ABSTRACT: Models of otoacoustic emission (OAE) generation mechanisms often attribute important features of OAEs to waves traveling along the cochlear partition. Since the lizard basilar papilla manifests no obvious analog of the mammalian traveling wave, detailed characterization of lizard OAEs offers an important opportunity to test and extend our knowledge of emission mechanisms. We report otoacoustic measurements (DPOAEs and SFOAEs) in the ears of adult leopard geckos (Eublepharis macularius) as well as humans. We compare and contrast the properties of gecko and human OAEs and discuss their implications for mechanisms of OAE generation.

A comparative study of evoked otoacoustic emissions in humans and geckos

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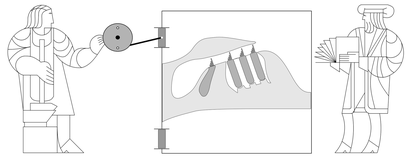


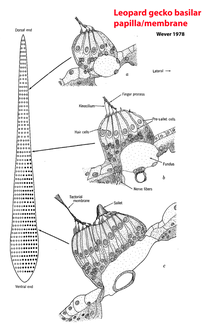
MIT Micromechanics Group

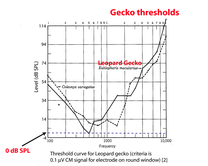
GECKO EARS

ANATOMY - There are significant differences between the inner ear anatomy of mammals and non-mammals. This diversity may have important implications for the mechanisms of frequency selectivity, signal amplification and OAE generation.

PHYSIOLOGICAL CONSEQUENCES - In mammals, current theories indicate that basilar membrane (BM) traveling waves may play an important role in OAE generation [1]. However, in the lizard ear, BM traveling waves are *presumably* absent. Are lizard OAEs therefore fundamentally different from mammalian OAEs?

PURPOSE - Our goal here is to make the first systematic comparison of human and lizard evoked OAEs. The results will serve to test theories of cochlear mechanics and OAE generation as well as better understand the underlying physiology.





Non-Mammalian Inner Ear (Leopard gecko)

- Middle ear plays similar role as in mammal (freq. filter and gain)
- Basilar papilla (BP) sits atop basilar membrane (BM) whose width and thickness vary significantly along its length of approximately 1.2-1.4 mm (in contrast to the Alligator lizard) [2]
- Hair cells (HCs) covered by a complex overlying tectorium (has both a continuous TM as well as discrete *sallets* which couple small groups of HCs in a single row radially), are also *efferently* innervated
- ANF data in similar species indicates tonotopic organization along the length of the BP as well as sharp tuning comparable to that of mammals[3,4]
- Cochlear microphonic measurements indicate leopard geckos have comparable thresholds to that of humans (~0 dB SPL) in their most sensitive frequency range of 500-800 Hz [2]
- A previous study has found spontaneous OAEs in this species, which had a wide spectral width relative to mammals [5]

UNKNOWN - Basilar membrane mechanical response and tonotopic mechanism(s); *presumably* BM traveling waves and somatic motility are absent [6]

MEASURING OAEs

- Two different types of emissions were examined:

1. *Stimulus Frequency Emissions* (SFOAEs) - when ear is stimulated with a **single tone** (f_p), these OAEs arise at that *probe* frequency
2. *Distortion Product Emissions* (DPOAEs) - occur when ear is stimulated with **two different tones** (f_1 and f_2), emissions arise at harmonic and intermodulation frequencies ($3f_1$, $2f_2 - f_1$, etc.)

- In addition to humans, we used adult **leopard geckos** (*Eublepharus macularius*) for the non-mammalian model. Animals (N=7) were lightly anesthetized (Nembutal, 20-25 mg/kg i.p.) for experiments, but all recovered completely and were subsequently used for multiple sessions. All experimental protocols were subject to the MIT DCM/CAC and COUHES approval.
- An Etymotic ER-10C probe containing a microphone and two earphones was tightly coupled to the outer ear and calibrated using flat-spectrum noise. Measurement system intermodulation distortion was small, however the harmonic distortion was not well characterized.
- A sample rate of 44.1 Hz was used with an encoding bit-depth of 24 bits. The system was capable of presenting/measuring frequencies down to 200 Hz. System I/O delays were subtracted out.
- A **suppression paradigm** is used in order to measure SFOAEs which consists of two intervals: the probe tone alone and probe plus a suppressor tone (f_s), where the emission is presumably reduced significantly. Subtraction in the complex plane reveals the emission [1]. This method takes advantage of ***cochlear non-linearity*** to measure SFOAEs.

OAE Parameters Used (both humans and geckos)

SFOAEs: $L_p = 40$ dB SPL, $L_s = 55$ dB SPL, $f_s = f_p + 40$ Hz

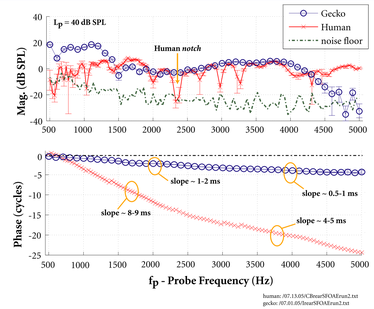
DPOAEs: $L_1 = L_2 = 65$ dB SPL, f_2/f_1 = const. (fixed ratio)

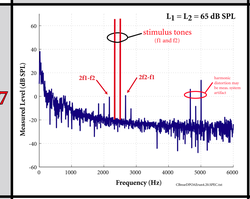
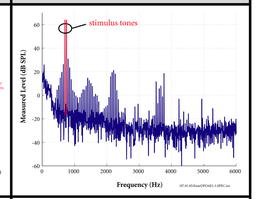
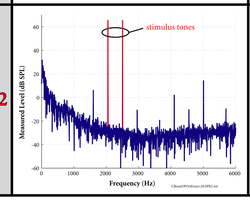
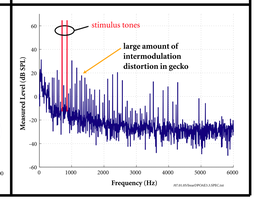
All error bars show standard error

SFOAEs & DPOAEs

1 - SFOAEs

- Both human and gecko ears show significant SFOAEs .
- The phase response shows a delay present in both ears (***phase gradient delay* is the slope of the phase**). It is significantly longer in the human ear [at 3-4 kHz, the delay is approximately 4-5 ms in the human and 0.5-1 ms in the gecko]. Also note that the delay varies with probe frequency in both ears (longer for lower f_p and shorter for higher f_p).
- Significant emissions were measured in the gecko between 0.2-4.5 kHz, quickly falling off beyond this upper limit (this correlates to upper bound of the gecko's hearing range).
- In both species, magnitude notches are manifest at certain frequencies which also usually show a corresponding phase jump. The notches are much more numerous in the human ear.



f2/f1 ratio	HUMAN	GECKO
1.07		
1.22		

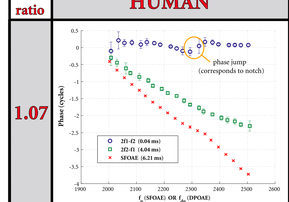
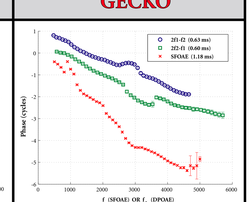
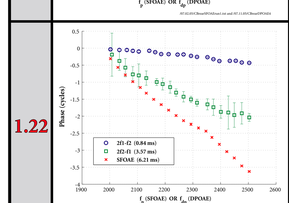
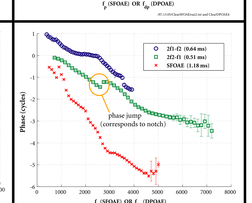
2 - DPOAEs (magnitude)

- Plots show comparison between humans and geckos for two different primary ratios
- Primaries illustrated here are centered about the frequencies of greatest sensitivity for each species
- While both ears manifest non-linear behavior, there is clearly more distortion being *emitted* by the gecko ear [DPs up to the 15'th order are clearly visible]
- Similarly to the SFOAEs, gecko DPOAEs disappear for distortion product frequencies (f_{dp}) above 4.5-5 kHz
- Notches/phase jumps were also seen in the DPOAEs as the primaries were swept (some as deep as 50 dB for the gecko!). The frequencies of DPOAE and SFOAE notches do not appear to be strongly correlated.

3 - PHASE GRADIENT DELAY (SFOAE and DPOAE phase)

- We focus our analysis here on $2f_1$-f_2 (lower side-band) and $2f_2$-f_1 (upper).
- Consistent with previous reports [7], the $2f_1$-f_2 phase in the human ear varies little with frequency, while both $2f_2$-f_1 and SFOAE phase rotate rapidly.
- The gecko ear also manifests significant phase gradients, although they are however much shorter than observed in the human ear [NOTE: the relative slopes depend upon the variable on the x-axis, here we plot vs f_{dp} so that slopes are proportional to the phase gradient delay]
- Both DPOAE phase gradients in the gecko ear are similar to that of the SFOAE, in contrast to the mammalian ear (and similar to the frog [8]). Some geckos showed a slightly shorter delay for $2f_1$-f_2 relative to $2f_2$-f_1. In both species, the SFOAE delay is longer than that of either DP.

NOTE wider range of frequencies in plots for geckos

f2/f1 ratio	HUMAN	GECKO
1.07		
1.22		

COMPARISON

OAE type	HUMAN	GECKO
SFOAEs	- magnitudes typically 0-10 dB SPL over a wide frequency range - magnitude punctuated by numerous deep notches with corresponding phase jumps - large phase gradient delays (~ 4-9 ms) which varied with probe frequency	- were similar to humans, if not larger (~0-20 dB SPL) over *entire* range of hearing (0.2-5 kHz) with fairly constant amplitude - occasional magnitude notches/phase jumps - shorter phase gradient delays (~ 0.5-2 ms) which also varied with frequency
DPOAEs	- modest magnitudes (~0 dB SPL) - few measurable higher order DPs - significant difference in phase gradient for $2f_1$-f_2 (*flat*), $2f_2$-f_1 (*steep*) and SFOAE (*steeper*)	- large magnitudes (~20 dB SPL) - many measurable higher order DPs - upper and lower-sideband DPOAEs have similar phase gradient delays

CAVEATS & QUESTIONS

SOAEs - We also examined spontaneous otoacoustic emissions, which had been previously reported in this gecko species [5]. While spontaneous activity was detected, it was for the most part inconsistent with the previous report (we saw fewer emissions, which were smaller in magnitude and had different spectral properties).

Plotting DP Data - There are many different ways to plot DPOAE data. We chose to plot vs. f_{dp} here for consistency with previous reports. However when plotting vs. f_1 or f_2 (which puts greater emphasis on the stimulus tones used to evoke the DPOAE), other properties may become apparent. It is important to keep this in mind when examining DPOAE data as a particular choice may lead to greater insight into the underlying physiology. Also, examining higher order DPs may provide additional information about cochlear non-linearity.

Some questions to keep in mind:

- How do lizard OAEs couple to the middle ear? Is it different than in humans?
- Do geckos have an *analogue* of mechanical traveling waves similar to that found in mammals?
- Is the gecko's cochlear non-linearity much stronger than that of the human? Or are human OAEs more highly *filtered* (e.g. by traveling waves) after *generation*?
- What accounts for the 0.5-2 ms phase gradient delay observed in gecko SFOAEs? And 0.5-1 ms in DPOAEs? Is it the same or different between the two? What type of information is the phase gradient delay telling us?
- What is the mechanism(s) for a gecko's frequency selectivity (micro- vs. macro-mechanical)?
- How might efferents affect OAEs in the lizard ear?
- Do gecko evoked OAEs arise from a single source or multiple sources as proposed for mammals? Is this source(s) the same one responsible for the generation of SOAEs? Does scaling symmetry play a role in the gecko ear?

SUMMARY

1 - Gecko ears show both significant DPOAEs and SFOAEs (nonlinear suppression paradigm worked well to reveal emissions)

2 - In comparison to humans, geckos appear to have more distortion (which manifests as OAEs)

3 - Phase gradients appear significantly shorter in the gecko ear than in humans

4 - In contrast to the human ear, both $2f_1$-f_2 and $2f_2$-f_1 phase gradients were similar and close to that of SFOAEs (particularly at lower primary ratios)

⟶ In comparing human and gecko OAEs, there are many striking qualitative similarities but also large quantitative differences

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- We would like to acknowledge insightful discussions with John Guinan, John Rosowski and AJ Aranyosi. This work was supported by R01 DC003687 (CAS), R01 DC0023821 (DMF) and T32 DC00038 (SHBT training grant) from the NIDCD, National Institute of Health.

The Harvard-MIT Division of Health Sciences and Technology