Kavli Institute for Theoretical Physics

- Optimization and constraints on anatomical form and circuit reconstruction methods
- Development of the brain and body
- Comparative evolution of brain structures

http://www.grc.org/programs.aspx?year=2008&program=neuroetho

Evolution of sound localization circuits

Shared computational principles

Catherine Carr

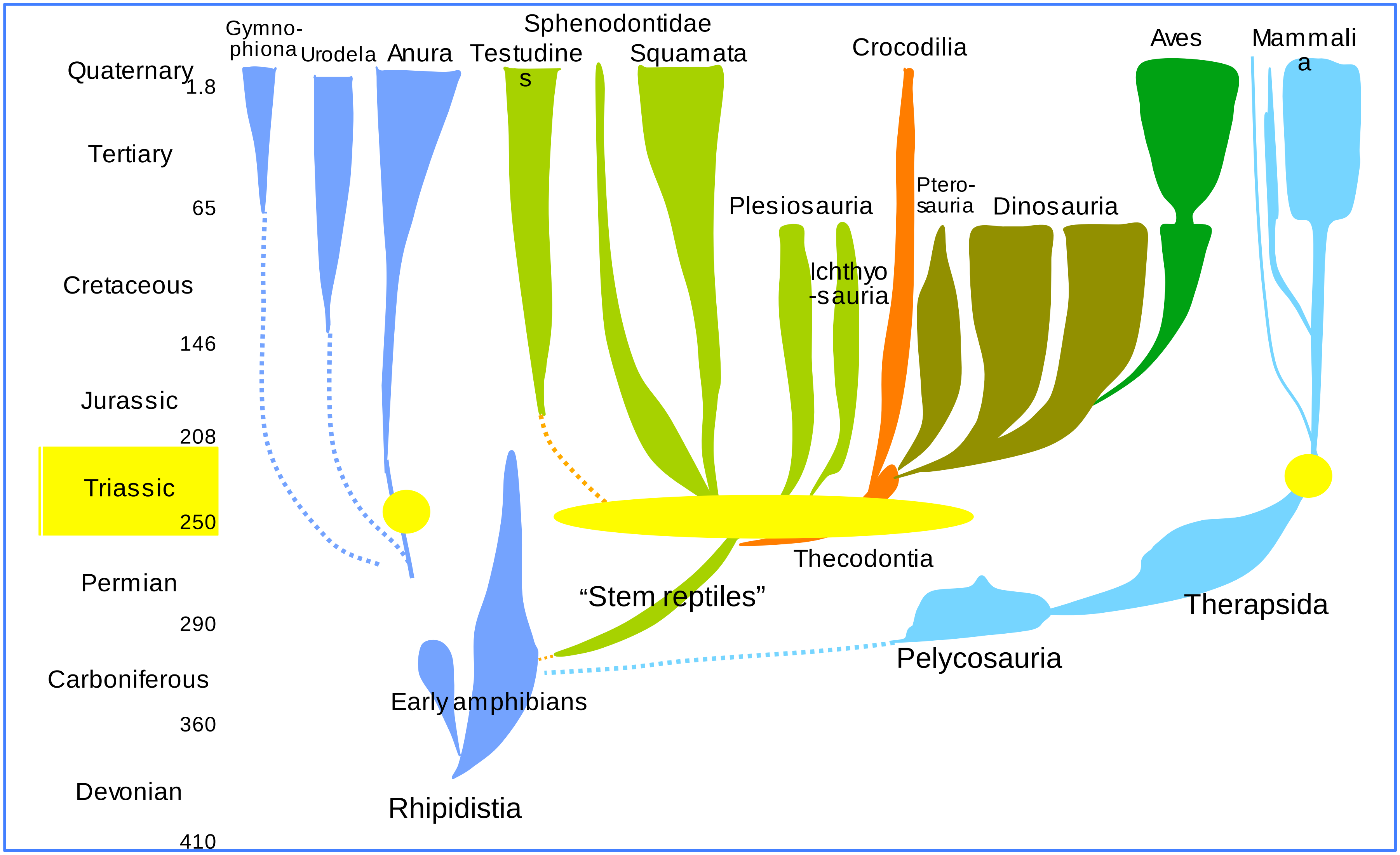
KITP

March

2008

Show how evolution shapes neural coding, using sound localization in land vertebrates as an example

Tetrapod ears evolved in parallel



Grothe, Nat. Rev. Neurosci, 2003

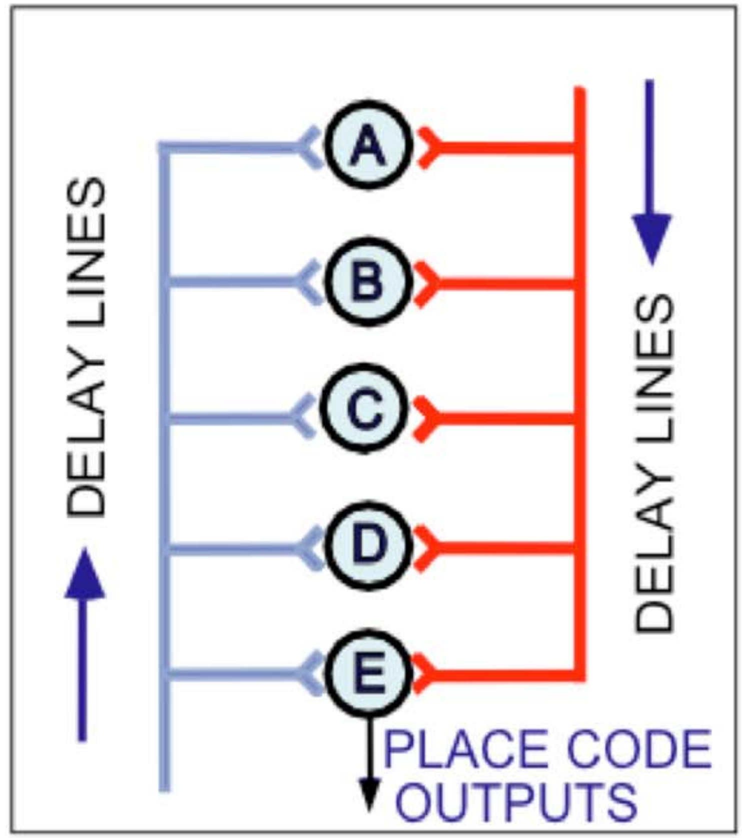
Sensitive, high-frequency hearing of airborne sound may be a recent event in vertebrate evolution

Hearing of airborne sound evolved multiple times - in parallel

- New ears lead to changes in the auditory centers of the brain
- Find similar (not identical) rules for localization in bird & crocodilian lineage and in mammals (different rules for lizards)
- Use parallel circuits to identify shared computational principles underlying sound localization
- Argue that these are suitable solutions to problems of coding

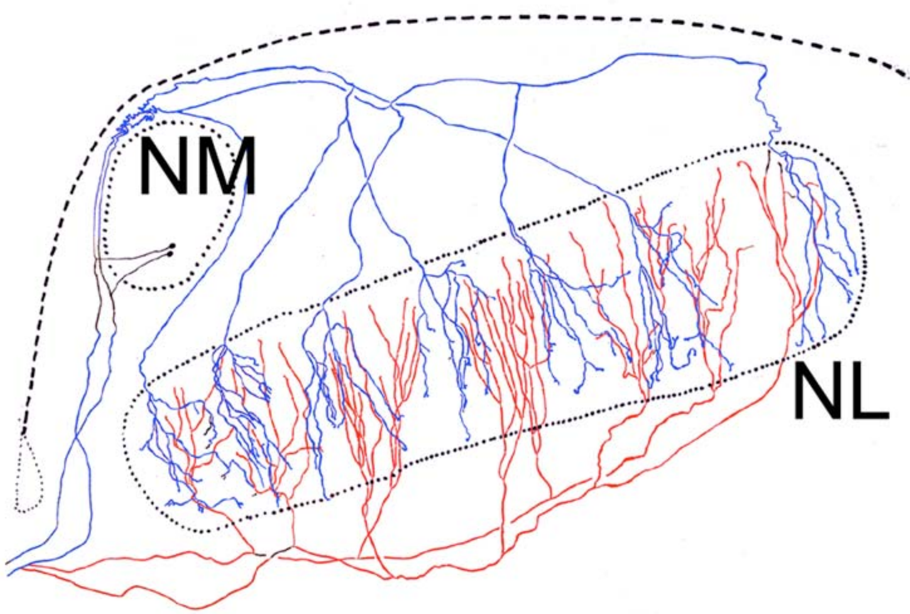
A circuit for detection of interaural time differences (ITD)

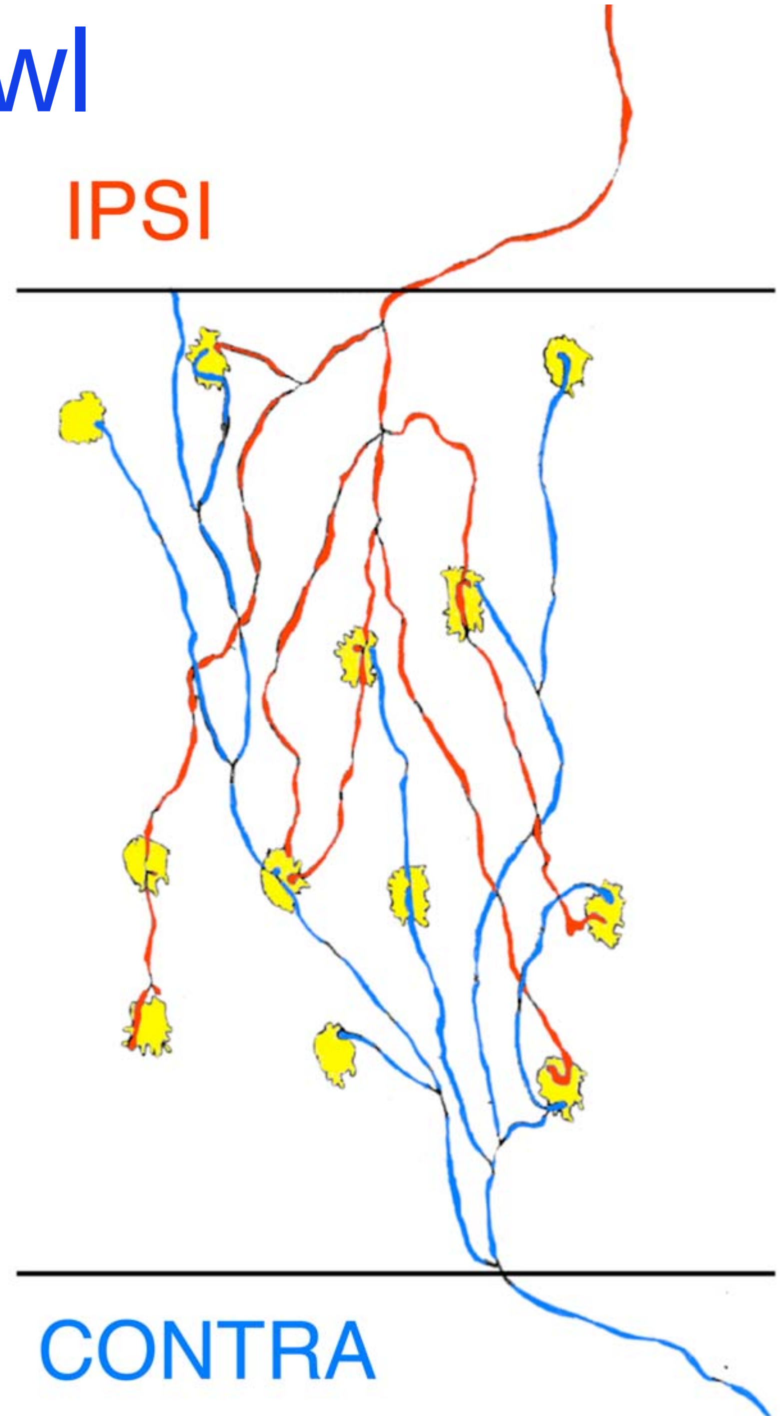
- Delay line inputs synapse on coincidence detector neurons.
- These neurons compute the new variable, ITD, and transform the time code into a place code



Jeffress model

ITD circuit in barn owl

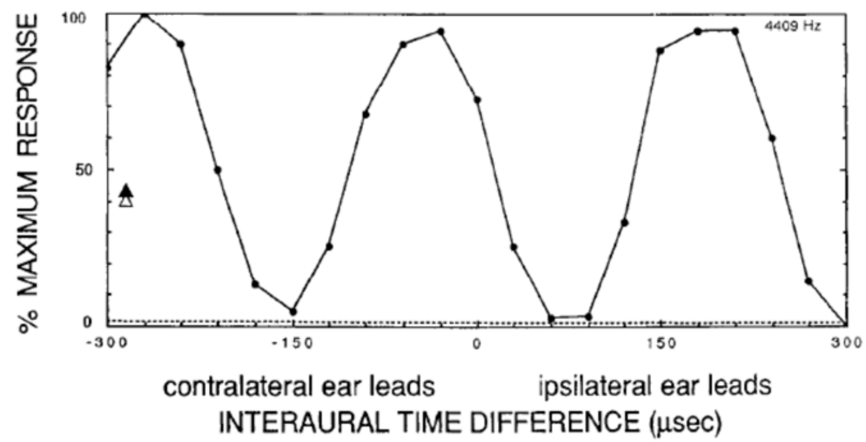


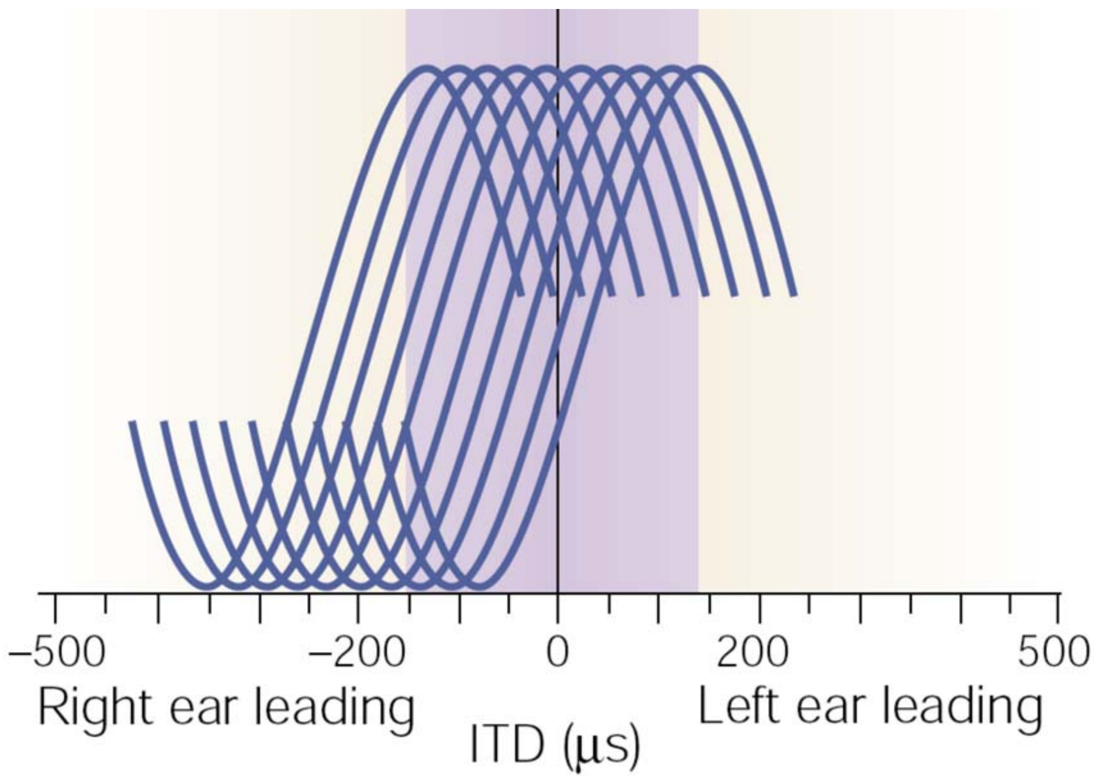


- Inputs from first order NM synapse on coincidence detector neurons in NL
- Create maps of ITD

ITD sensitivity in owl NL

- NL neurons tap into ITD map & encode ITD
- Until recently, it was assumed all ITD circuits employed similar algorithms

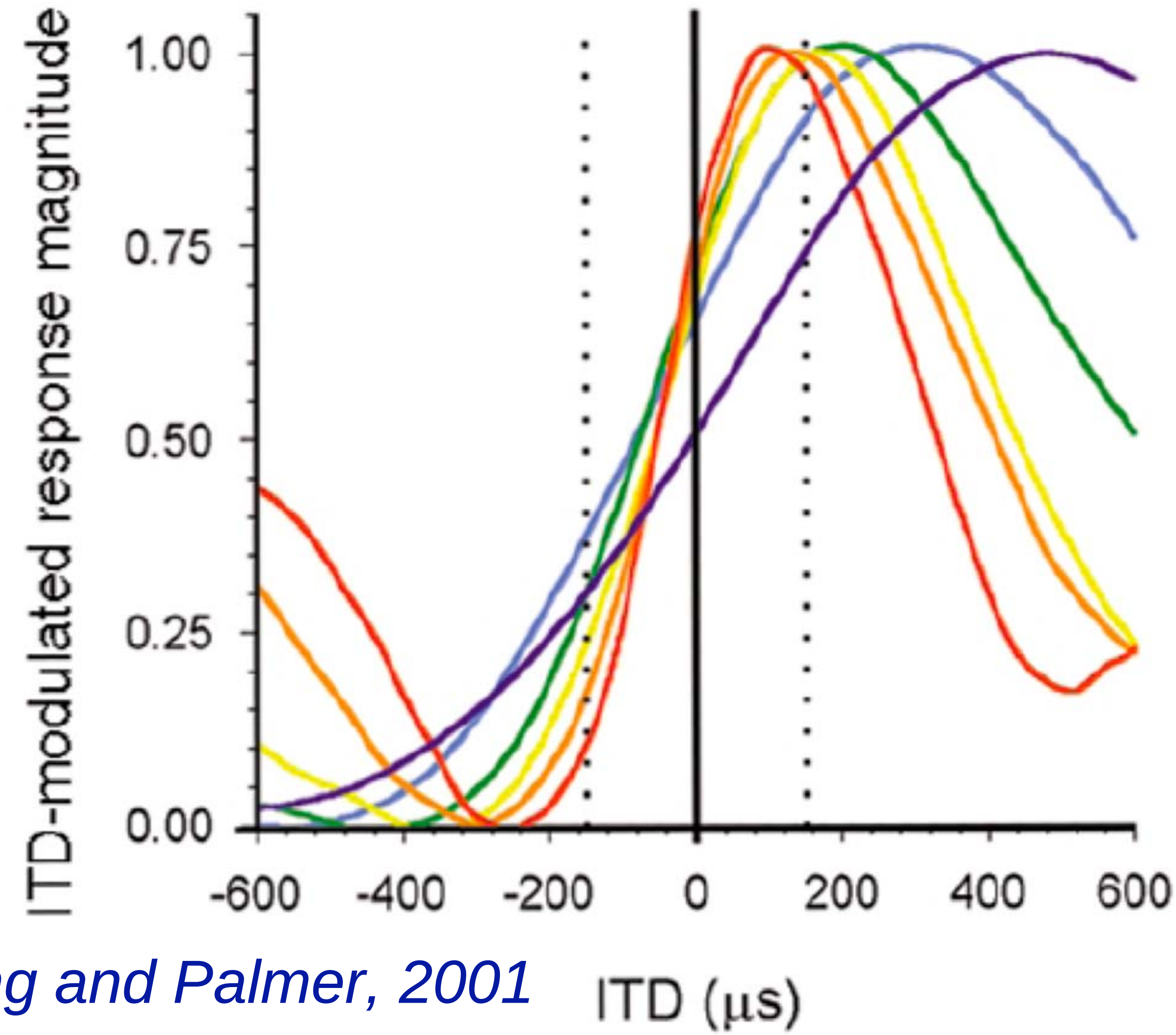




From Grothe 2003

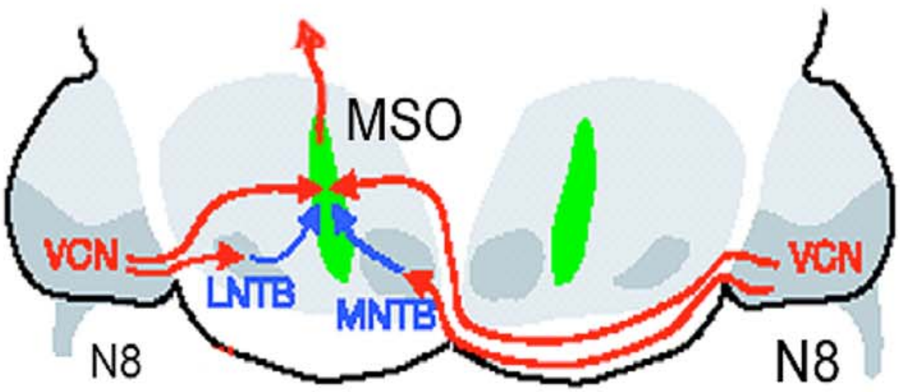
ITD responses in guinea pig IC

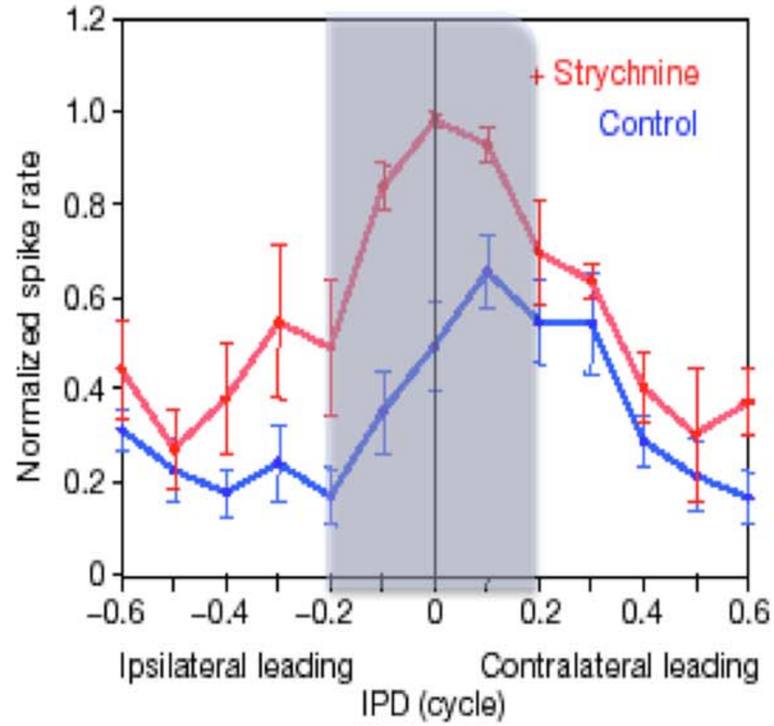
- Dotted line shows predicted biological range of ITDs
- Slopes, not peak, available at low BF



From McAlpine, Jiang and Palmer, 2001

Gerbil MSO data show slope of ITD curve in biological range





Inhibition shifts the slope of ITD function so it falls in the biological range

From: Brand, Behrend, Marquardt, McAlpine& Grothe NATURE 2002

NATURE | VOL 430 | 5 AUGUST 2004 | www.nature.com/nature

Optimal neural population coding of an auditory spatial cue

Nicol S. Harper[1,2] **& David McAlpine**[1]

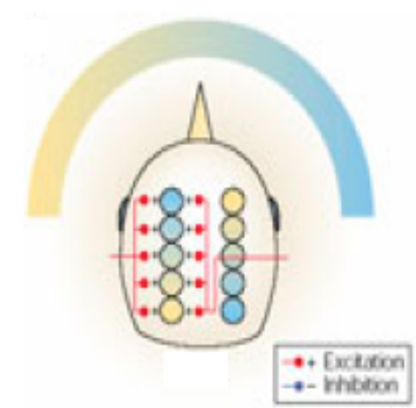
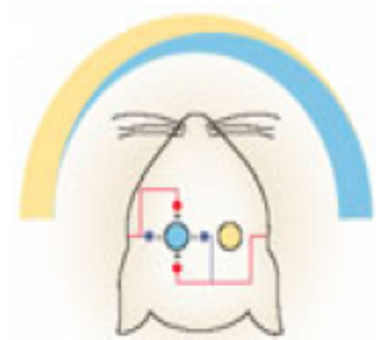
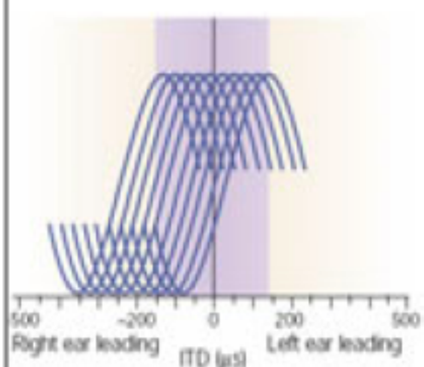
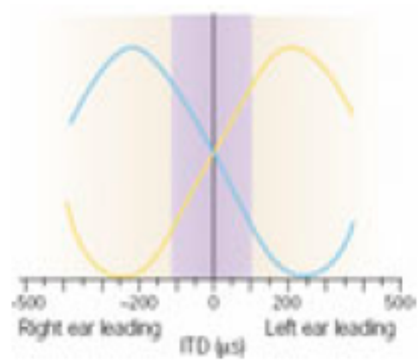
[1]*Department of Physiology and UCL Ear Institute and* [2]*CoMPLEX, University College London, London WC1E 6BT, UK*

A sound, depending on the position of its source, can take more

Harper and McAlpine (2004) proposed an unifying optimal coding strategy for ITD coding that depends on head size.

Unified theory of ITD coding?

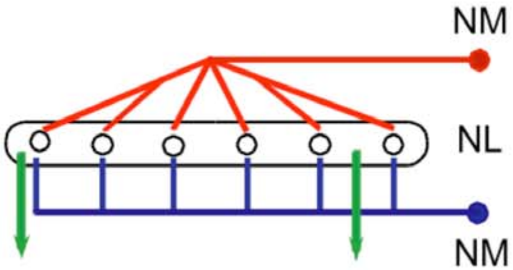
- Harper and McAlpine (2004) proposed optimal coding strategy for ITD depends on head size.
- Test their predictions in the chicken

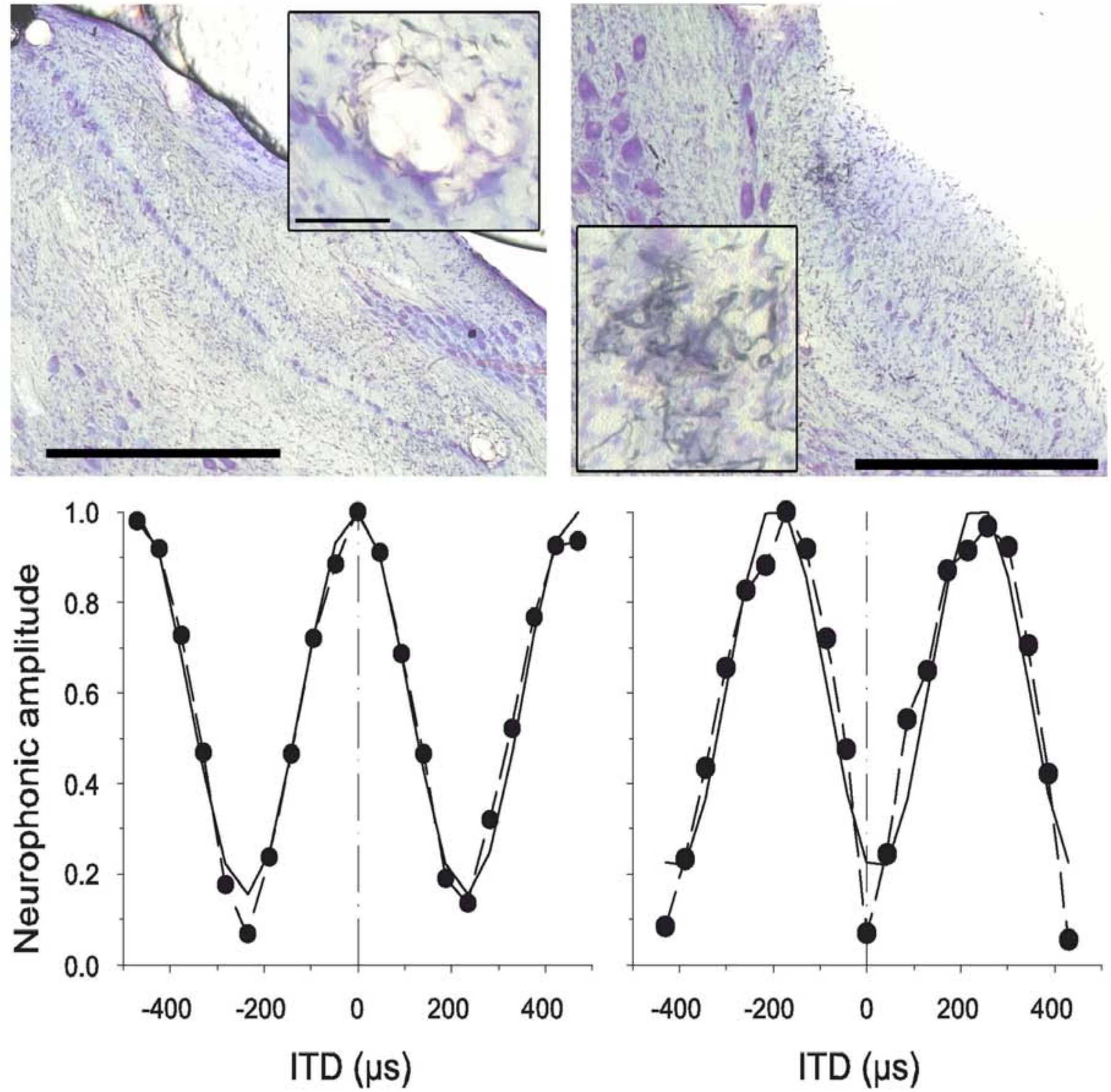
	Larger head and high-frequency phase locking: Barn owl	Small head and average phase locking: Gerbil, Guinea pig	Chicken
Model prediction:	Jeffress-like ITD coding above 3 kHz 	Two-channel ITD coding throughout phase-locking range 	
Data:	☑ consistent with prediction 	☑ consistent with prediction 	?

Schematic drawings from Grothe (2003)

ITD is systematically mapped in NL

- In chicken, ITDs near 0 mapped medially & ITDs from the side are mapped laterally
- corresponds to the biological range available to the chicken

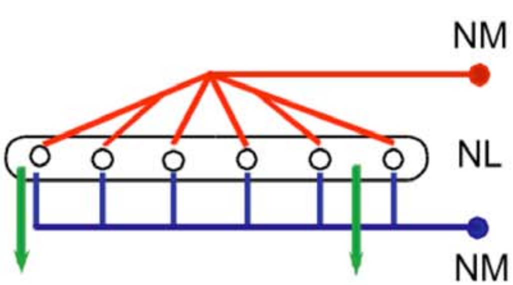


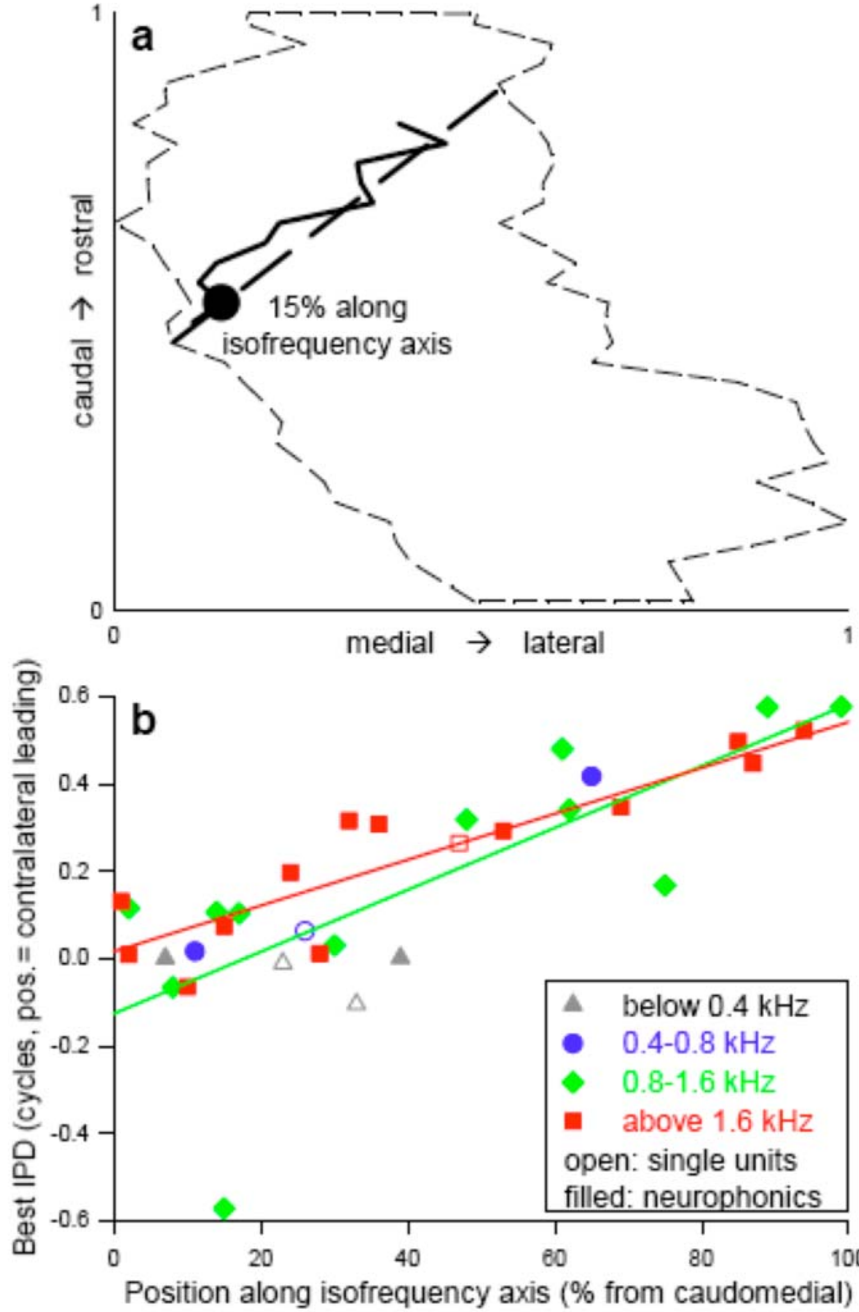


Medial lateral

ITD mapped in chicken NL

- Reconstruct labeled ITD sites in NL
- Medial points near 0 ITD
- Lateral points map progressively into contralateral space





Summary of ITD coding

- Owl and chicken use delay lines and coincidence detection to form ITD maps
- Functionally similar neurons in the gerbil act as coincidence detectors but may or may not be organized into a map
- Since chicken NL does not conform to optimal coding theory predictions,
  - Jeffress-like ITD coding mechanisms are an evolutionarily stable strategy (local minima?, good enough?)
  - evolutionary history influences coding
  - maps of ITD have computational utility

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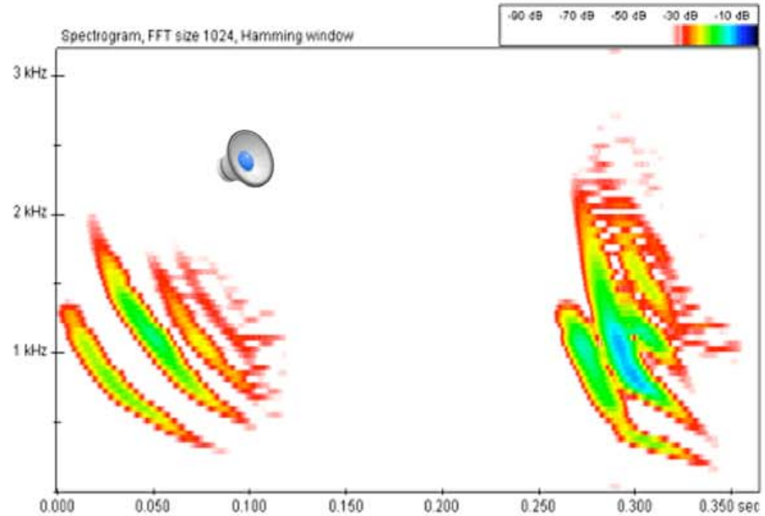
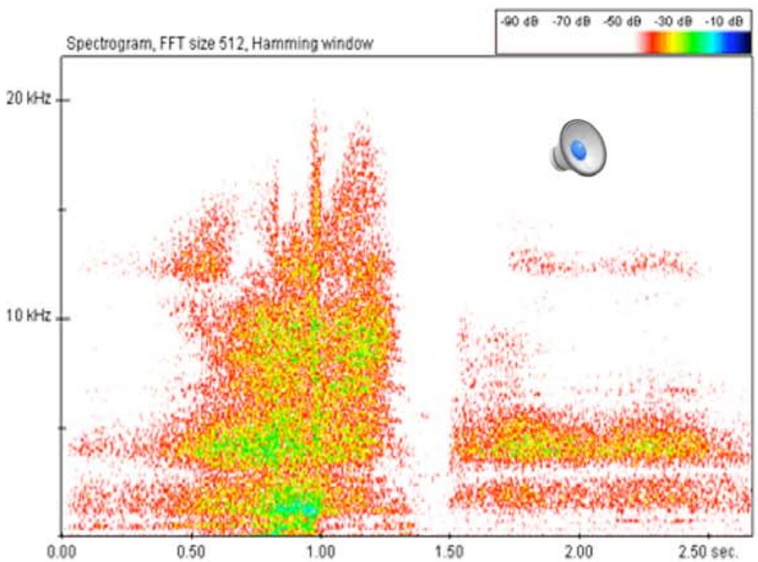
Sound localization circuits in alligators

Sister group to birds

- behavior
- brain slices
- ITD coding in brain

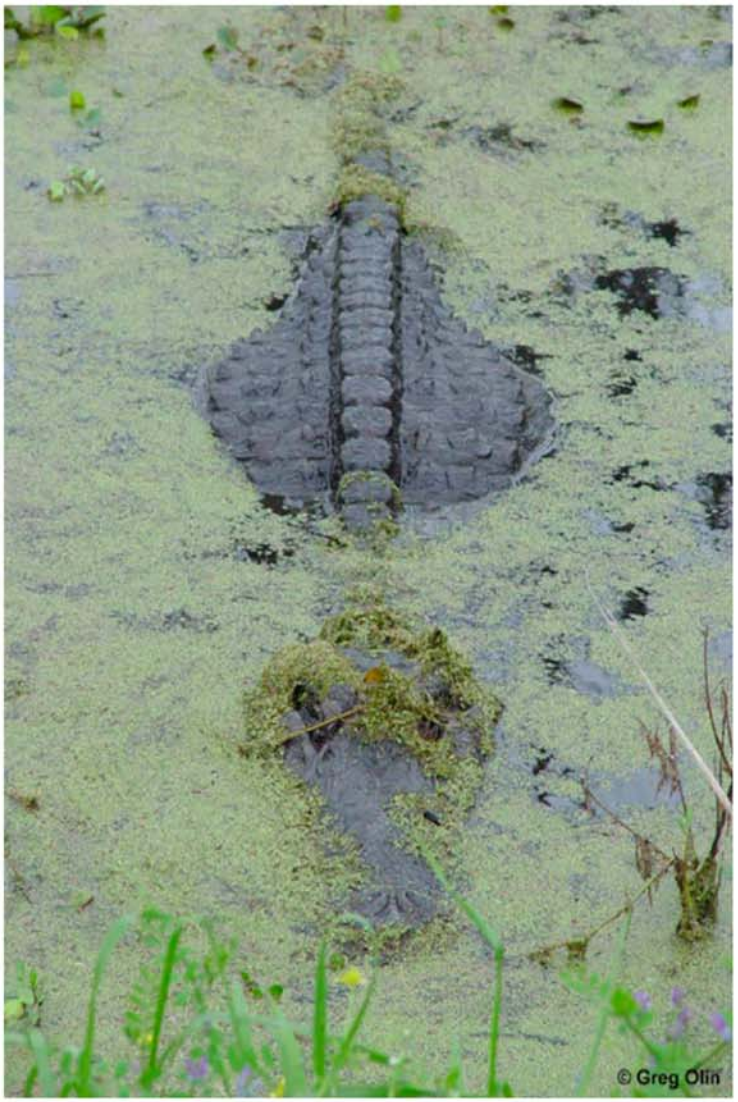
Alligators are very vocal and hear well at low frequencies



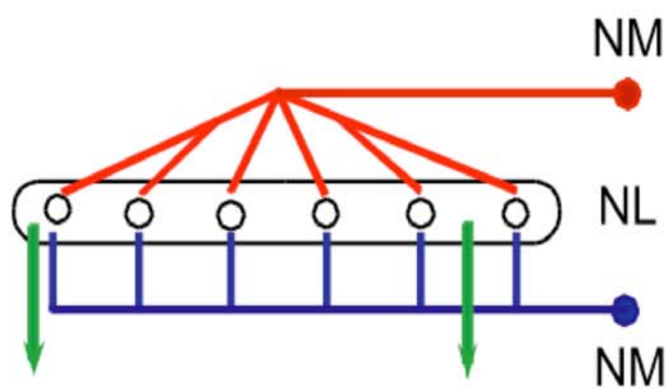


They have large ears covered by flaps

Sound localization circuits in alligators

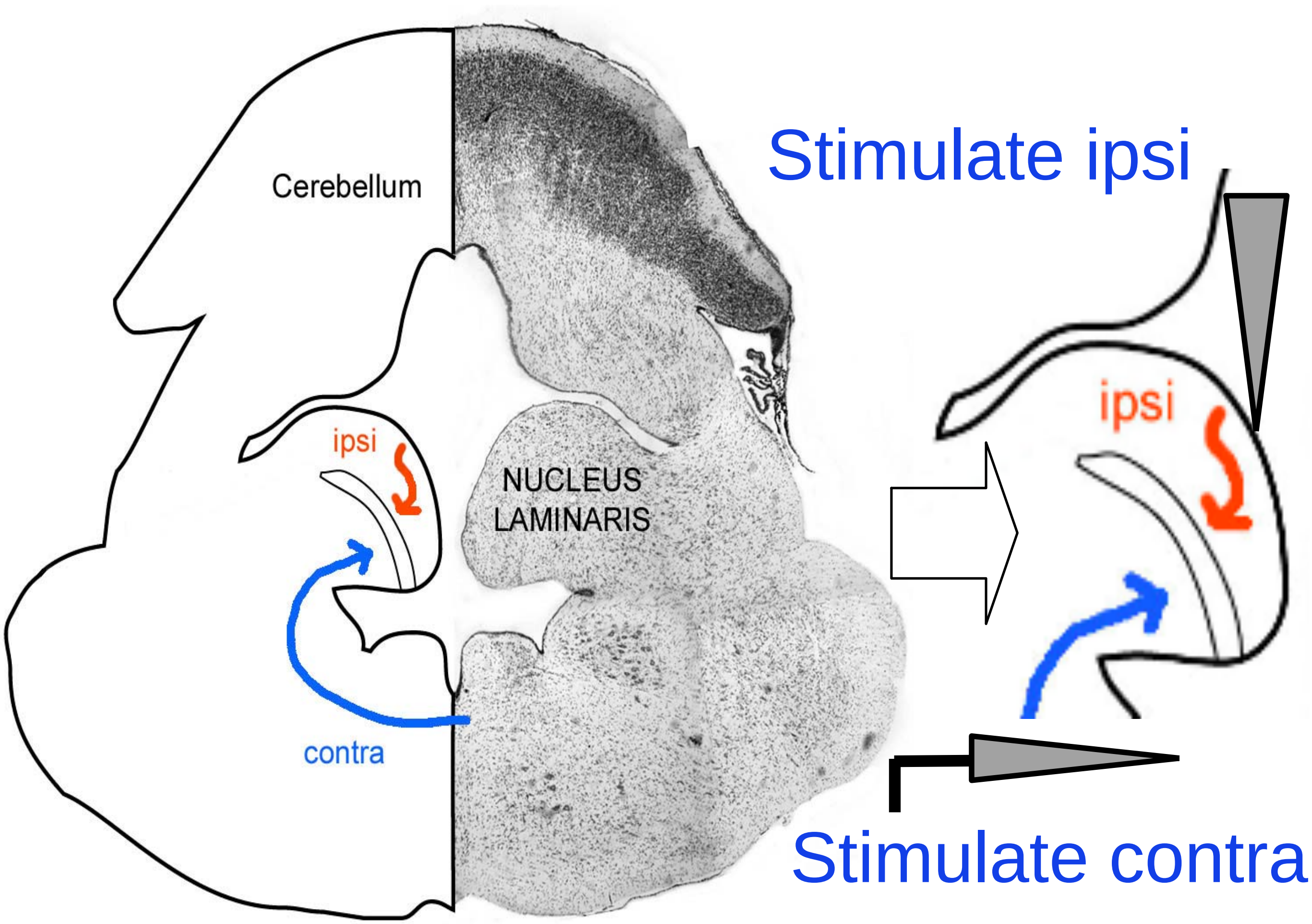


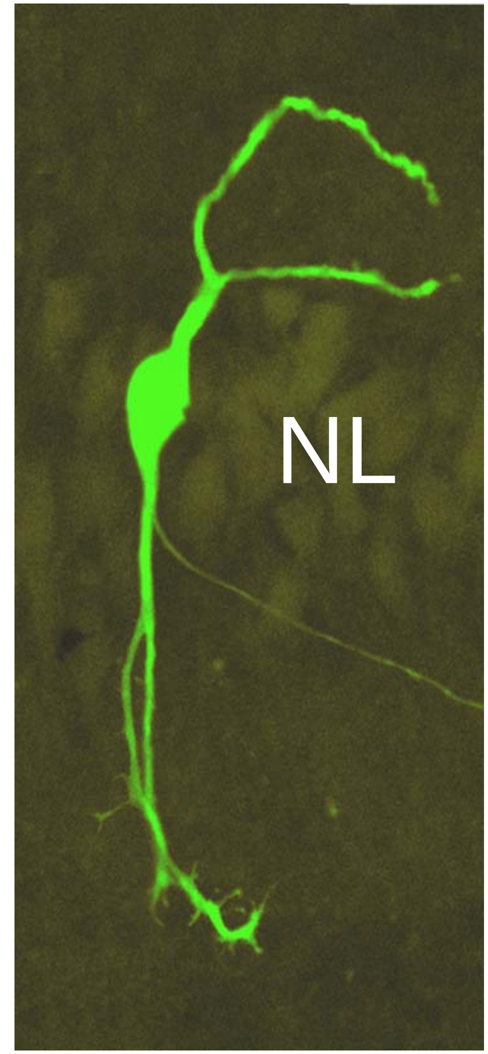
- behaviour
- brain slices
- ITD coding in brain



Alligator NL circuit resembles chick NL

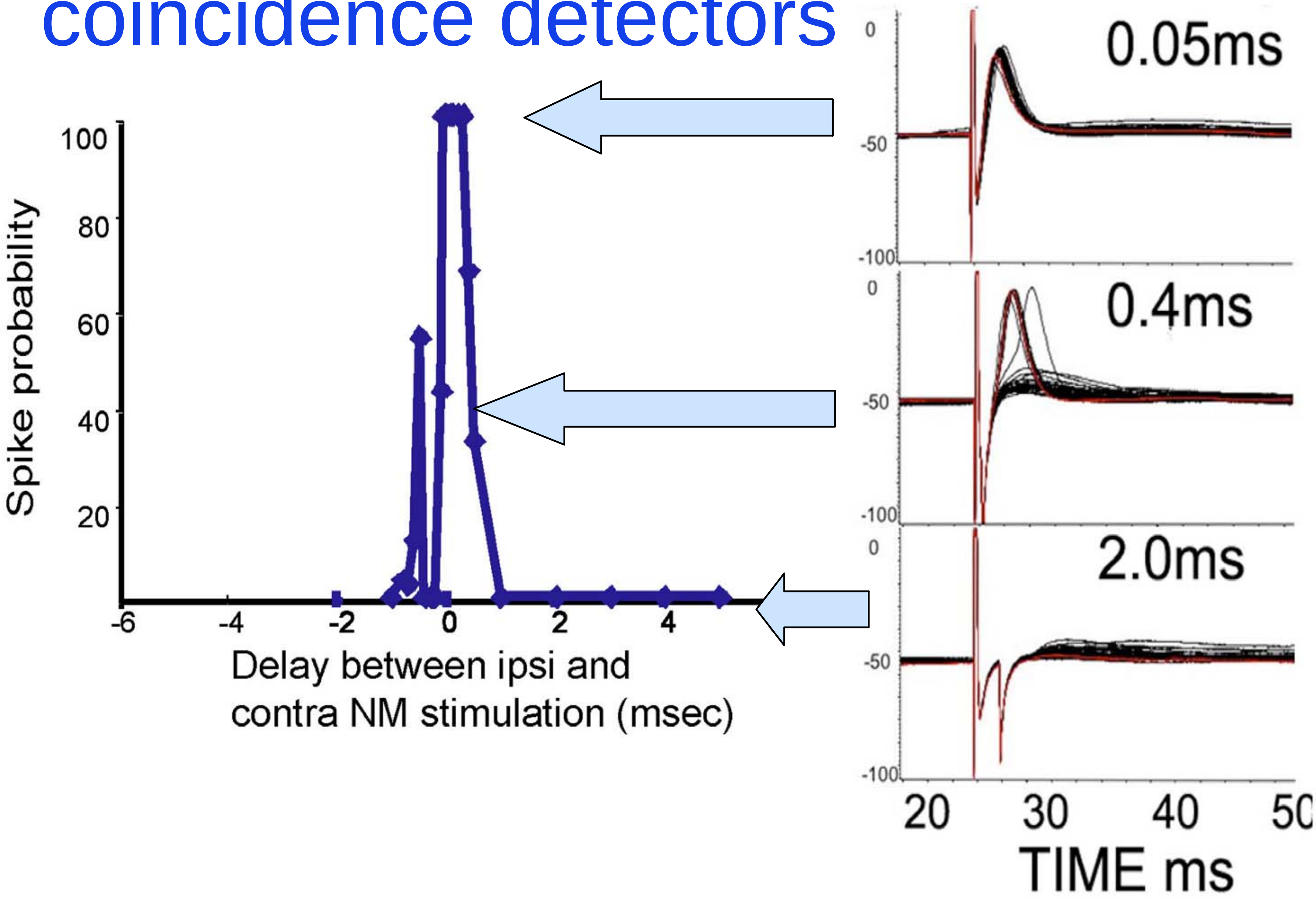
In alligator slices, record from NL while stimulating NM inputs





Record from NL

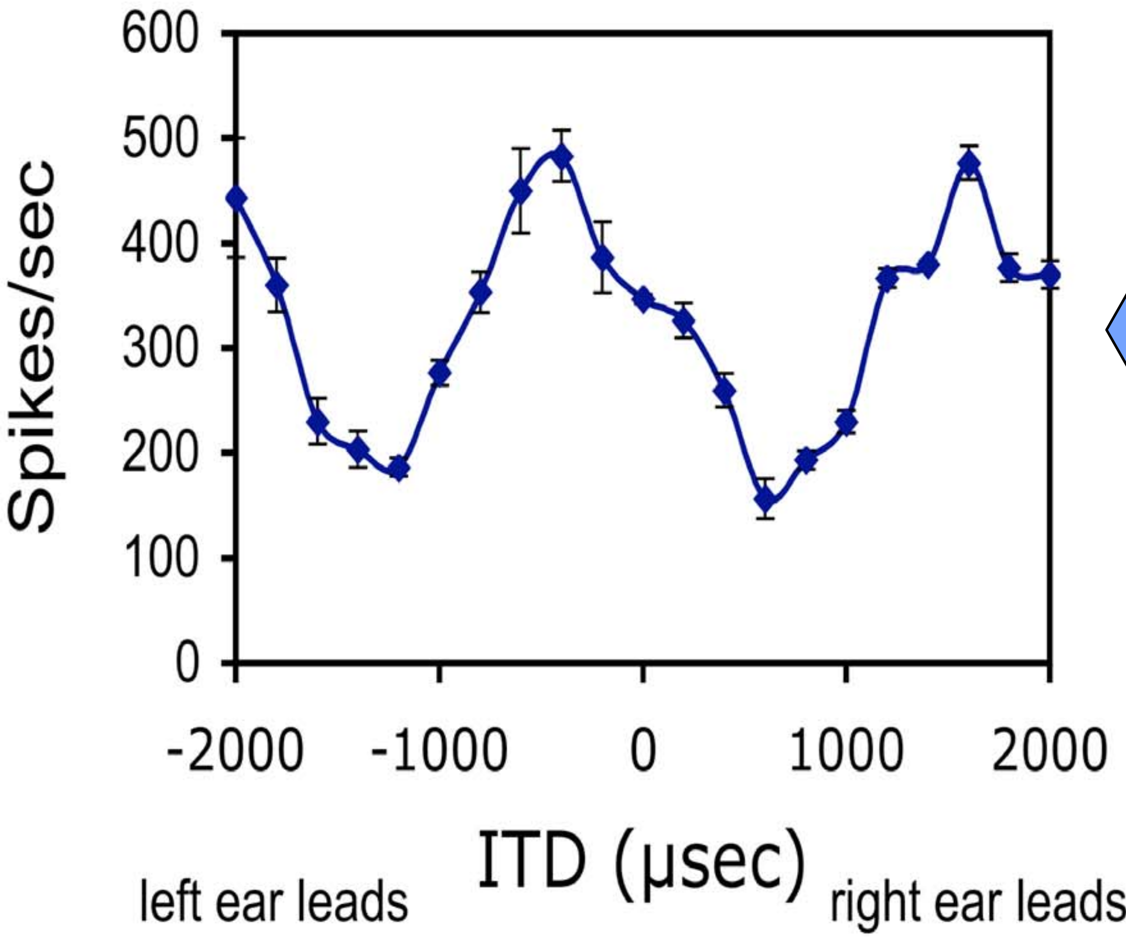
Alligator NL neurons act as coincidence detectors

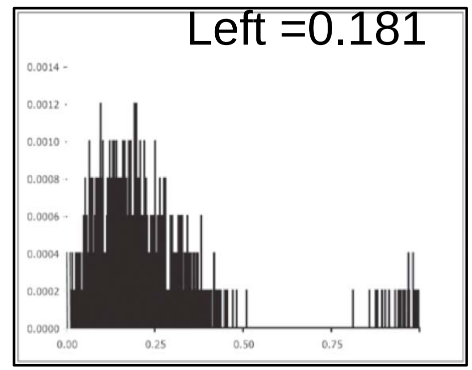


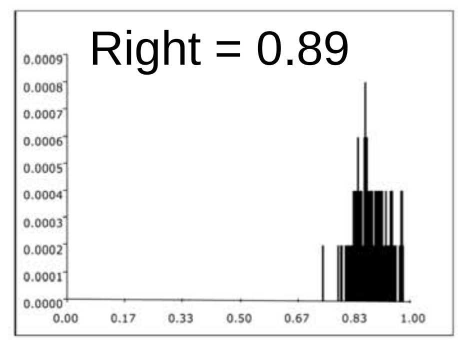
Alligator NL neurons act as coincidence detectors in vivo

Stimulate L <u>or</u> R ear and record phase of response in NL cell

-500μsec



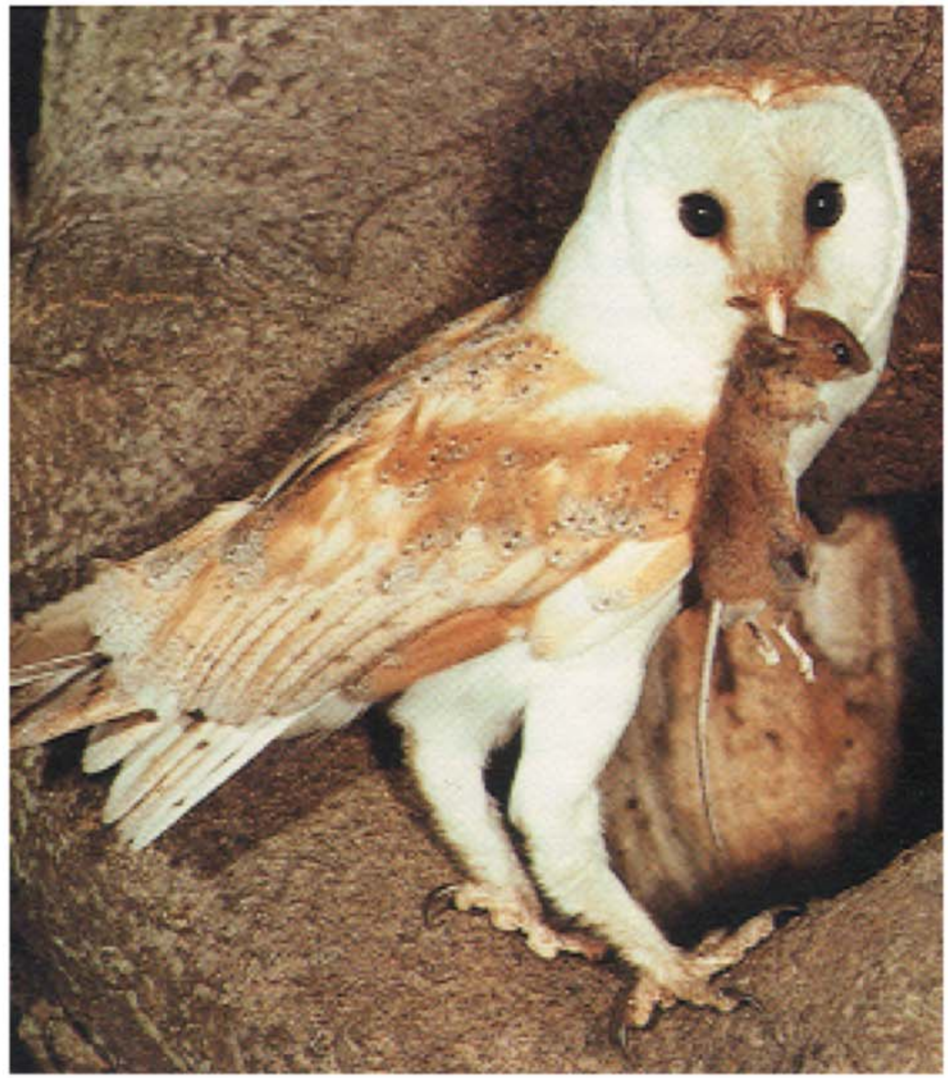




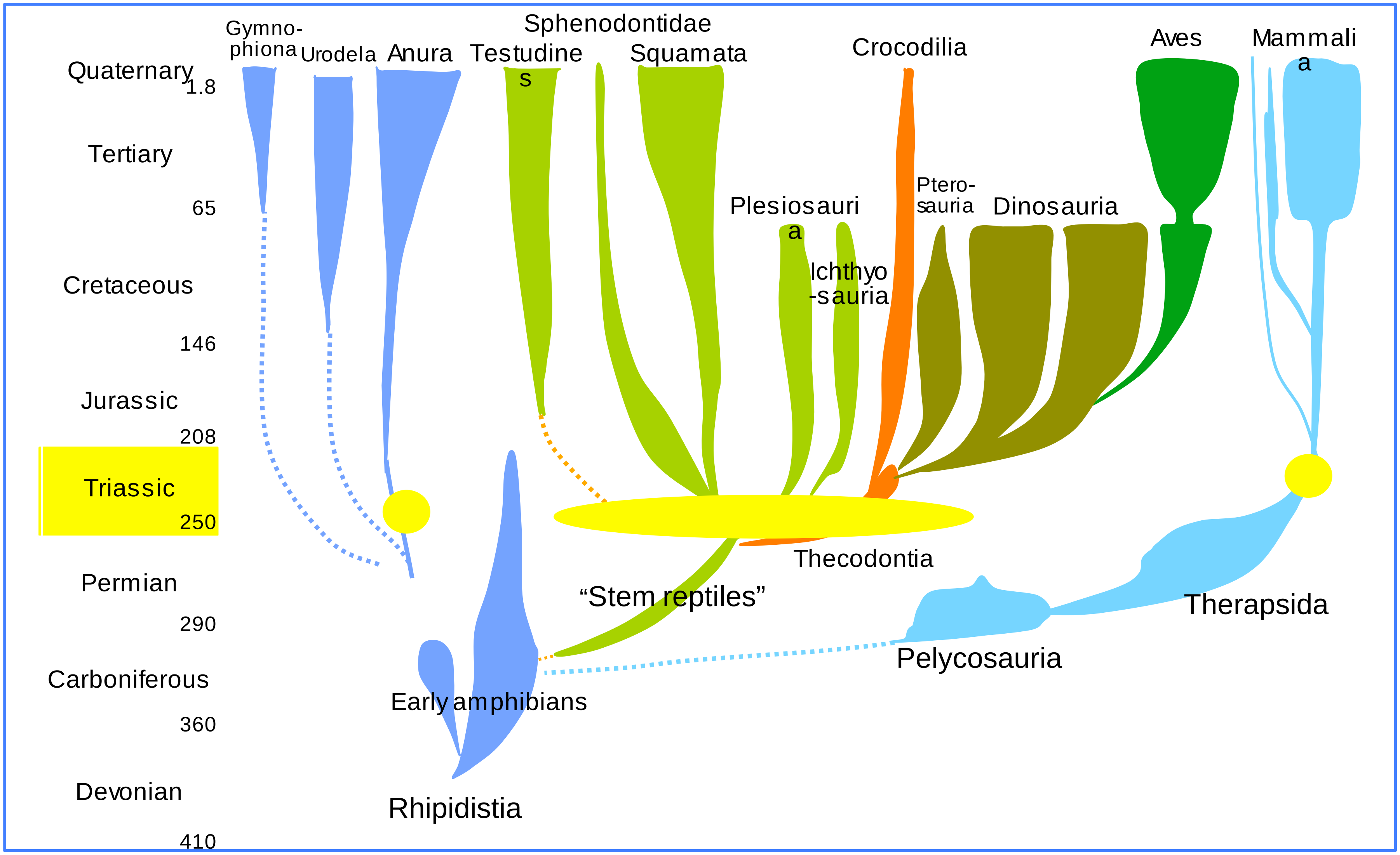
Best ITD is -500μsec
Right ear leads left by 0.284deg or -560μs.

Summary of ITD circuits in birds & crocodiles

- ITD coding circuits in closely related birds and crocodilians employ similar rules
- What about other Reptilia?



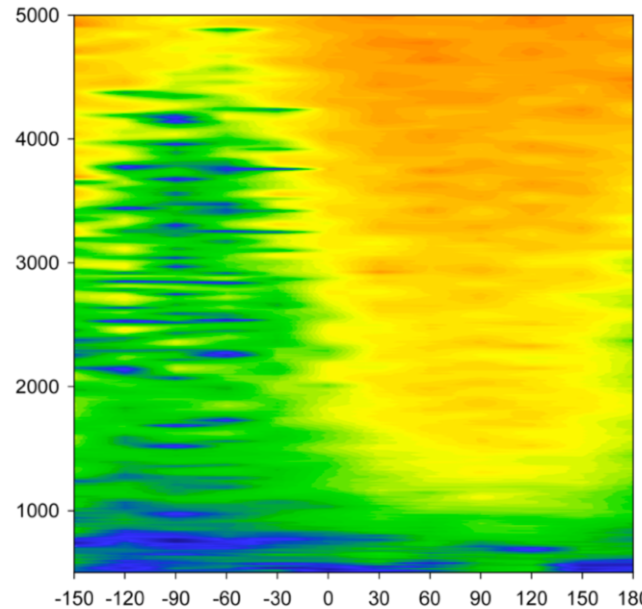
Tetrapod ears evolved in parallel



Grothe, Nat. Rev. Neurosci, 2003

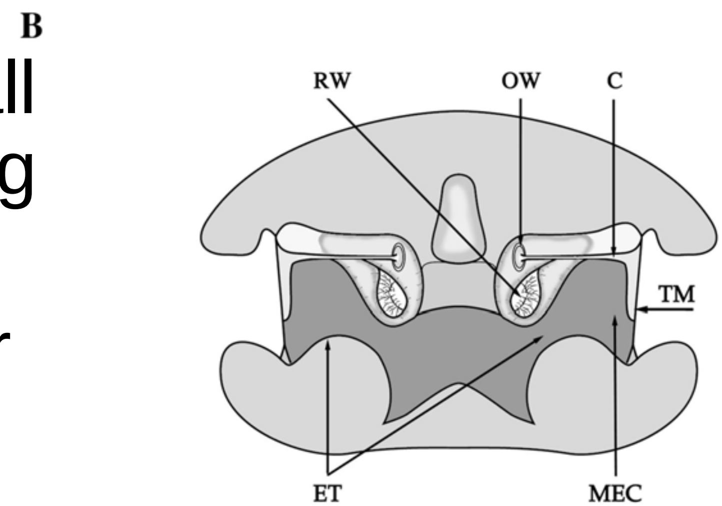
Sensitive, high-frequency hearing of airborne sound may be a recent event in vertebrate evolution

Sound localization in lizards

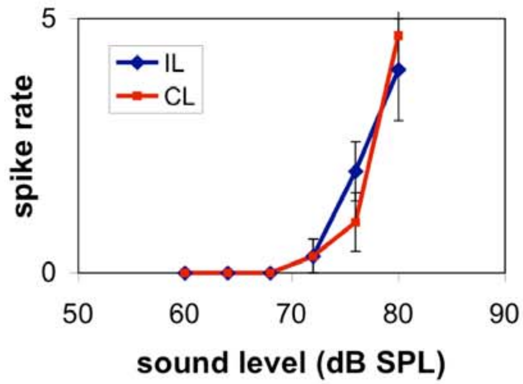


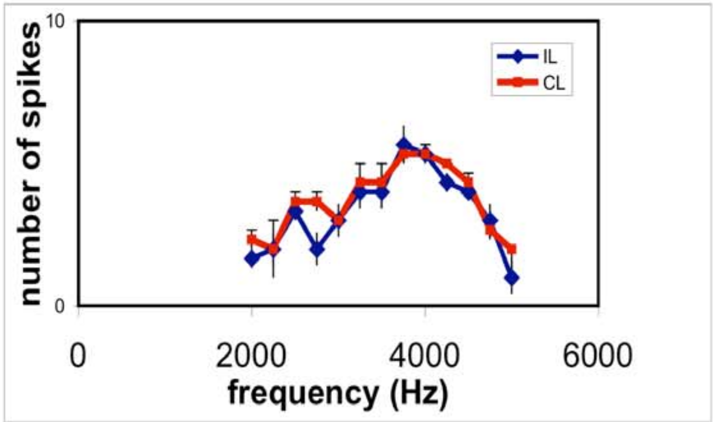
Ears of frogs, lizards & birds all show some acoustical coupling of the eardrums

Pressure gradient receiver ear is inherently directional

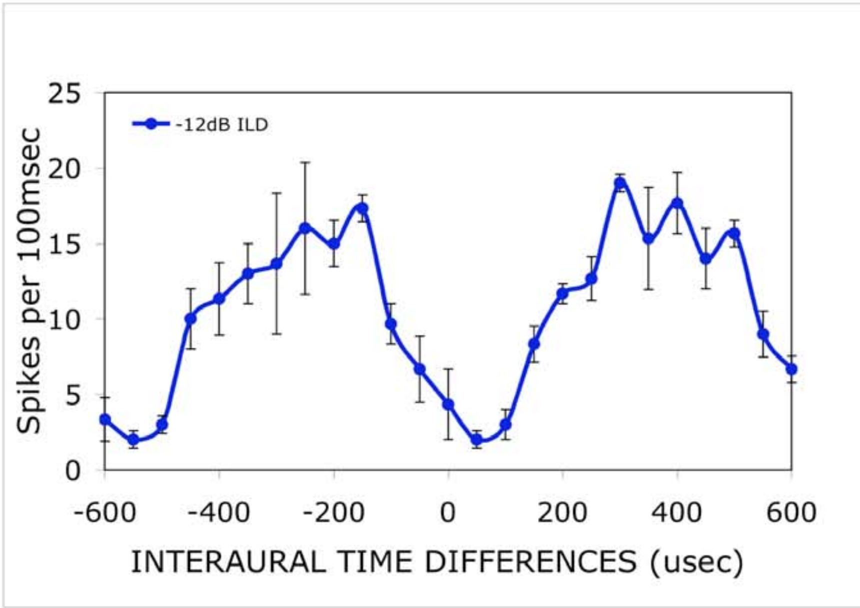


Without block: coupling of ears in Gekko





- similar sensitivity to ipsi- and contra sound
- strong acoustical binaural interactions at eardrum
- ITD and ILD sensitivity in nerve recordings



Predictions from gecko: Processing in early tympanic ears

- Directional responses in all brainstem nuclei
- The closure of the middle ear cavity in the mammals and some birds is a derived condition, and may have profoundly changed the operation of the ancestral tetrapod ear by decoupling the tympana
- A closed middle ear would improve the low-frequency response of the tympanum
- Would also lead to a requirement for neural computation of directionality in the brain
- Appears in parallel in archosaur and mammalian lineages

Shared computational principles in the auditory system

- Birds, crocodilians and mammals use similar coding strategies

- These parallel circuits reveal common computational principles for sound location which highlight evolutionary constraints in circuit design and coding