

Introduction to Neuroscience: Behavioral Neuroscience

- * Introduction to Neuroethology
- * Electrolocation in weakly-electric fish

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Outline of today's lecture

- **A primer on neurons and their activity**
- **Some principles of neuroethology**
- **Example system 1: Electrolocation in weakly-electric fish**
 - **Primer**

Outline of today's lecture

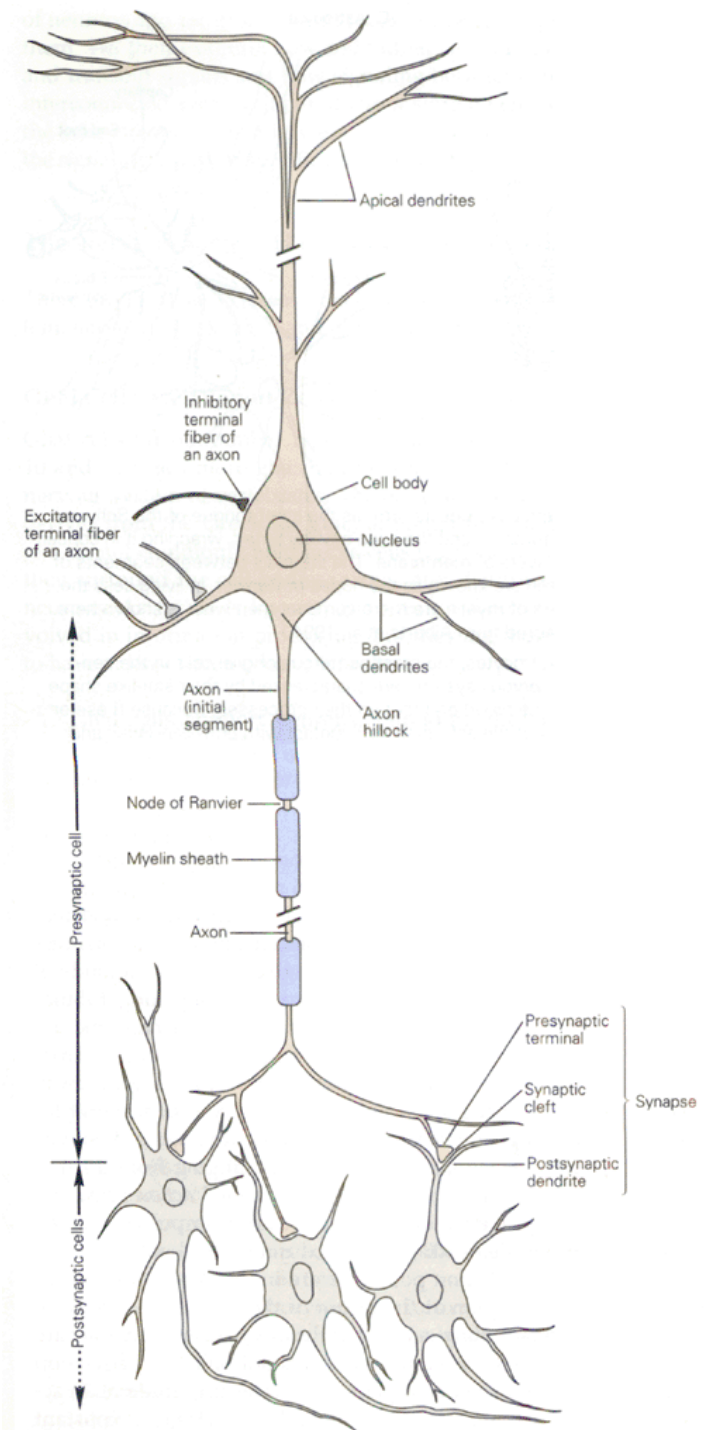
- **A primer on neurons and their activity**
- Some principles of neuroethology
- Example system 1: Electrolocation in weakly-electric fish

*These topics are expanded in the courses “**Intro to Neuroscience: Cellular and synaptic physiology**” (last semester) and “**Intro to Neuroscience: Systems Neuroscience**” (next year)*

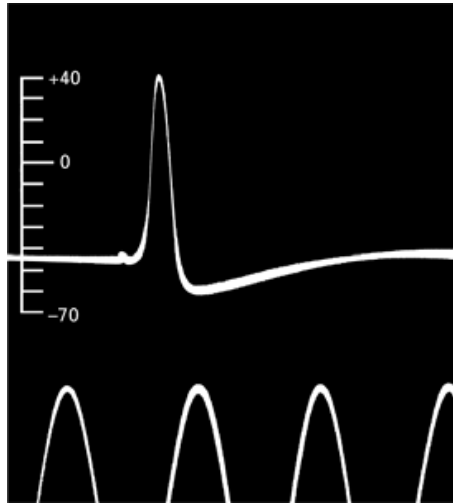
The structure of a neuron

Some basic terms:

- Cell body (soma)
- Dendrite
- Dendritic tree
- Axon
- Axon hillock
- Nodes of Ranvier
- Action potential (spike)
- Synapse



Neurons communicate with action potentials (spikes) *(with some exceptions in invertebrate brains)*

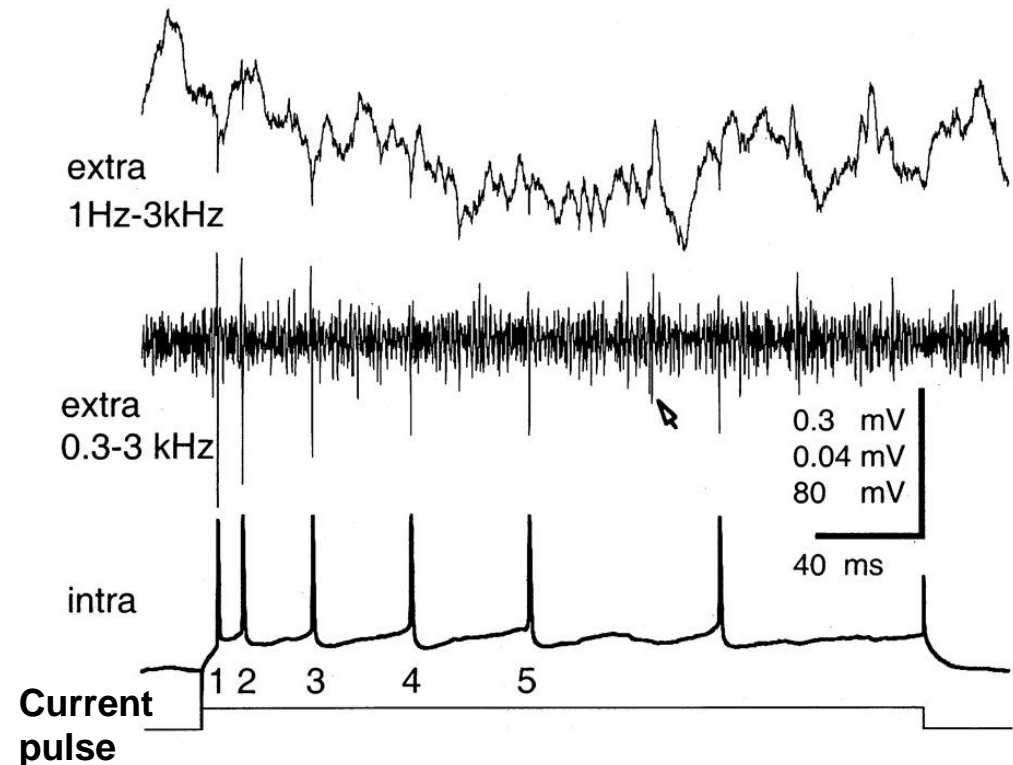


First published action potential (Hodgkin & Huxley 1939)

500 Hz sine wave (time marker)

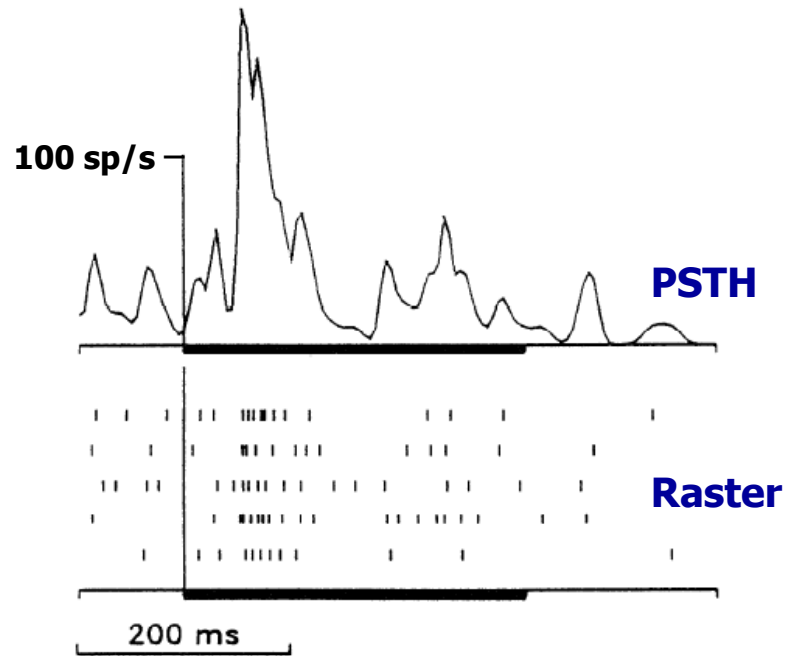
Some basic terms:

- Action potential (spike)
- Depolarization
- Hyperpolarization
- Intracellular recordings vs. Extracellular recordings

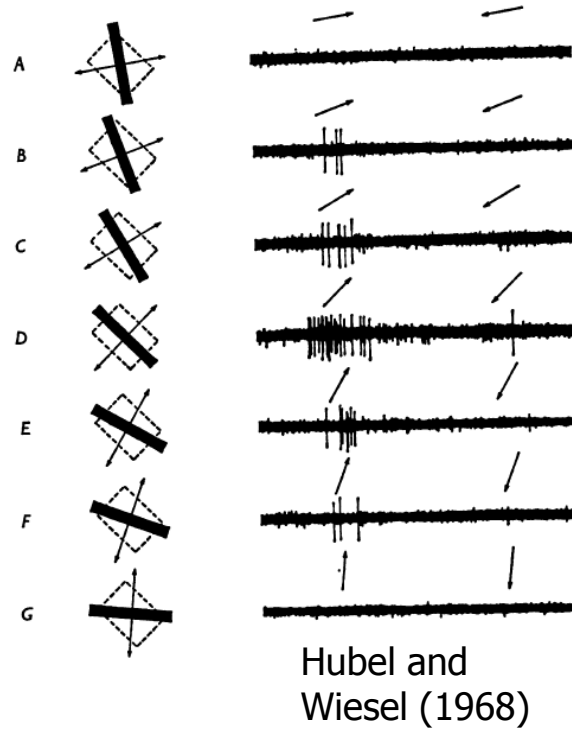


Henze et al. (2000)

Sensory neurons respond to stimuli with changes in firing-rate



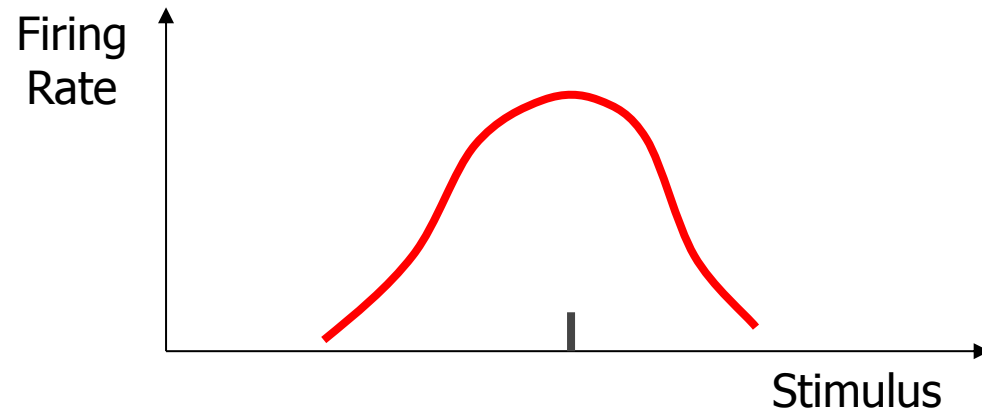
Richmond et al. (1990)
Responses of a V1 neuron
to complex patterns



Hubel and
Wiesel (1968)

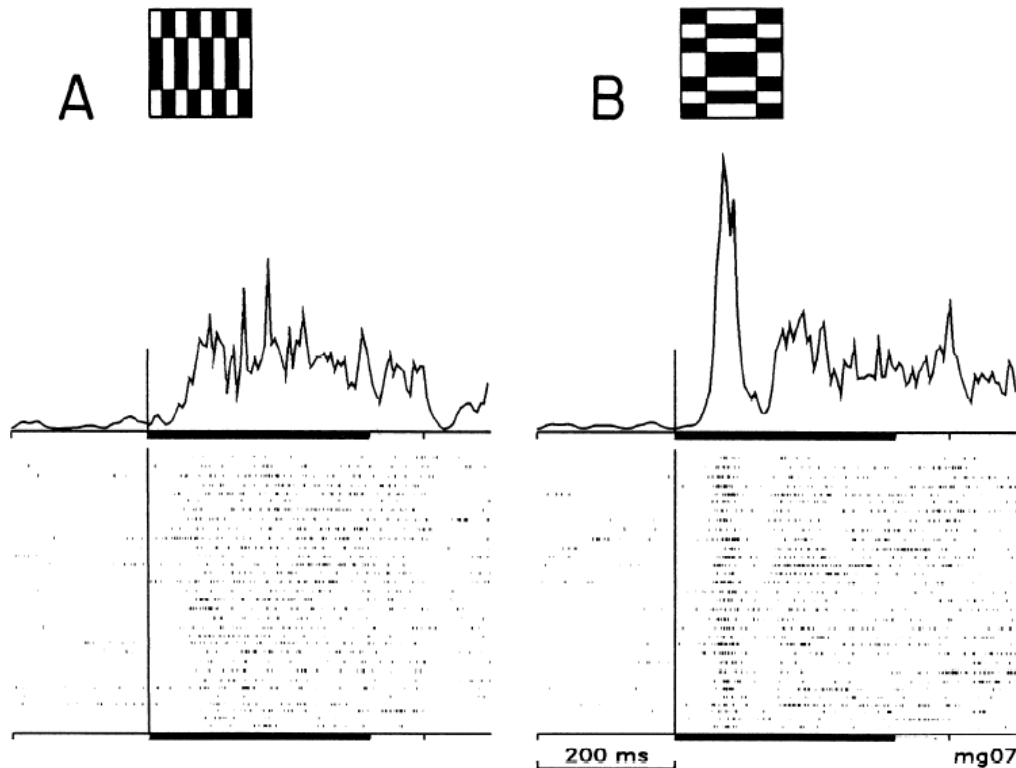
Some basic terms:

- Trial (of an experiment)
- Raster display of spikes
- Peri-stimulus time histogram (PSTH)
- Receptive field
- Tuning curve
- Best stimulus



Neurons may also use other neural codes

Temporal Coding: Example of one V1 neuron that responds with different temporal patterns to two stimuli

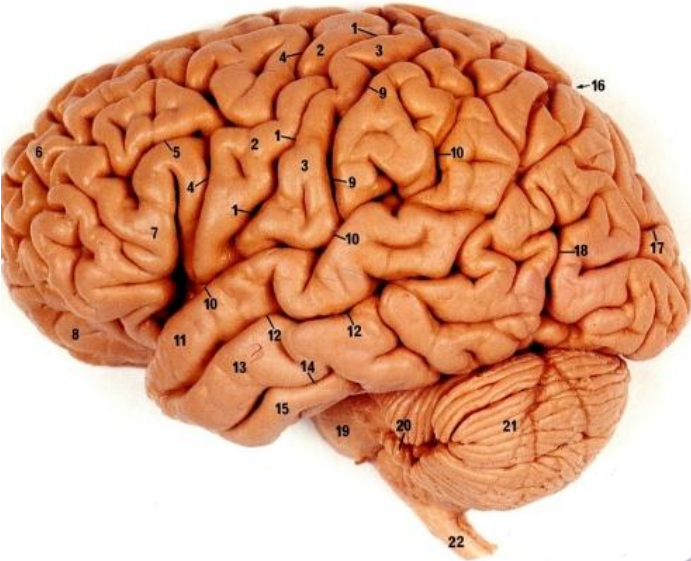


Richmond et al. (1990)

Some basic terms:

- Neural codes:
 - Rate code
 - Temporal code
 - Synchrony code
 - Labeled-line code
 - Other codes

Anatomy of a vertebrate brain



Beaver brain

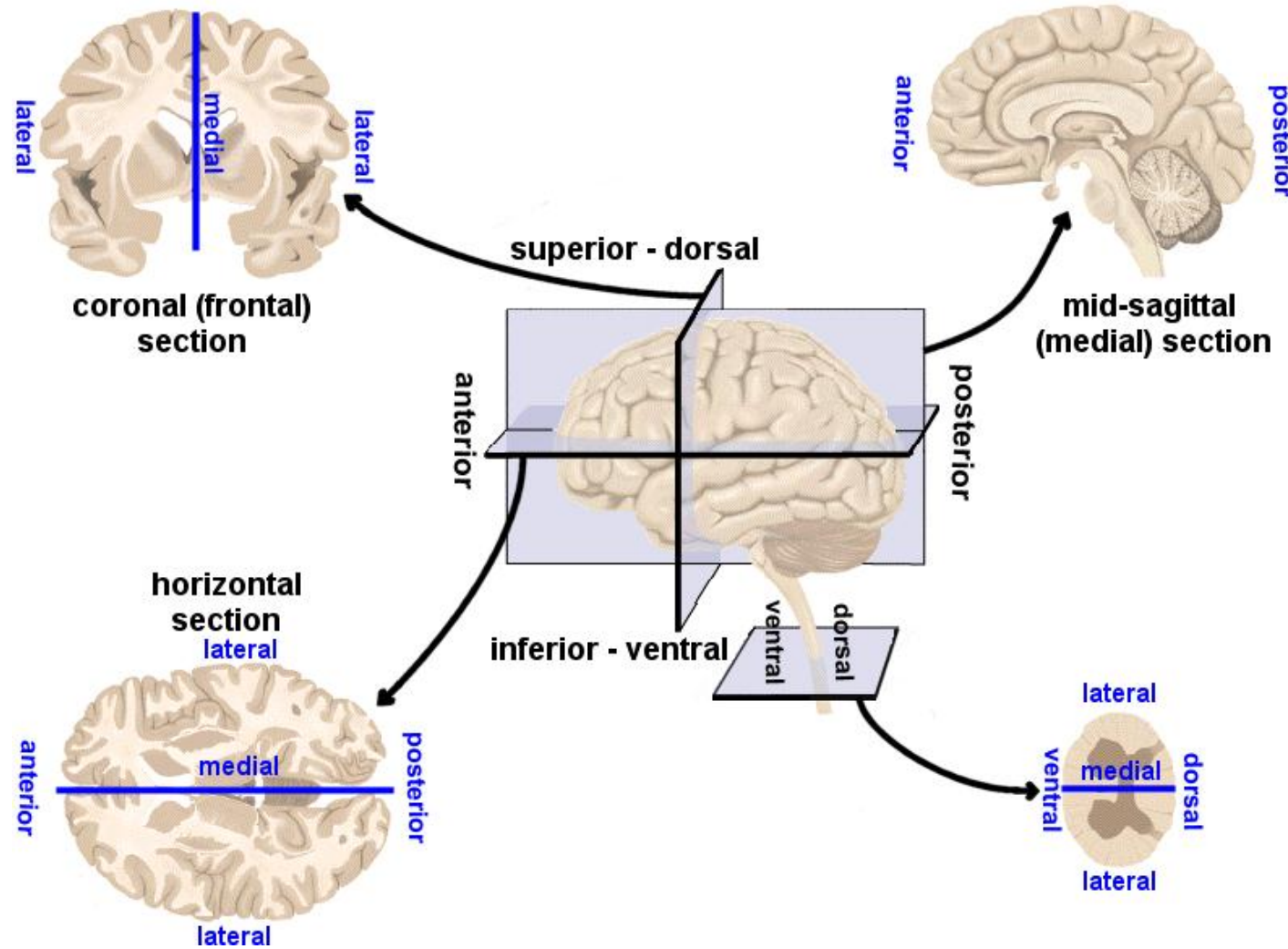


Some basic terms:

- Nucleus
- Gray matter / white matter
- Cortex (only in mammals)
- Sulcus, Gyrus
- Cerebellum
- Directions in the brain:
 - Dorsal/Ventral
 - Lateral/Medial
 - Anterior/Posterior
 - Rostral/Caudal

*These topics are expanded in the course
"Neuroanatomy" (every year)*

Anatomy of a vertebrate brain



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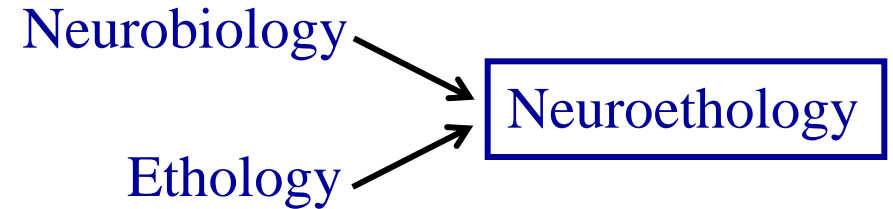
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- **Some principles of neuroethology**
- Example system 1: Electrolocation in weakly-electric fish

Principles of Neuroethology

Neuroethology seeks to understand the mechanisms by which the central nervous system controls the natural behavior of animals.



- **Focus on Natural behaviors:** Choosing to study a well-defined and reproducible yet natural behavior (either Innate or Learned behavior)
- **Need to study thoroughly the animal's behavior, including in the field:** Neuroethology starts with a good understanding of Ethology.
- **If you study the animals in the lab, you need to keep them in conditions as natural as possible,** to avoid the occurrence of unnatural behaviors.
- **Krogh's principle**

Krogh's principle

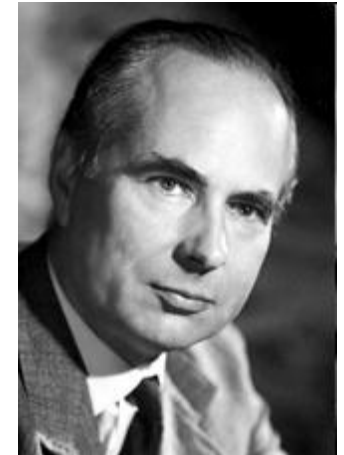


August Krogh
Nobel prize 1920

“For such a large number of problems there will be some animal of choice or a few such animals on which it can be most conveniently studied. Many years ago when my teacher, Christian Bohr, was interested in the respiratory mechanism of the lung and devised the method of studying the exchange through each lung separately, he found that a certain kind of tortoise possessed a trachea dividing into the main bronchi high up in the neck, and we used to say as a laboratory joke that this animal had been created expressly for the purposes of respiration physiology. I have no doubt that there is quite a number of animals which are similarly "created" for special physiological purposes, but I am afraid that most of them are unknown to the men for whom they were "created," and we must apply to the zoologists to find them and lay our hands on them.” (Krogh, 1929)

Krogh's principle and Neuroscience research

Studying the giant axon of the squid in order to understand mechanisms of action-potential generation



Alan Hodgkin Andrew Huxley
Nobel prize 1963

Q: Why was this species chosen?

A: Because of the huge **size** of its axon (~ 1 mm diameter), which allowed using macro-wires for recording electrical potentials - and doing voltage clamp.



Krogh's principle and Neuroscience research

Studying the frog neuromuscular junction in order to understand the physiology of synaptic transmission



Q: Why was this species chosen?

A: Because of the **size** of this synapse (end-plate) and the **simplicity** of the reflex circuit involved.



Sir John Eccles
Nobel prize
1963



Sir Bernard Katz
Nobel prize
1970



Krogh's principle and Neuroscience research

Studying the *Limulus* (horseshoe crab) retina in order to understand visual processing; discovery of the phenomenon of lateral inhibition



Haldan Hartline
Nobel prize 1967



Q: Why was this species chosen?

A: Because horseshoe crabs have long optic nerves that can be physically **split** to record from individual nerve fibers; and the retina circuitry is **simple**: the compound eye has one photoreceptor under each ommatidium, which facilitates the study of lateral inhibition

Krogh's principle and Neuroscience research

Studying the neurobiology of learning and memory in *Aplysia*



Eric Kandel
Nobel prize 2000

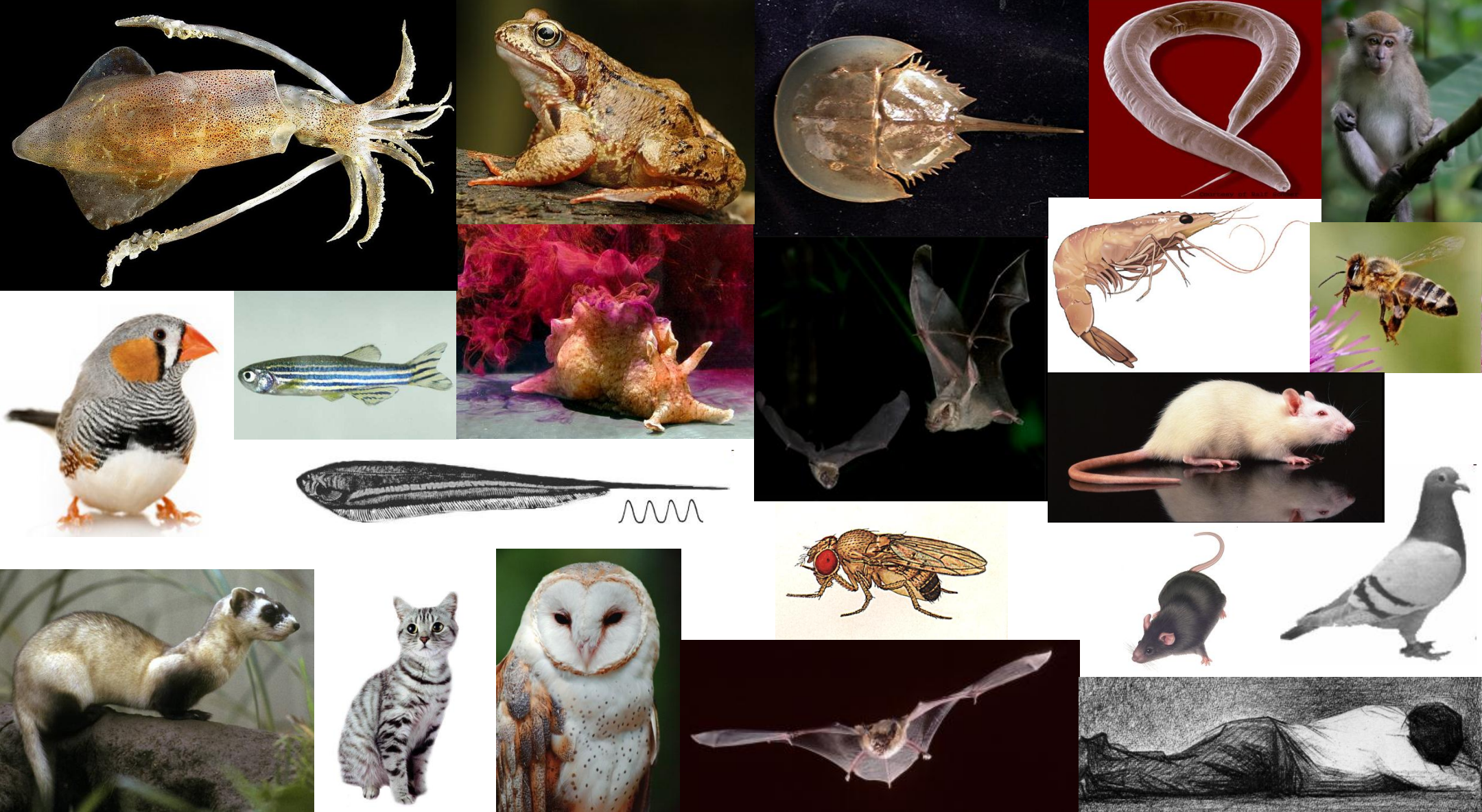
Q: Why was this species chosen?

A: Because of the **size** of its **identified** neurons; and not least importantly, because of the animal's robust **behaviors** (e.g. sensitization; or classical conditioning of the gill withdrawal reflex)



Some commonly used animal models in Neuroscience:

Past and Present *(Not showing less common species)*



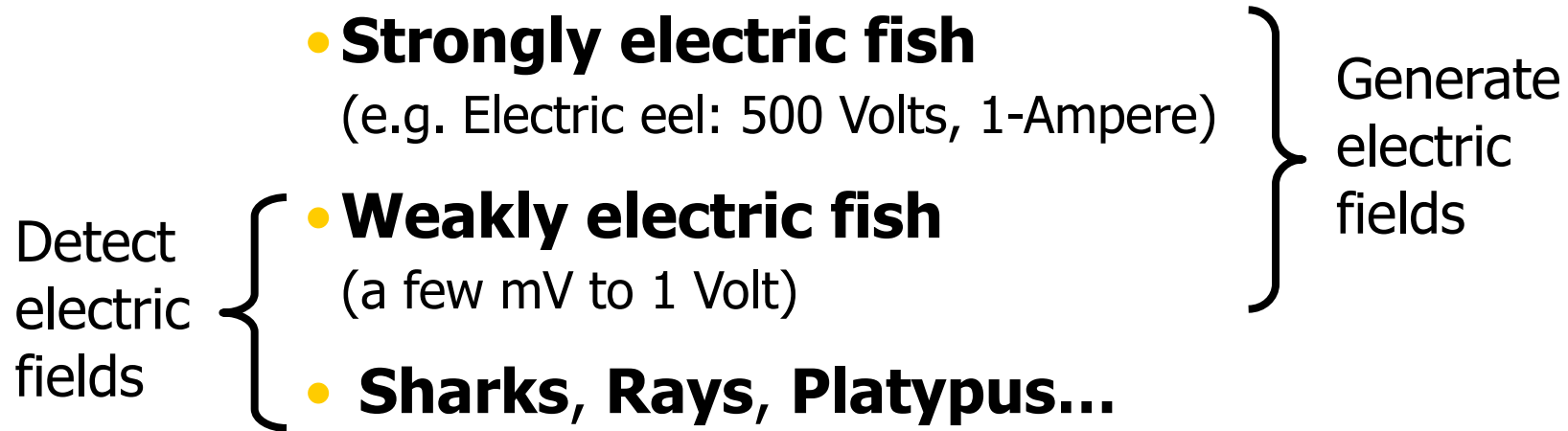
Krogh's principle vs. "standard animal models"

- **A corollary of Krogh's Principle – as viewed by Neuroethologists:**
You should choose the animal species that best fits your research question (fits either in terms of the animal's *behavior* or for technical reasons) – i.e., choose well your animal model – rather than studying all the possible questions using just a few "standard animal model species" (e.g., mouse, drosophila).
- **Advantages of "Standard animal models":** So much is known about their brains... Therefore, many people prefer this knowledge-base over Krogh's principle. Additionally, there are very powerful experimental tools available for these animals (particularly molecular tools).

Outline of today's lecture

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- **Example system 1: Electrolocation in weakly-electric fish**
[Electrolocation material is based primarily on the book:
Behavioral Neurobiology: An Integrative Approach, Zupanc (2004)]

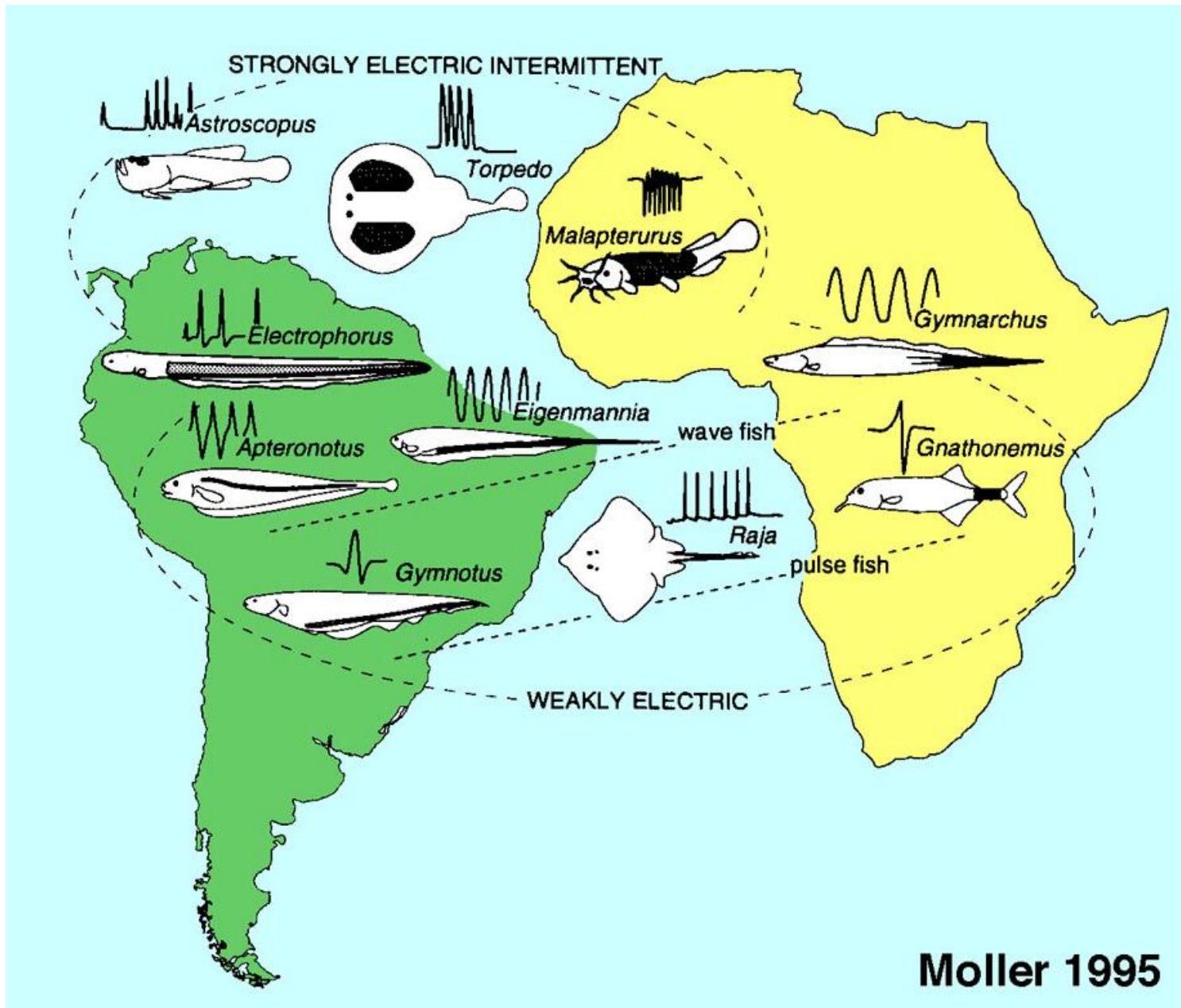
Fish and electric fields (and among mammals: *Platypus*)



Weakly electric fish **generate** and **detect** electric fields, and use this ability to localize objects in the environment: **Electrolocation.**

* A recent study by Kenneth Catania showed that electric eels cause involuntary muscle contraction in prey, in order to discover (via somatosensation) where the prey is hiding – and then launch a full attack on the prey (Catania, *Science* 2014).

Wave-type and Pulse-type weakly electric fish



Moller 1995

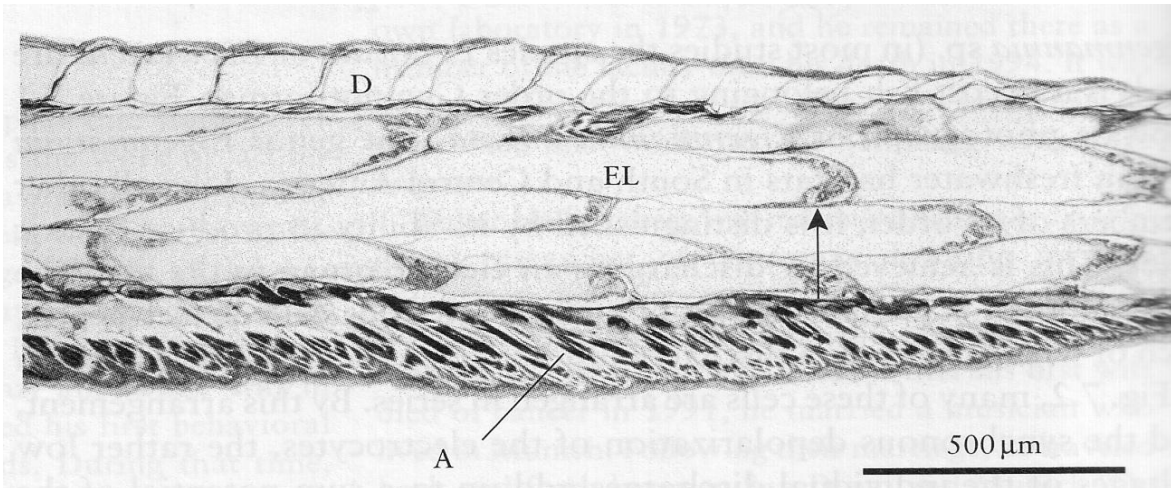
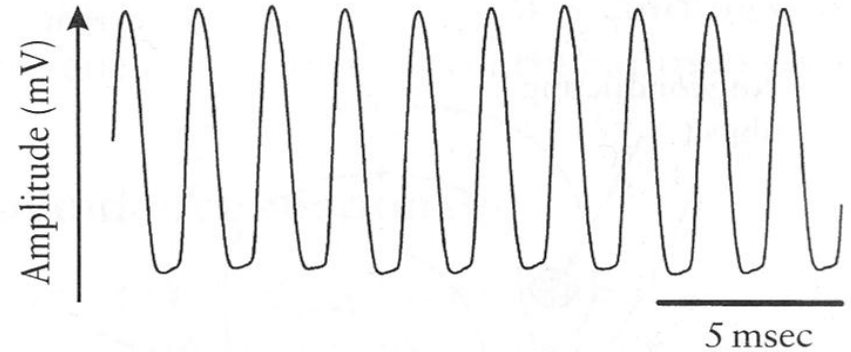
Why is it a good model system?

- **Animal model for sensory-motor integration:** Weakly electric fish are good animal model because sensory-motor integration is a closed-loop system (feedback system), and studying it requires “**opening the loop**” – which is possible in weakly electric fish (see next slides)
- **The Electric Organ Discharge (EOD) in *Eigenmannia* is the most stable biological oscillator in nature:** Hence it’s a good model system for studying questions of *neural coding*: temporal coding, rate coding, spike time variability, information transmission...
- **All sensory information to higher brain areas is funneled through a *single obligatory thalamic relay station*:** Simplicity.

Electric Organ Discharge

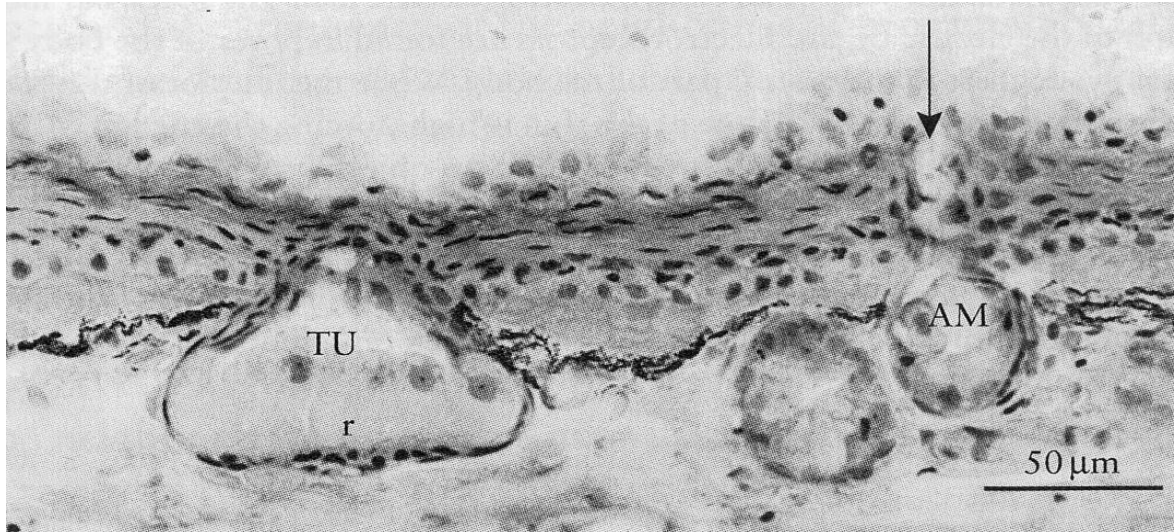


Eigenmannia virescens



EL cells – modified muscle cells
(in strongly electric fish they are stacked in series, so voltages can sum up to hundreds of volts)

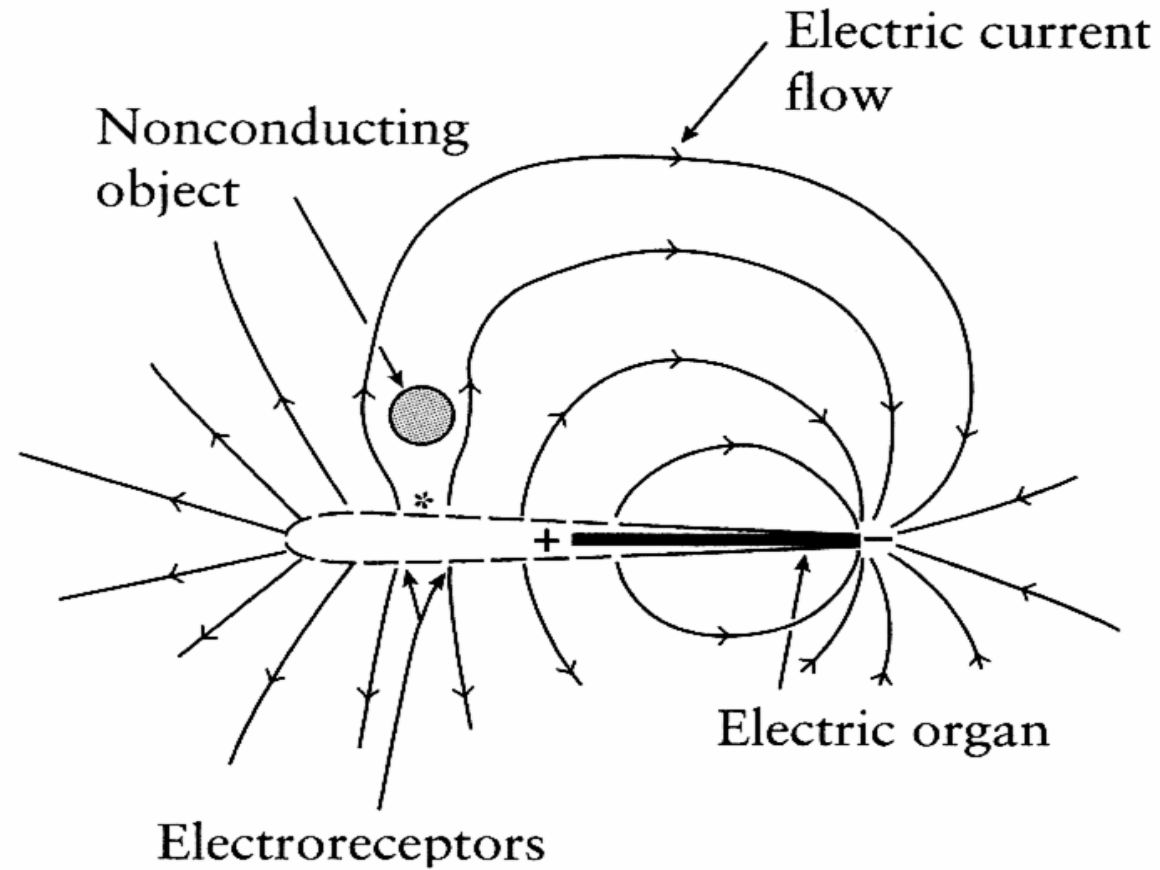
Electroreceptors



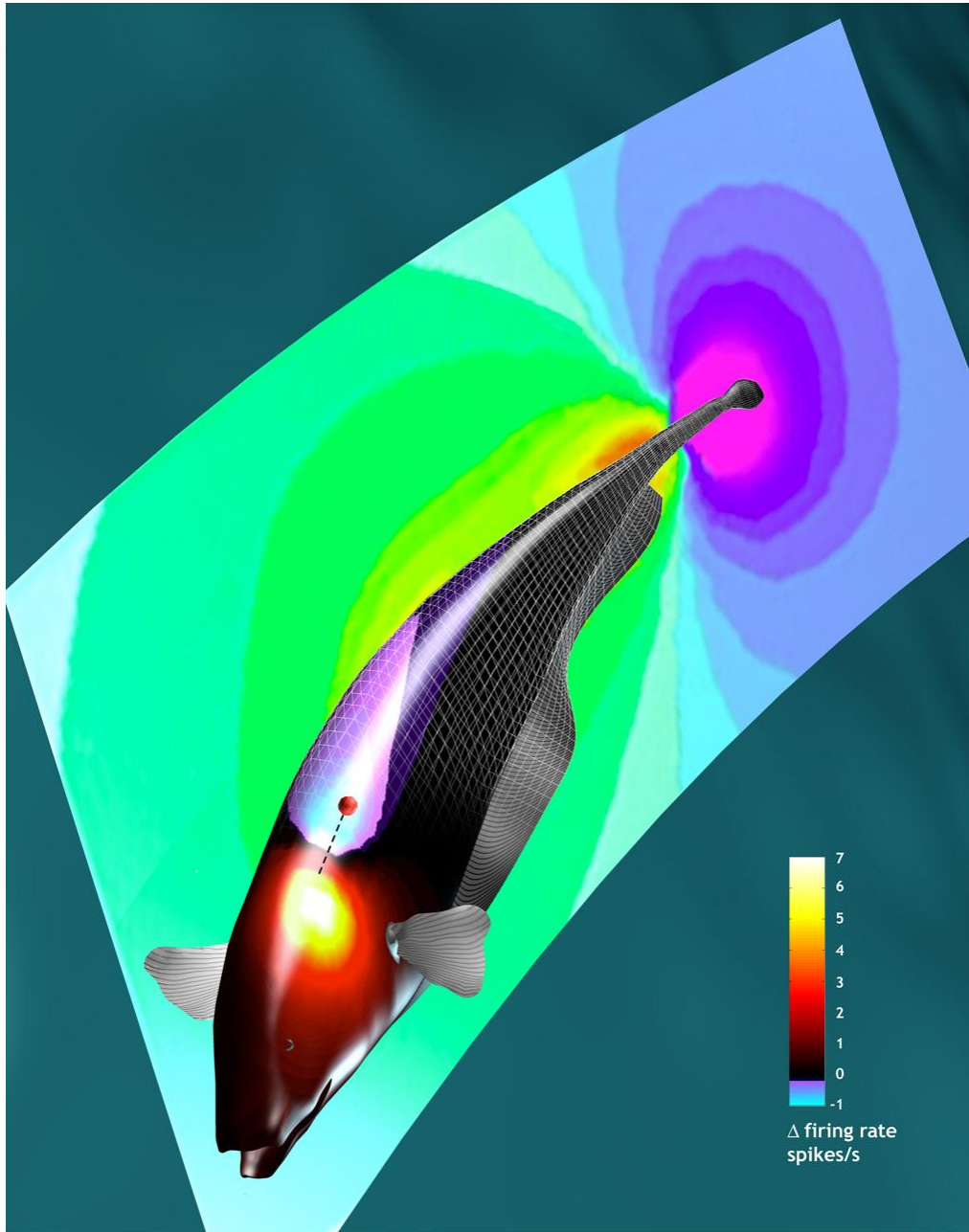
TU – Tuberous receptors (sensitive to high frequencies - most important for electrolocation). Each Tuberous receptor sends 1 axon to the brain.

AM – Ampullary receptors.

Electrolocation: putting production and reception together



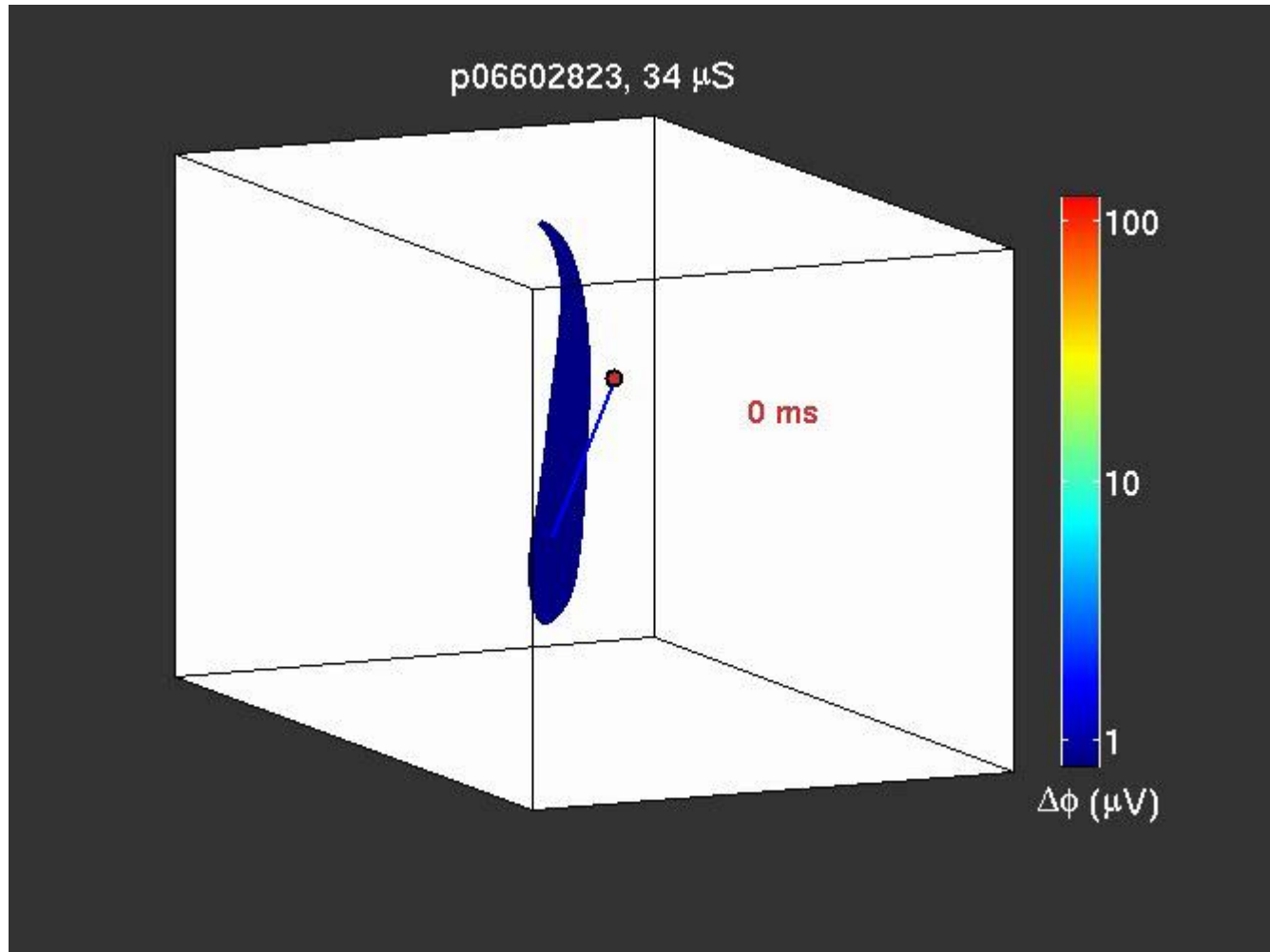
Electrolocation: putting production and reception together



Shown is the EOD dipole, as well as a false-color map on the skin indicating the change in firing-rate in sensory neurons (tuberous electroreceptors) caused by the presence of a small target (red dot).

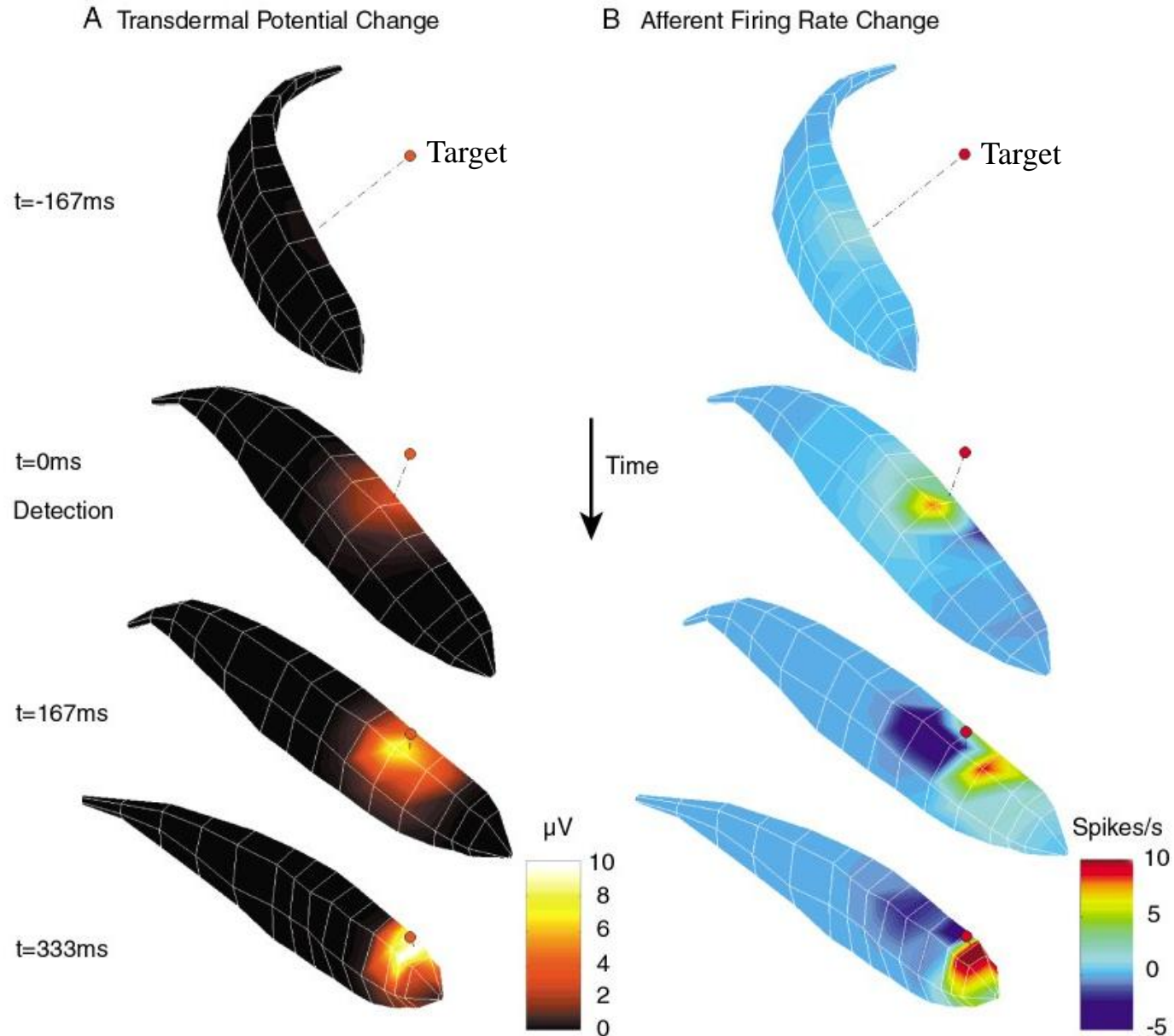
Electrolocation as Imaging:
The entire body surface of the fish is used for imaging the presence of conducting objects ("labeled-line code").

Electrolocation: putting production and reception together

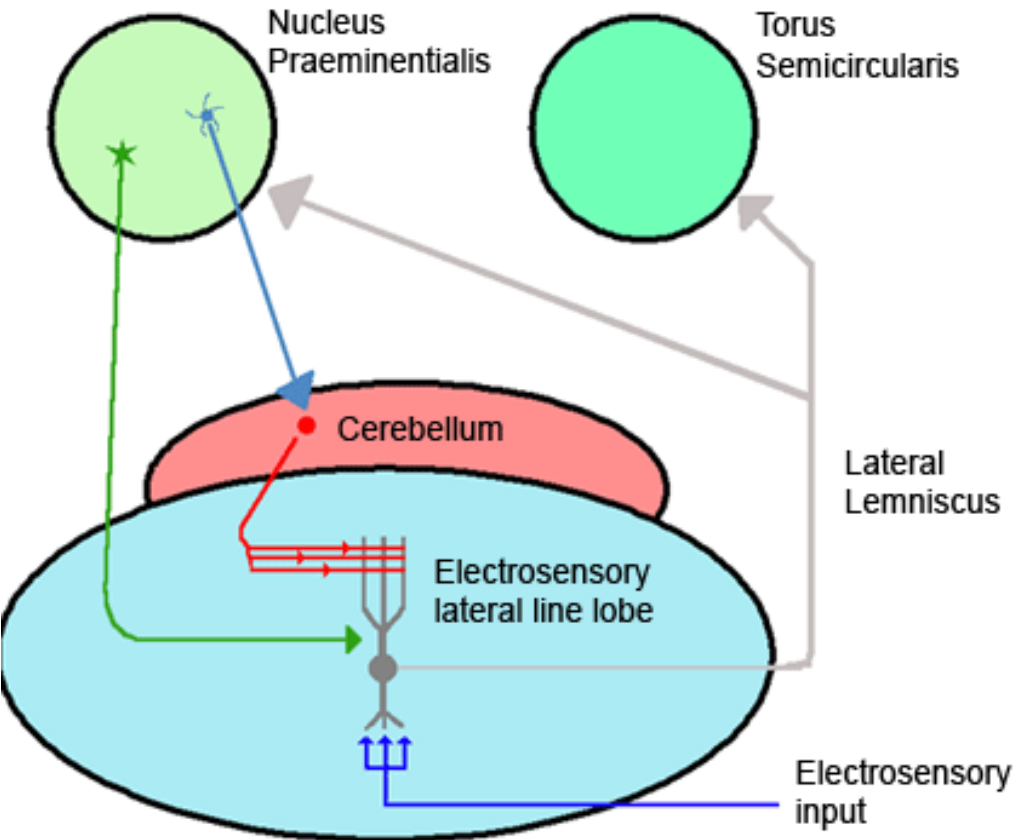


Simulation of weakly electric fish prey capture
(*Movie: Malcolm MacIver*)

Electrolocation: putting production and reception together



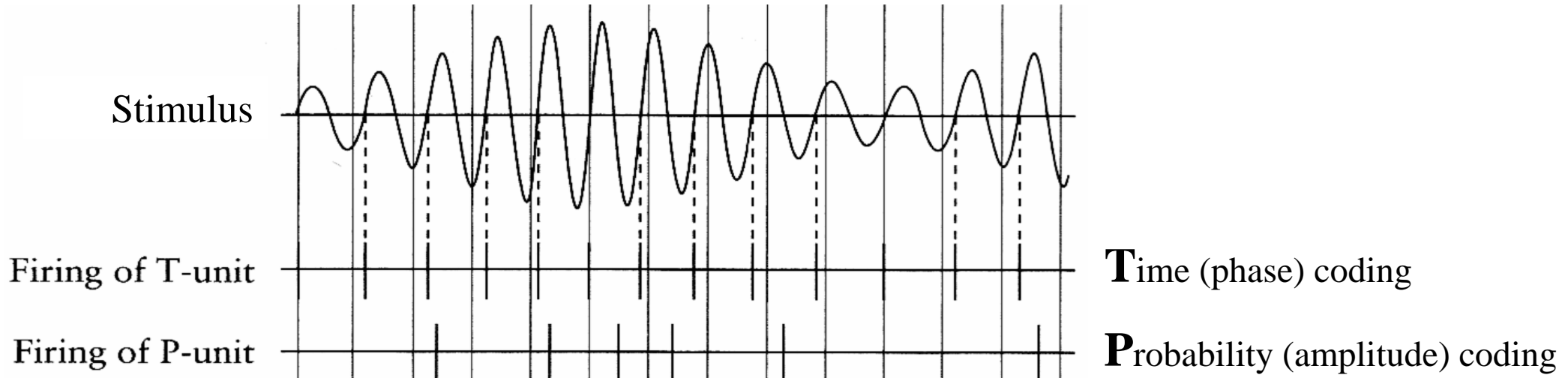
Cancellation of redundant stimuli by “negative image”



Electrosensory signals from electroreceptor afferents are cancelled by a “negative image” provided by feedback input – this is needed to eliminate the *huge* changes in received EOD due to changes in the animal’s posture during behavior → Thus, the afferents respond only to real targets in the environment.

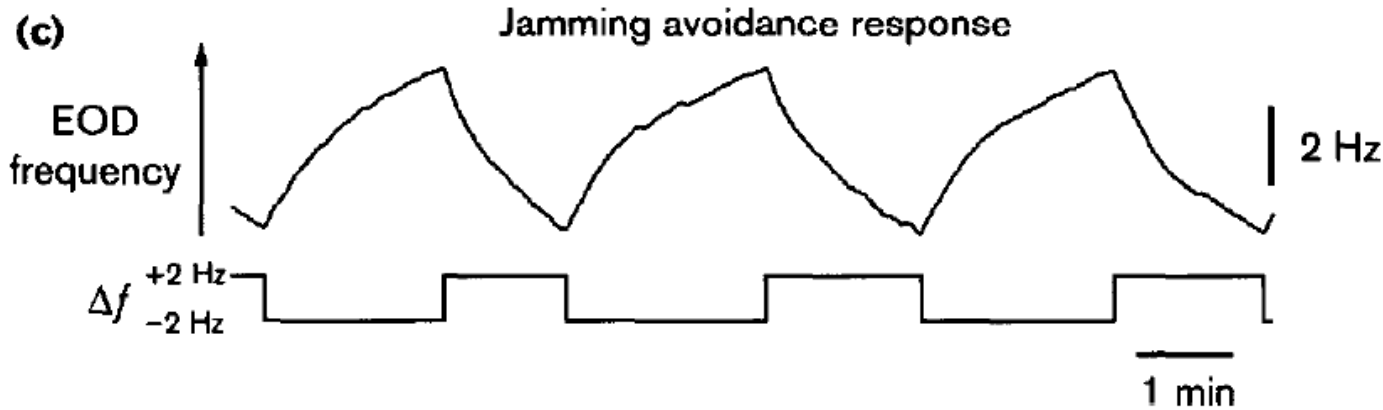
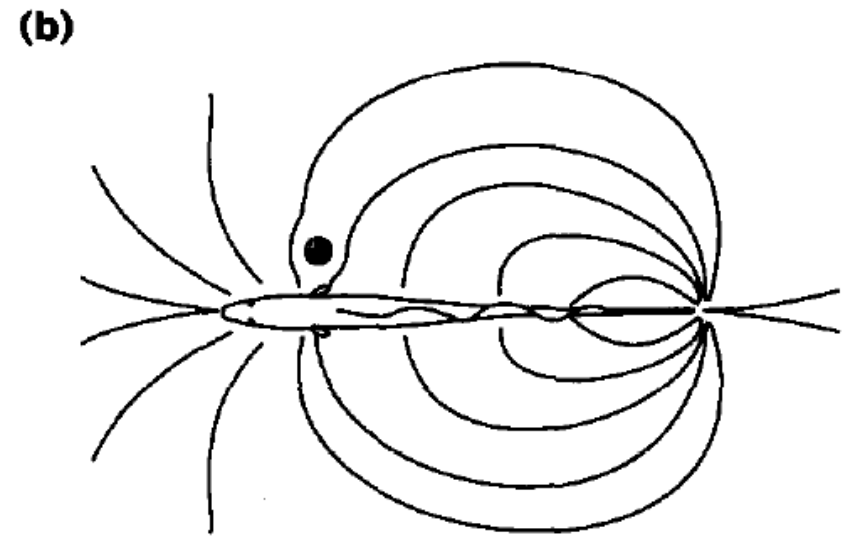
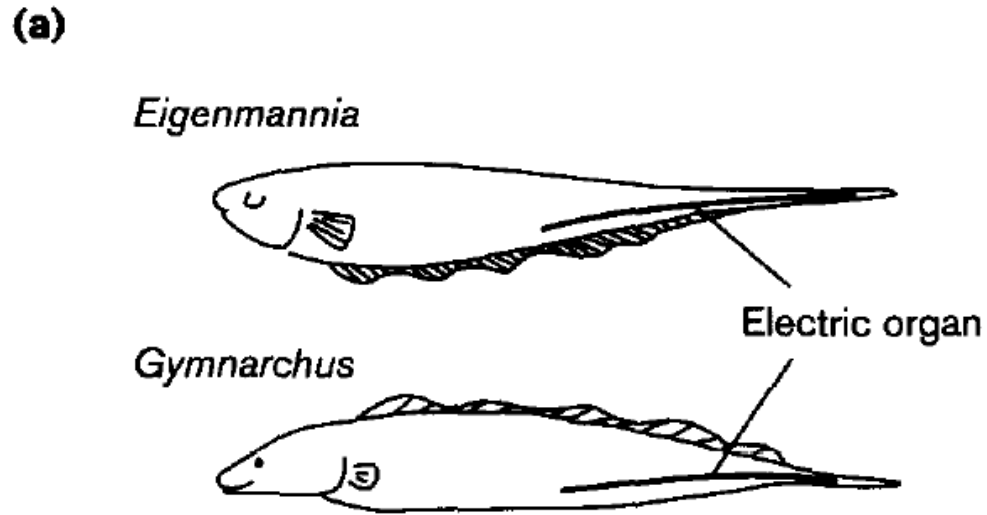
* The cerebellum is suggested to play a key role in this negative-image cancellation. Interestingly, the cerebellum of weakly electric fish has a *huge* size → Clue to the function of vertebrate cerebellum ??

Two type of electroreceptors encode time and amplitude



Behaviorally, weakly electric fish can detect **amplitude** changes $< 0.1\%$ in the input signal, and **temporal** changes $< 1 \mu\text{s}$.

Jamming Avoidance Response (JAR) in wave-type fish

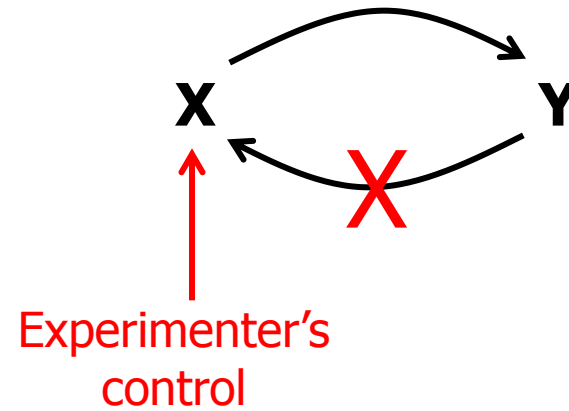


$$\Delta f = f_2 - f_1$$

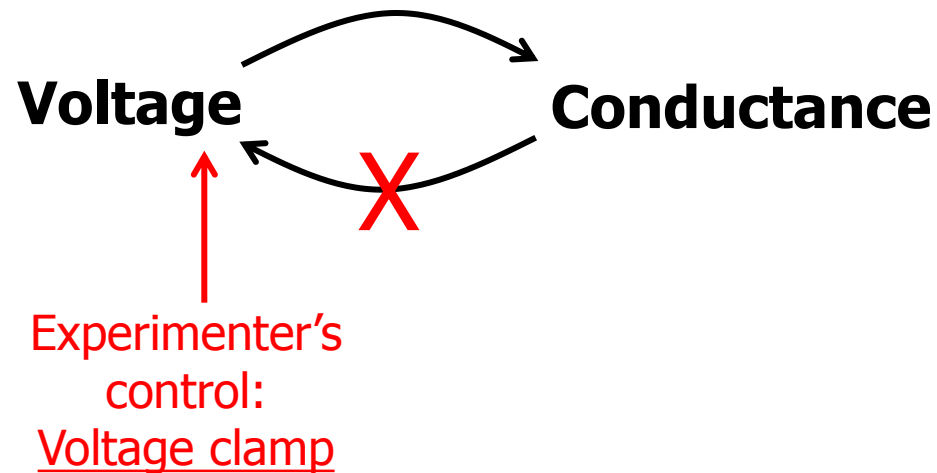
f_1 : fish's own EOD frequency

f_2 : neighbor's EOD frequency

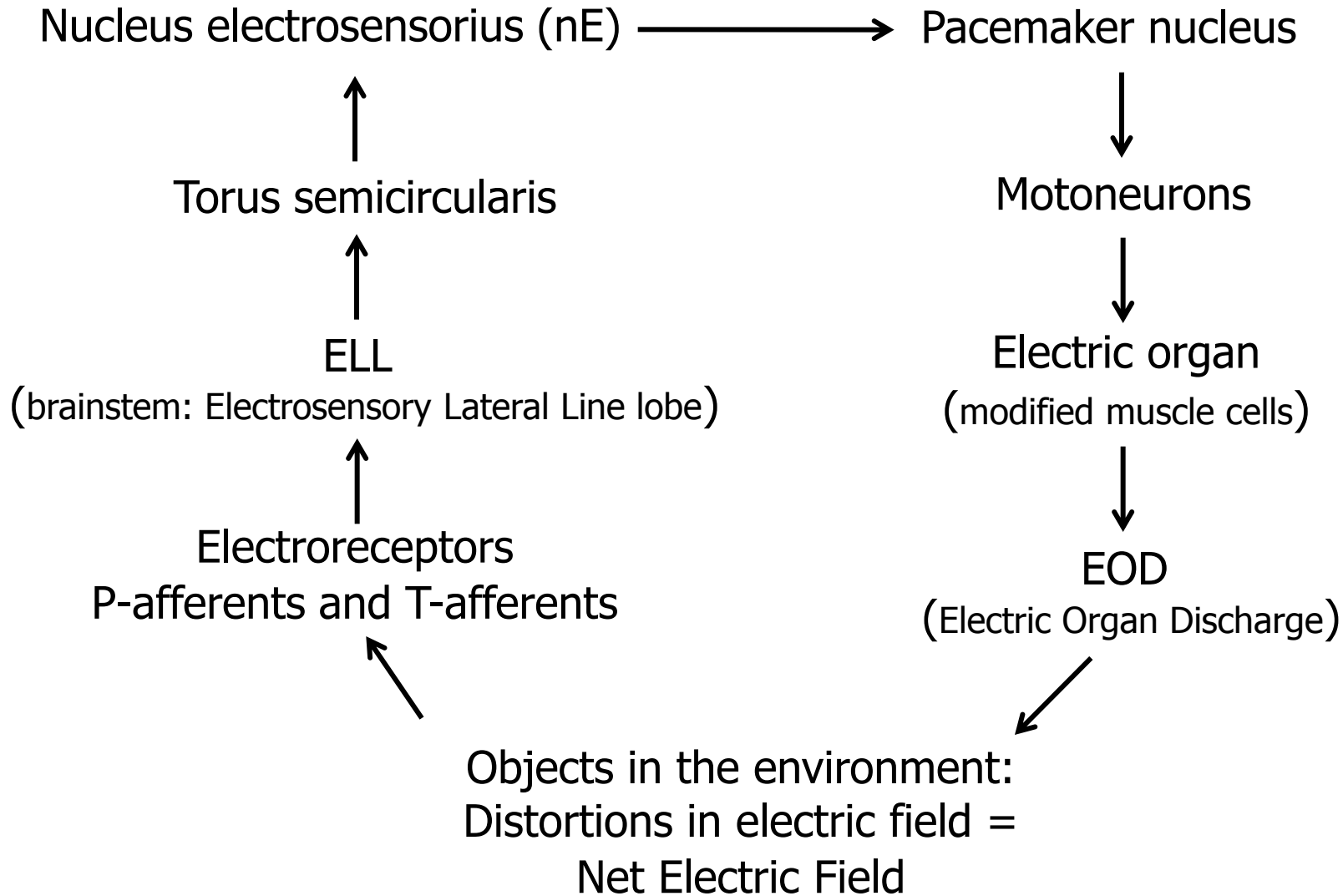
The concept of “opening the loop” in biological feedback systems



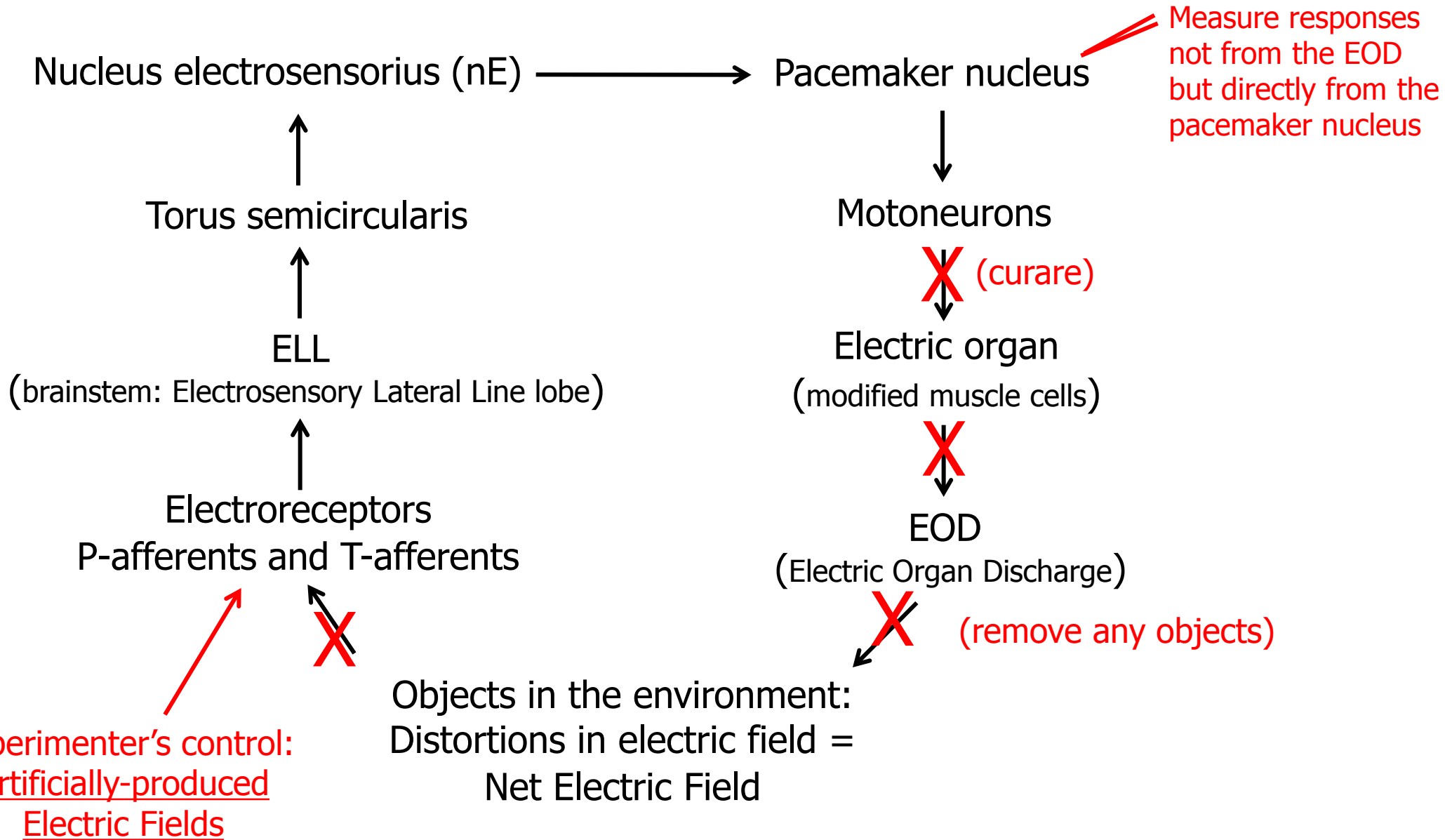
Example: Hodgkin & Huxley's elucidation of the mechanism of action potential generation



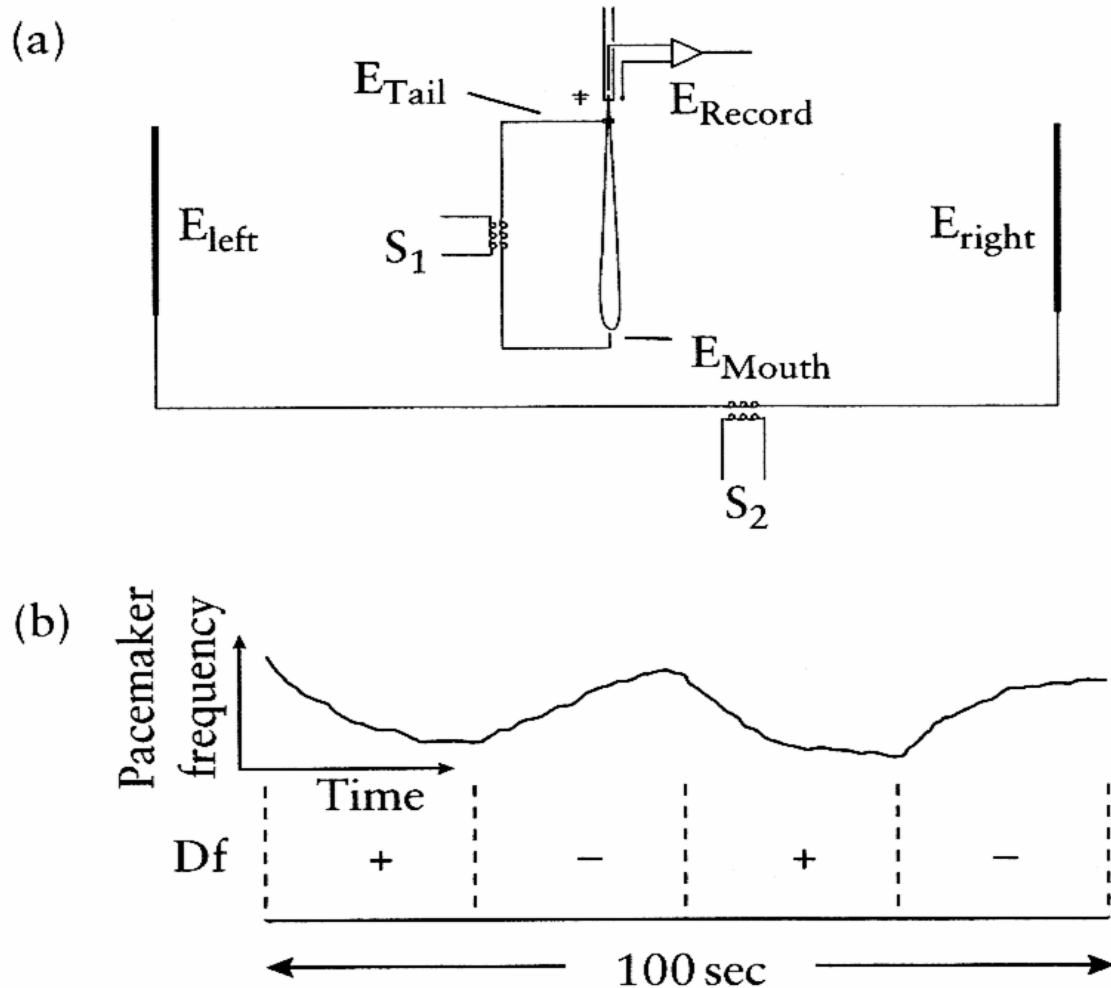
The concept of “opening the loop” in the Jamming Avoidance Response



The concept of "opening the loop" in the Jamming Avoidance Response



Eigenmannia do NOT compute the sign of Δf by comparing the sensory stimulus to the motor production

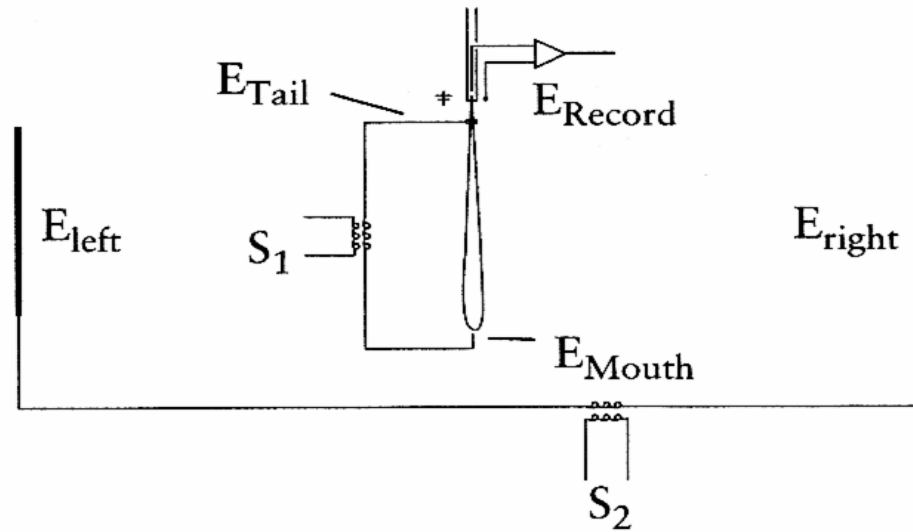


JAR is still present after blocking the EOD with curare and replacing it with artificial "self-produced" signal \rightarrow hence, JAR is purely sensory-based.



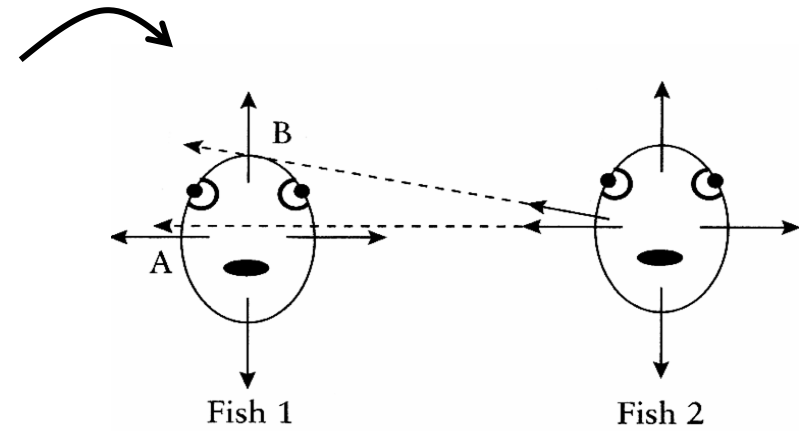
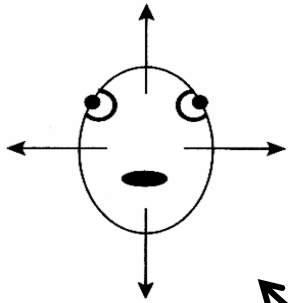
This is "opening the loop", because curare does NOT affect the pacemaker nucleus in the fish's medulla, which continues to oscillate normally and whose firing exhibits JAR

Natural geometry (two separate sources) is important for JAR

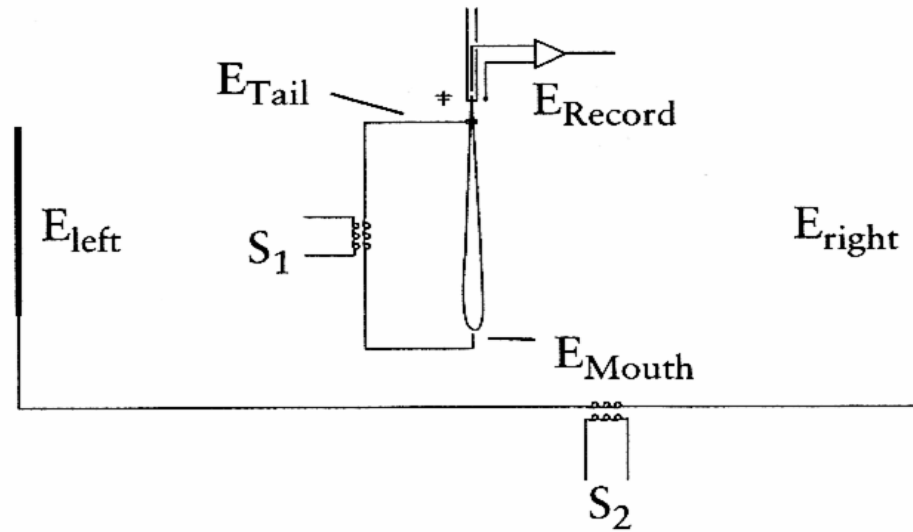


- If the two signals, S_1 and S_2 , are spatially separate sources – JAR is normal.

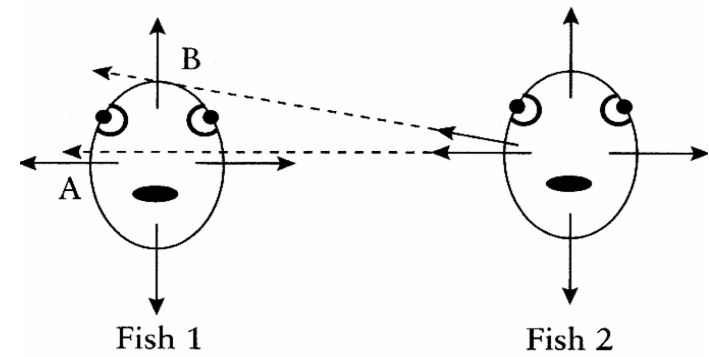
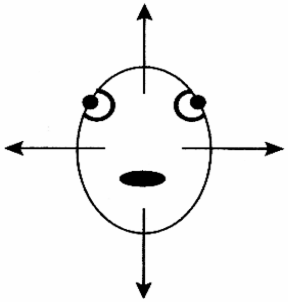
- If the two signals are added S_1+S_2 but this sum is presented from one location – no JAR occurs.



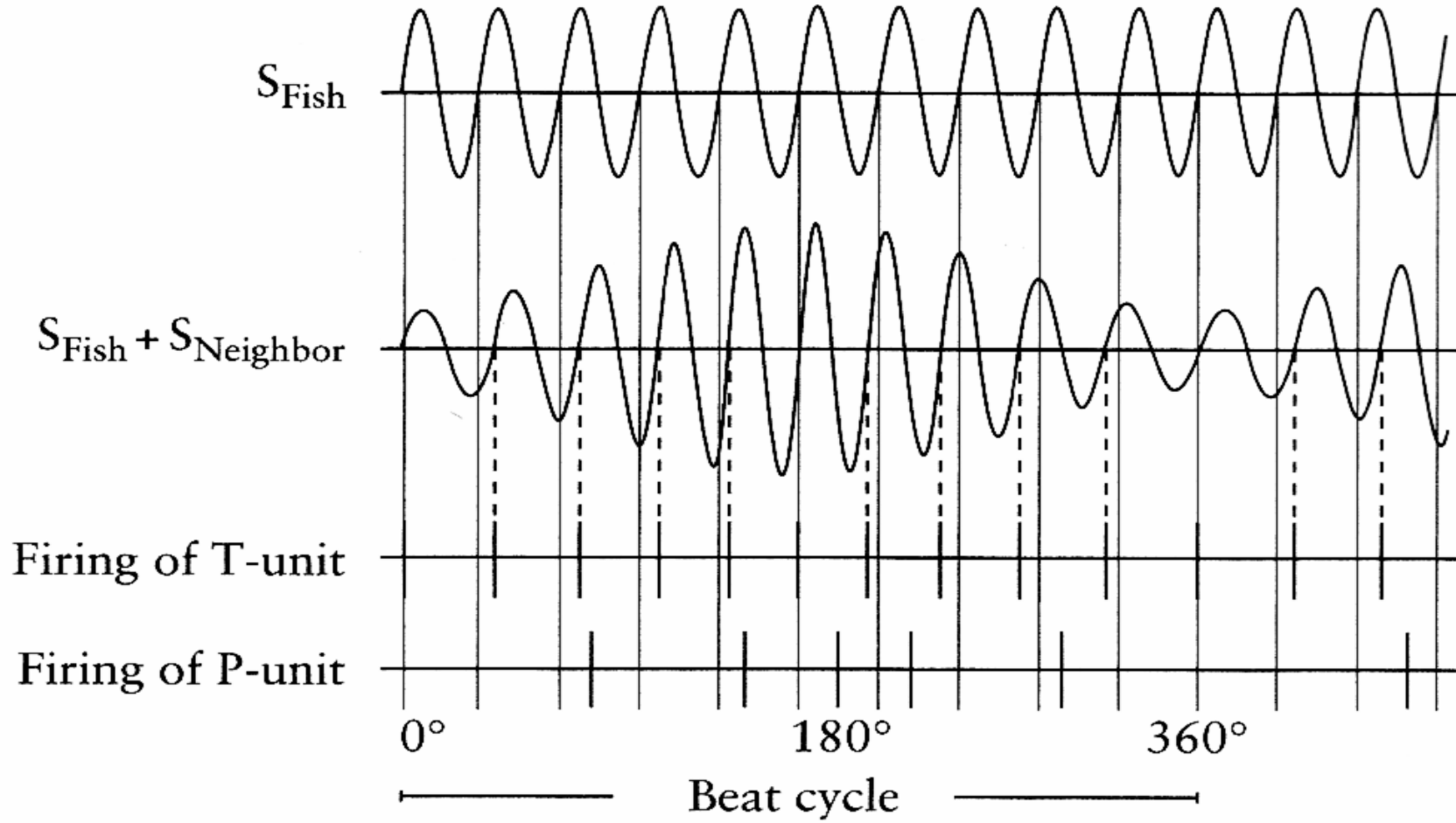
Natural geometry (two separate sources) is important for JAR



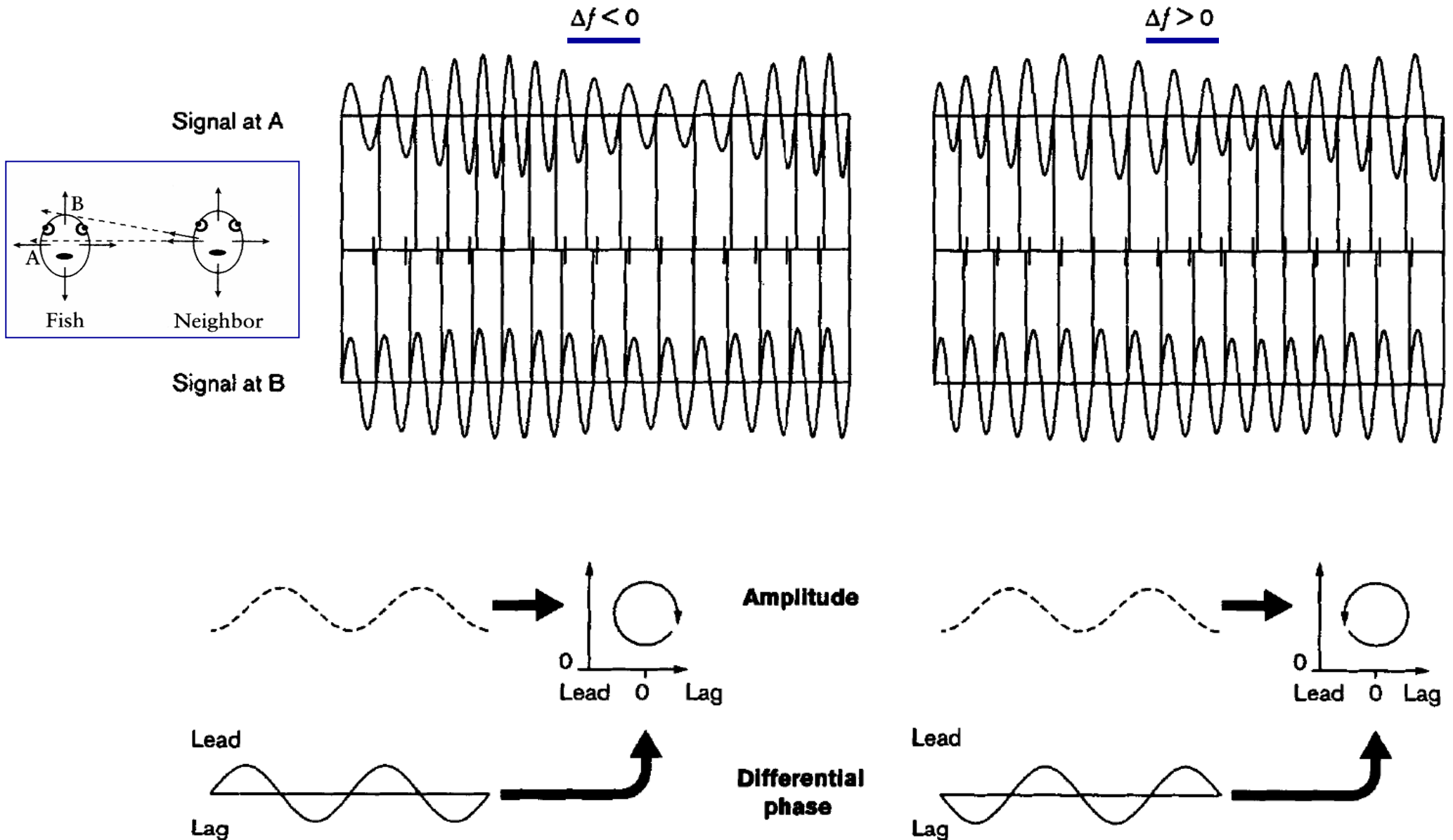
Hence: Variation of relative amplitudes S_1/S_2 across the body surface is important for JAR



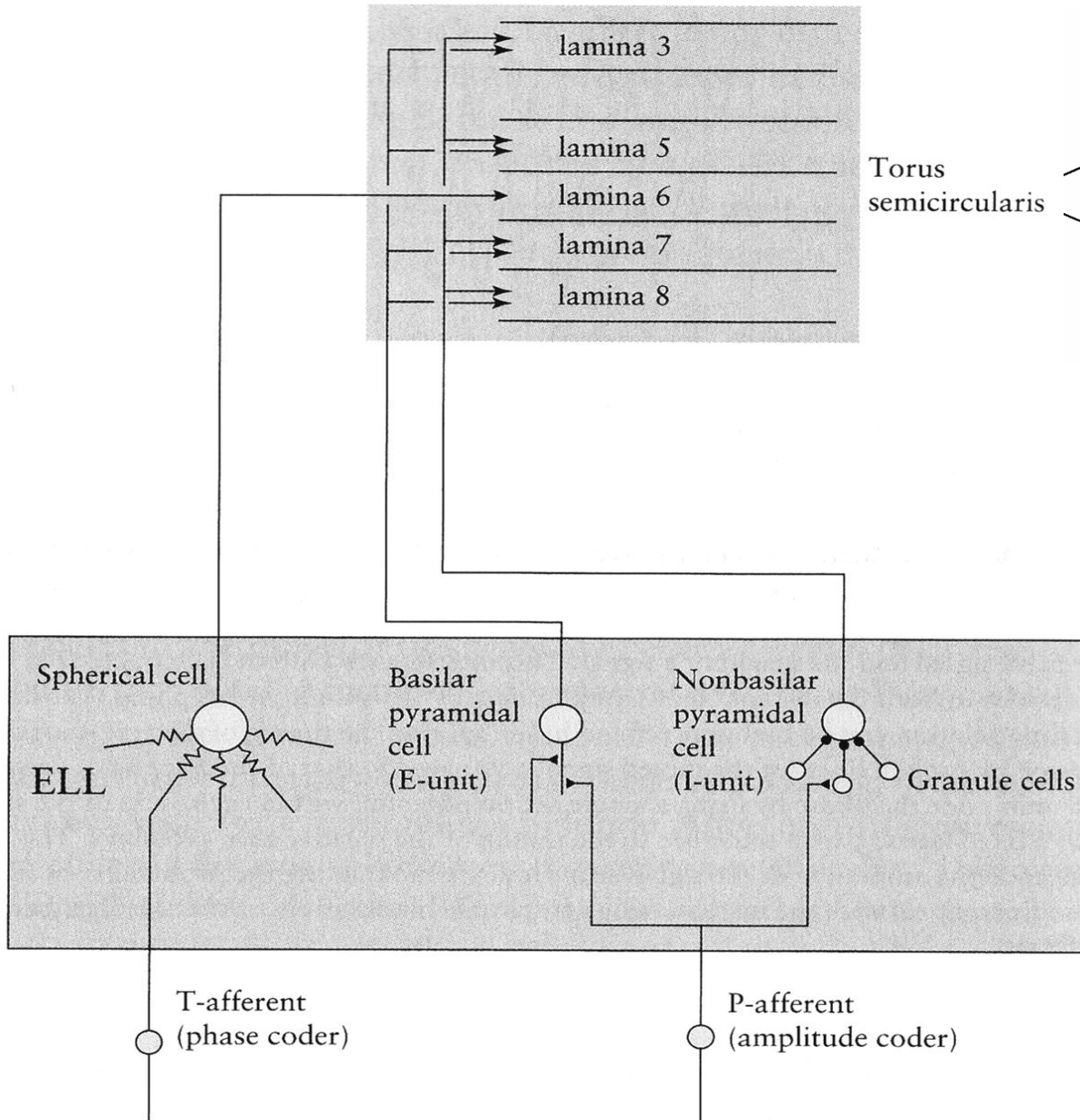
How does the fish know the sign of Δf ? That is, to shift \uparrow or \downarrow ?



How does the fish know the sign of Δf ? That is, to shift \uparrow or \downarrow ?



Neural circuits mediating JAR



Lamina 6: Differential phase computation

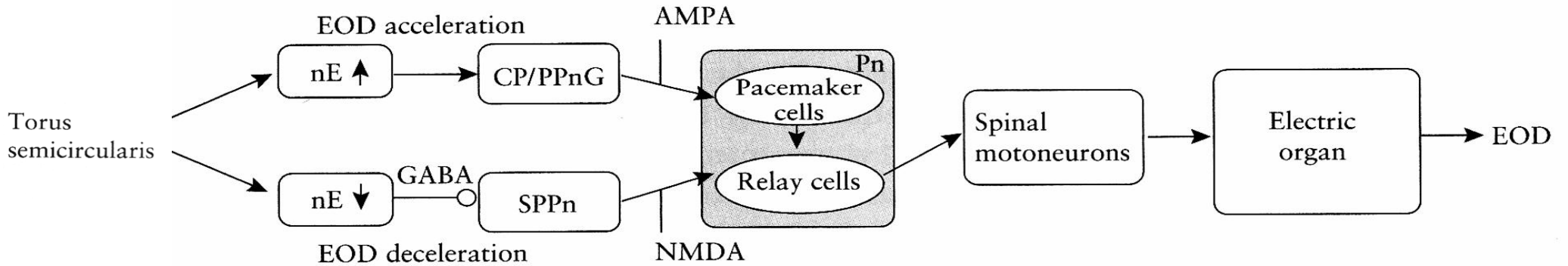
Laminae 5,7: Amplitude modulation computations

Lamina 8c: receives vertically signals from laminae 5,6,7: first station where neurons are coding for Δf

ELL: electrosensory lateral line lobe (contains three somatotopic electrosensory maps)

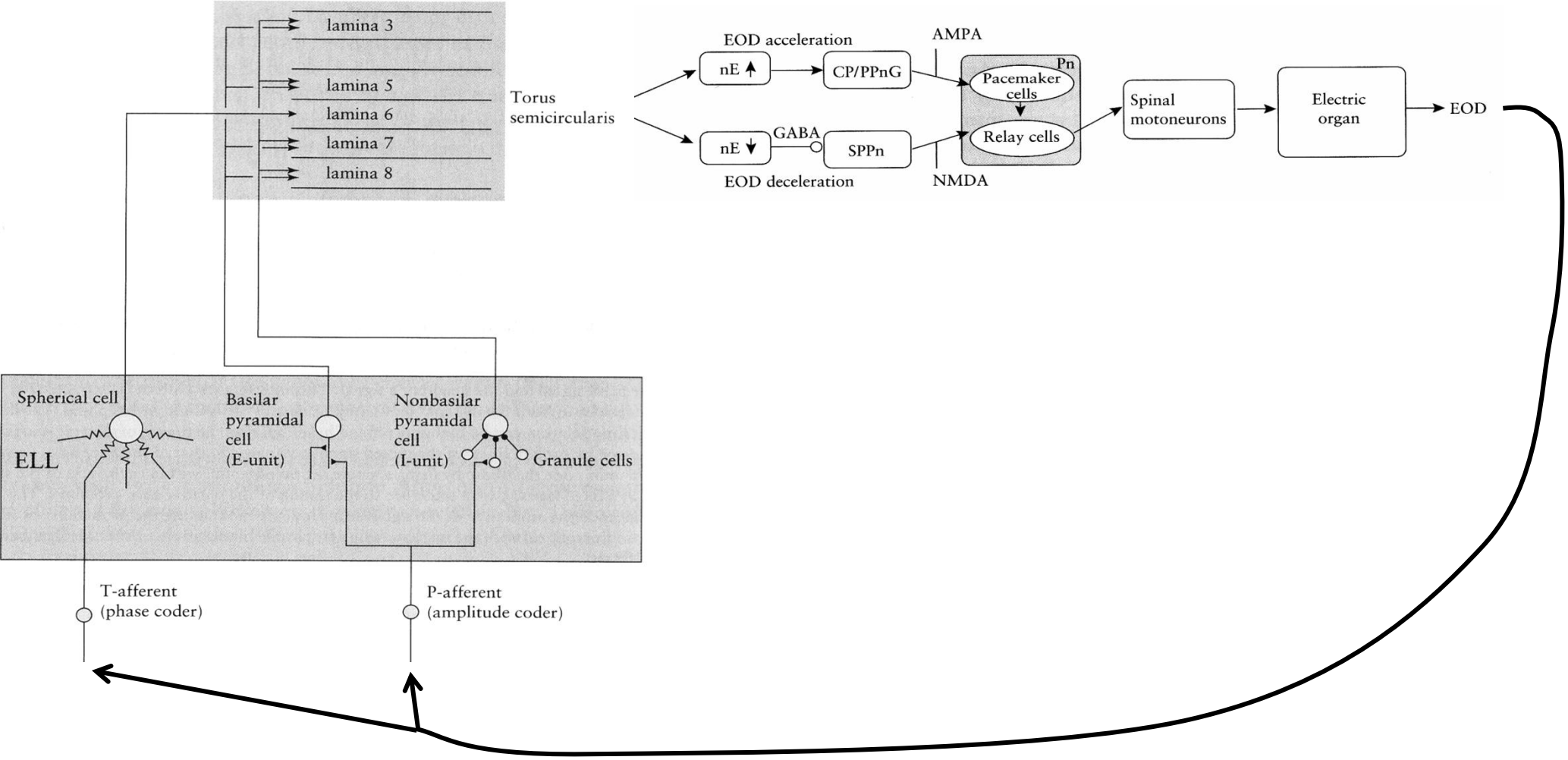
 **Electrical synapse**

Neural circuits mediating JAR

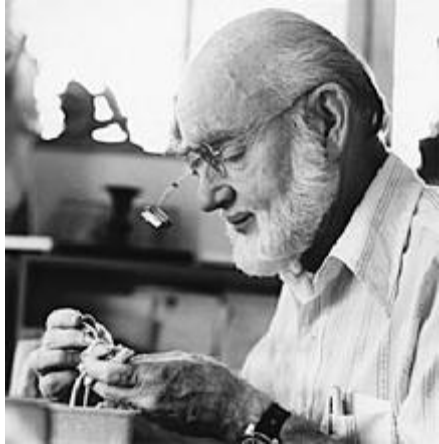


nE: *nucleus electrosensorius*: The first station where neurons are found that code for Δf irrespective of the geometric spatial arrangement of the jamming signal (i.e. no ambiguity)

Neural circuits mediating JAR – the full sensorimotor loop



The two founding fathers of electrolocation research



Theodore (Ted) Bullock:

- Discoverer of two (!) new sensory systems: Electrolocation in weakly-electric fish, and thermolocation by the snake's pit organs
- Founder of first Neuroscience department in the world (UCSD)
- Founder and 1st president of International Society for Neuroethology
- 3rd president of the Society for Neuroscience (SfN)



Walter Heiligenberg

- Pioneered the study of the brain mechanisms of the jamming avoidance response (JAR)
- Many electrolocation researchers worldwide are his ex-students
- One of the first Computational Neuroscientists, who combined experiments and modeling ("Neural nets in electric fish", 1991)