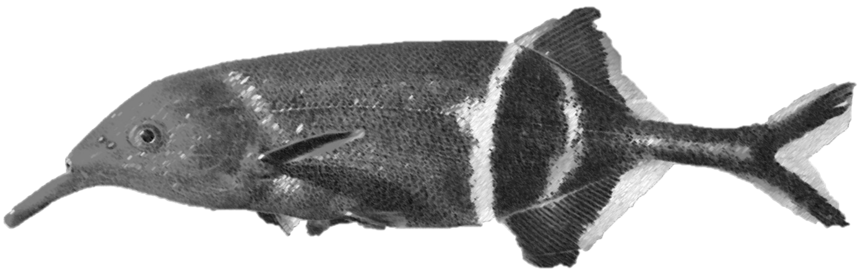
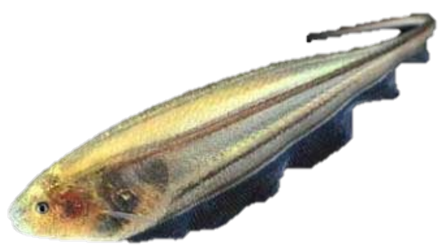
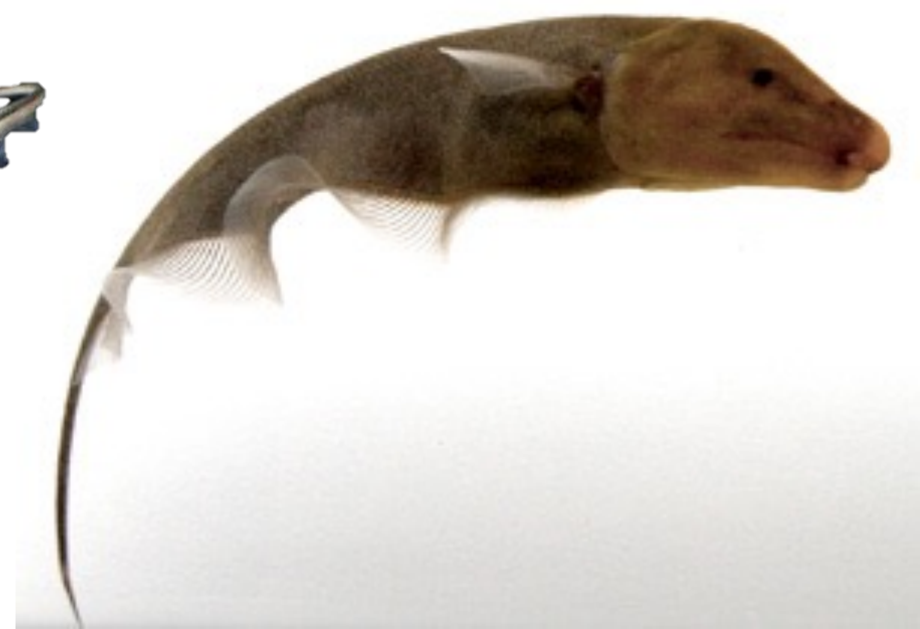
Sensory Systems: Electroreception







Presenting: Avner Wallach
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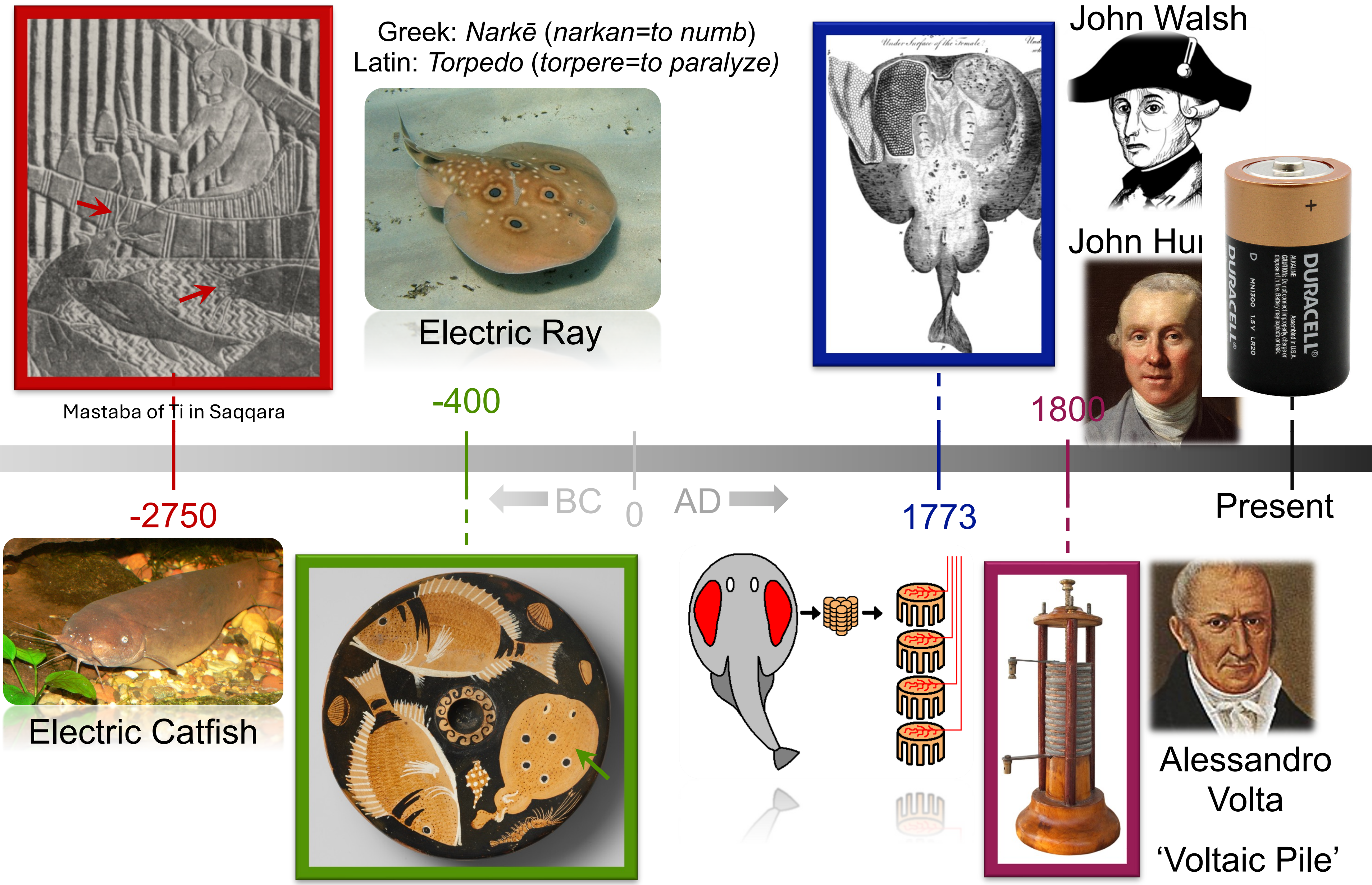
Overview

- Introduction:
  - Electrogenesis and electroreception
  - Active electrorecption: weakly electric fish
- Electrolocation in pulse type fish
  - Adaptive filtering of self-generated noise
- Electrocommunication in wave type fish
  - Jamming Avoidance
  - Neural correlates of social cognition

Electrogenesis

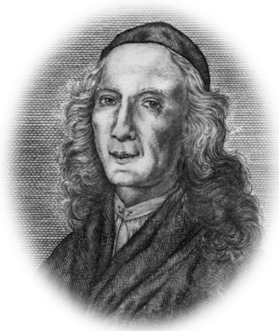
Electrogenesis: the biological ability to generate electrical signals

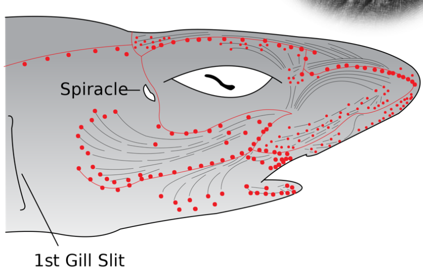


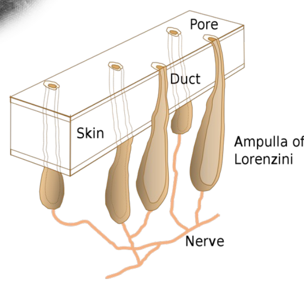
Electroreception

Electroreception: the biological ability to perceive electrical signals

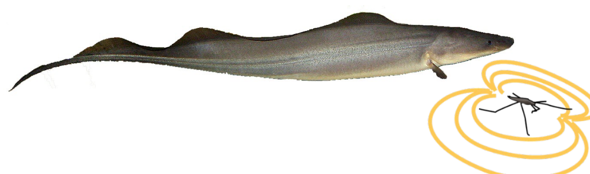
Stefano Lorenzini. 1678



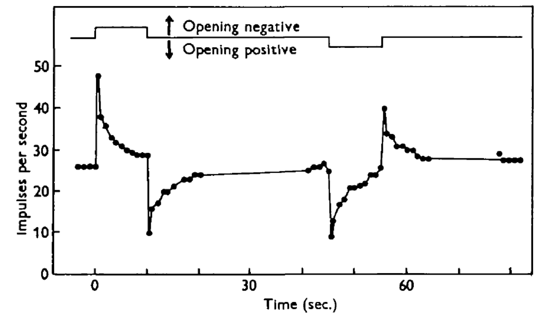




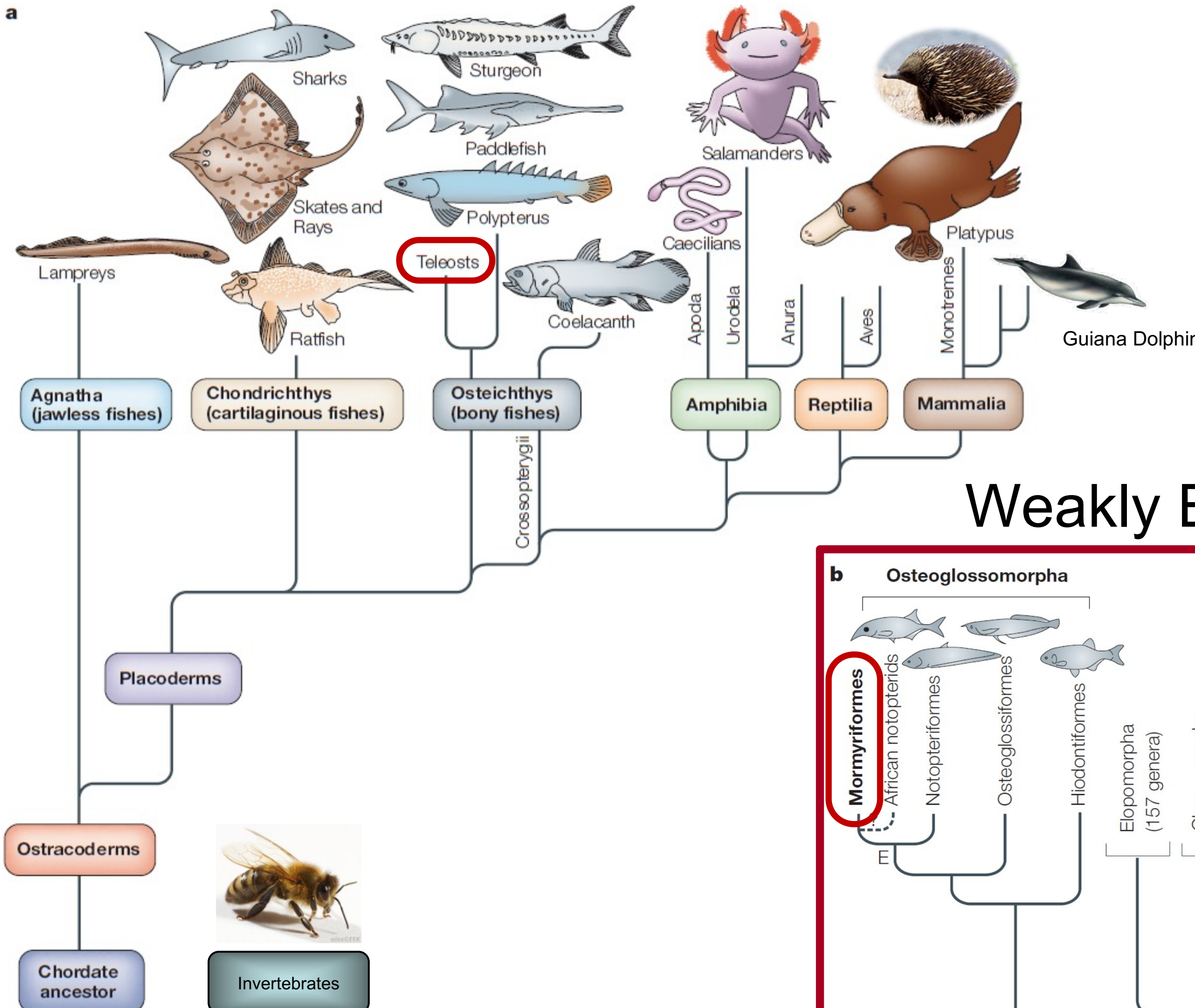
Hans Lissman, 1949



Richard W Murray, 1960

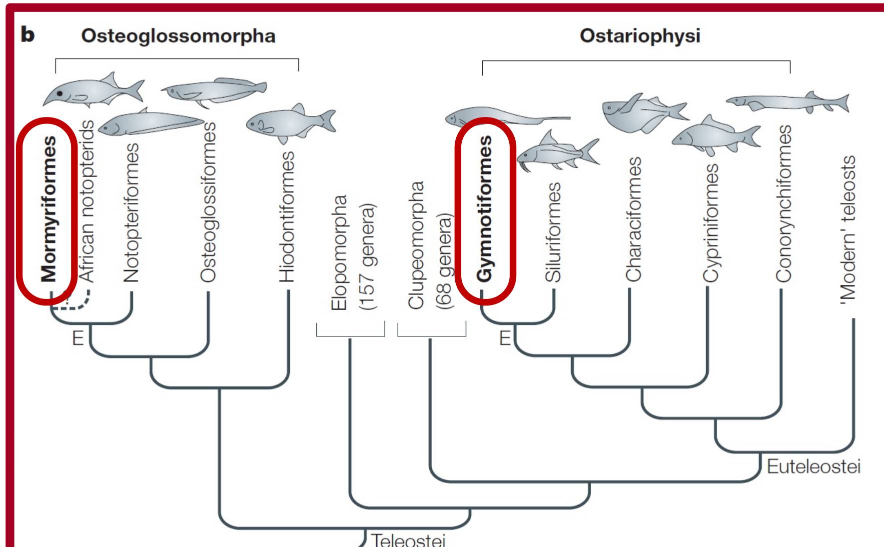


Electroreception in the Animal Kingdom

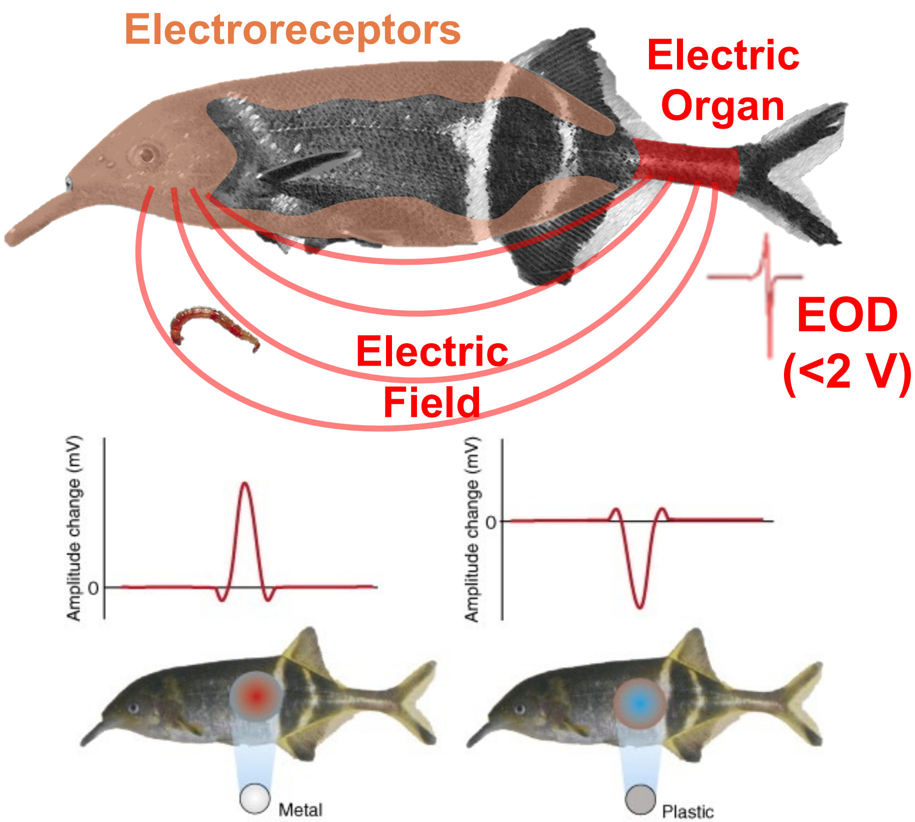


Rose, NRN 2004

Weakly Electric Fish

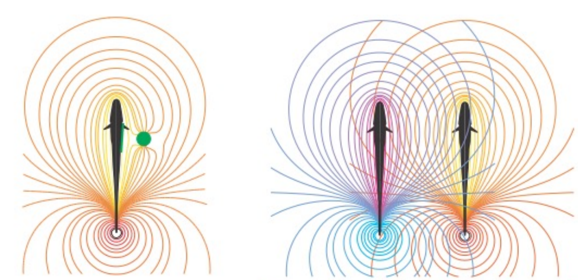


Active Electrorec



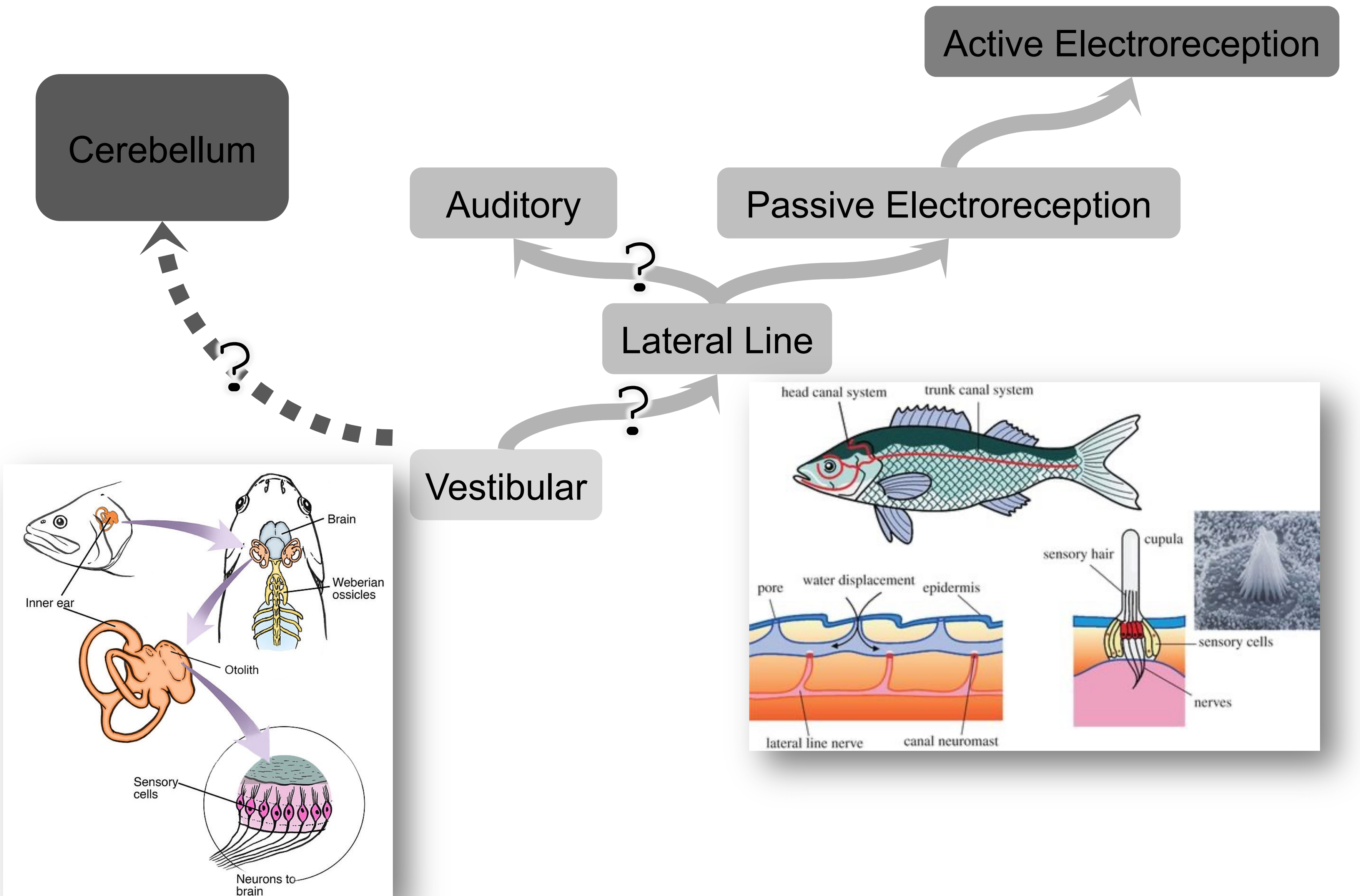
Electrolocation and Electrocommunication

- Electrolocation: perception of external objects based on their 'electric image'
- Electrocommunication: interactions between the electric discharge of neighboring fish

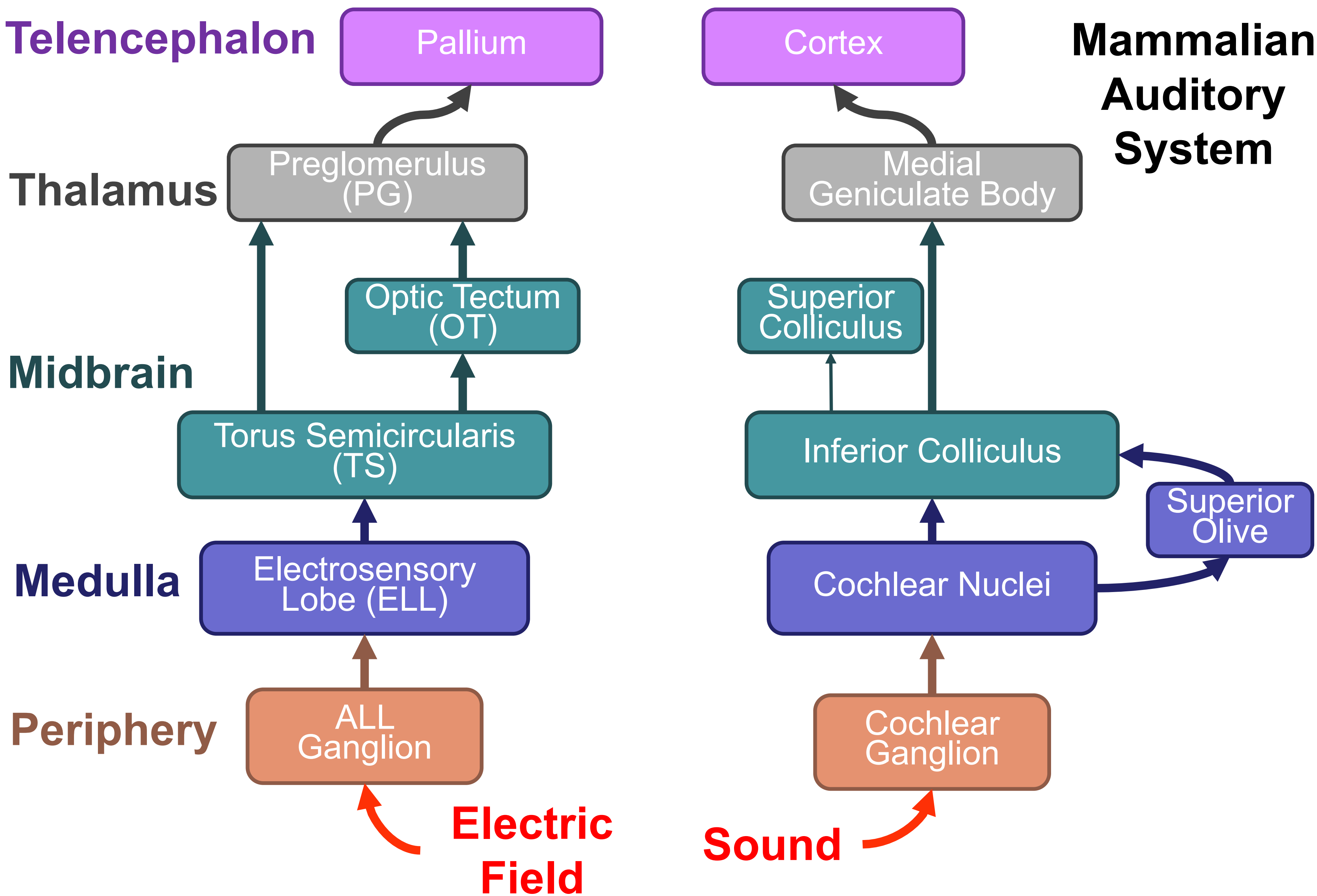


Electrolocation **Electro-communication**

Octavolateral (nVIII) Systems

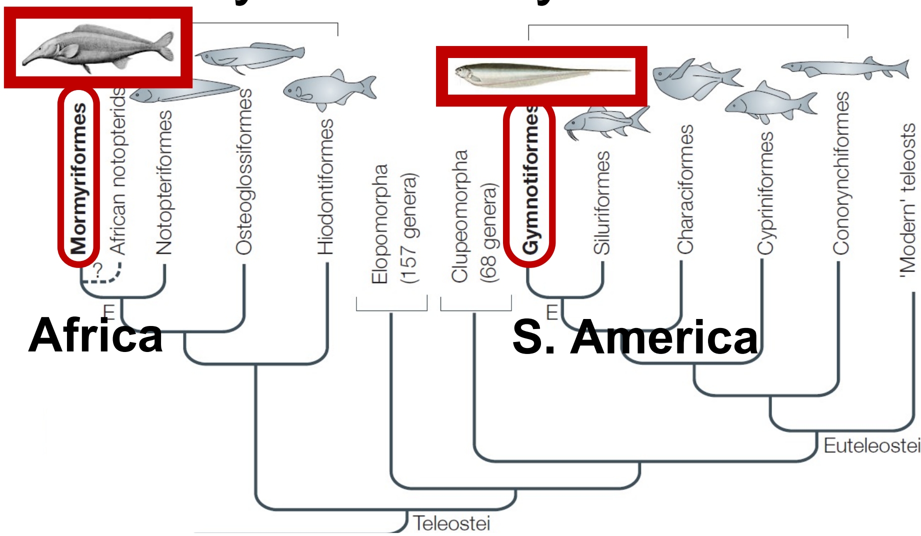


Ascending Electrosensory Pathway

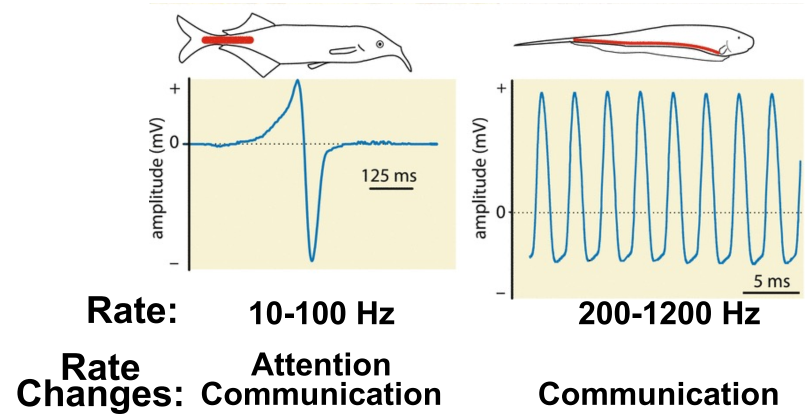


The Weakly Electric Fish

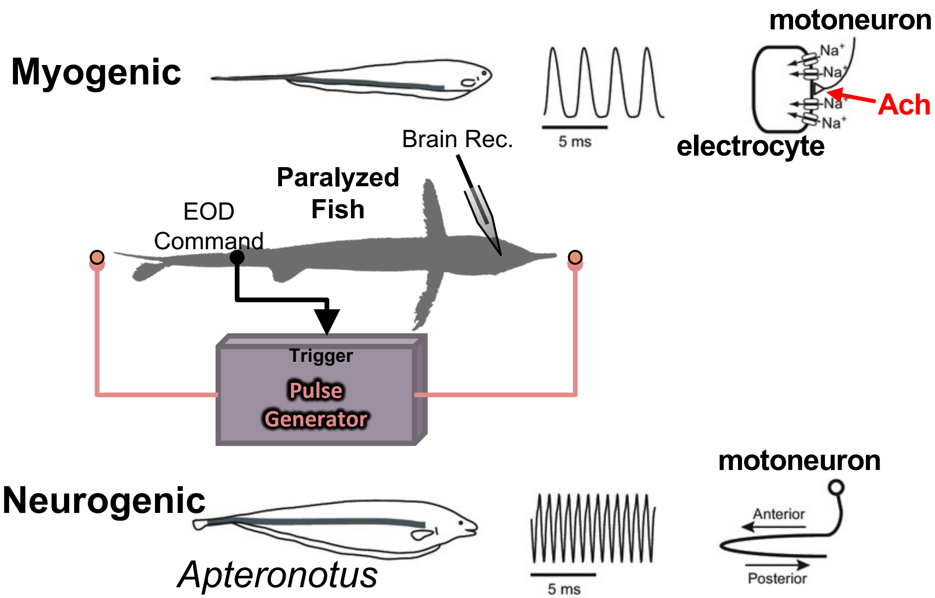
- Mormyrids vs. Gymnotids



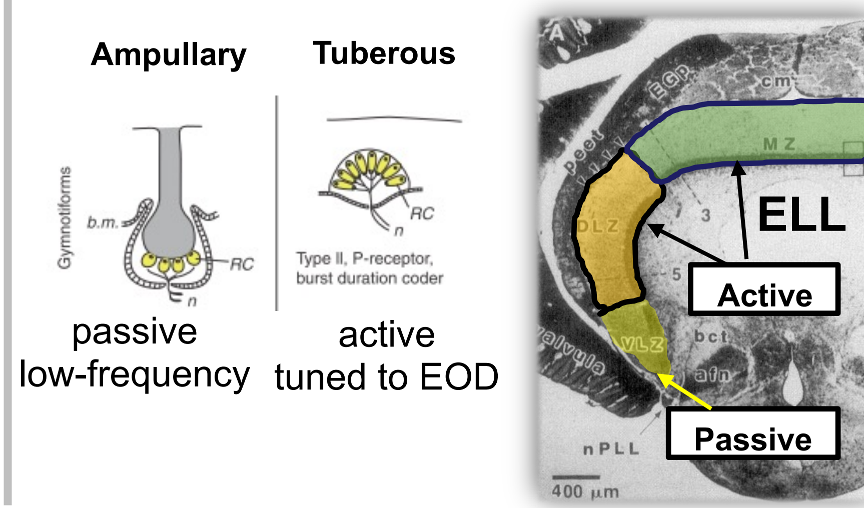
- Pulse vs. Wave



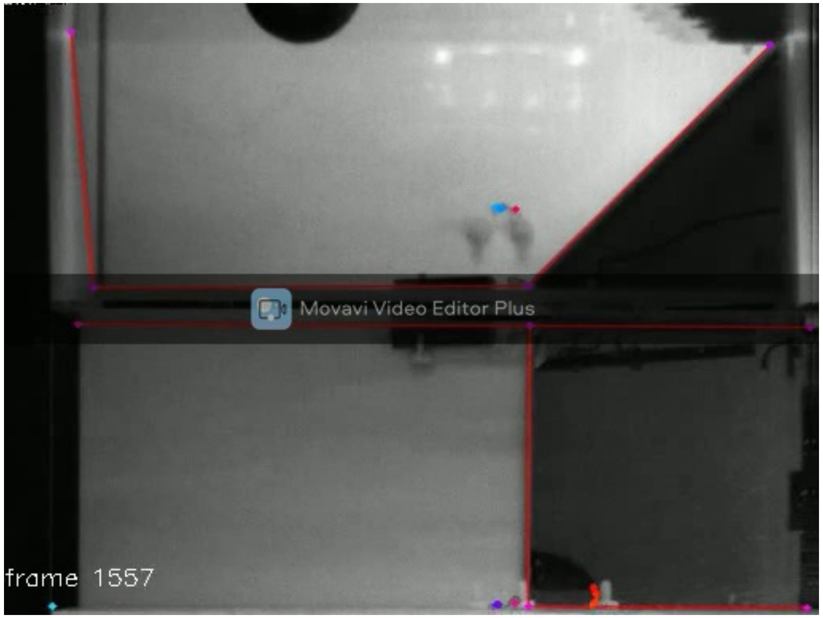
- Myogenic vs. Neurogenic



- Passive and Active



Electrolocation (pulse type fish)

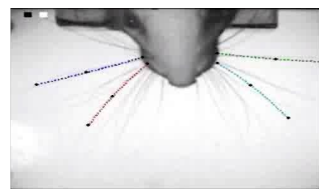


Schnauzenorgan

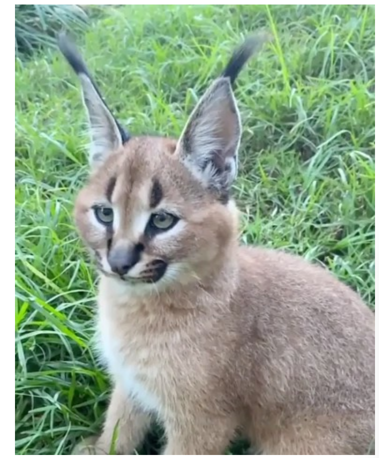
Elephantnose fish
(*Gnathonemus petersii*)
pulse type, Africa

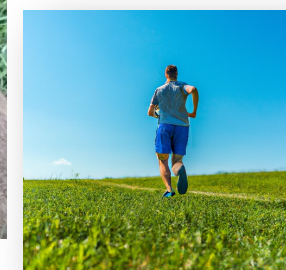
Active Sensing

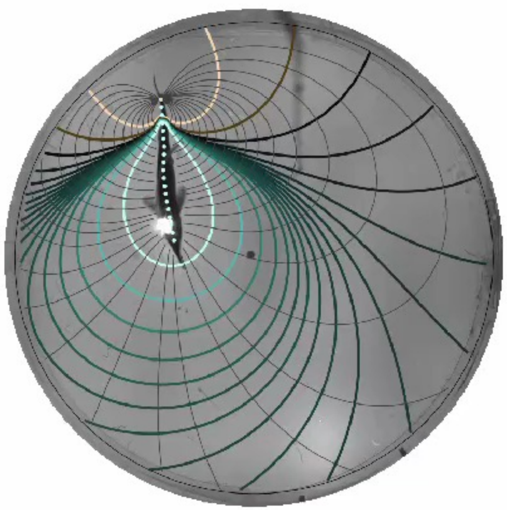
David Kleinfeld

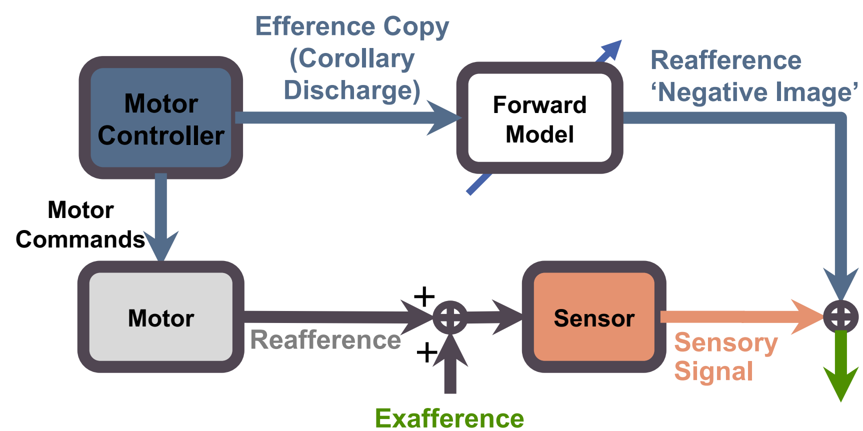


Ehud Ahissar









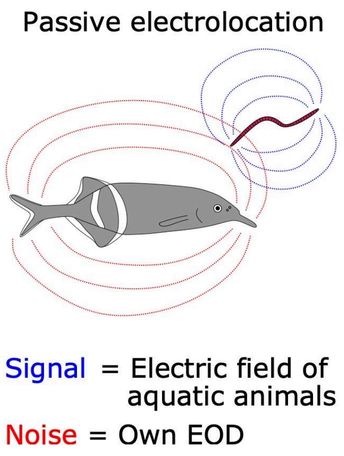
"We shall propose that the ***efference*** *leaves an "****image****" of itself somewhere in the CNS, to which the reafference... [is] the* ***negative****... so that when superimposed the image disappears."*

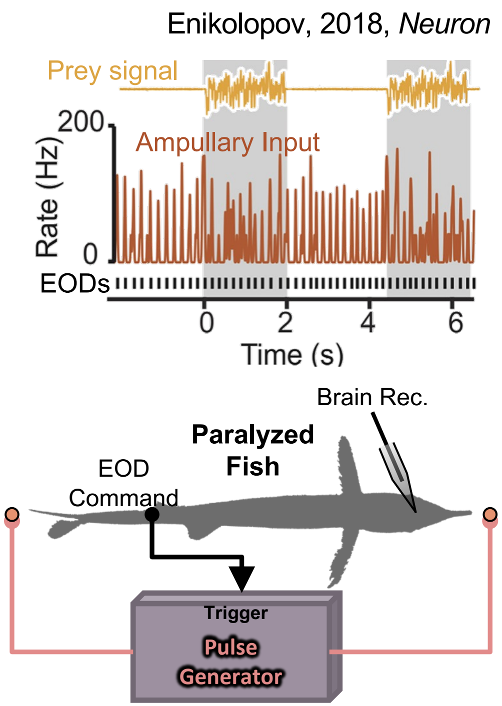
Von Holst, 1954

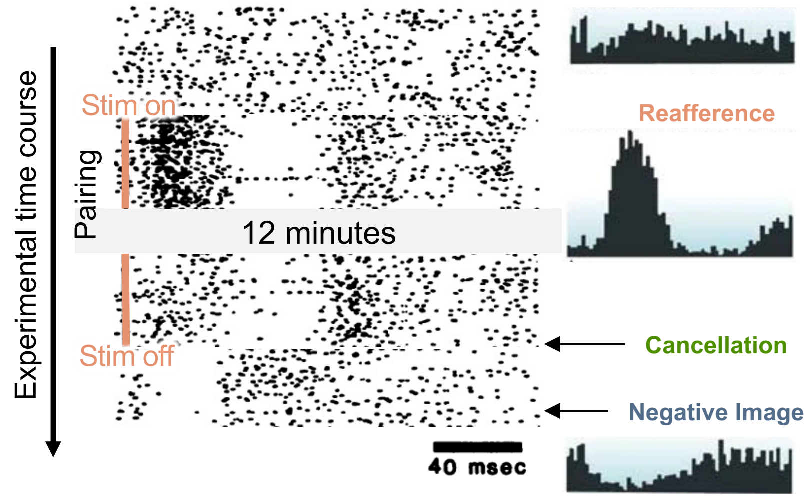
Reafference: self-generated sensations

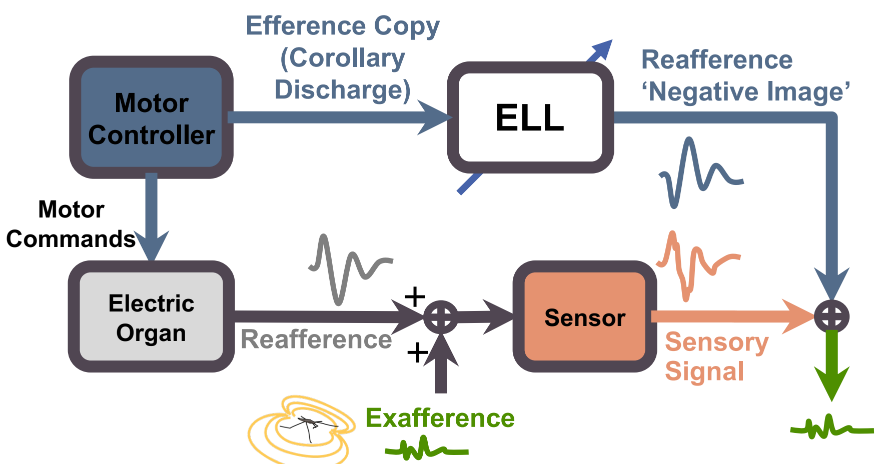
Exafference: externally generated sensations

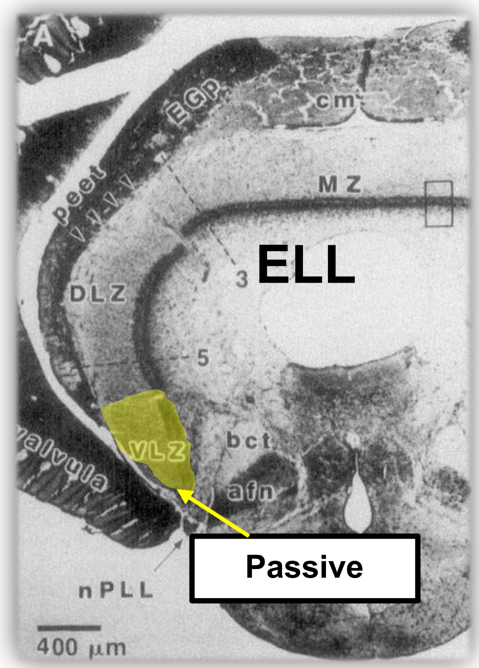
Cancellation of Self-Generated Sensations



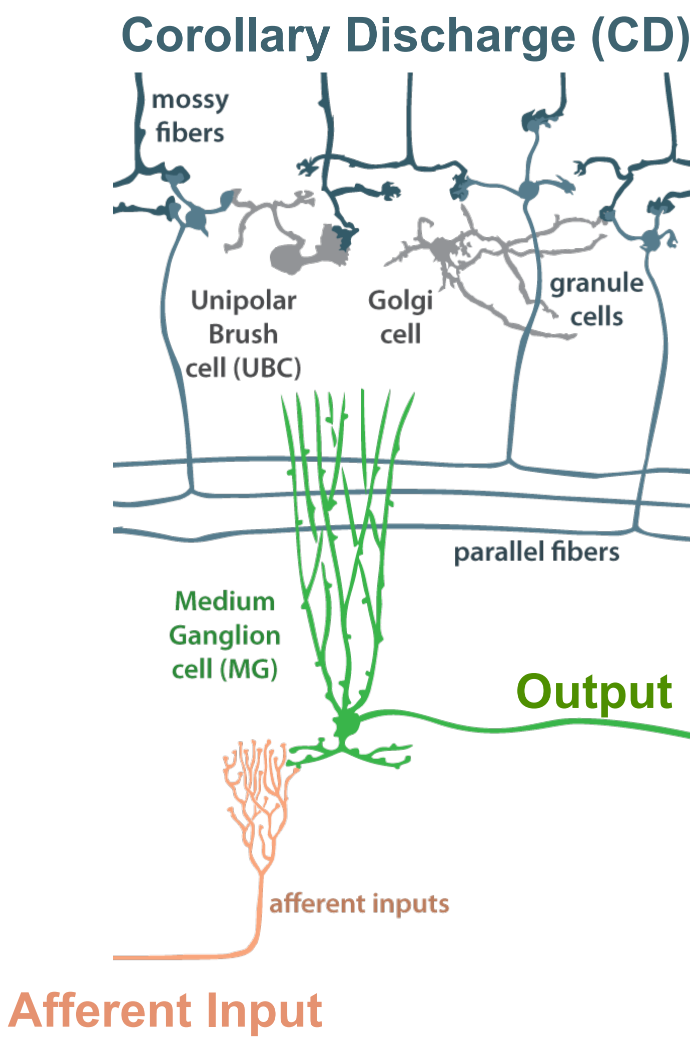


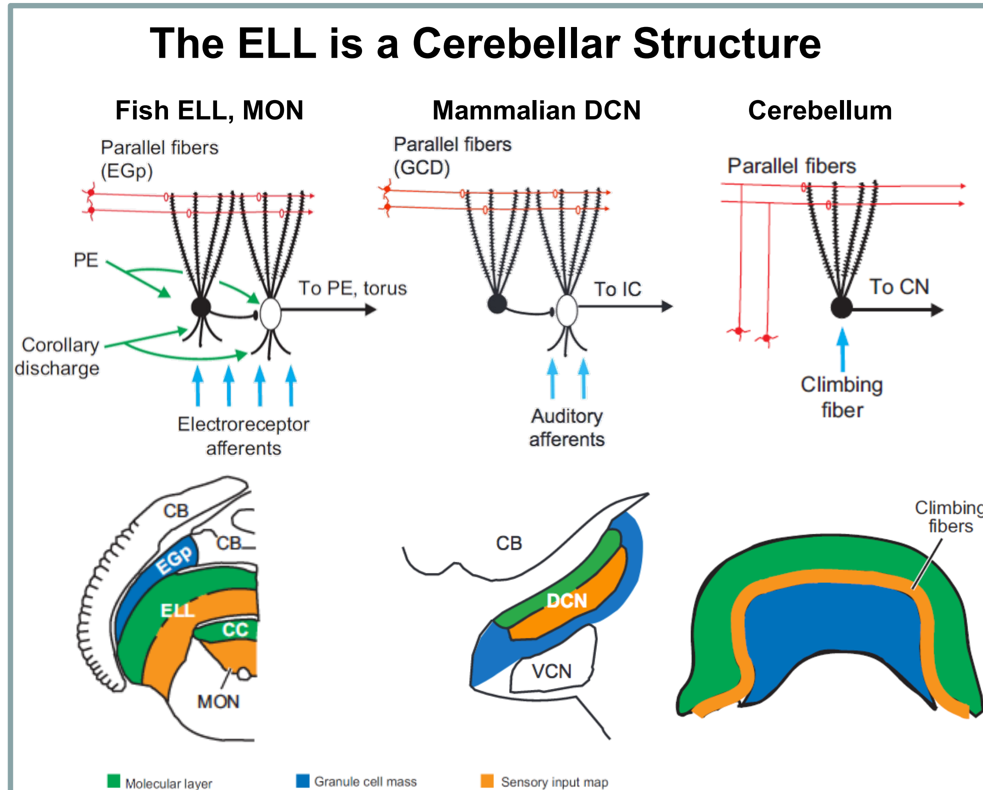






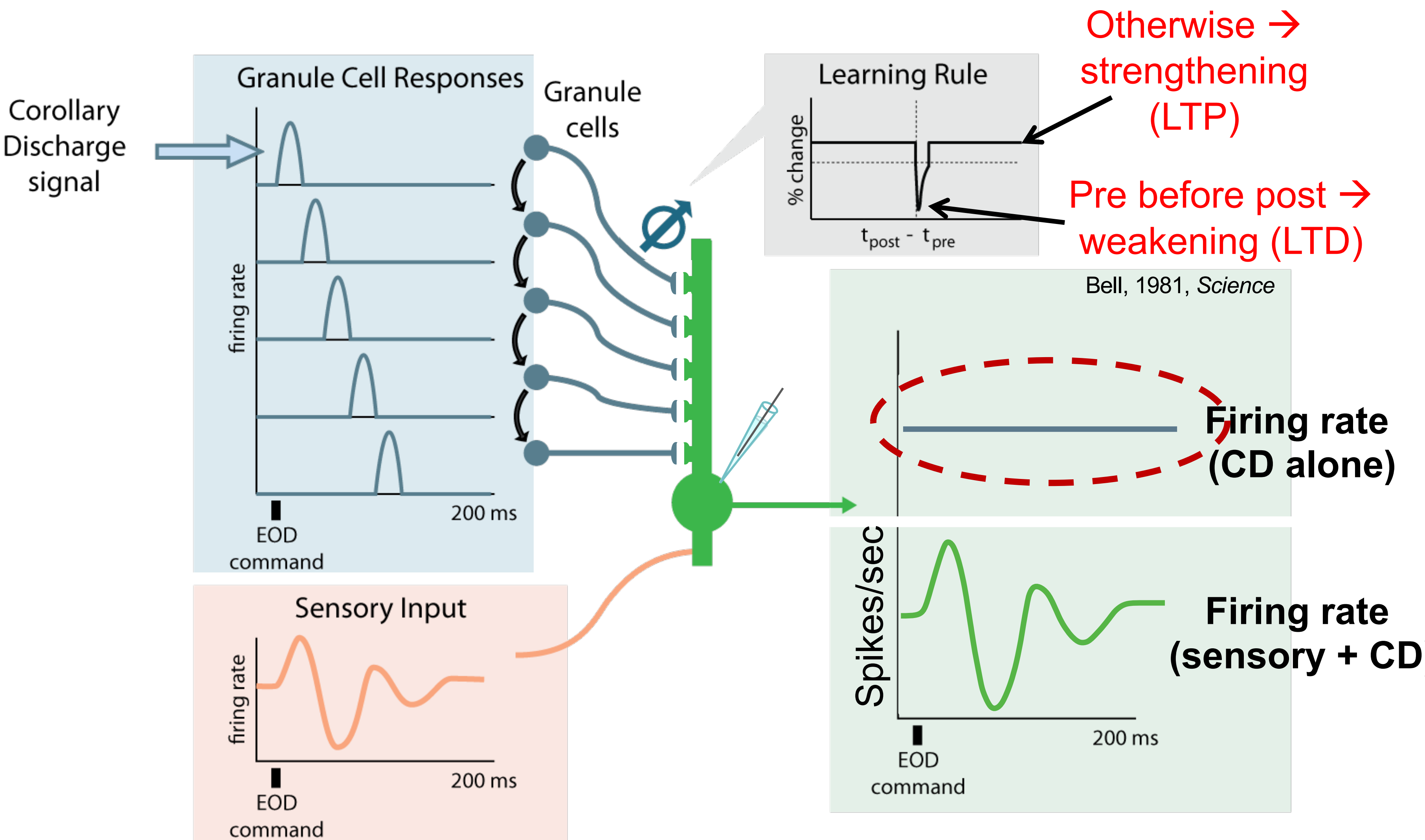
The ELL: Adaptive Reafference Filter

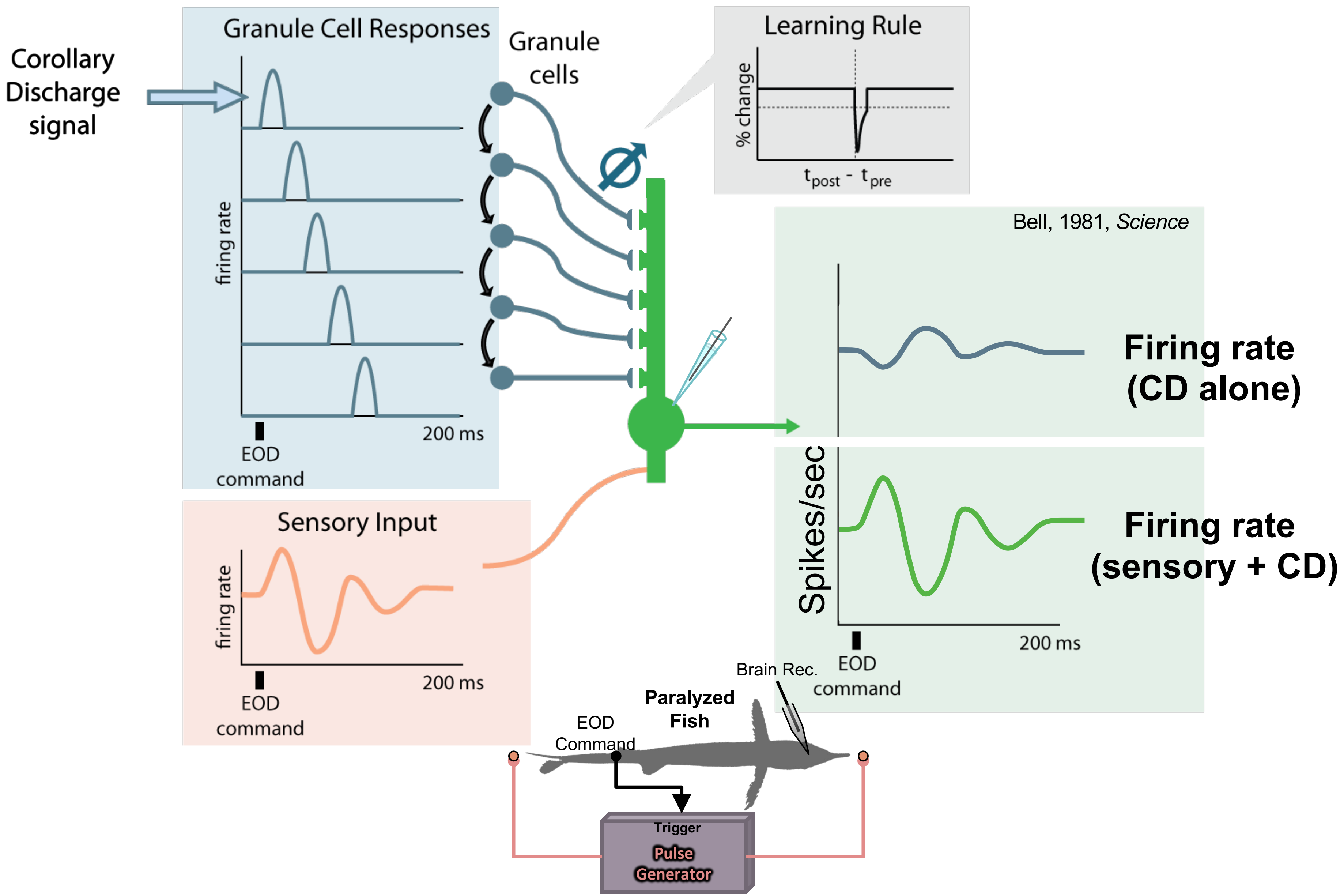




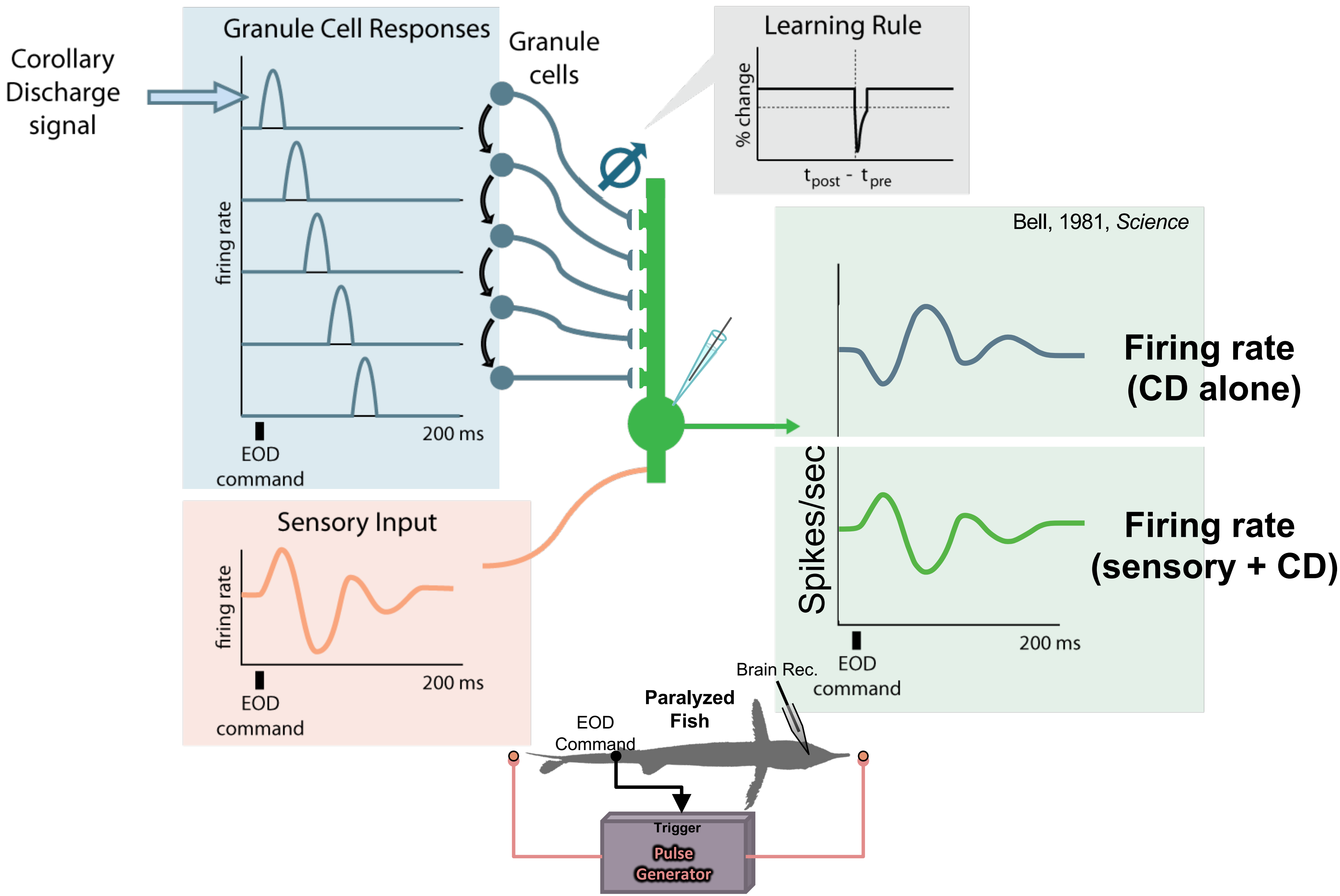
Bell et al, Annu. Rev. Neurosci. 2008

Anti-Hebbian Spike-Timing Dependent Plasticity

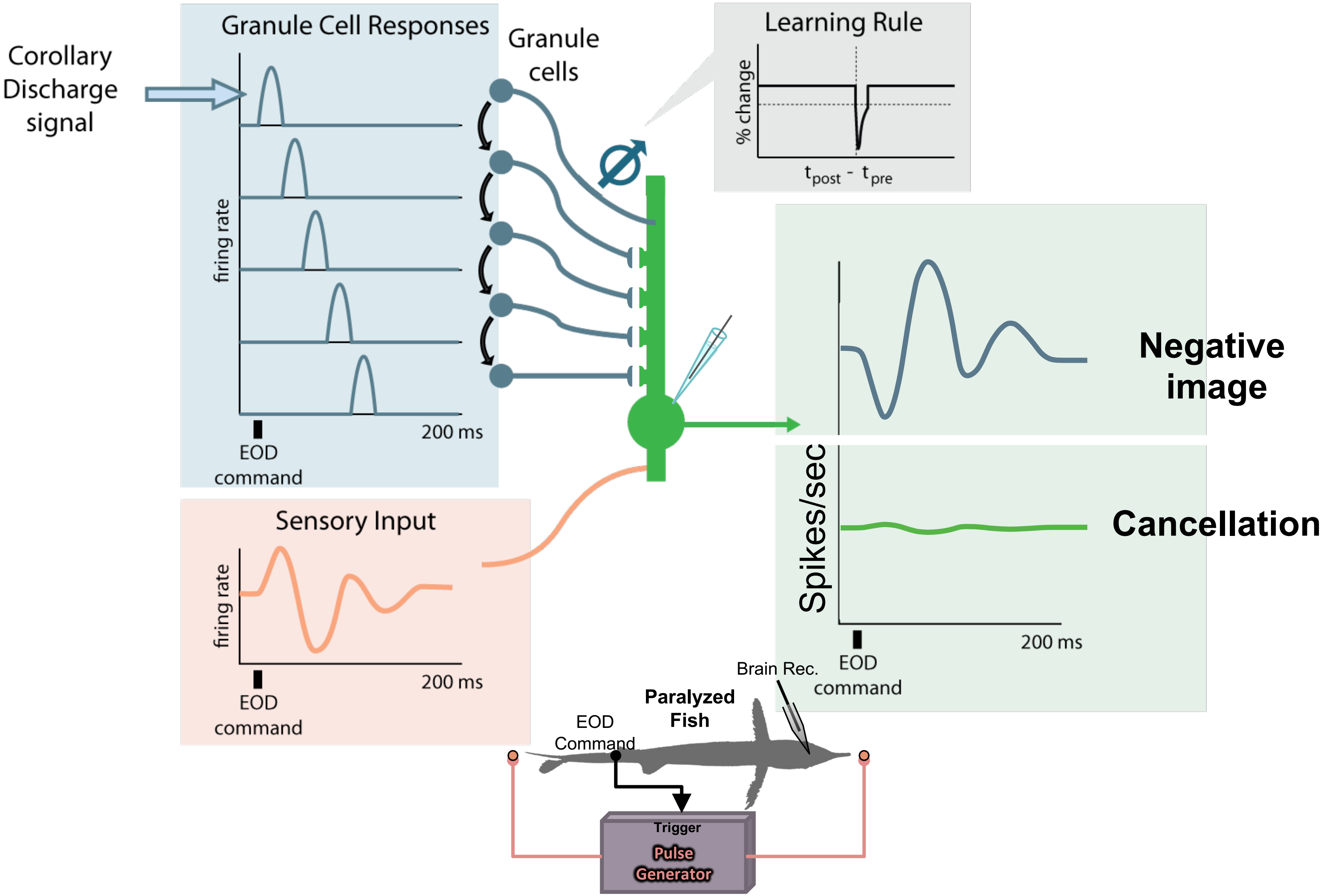




Corollary Discharge signal
Granule Cell Responses
firing rate
200 ms
EOD command
Granule cells
Learning Rule
% change
t post - t pre
Bell, 1981, Science
Firing rate (CD alone)
Spikes/sec
Firing rate (sensory + CD)
200 ms
EOD command
Sensory Input
firing rate
200 ms
EOD command
Brain Rec.
Paralyzed Fish
EOD Command
Trigger
Pulse Generator



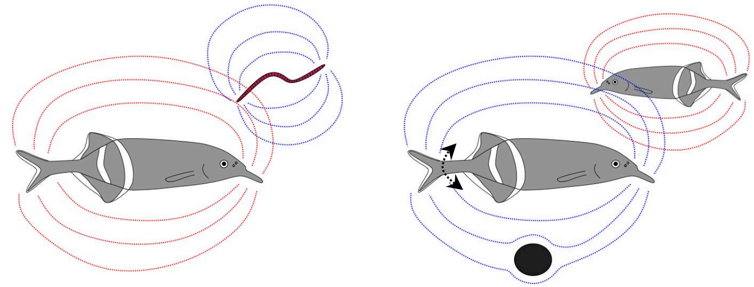
Corollary Discharge signal
Granule Cell Responses
firing rate
200 ms
EOD command
Granule cells
Learning Rule
% change
t post - t pre
Bell, 1981, Science
Firing rate (CD alone)
Spikes/sec
Firing rate (sensory + CD)
200 ms
EOD command
Sensory Input
firing rate
200 ms
EOD command
Brain Rec.
Paralyzed Fish
EOD Command
Trigger
Pulse Generator



Corollary Discharge signal
Granule Cell Responses
firing rate
200 ms
EOD command
Granule cells
Learning Rule
% change
t_{post} - t_{pre}
Negative image
Cancellation
Spikes/sec
200 ms
EOD command
Sensory Input
firing rate
200 ms
EOD command
Brain Rec.
Paralyzed Fish
EOD Command
Trigger
Pulse Generator

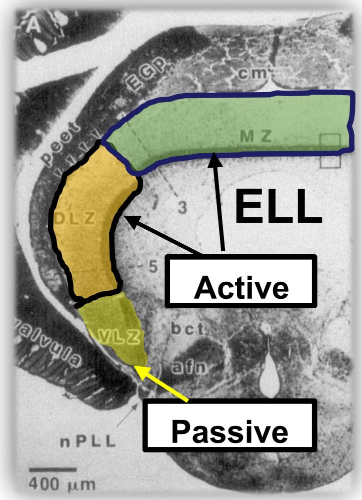
Reafference Cancellation in Active Electrolocation

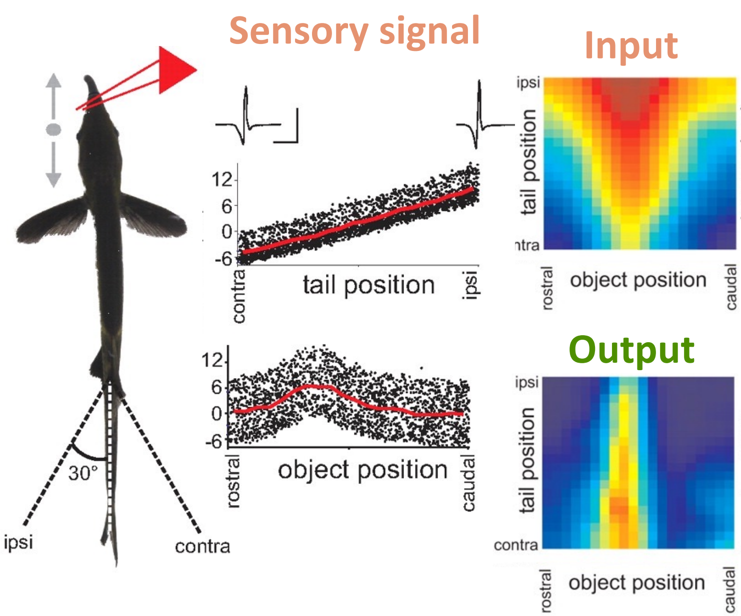
Passive electrolocation | Active electrolocation



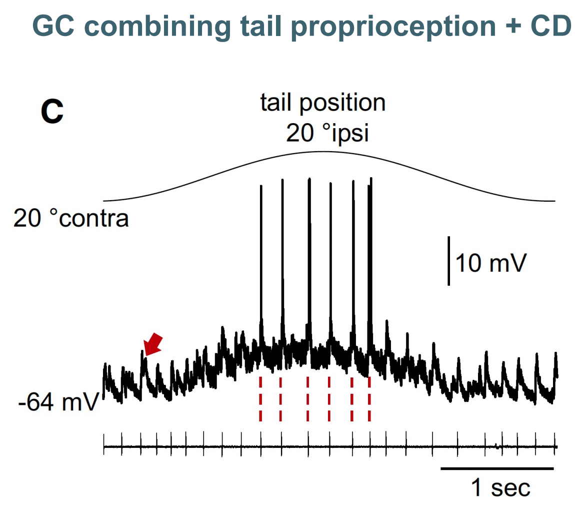
Signal = Electric field of aquatic animals
Noise = Own EOD

Signal = Own EOD
Noise = Other fish's EOD
Self-motion

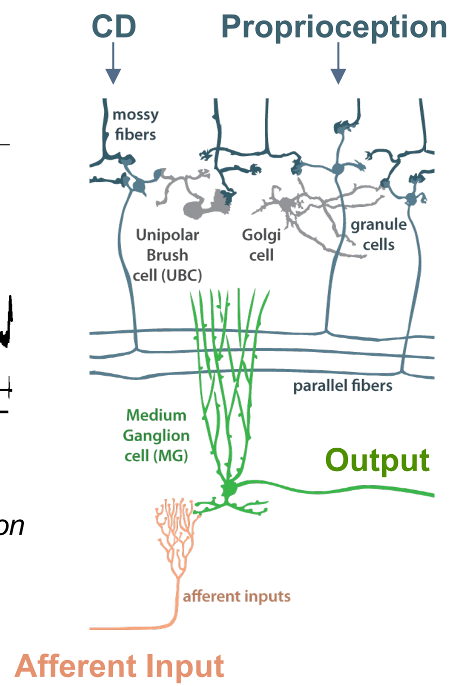


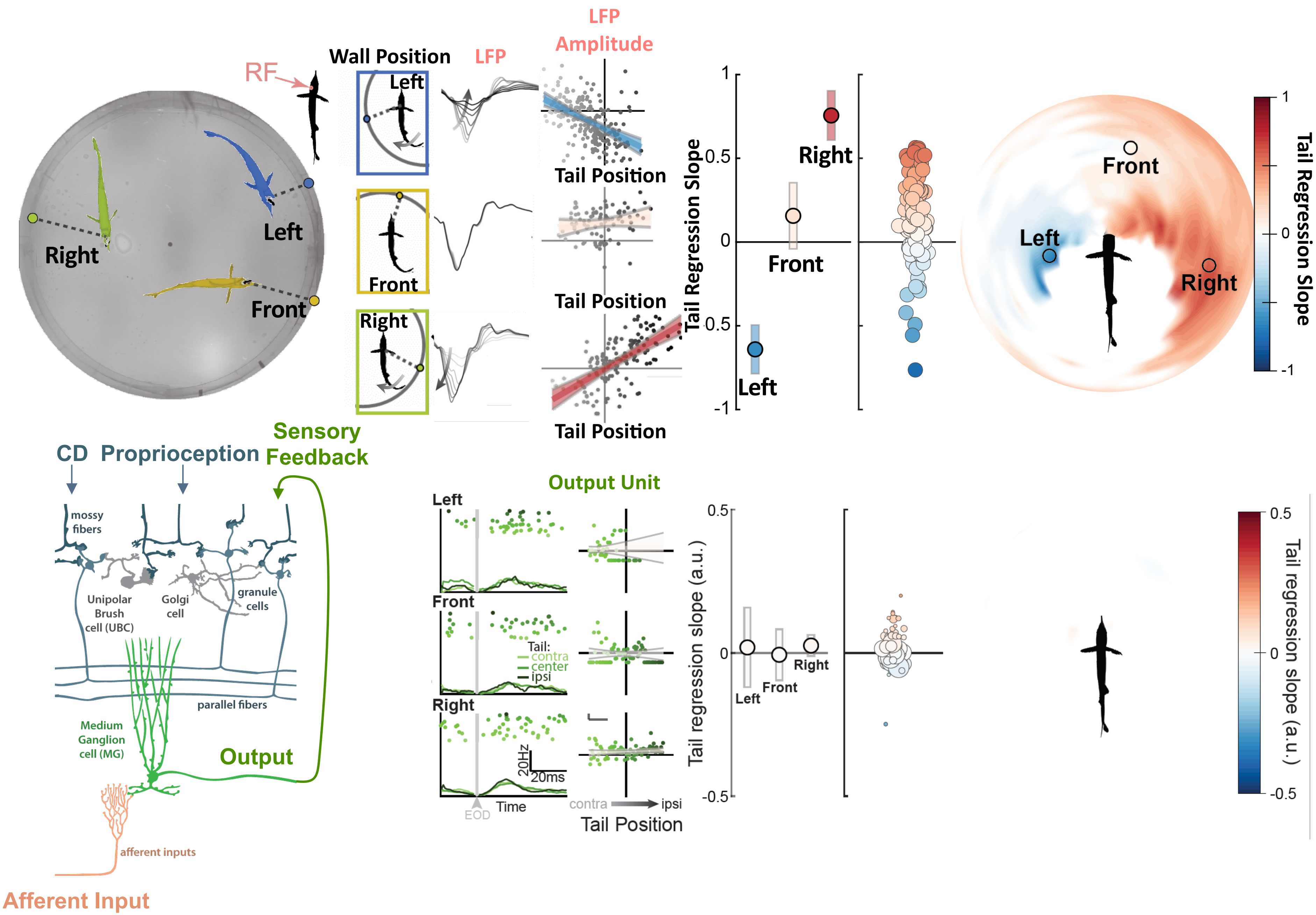


Sawtell & Williams, 2008, *JNS*



Sawtell, 2010, *Neuron*

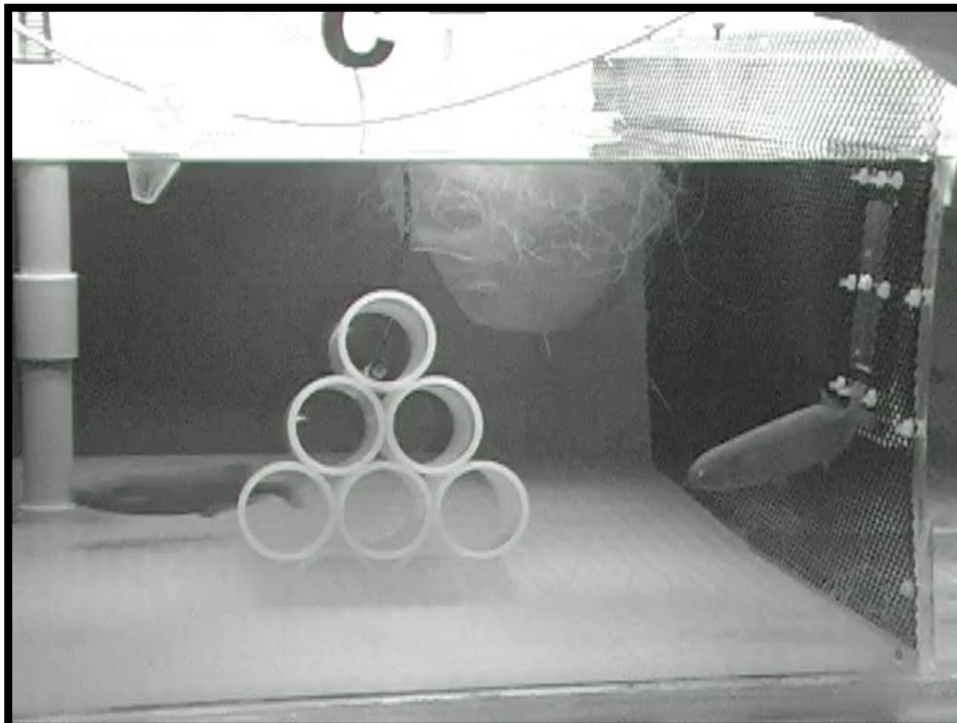




RF
Right
Left
Front
Wall Position
LFP
LFP Amplitude
Left
Front
Right
Tail Position
Tail Position
Tail Position
Tail Regression Slope
1
0.5
0
-0.5
-1
Right
Front
Left
Front
Left
Right
Tail Regression Slope
1
0
-1
CD
Proprioception
Sensory Feedback
mossy fibers
Unipolar Brush cell (UBC)
Golgi cell
granule cells
parallel fibers
Medium Ganglion cell (MG)
Output
afferent inputs
Afferent Input
Output Unit
Left
Front
Right
Tail:
contra
center
ipsi
20Hz
20ms
EOD
Time
contra
ipsi
Tail Position
Tail regression slope (a.u.)
0.5
0
-0.5
Left
Front
Right
Tail regression slope (a.u.)
0.5
0
-0.5

Electrocommunication

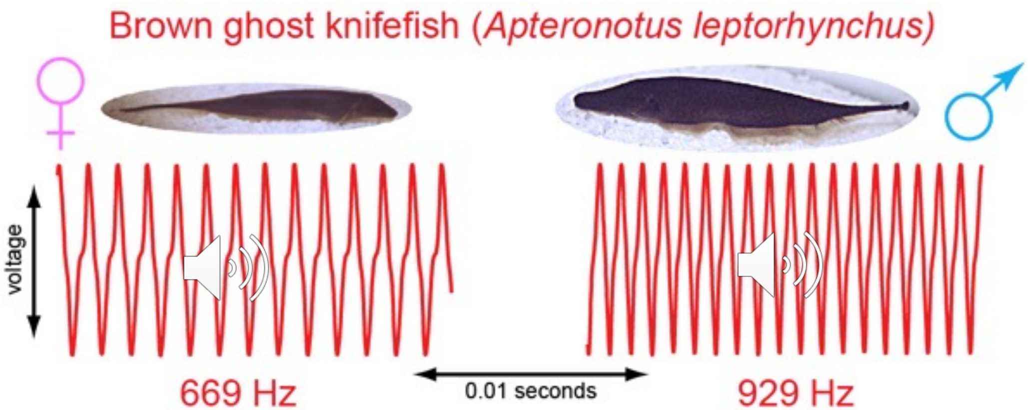
Electric fish use their discharge to communicate courtship, aggression, dominance etc



Very complicated in pulse fish

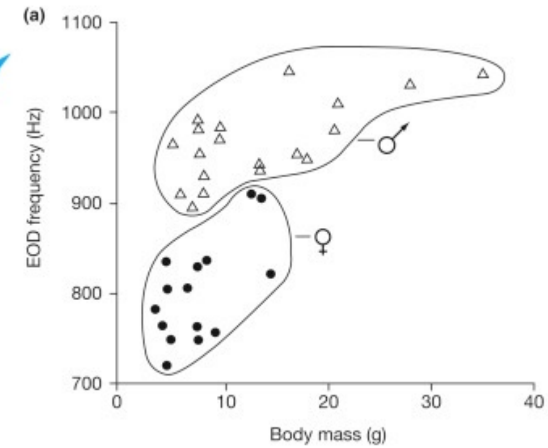
Electrocommunication (wave type fish)

EOD frequency conveys sex, status



600-900 Hz

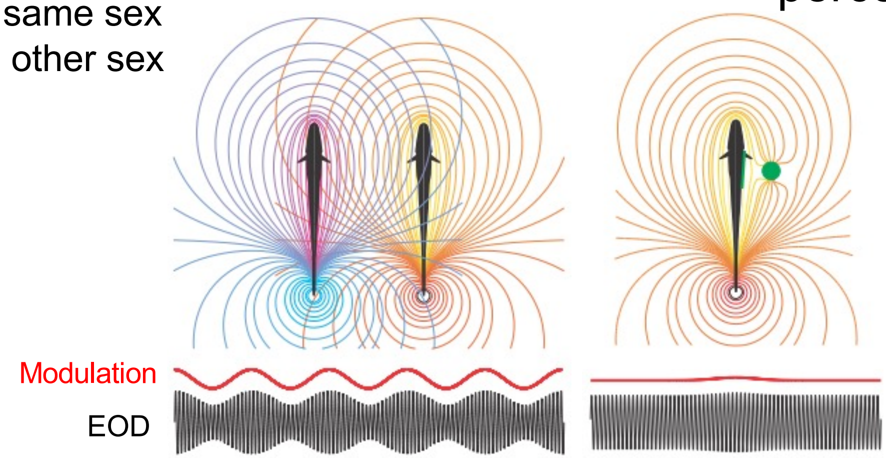
800-1100 Hz

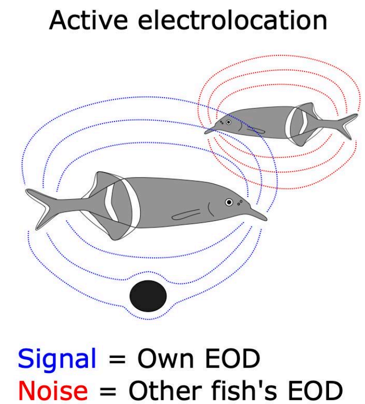


Beat: interference pattern between two EODs

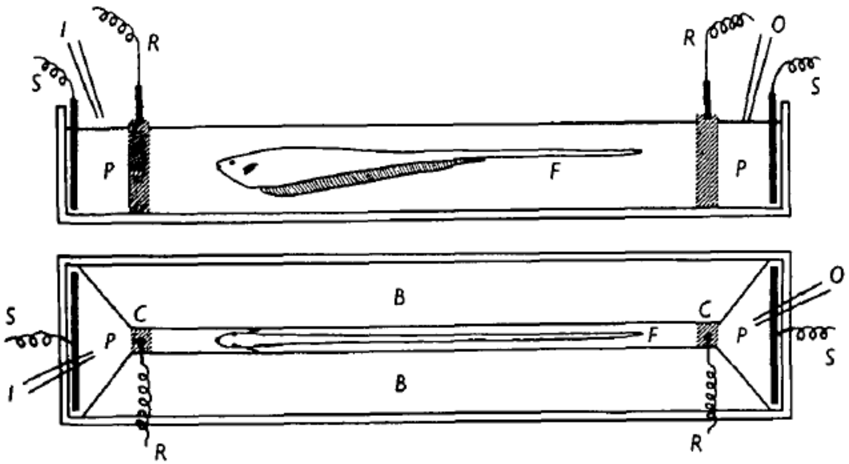
- Beat frequency = EOD freq. difference
  - Low beat freq = same sex
  - High beat freq = other sex

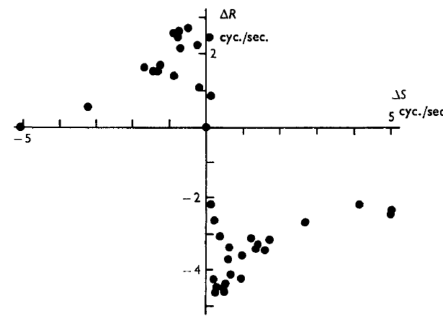
Jamming:
Low-frequency beat interferes with perception of objects

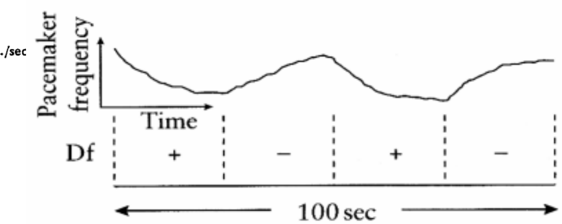




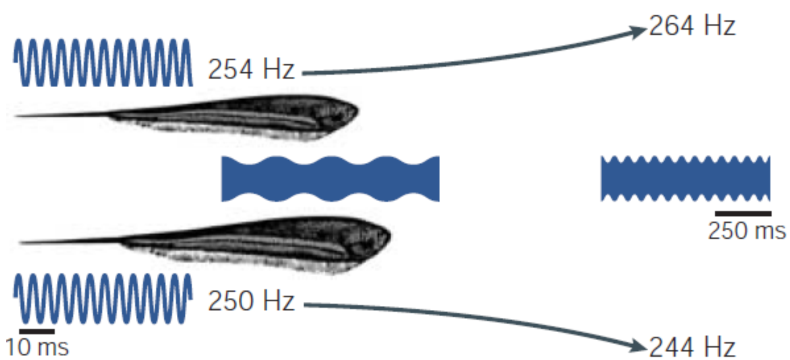
Jamming avoidance response

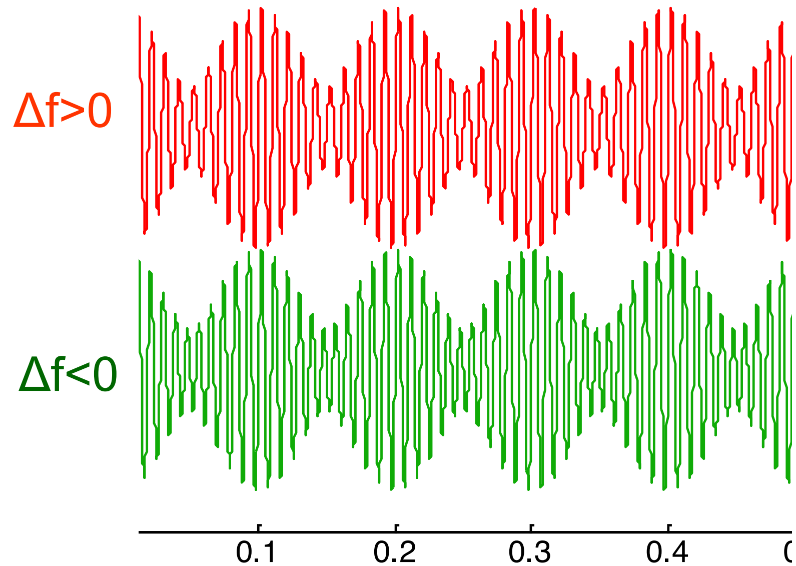






Watanabe & Takeda, J. Exp. Biol. 1963





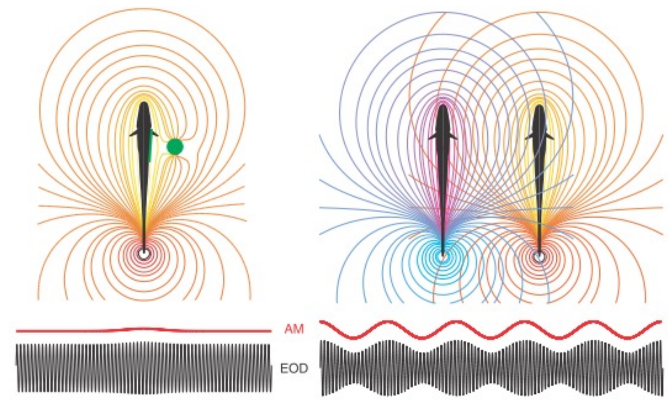
- Reproducible sensory-motor behavior of ethological importance.
- Requires non-trivial neuronal computation

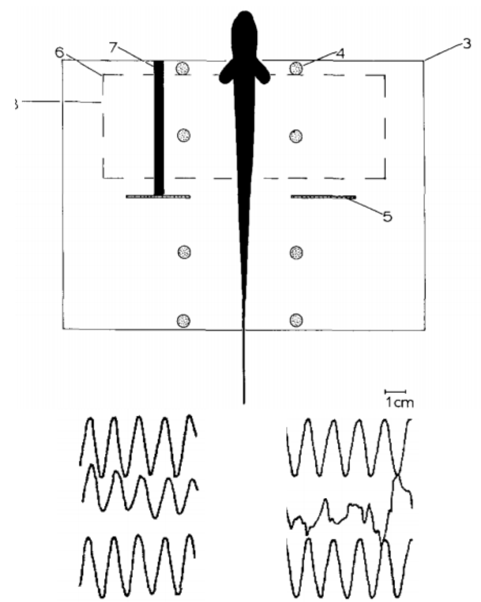
Jamming avoidance response

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

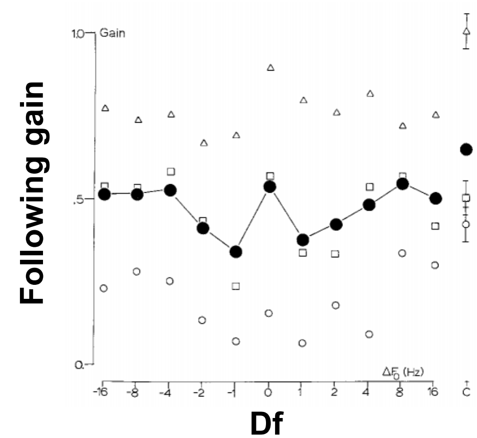
- Neighboring fish with similar EODr cause low-frequency interference which 'jams' perception.

- Solution: each fish alters its EOD rate so that the frequency difference will be outside the perceptual band (>20Hz)



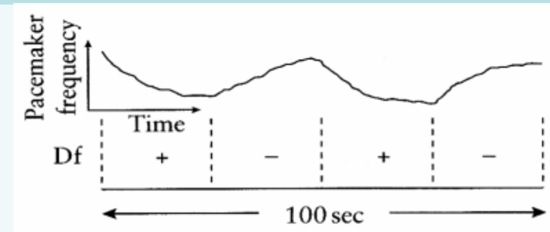
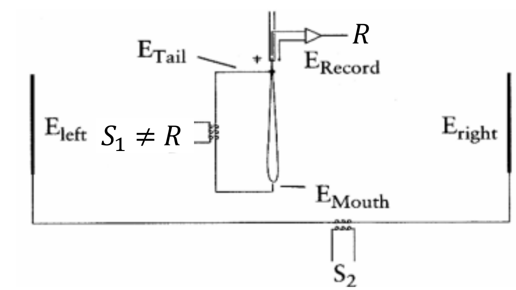
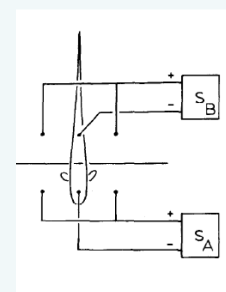
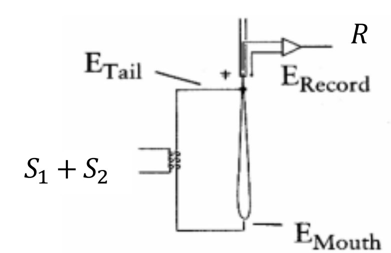


Plastic Agar



Heiligenberg J Comp Physiol. 1973,
Matsubara & Heiligenberg J Comp Physiol 1978

Possible mechanisms

Mechanism	Evidence	Experiment
Iterative search	❌ Immediate correct response	
Efference copy	❌ Open loop response according to mimic frequency ❌ No PPn→ELL pathway	
Using temporal interference pattern	✔ JAR abolished in split chamber stimulation	
Using spatial interference pattern	✔ Incorrect JAR in ‘identical geometry’ stimulation	

JAR computation

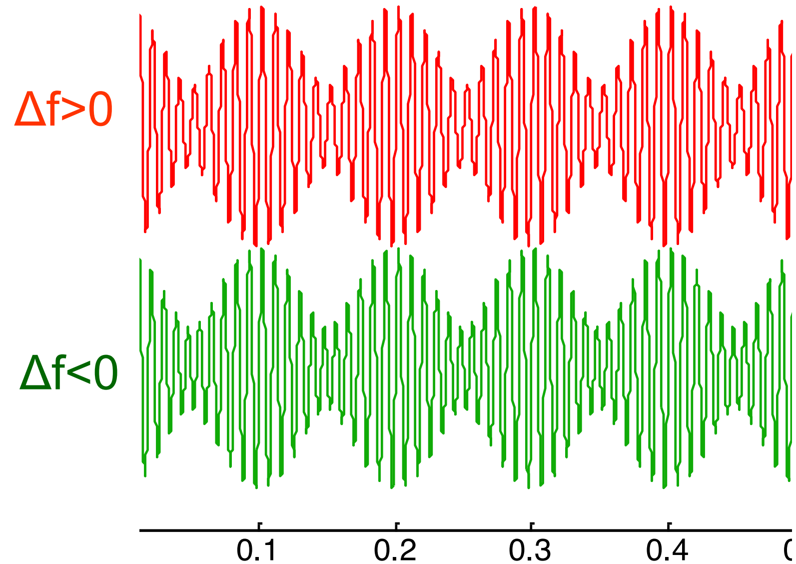
- f_1- Fish's own EOD rate
  f_2- Interefence EOD rate

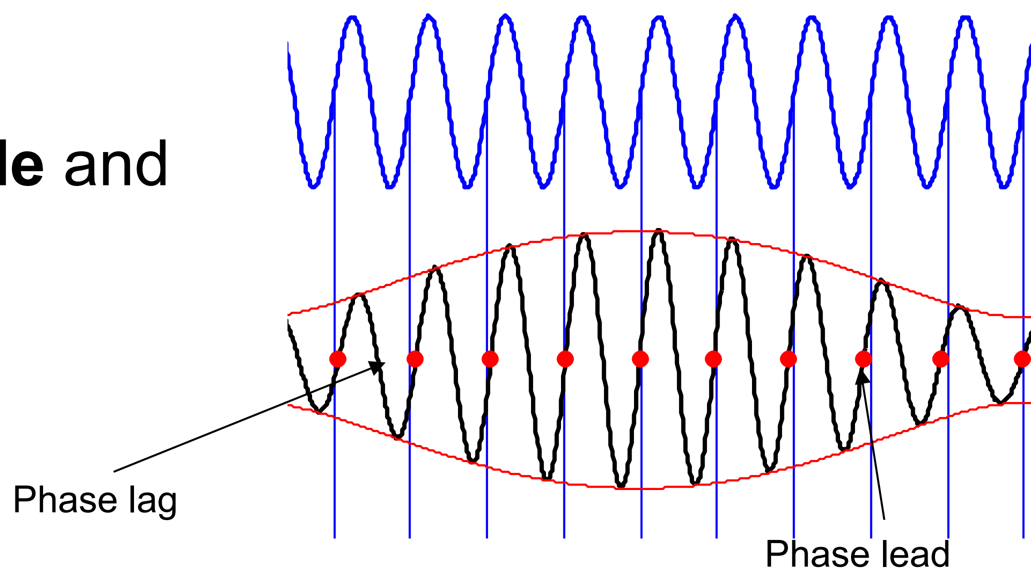
  $$\Delta f = f_2 - f_1$$

- The fish needs to compute if the neighbor is using a higher rate ($\Delta f>0$) or a lower rate ($\Delta f<0$).

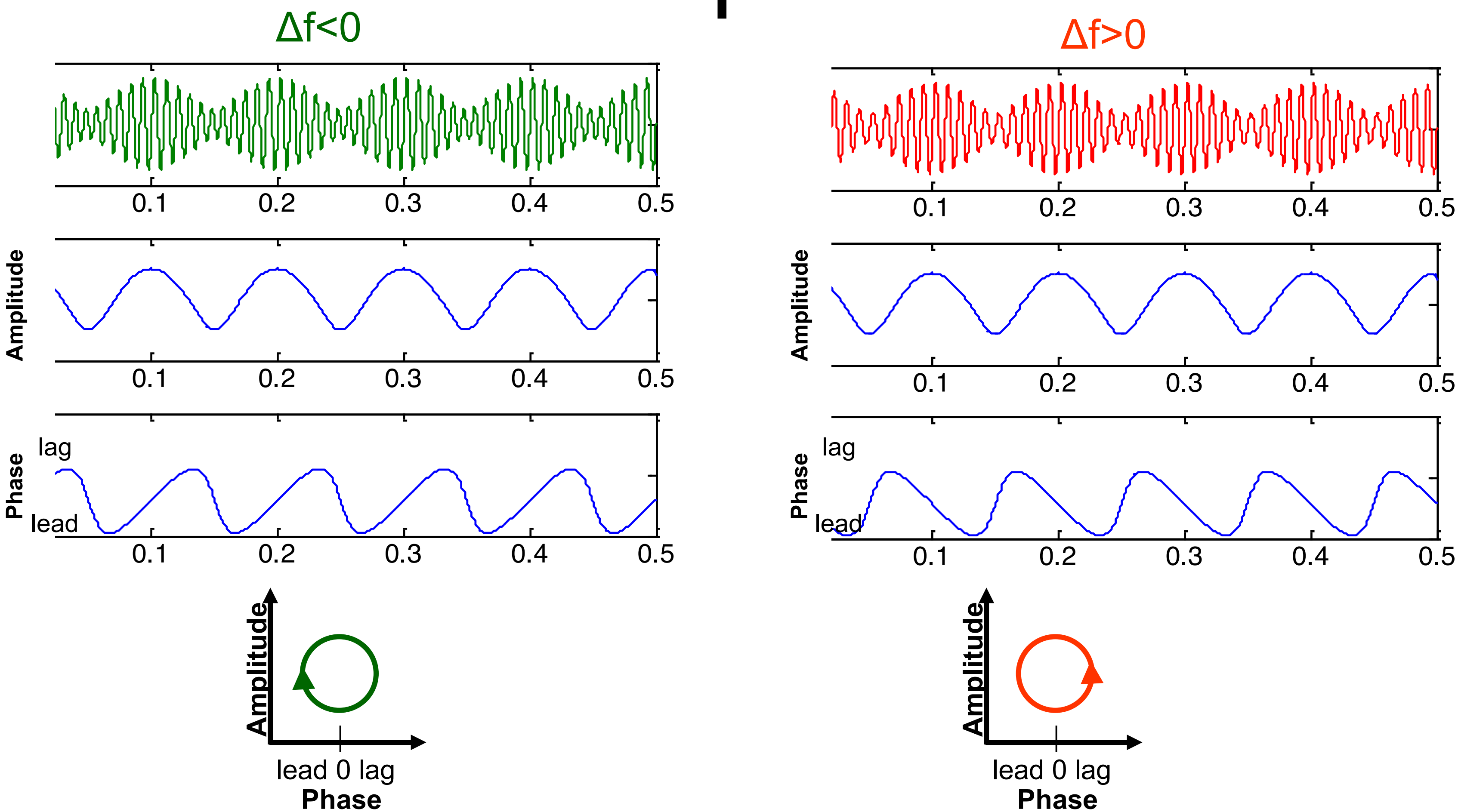
- The interference causes a modulation in both **amplitude** and **phase** called **'beat'**.

- The rate of the beat is $|\Delta f|$



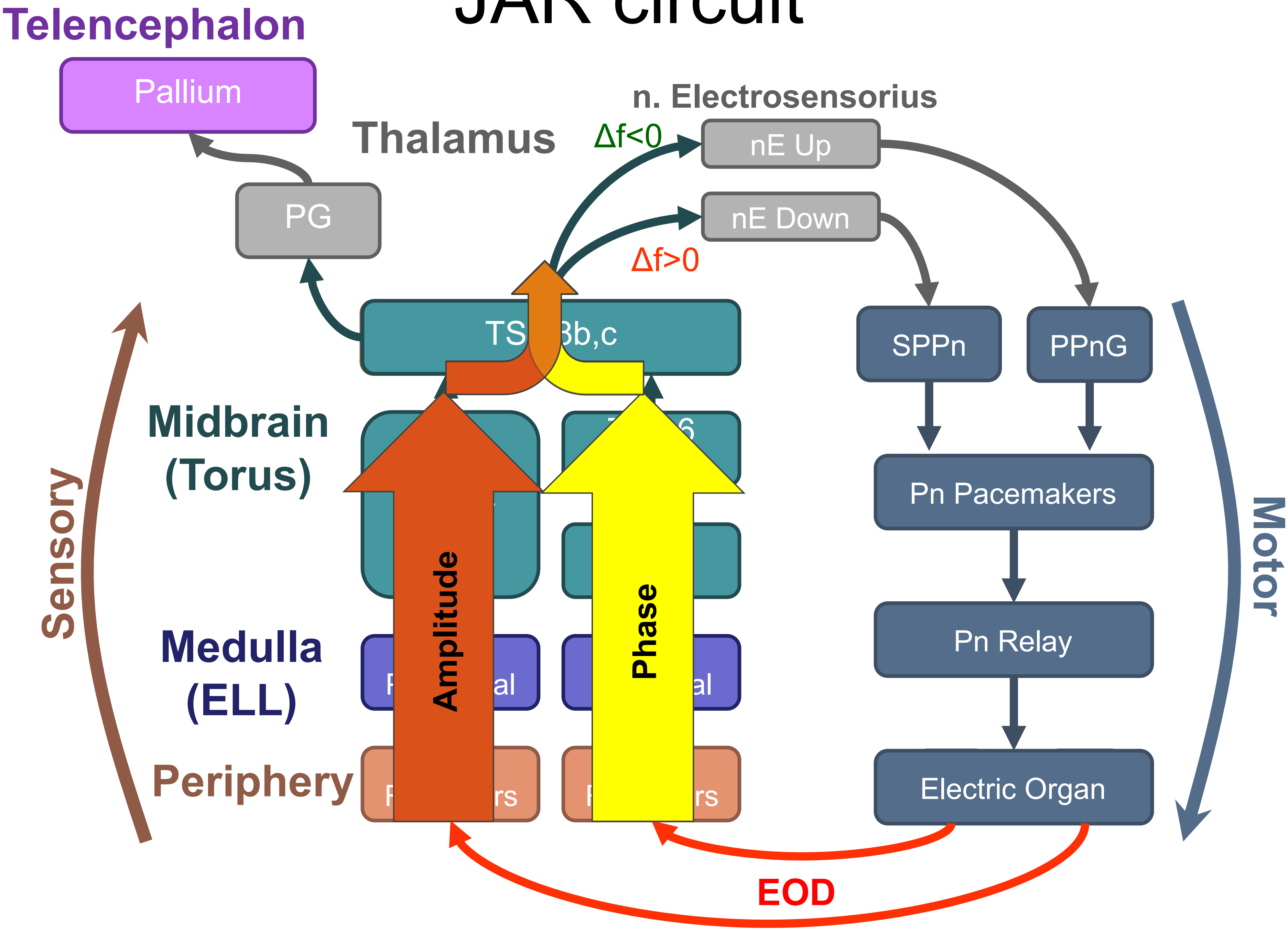


JAR computation



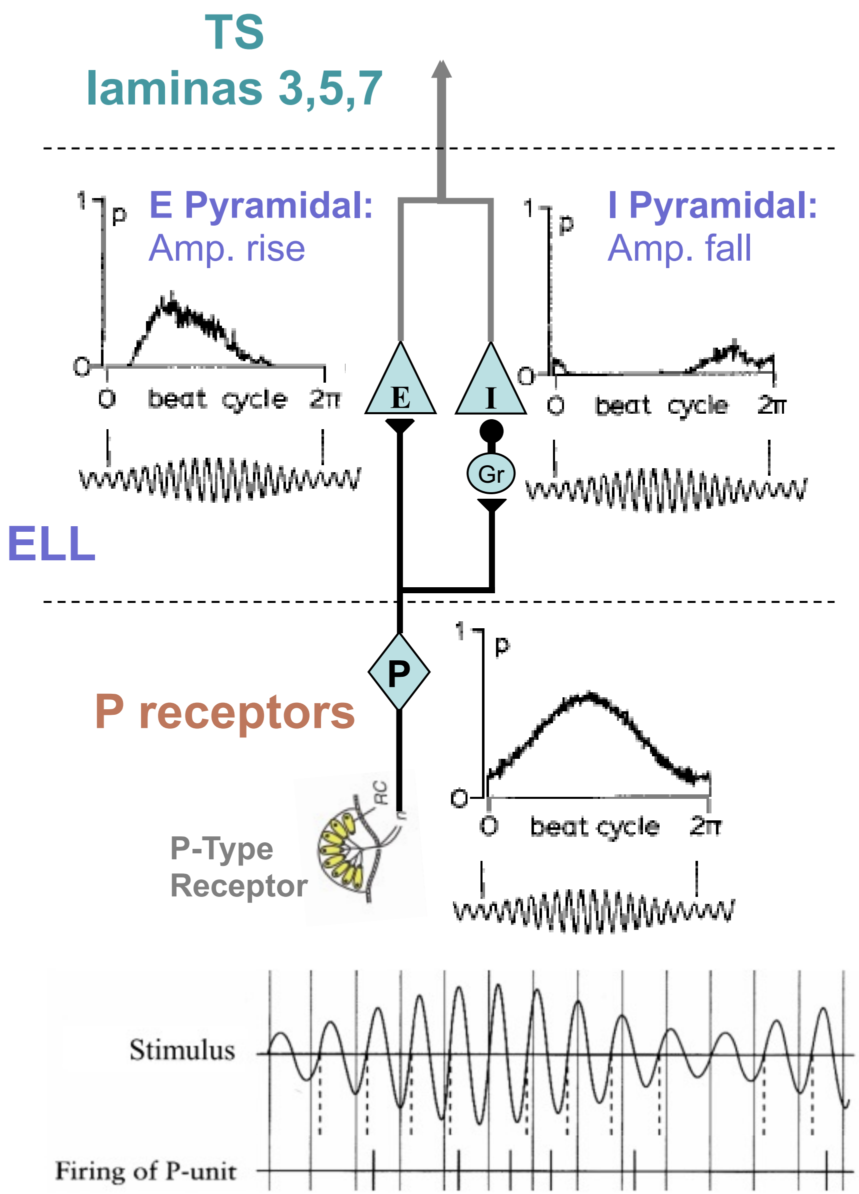
- Pattern of modulation in phase and amplitude holds information about sign of Δf:
  - When $\Delta f>0$ phase lag during amplitude rise and vice-versa.
  - When $\Delta f<0$ phase lead during amplitude rise and vice-versa.
- Rotations in different directions in amplitude/phase state-plane.

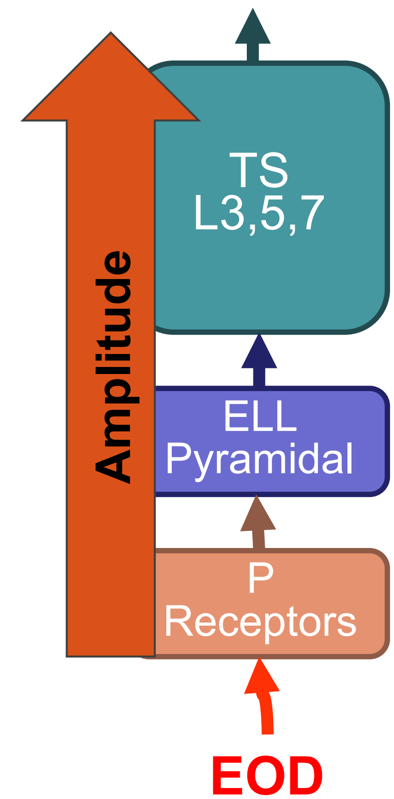
JAR circuit



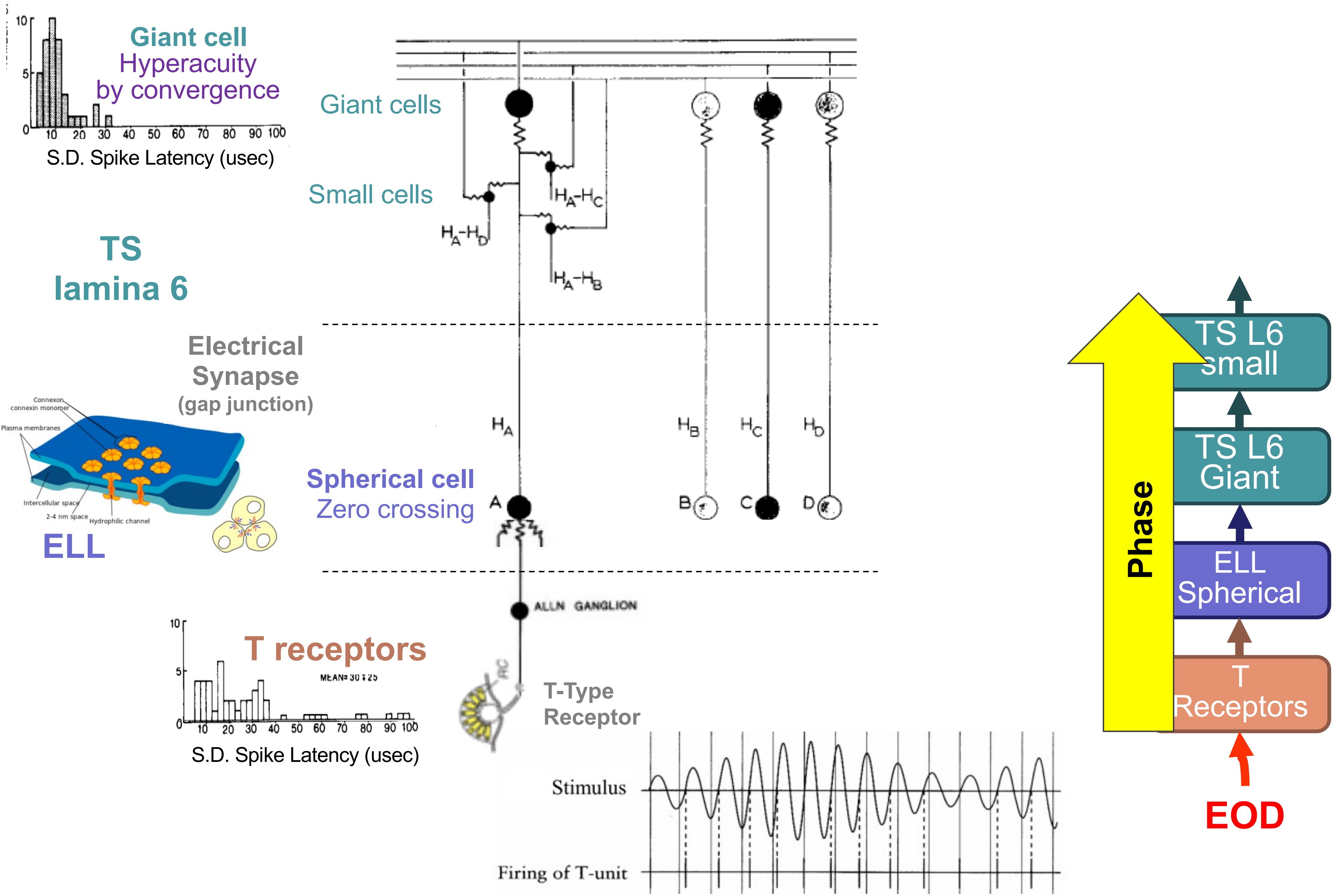
Telencephalon
Pallium
Thalamus
PG
n. Electrosensorius
Δf<0
nE Up
nE Down
Δf>0
SPPn
PPnG
Pn Pacemakers
Pn Relay
Electric Organ
Motor
Sensory
Midbrain
(Torus)
Medulla
(ELL)
Periphery
Amplitude
Phase
EOD

JAR physiology: Amplitude coding



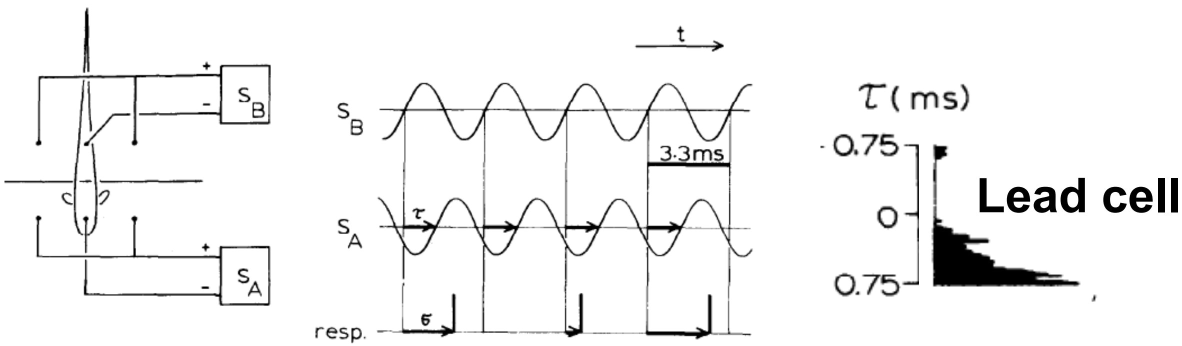


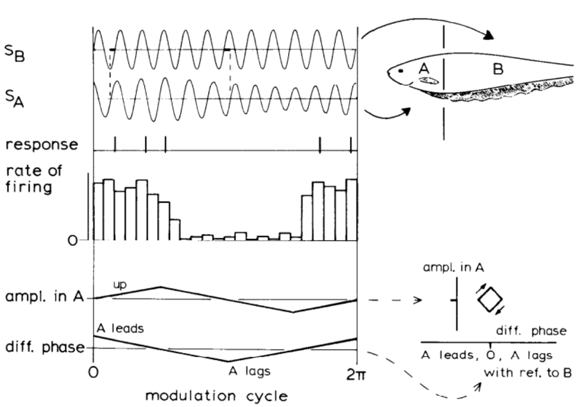
JAR physiology: Phase coding

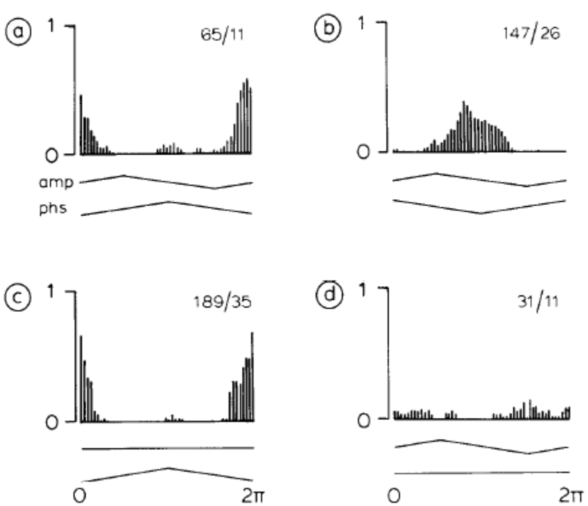


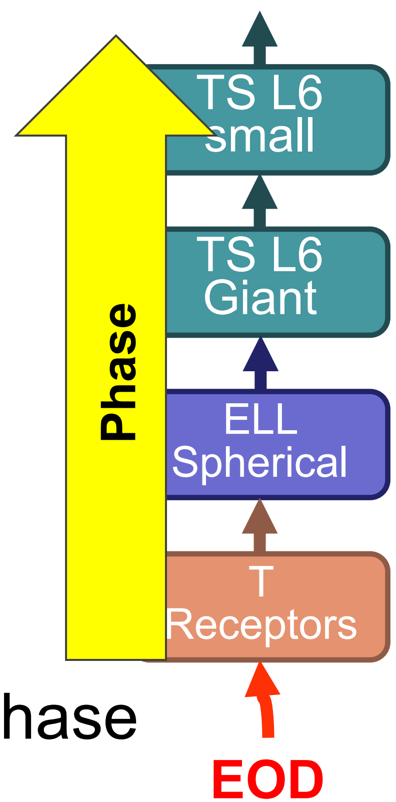
Phase coding

Split compartment experiments:
enable independent modulations of phase and amplitude



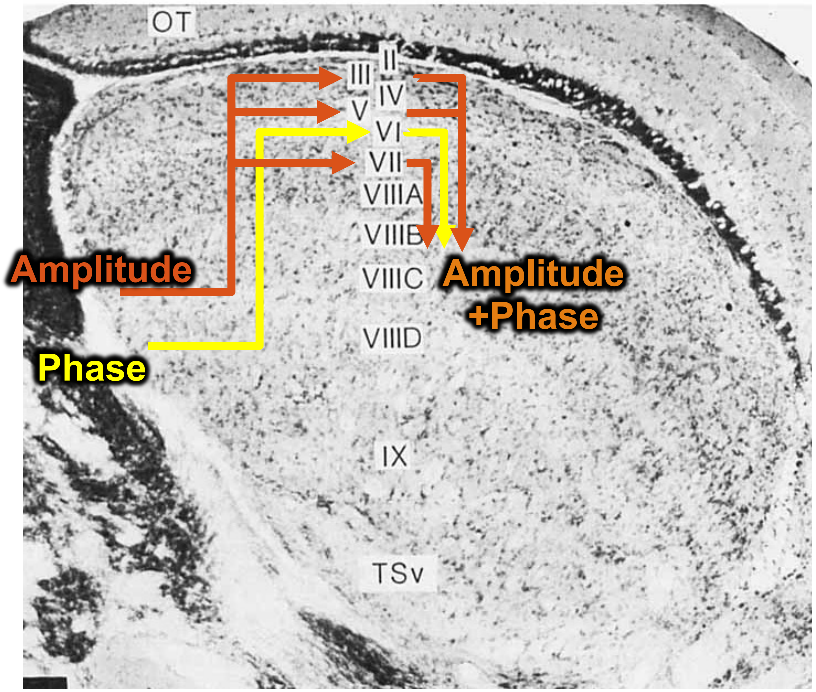


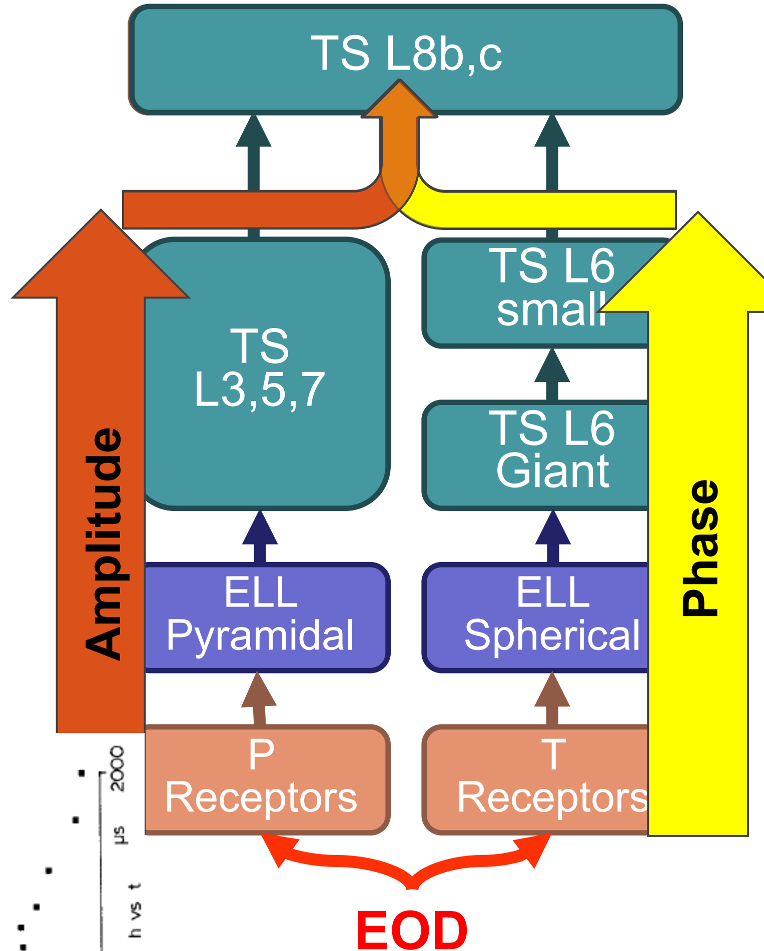


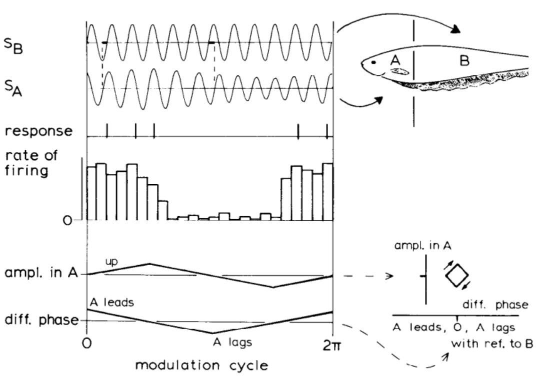


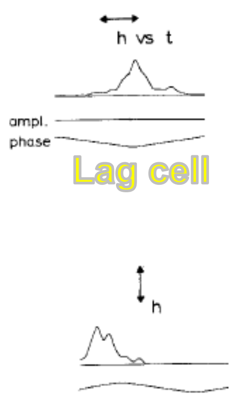
Small cells are coincidence detectors, reporting phase difference between two body regions.

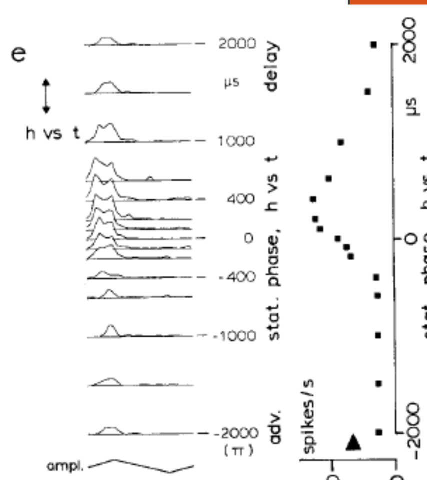
JAR physiology: Phase-amplitude coding

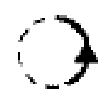








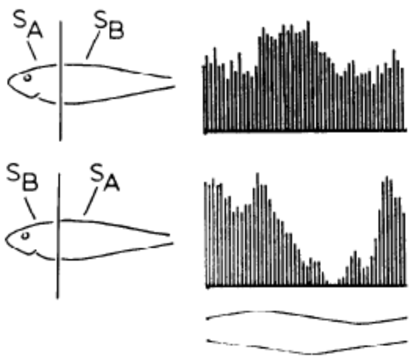




E-Lag cell

Phase-amplitude coding

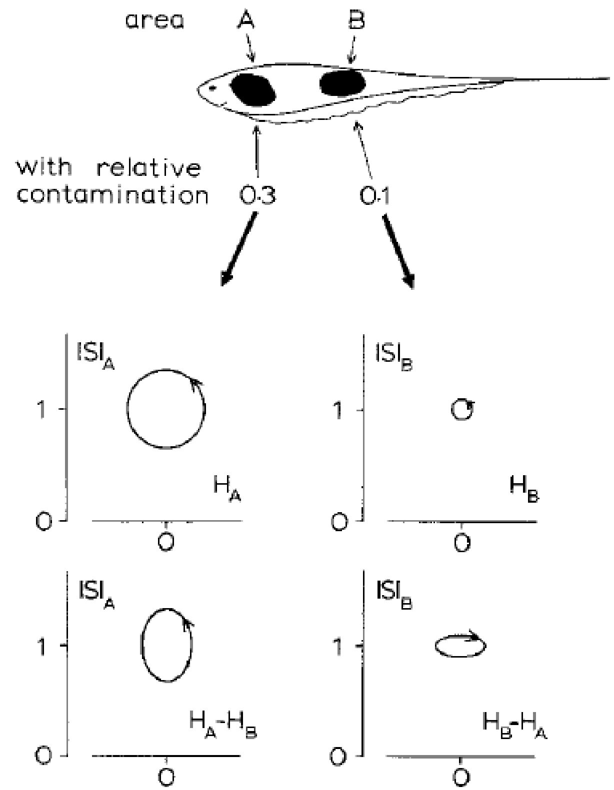
No Reference Signal- ambiguous code



E-advance

E-delay

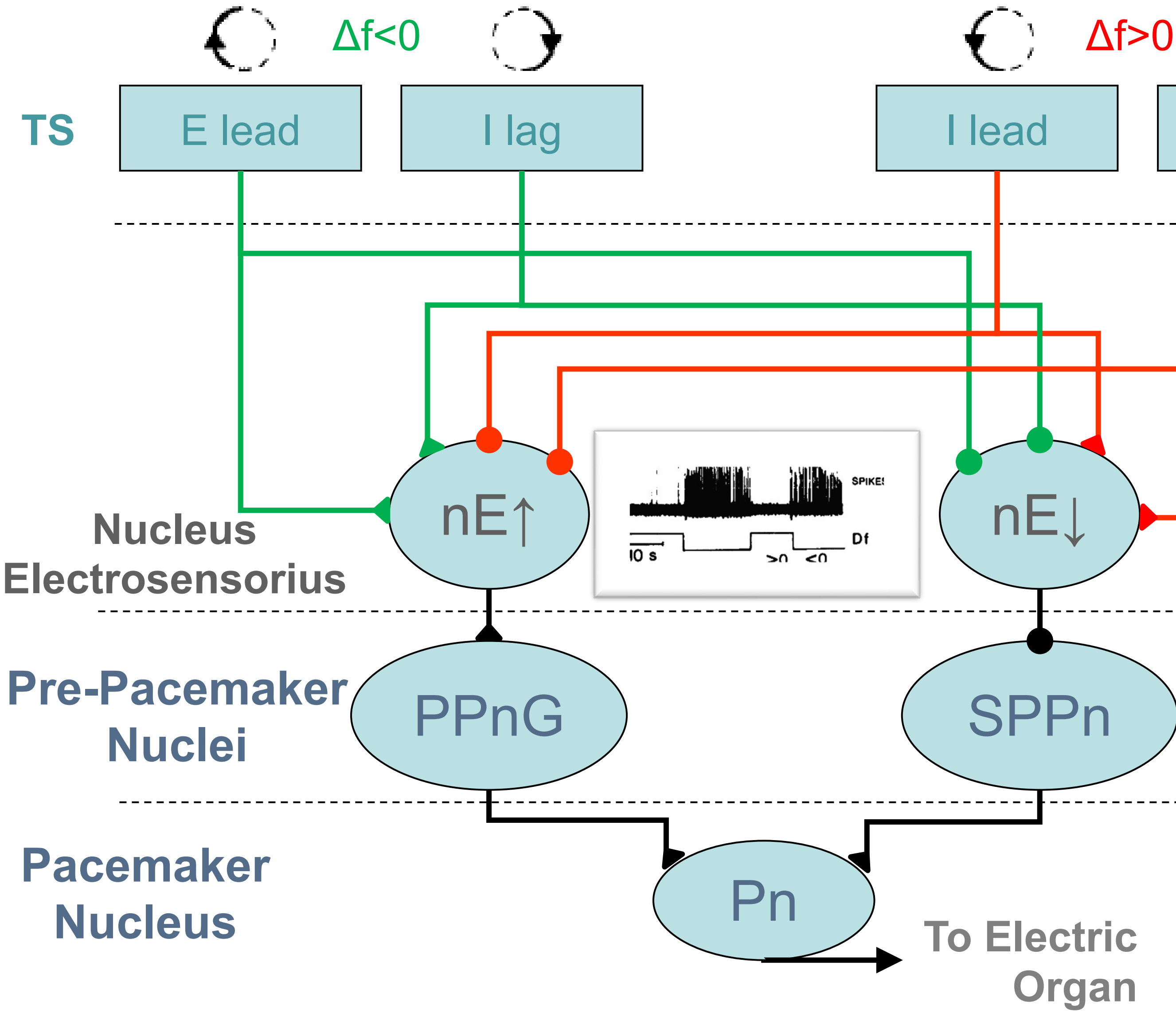
For each cell reporting Δf<0
there is a reciprocal cell reporting Δf>0

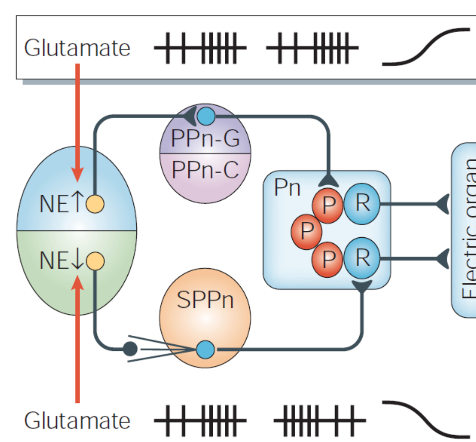


Solution: in natural geometry, different body regions are affected differently by the jamming interference.

Sensory-motor link

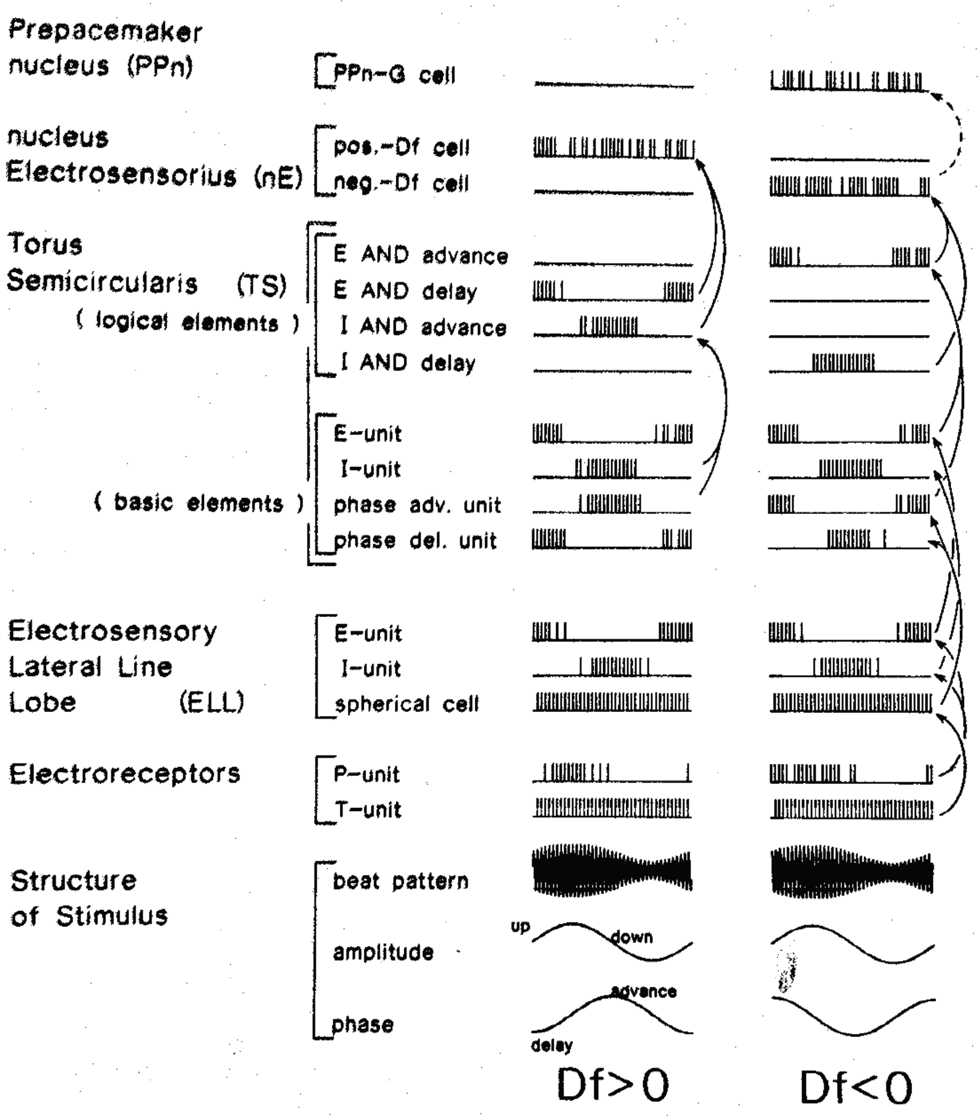
'Neural Democracy' (population code): the neurons 'vote' on the sign of Δf. The strongly affected regions get a stronger vote.

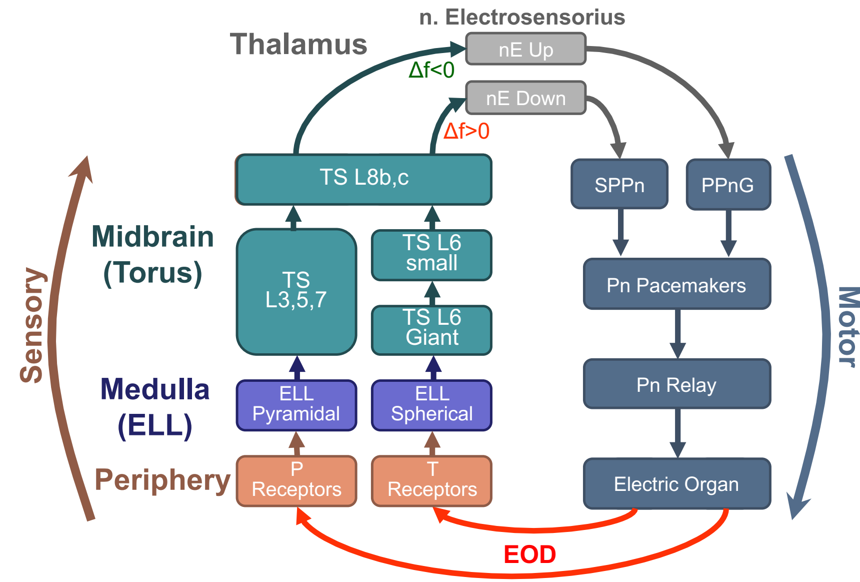


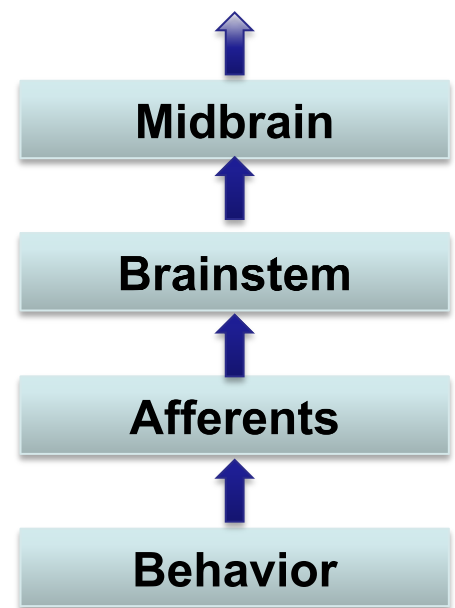


Rose, Nat. Rev. Neuro. 2004

JAR circuit- summary



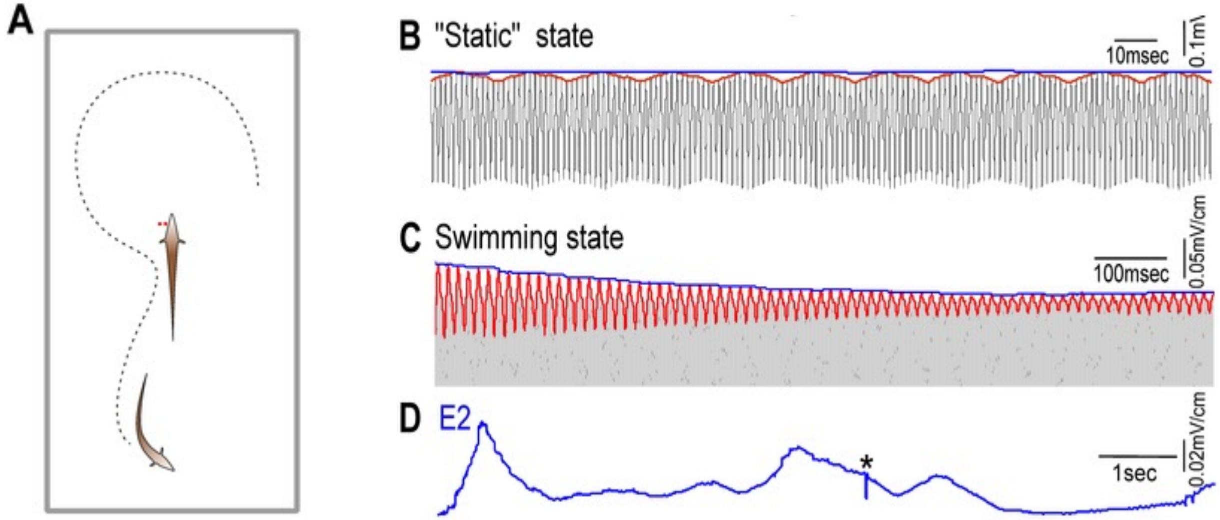




Chirps and Envelopes

The **beat frequency** depends on relative identity of other fish

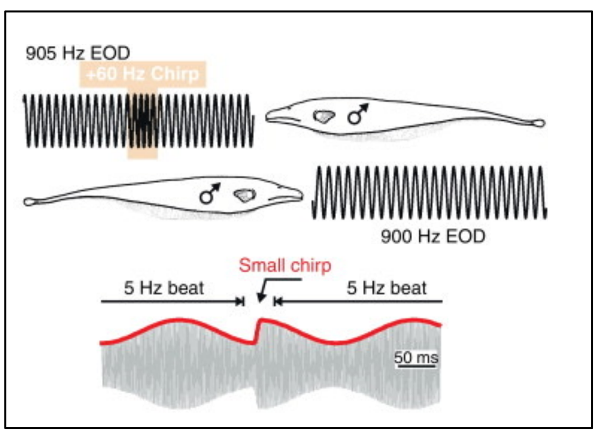
The ‘**beat envelope**’ (modulation depth) depends on relative position of other fish



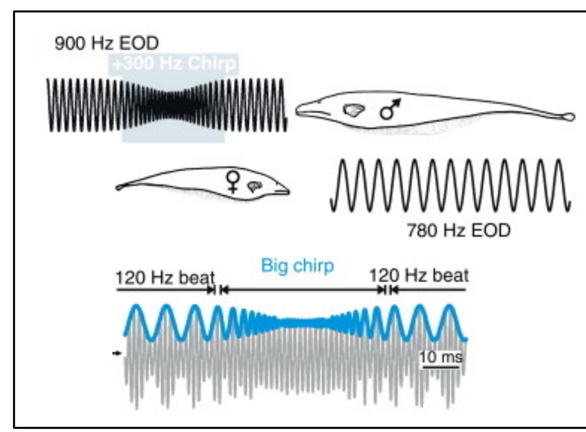
Yu et al, PLoS Comp. Biol. 2012

Chirps: transient changes in EOD frequency/amplitude, ‘communication tokens’

Small chirps

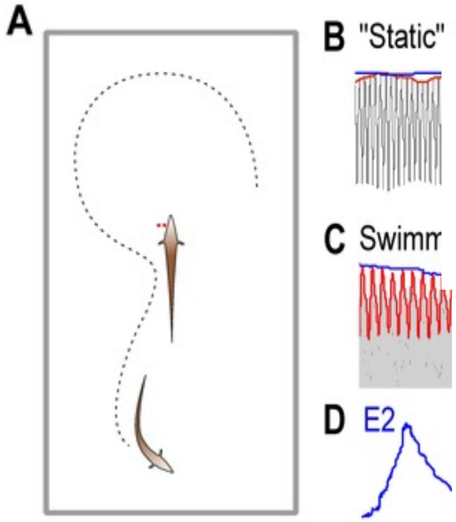


Long chirps

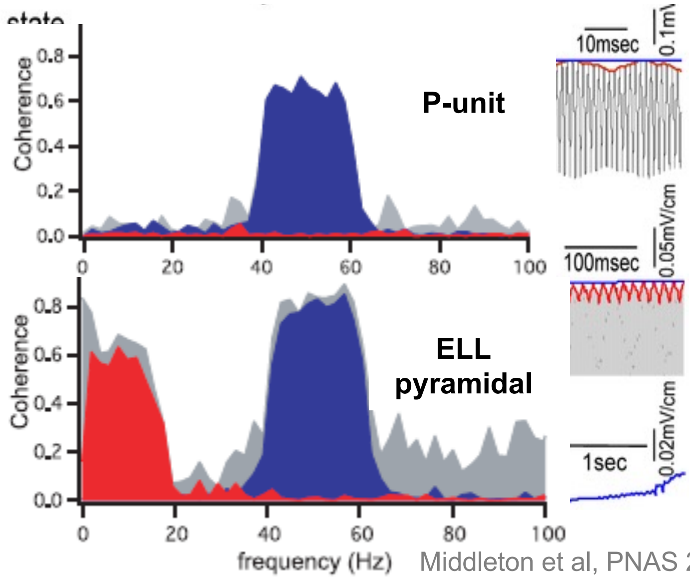


Marsat, Longtin & Maler, Curr. Op. Neurobiol. 2012

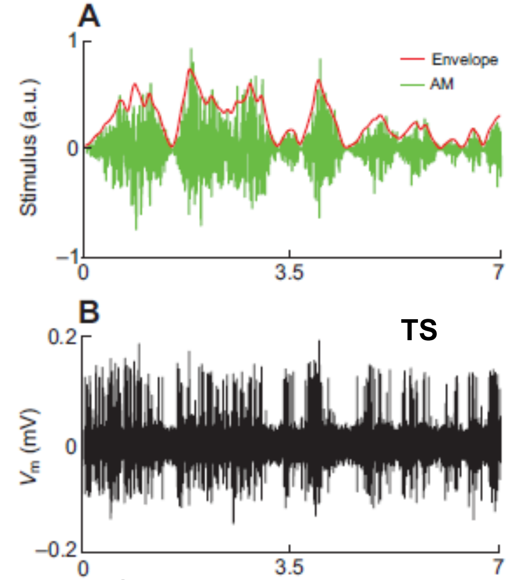
Motion induced envelopes



Yu et al, PLoS Comp. Biol. 2012



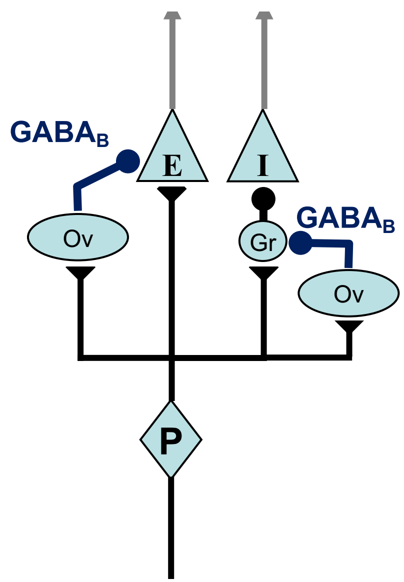
Middleton et al, PNAS 2006

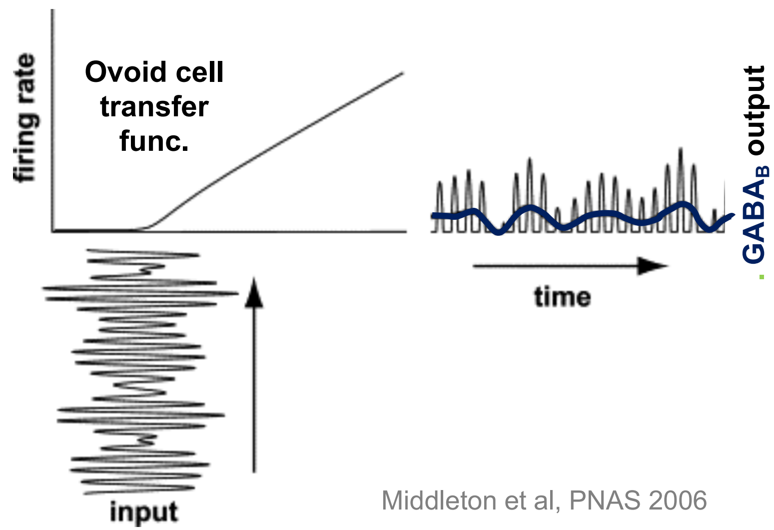


Stamper et al, J. Exp. Biol. 2013

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

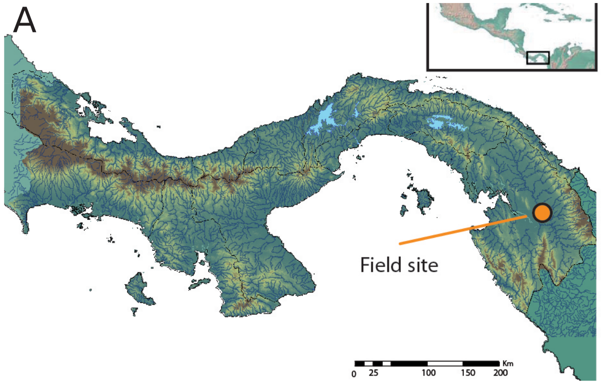
A: Ovoid cells: high-freq. response, slow GABA$_B$ output.

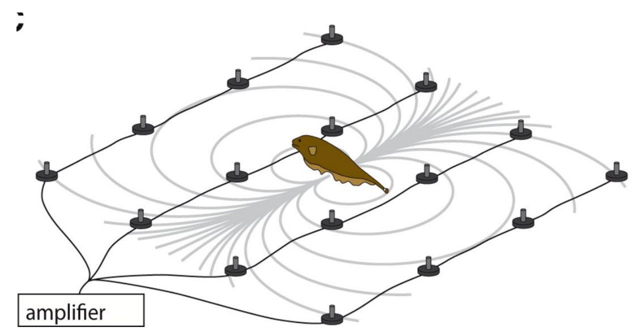


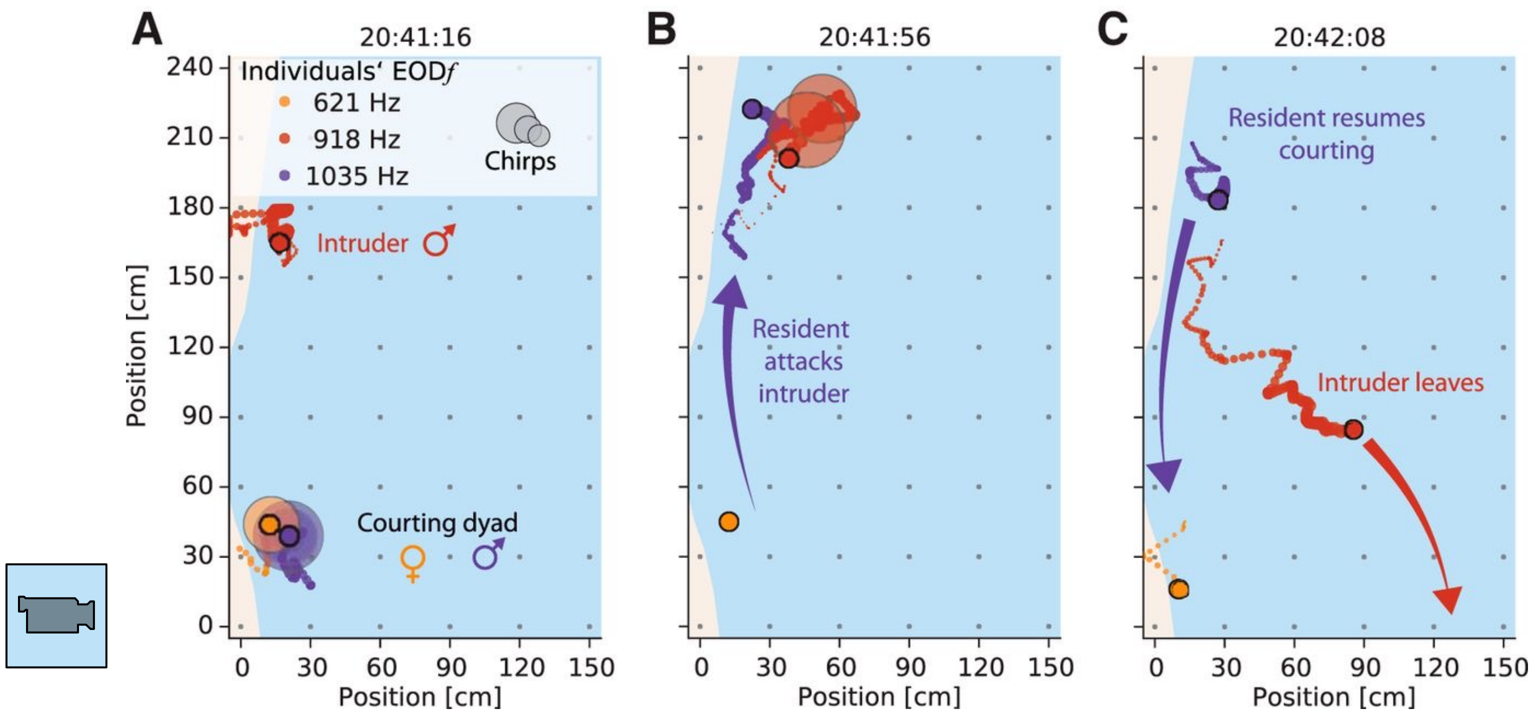


Middleton et al, PNAS 2006

Electrocommunication in the wild







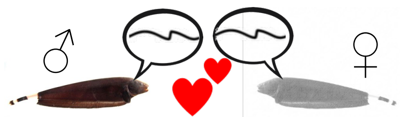
Henninger et al JNS 2018

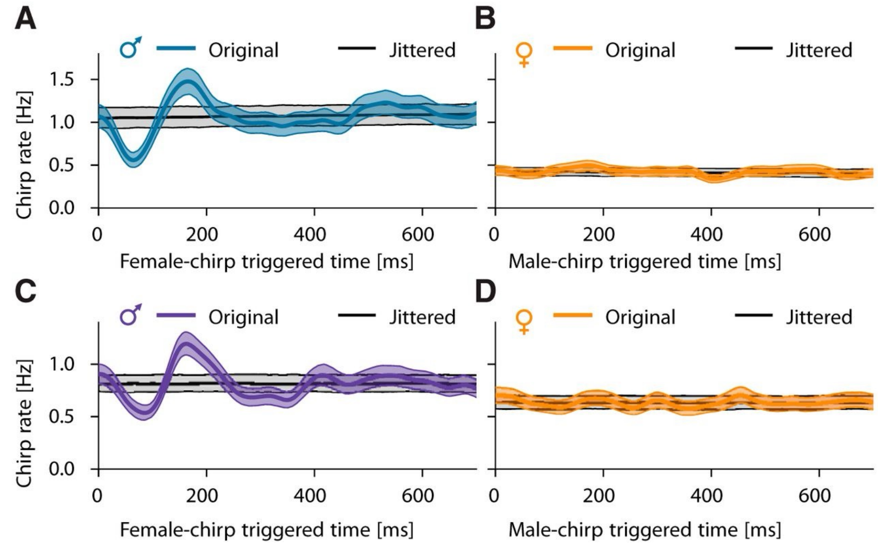
Electrocommunication in the wild

Small chirps:

Opposing sex (high freq beat)➢courtship

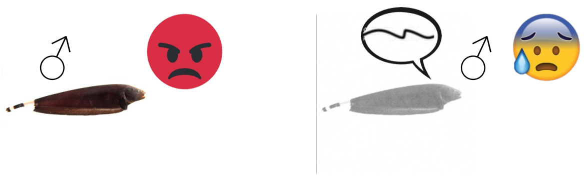
- Male echoes the female with precise latency





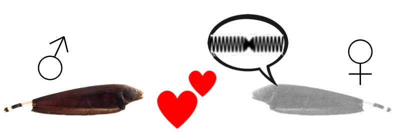
Same sex (low freq beat)➢submission

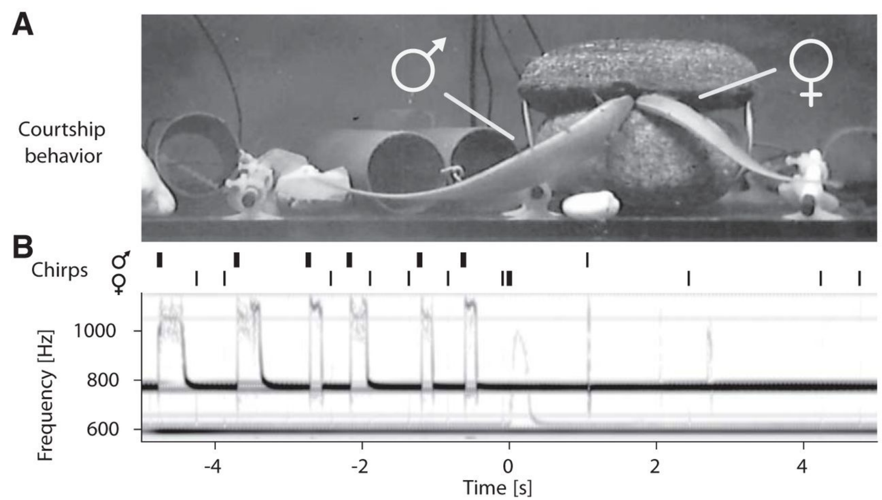
- Emitted by retreating intruder



Long chirps:

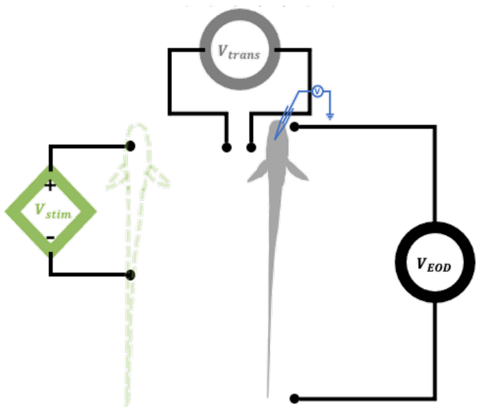
Courtship only ➢ female acceptance, spawning synchronization

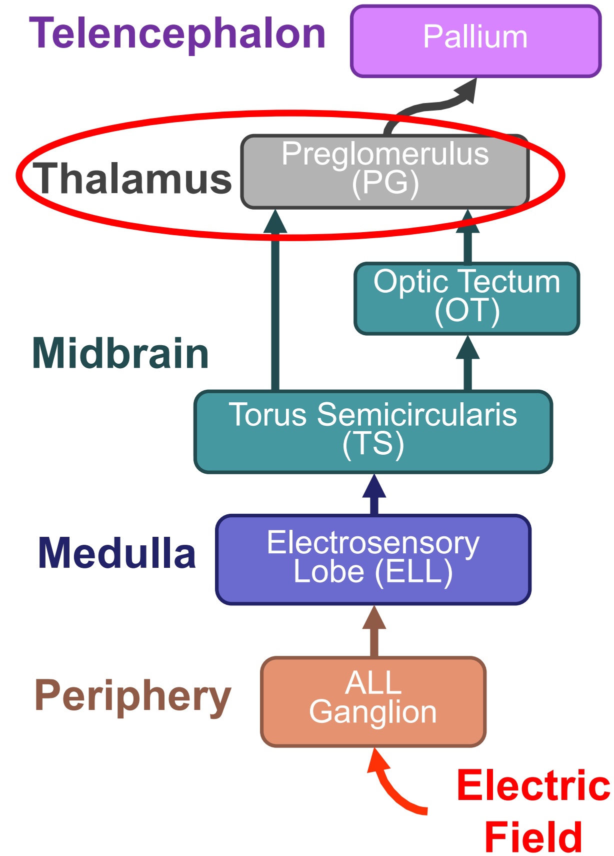


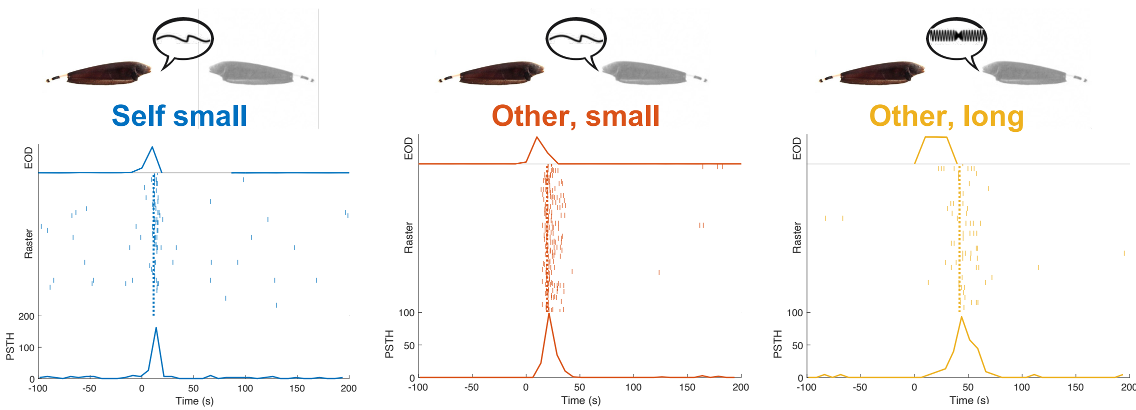


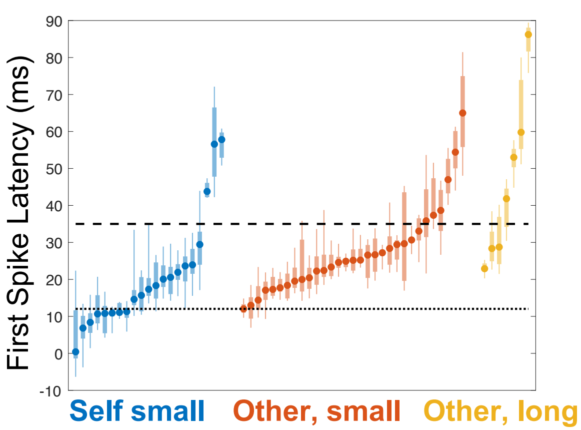
Henninger et al JNS 2018

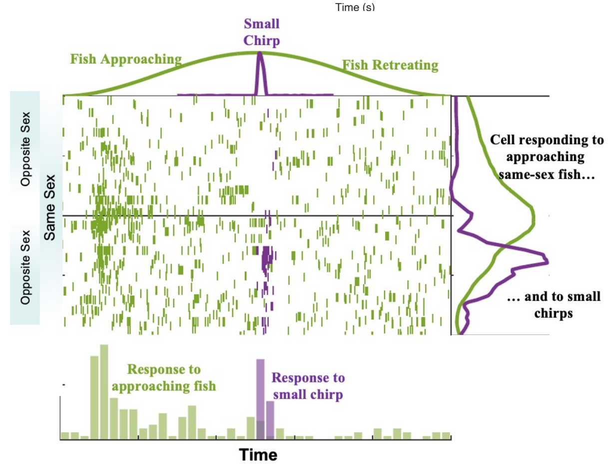
Thalamic Representation of Electrocommunication











Wallach et al, Curr. Bio. 2022

Pros and Cons of Electric Fish as an experimental system

Pros

- Convergent evolution
- Relatively few ethical constraints
- Low-dimensional behavior- easy to record and interpret
- Easy to mimic
- Easy to model
- Tractable neural circuitry
- Analogous to other modalities
- Highly-developed brain

Cons

- High-tech methods (imaging, genetics etc) are less-developed
- Captive breeding is challenging.
- Lives underwater…