The electric sense of weakly electric fish

Presenting: Avner Wallach

Why study ‘exotic’ neural systems?

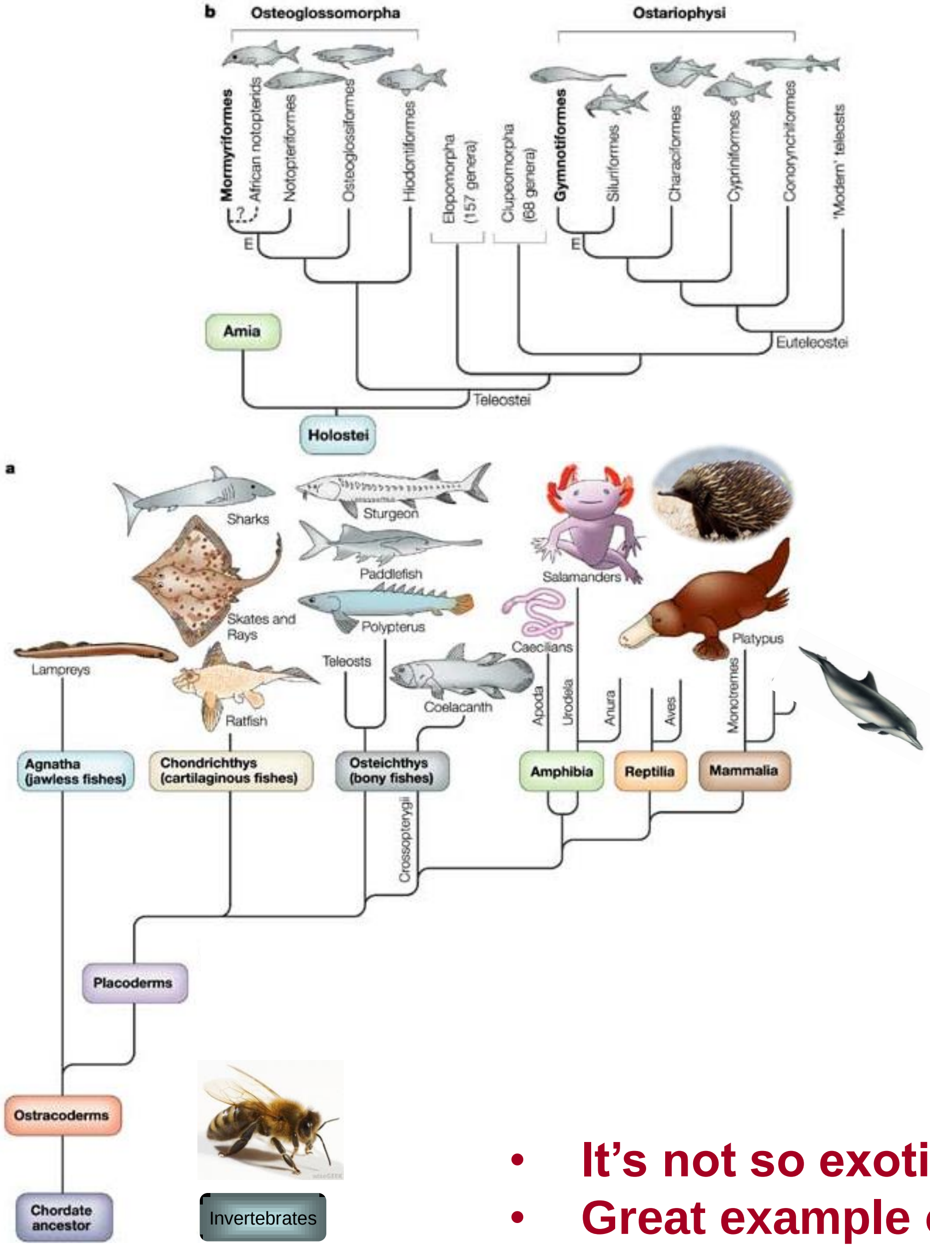
The *credo* of neuroethology-
choosing ‘champion’ animals that:

- Offer experimental access to important questions. Examples for this are colored in brown.
- Evolved to maximize the computational performance of their nervous system. Examples for this are colored in purple.

Overview

- Introduction
  - Taxonomy
  - Sensors and Actuators
  - Active Electroception
- Electrocommunication
  - The **Jamming Avoidance Response:** behavior, anatomy, physiology
  - Envelopes
  - Chirps
- Electrolocation
- The nP-EGp feedback loop
- High-level functions: the Telencephalon

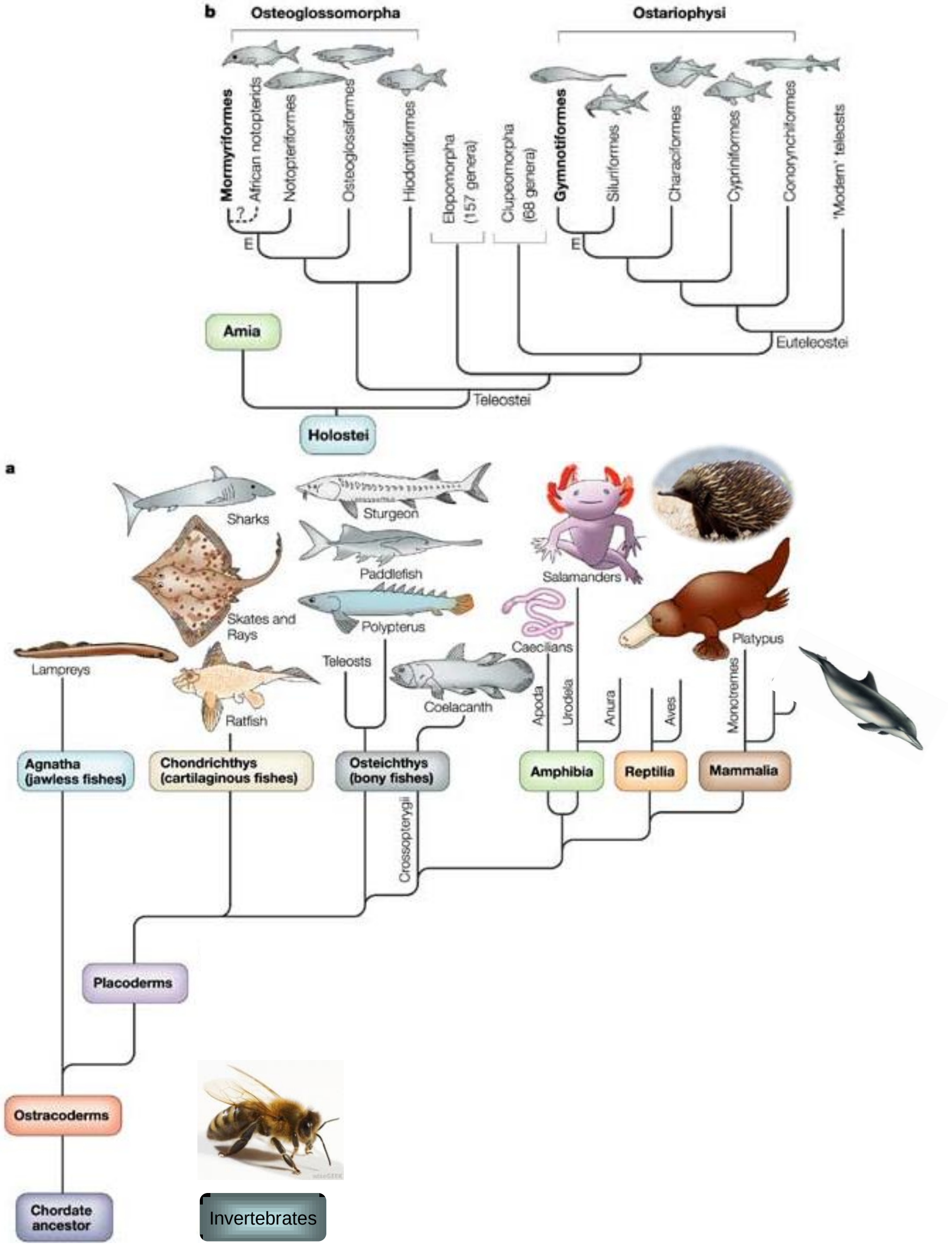
Electroception in the animal kingdom



- Most electroceptive animals have passive (**ampullary**) receptors: sense weak, low frequency electric fields (e.g., caused by prey's respiratory system).
- Some fish developed an **electric organ:** generate strong electric fields (e.g., to stun prey).
- Two families of bony fish- the **South American Knifefish** (*gymnotiforms*) and the **African Elephantfish** (*Mormyriforms*): both electric organs and special receptors (**tuberous**) that sense the self-generated electric field.

- **It's not so exotic**
- **Great example of convergent evolution**

Electroception in the animal kingdom

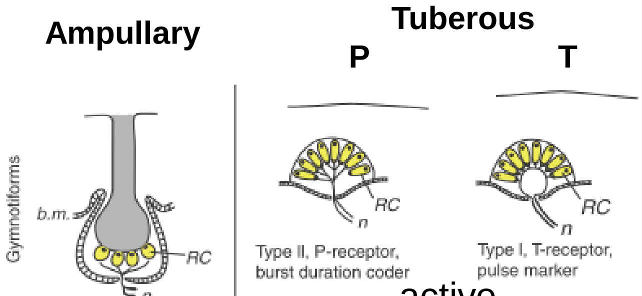


Why did electroception evolve so many times?

- Occupy a cornucopious ecological niche: enables detection of prey in darkness, murky water or mud, while being safe from most predators.
- Use of existing ‘hardware’.

Sensors and Actuators

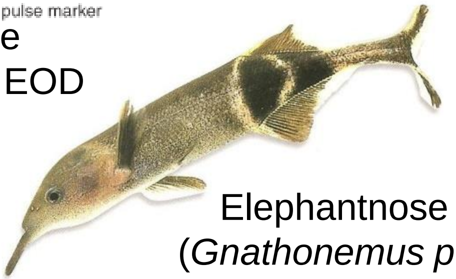
- Receptors derived from lateral-line acoustic receptors (or from trigeminal mechanoreceptors in mammals).
- Distributed on the skin. Highest density in the head ('electric fovea').



passive
low-frequency

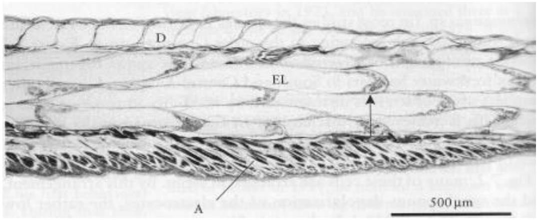
active
tuned to EOD

Schnauzenorgan



Elephantnose fish
(*Gnathonemus petersii*)
pulse type, Africa

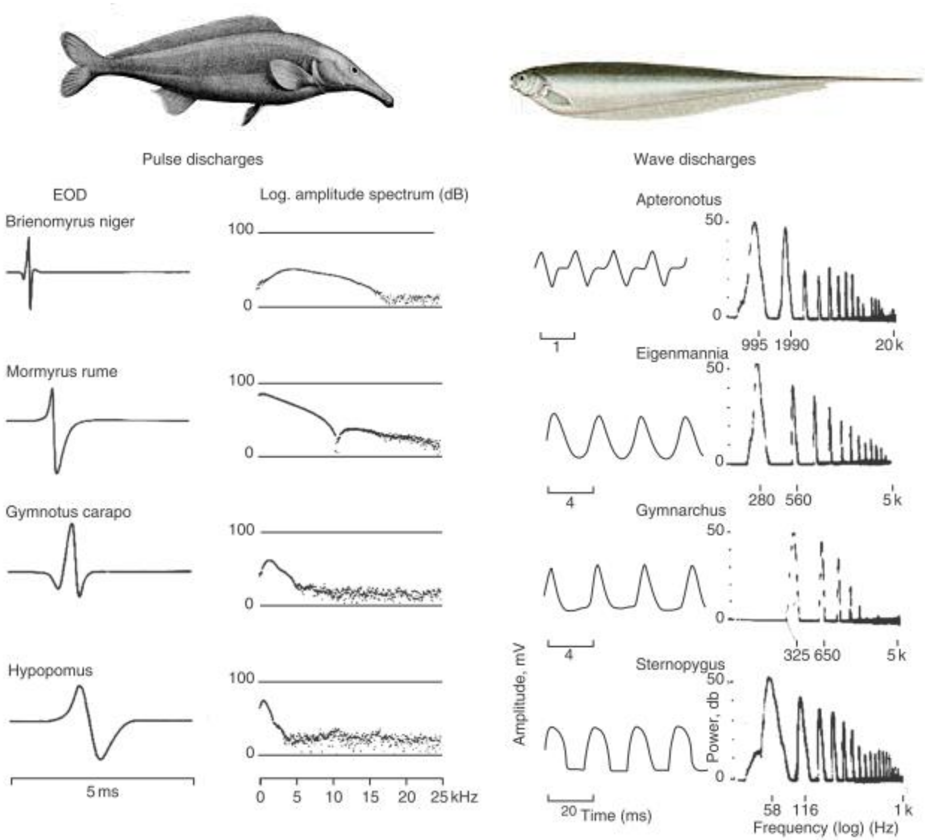
- Actuators are called **electrocytes**, derived from muscles-cells (myogenic) → silenced by curare (enables opening of loop).
- In one family (*apteronotidae)* derived from nerve-cells (neurogenic) → **not** silenced by curare (enables recording awake behavior in immobilized fish).

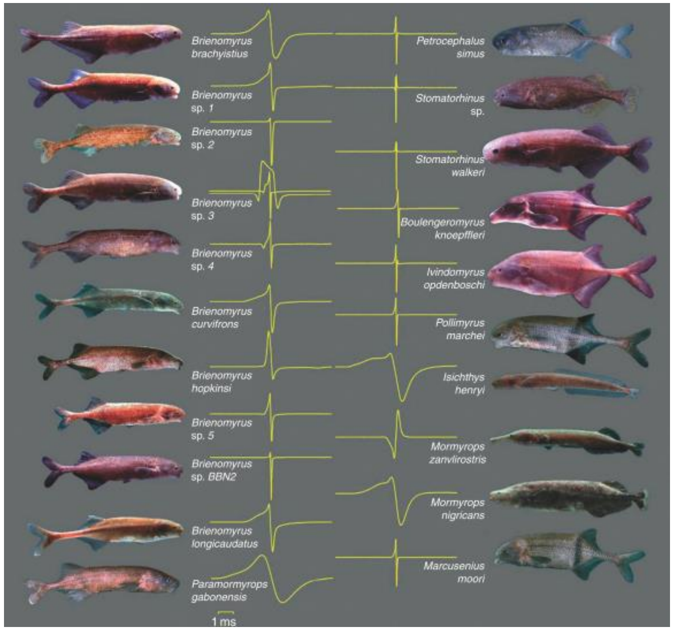


Curare: paralytic drug, blocks the nicotinic acetylcholine receptors found in neuromuscular junctions.

- **Relatively few ethical constraints**

EOD: Electric Organ Discharge





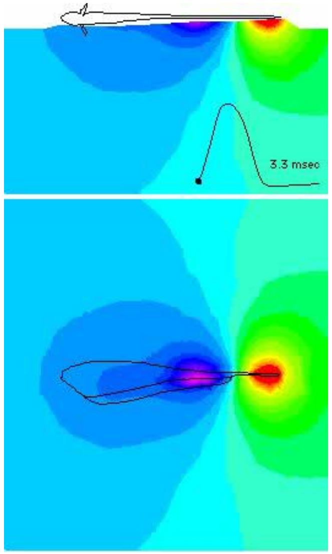
Low-jitter oscillations

- **Behavior in relevant modality is easy to record and interpret**

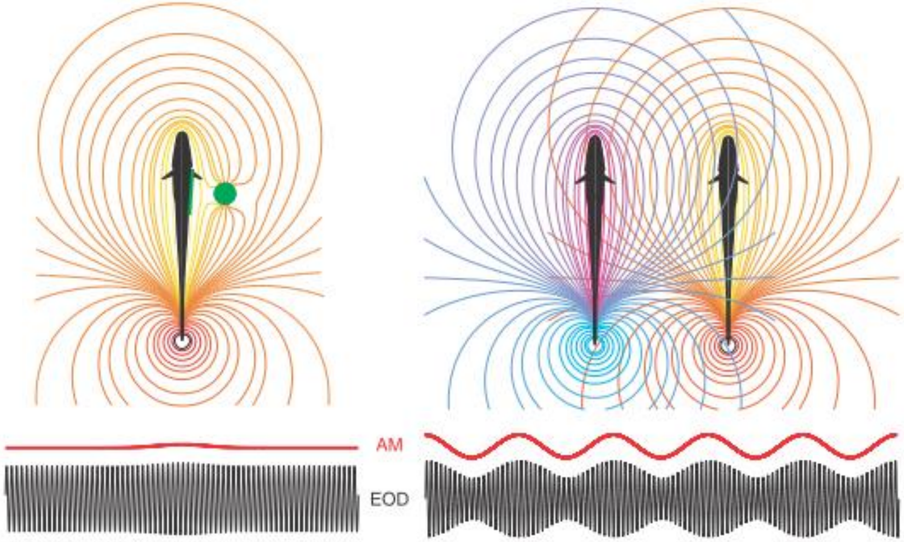
Active electroception

Electric organ creates an alternating electric **dipole**

$E \sim 1/R^2$ → Proximal sense (like whisking in rodents)



Assad & Rasnow, Bower lab



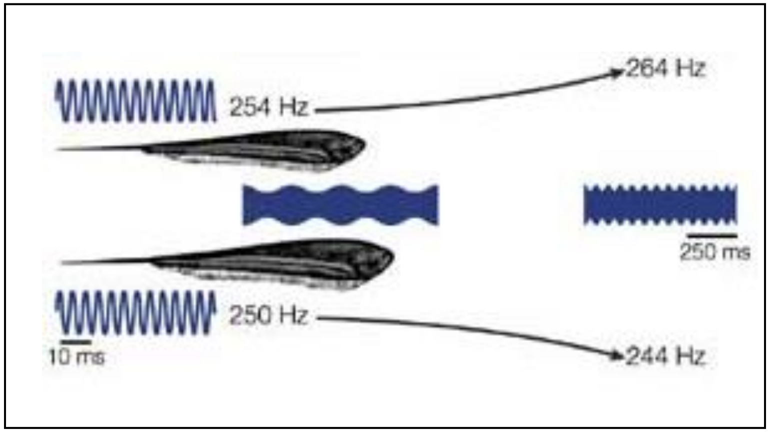
- Presence of external objects exerts low frequency (<20Hz) modulations of the EOD ‘image’ on the skin.

- Problem: neighboring fish causes low-frequency interference which ‘jams’ perception.

Jamming Avoidance Response (JAR)

From: Walter Heiligenberg, Neural Nets in Electric Fish, 1991

- Solution: each fish alters its EOD rate so that the frequency difference will be outside the perceptual band (>20Hz).
- JAR is a useful subject for neuroscience:
  - Reliably reproducible sensory-motor behavior of ecological importance.
  - Requires non-trivial neuronal computation



Gary J. Rose, Nature Reviews Neuroscience, 2004

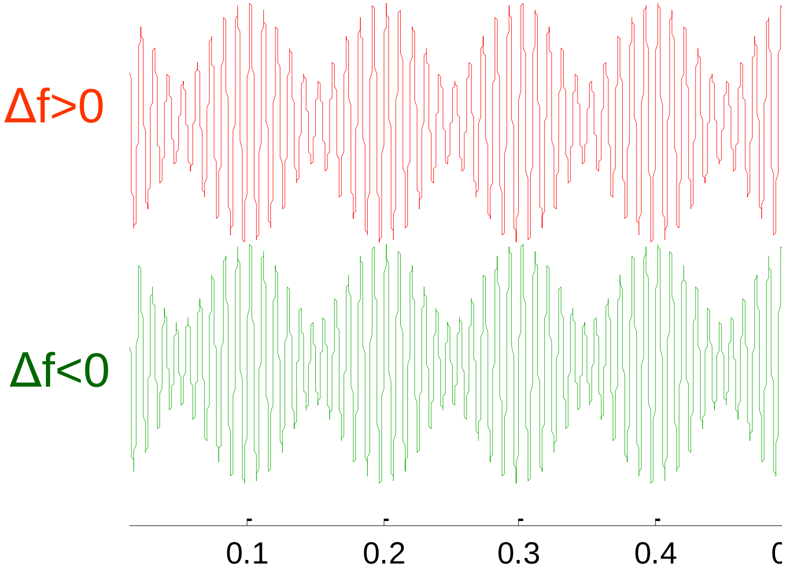
- **Provides reliable, non-trivial sensory-motor behaviors**
  - **Easy reduction of experimental variables**

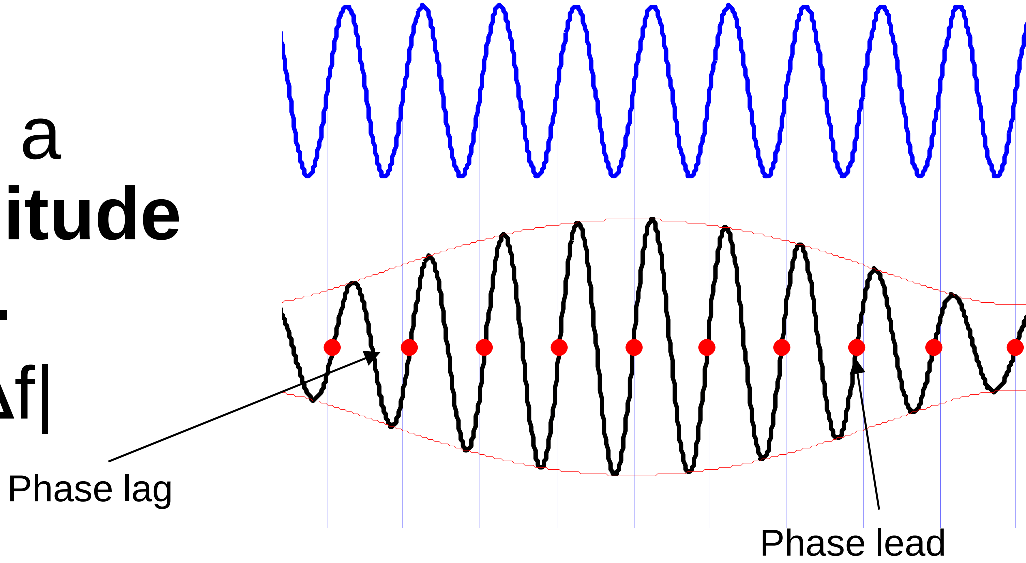
JAR behavior I

- f_1- Fish’s own EOD rate
  f_2- Interefence EOD rate

$$\Delta f=f_2-f_1$$

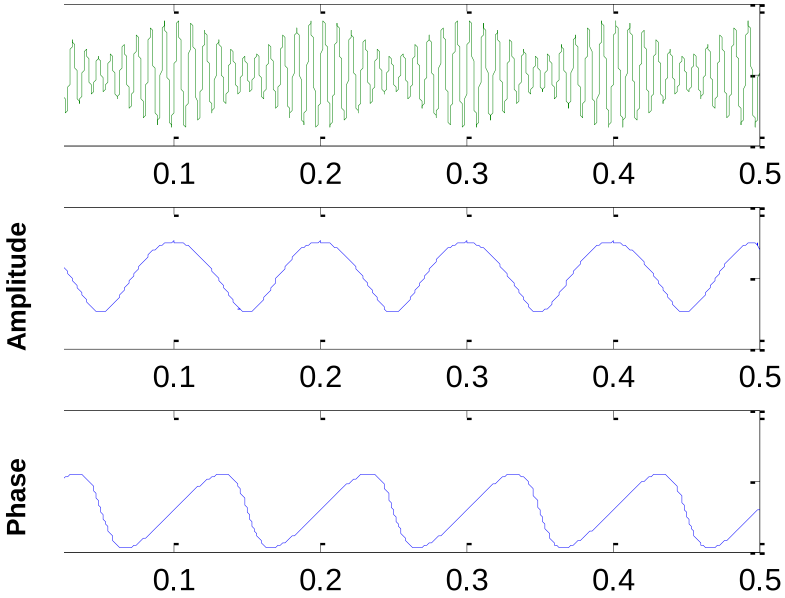
- Each fish needs to ‘decide’- is the neighbor using a higher rate ($\Delta f>0$) or a lower rate ($\Delta f<0$).
- The interference causes a modulation in both **amplitude** and **phase** called **‘beat’.**
- The rate of the beat is $|\Delta f|$



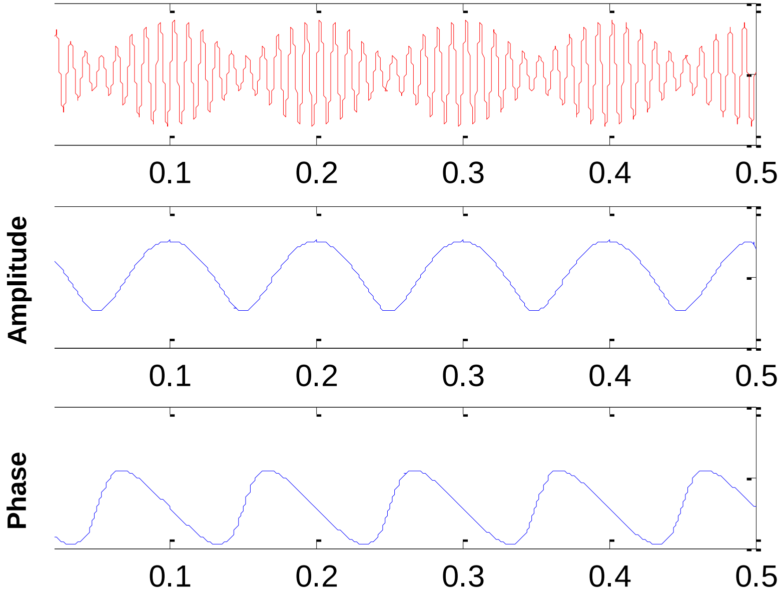


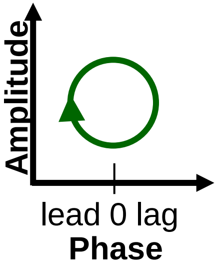
JAR behavior II

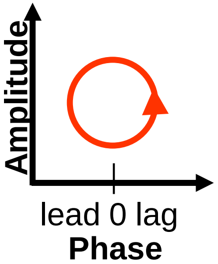
Δf<0



Δf>0



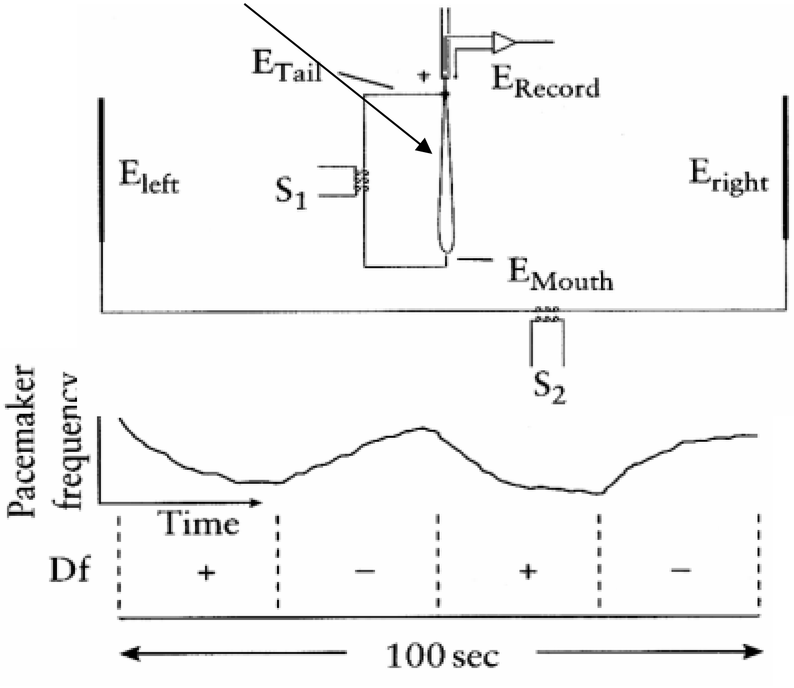




- Pattern of modulation in phase and amplitude holds information about sign of Δf:
  - When Δf>0 phase lag during amplitude rise and vice-versa.
  - When Δf<0 phase lead during amplitude rise and vice-versa.
- Rotations in different directions in amplitude/phase state-plane.

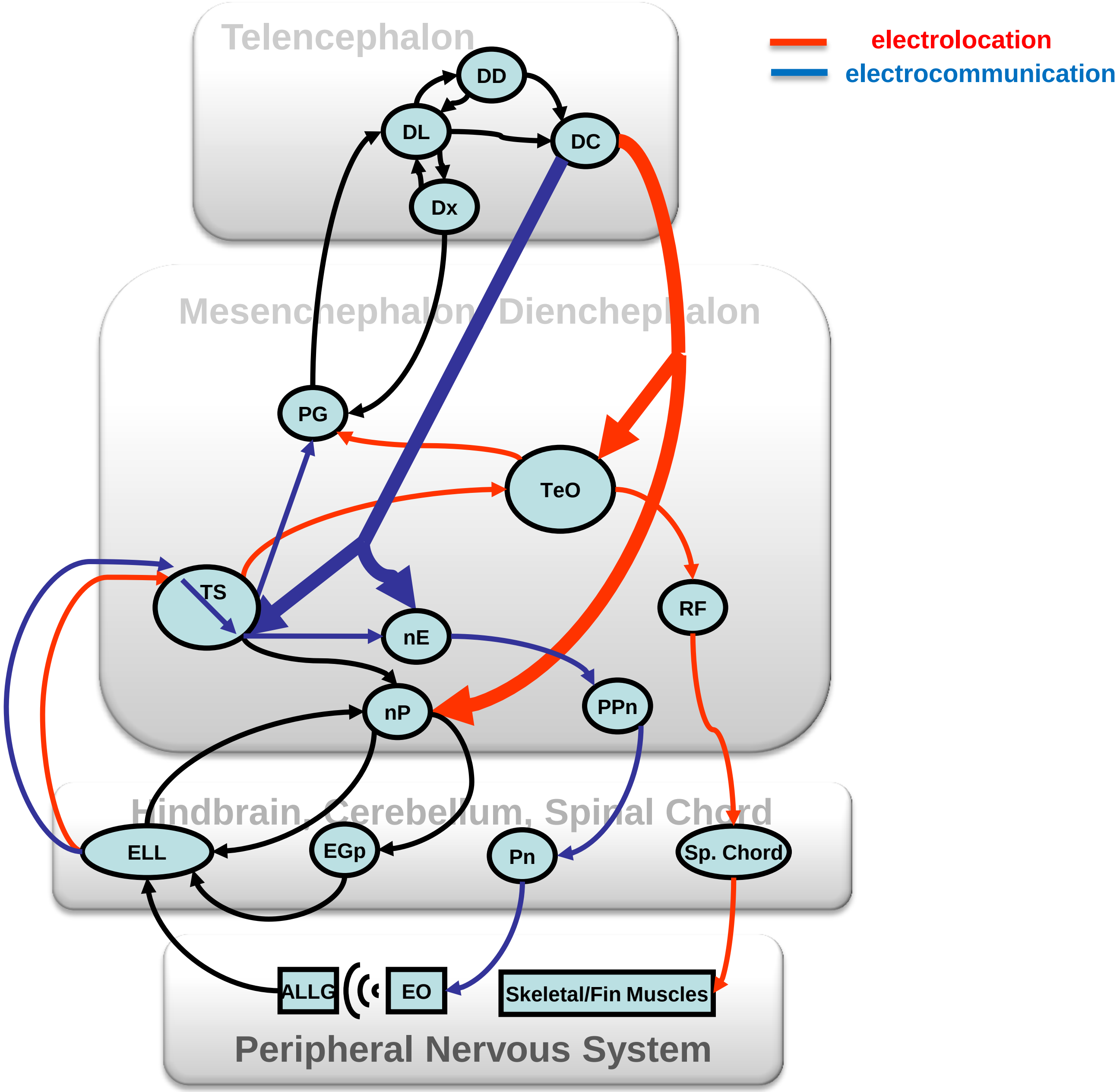
JAR behavior III

- Coding amplitude changes can be done locally, but phase coding requires a **reference**.
- One solution: use own motor output (‘efference copy’) as reference. However:
  - JAR elicited in curarized fish.
  - No JAR when interference is applied equally on entire body surface.

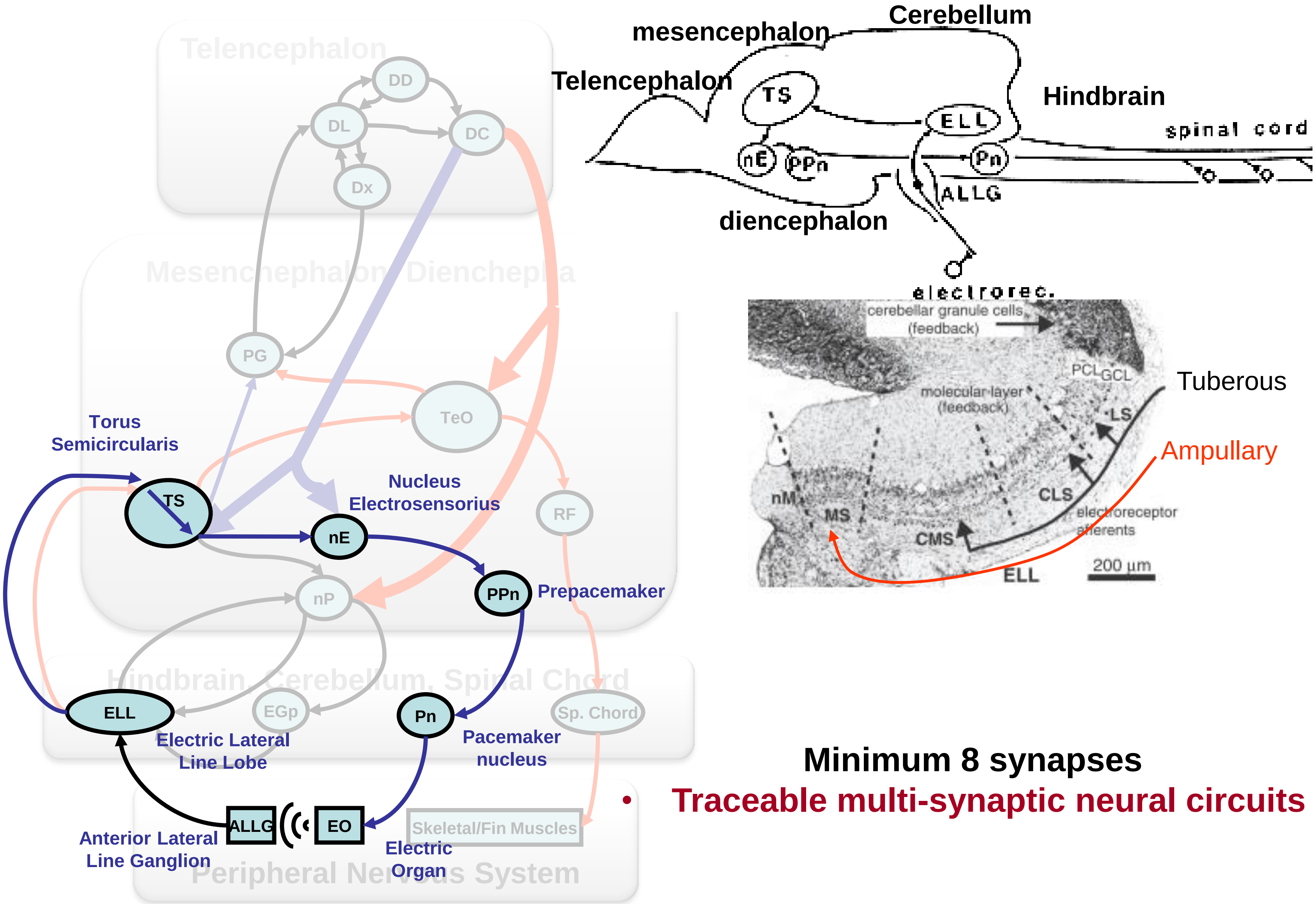

Curarized fish

Conclusion: The fish compares the differential effect of interference across the body surface.

Electrosensory related neural circuits



JAR anatomy

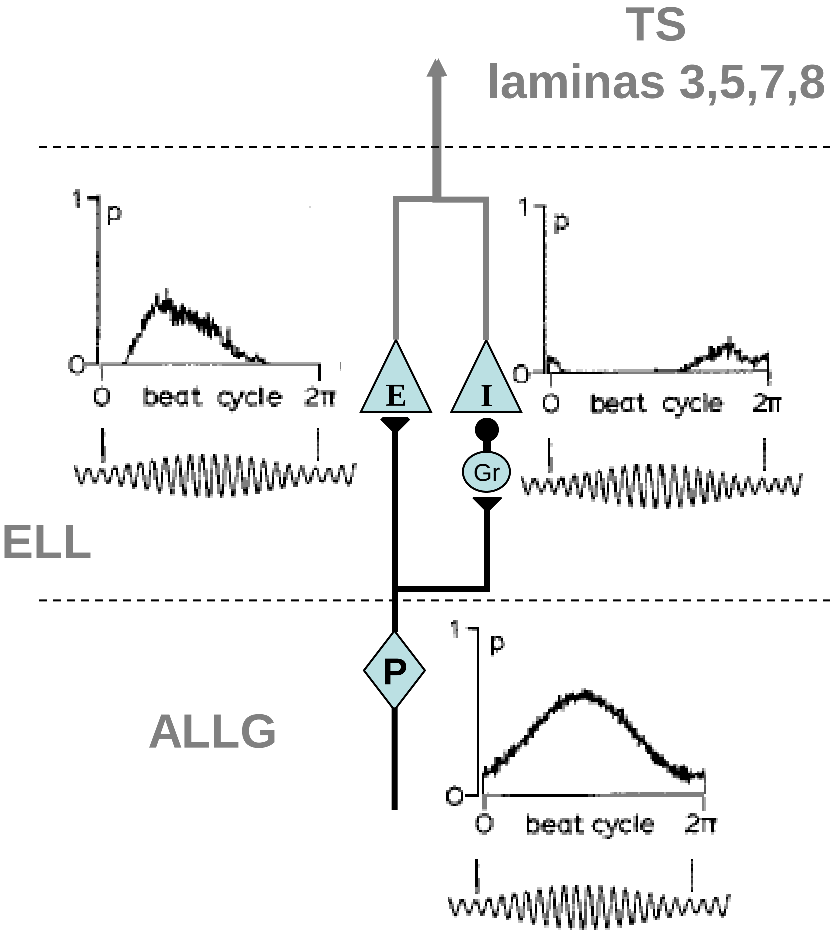


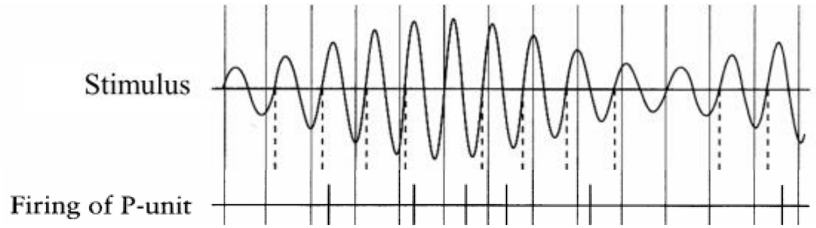
Minimum 8 synapses

- Traceable multi-synaptic neural circuits

JAR physiology: Amplitude coding

- **ALLG: P type** tuberous receptors encode wave amplitude (rate code).
- **ELL**: P-afferents excite **E-cells** and inhibit (via local granule cells) **I-cells**. E-cells fire on amplitude rise and I-cells fire on amplitude fall.
- **TS**: superficial laminas (3,5,7) contain mostly E and I type cells.

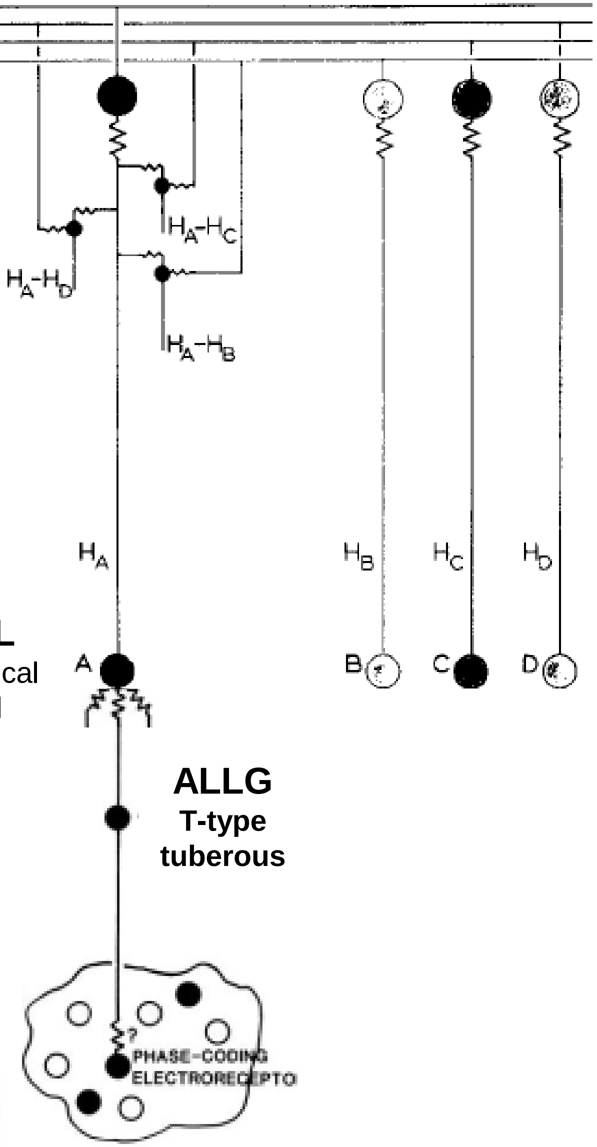




JAR physiology: Phase coding I

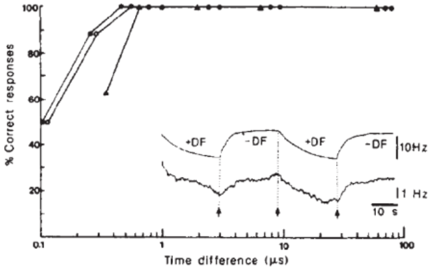
- **ALLG:** T-type tuberous receptors fire one spike at zero-crossing of wave (temporal code).
- **ELL**: Somatotopic organization. Multiple T-afferents form electrical synapses (gap junctions) with **spherical cells**.
- **TS lamina 6**: spherical cells form electrical synapses in somatotopic order onto **giant cells** and **small cells**.
  - Giant cells relay the information horizontally.
  - Each small cell receives direct local input in dendrites and indirect input from one distant giant cell.

TS
lamina 6

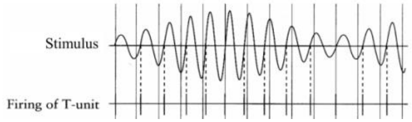


ELL
spherical cell

ALLG
T-type
tuberous

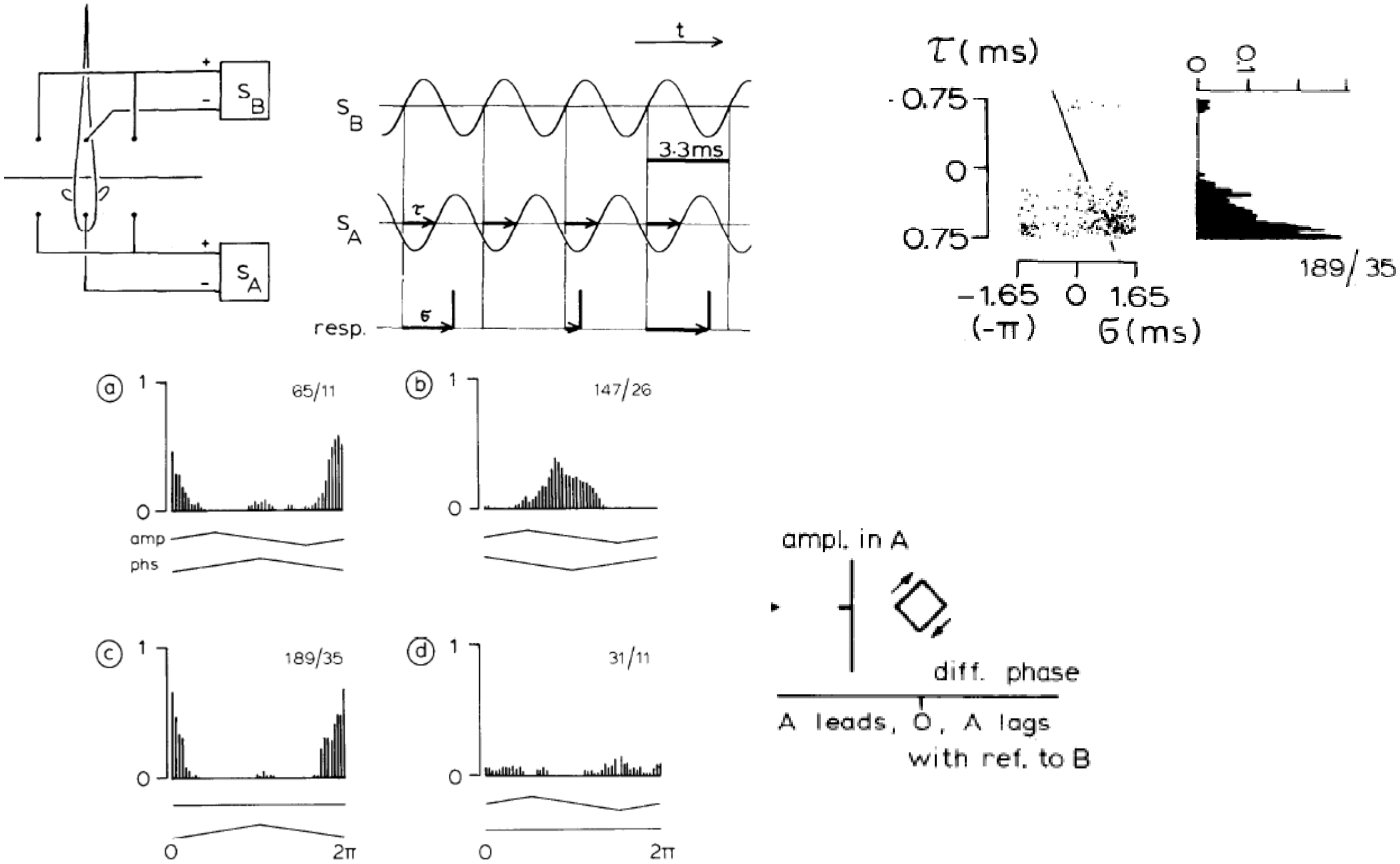


Hyperacuity
by convergence



JAR physiology: Phase coding II

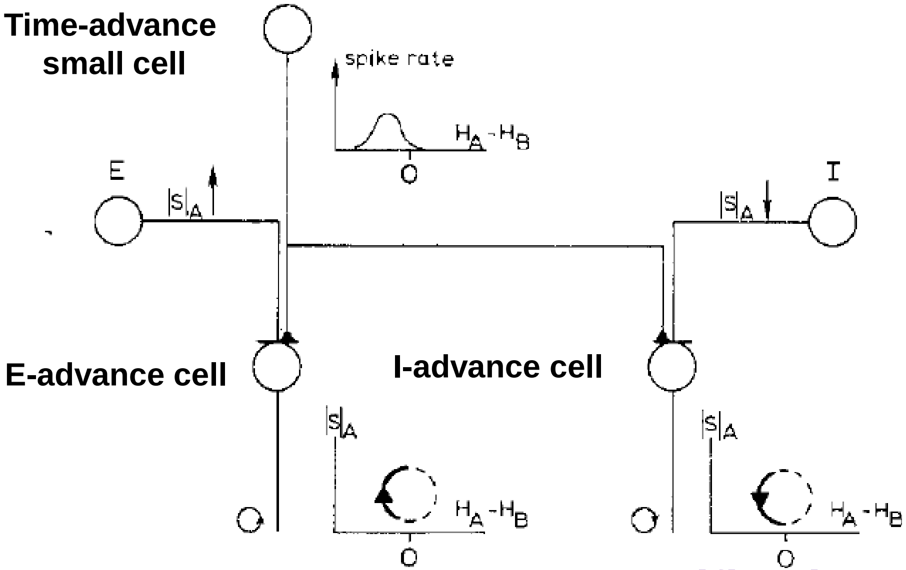
Split compartment experiments:
enable independent modulations of phase and amplitude

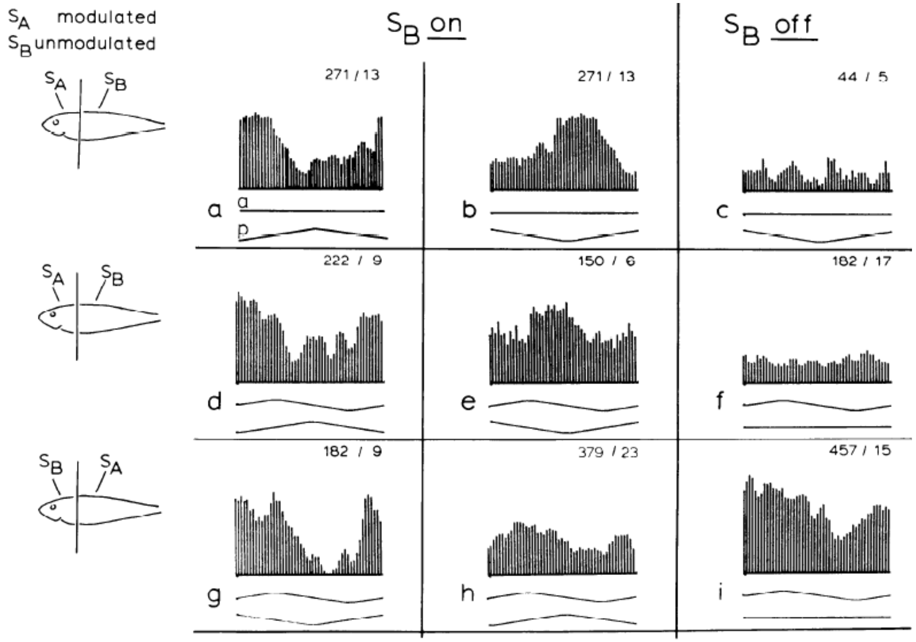


Small cells are coincidence detectors, reporting phase difference between two body regions.

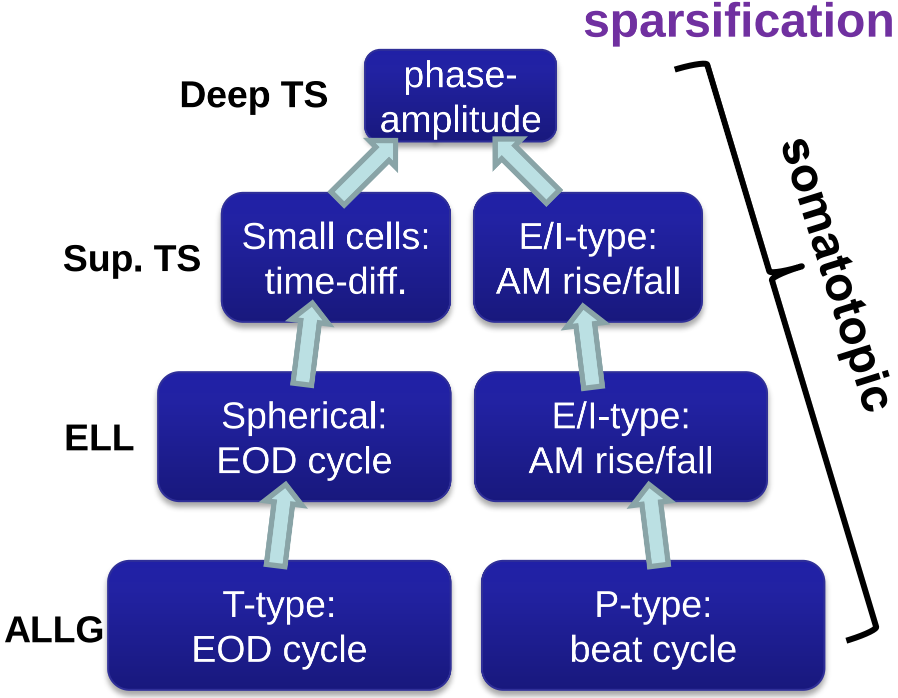
JAR physiology: Phase-amplitude coding I

- Differential phase and amplitude information converge onto cells in the deep lamina of TS (8b and 8c).
- Four types of cells: E-advance, E-delay, I-advance, I-delay.





E-advance cell (8c)



sparsification

Deep TS

phase-amplitude

Sup. TS

Small cells: time-diff.

E/I-type: AM rise/fall

ELL

Spherical: EOD cycle

E/I-type: AM rise/fall

ALLG

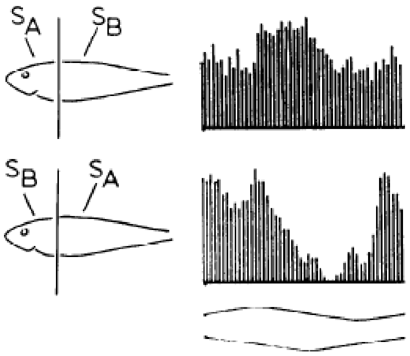
T-type: EOD cycle

P-type: beat cycle

somatotopic

JAR physiology: Phase-amplitude coding II

Problem: Δf sign representation is still somatotopic and ambiguous; differential phase between regions A and B: which one is the ‘reference’ signal?



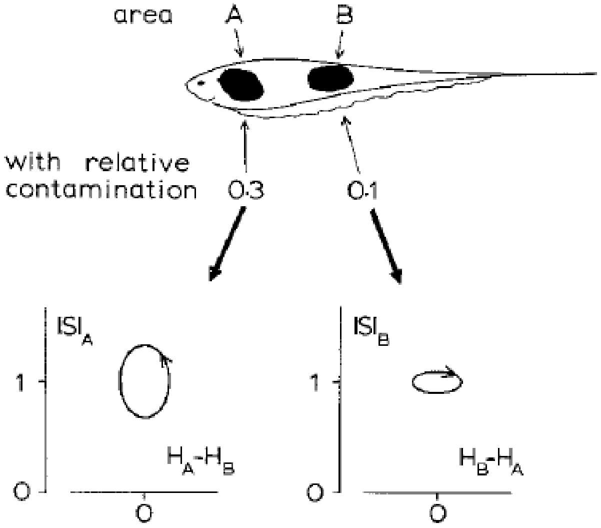
E-advance

E-delay

For each cell reporting Δf<0
there is a reciprocal cell reporting Δf>0

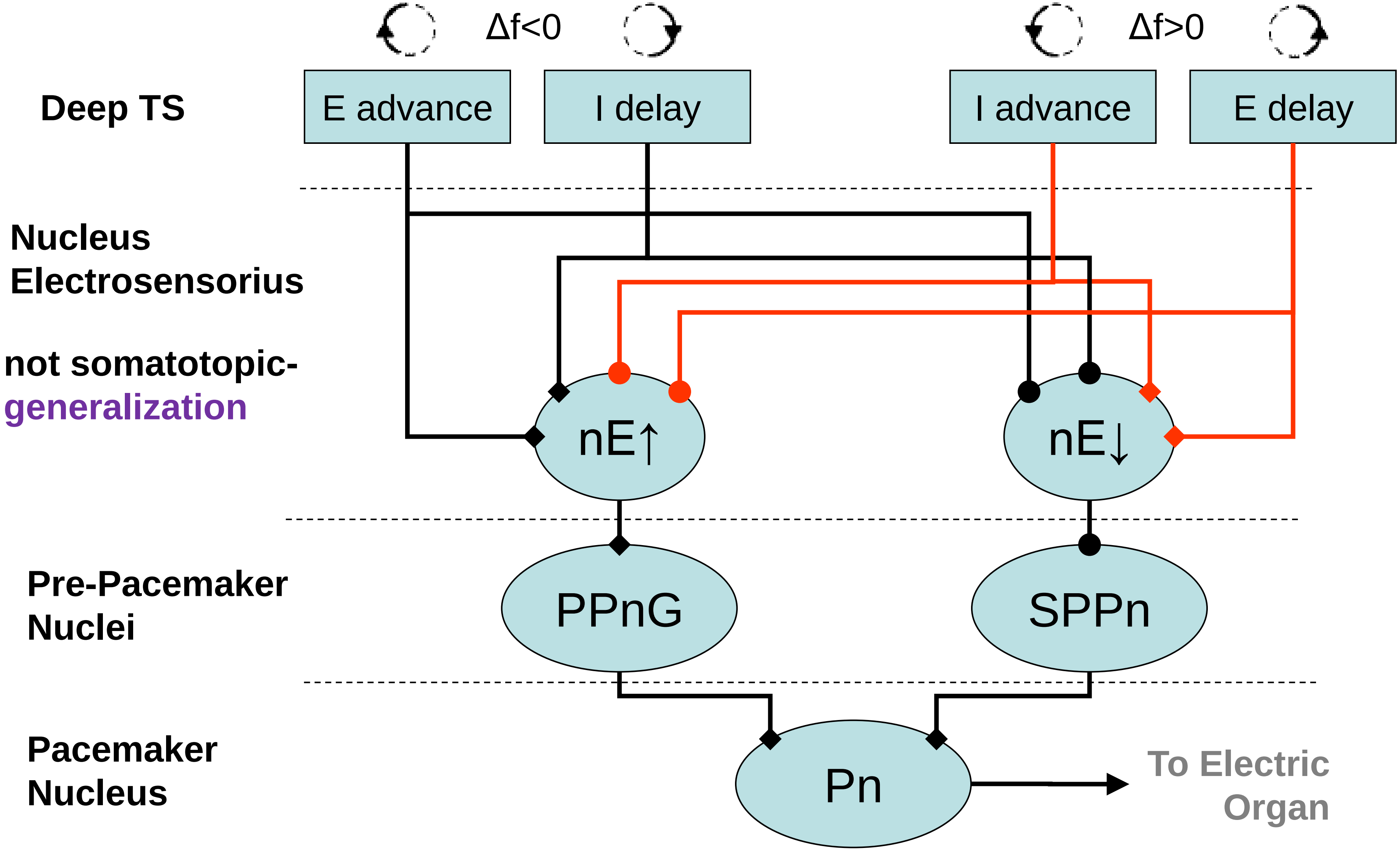
Solution: in natural geometry, different body regions are affected differently by the jamming interference.

In this example- the head region reports Δf>0 while the trunk reports Δf<0, but the head has stronger response.



JAR physiology: Sensory-motor link

Population coding: the neurons ‘vote’ on the sign of Δf. The more affected regions get a stronger vote.



Δf<0

Δf>0

Deep TS

E advance

I delay

I advance

E delay

Nucleus Electrosensorius

not somatotopic-generalization

nE↑

nE↓

Pre-Pacemaker Nuclei

PPnG

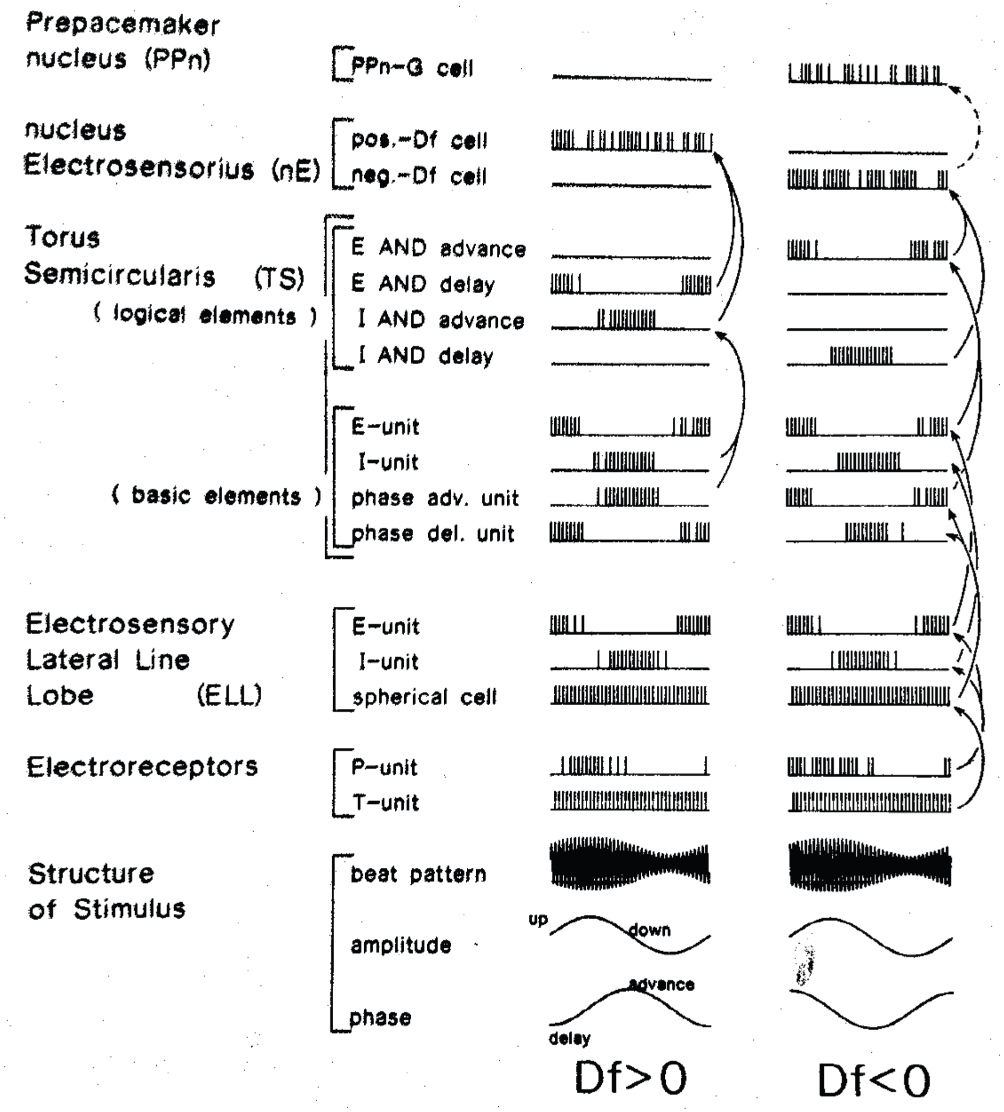
SPPn

Pacemaker Nucleus

Pn

To Electric Organ

JAR circuit- summary



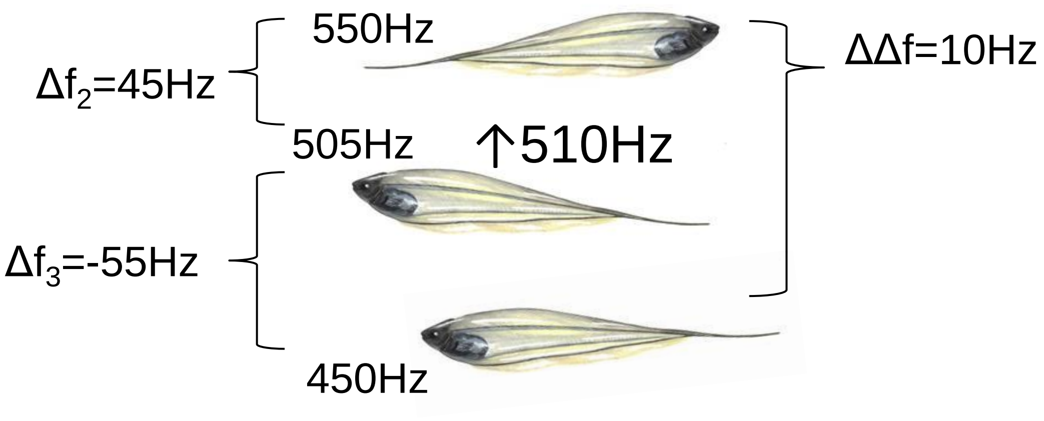
Midbrain

Brainstem

Afferents

Behavior

Social Envelope Response (SER)



550Hz

Δf_2=45Hz

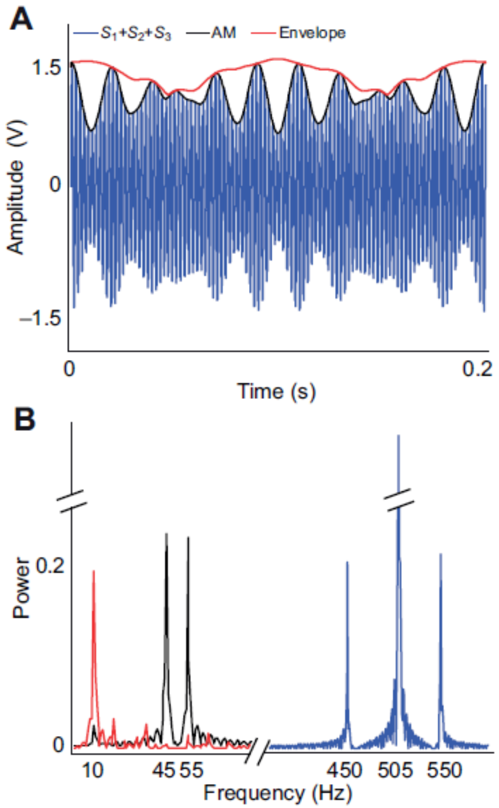
505Hz

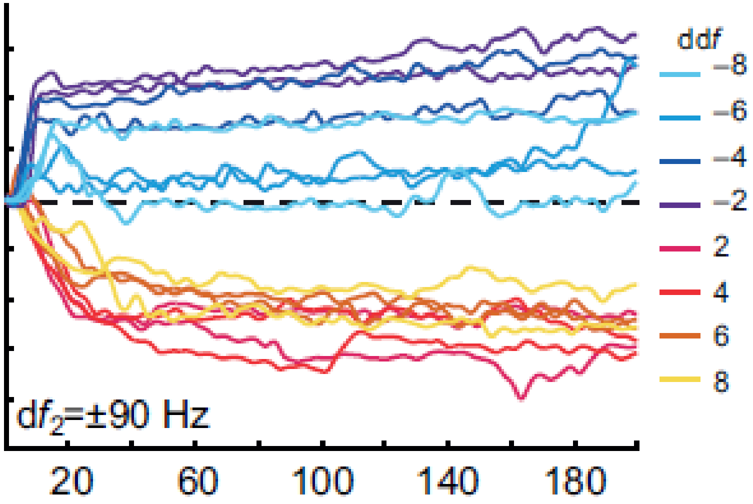
↑510Hz

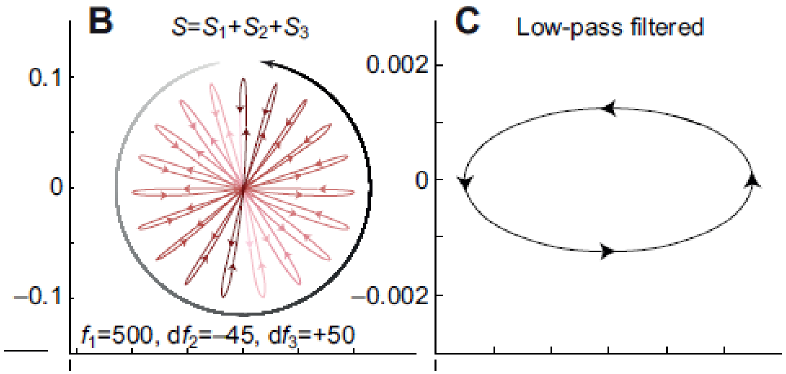
Δf_3=-55Hz

450Hz

$\Delta\Delta f$=10Hz

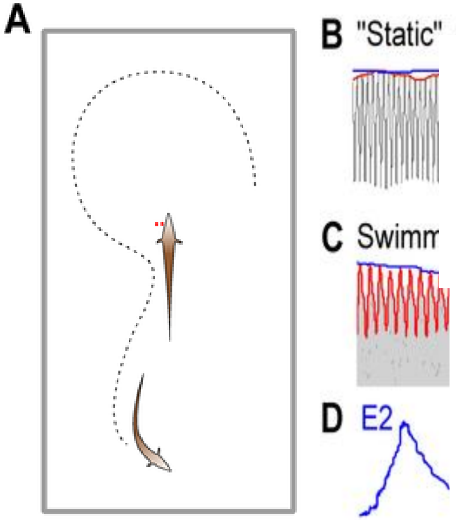




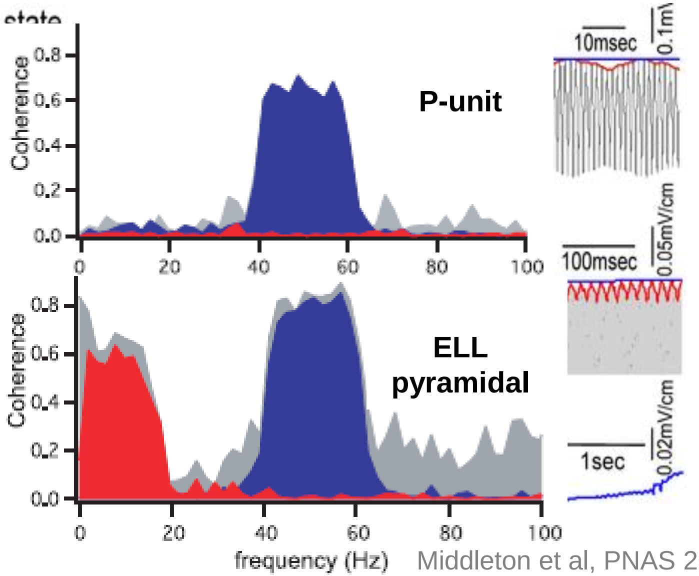


Stamper et al, J. Exp. Bio. 2012

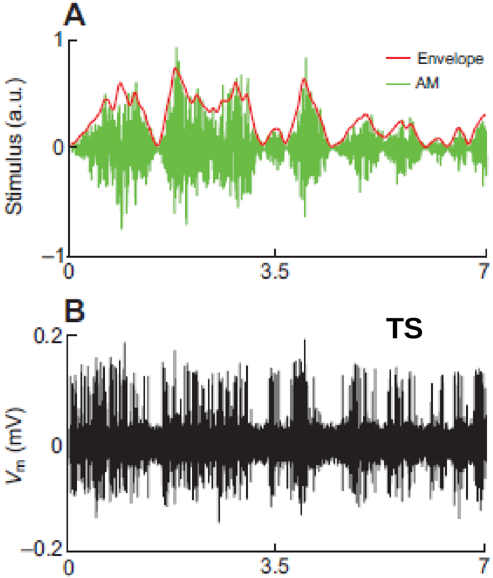
Motion induced envelopes



Yu et al, PLoS Comp. Biol. 2012



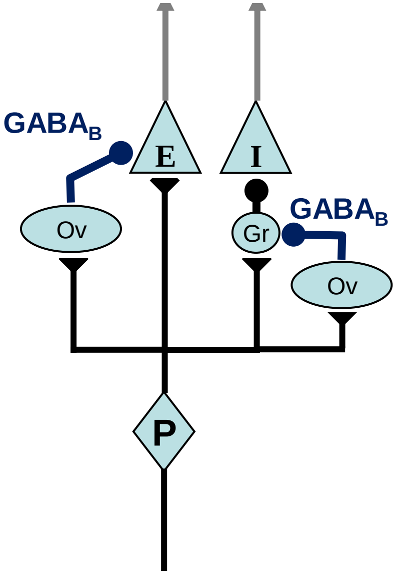
Middleton et al, PNAS 2006

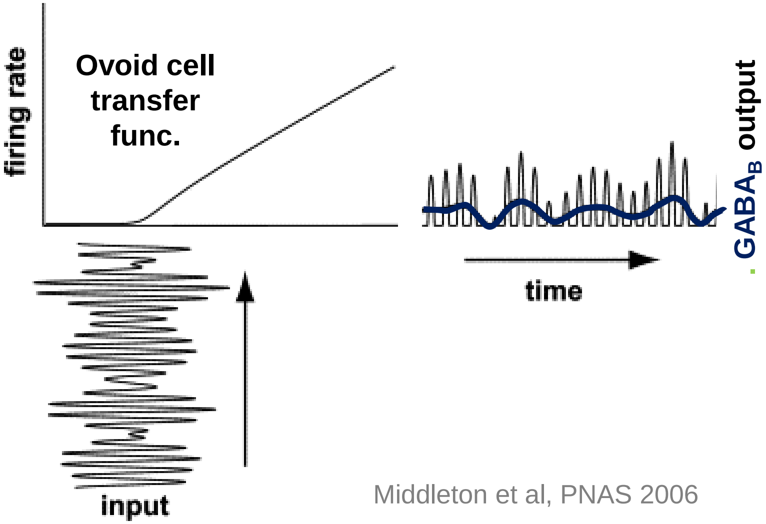


Stamper et al, J. Exp. Biol. 2013

Q: How can pyramidal cells and TS cells encode envelopes when P-afferents don't?

A: Ovoid cells: high-freq. response, slow GABA_B output.

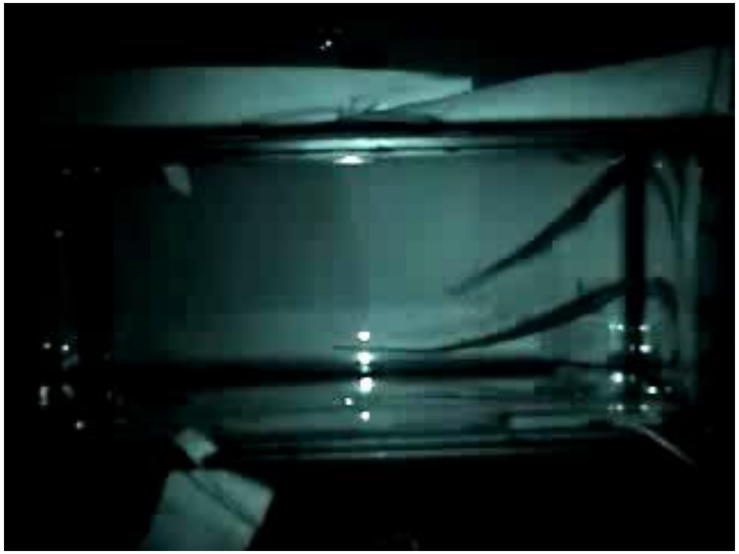




Middleton et al, PNAS 2006

Chirps- behavior

- The electric sense is used for conspecific communication:
  aggression ,courtship, spawning, parental care.
- Communication signals consist of short modulations of EOD called ‘chirps’.

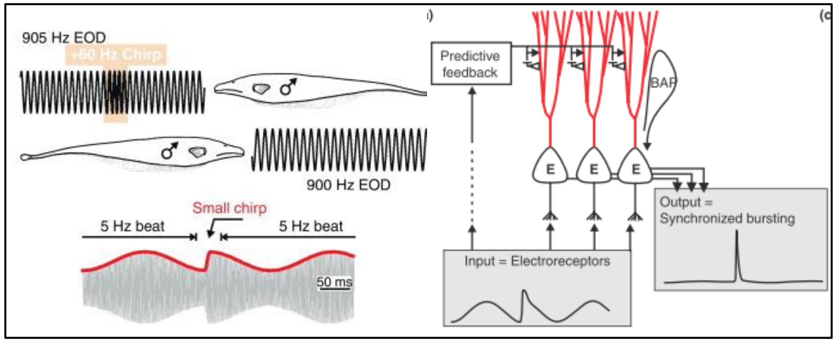


Hupe & Lewis, Maler lab

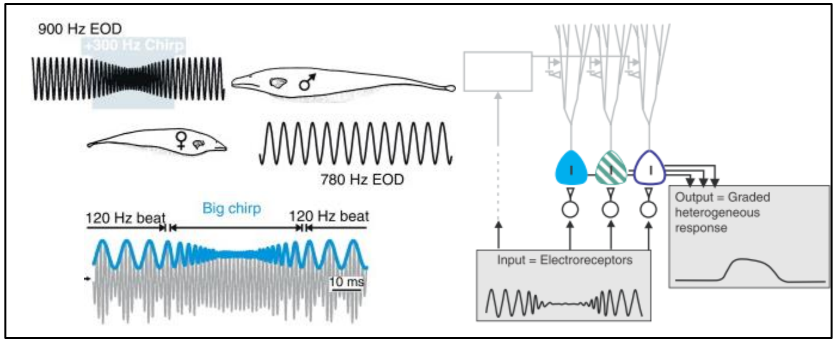
Chirps- physiology

Neural circuit closely related to JAR circuit.

- **Small chirps** (male aggression): sudden shift in phase. Encoded by ELL E-cells with predictive feedback.



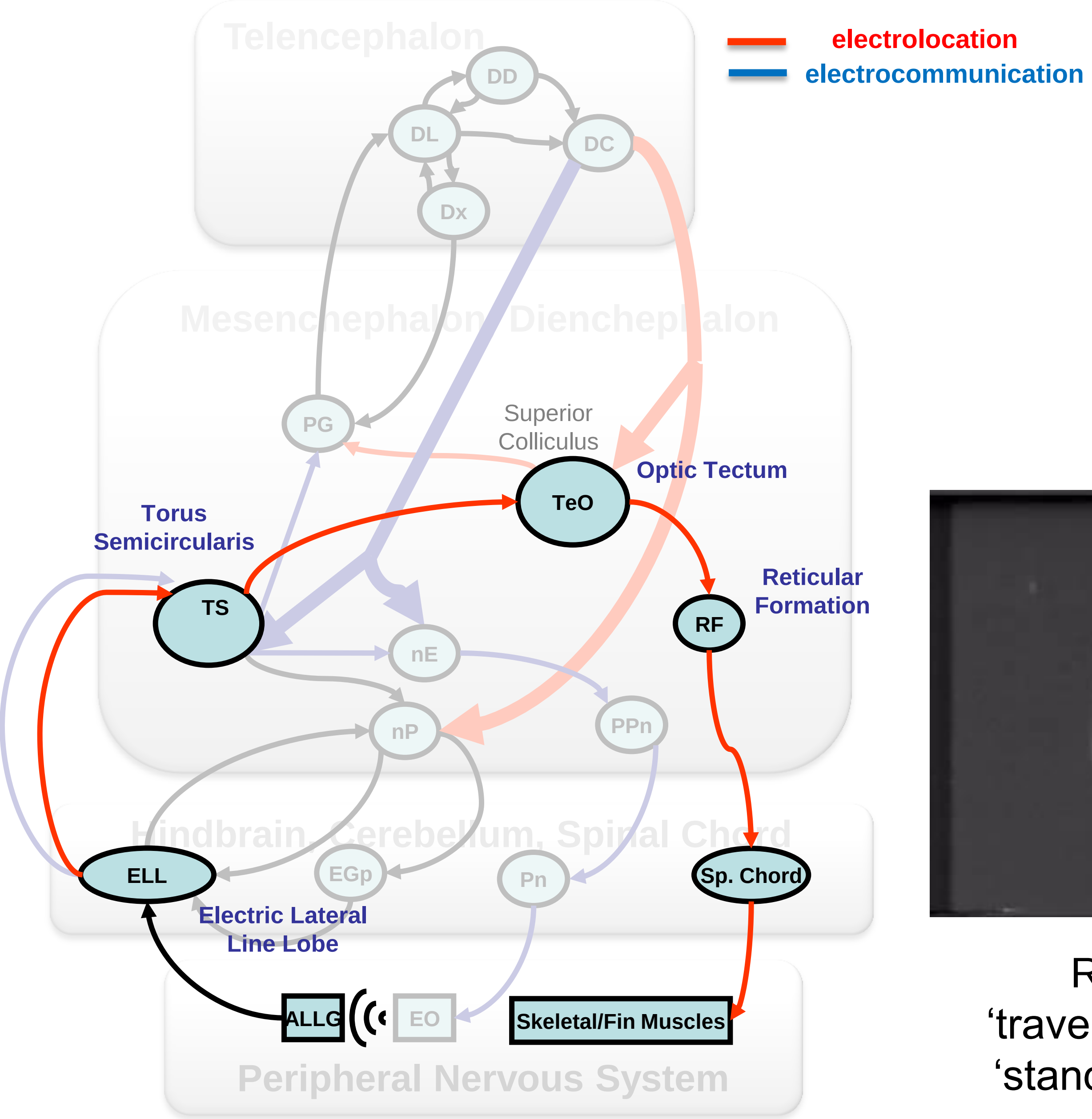
- **Big chirps** (courtship): transient rise in frequency + drop in amplitude. Encoded by ELL I-cells (and envelope cells).

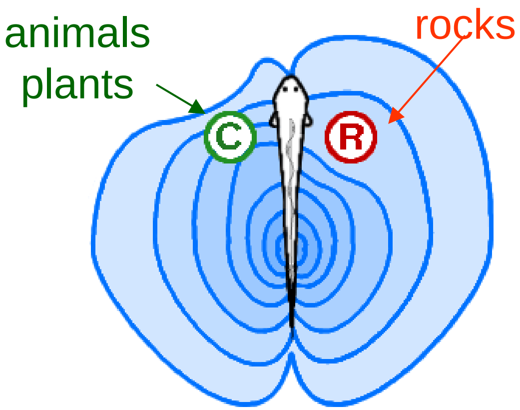


Marsat, Longtin & Maler, Curr. Op. Neurobiol. 2012

- In addition:
  - nEb: representation of beat frequencies (Δf), not involved in JAR. Perhaps used for conspecific recognition.
  - PPnC: prepacemaker section that induces chirp signals.

Electrolocation



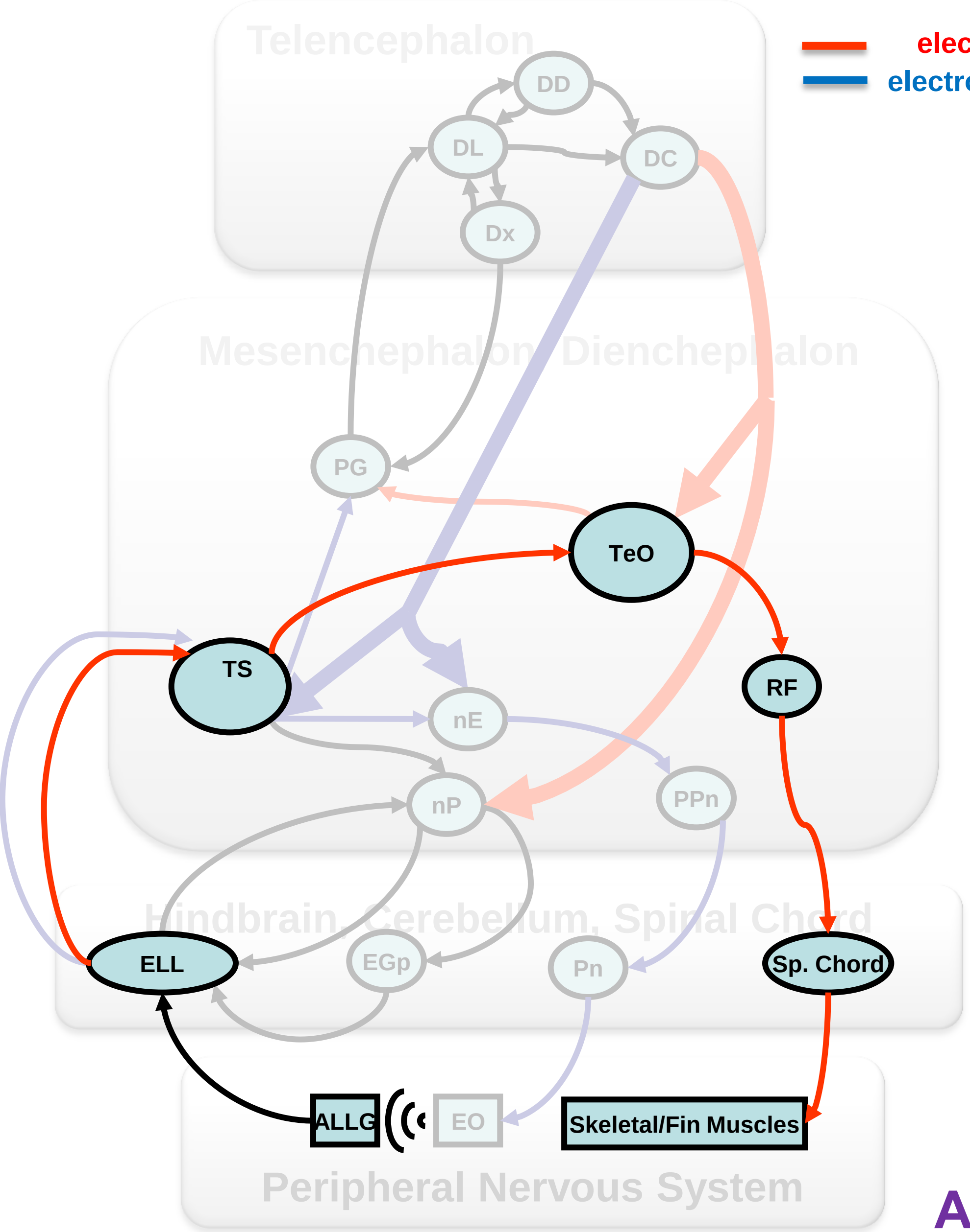


Prey capture

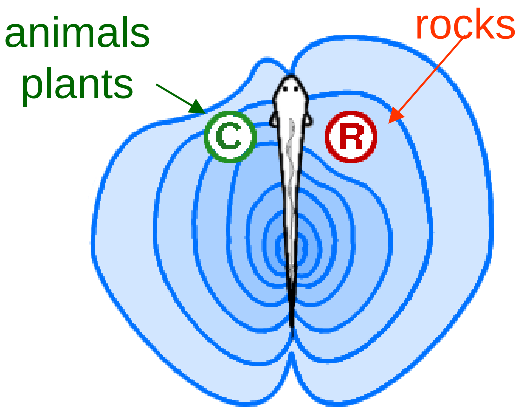
Nelson & MacIver

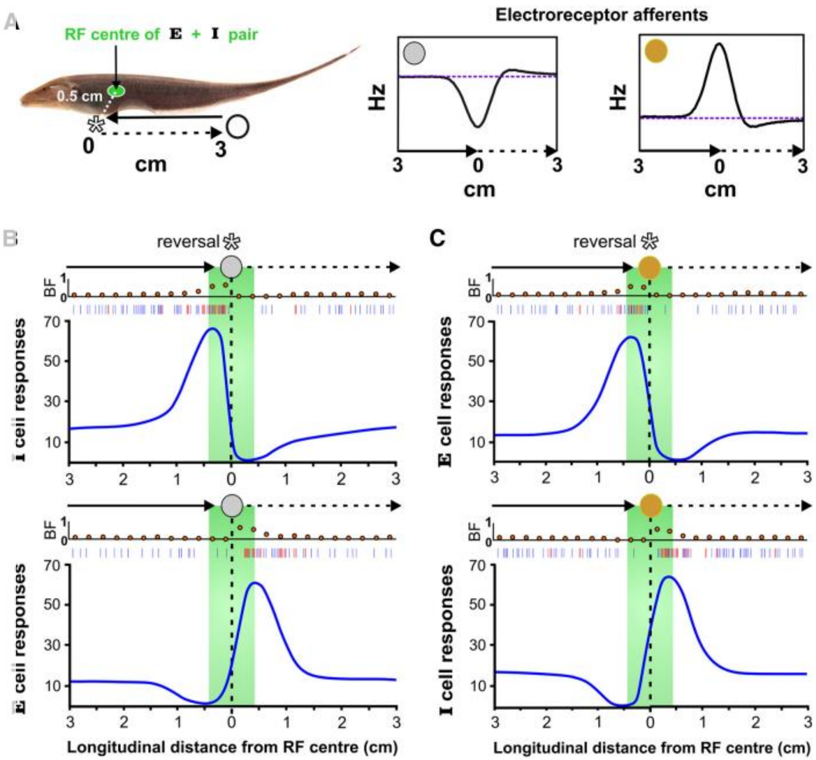
Ribbon fin locomotion:
‘traveling wave’=back-and-forth
‘standing wave’= up-and-down

Electrolocation



🟥 electrolocation
🟦 electrocommunication

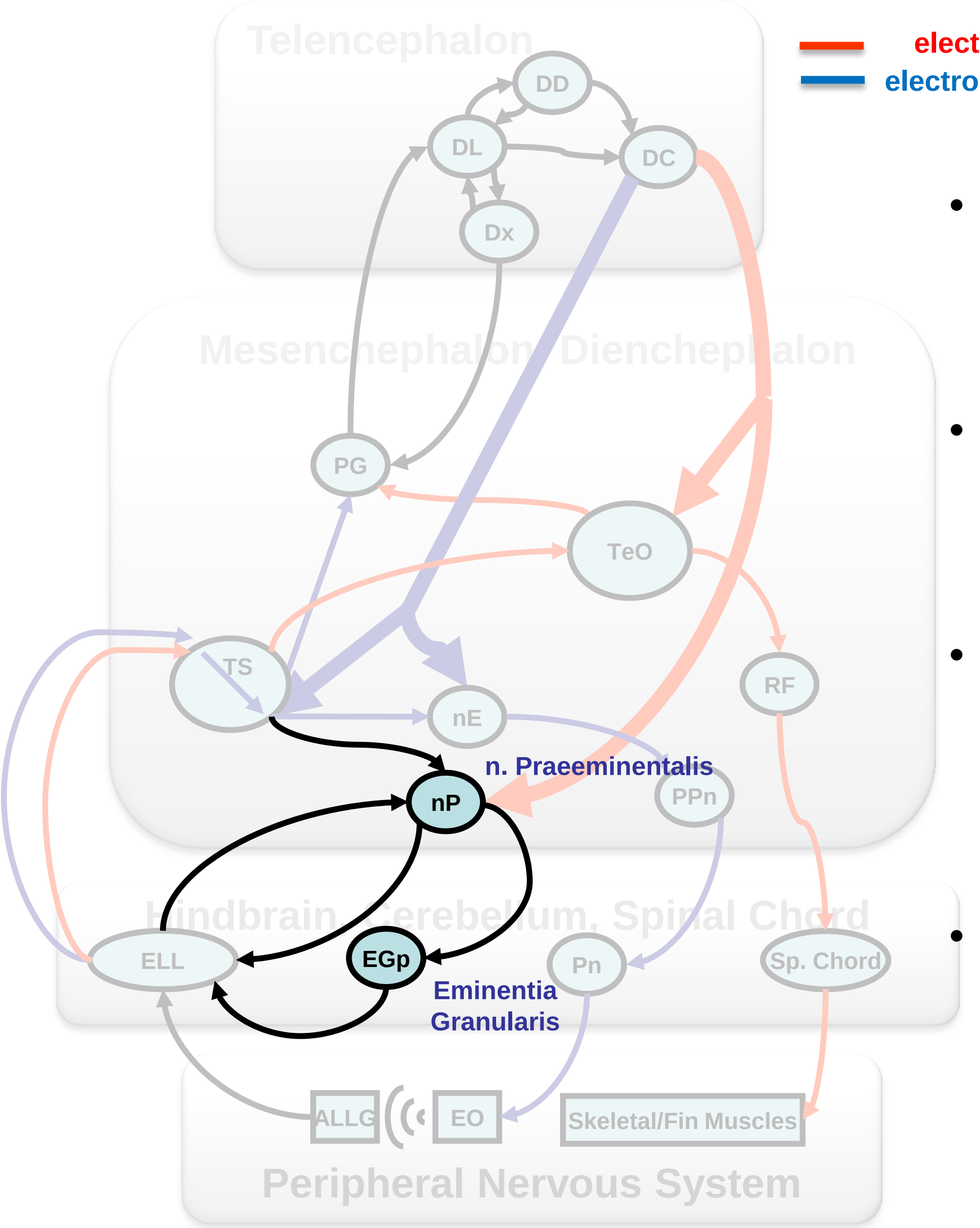




Clark et al, J Neurosc. 2014

Absence of ‘labeled line’ coding

Channel separation



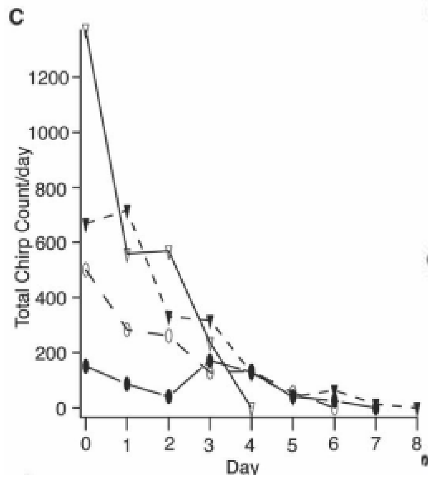
🟥 electrolocation

🟦 electrocommunication

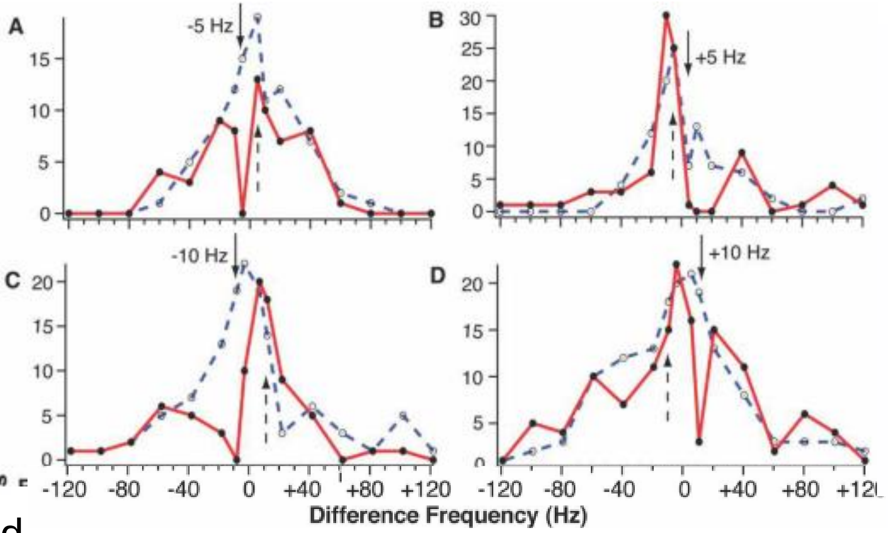
- P-afferents convey information related to both ‘channels’. How is the information separated in the ELL?
- JAR and SER provide a mechanism for **frequency separation** (useful for persistent interference).
- Another mechanism is **spatial separation**- electrolocation related information is **local**, while communication is **global**.
- This mechanism is realized by the **nP-EGp feedback loop**.

High-level functions

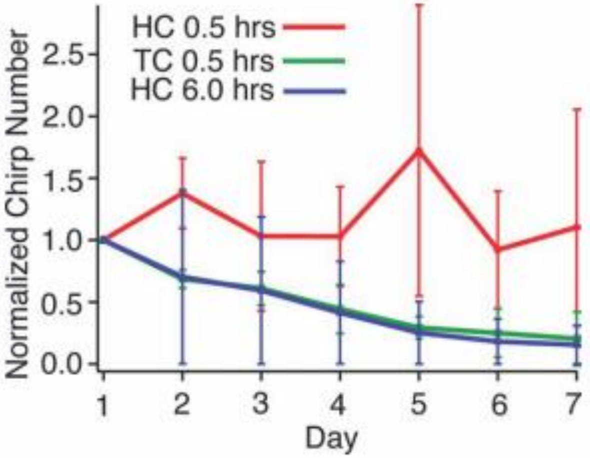
- Fish were stimulated with mock EODs of a specific frequency (simulating rival fish)
- Fish responded with aggression chirps.



Response decreased from day to day



Decrease is stimulus specific

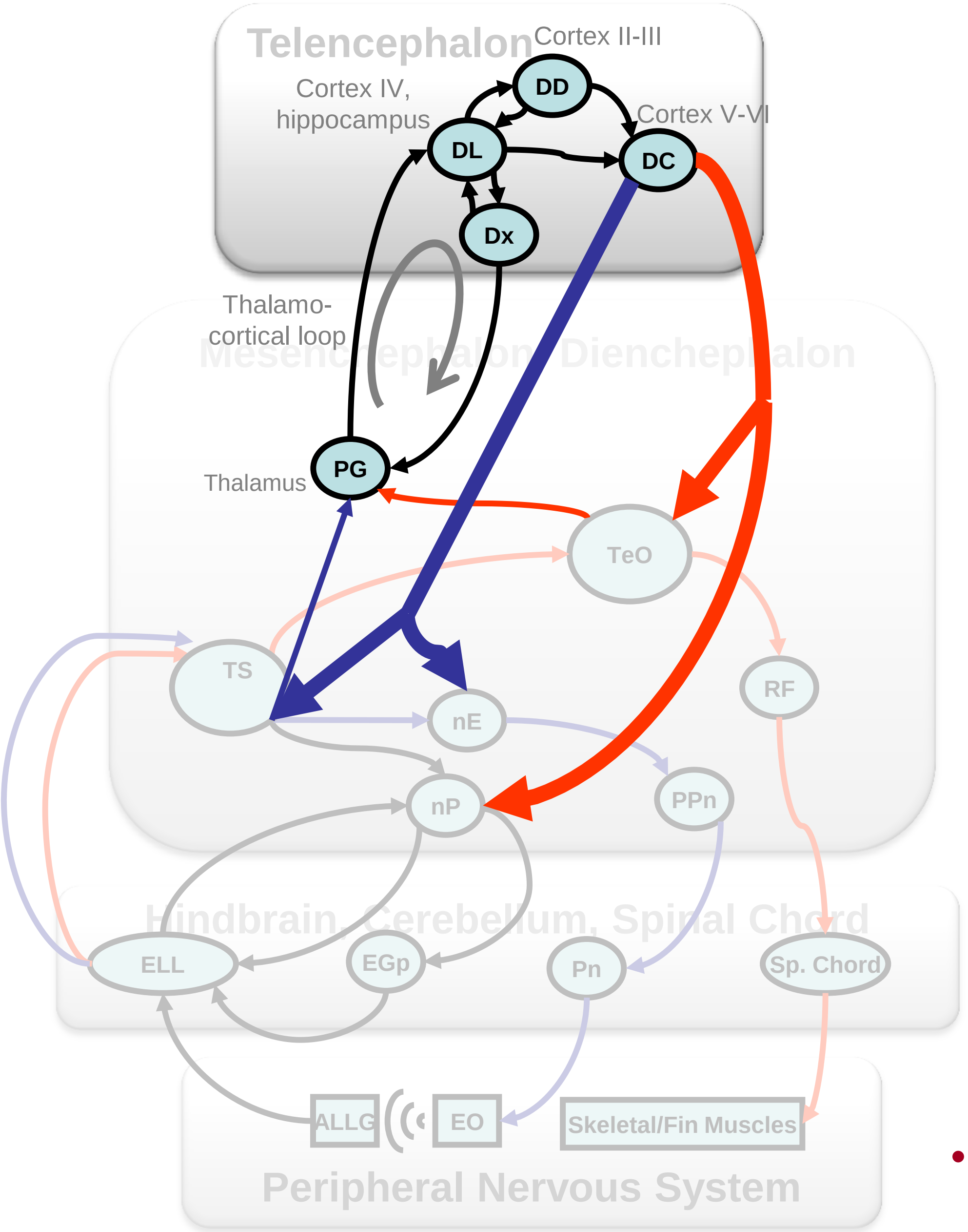


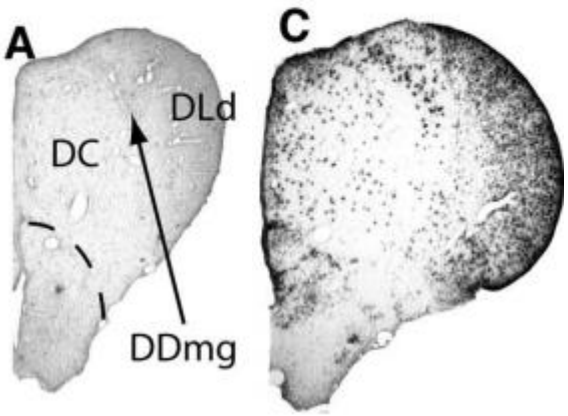
Requires consolidation

Harvey-Girard et al, J. Comp. Neurol. 2010

- Conclusion: Fish can learn to identify individual rivals and ignore them.
- They can also:
    - Perform spatial navigation.
    - Learn classical (Pavlovian) conditioning (associate landmarks with food).
    - Execute experience-based decisions (to eat or not to eat?).

High-level functions: The Telencephalon





Harvey-Girard et al, J. Comp. Neurol. 2010

Markers of learning were found in Telencephalon

- **The Pallium:** the dorsal part of the fish’s forebrain (Telencephalon).
- **Cortex + Hippocampus Homologue,** but has:
  - **Single Input (DL)**
  - **Single Output (DC).**

- **Relatively simple neural architecture**

Summary: pros and cons of Electric Fish as an experimental system

Pros

- Ubiquitous in nature.
- Convergent evolution
- Relatively few ethical constraints
- Behavior in relevant modality is easy to record and interpret
- Reliable, non-trivial sensory-motor behaviors
- Easy reduction of experimental variables
- Traceable multi-synaptic neural circuits
- Anatomy homologous to other vertebrates
- Relatively simple neural architecture

Cons

- High-tech methods (imaging, genetics etc) are less-developed (due to small scientific community).
- Captive breeding is challenging.
- Difficult to train (if you're into neuropsychology).
- Lives underwater…