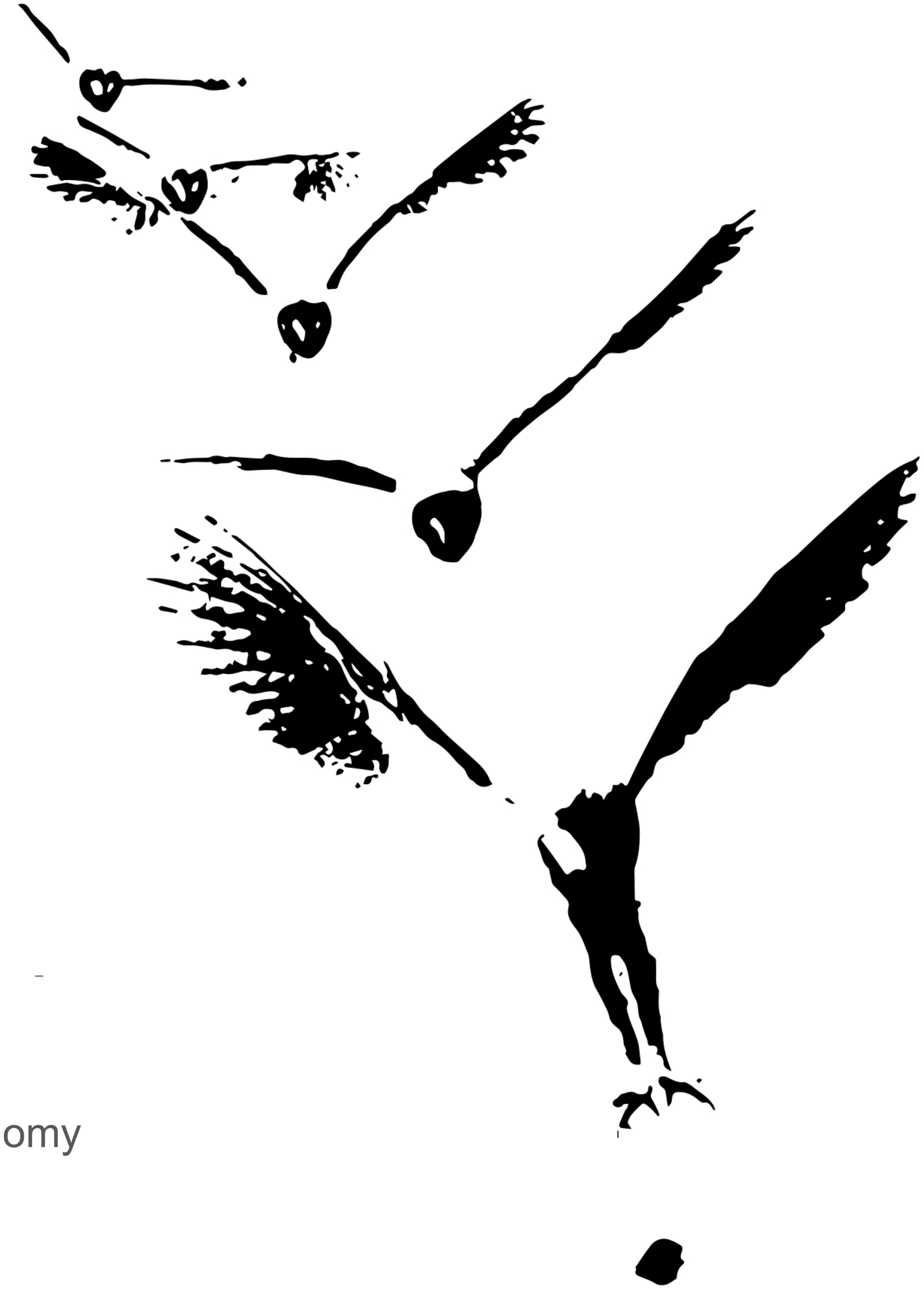
Recasting Coherent Reflection



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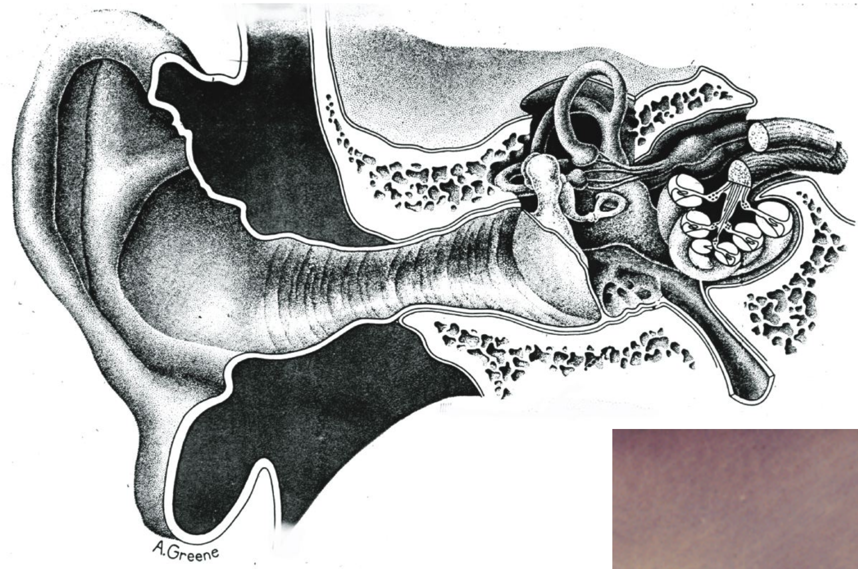
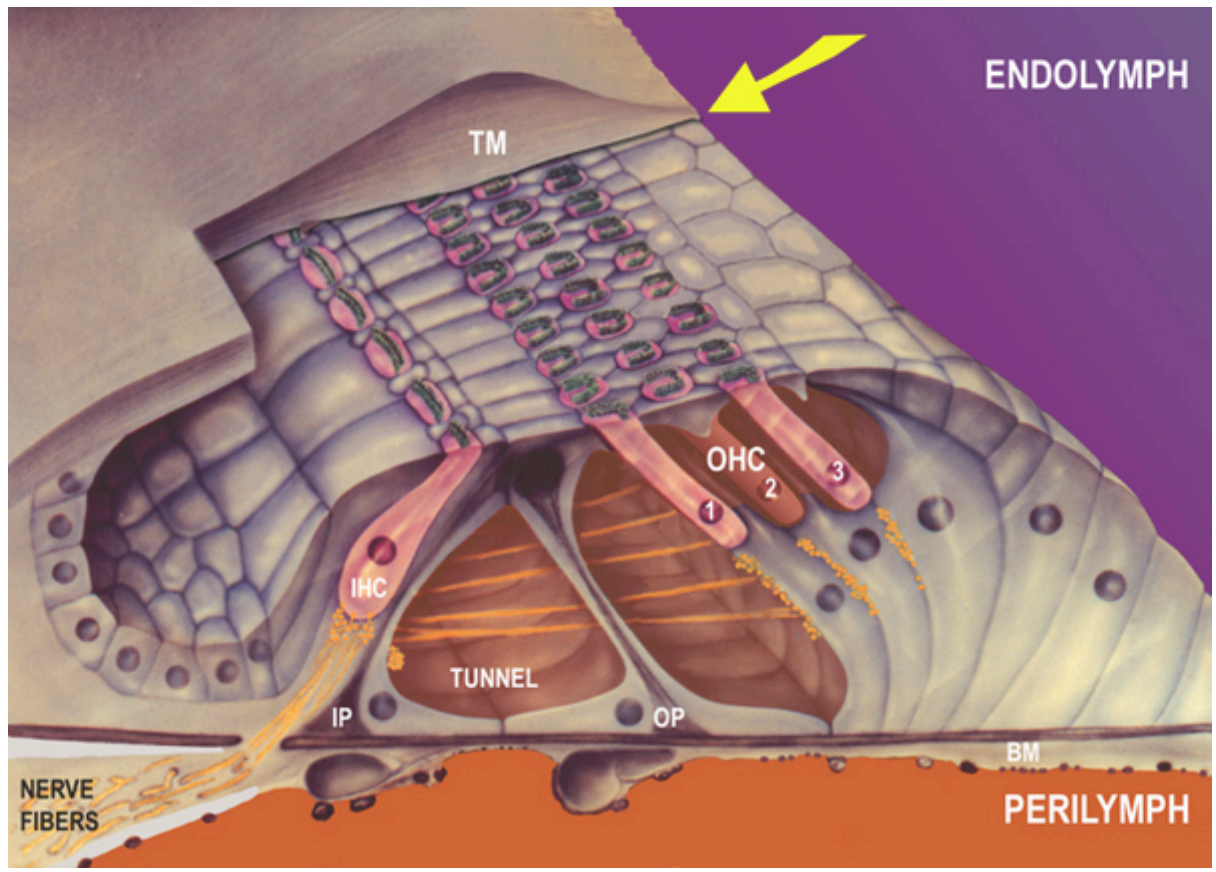
GRC 2014



➢ Cochlear (i.e., mammalian) micromechanics still not well understood

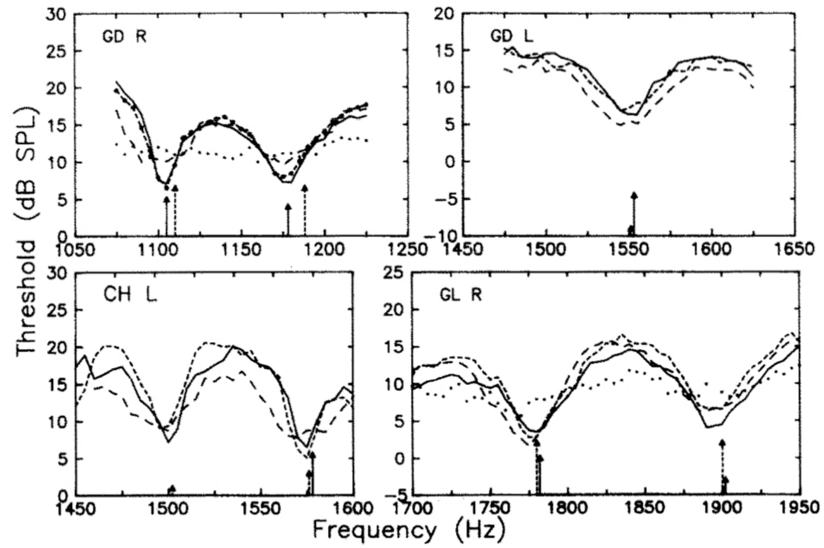


Bohne

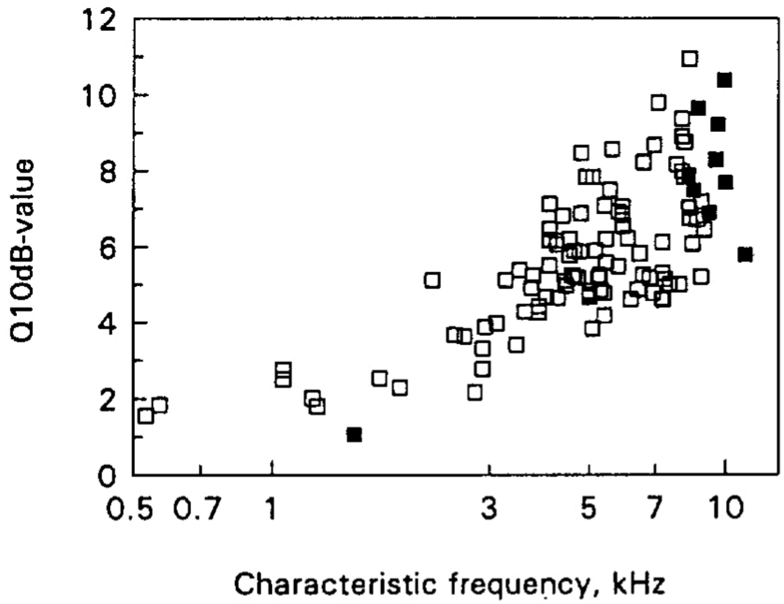
➢ Increasing focus on structural detail
(e.g., tectorial membrane, organ of Corti geometry)

OAEs tied to forward auditory transduction

- ➢ Audiometric 'dips' correlate to presence of SOAEs



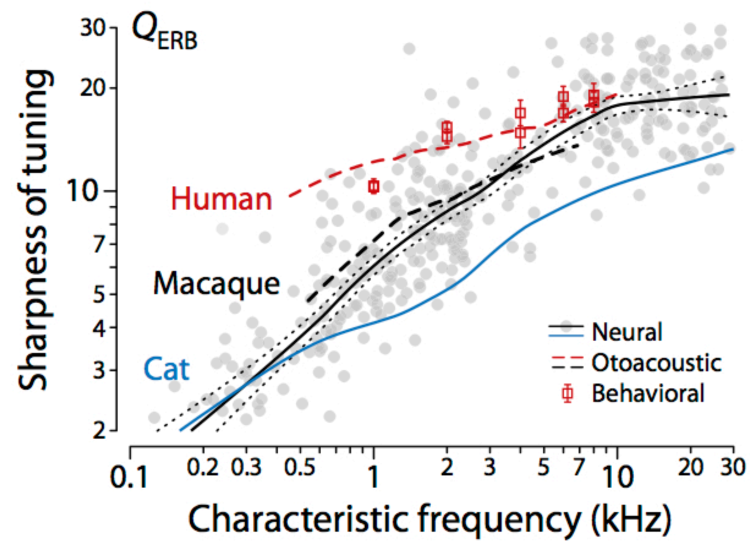
Long & Tubis (1988)



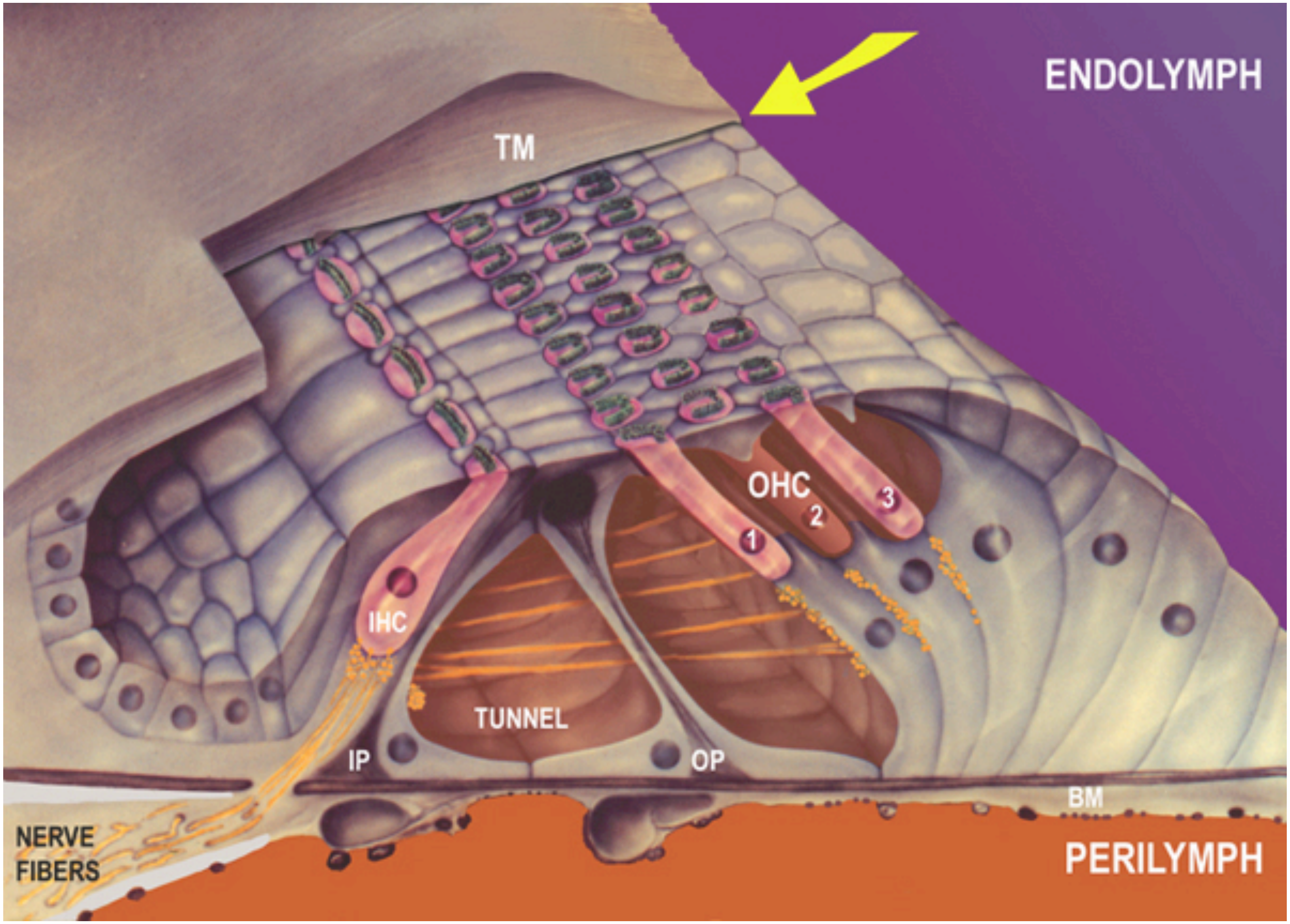
Taschenberger et al (1997)

- ➢ SOAE 'suppression' tuning curves match those of ANFs

- ➢ SFOAE 'phase-gradient delays' also accurately estimate ANF sharpness of tuning



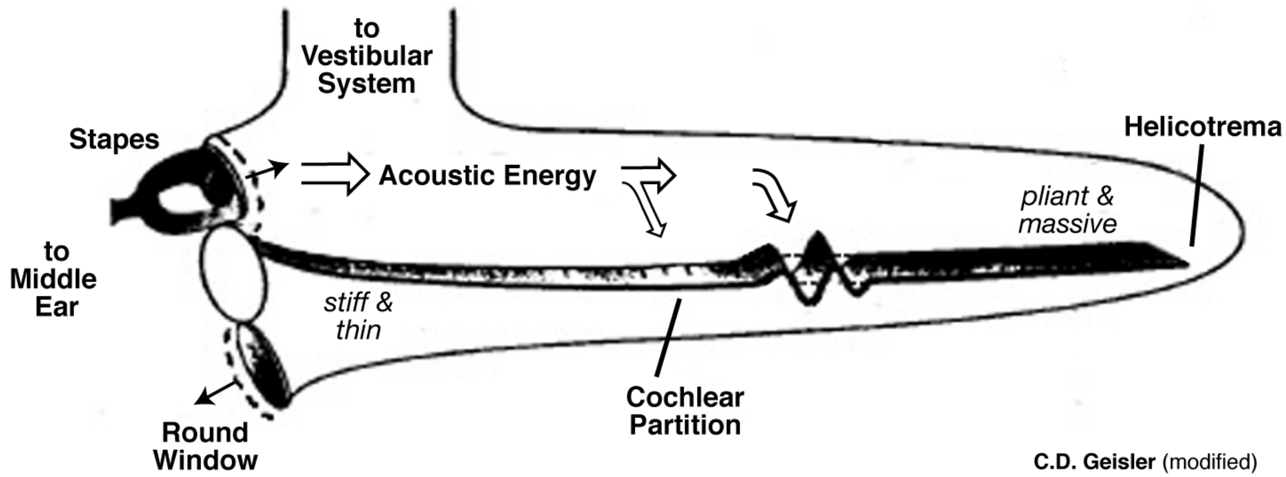
Joris et al (2011)



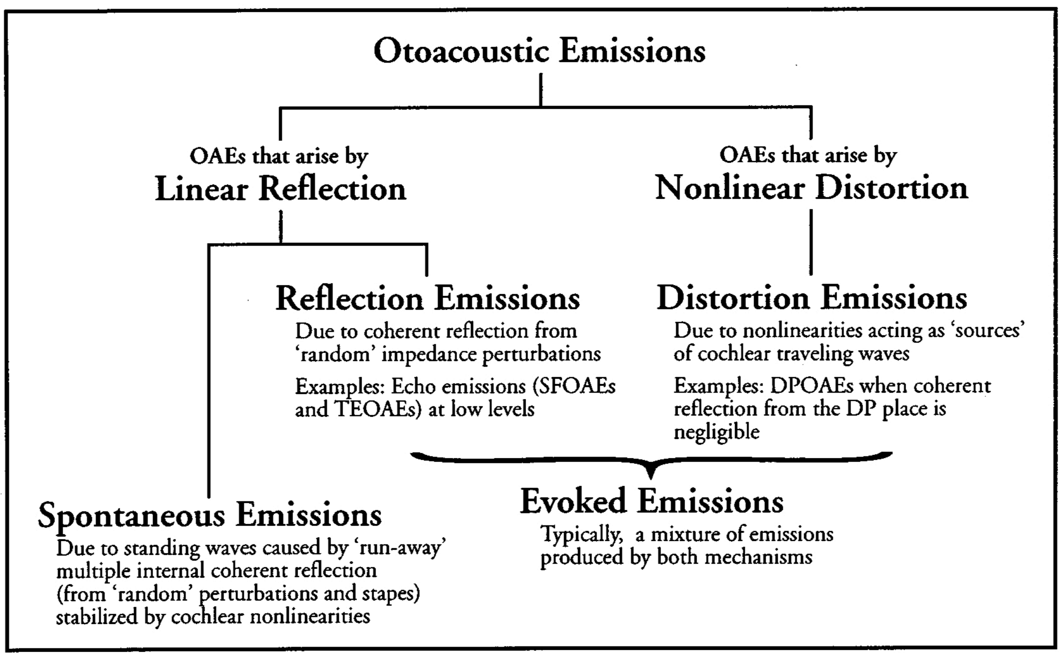
→ But what do OAEs tell us about cochlear mechanics?

OAE Taxonomy

➢ BM traveling waves



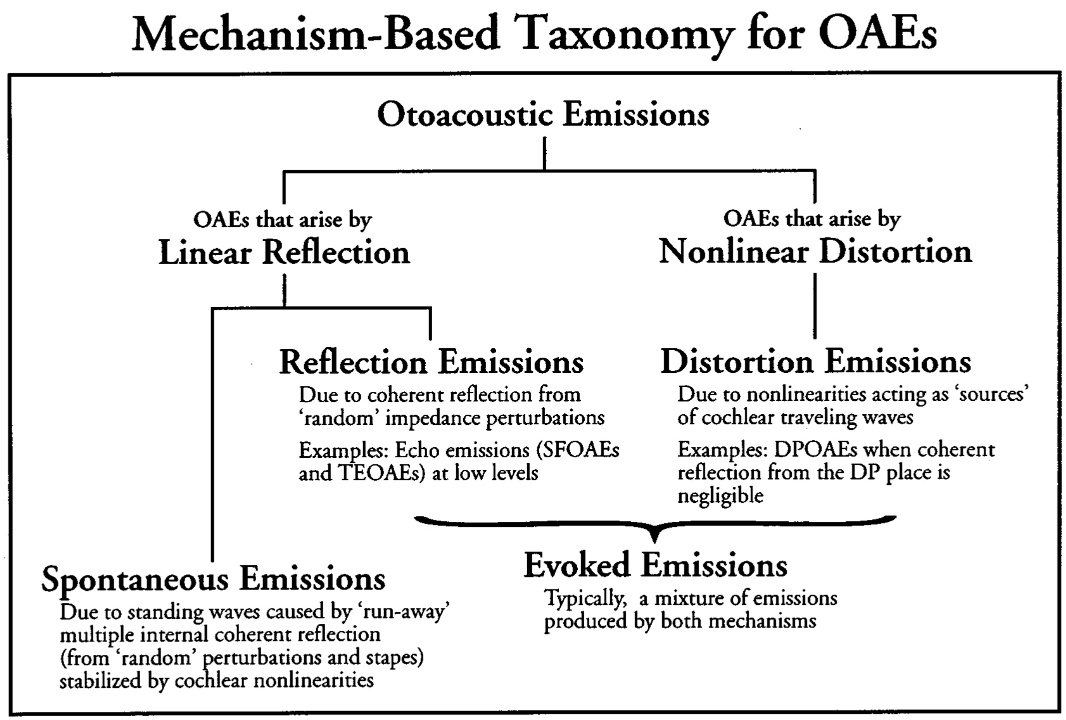
Mechanism-Based Taxonomy for OAEs



Shera & Guinan (1999)

➢ Wave-centric framework, including notion of 'coherent reflection'

Present goal



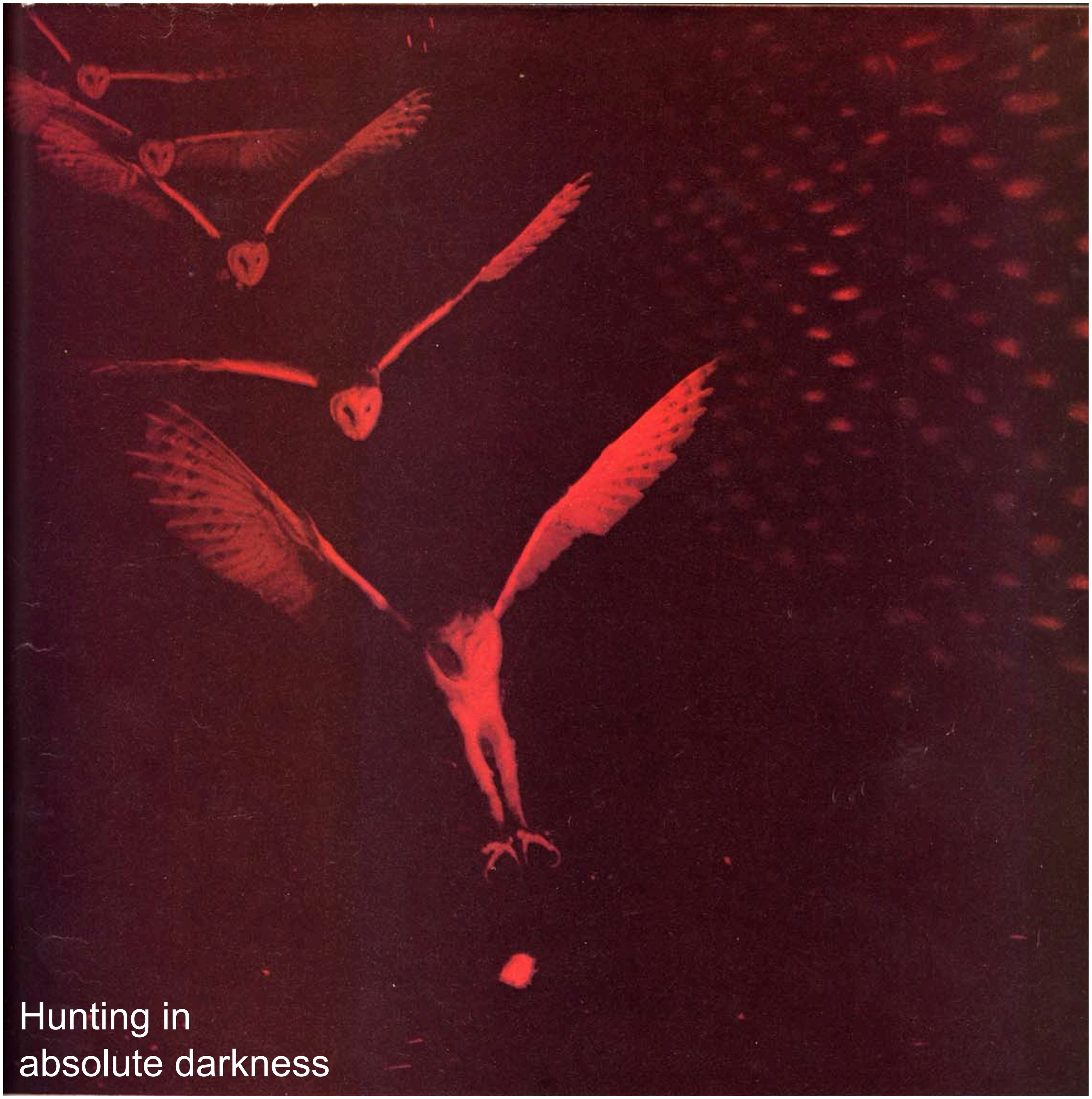
Shera & Guinan (1999)

Argue that:

- ➢ Useful framework, but...
- ➢ ... wave-centric focus hides a more general/ powerful biophysical principle at work

→ Illustrate via a comparative viewpoint

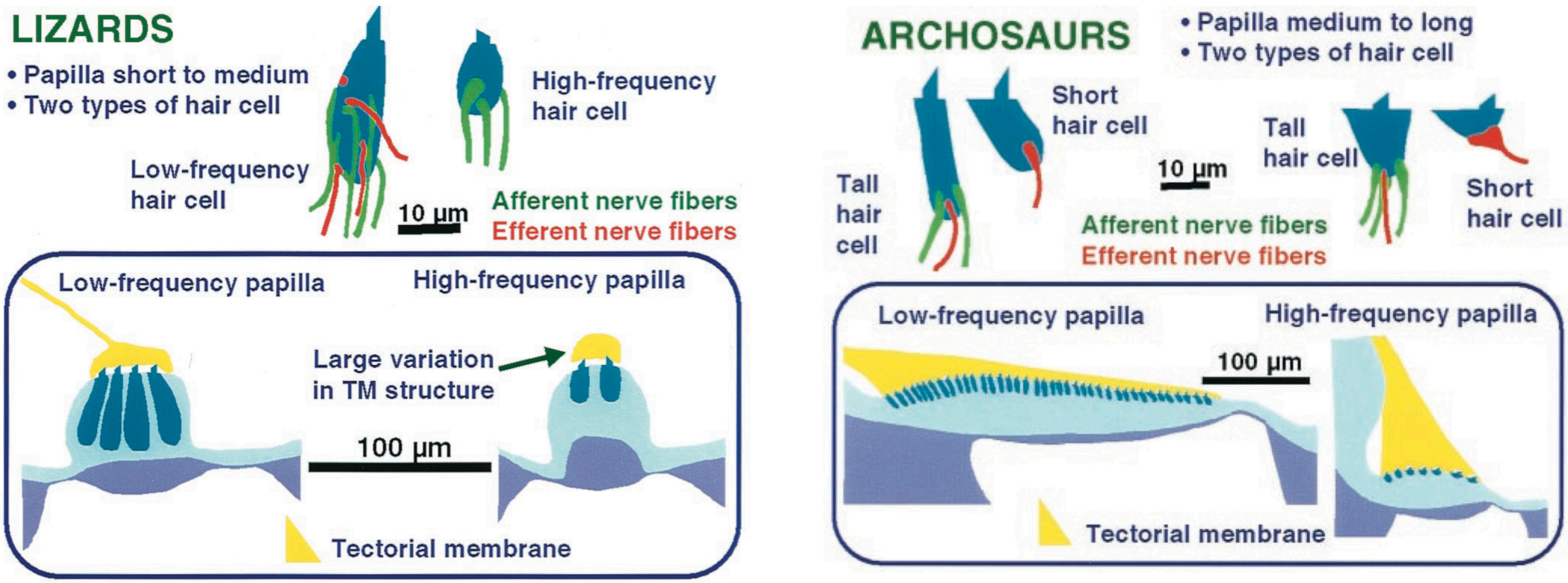
Tyto alba



Konishi (1973)

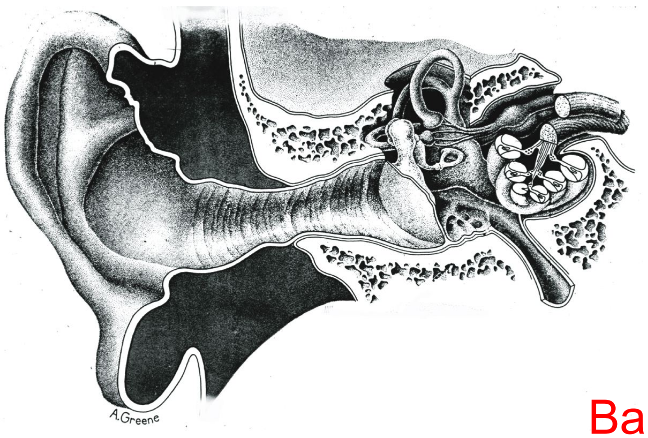

Anolis carolinensis

Comparative Approach: Morphological differences



Manley (2000)

<u>Comparative approach</u>: Morphological differences



<u>Human</u>

- BM length: ~30-35 mm
- # of hair cells: ~20000
- overlying tectorial membrane (TM)

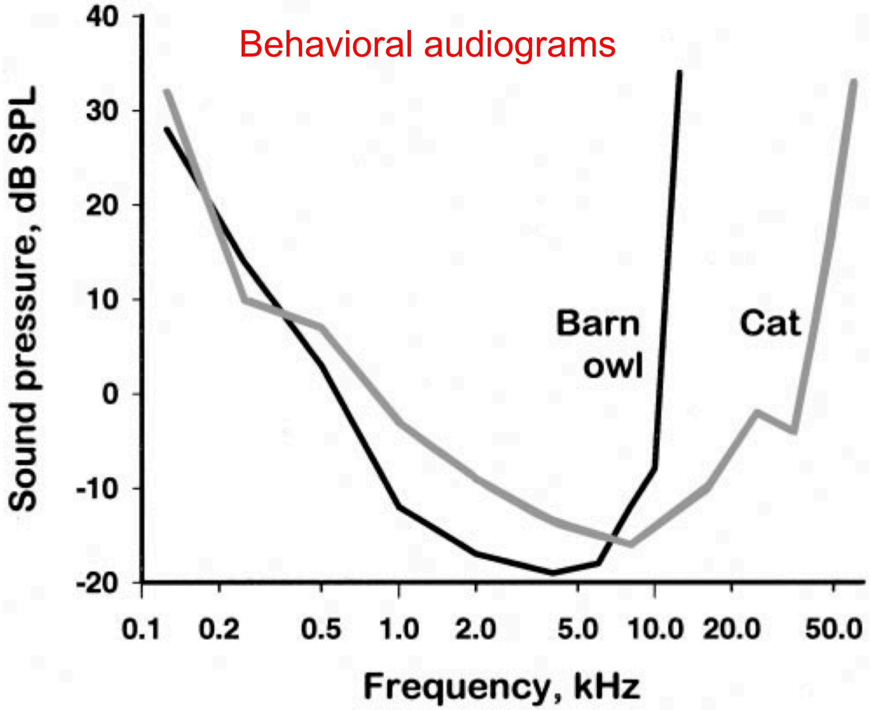
<u>Barn owl</u> (*Tyto alba*)

- BM length: ~10 mm
- # of hair cells: ~16000
- Thick TM coupled to papilla
- BM waves = ???

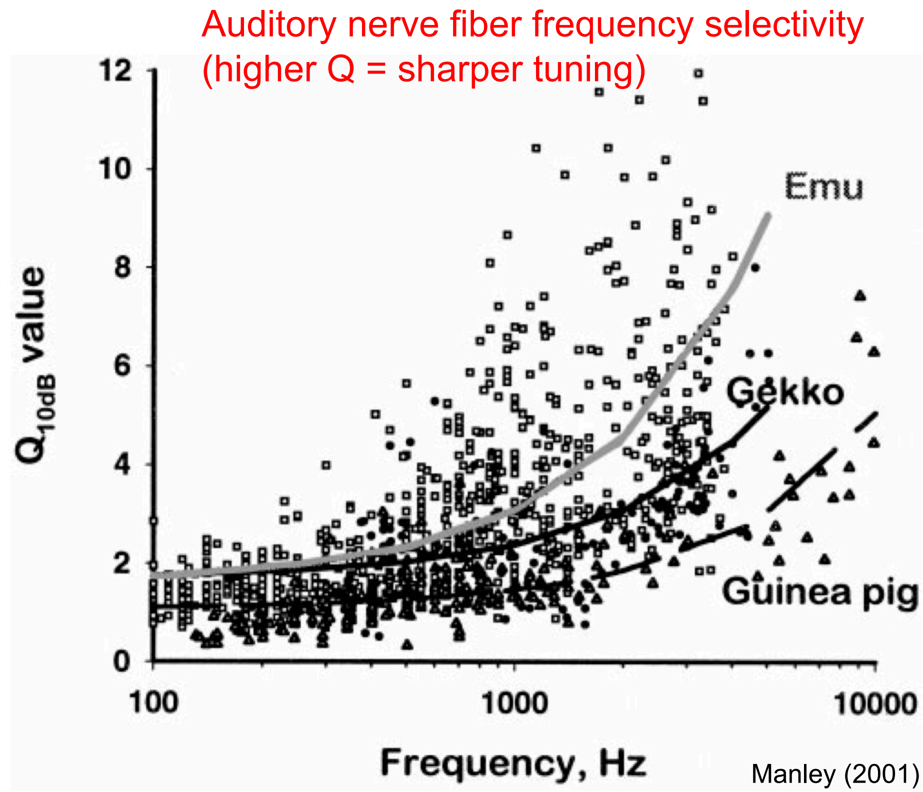
<u>Lizard</u> (*Anolis*)

- BM length: ~0.45 mm
- # of hair cells: ~150
- free-standing bundles (i.e., no TM)
- <u>no BM traveling wave</u>

How does morphology affect performance?



Manley (2001)



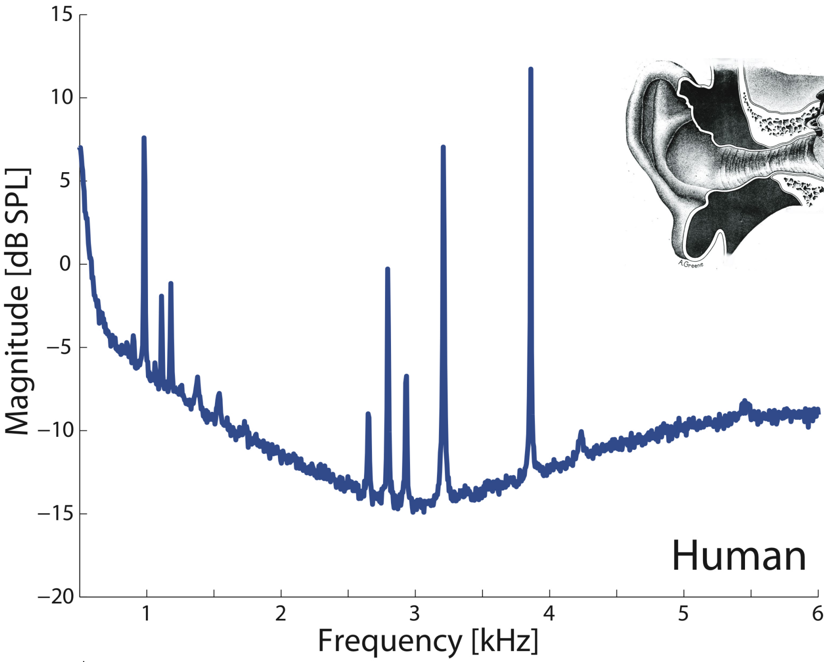
Manley (2001)

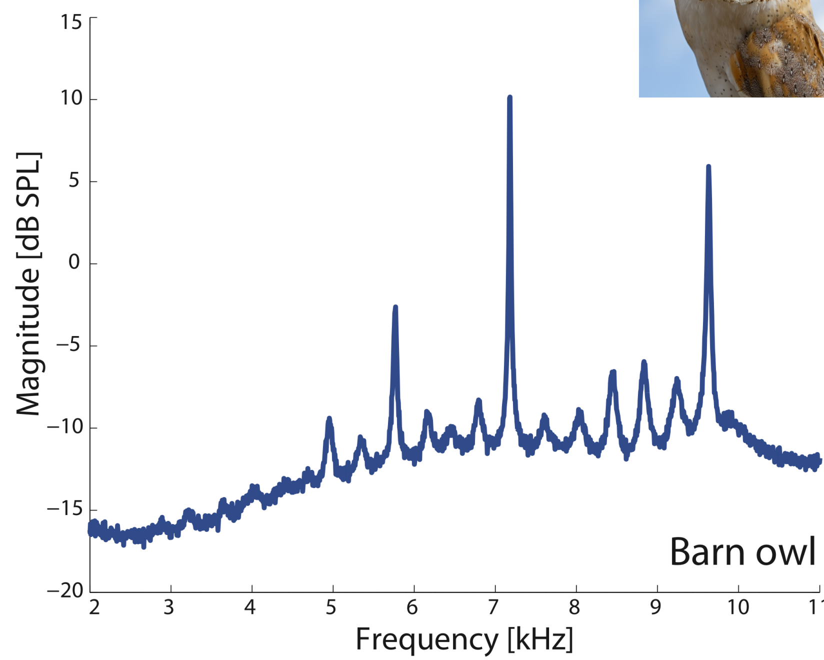
→ Non-mammalian ears can exhibit similar thresholds/tuning as mammals*

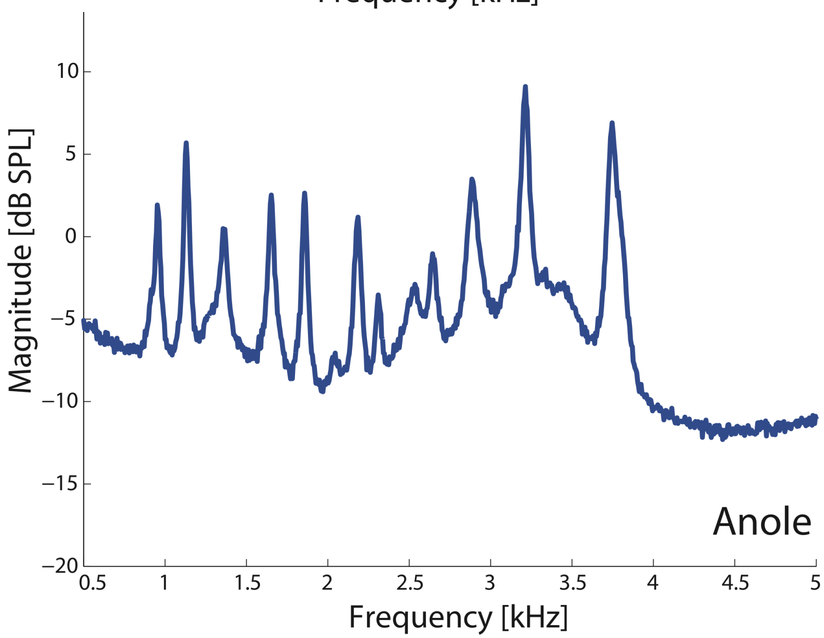
* In general, high frequency hearing (>10 kHz) is unique to mammals

- Lightly anesthetized
- Middle ear vented

Results: Spontaneous OAEs (SOAEs)







Dynamics of spontaneous otoacoustic emissions

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Background

Active mechanisms & OAEs - Otoacoustic emissions (**OAEs**) are a universal feature across a broad range of the animal kingdom [e.g., Koppl, 1995] and have correlates at the level of the single hair cell [Crawford & Fettiplace, 1985; Martin et al. 2003]. There appears wide agreement that OAE generation is ultimately an epiphenomenon associated with a nonlinear 'active' mechanism(s) (i.e., power amplification of low-level external stimuli) that can facilitate forward auditory transduction. However, though often cited as compelling evidence for such an active process, spontaneous emission (**SOAE**) generation remains poorly understood. Of all OAE types, SOAEs are arguably the simplest to measure and require the fewest assumptions to explain, yet are the relatively least reported.

Morphology & Comparative Approaches - Across the vertebrate subphylum, hair cells (**HC**, i.e., stereovillar bundle containing mechanically-activated transduction channels) appear a relatively universal feature. However, there is otherwise significant variation in the structure of the auditory periphery, especially at the level of the inner ear [e.g., Manley, 2000]. For example, ears exhibiting SOAE activity can have anywhere from approximately 40 to 20000 HCs, can have a thick overlying tectorial membrane (**TM**) or none at all, and can exibit basilar membrane (**BM**) traveling waves or not. There is thus a rich basis for comparative study of SOAEs to examine what biomechanical features are (or are not) essential in OAE generation.

FIGURE 1 - Basic schematics for different model classes of SOAE generation

Models for SOAE Generation - Various classes of theoretical models have been developed to explain SOAE generation. Initial models chiefly considered only a single self-oscilloatory element (e.g., a limit-cycle oscillator such as a van der Pol system) [Wit, 1985; Talmadge et al. 1991]. Other model classes have considered coupled oscillators [e.g., Murphy et al. 1995; van Hengel et al. 1996]. 'Global' models (i.e., more than one oscillator) however have, given the morphological variation noted above, come in a wider variety of flavors in terms of the assumed underlying biomechanics [**Fig.1**]. For example, one model [Shera, 2003] focuses on energy reflected by BM traveling waves that gives rise to standing waves. Another model type [Vilfan & Duke, 2008] considers the ear as a collection of coupled nonlinear oscillators and neglects the BM altogether. Common ground between these models is unclear, as basic underlying biophysical assumptions remain under debate. For example:

- What are the energy sources for SOAE generation?
- How do different HC types (inner vs outer, short vs tall) play complementary roles?
- What is the role of inertia at the level of the HC bundle and how does such contribute to tuning in both 'active' and 'passive' conditions?
- How are HCs mechanically coupled together? Relative contributions of viscous vs. elastic coupling? Tectorial membrane?
- What is the role of stochasticity? For example, dynamic features such as thermal noise? Or static ones such as anatomical irregularity?

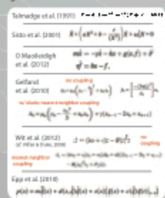


FIGURE 2 - Overview of equations of motion for different assumed types of 'active oscillators'

Present Goals - Numerous studies have reported aspects of SOAEs that extending beyond averaged spectra. For example, dynamic responses [e.g., Sisto et al. 2001], influence of external tones [e.g., Zwicker & Schloth, 1984] and the associated 'suppression tuning curves' [Koppl & Manley, 1994], pharmocological effects [Long et al. 1991; Stewart & Hudspeth, 2001], and other behavior such as temperature dependence and noise exposure [e.g., Manley, 2006]. The goal of the present study is to further examine SOAE dynamics over a range of timescales. For example, how does SOAE activity respond to swept tones (**S-SOAE**) and tone bursts (**B-SOAE**)? We adopt a comparative point of view, capitalizing upon gross morphological distinctions of those vertebrate species that exhibit robust SOAE activity.

Methods

- Data reported here come from representative individuals of three different groups, with morphological aspects summarized below. As SOAE prominence varies significantly across individuals, ears indicated here can be considered relatively strong emitters.

Human
> BM Length: ~35 mm
> Hair cell count: ~20000
> TM: thin ribbon
> BM traveling wave: Yes

Barn owl (Tyto alba)
> BM Length: ~12 mm
> Hair cell count: ~16000
> TM: thick, coupled to papilla
> BM traveling wave: Unknown

Lizard (Anolis carolinensis)
> BM Length: ~0.5 mm
> Hair cell count: ~180
> TM: None (over most of papilla)
> BM traveling wave: No

- All measurements were made using an Etymotic ER-10C probe system, connected to a PC running custom software. All data was sampled at 44.1 kHz at 24 bits. For lizard and owl recordings, animals were lightly anesthetized and kept at a stable body temperature via a heating blanket. Earphones were calibrated in-situ using flat-spectrum noise and unless noted otherwise (i.e., Fig.8), stimulus levels were flat across frequency. Tone-bursts were cosine-ramped to minimize spectral splatter.

- Analysis was performed using custom software written in Matlab. Two primary methods employed were the Fourier and Hilbert transforms. Spectrogram analyses [e.g. **Fig.5**] were done via a short-time Fourier transform (**STFT**), whose parameters (window type, segment length, fractional overlap) were chosen with the goal of optimizing time-frequency representation.

Results

> **Intrapeak statistics** - As shown in **Fig.3**, there is both a variety in SOAE spectra characteristics across species as well as diversity within a given spectrum. A wide range of behaviors of individual peaks are observed: stable sinusoids with varying degrees of envelope modulation, noisy peaks with large fluctuations, peaks whose filtered signal appears to (limitedly) turn on/off, and the existence of broad 'baseline' plateaus (lizard). Note that the owl shows prominent peaks, yet their distributions are relatively noisy. This variety strengthens the broad notion that *"Any investigation of the properties of spontaneous emissions must take into account that they fall into several different classes"* [Talmadge et al., 1991] and that such applies broadly across species.

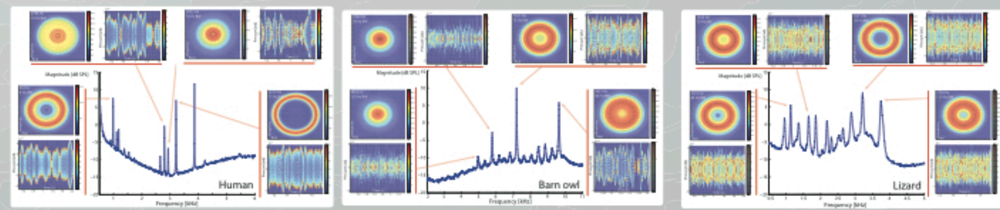


FIGURE 3 - Intrapeak Statistics Data from a representative ('robust emitter') ear for each species. SOAE spectra were computed by averaging the magnitudes of four hundred 0.19 s sequential buffers (~74 s total). Note the difference in the horizontal axes. For each representative peak indicated, the distribution of the (filtered) analytic signal [Shera, 2003] is shown, as is the timecourse of the amplitude distribution over an arbitrary shorter segment. Filter properties are indicated in upper left corners.

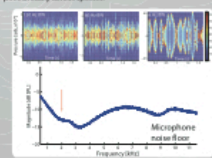


FIGURE 4 - Microphone Noise Floor Similar to Fig.3, but with the probe coupled to a plastic tube to demonstrate the noise floor. The analytic signal distributions have been excluded for clarity, but all appeared as centroids (i.e., Gaussian amplitude distributions, Bialek & Wit, 1984). The temporal distribution indicates that when the filter bandwidth is sufficiently narrow (6 Hz), behavior reminiscent of a sinusoid (with large amplitude variations) becomes apparent, as are on/off periods.

> **S-SOAE** - The effect of swept tones upon SOAEs (**Figs.5 & 6**) reveals features consistent with those previously reported for discrete tones [e.g., Manley, 2006], such as regions of 'suppression' about the tone complemented by 'facilitation' effects (i.e., increased magnitude), pushing/pulling of peaks as the tone approaches or moves away, and sub-harmonic distortion effects. S-SOAE responses reported here used relatively slow sweep rates (1-2 kHz/s) and appear to be in a pseudo-steady state.

> **B-SOAE** - The effect of tone bursts upon SOAEs (**Figs.7 & 8**) reveals several complex features. First, there is typically a confined region of 'suppression' (vertical bands) about the burst. The associated dynamics appear relatively fast, at least compared to the time resolution shown here. Second, while not always observed, numerous instances of entrainment are apparent: an SOAE peak is drawn across frequency 'into' a burst, and then relaxes back as the burst ramps down. In some cases, the opposite happens and peaks are pushed away until a 'break' into a region of suppression (e.g., Fig.8).

> **TBOAE** - The burst data can also be analyzed by subtracting (appropriately scaled) runs obtained at different stimulus levels to extract a residual as the evoked tone-burst emission (TBOAE). Unlike the data shown in Figs.5-8 that were spectrally averaged, temporal averaging here (**Figs.9 & 10**) allows visualization of the 'residual' activity entrained to the stimulus. The lizard data in **Fig.10** indicate that TBOAEs are chiefly confined to regions where SOAE could occur, at least below a higher frequency limit. The human data in **Fig.9** show two salient features. First, when the burst is close to an SOAE peak, there can be a relatively slow de-synchronization [e.g., Sisto et al. 2001] that glides across frequency [e.g., Carney et al. 1999]. Second, in the time-frequency plane, the bursts take on a variety of shapes, indicating changes in energy across both frequency and time.

> **Interpeak correlations** - While not shown here, previous studies [e.g., van Dijk et al., 1998] motivated us to examine evidence for inter-peak interactions. Initial efforts extracted (variable-length) filtered envelope segments and performed a cross-correlation between such for two peaks. Preliminary results for the lizard indicate no clear correlations: It is presently unclear if this is due to peaks ultimately being weakly/not correlated or if more sophisticated methods are needed due to nonlinearities.

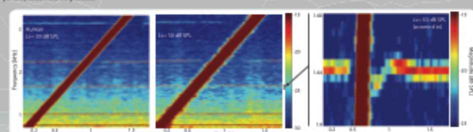


FIGURE 5 - S-SOAE (Human) - Response to swept tones. Data shown here comes from a single human subject. The two sweep conditions (left panel at 30 dB SPL, center at 50 dB SPL) were measured in an interleaved fashion. The right panel shows a zoom-in of the 1.6-1.68 kHz range for the 50 dB SPL condition. STFT analysis properties used a 8192 point window with 97% sliding overlap, spectrally averaged across 35 stimulus presentations.

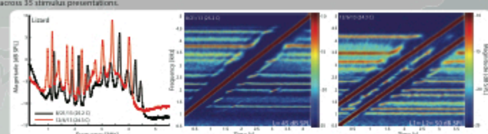


FIGURE 6 - S-SOAE (Lizard) - Response to swept tones. Data shown here comes from a single lizard, the same ear measured on two separate occasions. Note that body temperature was not the same for both recordings. For the 8/21/13 session (black trace in left panel), a single 45 dB SPL tone was swept across frequency (middle panel). For the 12/6/13 session (red trace in left panel), two 50 dB SPL tones were swept (right panel) with a fixed frequency separation of 0.85 kHz. STFT analysis properties used a 8192 point window with 99% sliding overlap, spectrally averaged across 35 stimulus presentations.

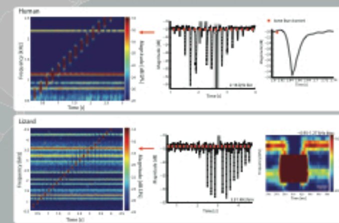


FIGURE 7 - B-SOAE - Response to tone bursts. Top row shows response from a human ear, bottom row is from a lizard. Peak burst level was 60 dB SPL in both cases (cosine ramping). Each presentation period containing a burst was 186 ms long, the human's ramped portion 23 ms long (i.e., 12% duty cycle) while the lizard's ramped portion was 45 ms long (24% duty cycle). For the human, middle panel shows the waveform associated with the 2.153 kHz bin (see red arrow), with right panel zooming in upon the shaded region. Note that onset of burst is designated via a red square. For the lizard, middle panel shows the waveform associated with the 3.5 kHz bin, while the right panel shows a zoomed in section of the left panel (0.95-1.27 kHz region).

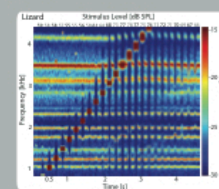


FIGURE 8 - B-SOAE Similar to Fig.7, but with burst were presented with a flat voltage (corresponding peak dB SPL appears on top). Data shown here are from a lizard. Individual burst duration was 113 ms.

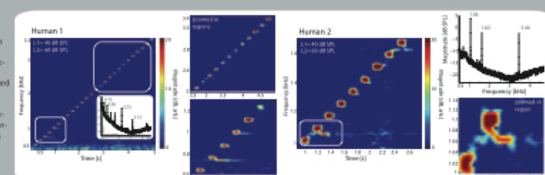


FIGURE 9 - Human TBOAE The tone-burst OAE (TBOAE) shown here is the 'residual' obtained by taking two separate B-SOAE runs acquired sequentially using different stimuli, the lower level time-averaged waveform then scaled up and subtracted from the higher level run. Data from two different human subjects are shown, along with their corresponding SOAE spectra as well as zoomed-in regions of the spectrogram.

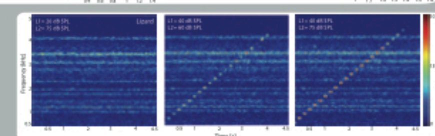


FIGURE 10 - Lizard TBOAE Similar to Fig.9, but from a lizard ear. Here, all data are from the same ear, but each panel shows a different combination of stimulus levels. The residual 'TBOAE' can be seen via the discrete diagonal trace. These residuals were only present over the frequency range where SOAE activity could be observed. Note that while the waveforms were time-averaged, SOAE activity is still be seen via the horizontal traces.

Discussion

Time-Frequency Tradeoff - We are ultimately limited here in terms of temporal resolution. Different transforms [e.g., Wit et al, 1994; Jedrzejczak et al. 2005; Moleti et al. 2012] may improve such.

Entrainment vs. Suppression - B-SOAE data suggest a complicated mix between entrainment effects (i.e., correlated behavior of underlying oscillators, either relative to the external stimulus or each other) [van Hengel et al. 1996] and suppression (i.e., cessation of self-sustained motion). One hypothesis is that entrainment typically acts relatively 'local', but for oscillators further away from the external stimulus frequency, they are pushed into a quiescent state. More generally, stricter definitions of these two states is desirable (e.g., how is entrainment related to 'phase-locking'?).

Spontaneous vs. Evoked OAEs - Most evoked emissions are likely associated with underlying SOAE activity, regardless of whether such can be detected or not [e.g., Shera, 2003; Bergevin et al. 2012]. For example, using a nonlinear 'subtraction' to extract a TBOAE (e.g., Fig.9), the residual suggests some indication of what was (or was not) 'entrained' to the stimulus between the two conditions.

SOAE Stability - Within a given ear, the idiosyncratic nature of the SOAE spectra is highly stable (e.g., relaxation following stimulus offset returns to original pattern). What precisely is the physical mechanism governing such an underlying pattern? 'Irregularity' in the invidual hair cells? Their coupling? The substrate upon which they rest (i.e., BM)? A mix of all these? Conversely, on shorter timescales, SOAE peaks are noisy. What drives such? Lastly, why are some healthy ears 'robust' emitters, and others not? Middle ear effects?

Coupling - The basic biophysical question remains as to how the individual generators are coupled to one another. For example, consider nearest-neighbor coupling (via viscous fluid or elastic tectorial structures) versus all generators equally coupled (via a rigid papilla, in the case of the lizard). Furthermore, it is unclear if the SOAE signal we see ultimately reflects how the underlying generators interact (**Fig.11**). For example, do all the individual generators each individually drive the stapes via fast compressional waves, and thus what we see is a summed response? Or might the generators drive the BM (thereby coupling all of them together), which then in turn drives the stapes?

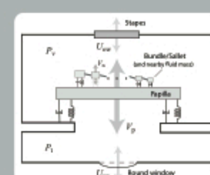


FIGURE 11 - Model schematic for lizard ear [cf. Bergevin & Shera, 2010]. Note that individual 'bundles' can be coupled in two different ways: either locally via nearest-neighbor connections (e.g., fluid boundary layer, elastic tectorium) or globally via the (relatively rigid) papilla.

Comparative Considerations - Various aspects noted above such as coupling might be quite different across morphologies. For example, differential longitudinal motion in the mammalian cochlea (as apparent in traveling waves) could give rise to a different type of collective dynamic, such as a standing wave-type mechanism [e.g., Shera 2003]. Consider further that some species that exhibit SOAEs, such as frogs, don't even have a flexible BM. Furthermore, insects do not even have hair cells [Mhatre & Robert, 2013].

References

Acknowledgements

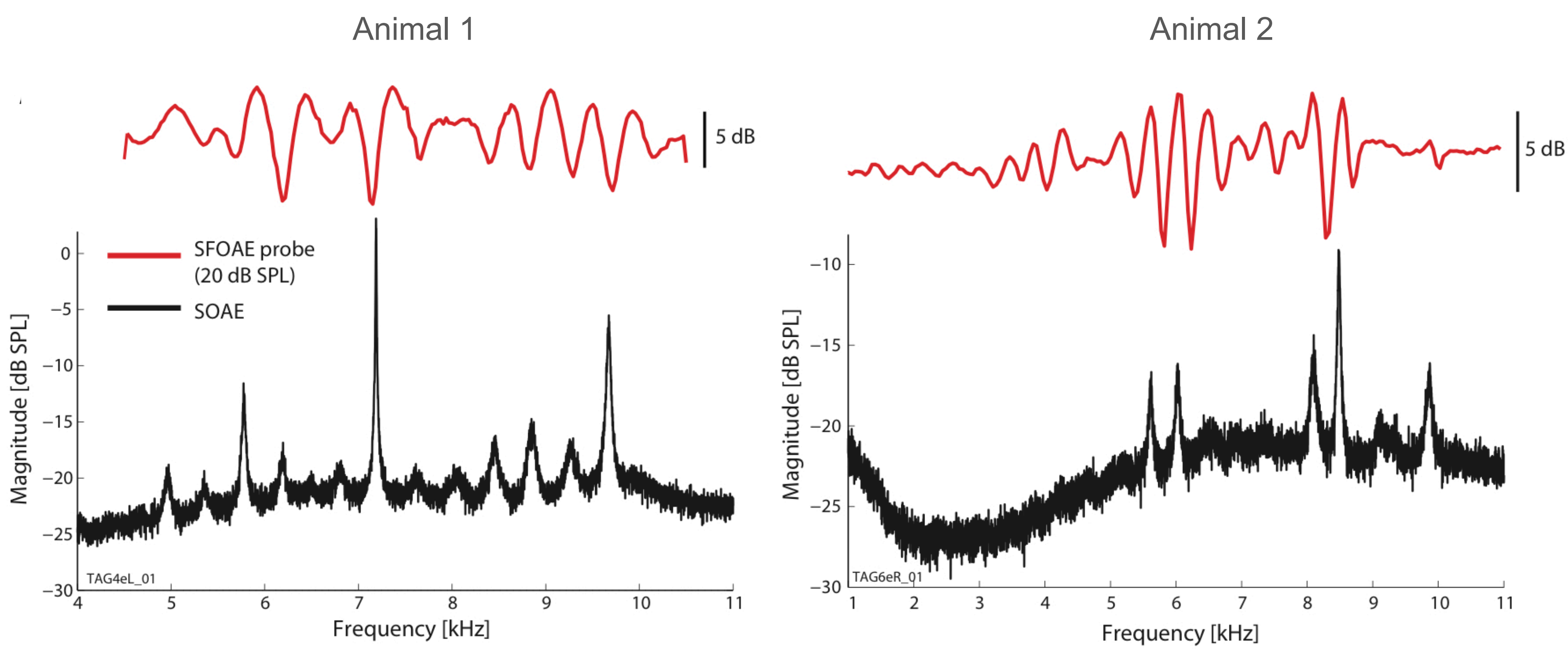
Biophysics

YORK UNIVERSITY

Results (owl): SOAE Interactions with (External) Swept Tones

Data from two representative animals

Tone level = 20 dB SPL

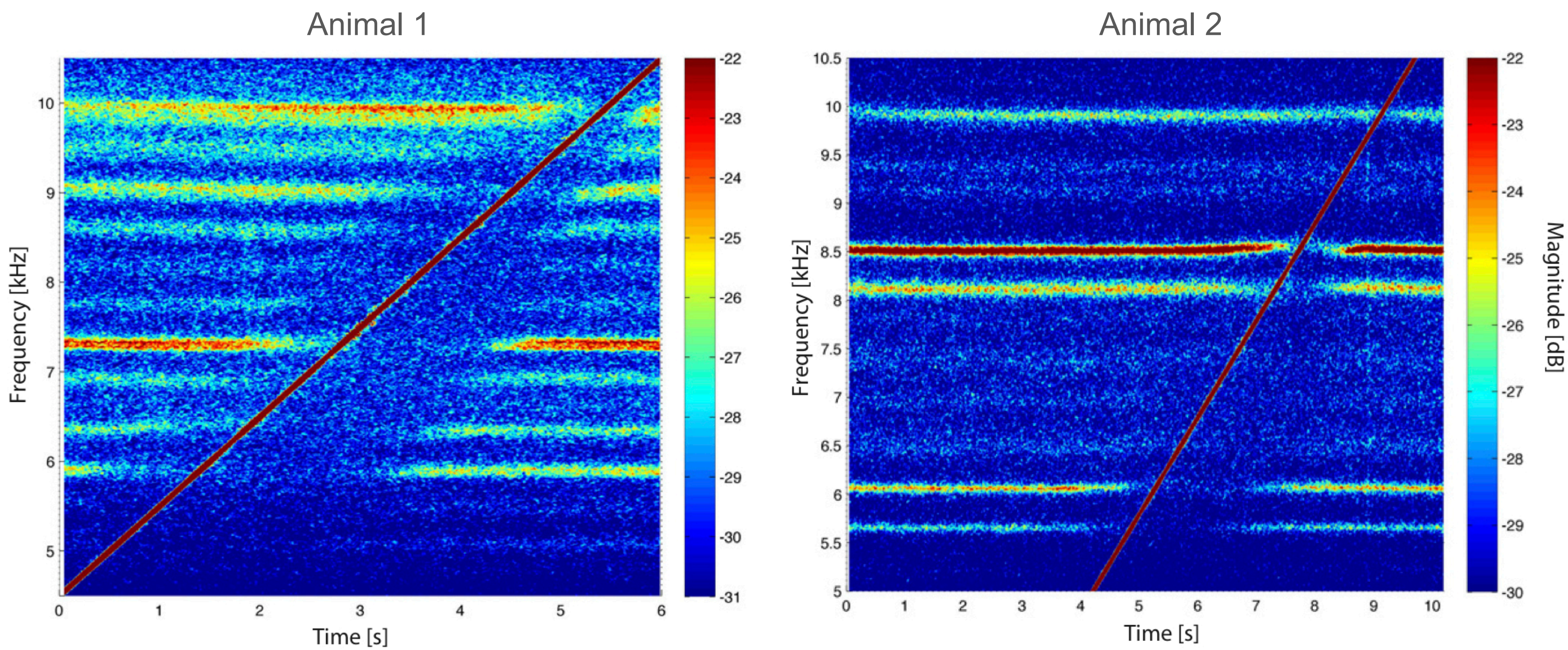


- ➢ Strong interactions with (flat-level) stimulus tone at ear canal (even for small SOAE peaks)

Results (owl): SOAE Interactions with (External) Swept Tones

Tone level = 20 dB SPL

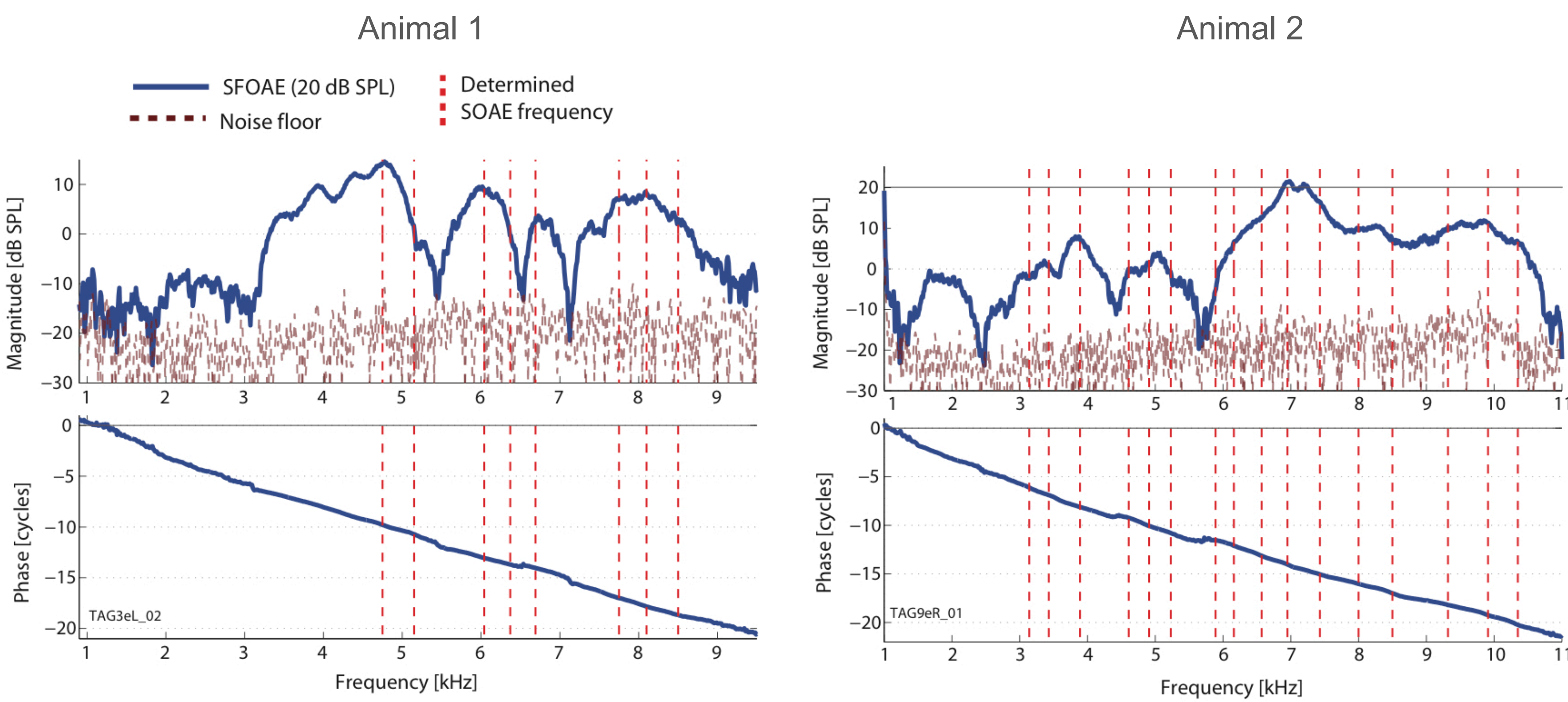
Data from two representative animals



- SOAEs appear as horizontal lines, (external stimulus) swept tone as diagonal
- Localized interactions (e.g., 'suppression') apparent
- Allows for determinations of SOAE frequencies during SFOAE measurements

Results (owl): SFOAEs

Lp = 20 dB SPL
Ls= 35 dB SPL
fs= fp+ 40 Hz

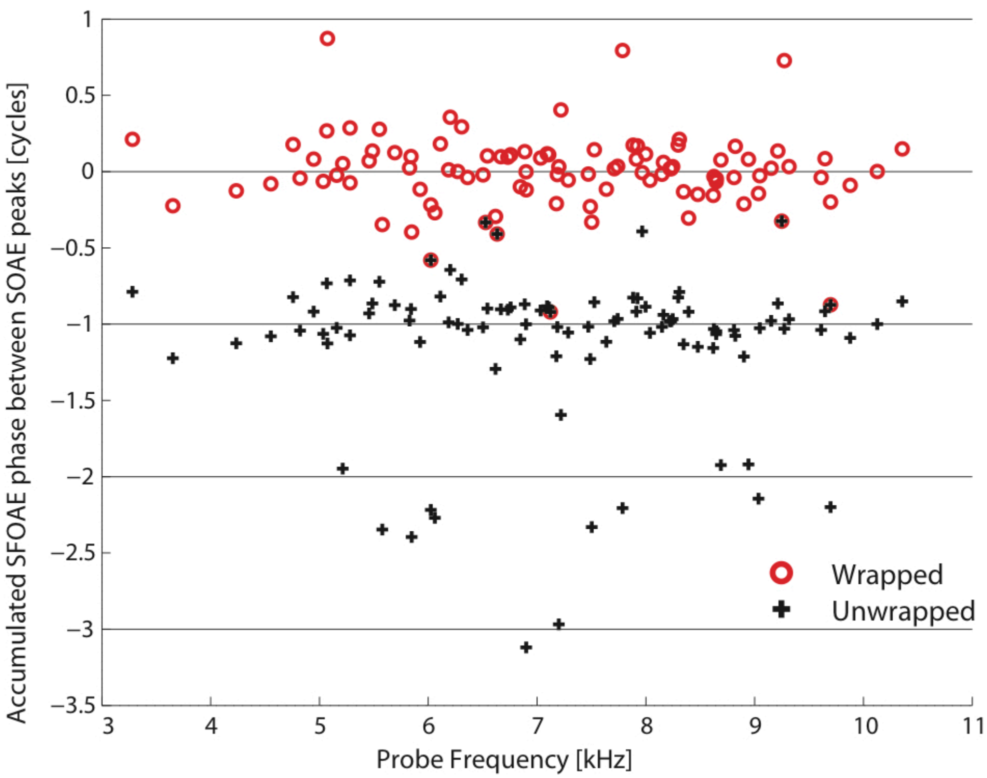


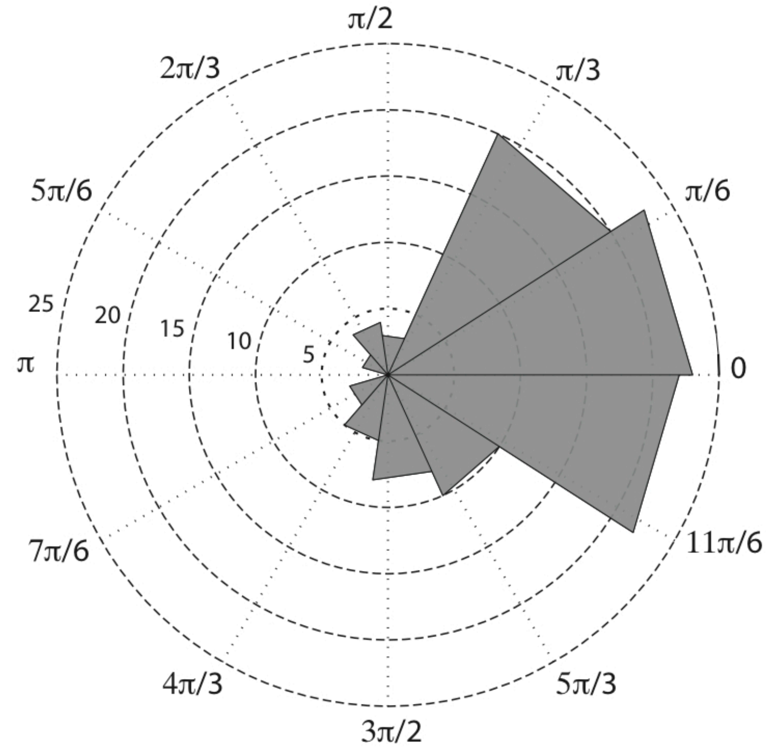
- Robust SFOAEs (e.g., residual can be stronger than evoking stimulus!)
- SOAE and SFOAE peak locations not always correlated
- Allows estimation of SFOAE phase accumulation between adjacent SOAEs

<u>Results (owl)</u>: SFOAE phase accumulation re SOAEs

Data compiled from
15 ears of 9 owls

Lp = 20 dB SPL

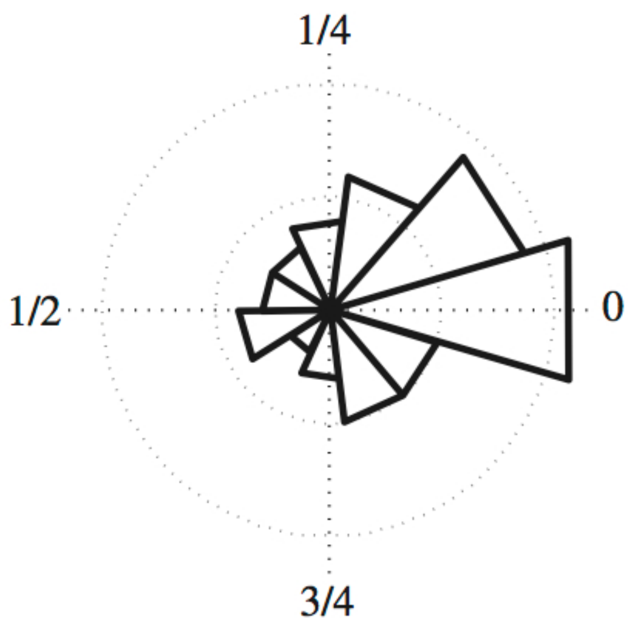




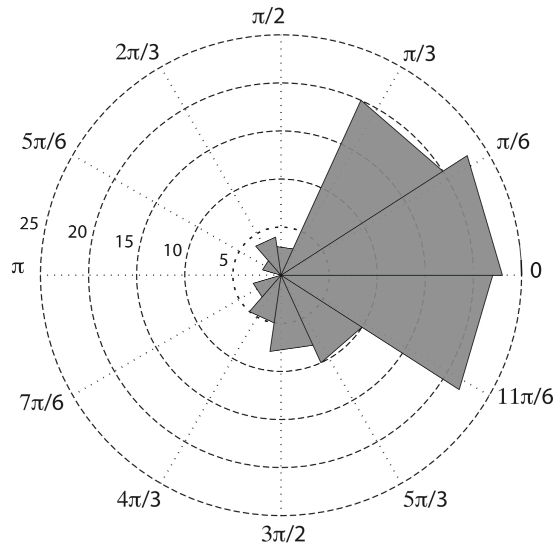
- ➢ Integral number of cycles of phase accumulation between SOAE peaks
- ➢ Independent of frequency and phase (un)wrapping

Putting the pieces together...

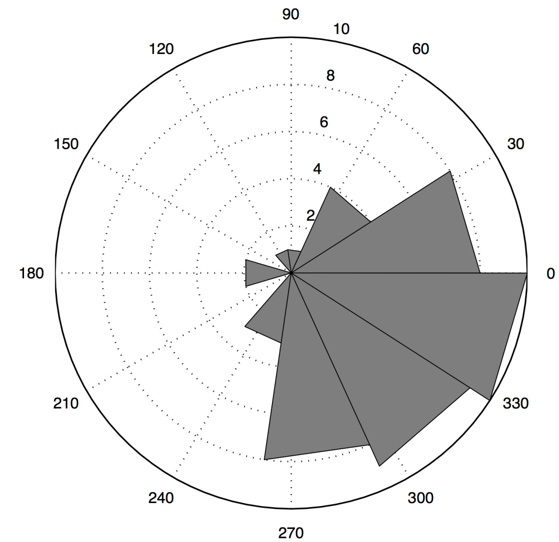
Human



Owl



Anolis



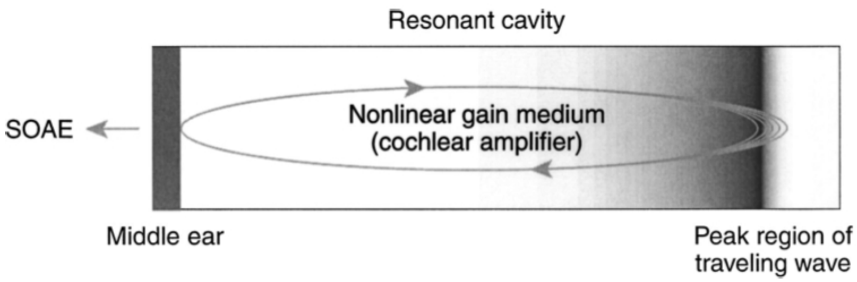
All species show integral # of cycles of SFOAE phase accumulation between adjacent SOAE peaks......

.... despite gross morphological/biomechanical differences (e.g., no BM waves)

Bergevin et al. (2012)

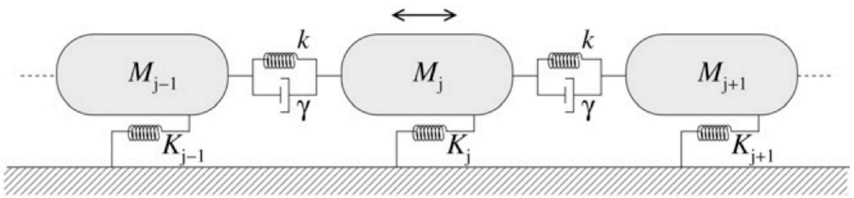
<u>Connecting back to models</u> (of SOAE generation)

Traveling wave framework

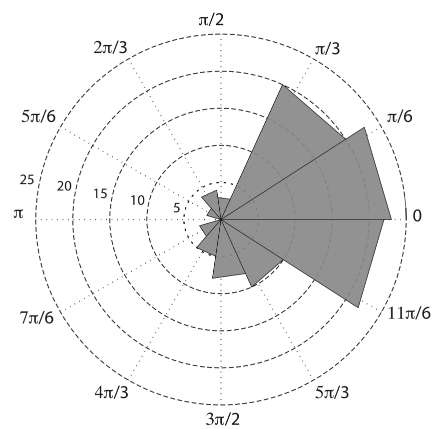


Shera (2003)

Coupled oscillator framework



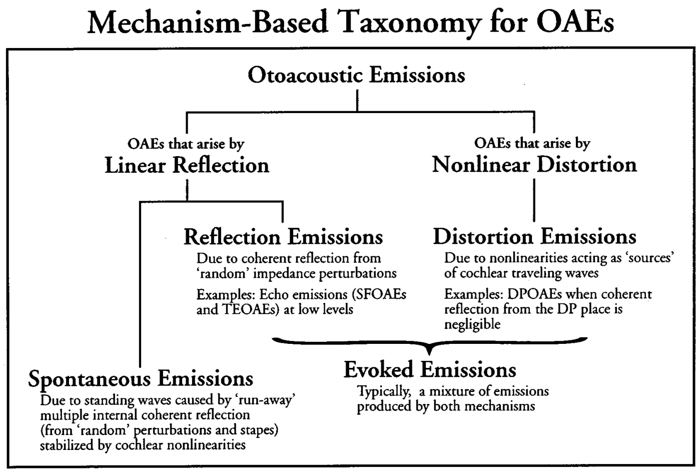
Vilfan & Duke (2008)
Wit et al. (2012)

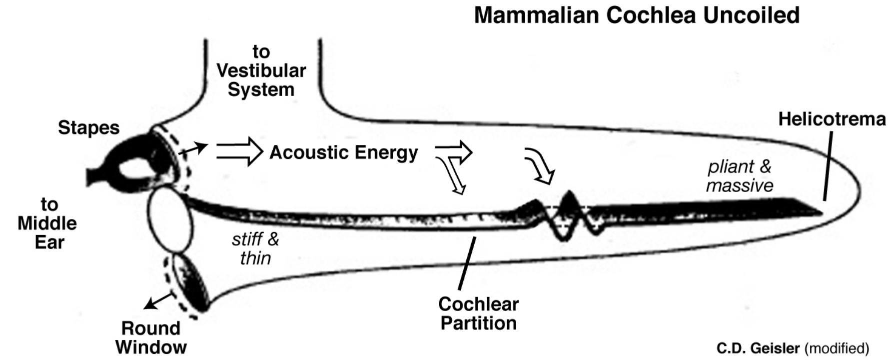


- To first order, data consistent with seemingly disparate models

→ Is this telling us something important?

De-waving coherent reflection





Recast the basic biophysical picture:

Coherent reflection → *'phase coherence of coupled oscillators'*

Basic gist:

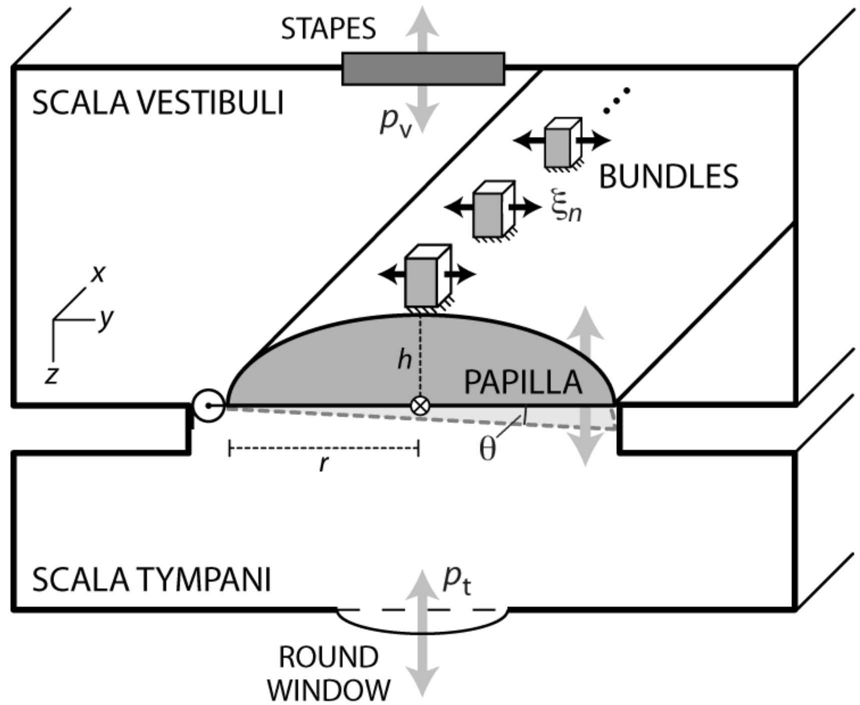
- Consider inner ear as collection of coupled nonlinear/active oscillators
- 'Systems' view: *The whole is more than the sum of the parts*

A more general biophysical principle emerges...

phase coherence of coupled oscillators

- ➢ More universal/parsimonious framework for describing/ understanding inner ear mechanics

  (i.e, human/owl/lizard ears are both similar & different)



Bergevin & Shera (2010)

Entrainment of Neuronal Oscillations as a Mechanism of Attentional Selection

Peter Lakatos,[1,2] George Karmos,[2,3] Ashesh D. Mehta,[4] Istvan Ulbert,[2,3] Charles E. Schroeder[1,5]*

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- ➢ Basic idea likely holds in other areas of hearing (and beyond)...

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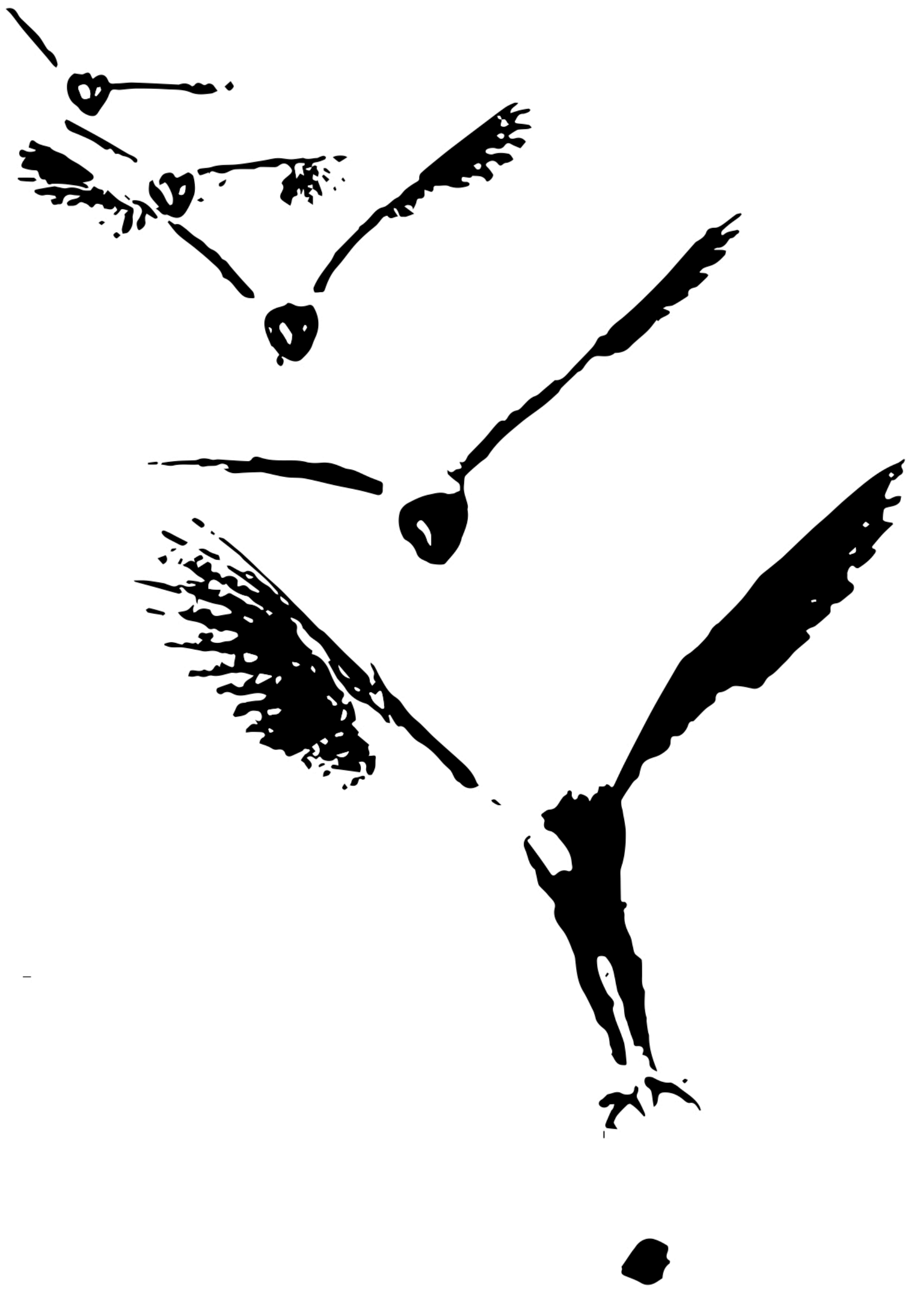
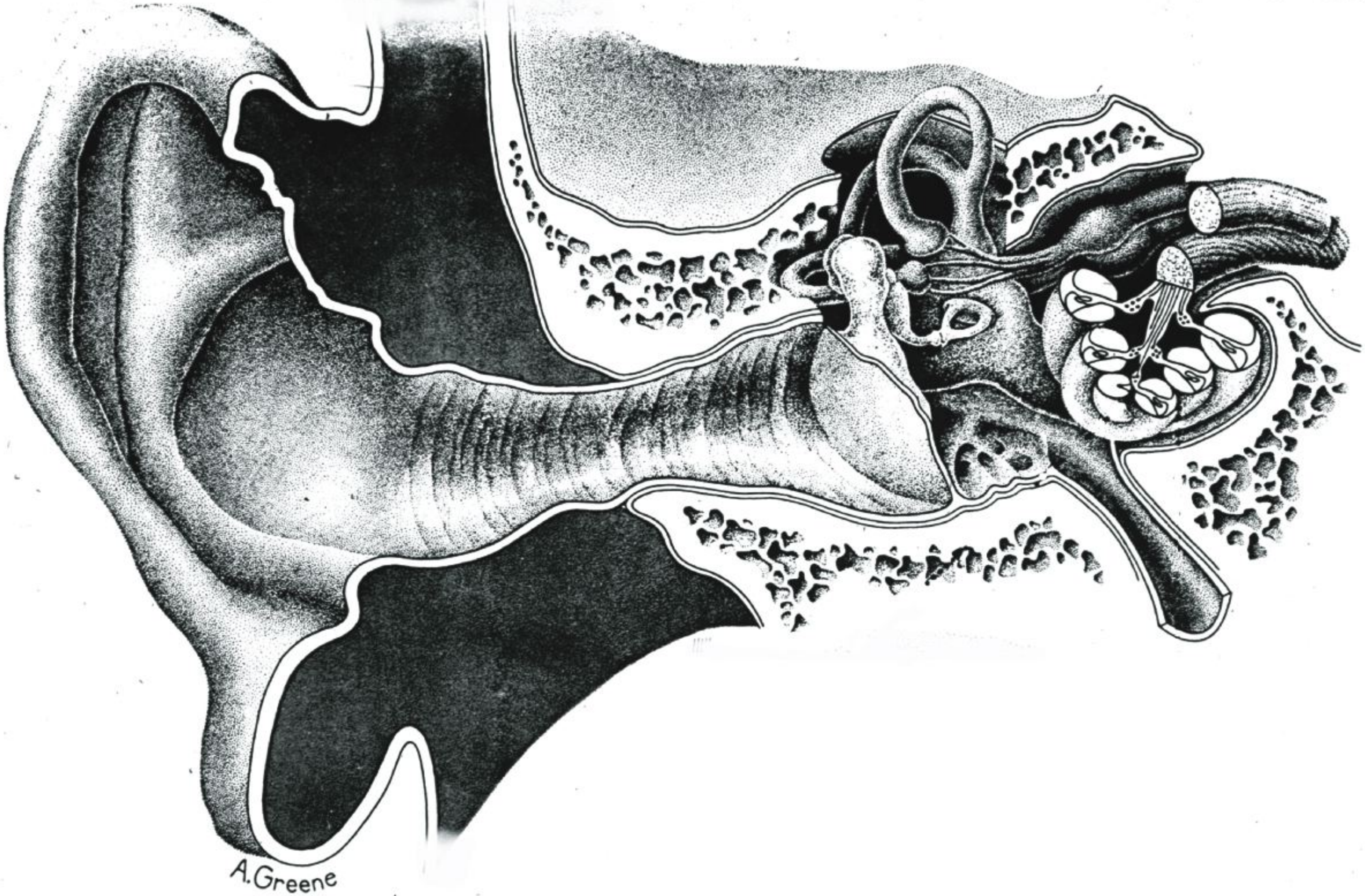
- Deutsche Forschungsgemeinschaft (CRC/TRR 31 “Active Hearing")



Fini


A.Greene

Otoacoustic Emissions (OAEs)

- Presumably by-product of amplification mechanism

- OAEs used for newborn hearing screening *(only ‘healthy’ ears emit)*

- Much faster/easier than evoked electrical potentials