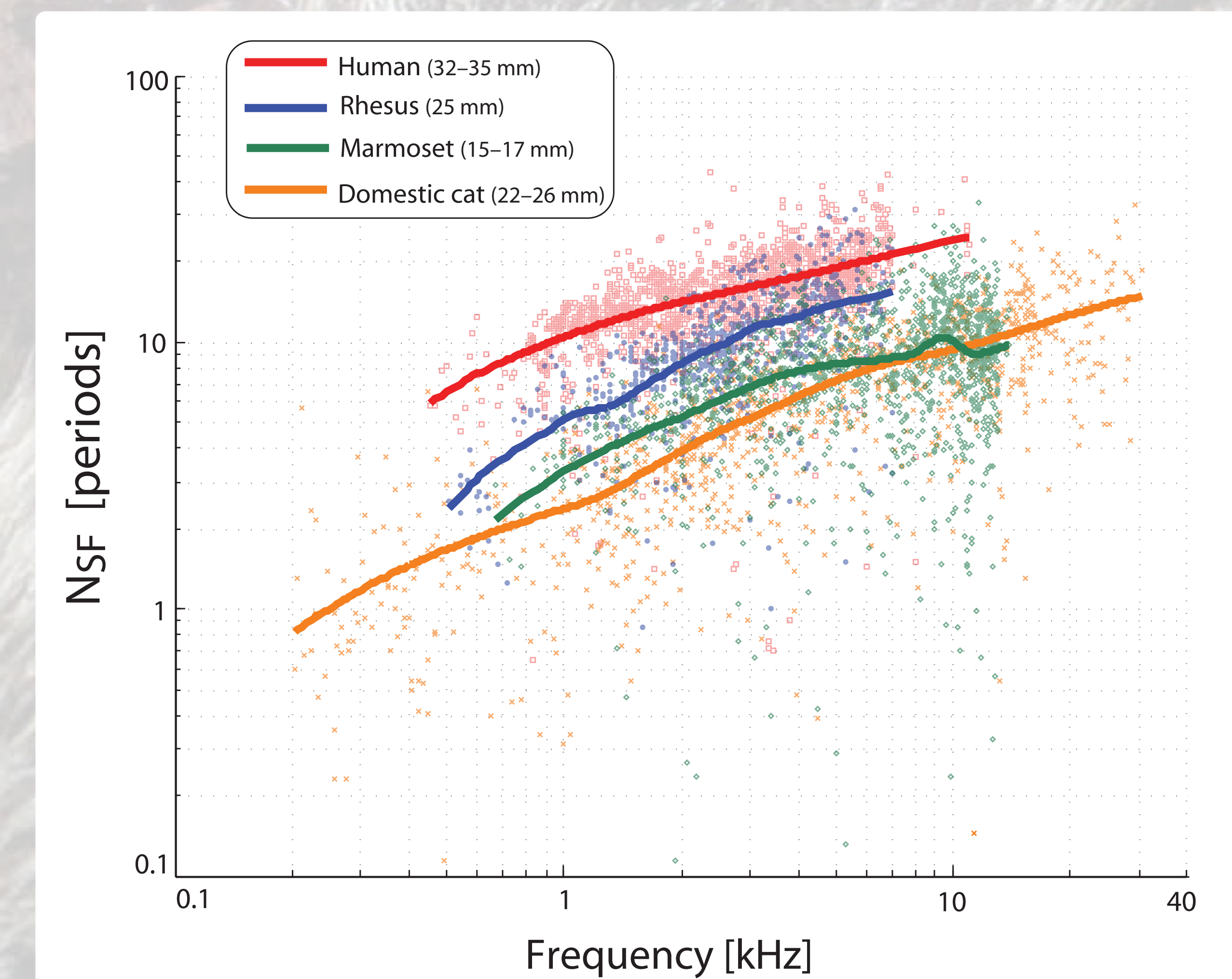


FIGURE 5 - Cross-species comparison of SFOAE phase-gradient delays in stimulus periods (N_{SF}). Data points and trends are shown for all species. Confidence intervals (e.g., Fig. 4) excluded for clarity. Human and domestic cat data are from Shera & Guinan (2003) while the rhesus data are from Joris et al. (submitted), and were measured using the same paradigms and stimulus levels (40 dB SPL). The legend gives approximate BM lengths for each species.

References

- Bergevin, C., Freeman, D.M., Saunders, J.C. & Shera, C.A. Otoacoustic emissions in humans, birds, lizards, and frogs: evidence for multiple generation mechanisms. *J. Comp. Physiol. A*. 194:665-683 (2008)
- Greenwood, D.D. A cochlear frequency-position function for several species—29 years later. *J. Acoust. Soc. Am.* 87:2592-2605 (1990)
- Guinan, J.J. Changes in stimulus frequency otoacoustic emissions produced by two-tone suppression and efferent stimulation in cats. In *Mechanics and Biophysics of Hearing*, edited by P. Dallos et al. (Springer-Verlag, 1990)
- Heffner, H.E. & Heffner, R.S. Hearing Ranges of Laboratory Animals. *J. Am. Assoc. for Lab. Animal Sci.* 46:20-22 (2007)
- Johnson, L. & Wang, X. Characterization of the Marmoset Monkey Temporal Bone: A Cochlear Implant Feasibility Study. ARO 23rd Mid-Winter Meeting Abstracts (2009)
- Joris, P.X., Bergevin, C., Kalluri, R., McLaughlin, M., Michelet, P., van der Heijden, M. & Shera, C.A. Frequency selectivity in Old World monkeys corroborates sharp cochlear tuning in humans [submitted]
- Osmanski, M. & Wang, X. Measurement of absolute auditory thresholds in the common marmoset (*Callithrix jacchus*). *Hear. Res.* [in press] (2011)
- Shera, C.A. & Guinan, J.J. Evoked otoacoustic emissions arise by two fundamentally different mechanisms: A taxonomy for mammalian OAEs. *J. Acoust. Soc. Am.* 105:782-798 (1999)
- Shera, C.A. & Guinan, J.J. Stimulus-frequency-emission group delay: A test of coherent reflection filtering and a window on cochlear tuning. *J. Acoust. Soc. Am.* 113:2762-2772 (2003)
- Shera, C.A., Guinan, J.J. & Oxenham, A.J. Revised estimates of human cochlear tuning from otoacoustic and behavioral measurements. *Proc. Natl. Acad. Sci. USA* 99:3318-3323 (2002)
- Shera, C.A., Guinan, J.J. & Oxenham, A.J. Otoacoustic estimation of cochlear tuning: validation in the chinchilla. *J. Assoc. Res. Otolaryng.* 11:343-365 (2010)
- Shera, C.A. & Bergevin, C. Estimating trends in reflection-source otoacoustic emission phase-gradient delay data. [in preparation]
- Valero, M.D., Pasanen, E.G., McFadden, D. & Ratnam, R. Distortion-product otoacoustic emissions in the common marmoset (*Callithrix jacchus*): Parameter optimization. *Hear. Res.* 243:57-68 (2008)
- Wang, X. On cortical coding of vocal communication sounds in primates. *Proc. Natl. Acad. Sci. USA* 97:11843-11849 (2000)
- Wang, X. Neural coding strategies in auditory cortex. *Hear. Res.* 229:81-93 (2007)
- West, C.D. The relationship of the spiral turns of the cochlea and the length of the basilar membrane to the range of audible frequencies in ground dwelling mammals. *J. Acoust. Soc. Am.* 77:1091-1101 (1985)

Acknowledgements

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