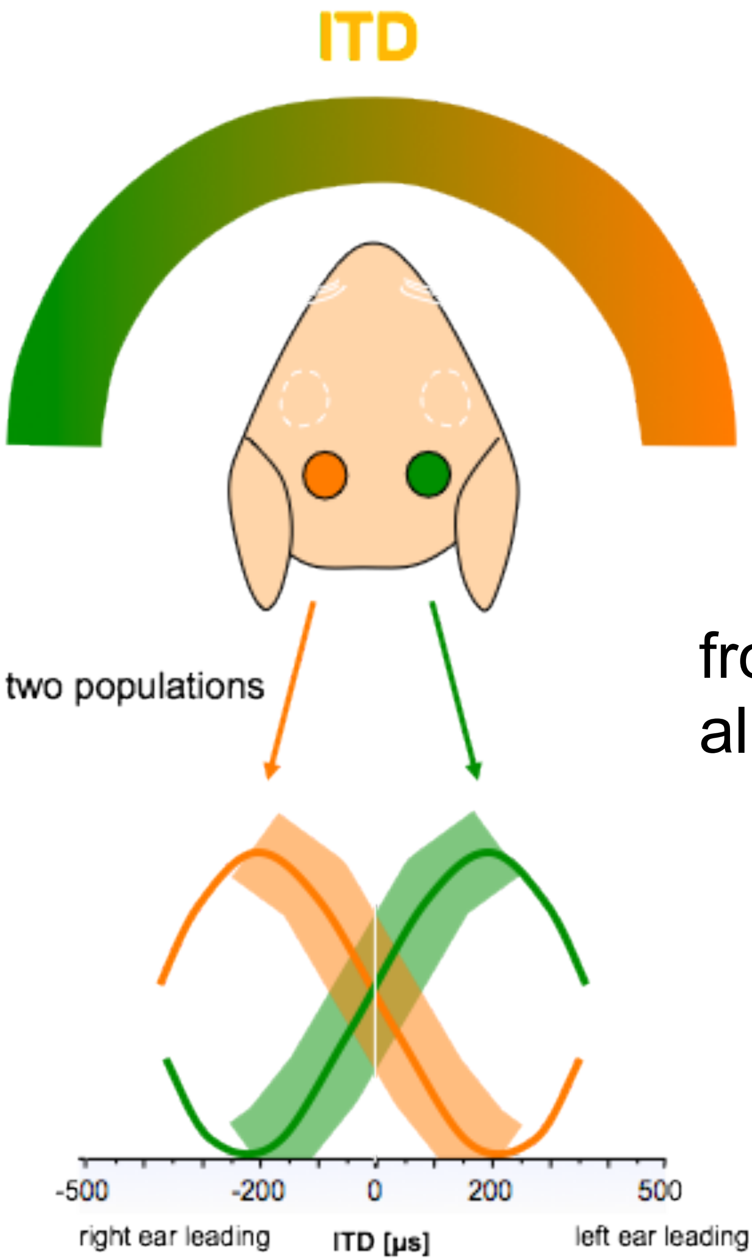
Tutorial

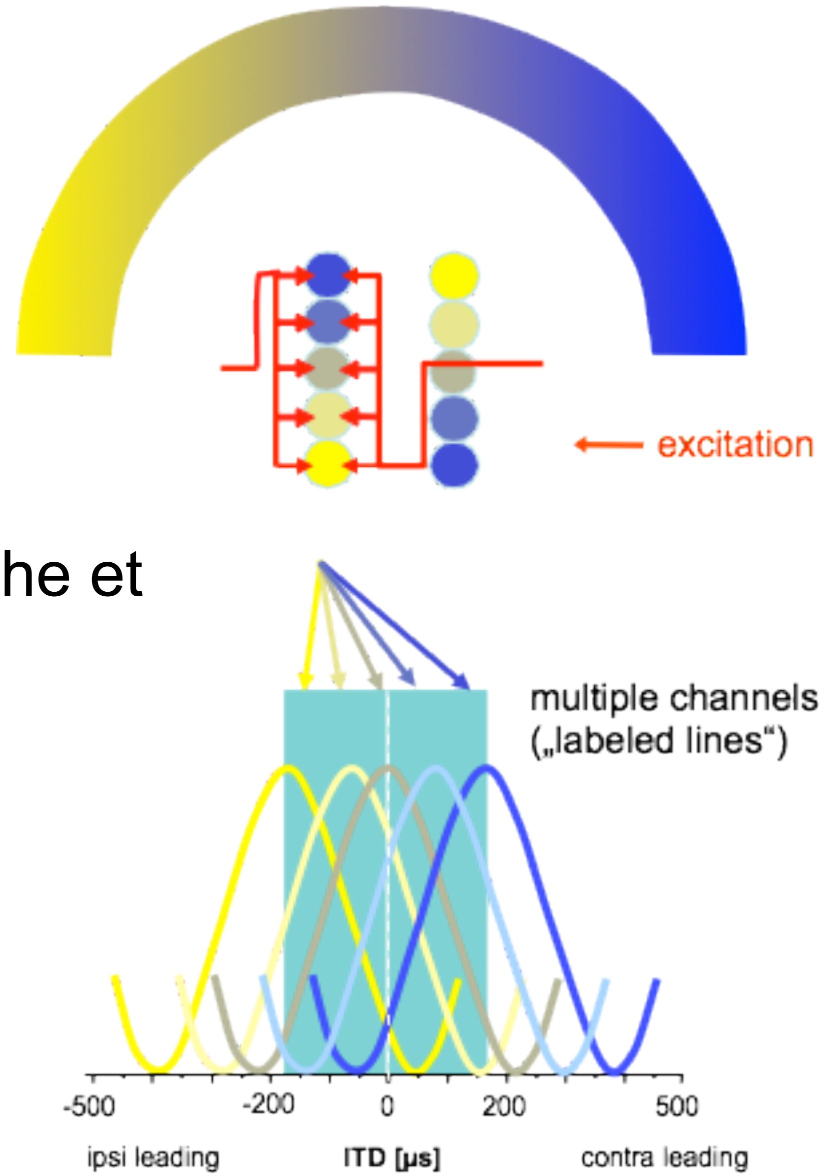
Evolution of sound localization circuits

Catherine Carr

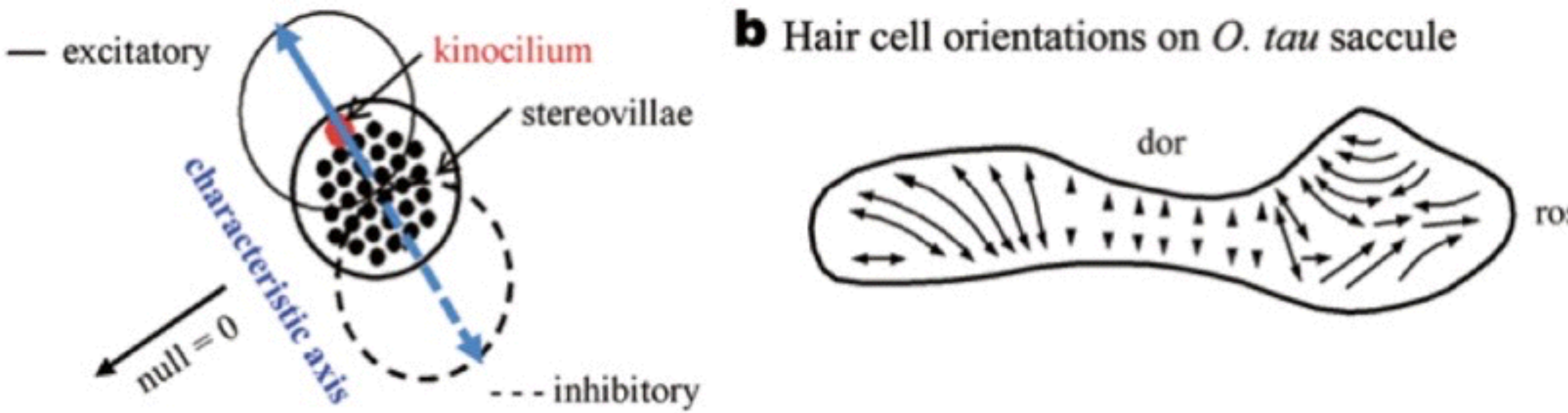
More than one way to encode ITD



from Grothe et al. 2010



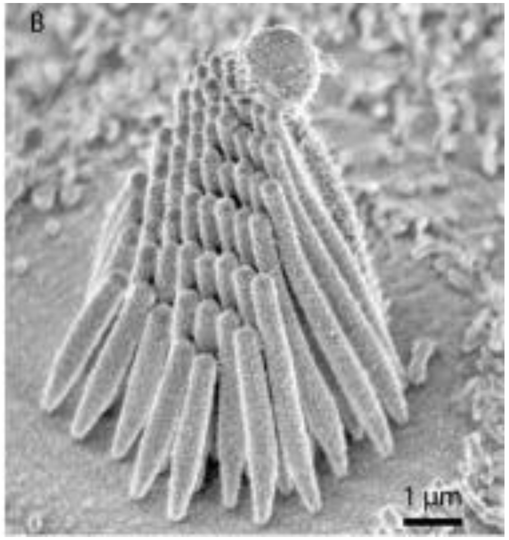
1. Hair cell patterns convey source direction



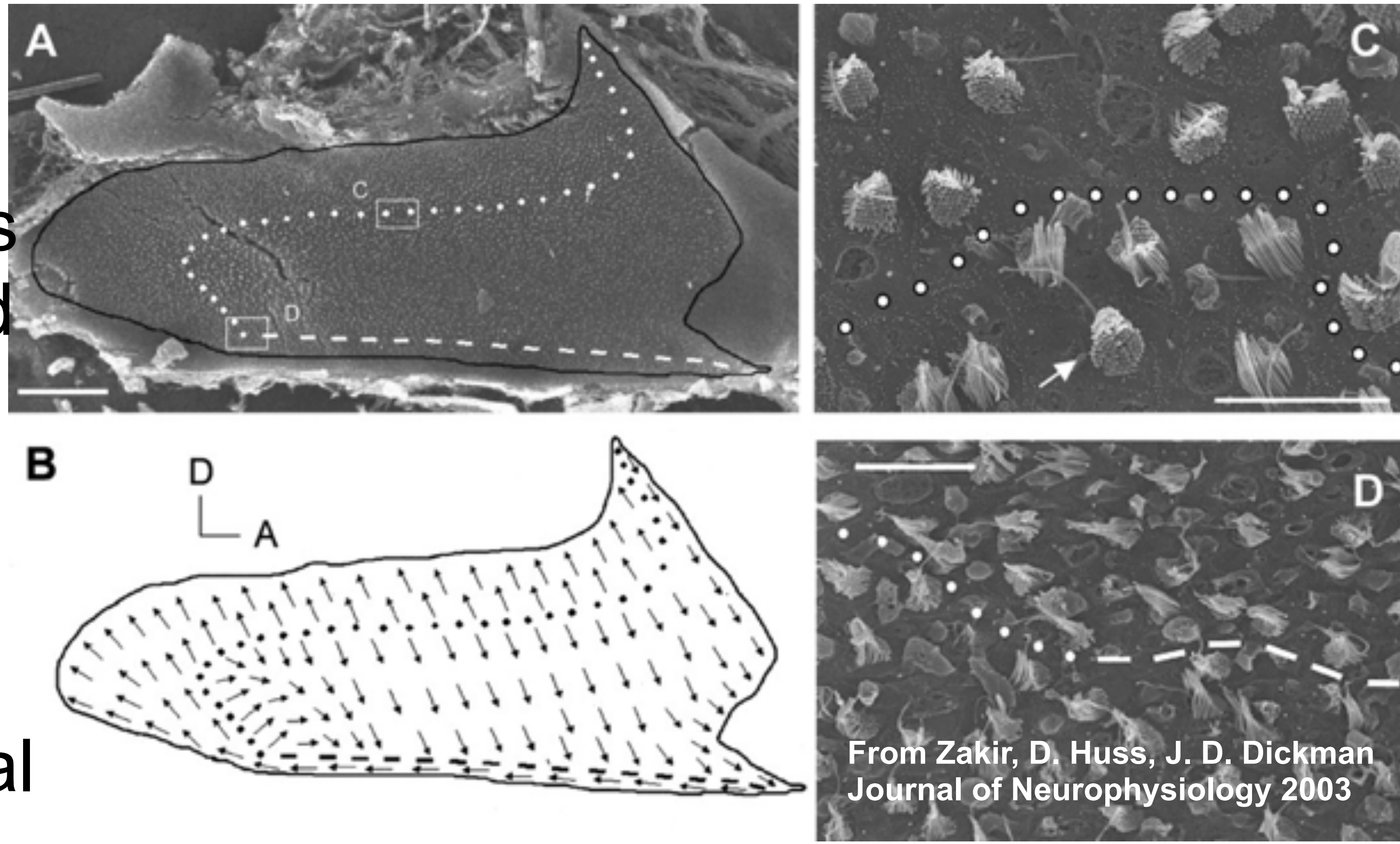
- Hair cells have a preferred direction of stimulation
- Hair cell orientation varies systematically in end organs
- Hearing in aquatic animals is likely directional

from Edds Walton, 2016

Hair cells have different, conserved polarities



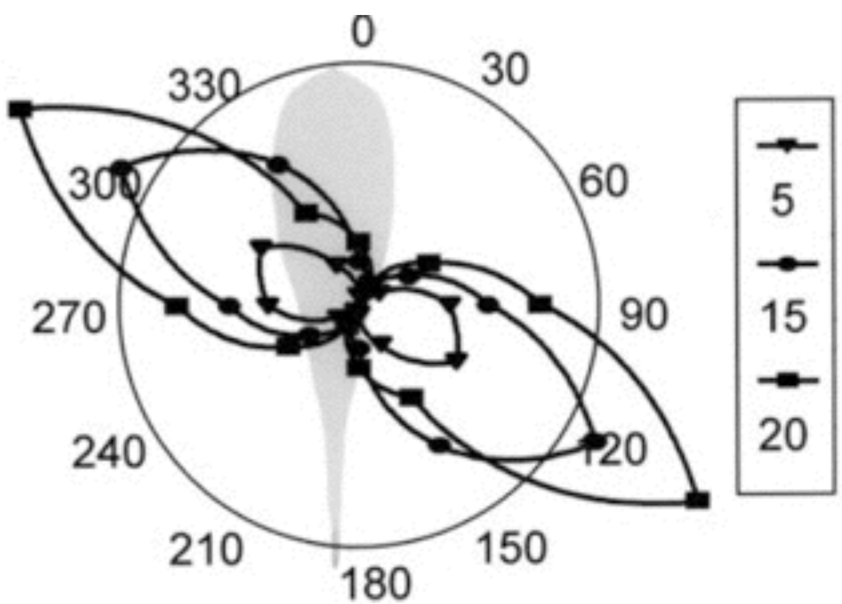
- Hair cells polarized
- Example from saccule
- bi-drectional



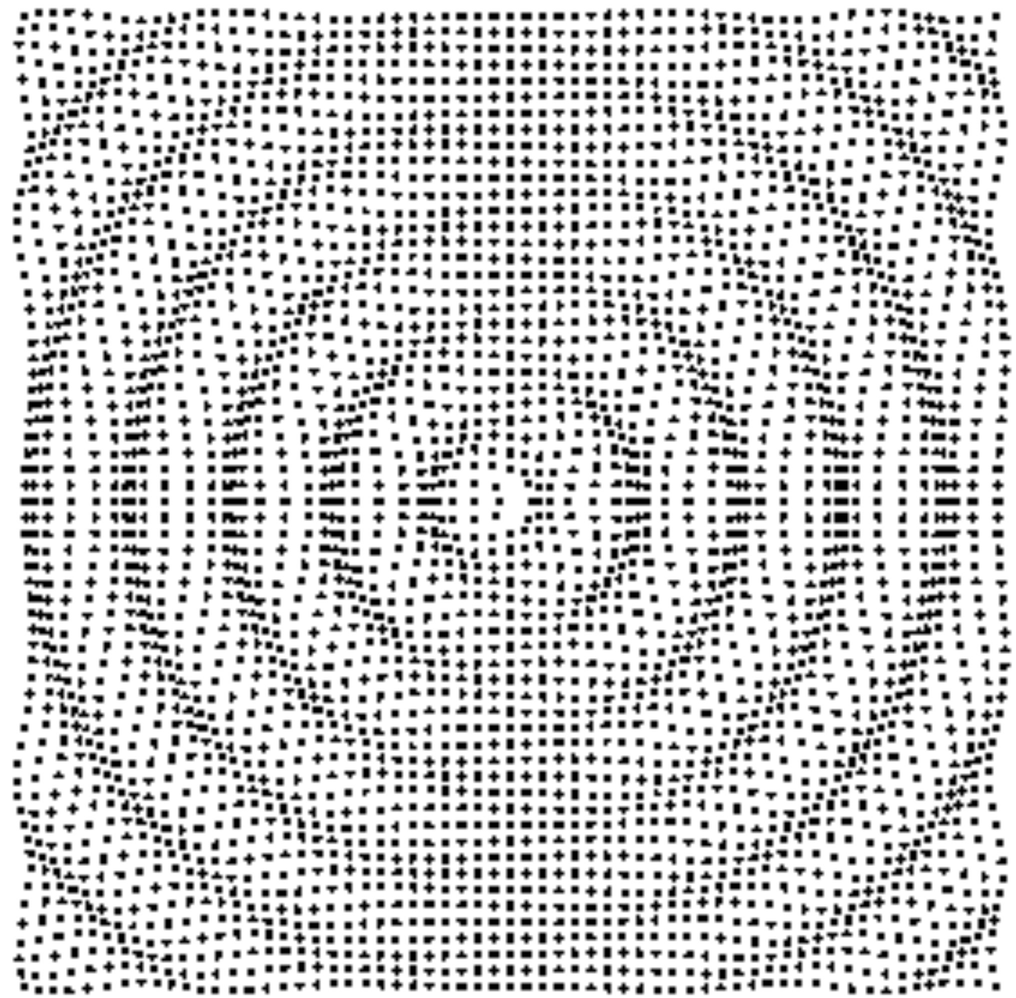
From Zakir, D. Huss, J. D. Dickman
Journal of Neurophysiology 2003

Particle motion

- Dipole source radiates, particles move back & forth
- Hair cells sensitive to particle motion, best in preferred direction. Short range.
- Record saccular fibers in 8th nerve



Saccule afferent, from Edds Walton & Fay



Animation courtesy of Dr. Dan Russell, Grad. Prog. Acoustics, Penn State

Particle motion

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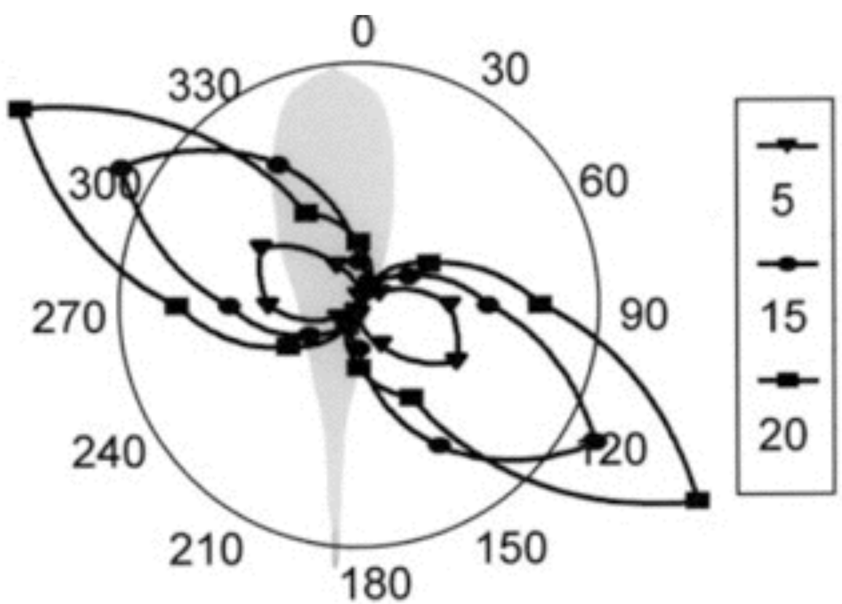

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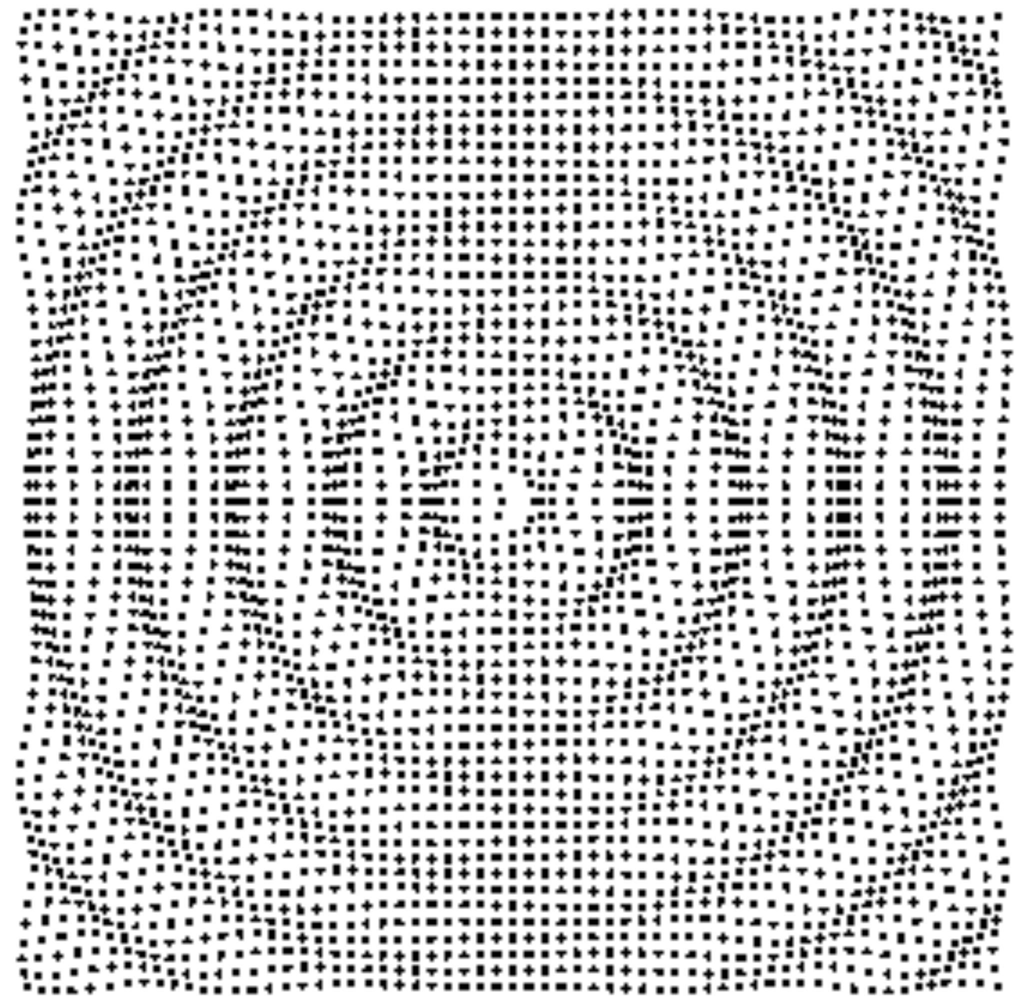
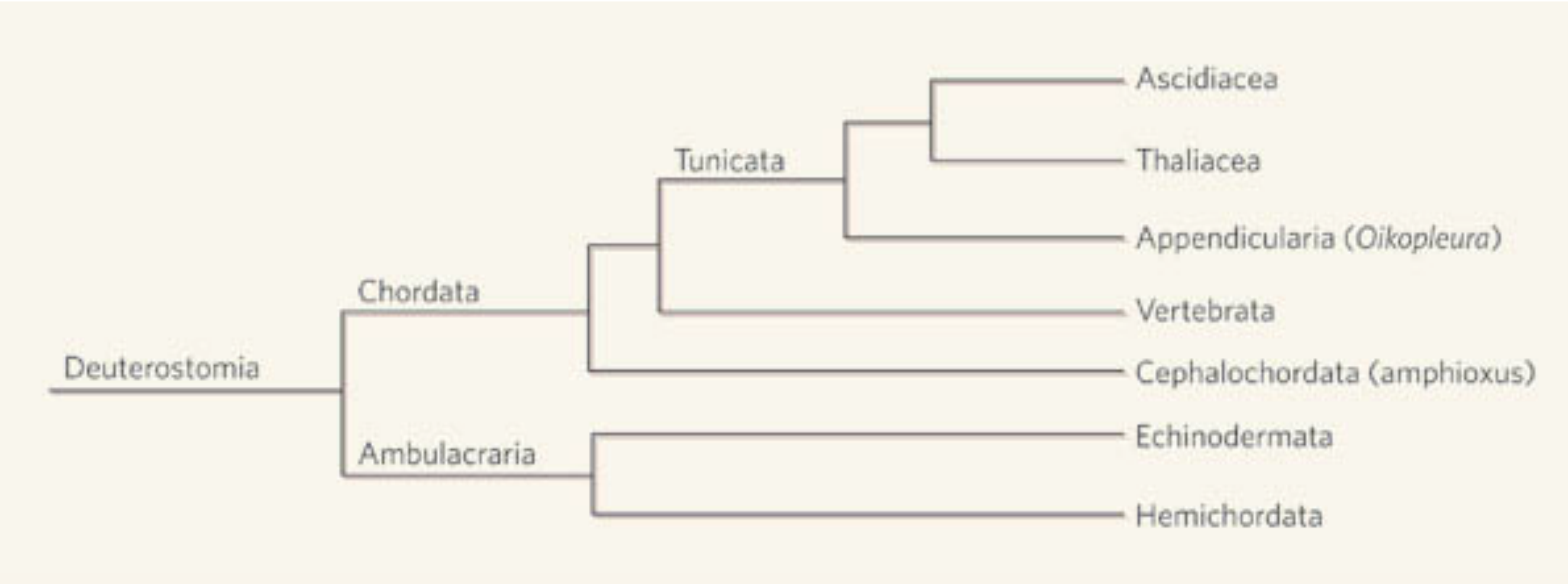
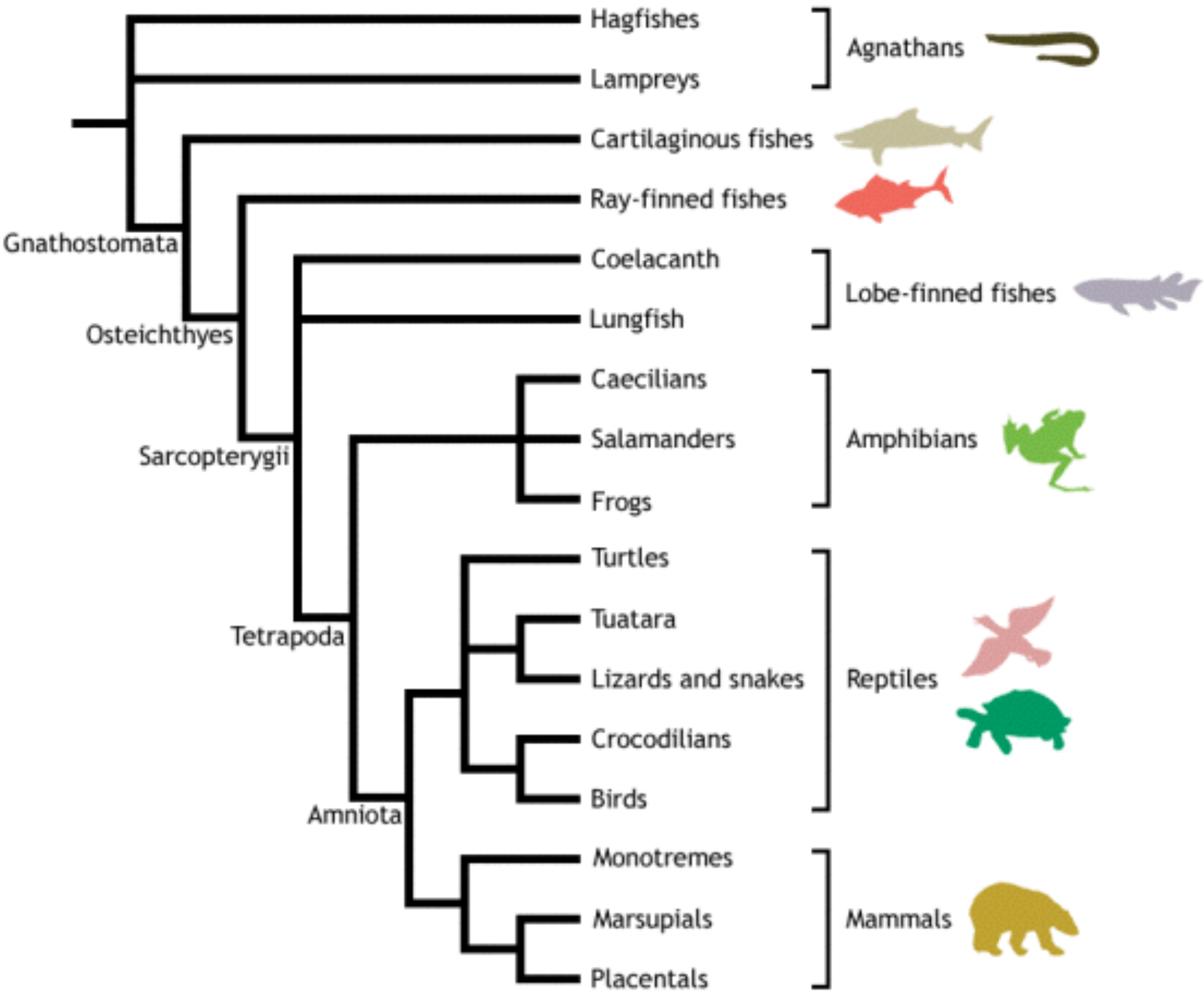


Animation courtesy of Dr. Dan Russell, Grad. Prog. Acoustics, Penn State

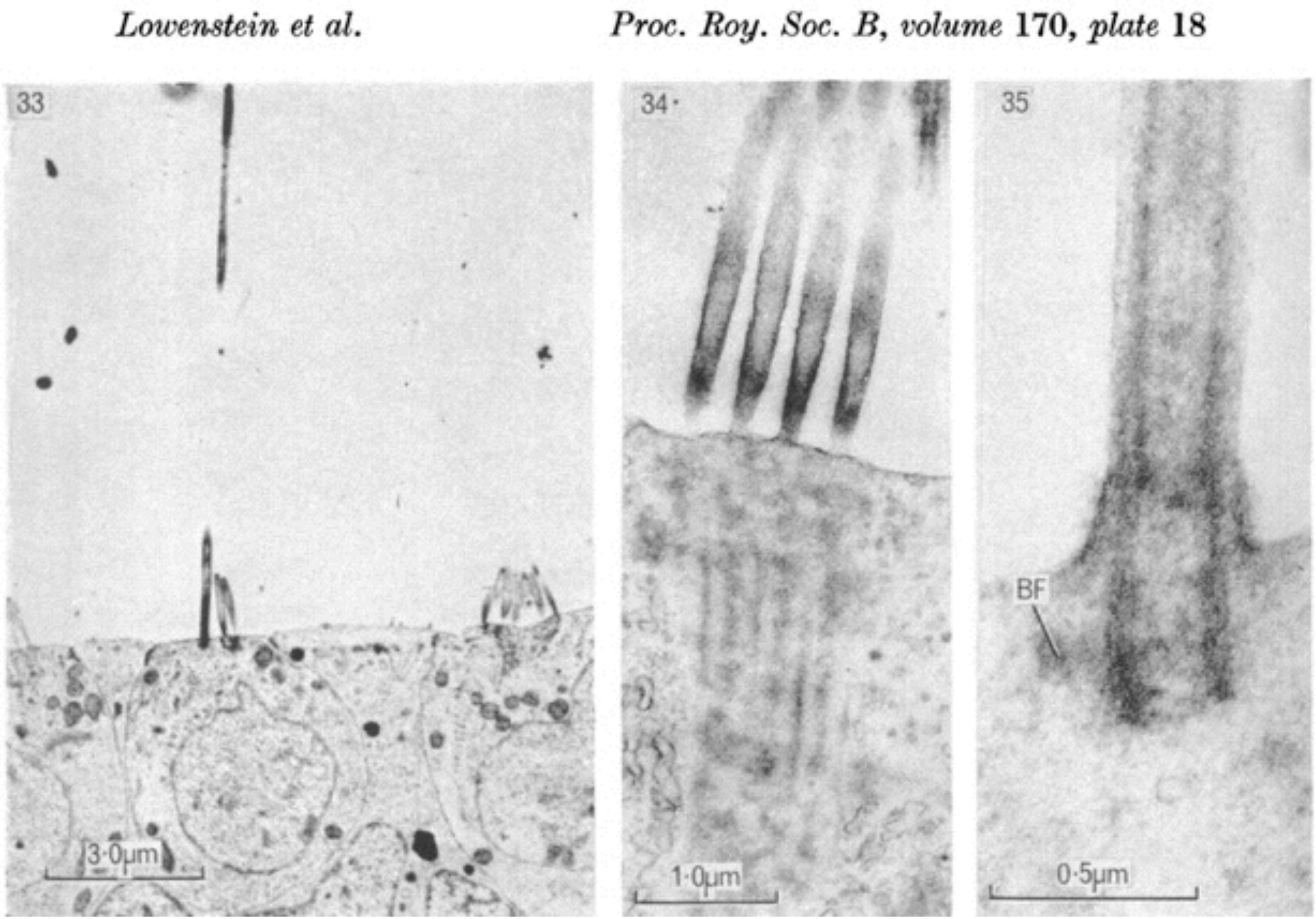
2. Phylogeny



- Chordate tree

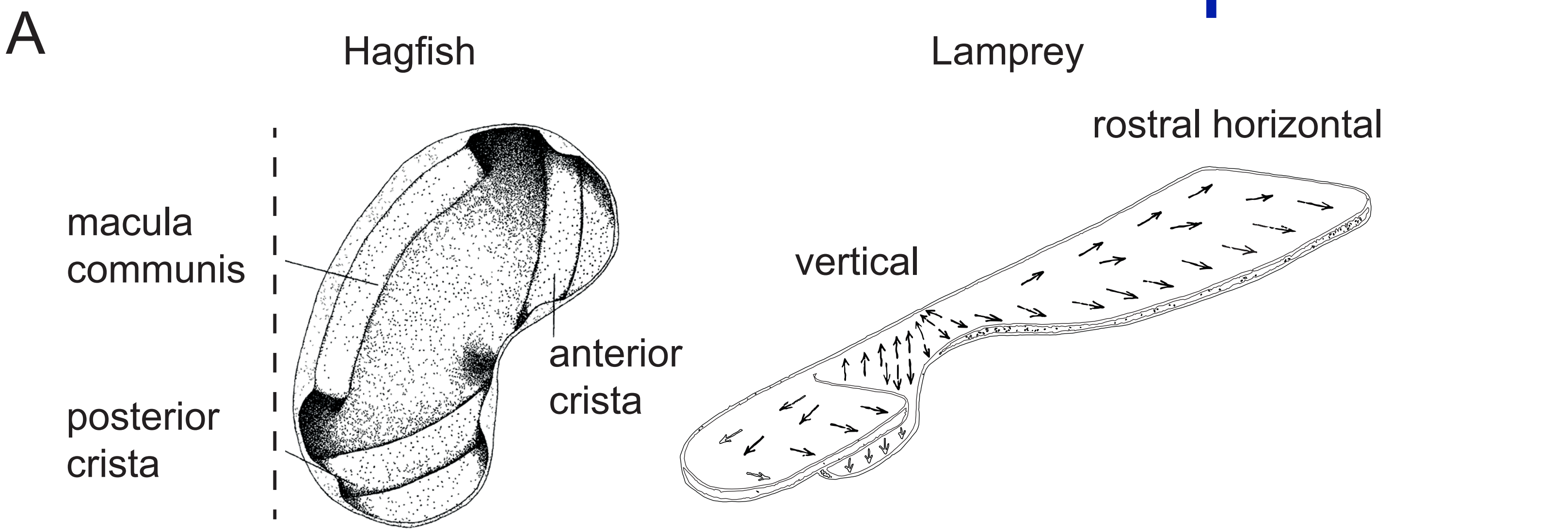

Hagfishes
Lampreys
Agnathans
Cartilaginous fishes
Ray-finned fishes
Gnathostomata
Coelacanth
Lungfish
Lobe-finned fishes
Osteichthyes
Caecilians
Salamanders
Frogs
Amphibians
Sarcopterygii
Turtles
Tuatara
Lizards and snakes
Crocodilians
Birds
Reptiles
Tetrapoda
Amniota
Monotremes
Marsupials
Placentals
Mammals

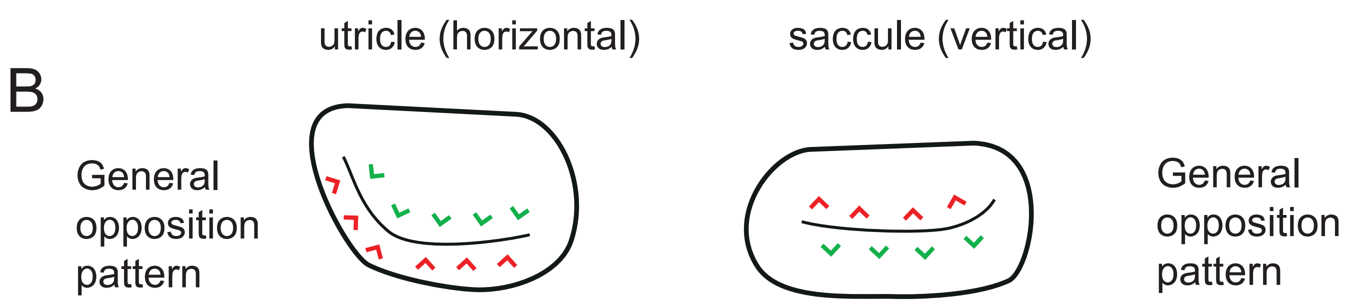
Agnathans have hair cells



- Lowenstein, lamprey anatomy & physiology

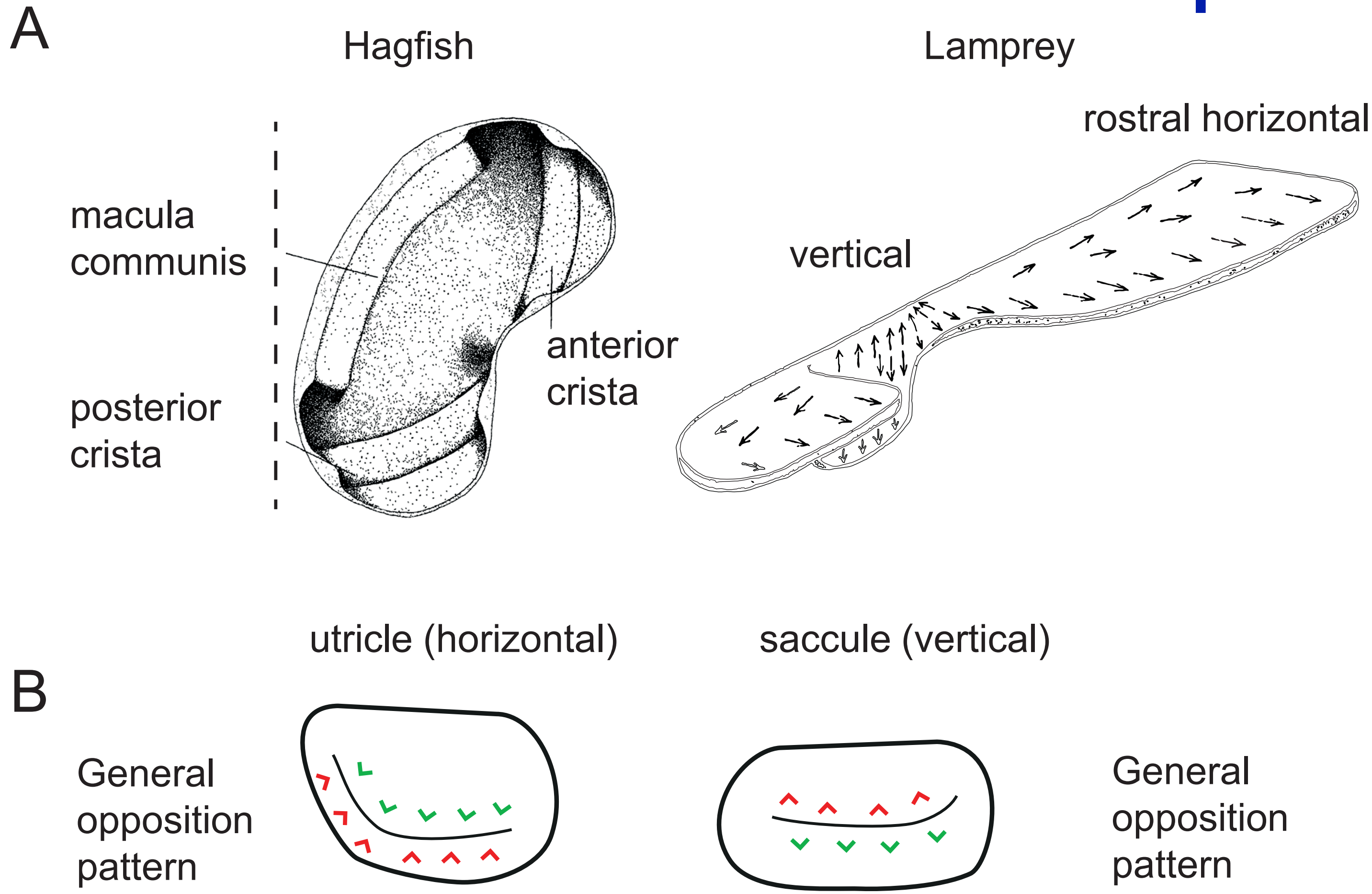
Consistent hair cell patterns

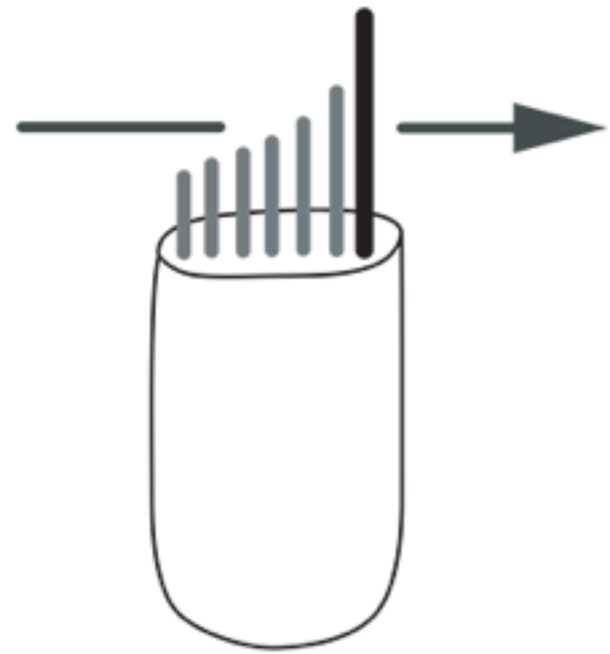




- varied directionality should create sensitivity to sound source locations

Consistent hair cell patterns

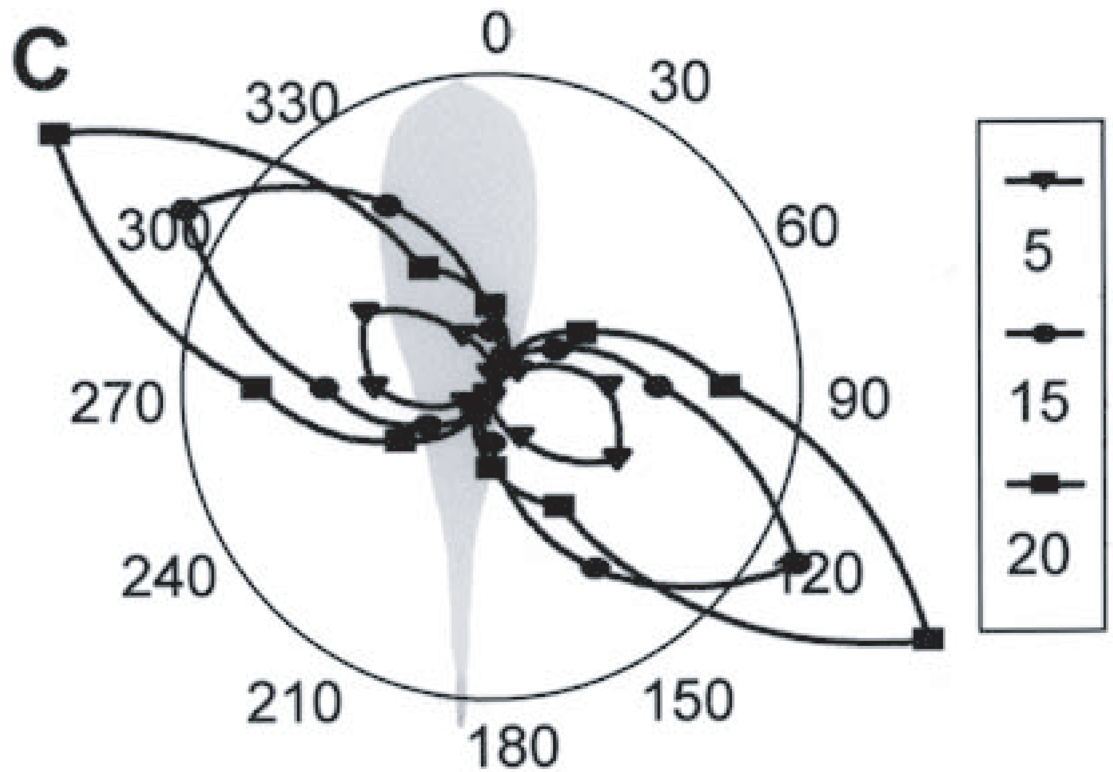




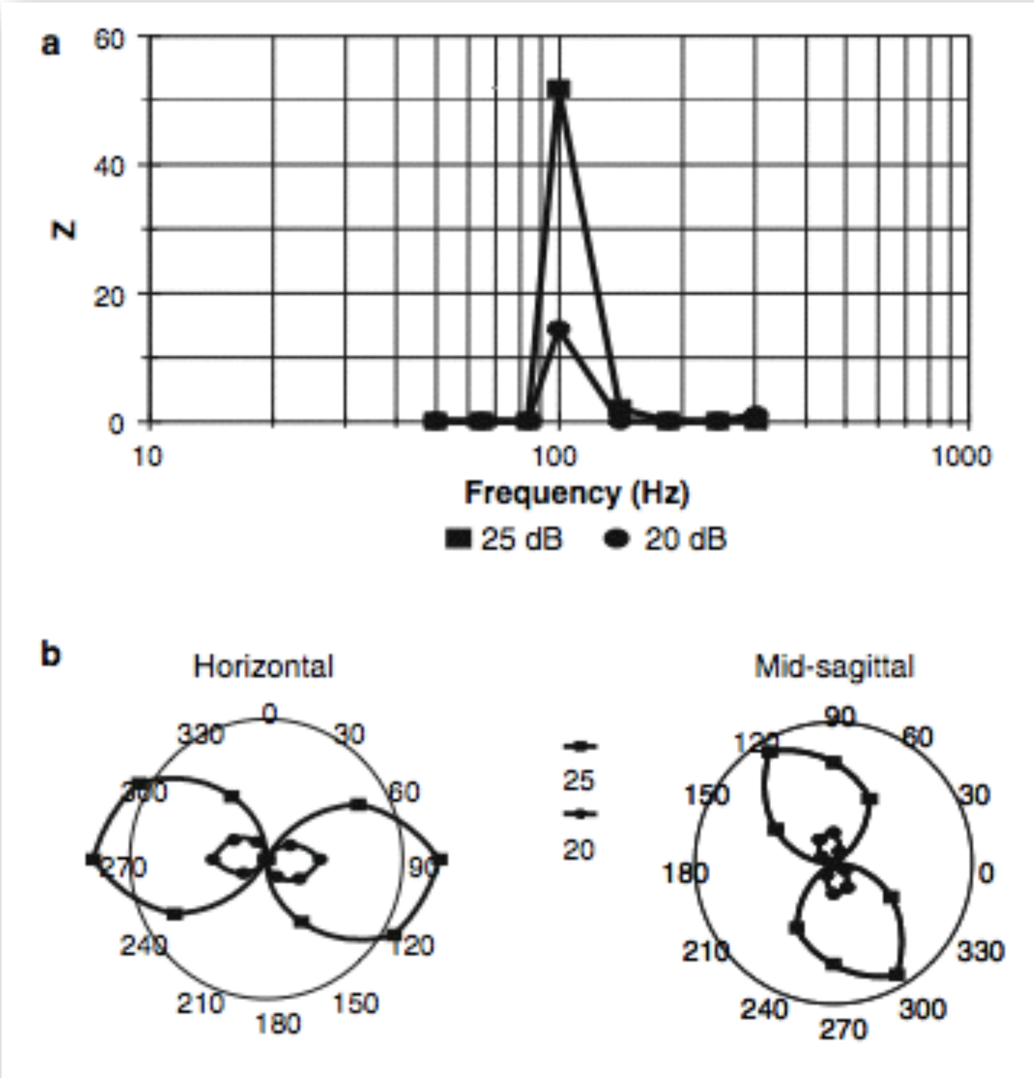
- varied directionality should create sensitivity to sound source locations

3. Directional sensitivity in fishes

- consistent with hair cell orientation
- Recordings from toadfish show strong directionality
- 180° ambiguity - direction and not source location



Saccule - short range & low frequency

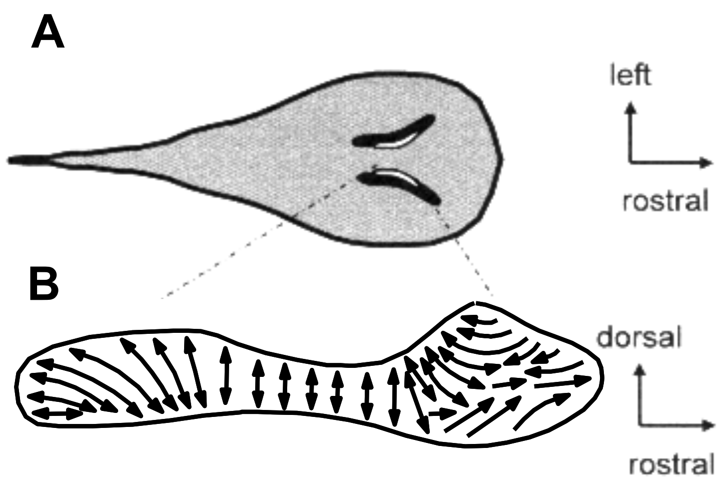


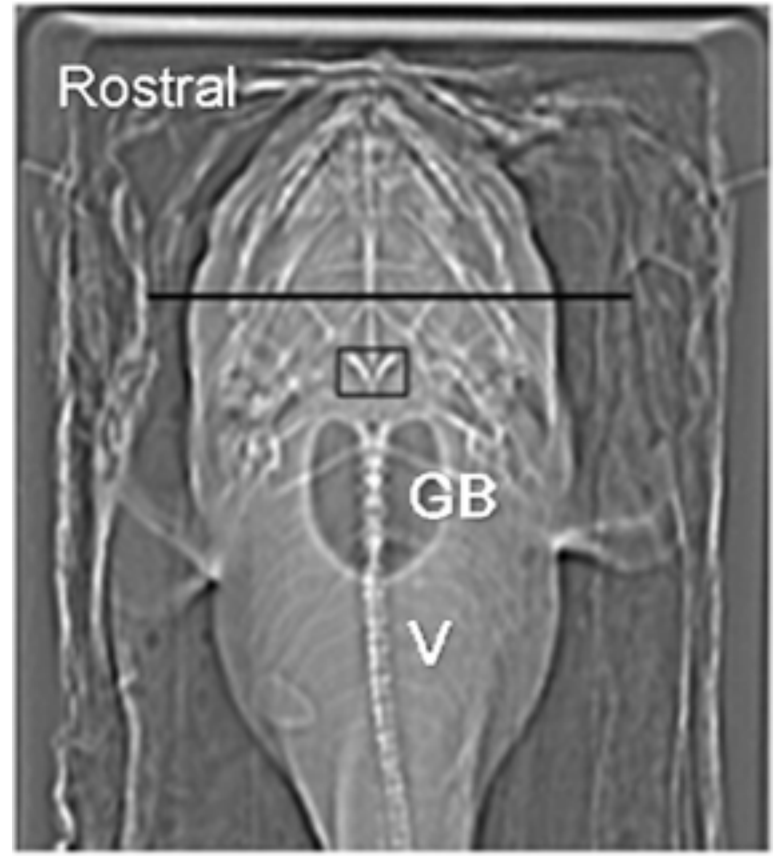
Edds-Walton and Fay, 2008

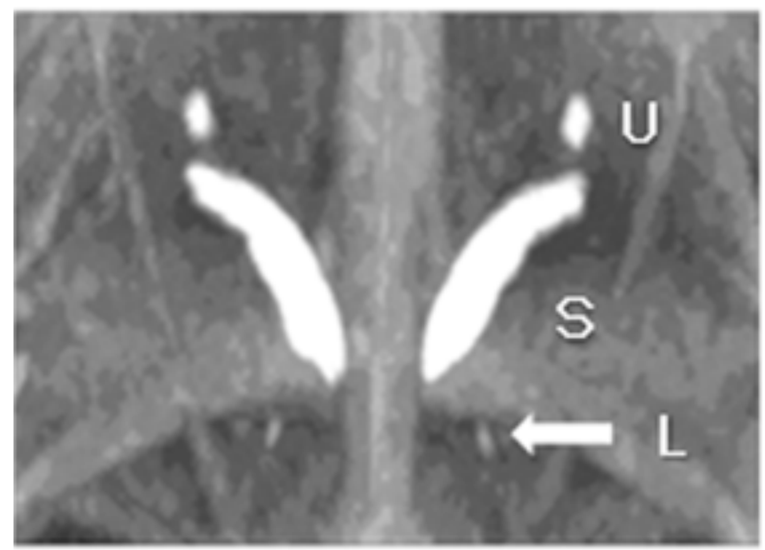
- Hearing in aquatic ancestors would likely have been directional
- Unless teleosts specialize by adding bubbles, or Webberian ossicles, frequency range is small

From directionality to source localization

- x-ray of toadfish shows saccule orientation
- not parallel, so homotypic hair cells not stimulated equally

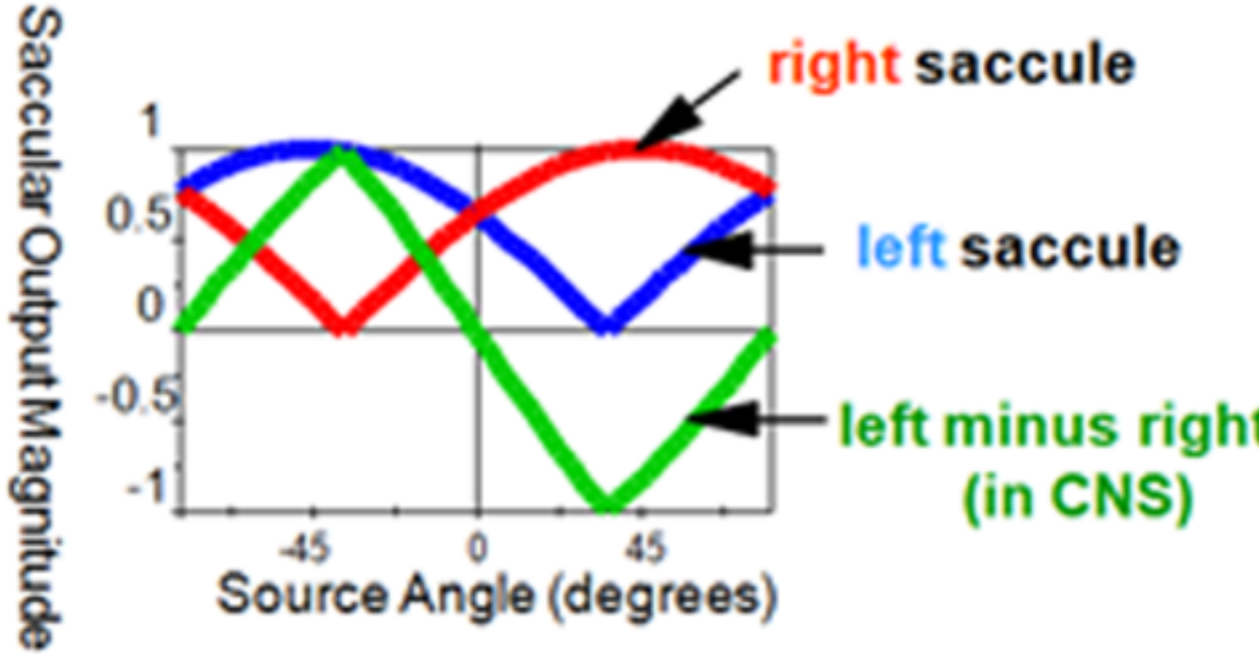


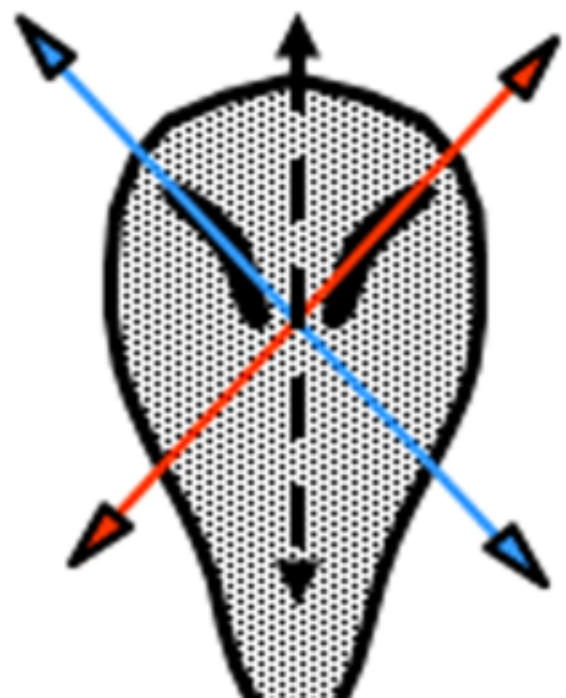




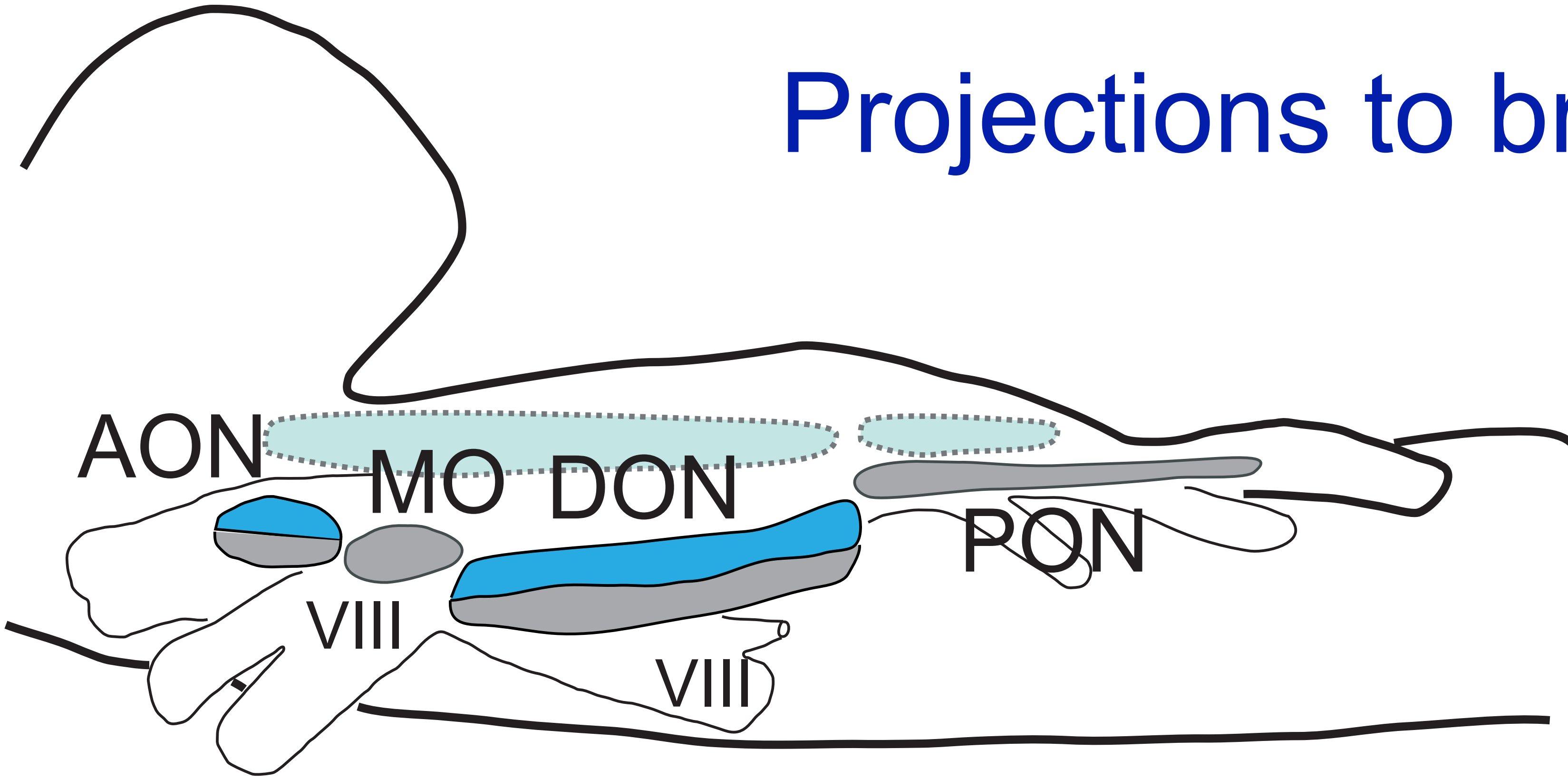
compare across midline

- Behavior - sound producing fish can localize mates
- anatomy - connections across midline
- physiology -





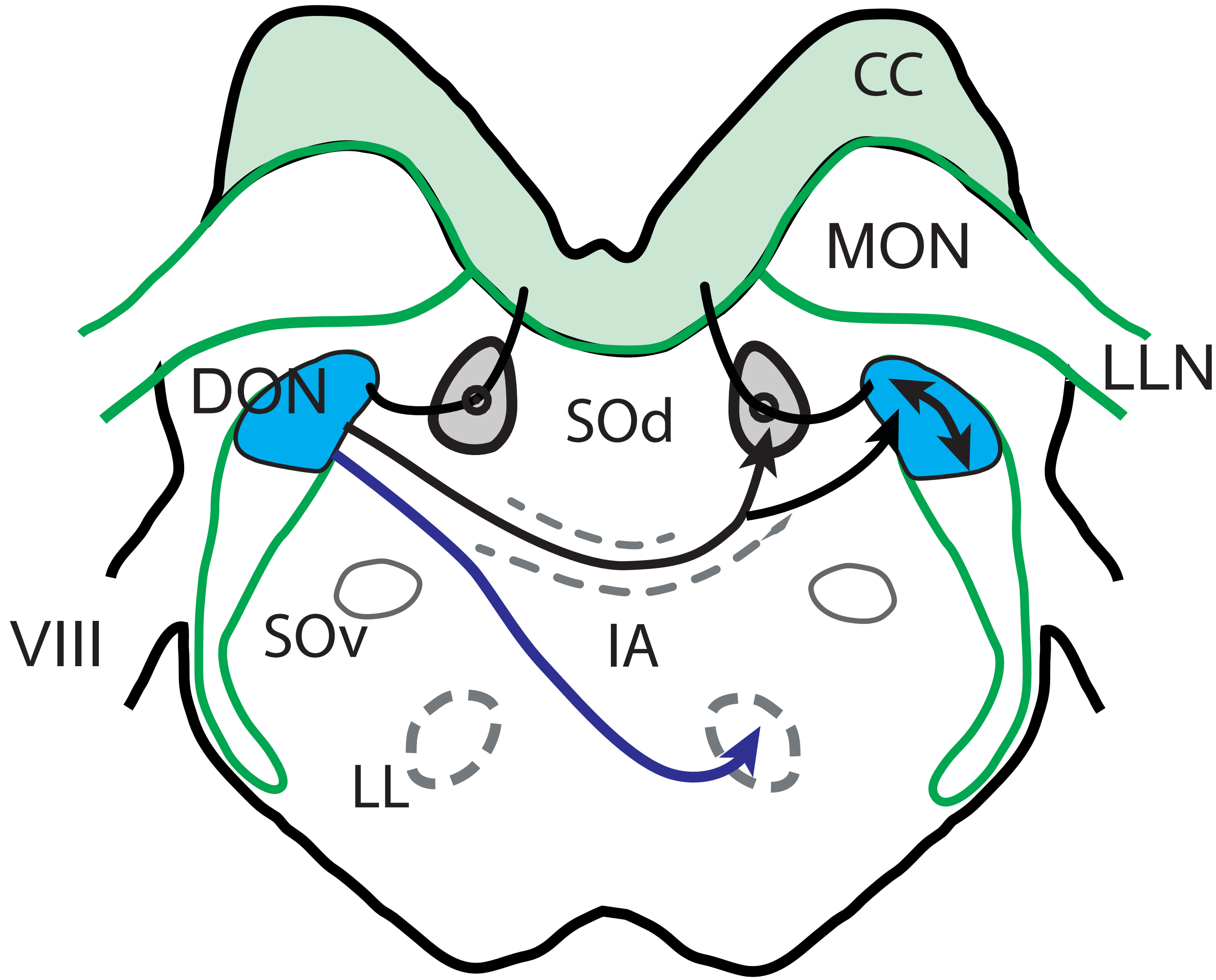
Projections to brain



- Auditory inputs (usually from saccule)
- Project to two targets, anterior and descending
- No apparent tonotopy

Directional circuits in fishes

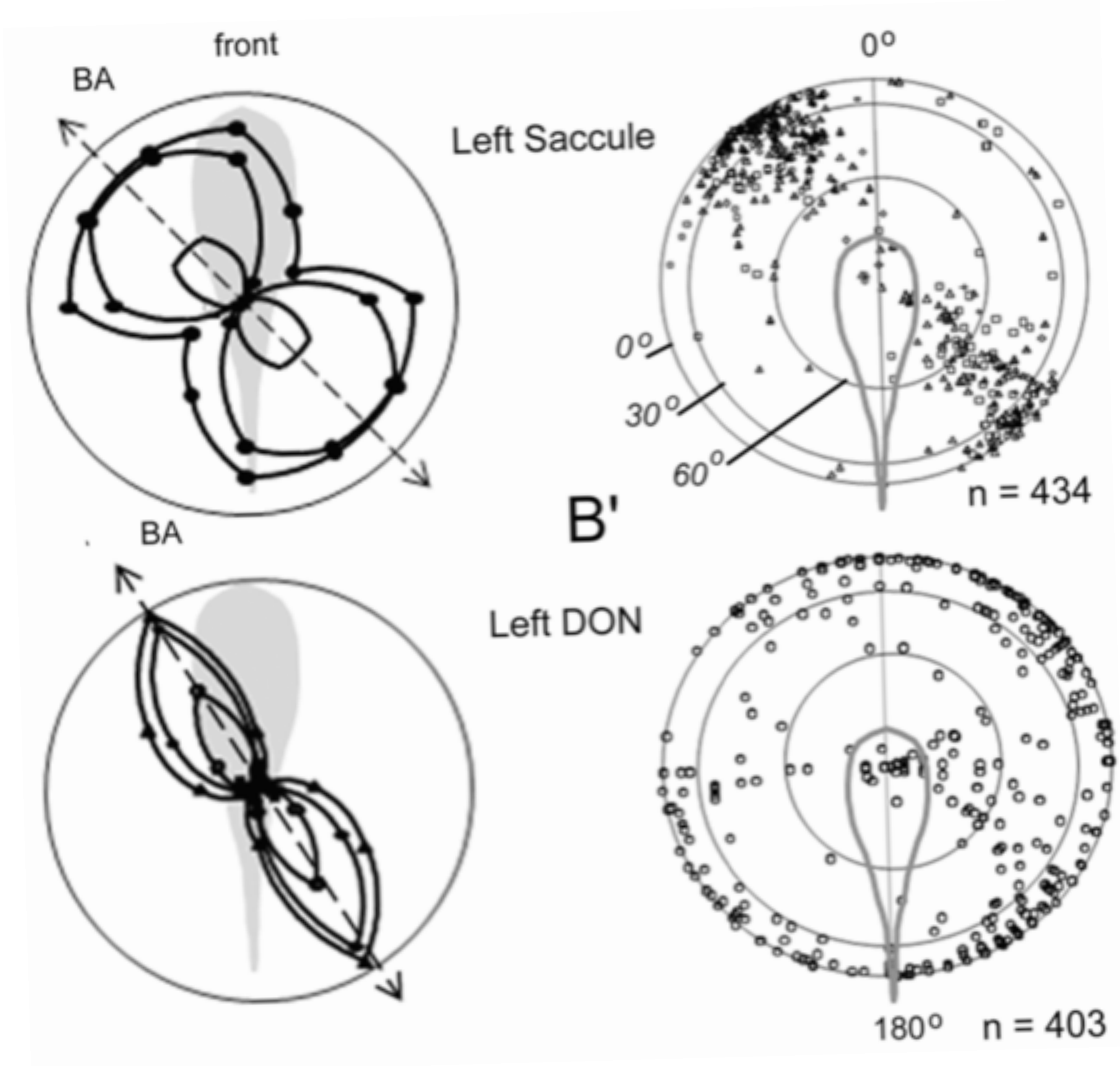
- Teleost auditory brainstem has strong EI connections across midline
- Projects within DON & projects across midline in internal arcuate tract



from Edds Walton, 2017

Nerve to brain

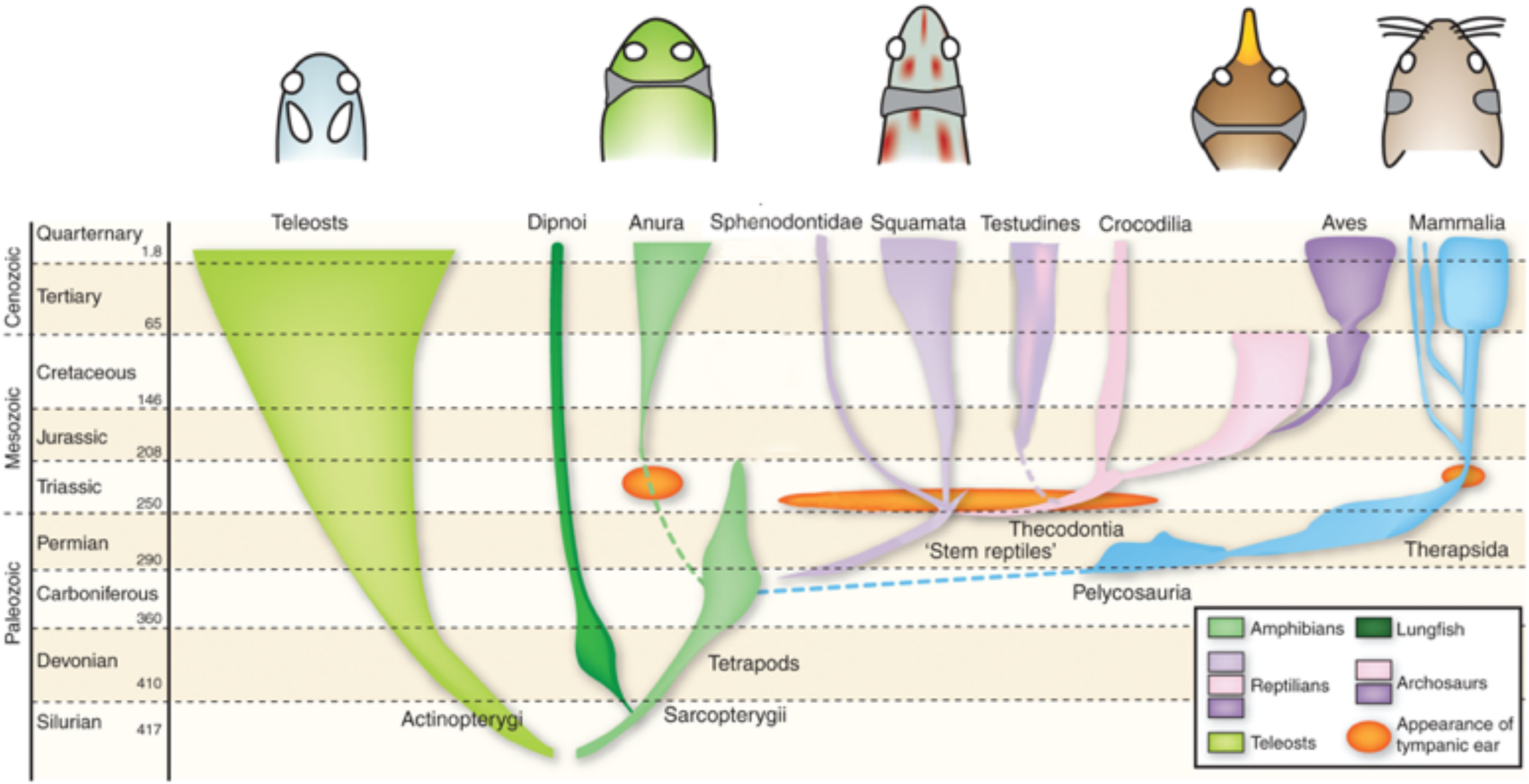
- responses sharpen in brain
- range of directions increases



Can’t do physiology on fossils

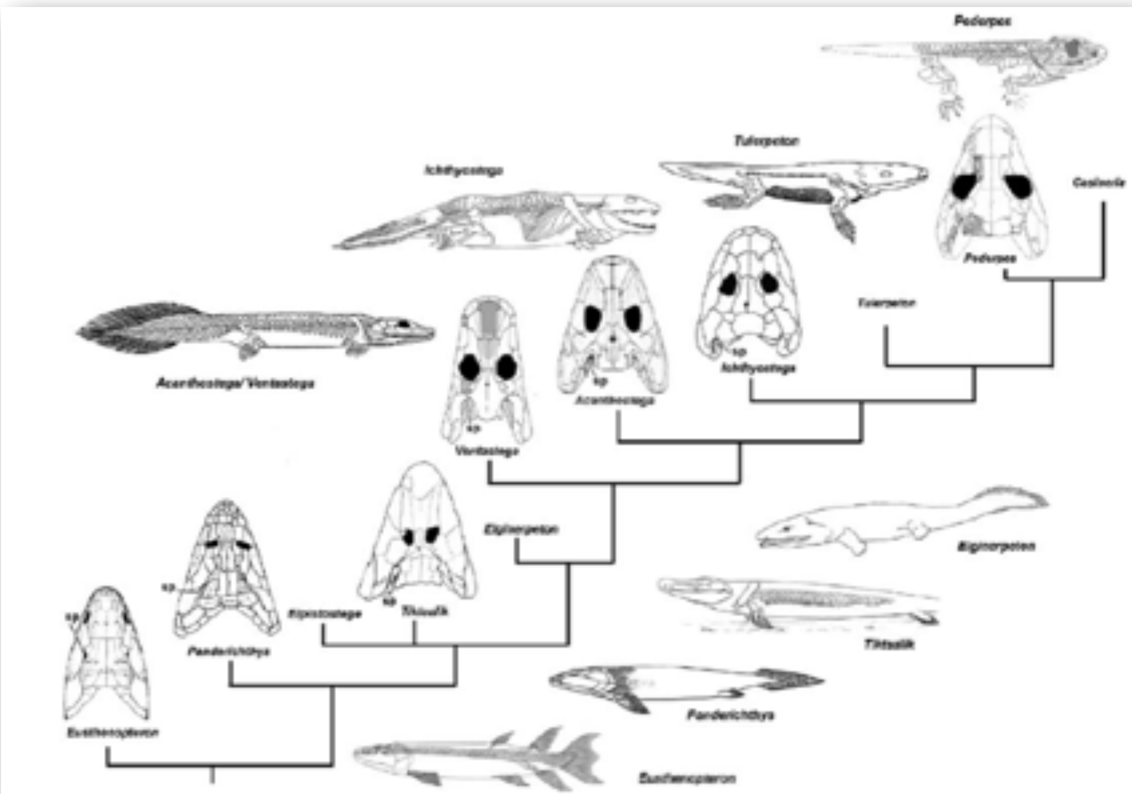
- assume early tetrapods similar to non-specialist fish
- therefore possessing directional hearing
- review tetrapods
- ask what happens with movement onto land

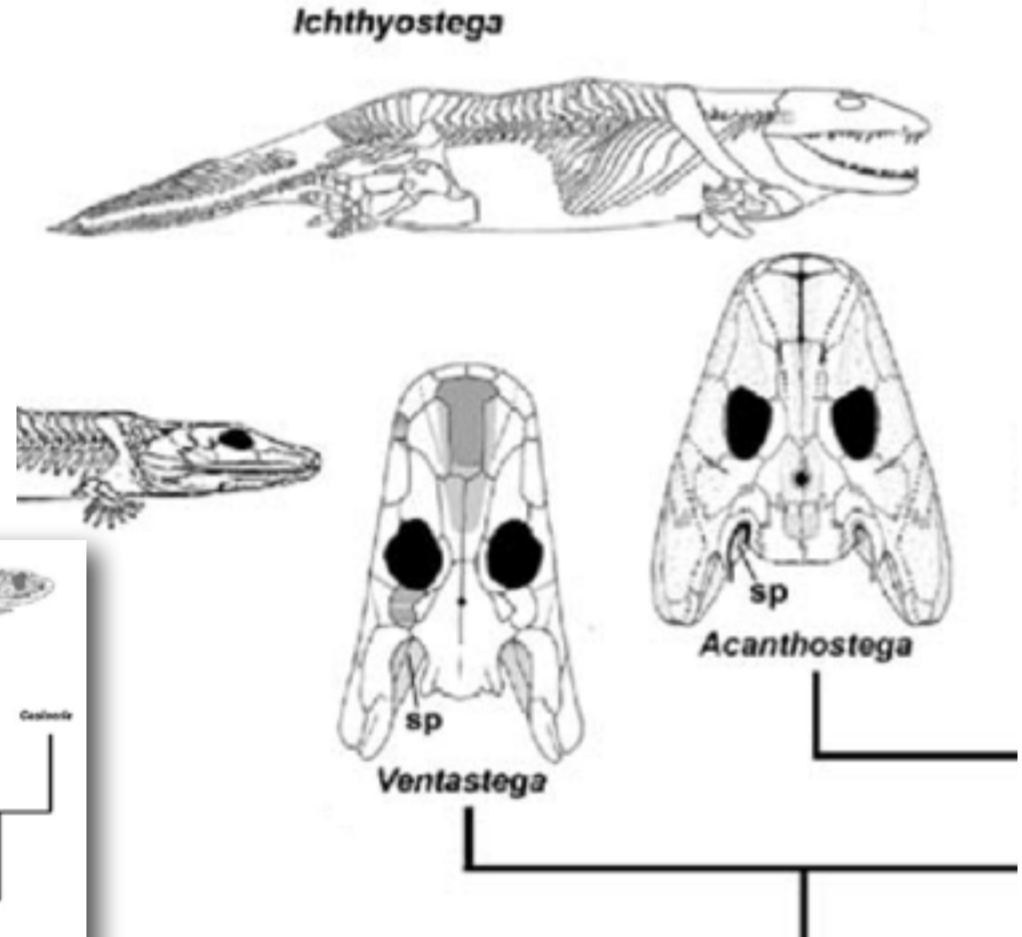
4. capabilities of early tetrapods



- Lobe finned fishes,
tetrapods

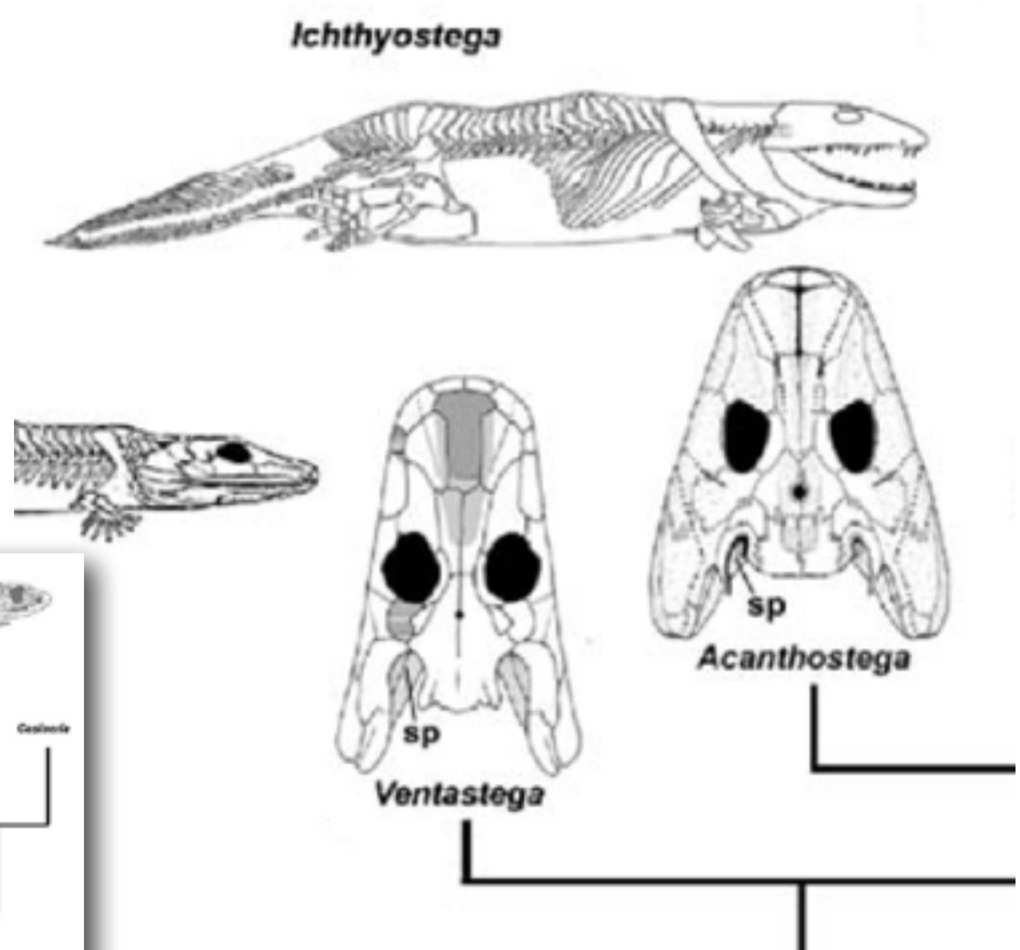
Ancestral tetrapods

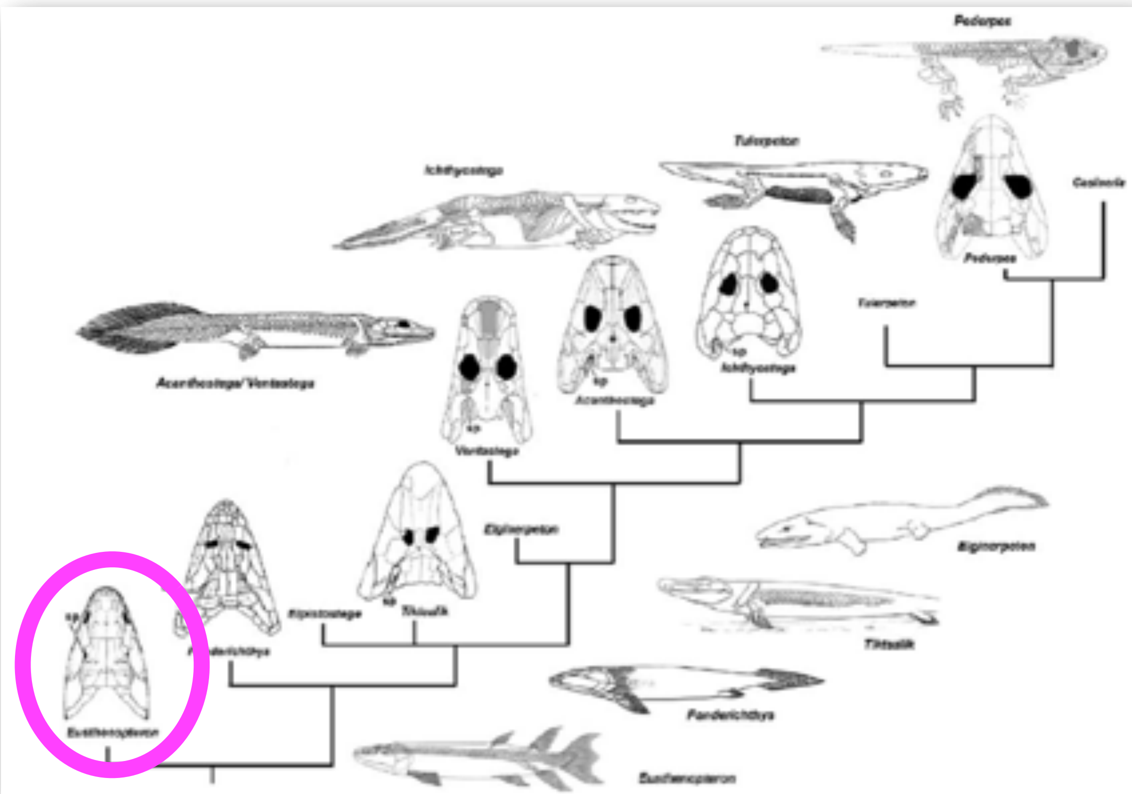




From Clack, 2009

Ancestral tetrapods





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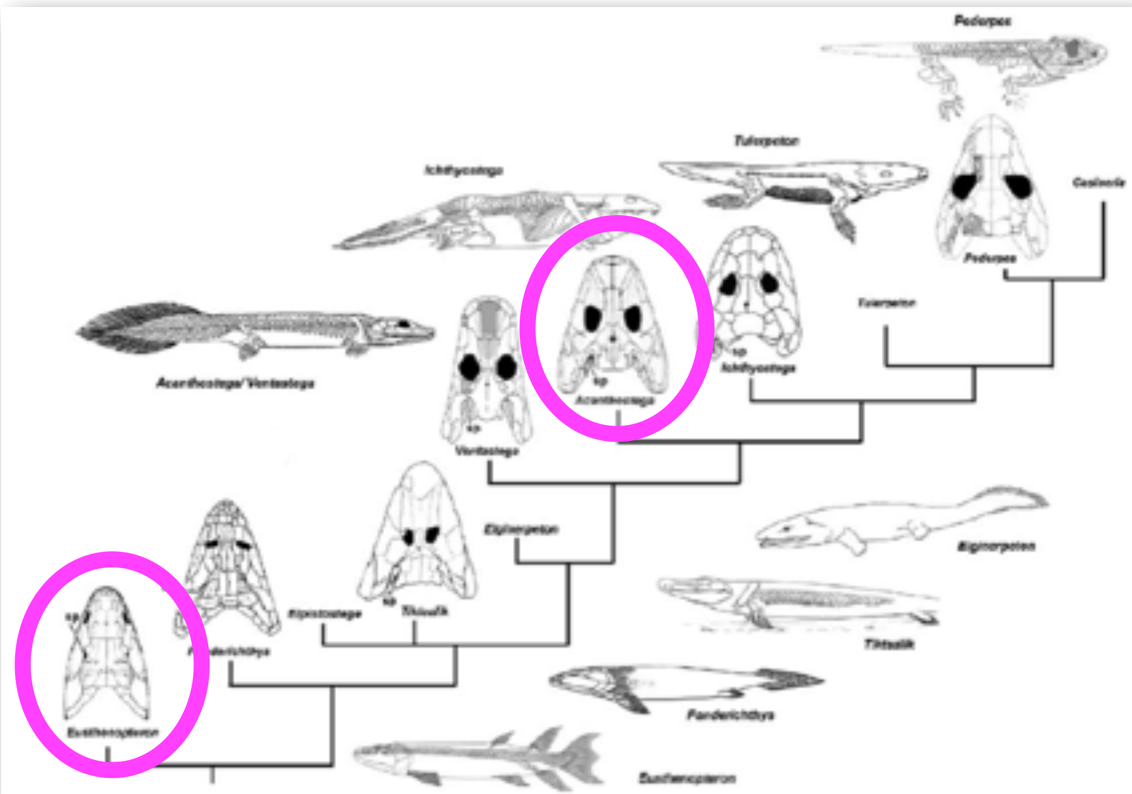
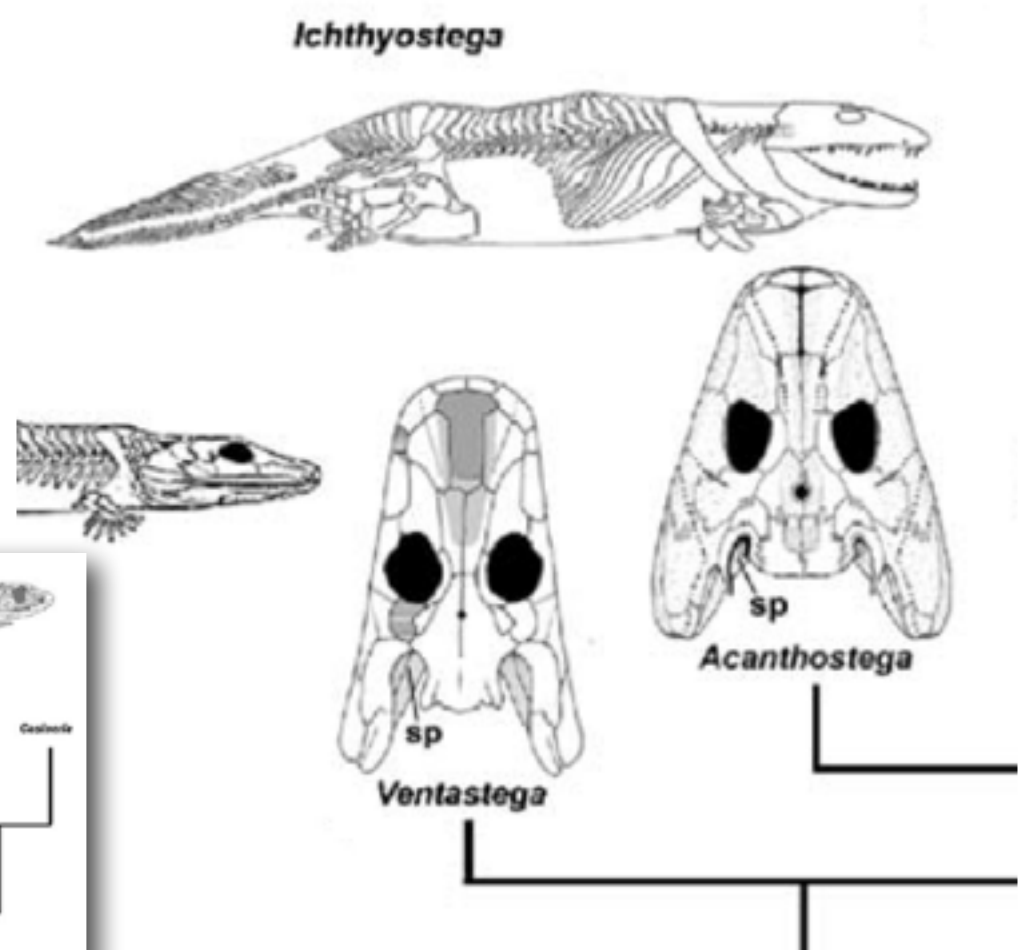
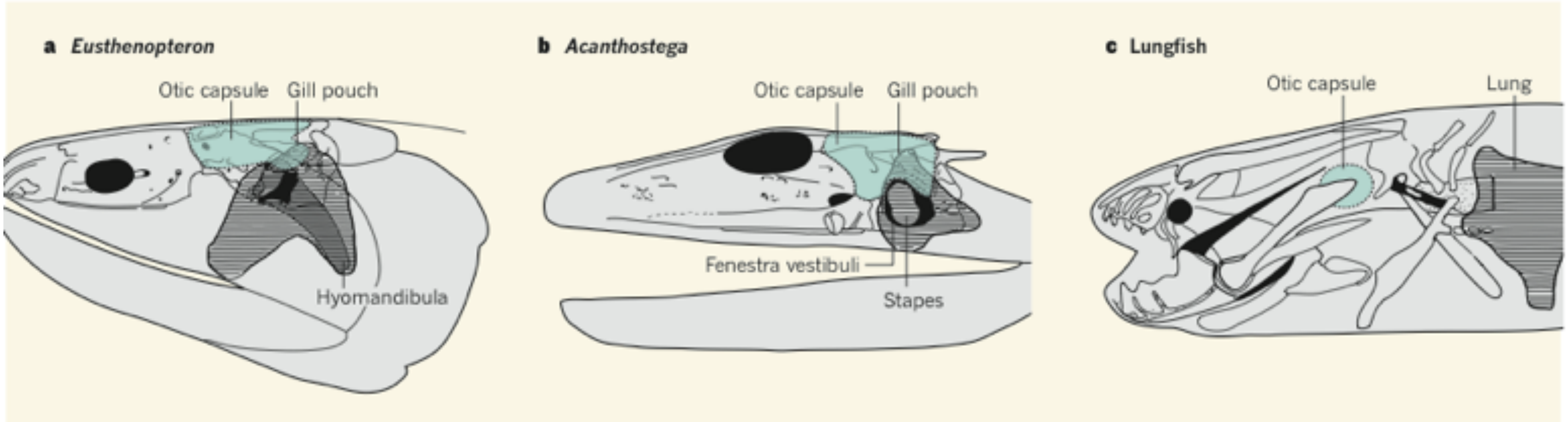




From Clack, 2009

Clack: What could early tetrapods hear?



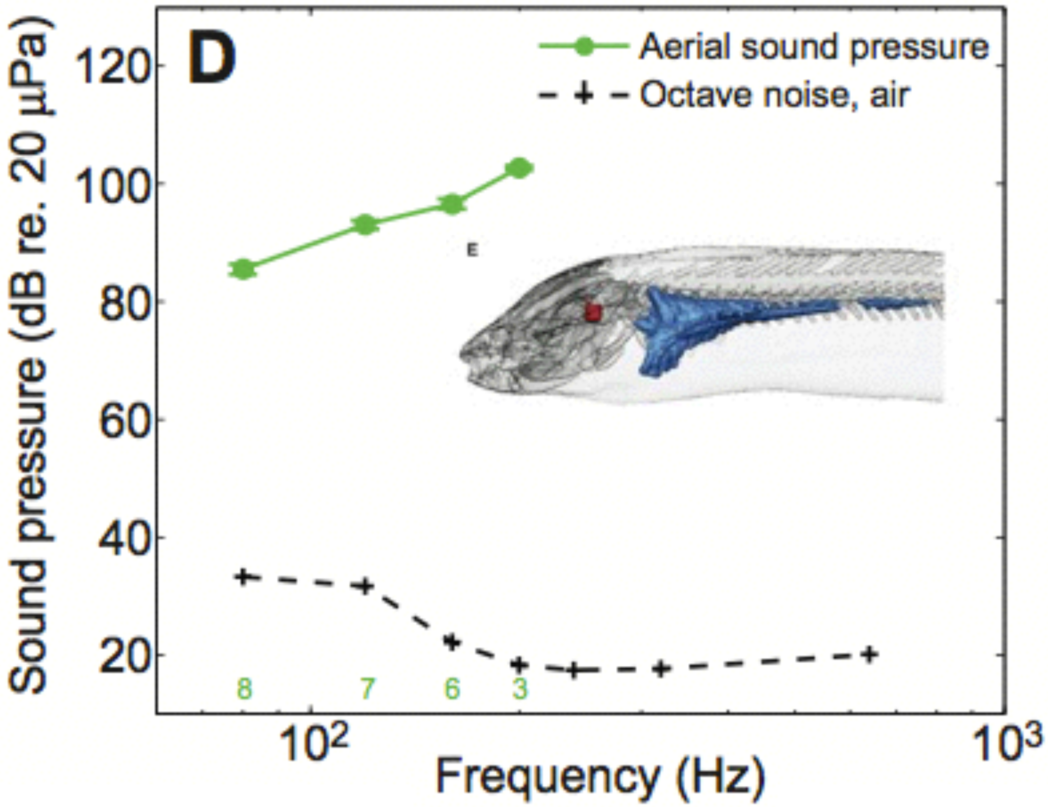
from Clack 2015 News & views

- Earliest tetrapods seem not to have had a specialized apparatus (tympanum) for terrestrial hearing, so to what extent could they hear air borne sound?

Clack hypotheses

- In the earliest osteichthyans, proximity of the mobile hyomandibula to an **air-filled chamber** could have allowed pressure-induced vibrations to be transmitted to the inner ear.
- If air breathing were a primitive osteichthyan characteristic, then could have detected sound propagated in water, through the substrate, or even in air
- may have heard better than modern lungfishes.
- discuss early hearing, ears and neural circuits

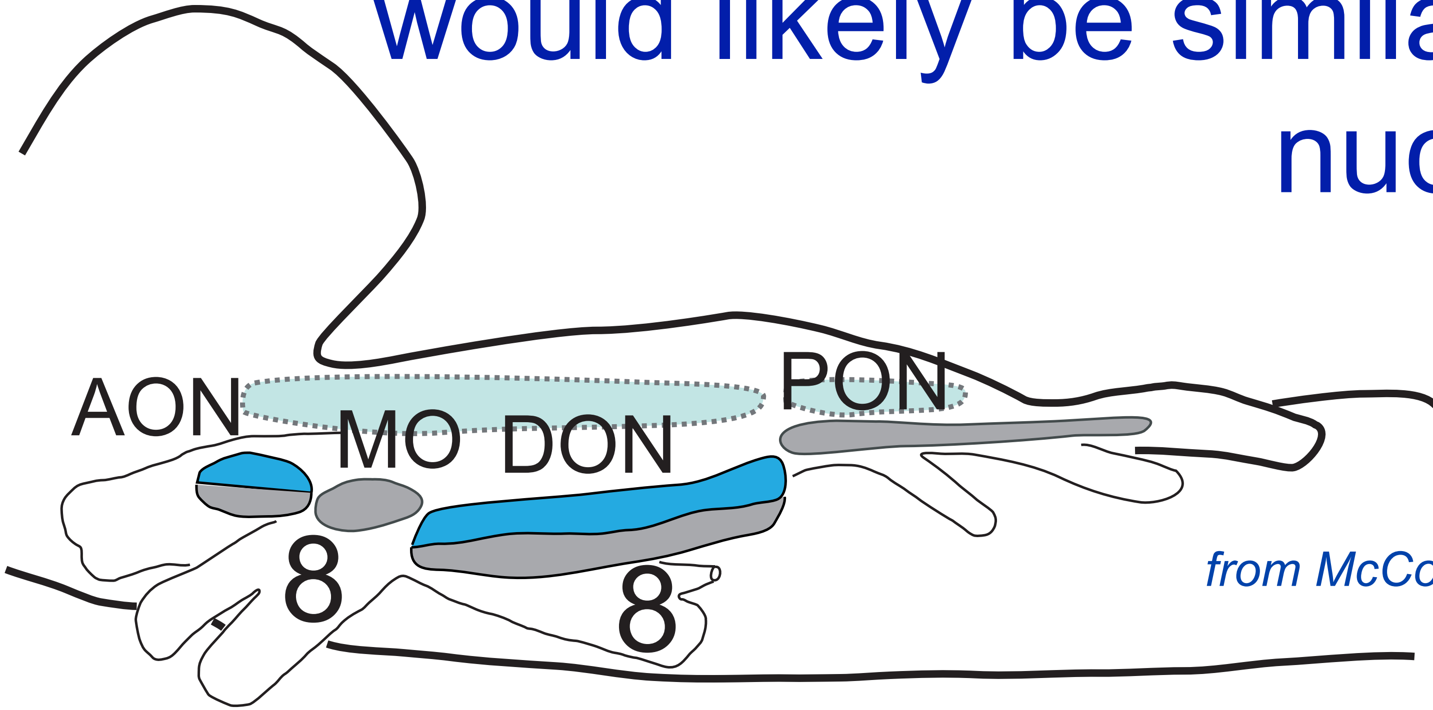
First terrestrial tetrapods could have had similar hearing to lungfish



- Lung can transmit sound vibrations to the otic capsule
- Thus some sensitivity to low frequency airborne sound, even though they lacked middle ear adaptations

Hearing of the African lungfish (Protopterus annectens) suggests underwater pressure detection and rudimentary aerial hearing in early tetrapods. 2015. Bech Christensen, Christensen-Dalsgaard and Madsen J. Exp. Biol.

Brainstem targets in early tetrapods would likely be similar to octaval nuclei in fishes

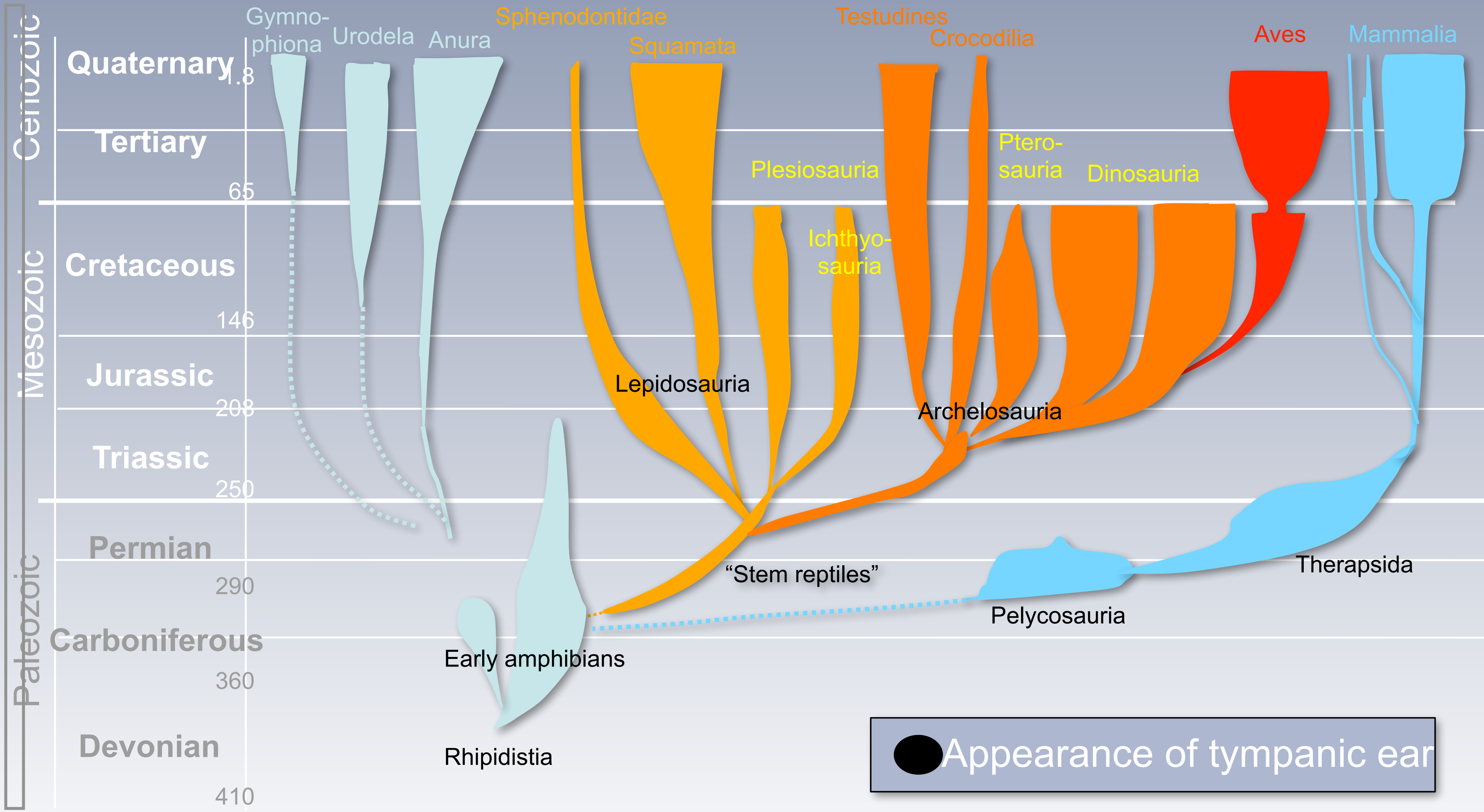


from McCormick 1981

Actinopterygian pattern

- Auditory and vestibular projections overlap, auditory dorsal
- Descending & anterior project to midbrain (McCormick 1981)
- Overlying (electrosensory), lateral line and cerebellar crest

Evolution of tetrapod hearing



Grothe at al (2010) *Physiol Rev*

partially adapted from: Walker & Liem (1994) *Functional anatomy of vertebrates - An evolutionary perspective.* Saunders College Publishing

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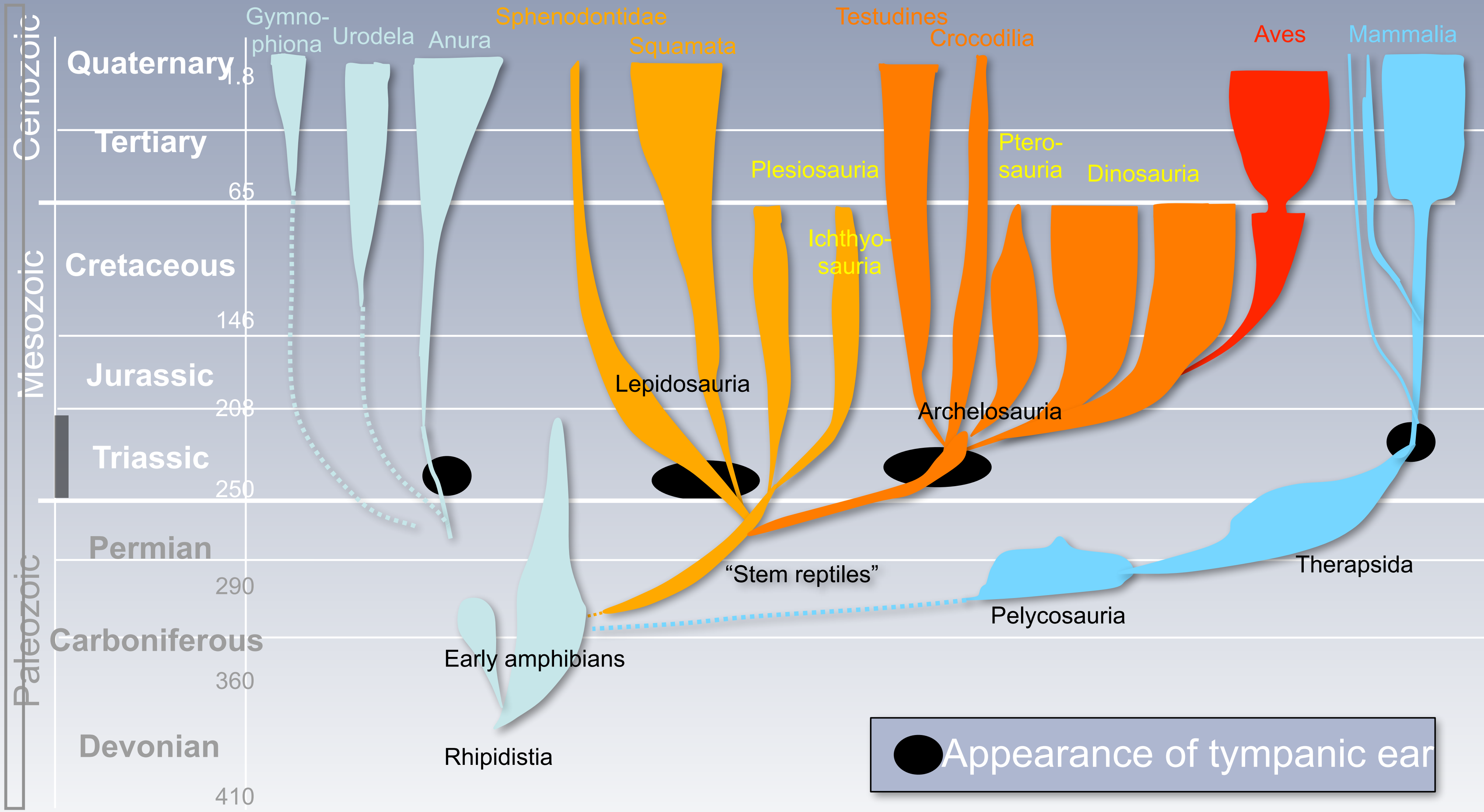
Evolution of tetrapod hearing



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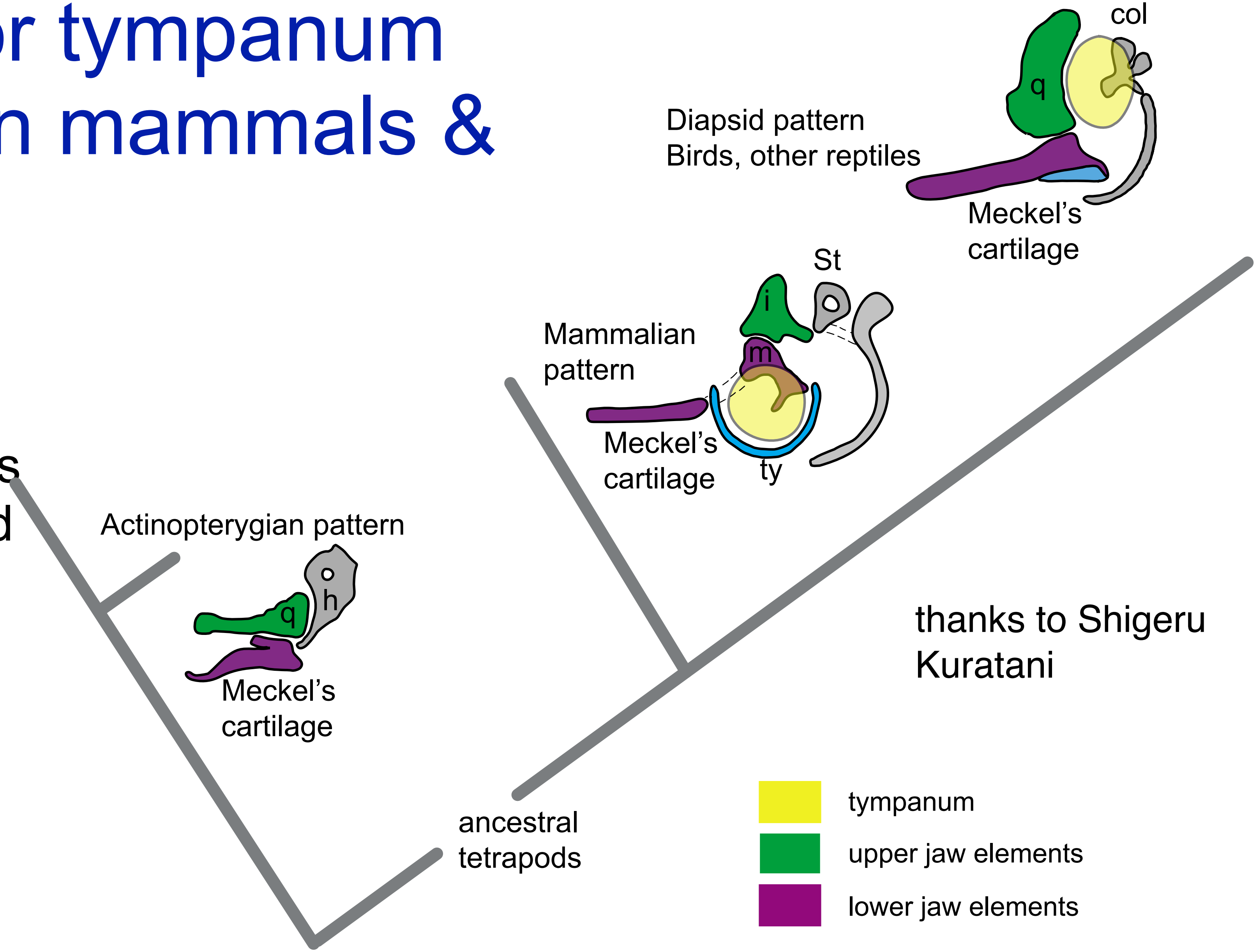
5. Hearing of airborne sound evolved multiple times - in parallel

- Review scenarios for how this occurred
  - use comparative approach to identify rules for localization of air born sound
- Ear development would have led to changes in the auditory centers of the brain
- Begin with ancestral tetrapods
  - what they could hear
  - auditory properties
  - auditory circuits

scenario for tympanum formation in mammals & diapsids

- tympanum forms in different ways in mouse and chicken
- confirms the parallel evolution of eardrums
- new ear should organize the

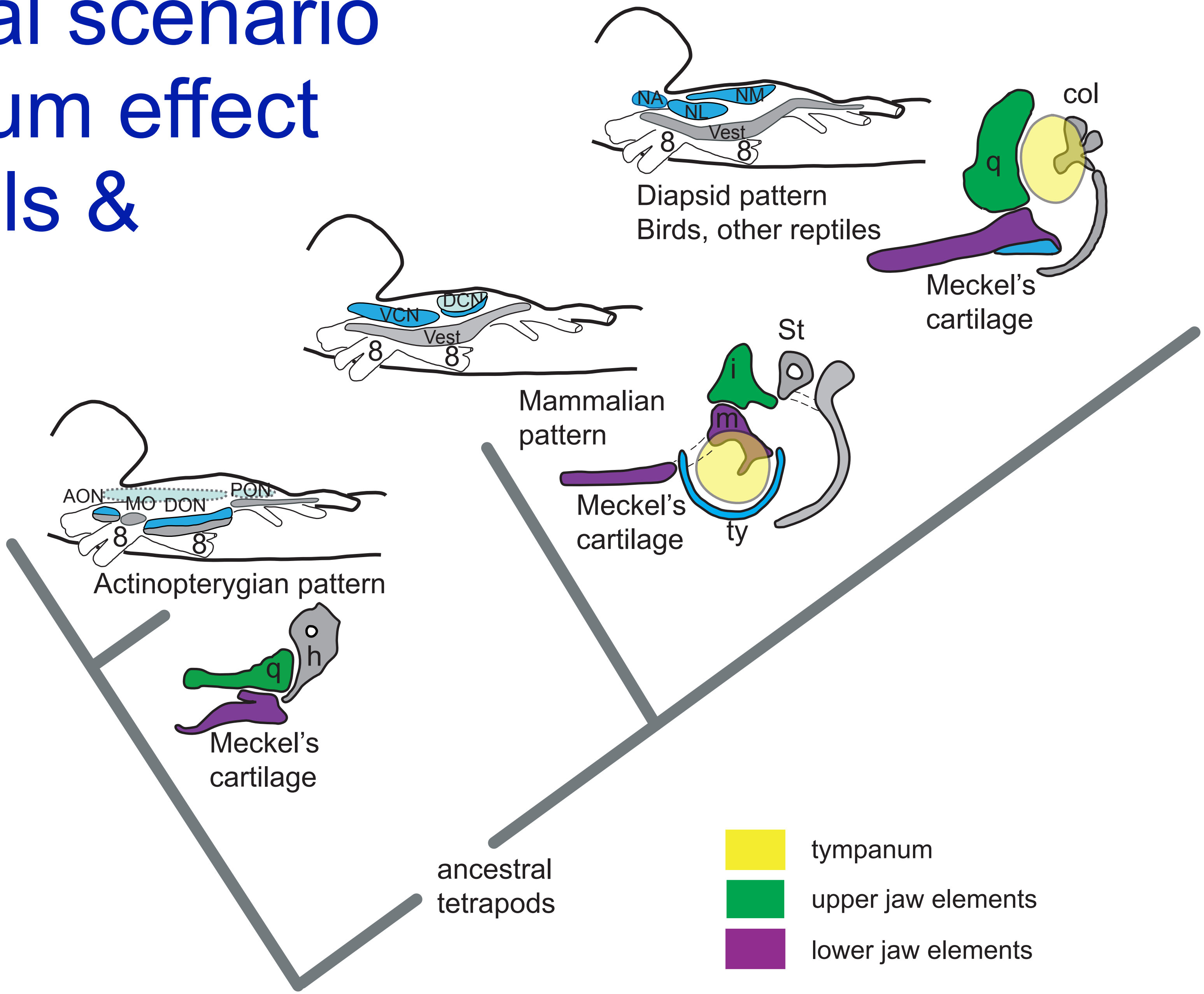


thanks to Shigeru Kuratani

Taro Kitazawa, Masaki Takechi, Tatsuya Hirasawa, Noritaka Adachi, Nicolas Narboux-Nême, Hideaki Kume, Kazuhiro Maeda, Tamami Hirai, Sachiko Miyagawa-Tomita, Yukiko Kurihara, Jiro Hitomi, Giovanni Levi, Shigeru Kuratani & Hiroki Kurihara Developmental genetic bases behind the independent origin of the tympanic membrane in mammals and diapsids. Nature communications. 2015 Apr 22;6.

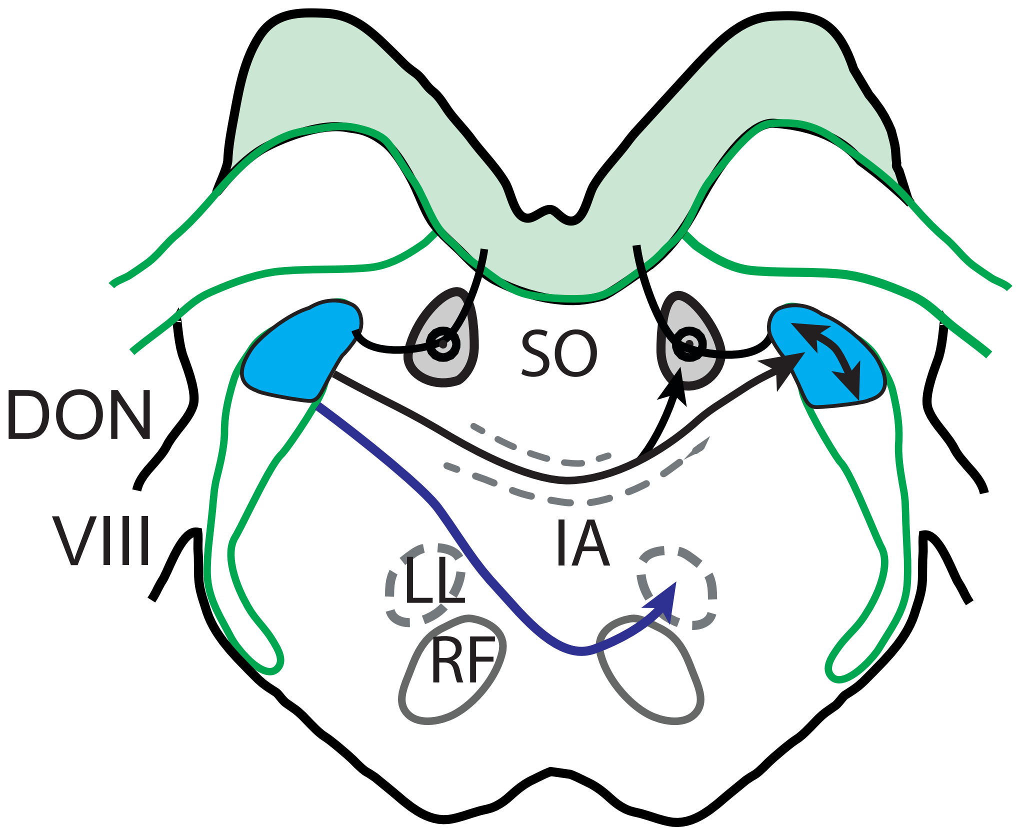
Hypothetical scenario for tympanum effect on mammals & diapsids

- Tympanum should increase sensitivity & frequency range
- “new” ear should organize brain



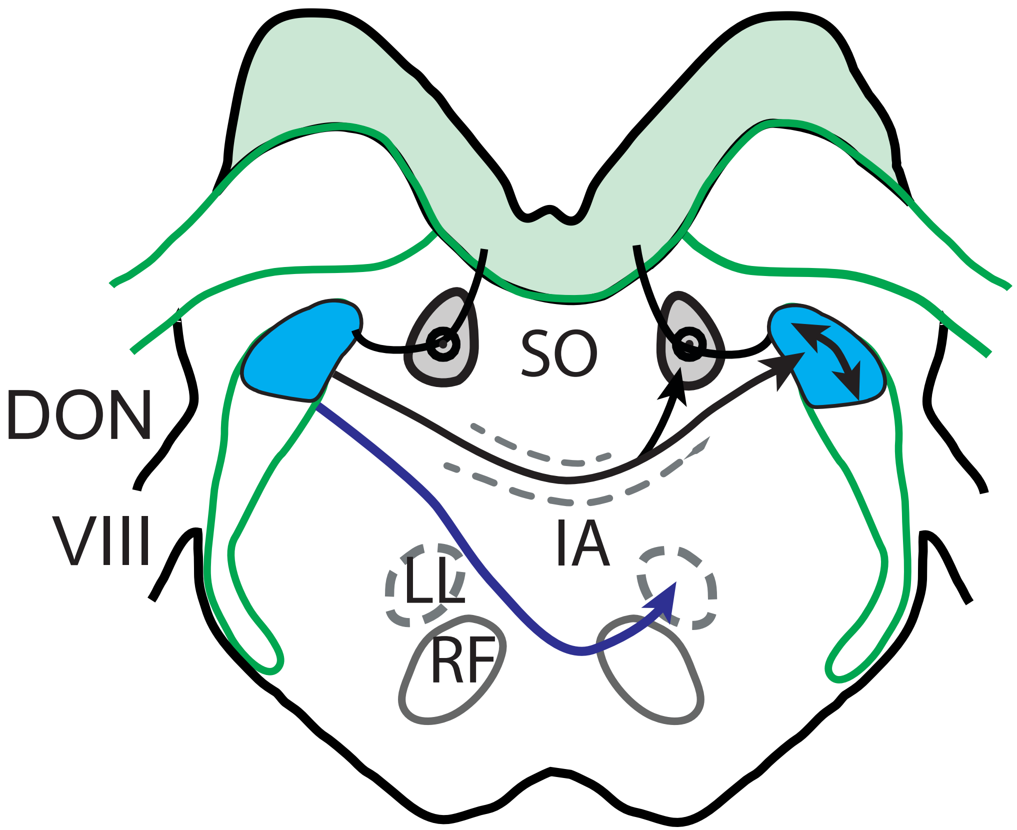
Current Opinion, 2016

Hypothetical transformation of basal to reptilian circuit



Teleost

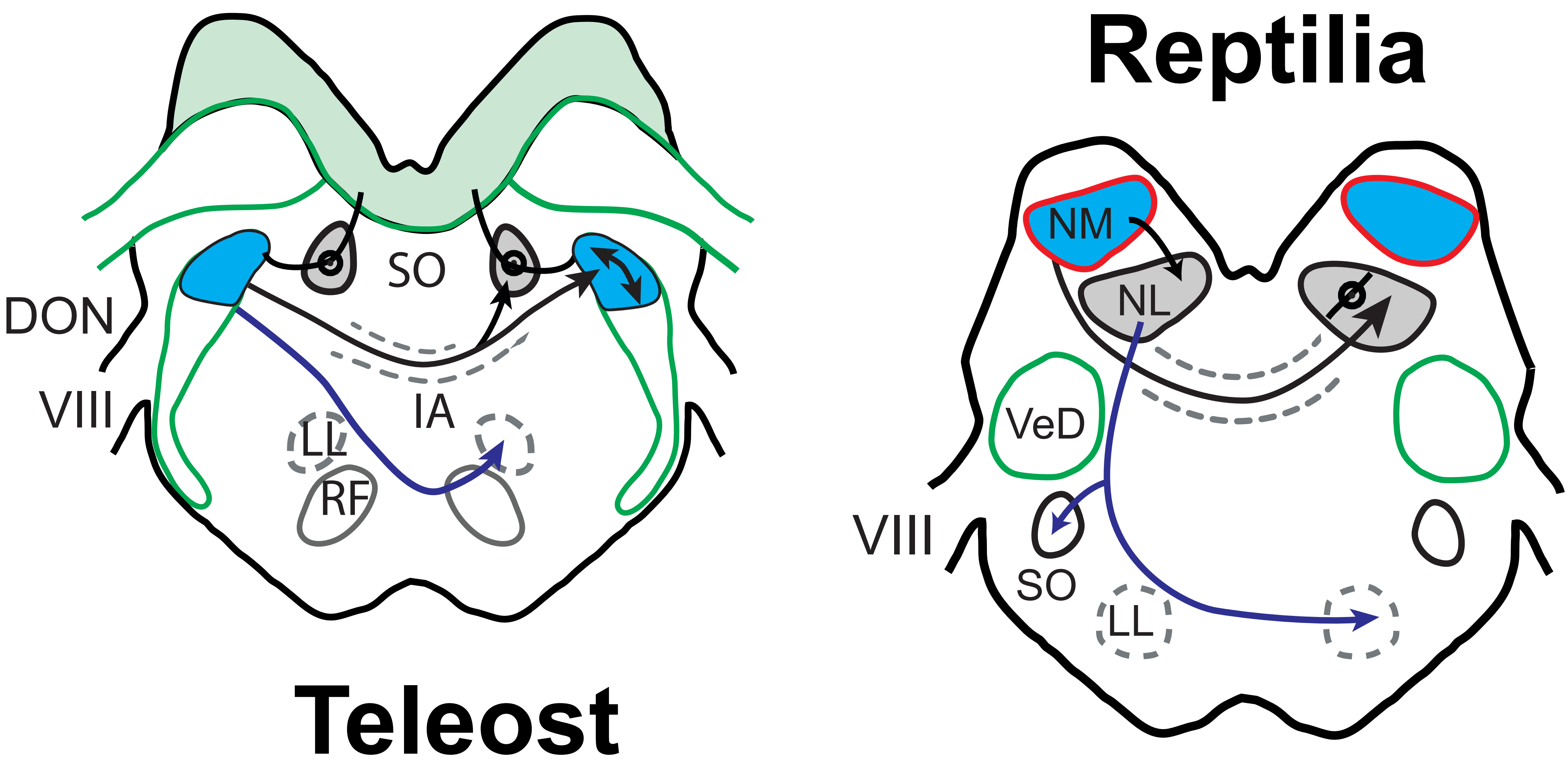
Hypothetical transformation of basal to reptilian circuit



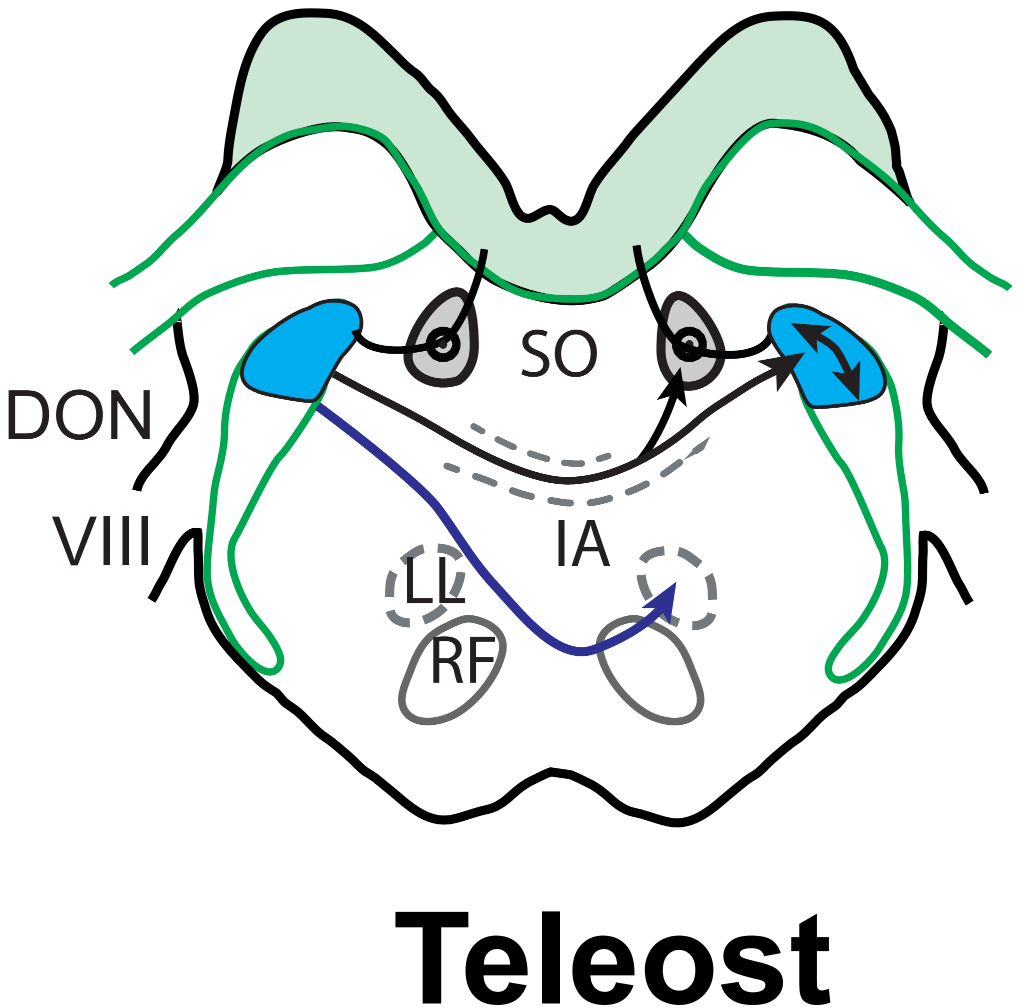
Teleost

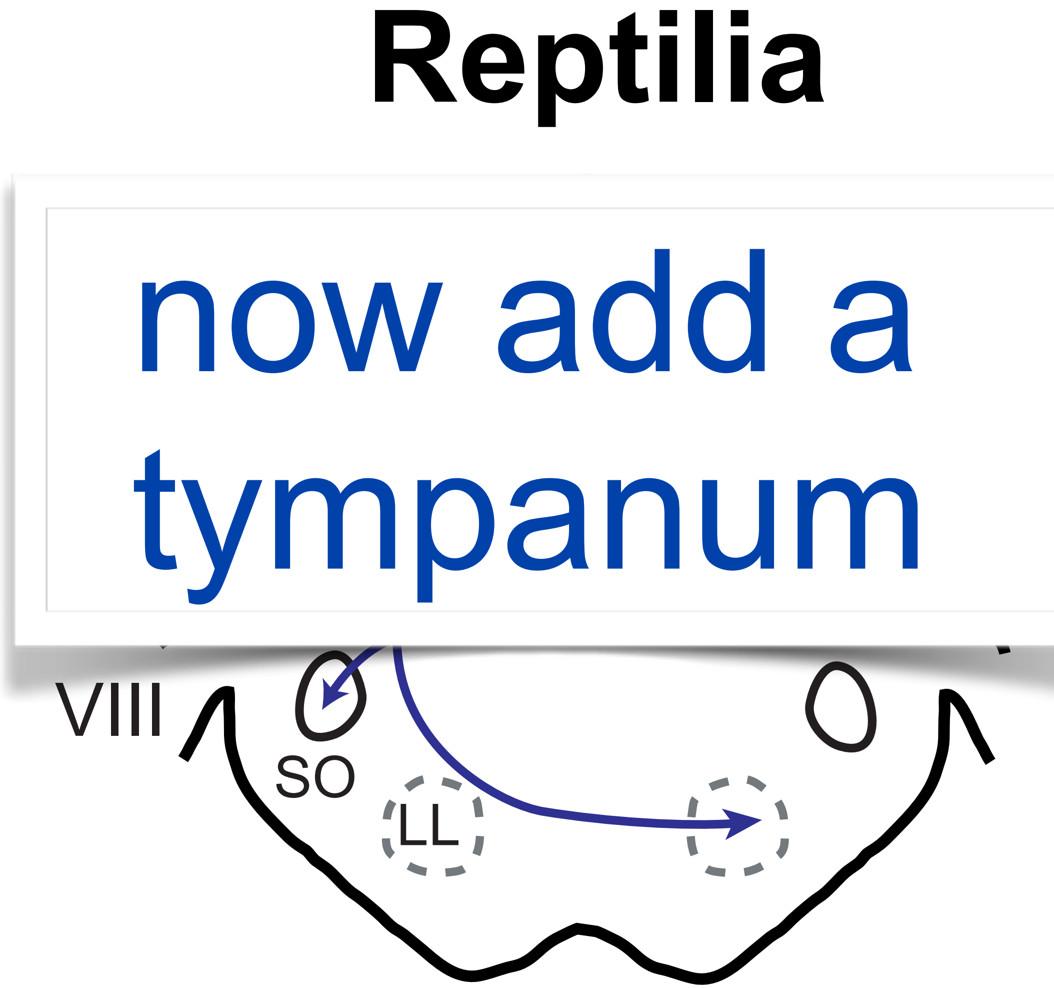
Reptilia

Hypothetical transformation of basal to reptilian circuit



Hypothetical transformation of basal to reptilian circuit

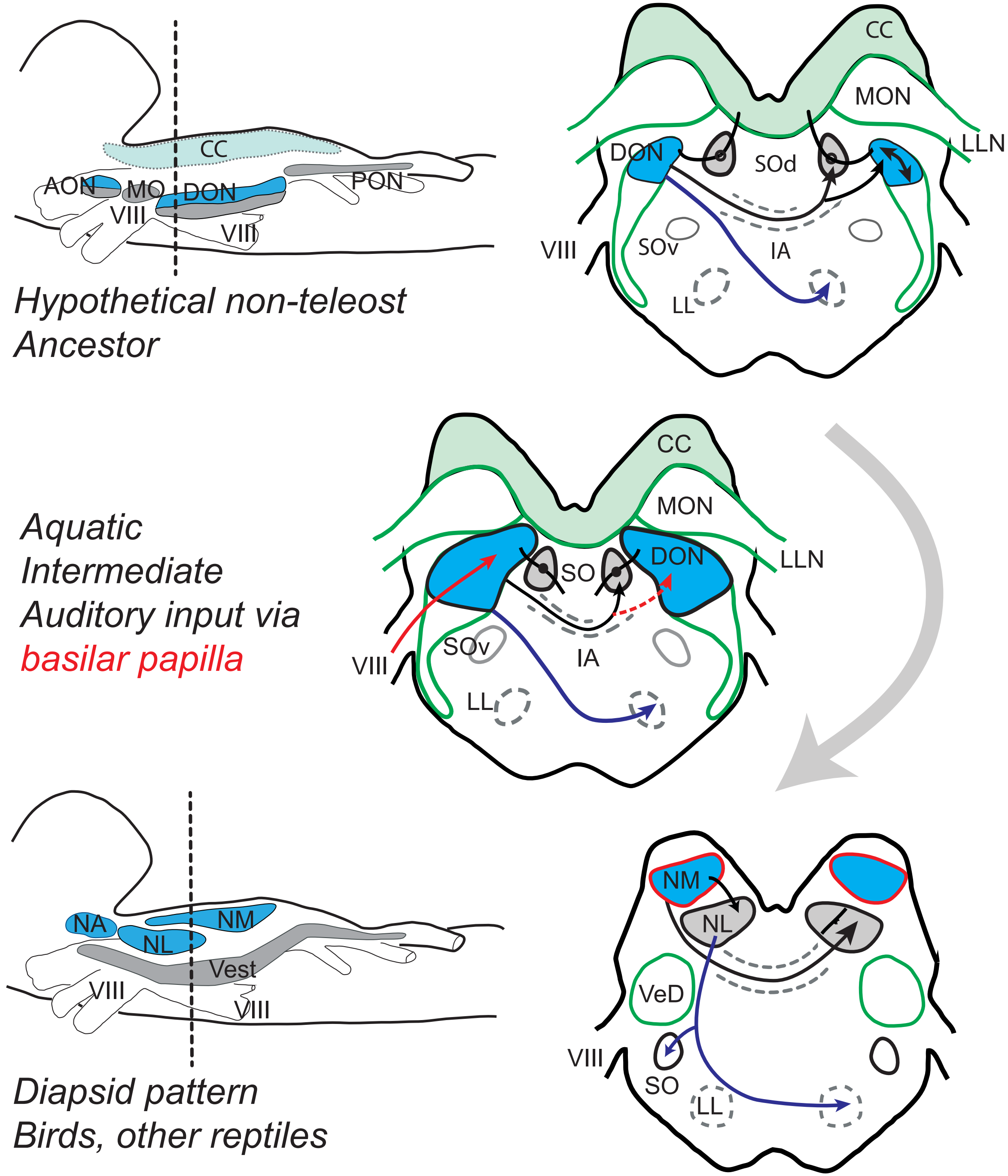




now add a tympanum

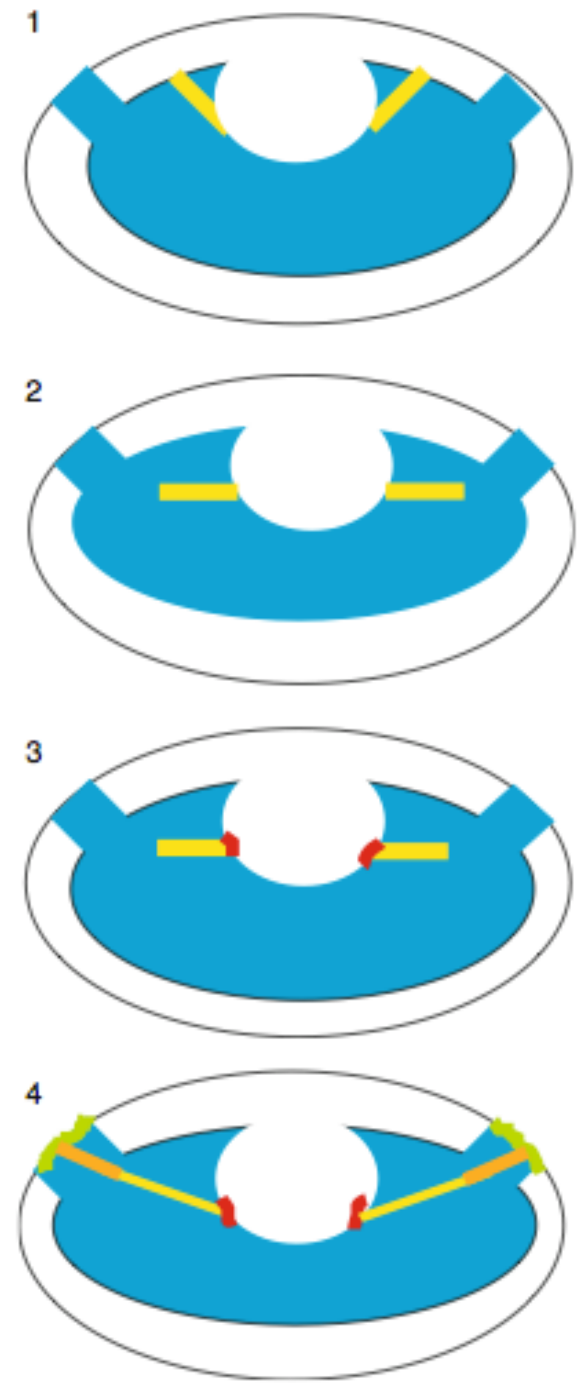
Hypothetical transformation for reptiles

- what came first?
- new papillae
- tympanum
- impedance matching ear



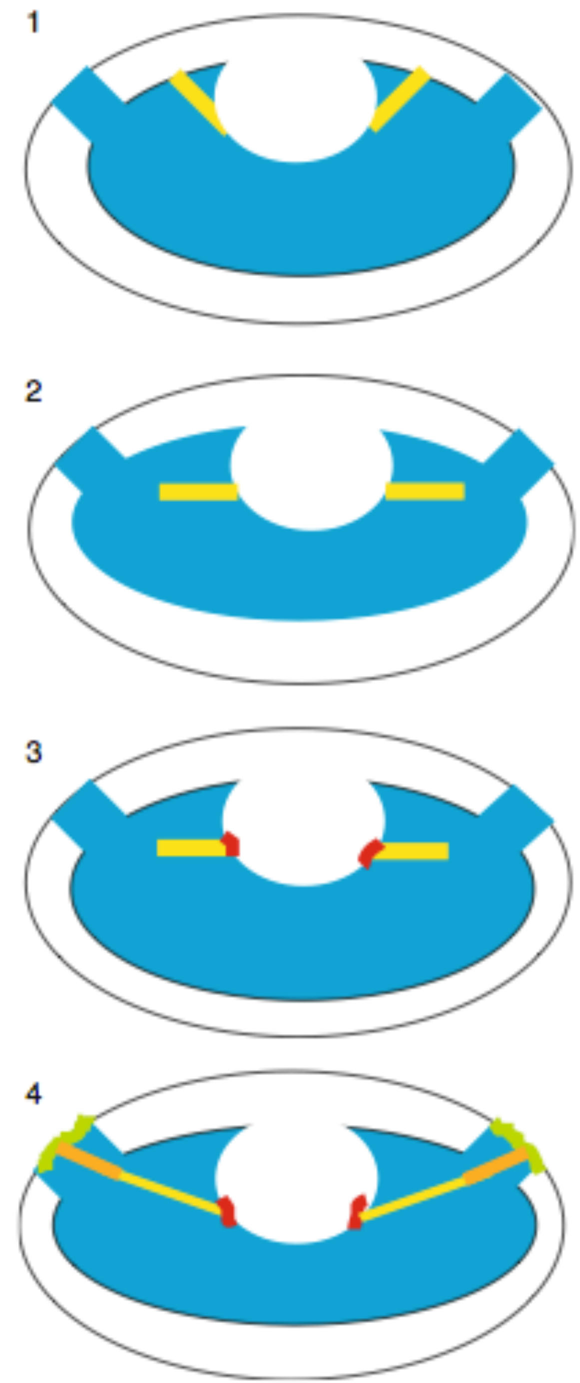
Manley & Christensen-Dalsgaard's 4 stages of ear morphology leading to increased sensitivity

1. Early inner ear similar to lungfish ear, sensitive to very low-frequency sound and vibration
2. High-frequency sensitivity of the inner ear could be increased by reducing the mass of the otolith(s).

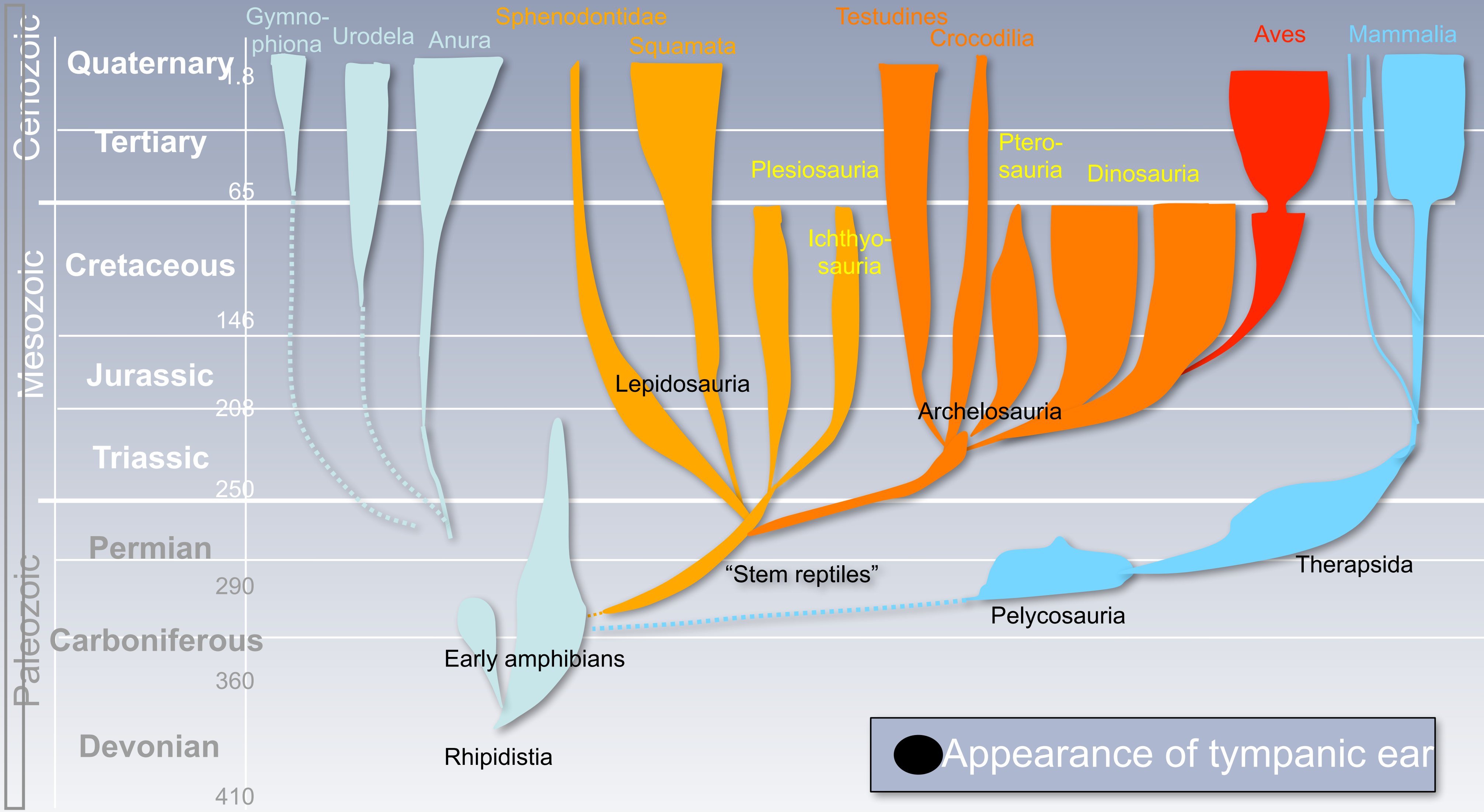


Manley & Christensen-Dalsgaard's 4 stages of ear morphology leading to increased sensitivity

3. large columella acts as an inertial element.
4. Tympanic ear achieved by joining smaller columella to the surface of the skull in the region where the skin covered the former spiracle



Evolution of tetrapod hearing



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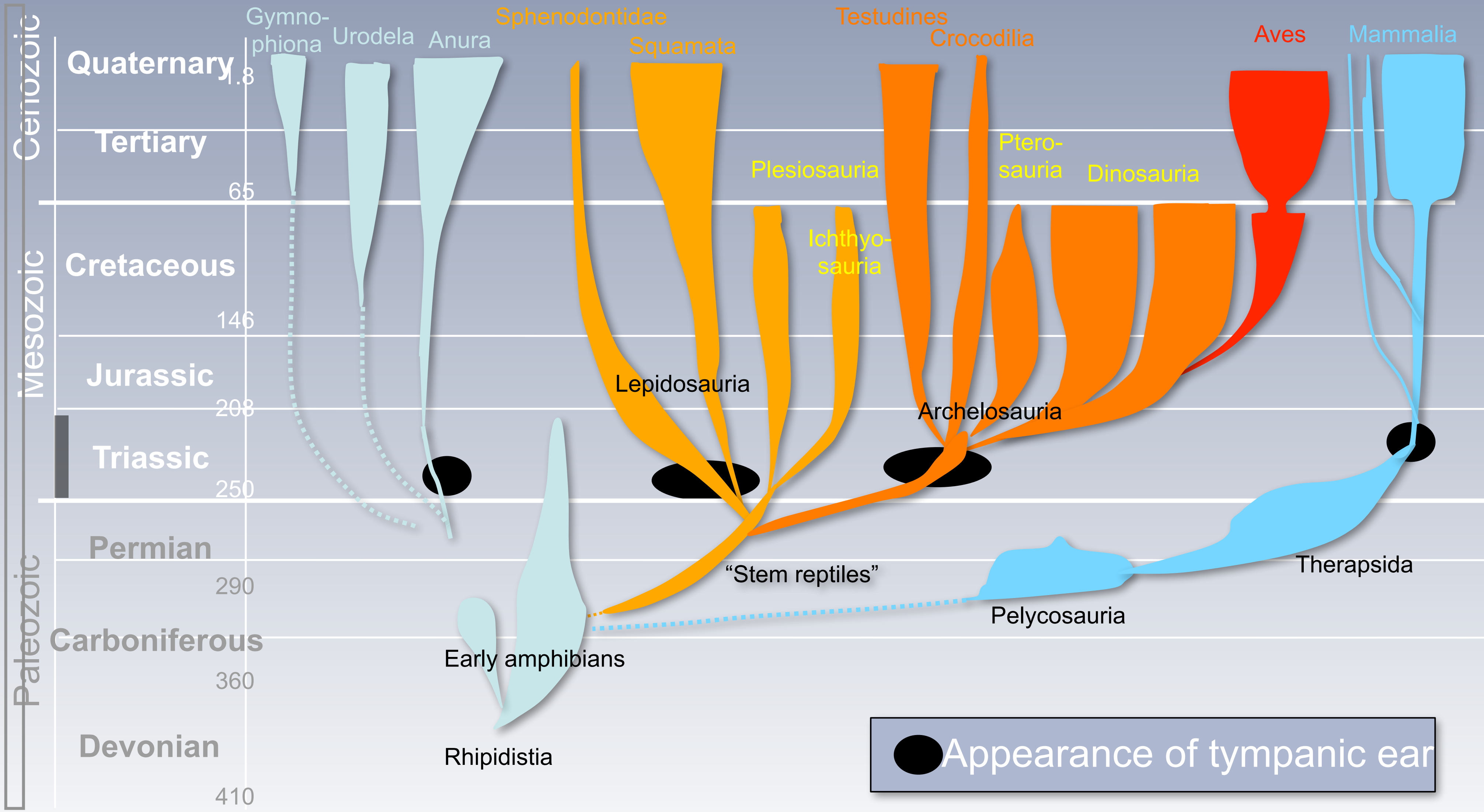

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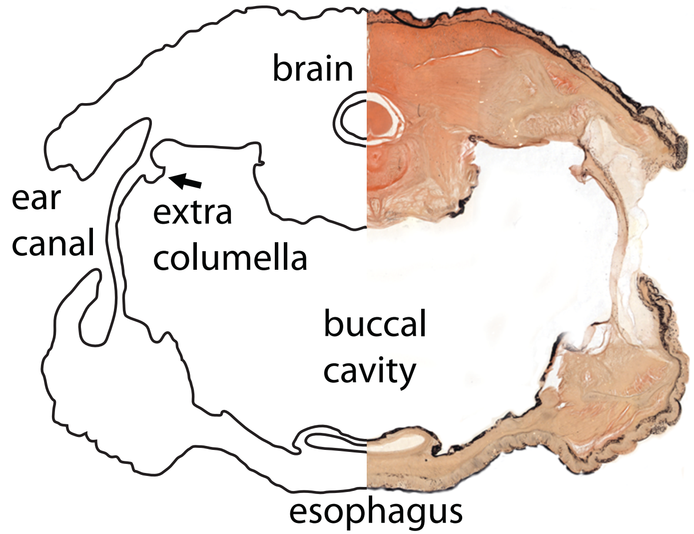
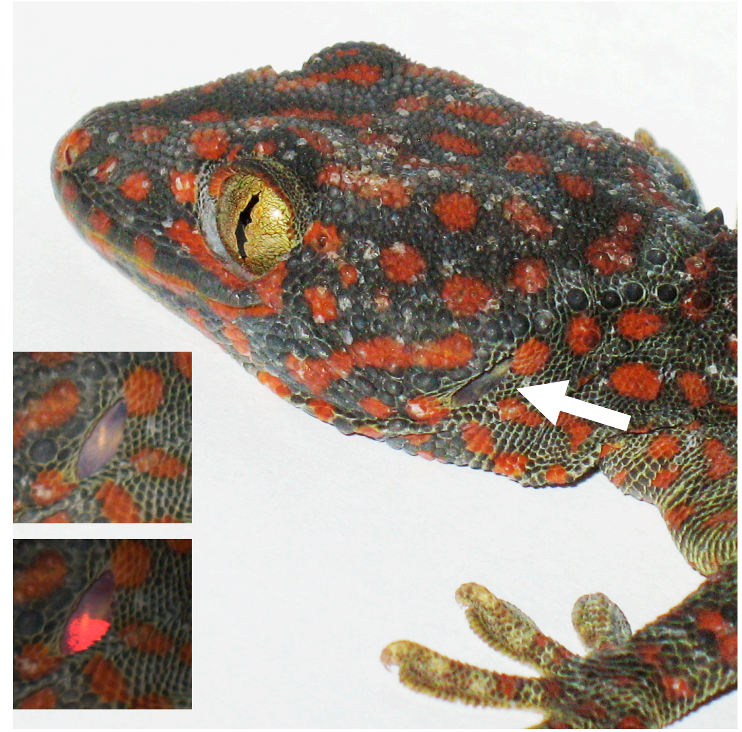
how did animals localize sound after acquiring tympana ?

- many unknowns
- in most cases (except mammals) eardrums coupled through mouth cavity
- lizards
- frogs

- Lizards
- Turtles
- Alligator
- Barn ow

Lizard ears

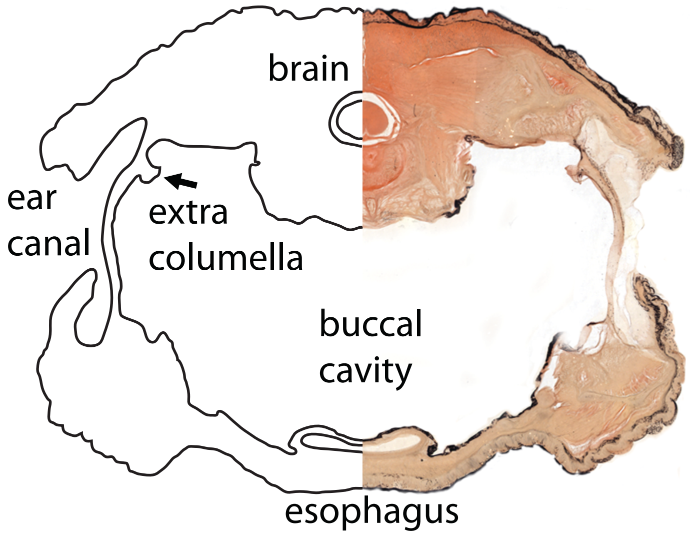


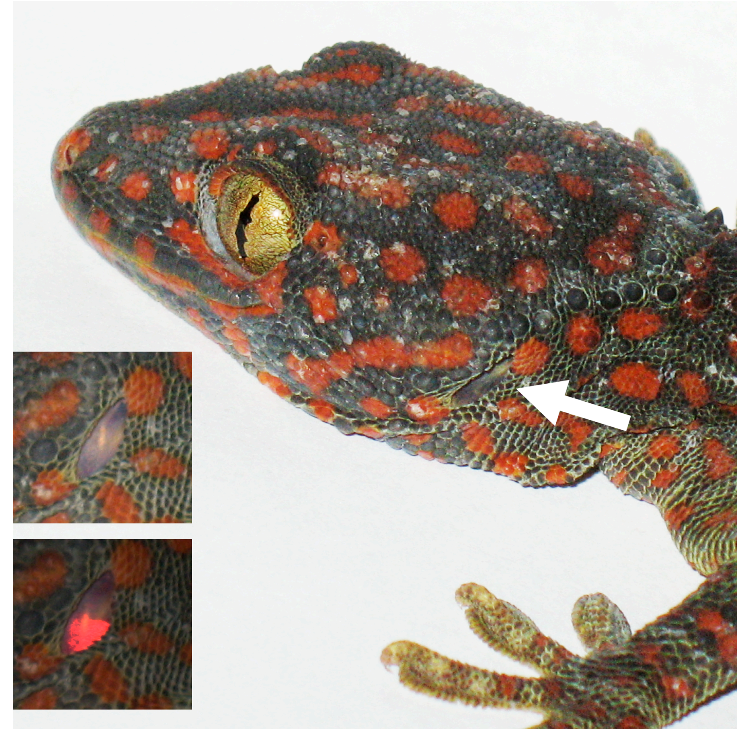


- lizards hear well, and a few are vocal
- eardrums coupled by middle ear cavity, creating a **pressure difference** receiver
- primitive condition ?

From Jakob Christensen-Dalgaard

Lizard ears





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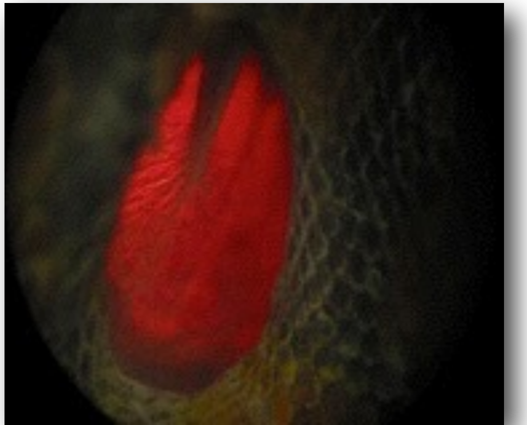
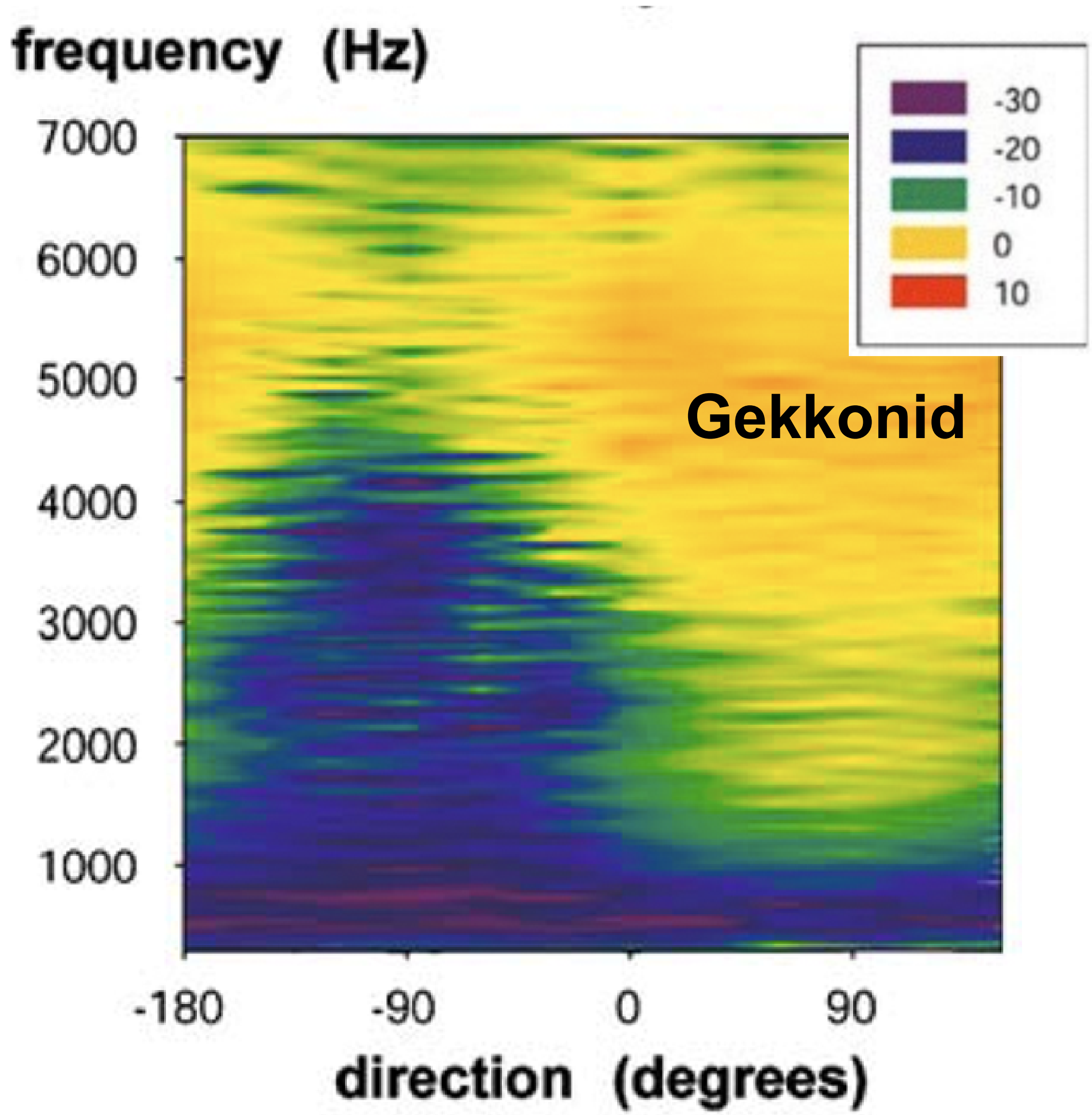
From Jakob Christensen-Dalgaard

Coupled ears are directional



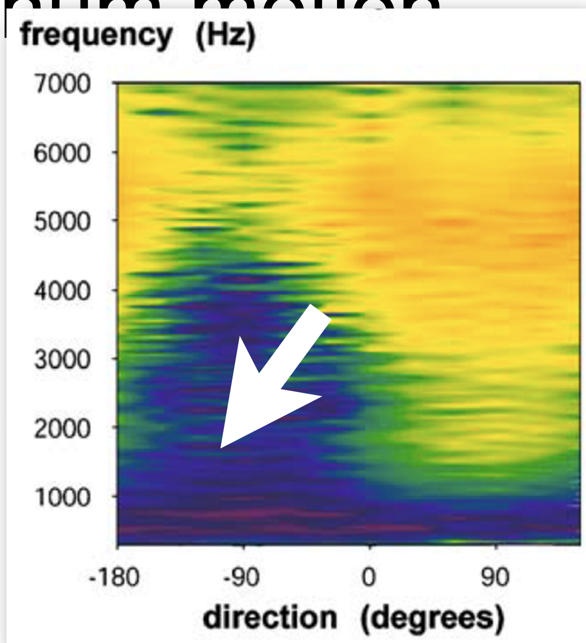
- Laser measures of eardrum vibrations & changing sound location
- color scale shows eardrum velocity (in dB) with varying speaker locations

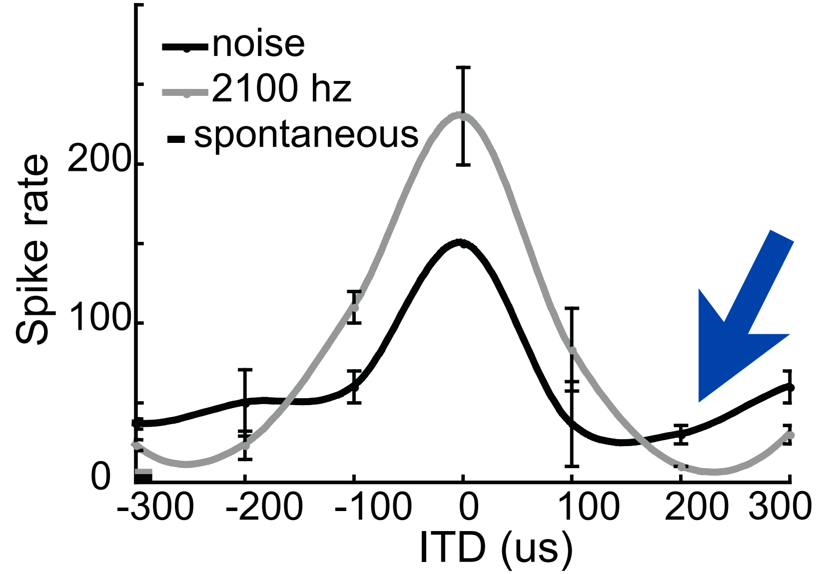
From Christensen-Dalsgaard & Manley, 2005, 2008

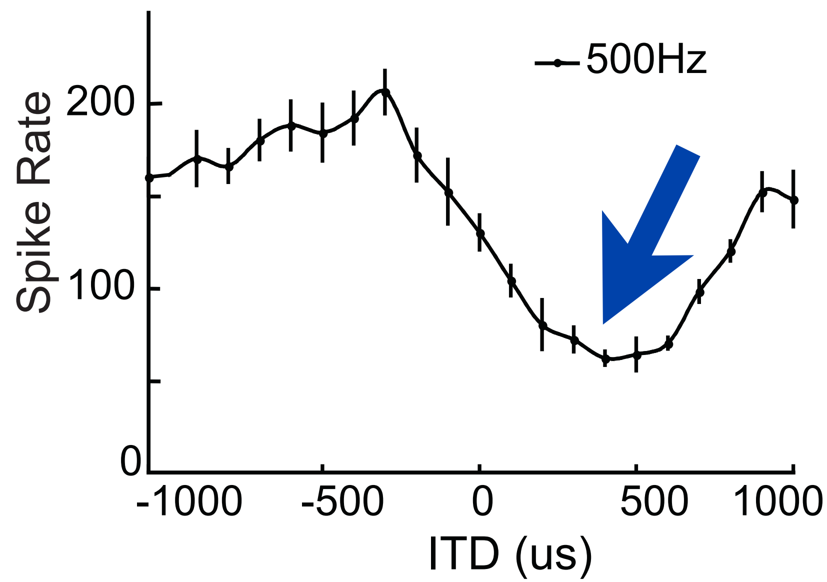


ITD sensitivity in auditory nerve

- Sound sources to the side of gecko "cancel" tympanum motion

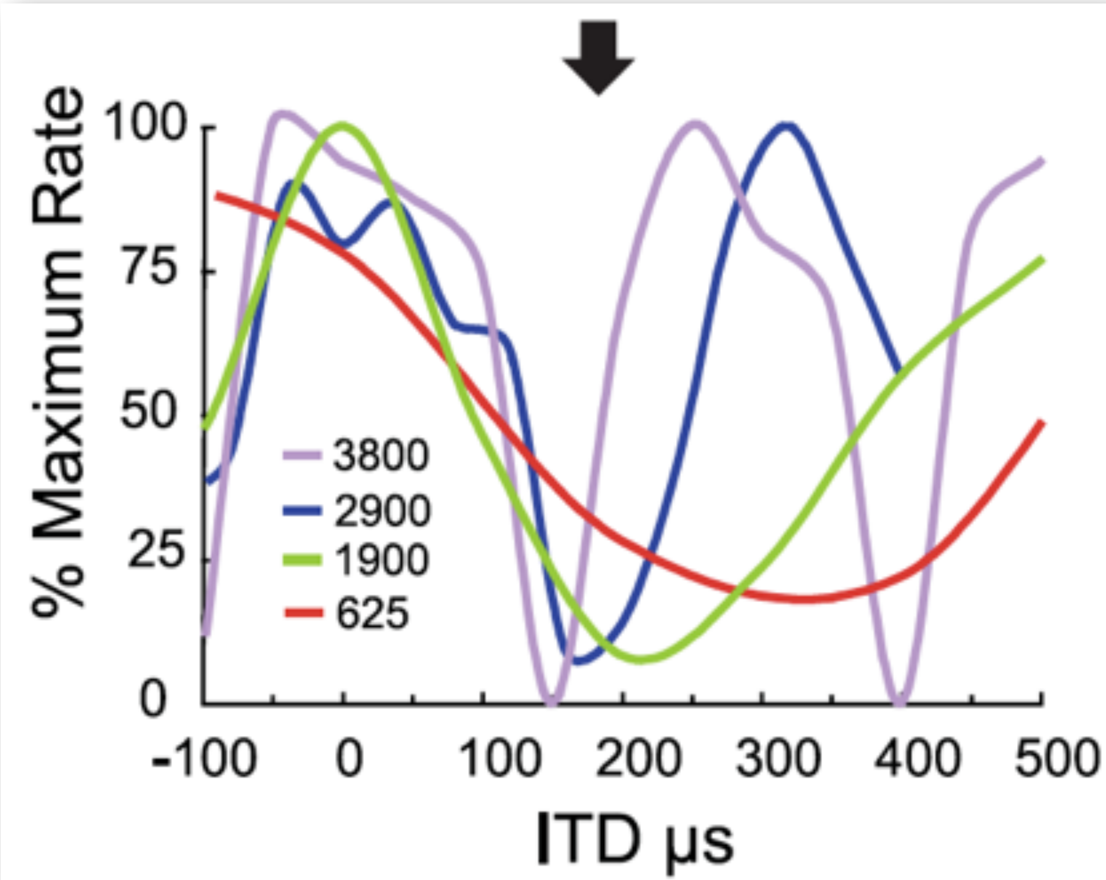


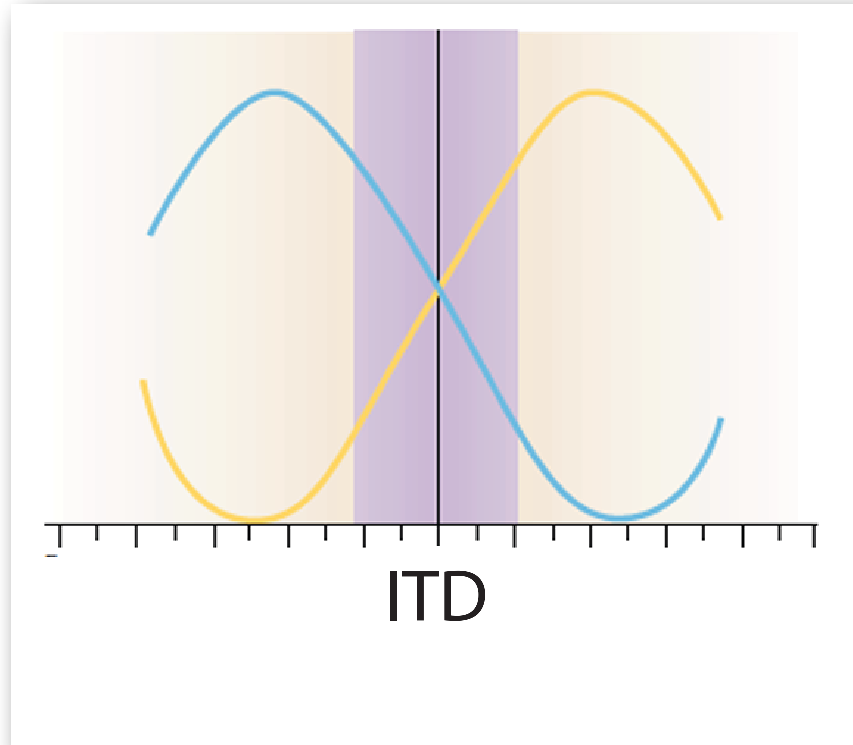




- ITD/ILD sensitive rate code in gecko auditory nerve.

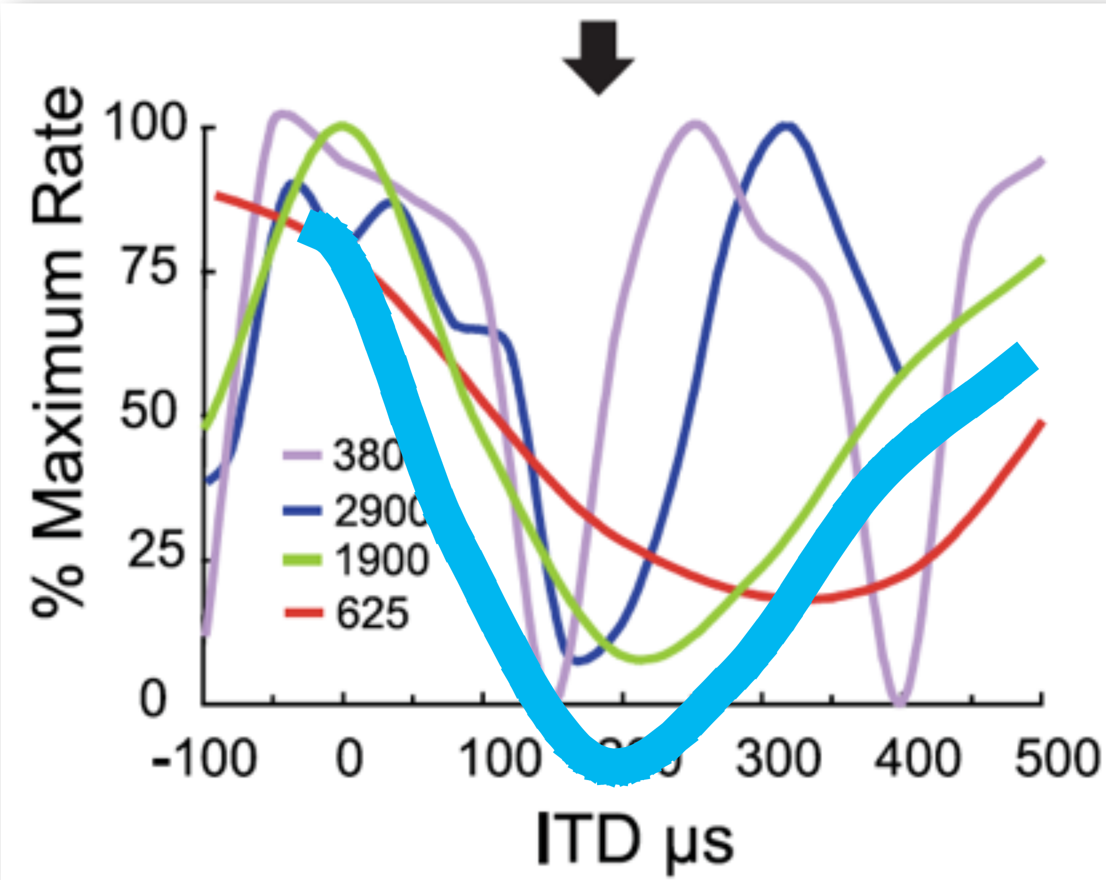
All responses sensitive to sound location

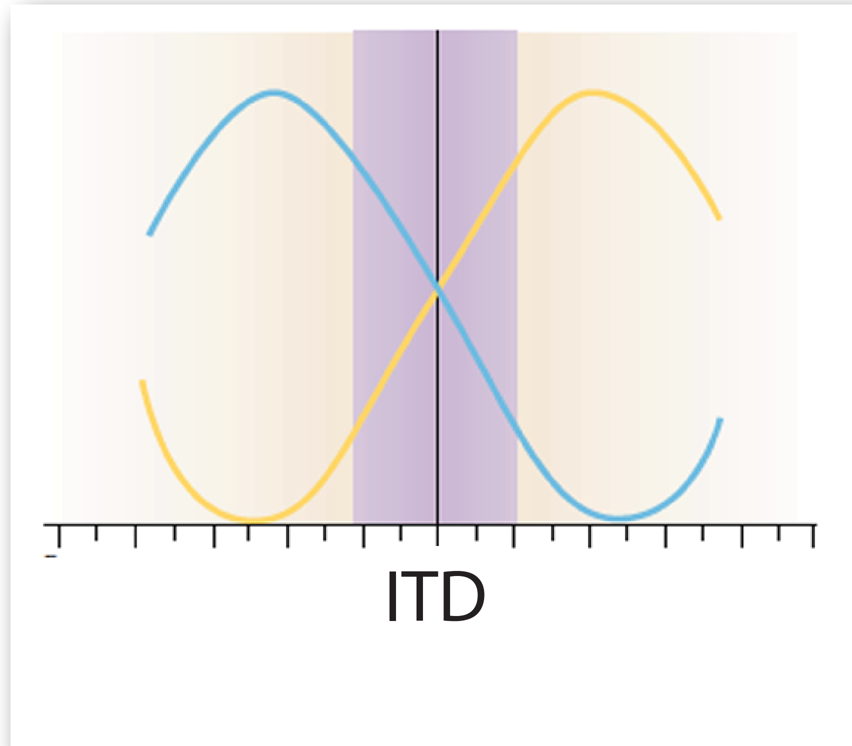




J Neurophys, 2011

All responses sensitive to sound location

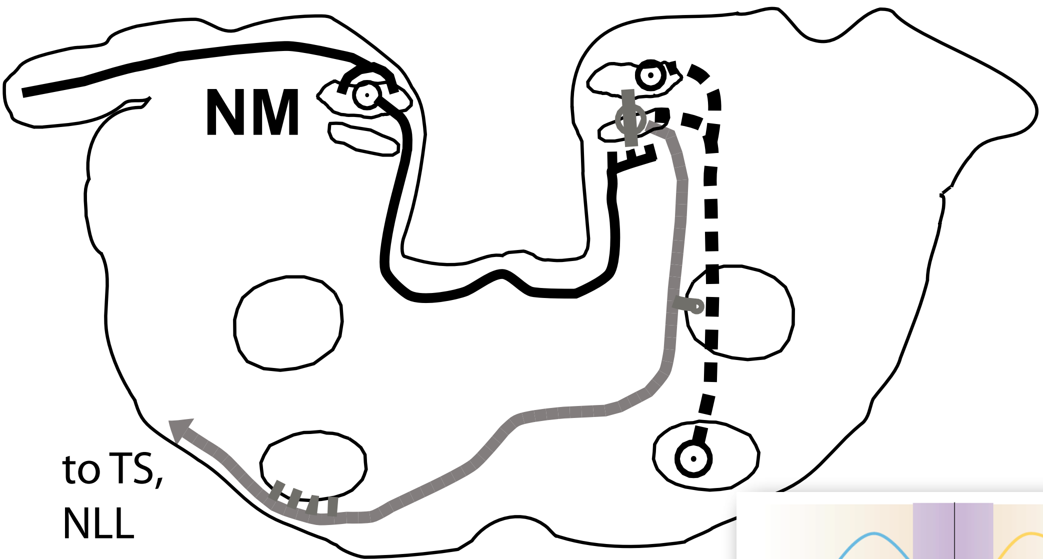




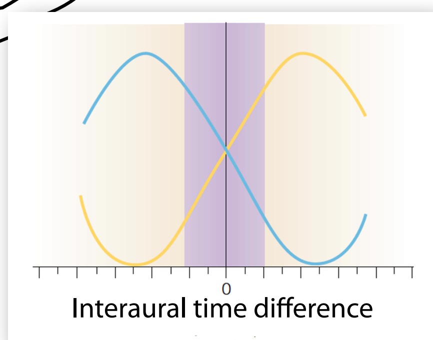
J Neurophys, 2011

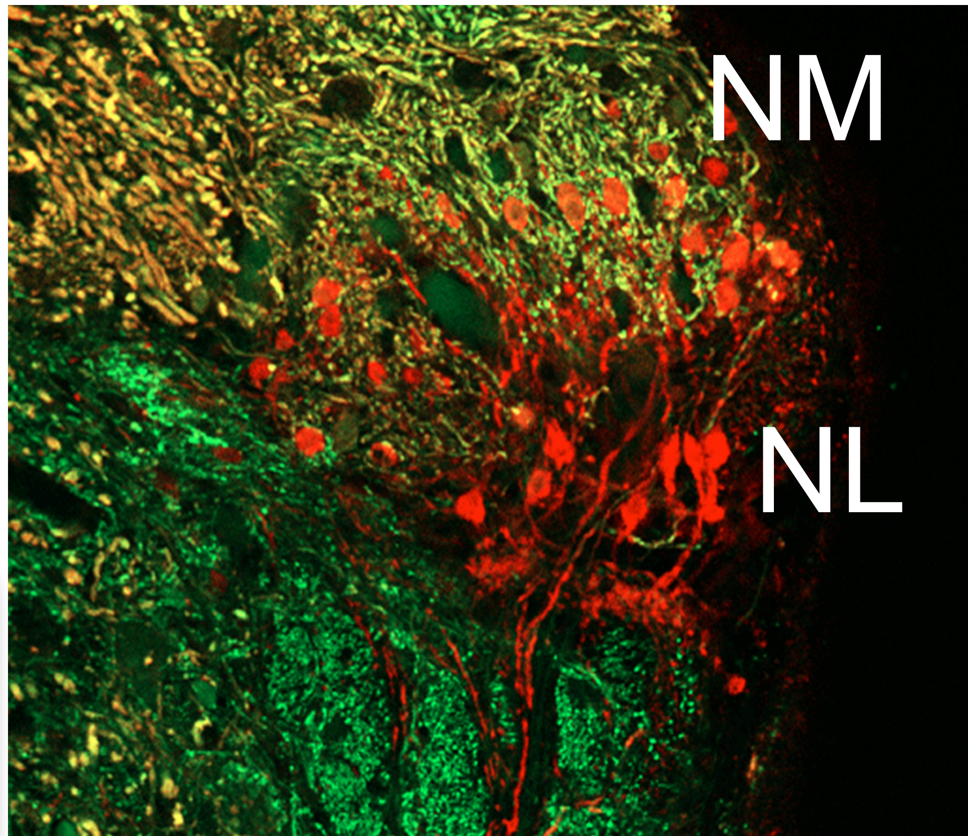
What happens to directional signal in brain?

- Nerve signal must be compared in brain to disambiguate loudness information
- circuit organized in Reptilian morphotype



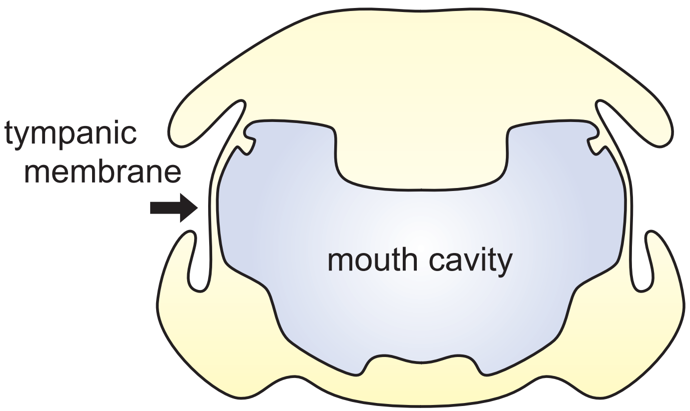
J Comp Neurol 2011

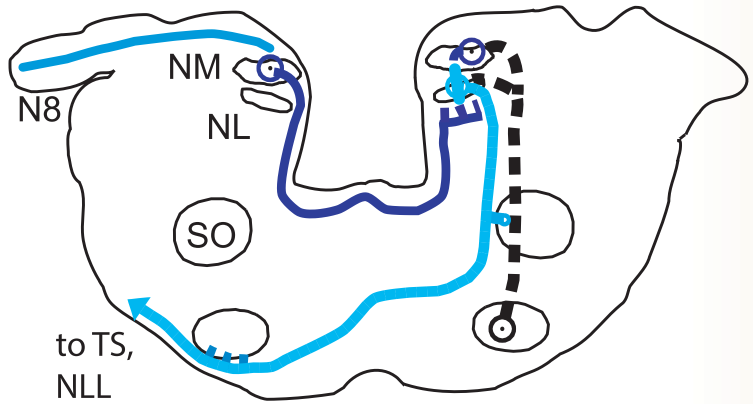


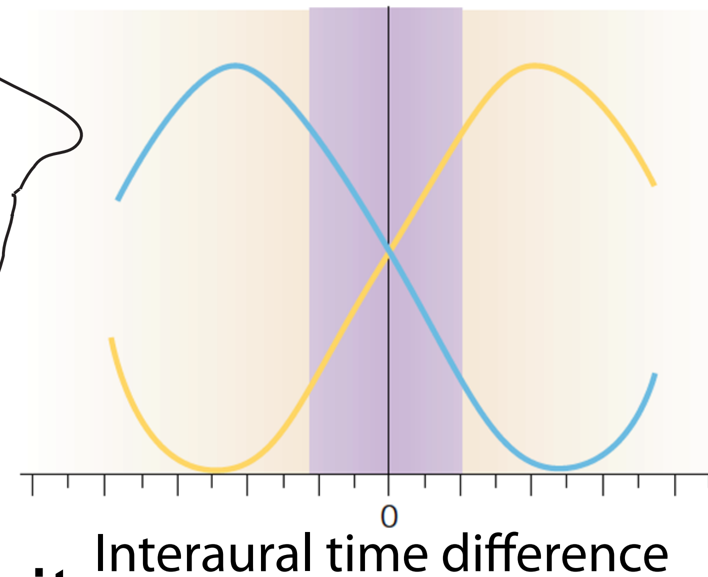


J Comp Neurol 2010

Summary of lizard ITD coding







- coupled ears creates ITD sensitivity

- Nerve signals directional, but must be compared in brain to disambiguate loudness information
  - reptilian circuit

Evolution of hearing in tetrapods

- Early tetrapods either developed a new macula (hair cells) or enlarged a pre-existing one
- And after radiated, developed tympana, which increased frequency range and sensitivity
- these “new” ears should organize the central auditory system (more cells, tonotopy etc)
- Likely neural circuits **already adapted** to process directional information
- Bilateral comparisons, e.g. vestibular system
- Comparisons of circuits in tetrapods reveal similar coding strategies (Manley)

Thank you

Hilary Bierman
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