Introduction to Neuroscience: Behavioral Neuroscience

* Introduction to Neuroethology

* Electrolocation in weakly-electric fish

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2009-2010, 1st semester

Outline of today's lecture

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

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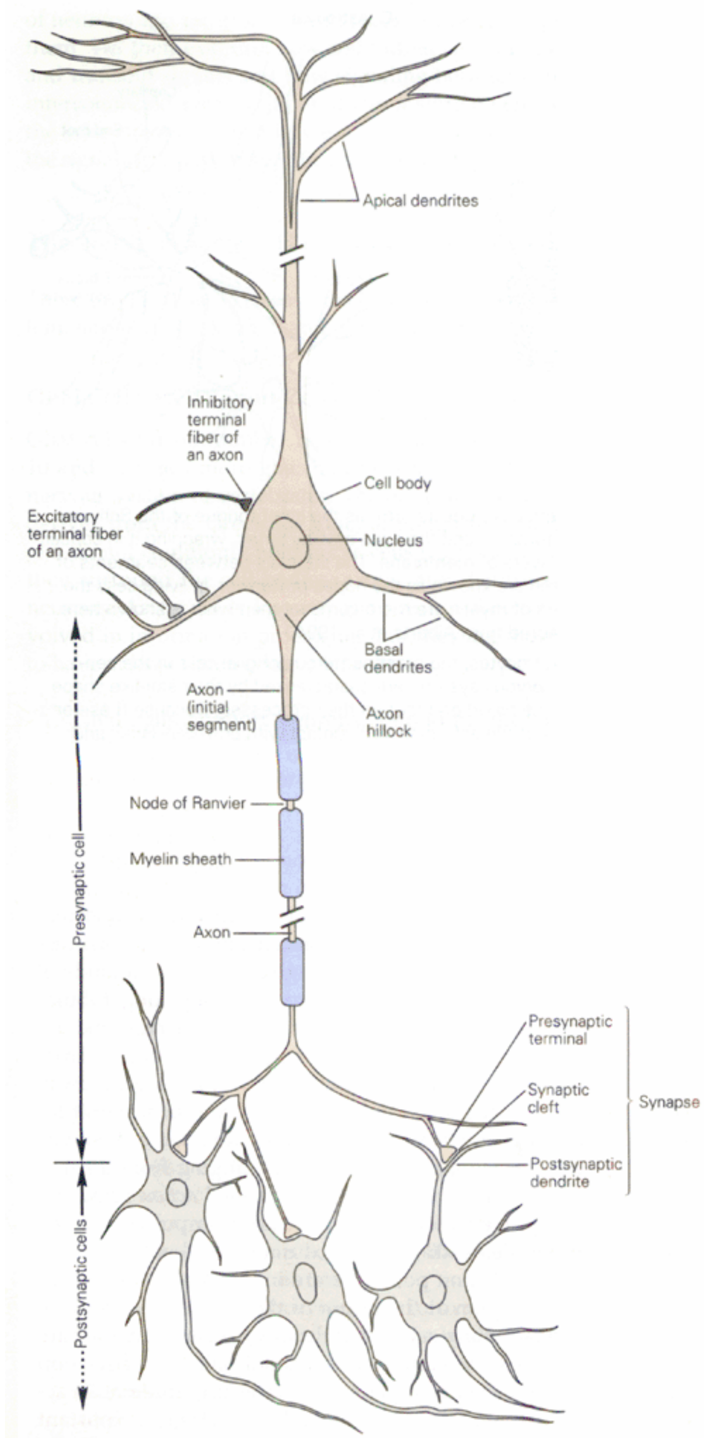
*These topics will be expanded in the courses **"Intro to Neuroscience: From Neuron to Synapse"** (next semester) and **"Intro to Neuroscience: Sensory, Motor and Memory Systems of the Brain"** (next year)*

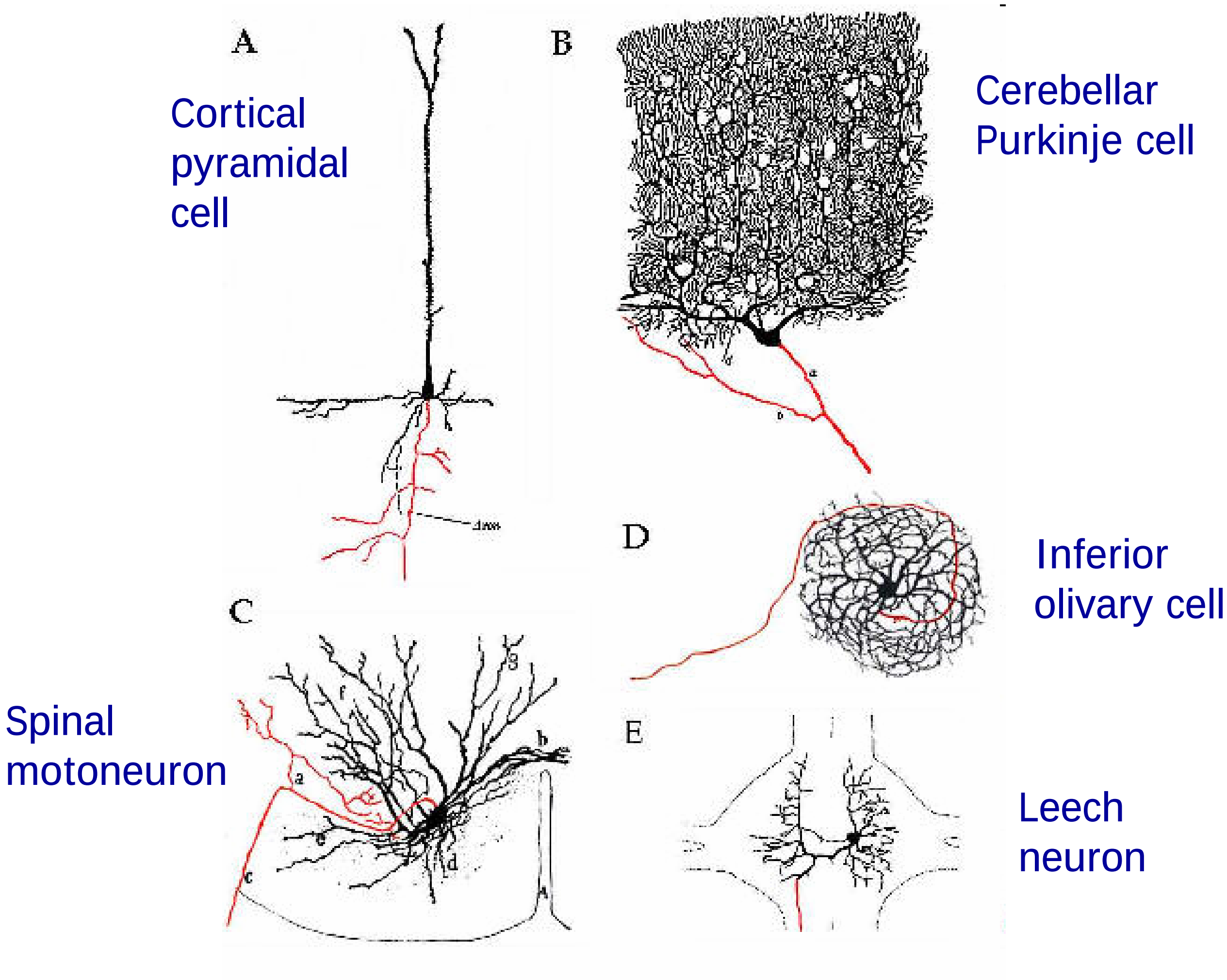
The structure of a neuron

Some basic terms:

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



Heterogeneity of neuronal morphology is likely related to the different functions of different neurons



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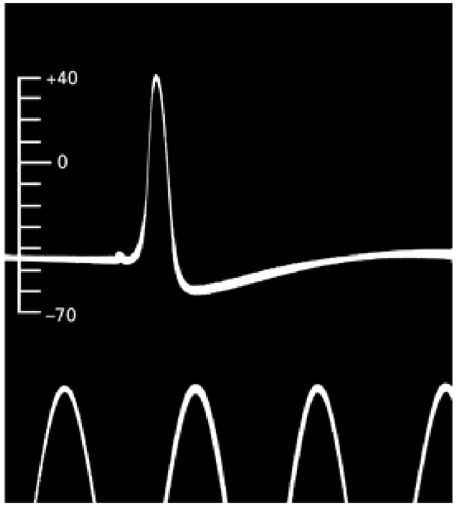
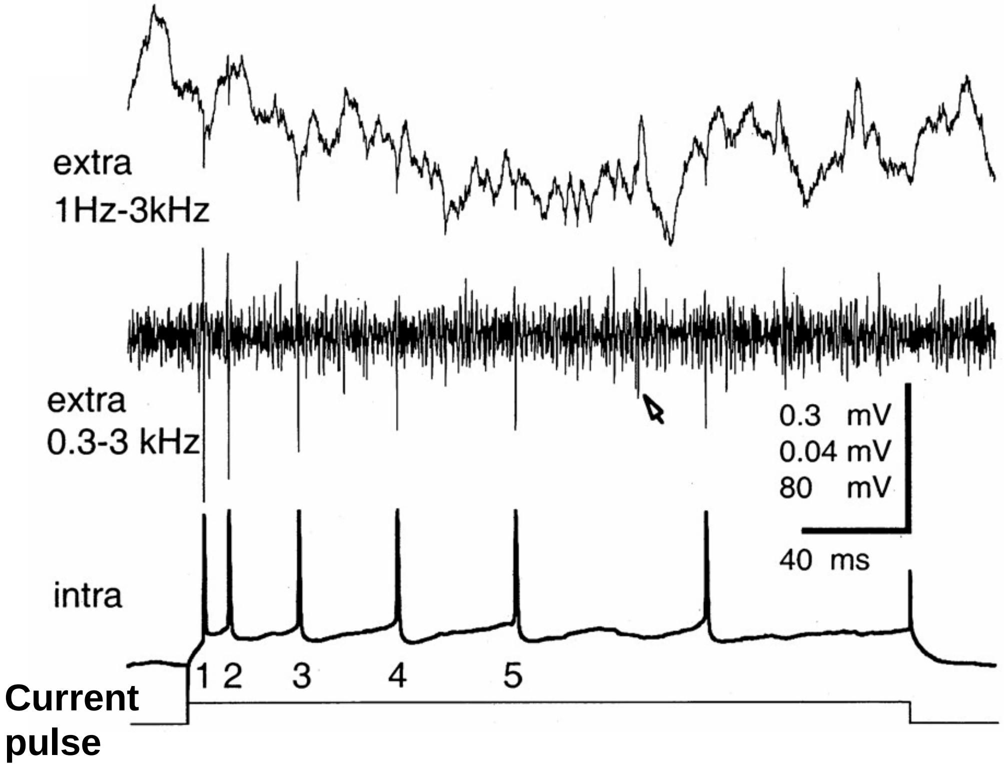
Neurons communicate with action potentials (spikes)

(with some exceptions in invertebrate brains)



First published action potential (Hodgkin & Huxley 1939)

500 Hz sine wave (time marker)

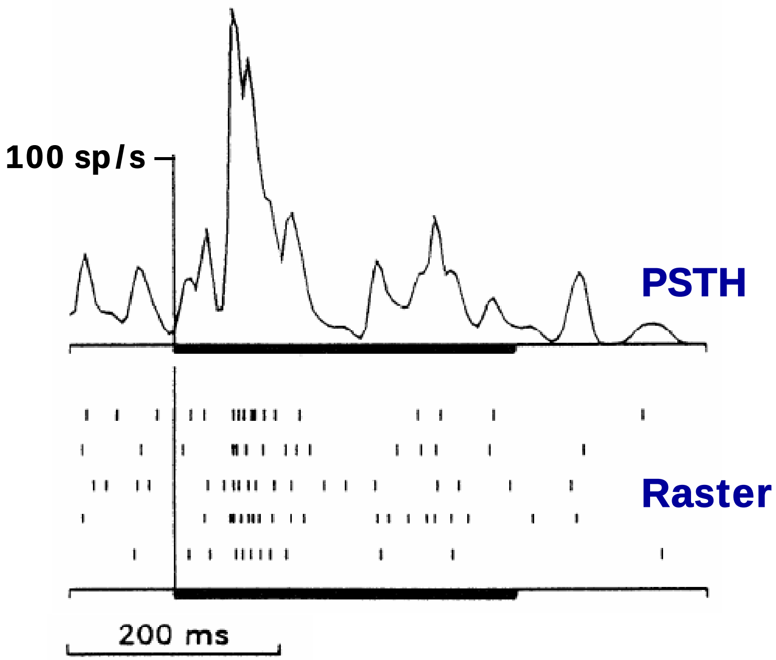


Henze et al. (2000)

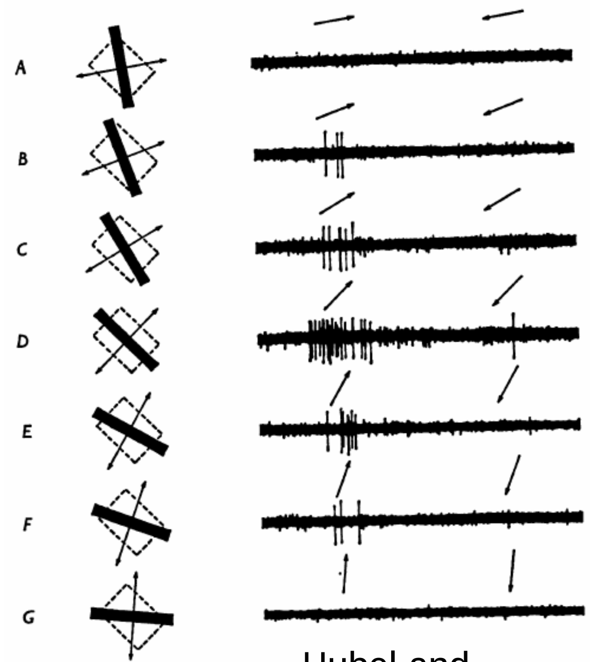
Some basic terms:

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

Sensory neurons respond to stimuli with changes in firing-rate



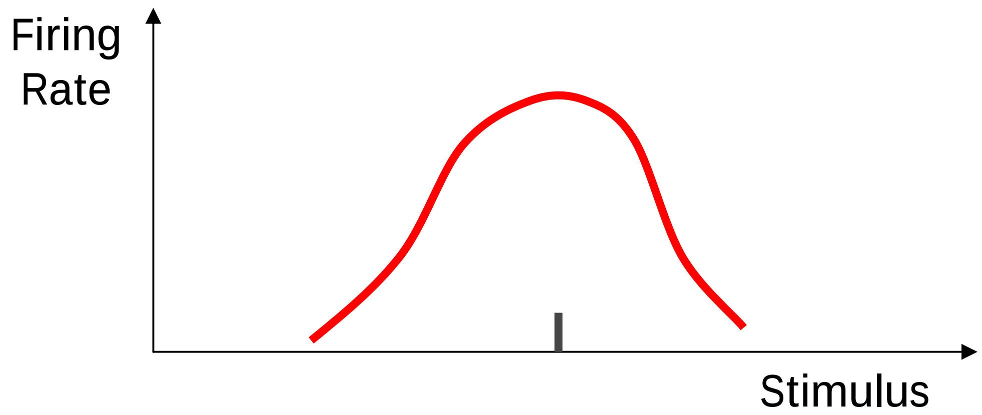
Richmond et al. (1990)
Responses of a V1 neuron
to complex patterns



Hubel and
Wiesel (1968)

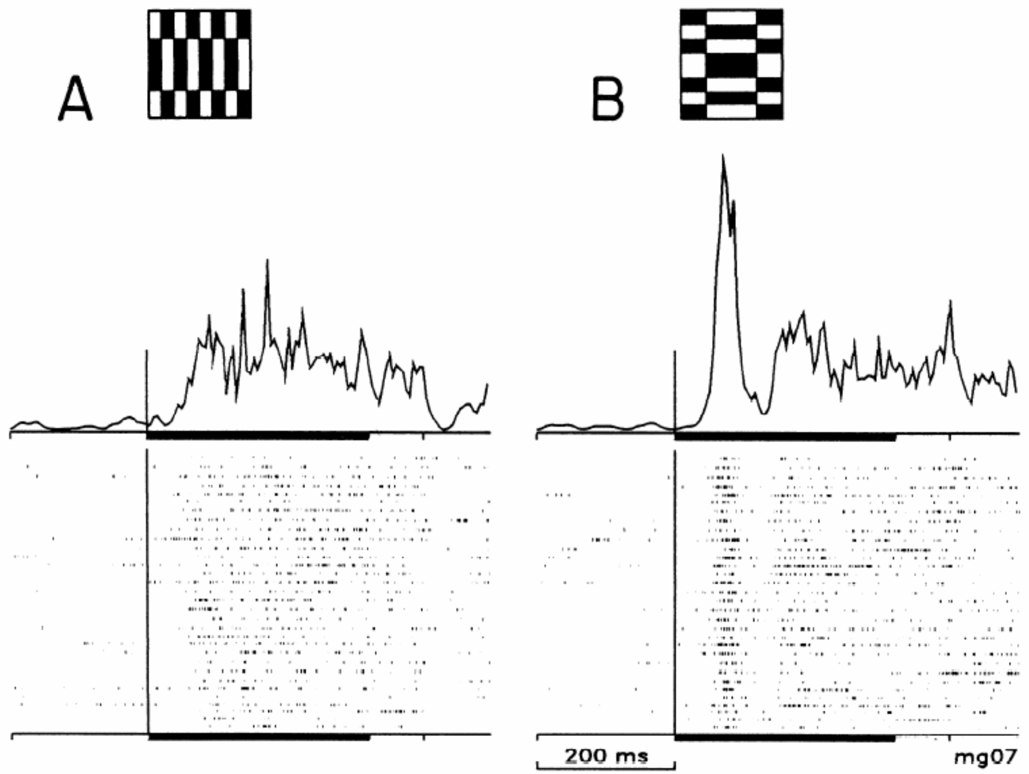
Some basic terms:

- 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



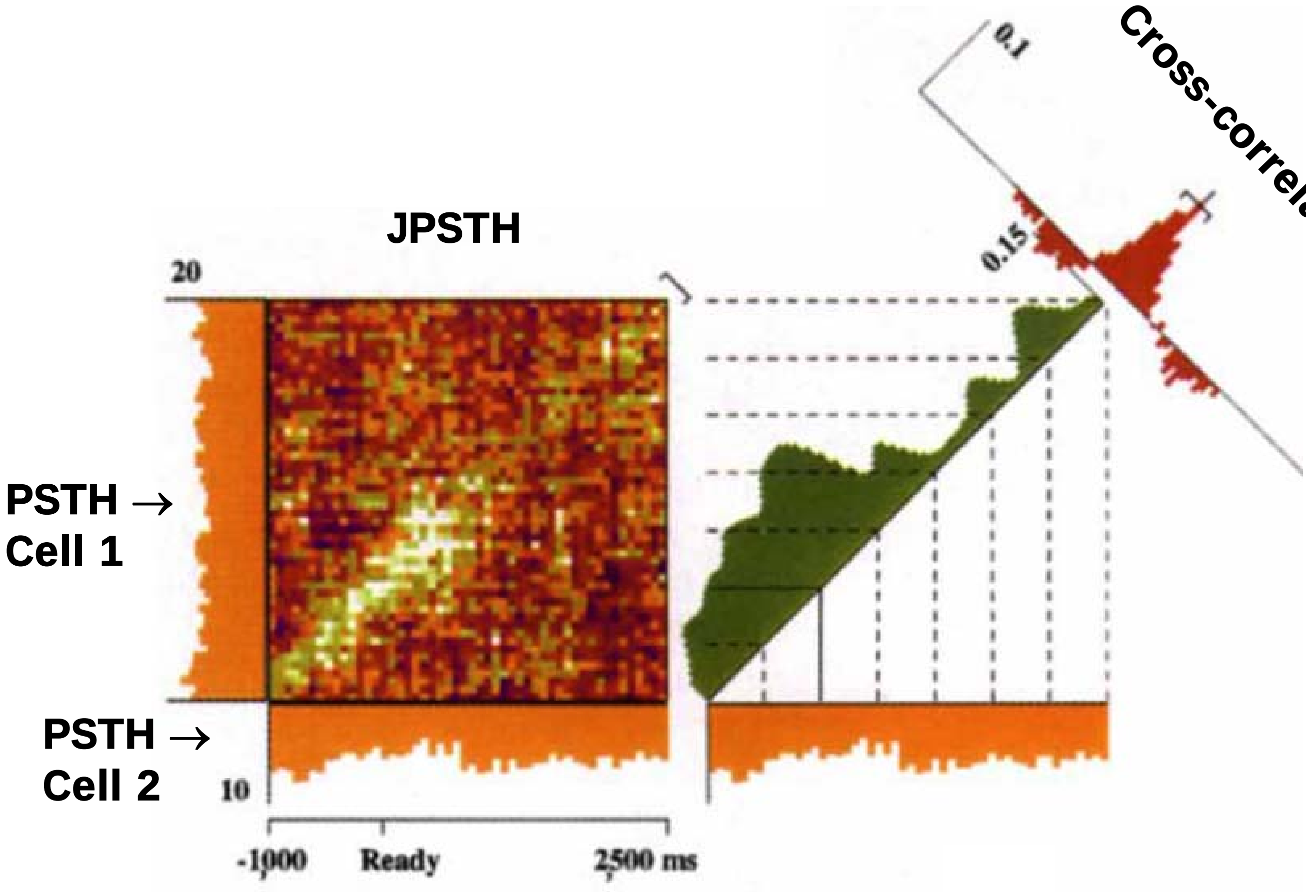
Richmond et al. (1990)

Some basic terms:

- Cross-correlation
- Joint peri-stimulus time histogram (JPSTH)
- Neural codes:
    - Rate code
    - Temporal code
    - Synchrony code
    - Labeled-line code
    - Other codes

These topics will be expanded in the courses "Intro to Neuroscience: Sensory, motor and memory systems of the brain" (next year) and "Computational Neuroscience"

Neurons may also use other neural codes



Vaadia et al. (1995)

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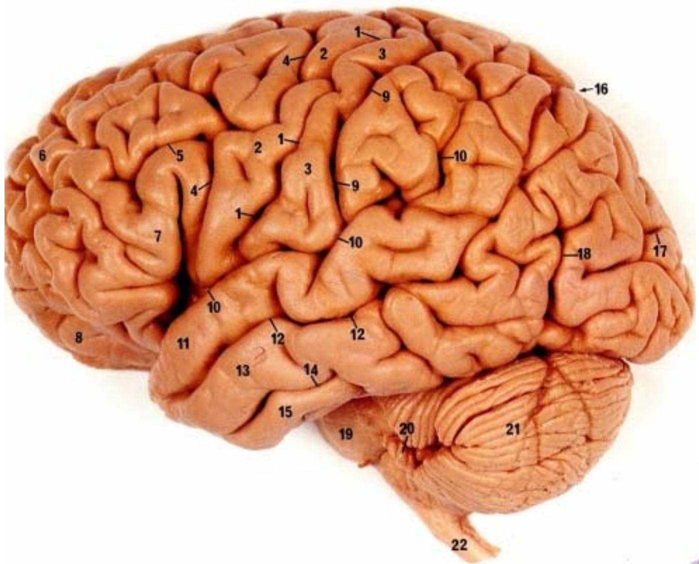
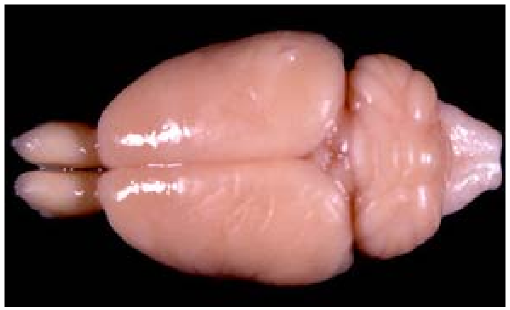
Anatomy of a vertebrate brain





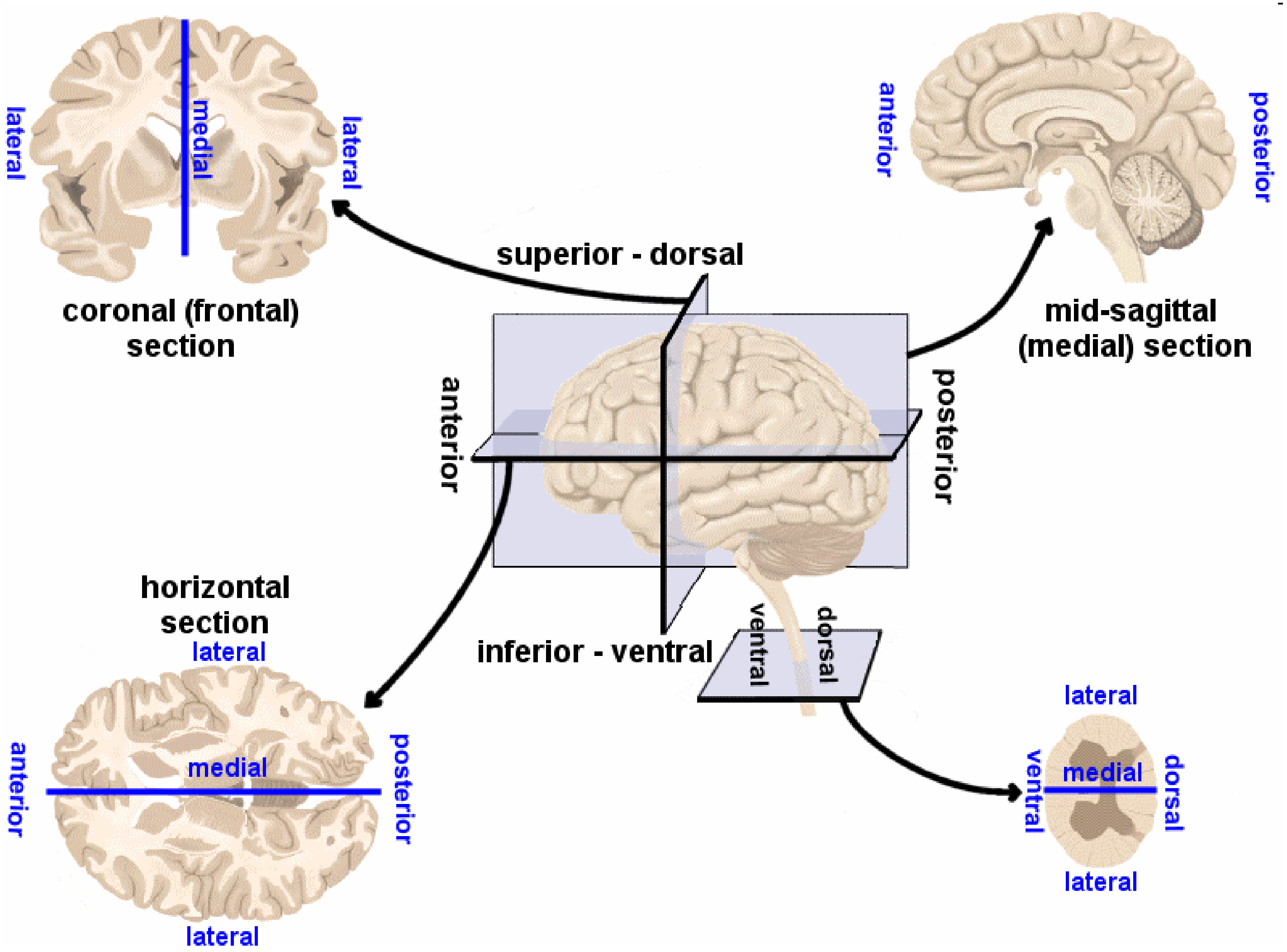
Beaver brain

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 will be expanded in the courses “Neuroanatomy” (this year)

Anatomy of a vertebrate brain



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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.

$$\begin{array}{l} \text{Neurobiology} \searrow \\ \qquad\qquad\qquad \boxed{\text{Neuroethology}} \\ \text{Ethology} \nearrow \end{array}$$

- **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**

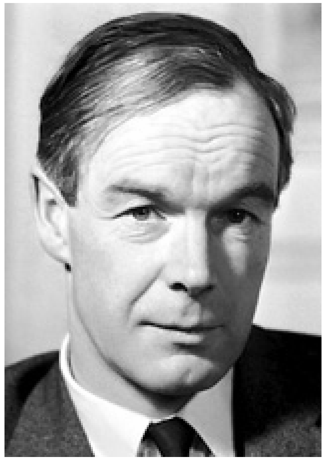
Krogh’s principle

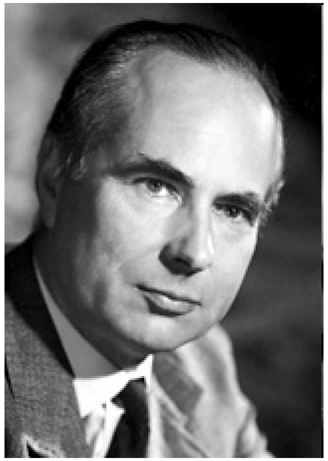
August Krogh
Nobel prize 1920

“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





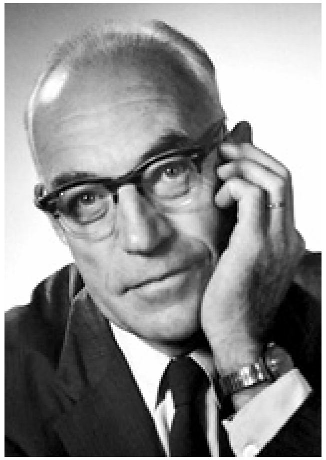
Alan Hodgkin   Andrew Huxley
Nobel prize 1963

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



Sir John Eccles
Nobel prize
1963

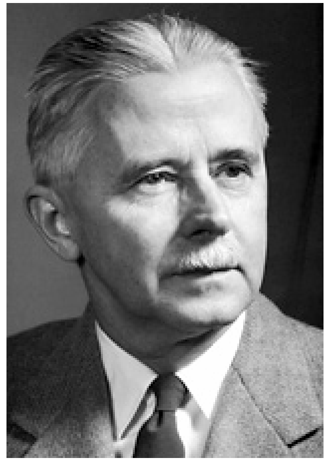
Sir Bernard Katz
Nobel prize
1970

Q: Why was this species chosen?

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

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*

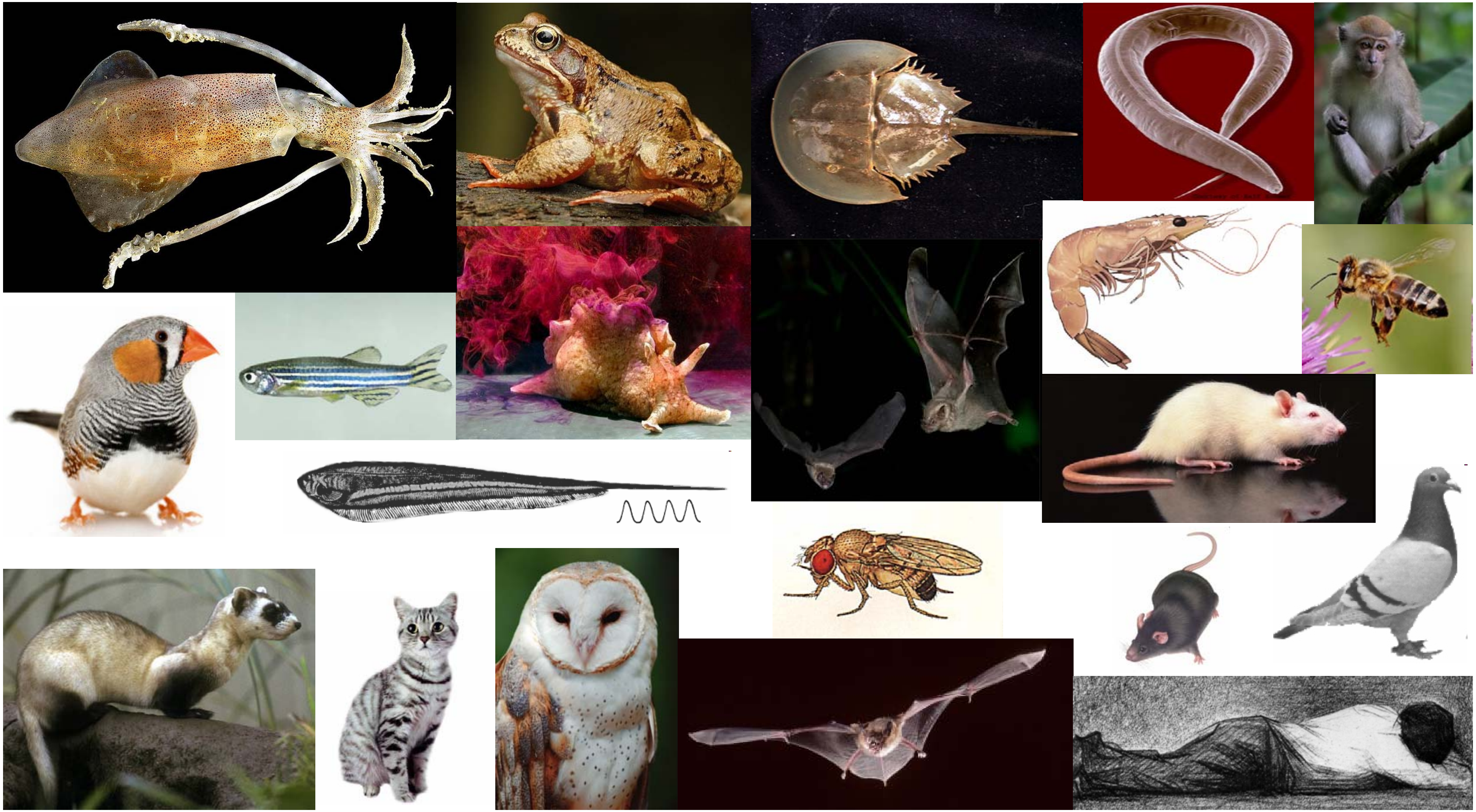
Eric Kandel
Nobel prize 2000

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 **behavior** (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, e.g. Elephant)*



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" (rat, mouse, monkey).

- **Advantages of "Standard animal models":** So much is known about their brains... Therefore, many people prefer this knowledge-base over Krogh's principle.

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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 (*Platypus also added here*)

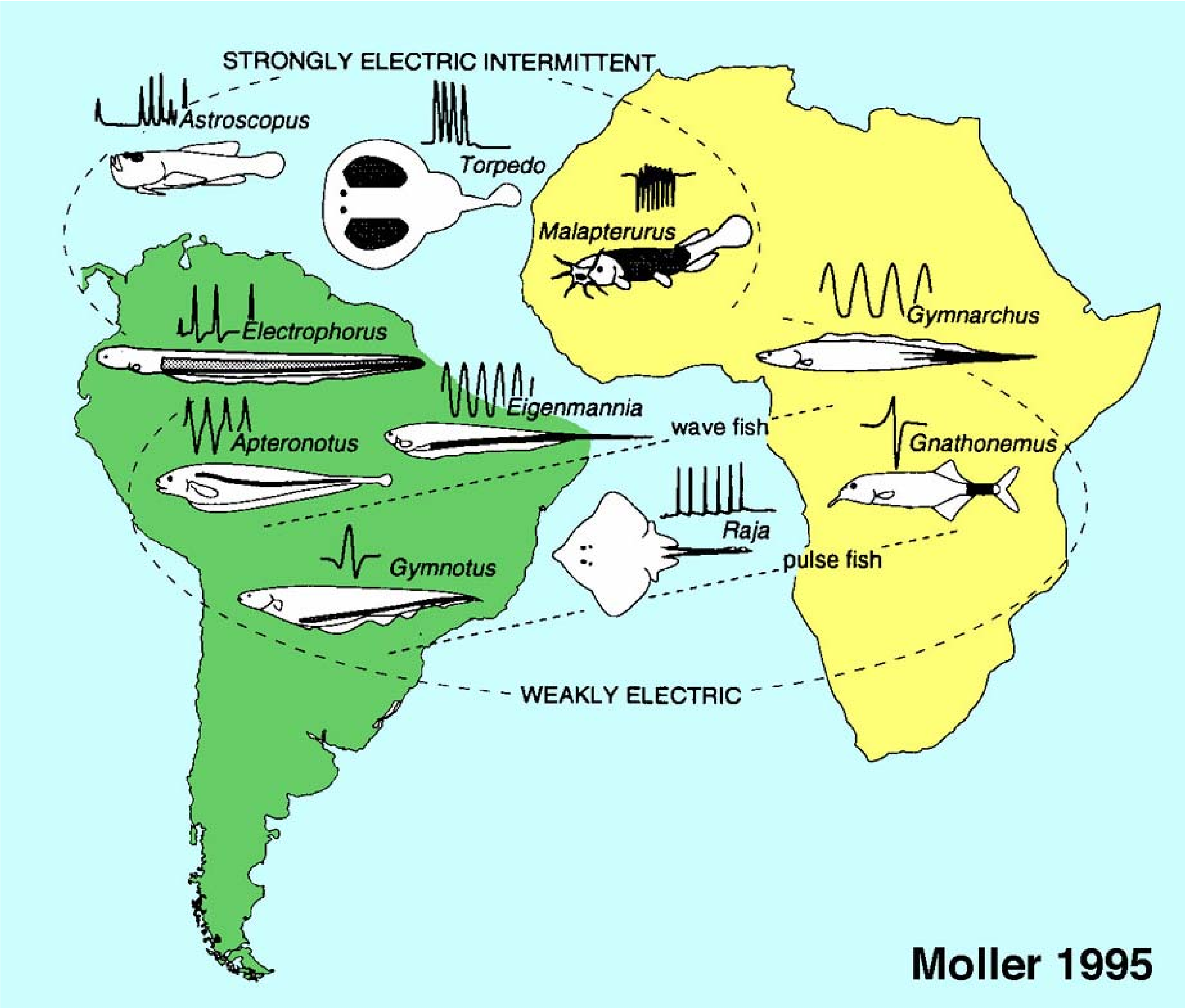
- **Strongly electric fish**
  (e.g. Electric eel: 500 Volts, 1-Ampere)
- **Weakly electric fish**
  (a few mV to 1 Volt)
- **Sharks**, **Rays**, **Platypus…**

Generate electric fields

Detect electric fields

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

Wave-type and Pulse-type weakly electric fish



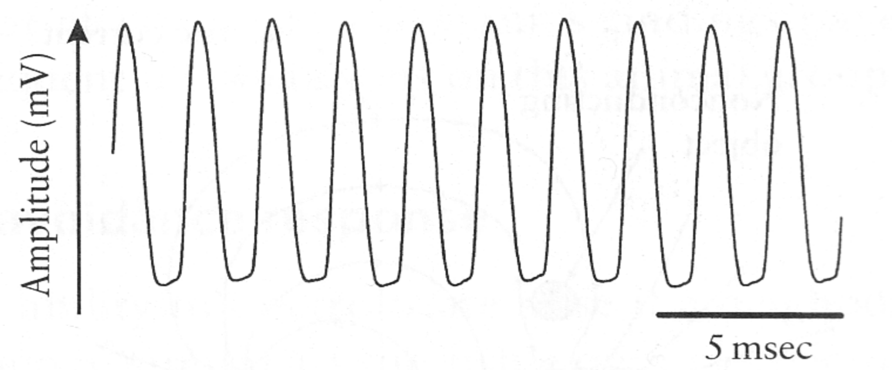
Why is it a good model system?

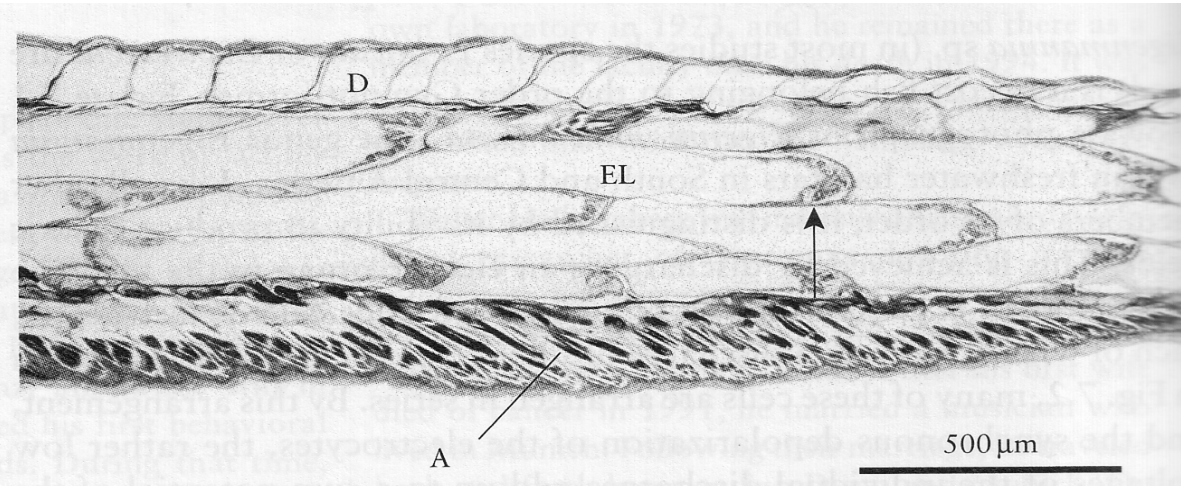
- **Animal model for sensory-motor integration:** Weakly electric fish are good animal model because sensory-motor integration is a closed-loop system (negative feedback), and studying it requires **“opening the loop”** – which is possible in weakly electric fish (see next slides)

- **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...

Electric Organ Discharge

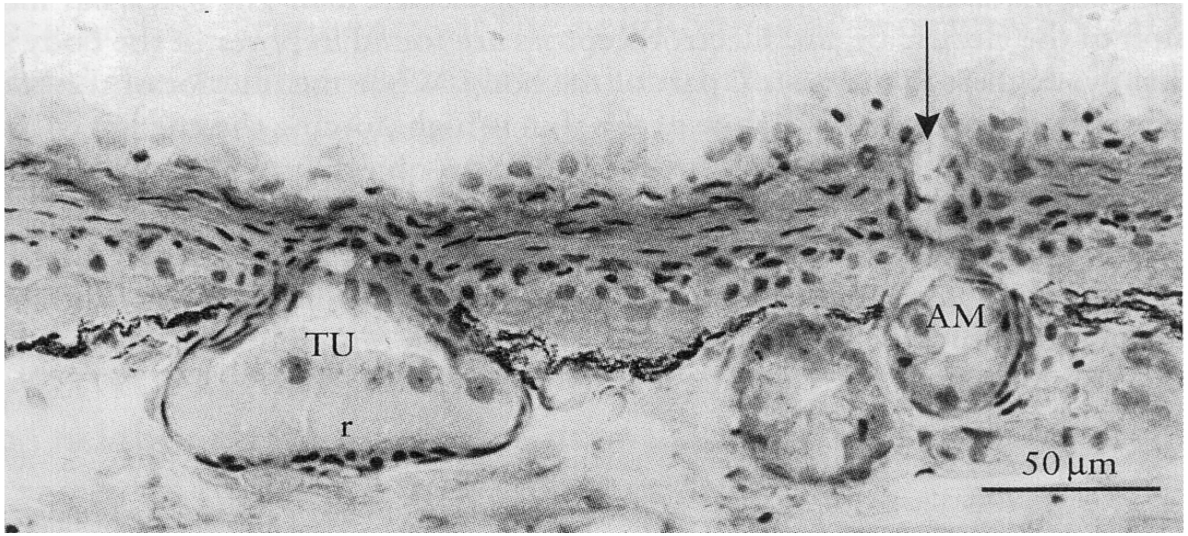
Eigenmannia virescens





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

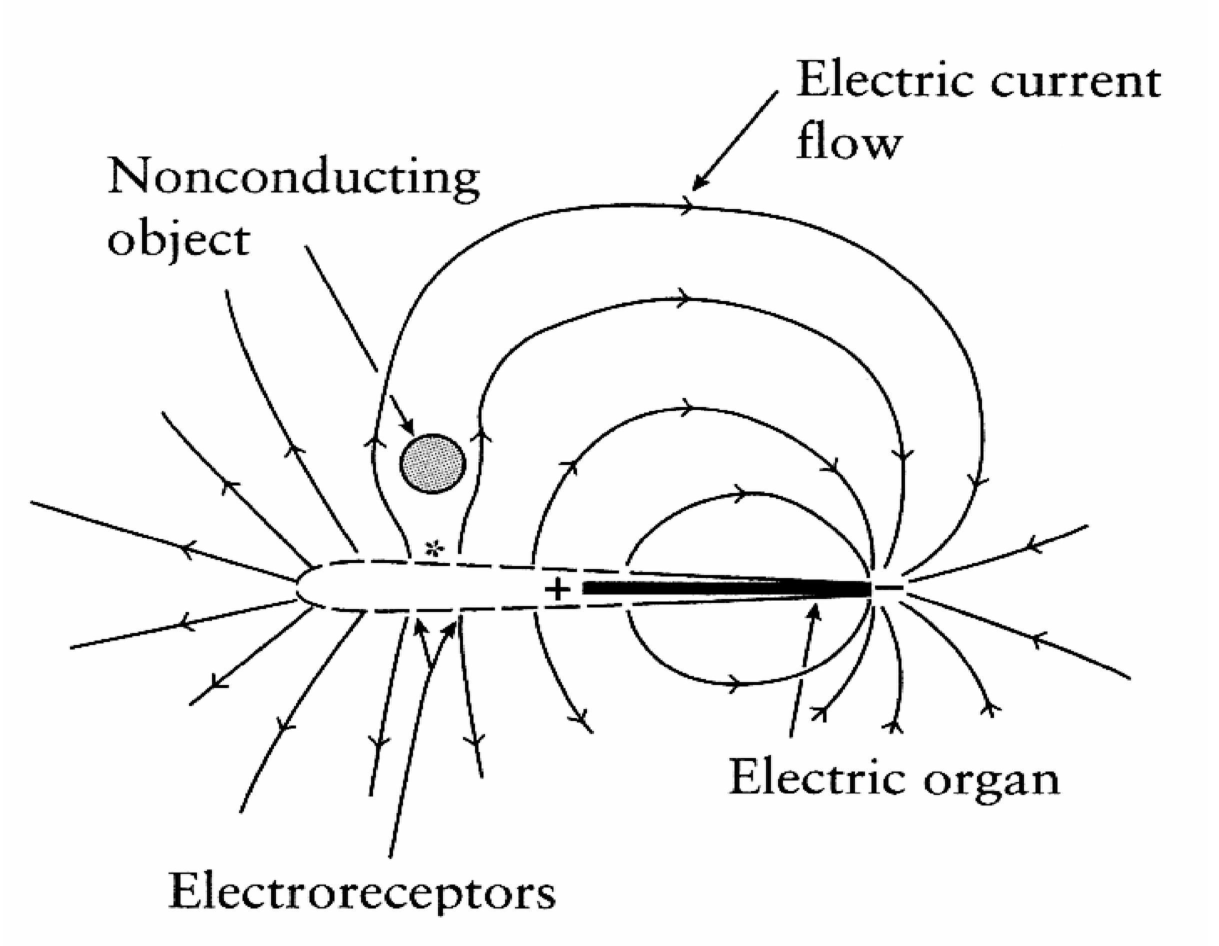
Electroreceptors



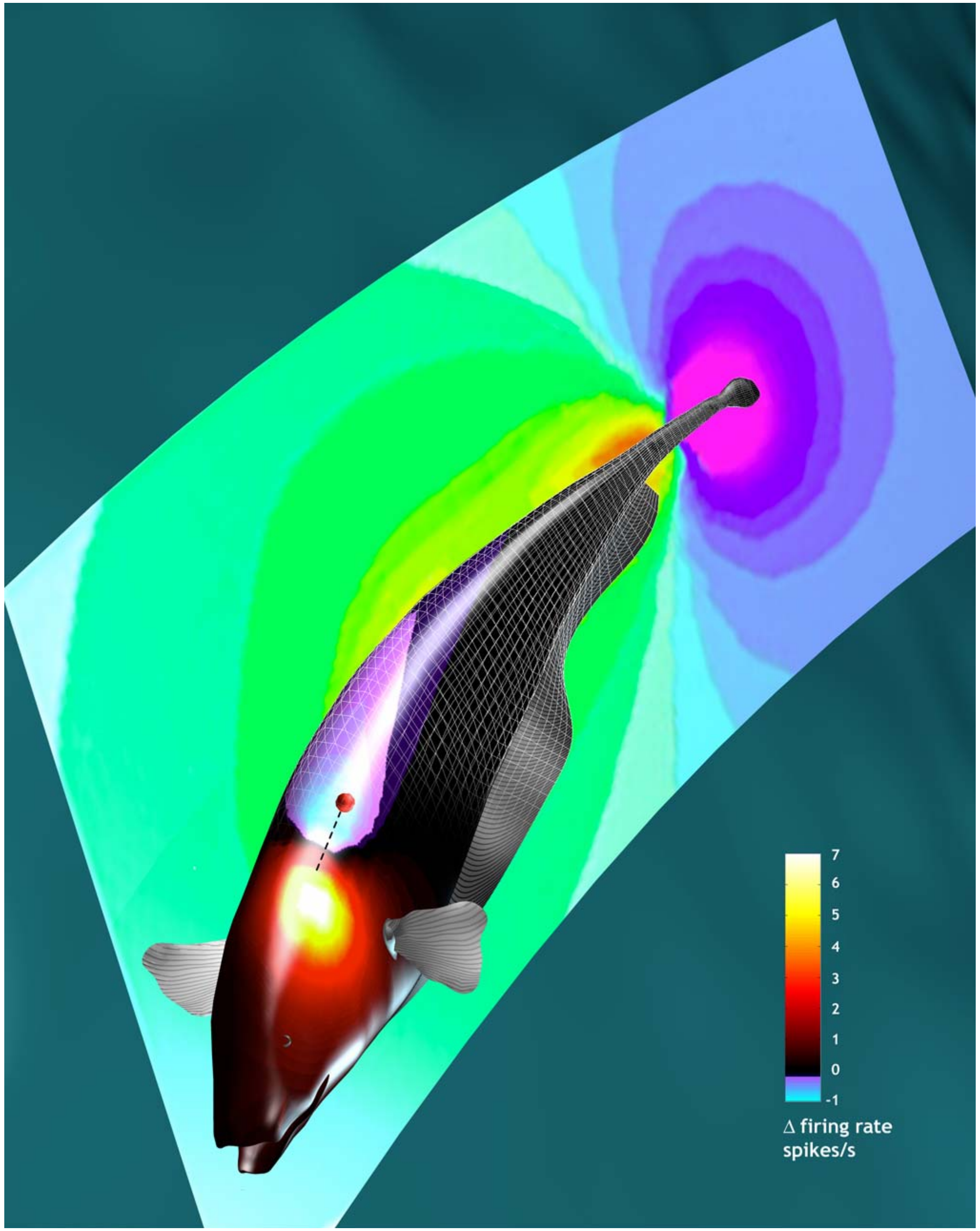
TU – Tuberous receptors (sensitive to high frequencies - most important for electrolocation). Each Tuberous receptor sends 1 axon to the brain.

AM – Ampullary receptors.

Electrolocation: putting production and reception together



Electrolocation: putting production and reception together



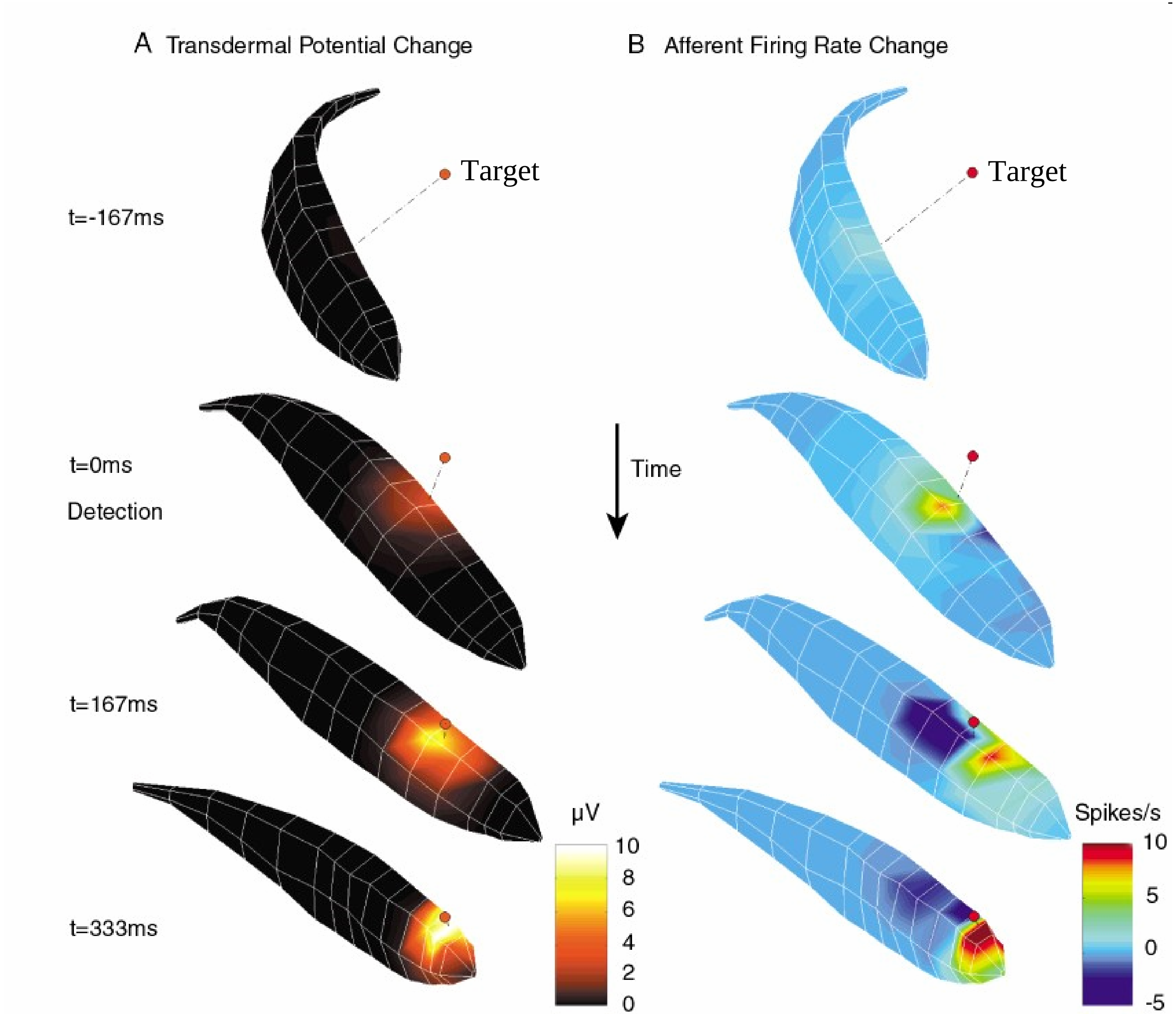
Shown is the EOD dipole, as well as a false-color map on the skin indicating the change in firing-rate in sensory neurons (tuberous electroreceptors) caused by the presence of a small target (red dot).

Electrolocation: putting production and reception together

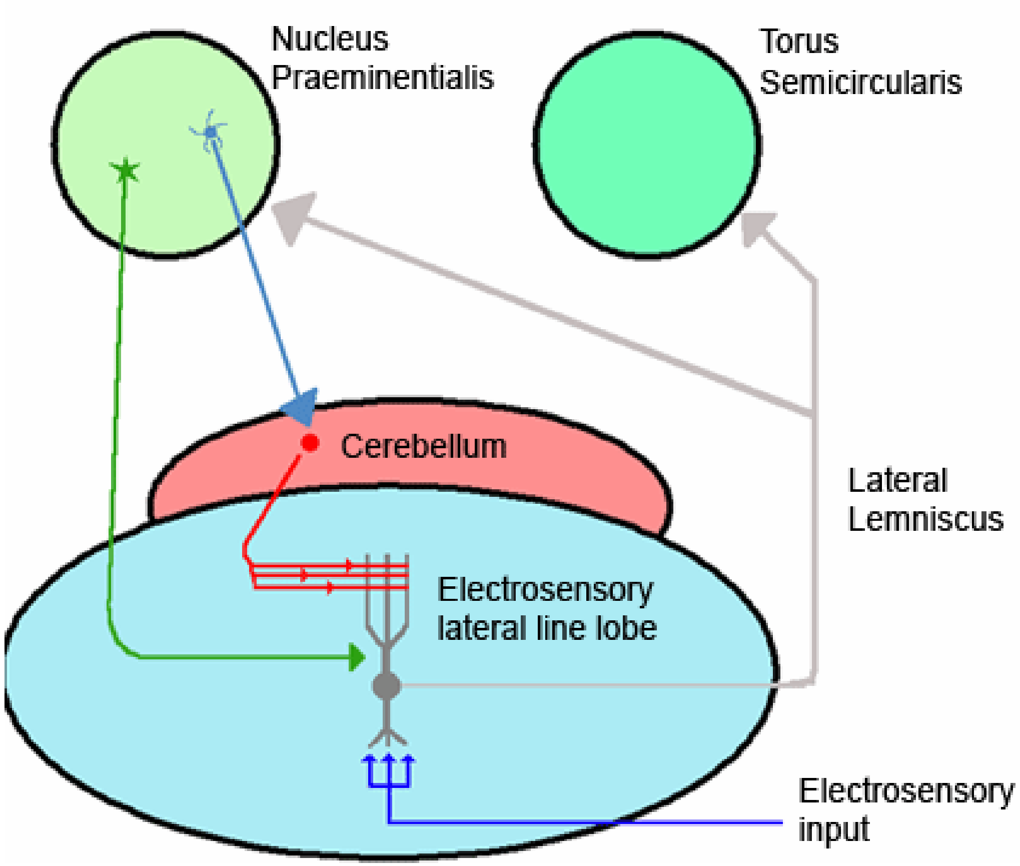
Show Movie of simulation of
weakly electric fish prey capture

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

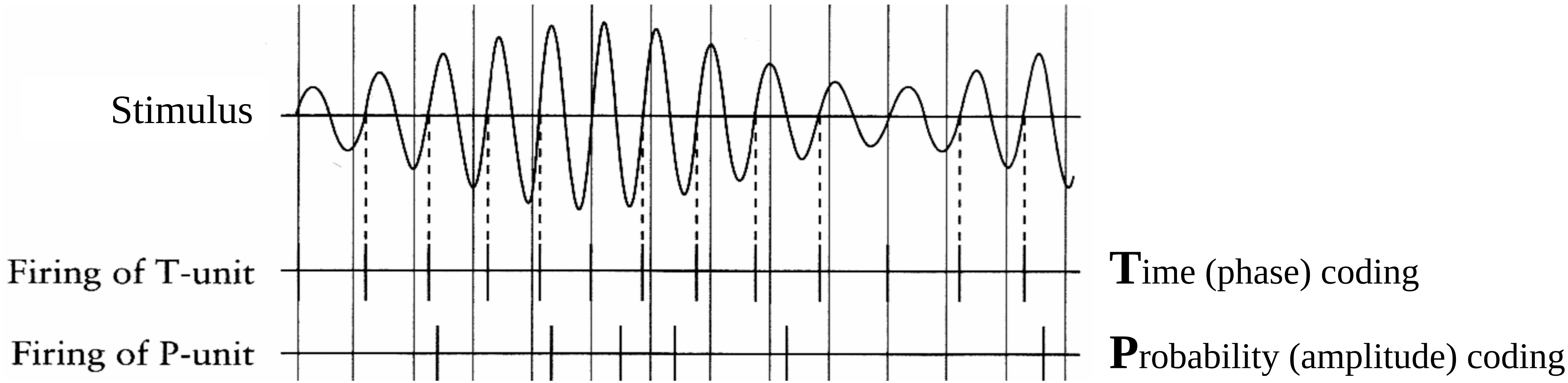


Cancellation of redundant stimuli by "negative image"



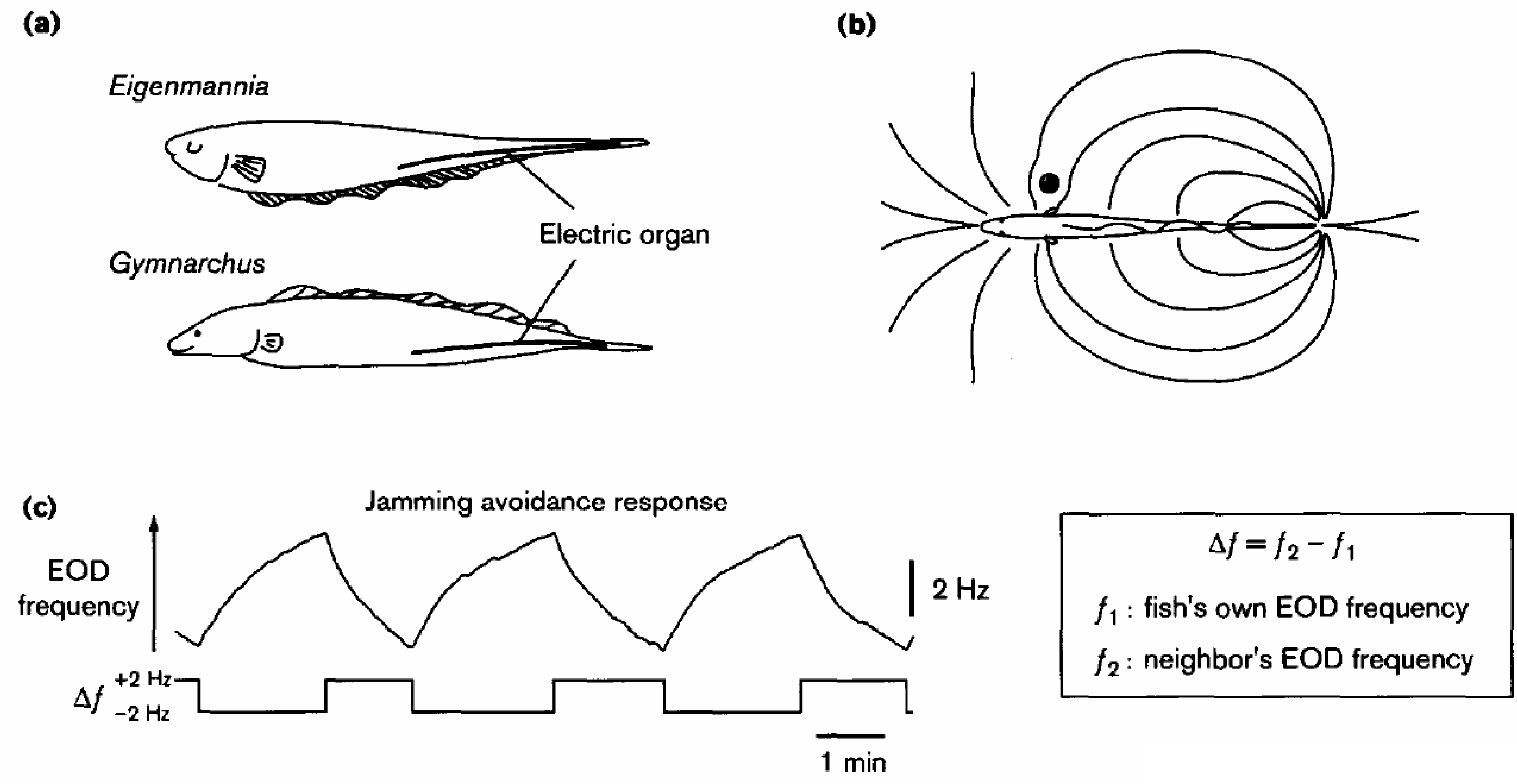
Electrosensory reafferent signals from electroreceptor afferents are cancelled by a "negative image" provided by feedback input – this is needed to eliminate the large changes in received EOD due to changes in the animal's posture during behavior

Two type of electroreceptors encode time and amplitude

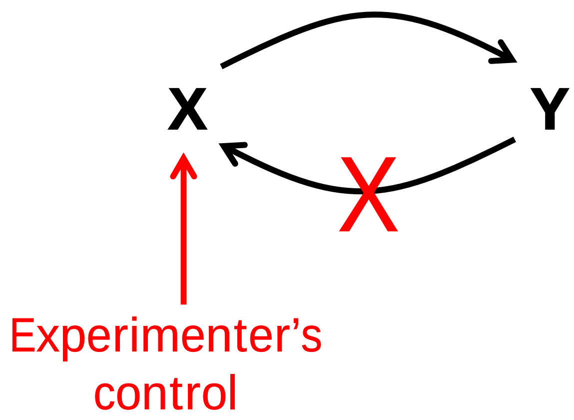


Behaviorally, weakly electric fish can detect **amplitude** changes < 0.1% in the input signal, and **temporal** changes < 1 μs.

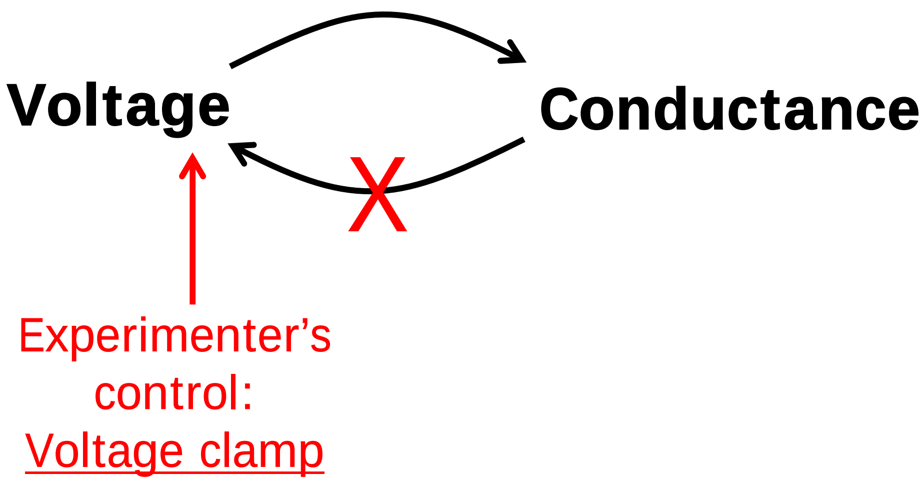
Jamming Avoidance Response (JAR) in wave-type fish



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

Nucleus electrosensorius (nE) → Pacemaker nucleus

Torus semicircularis

Motoneurons

ELL
(brainstem: Electrosensory Lateral Line lobe)

Electric organ
(modified muscle cells)

Electroreceptors
P-afferents and T-afferents

EOD
(Electric Organ Discharge)

Objects in the environment:
Distortions in electric field =
Net Electric Field

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

Nucleus electrosensorius (nE) → Pacemaker nucleus

Measure responses not from the EOD but directly from the pacemaker nucleus

Torus semicircularis

Motoneurons

(curare)

ELL
(brainstem: Electrosensory Lateral Line lobe)

Electric organ
(modified muscle cells)

Electroreceptors
P-afferents and T-afferents

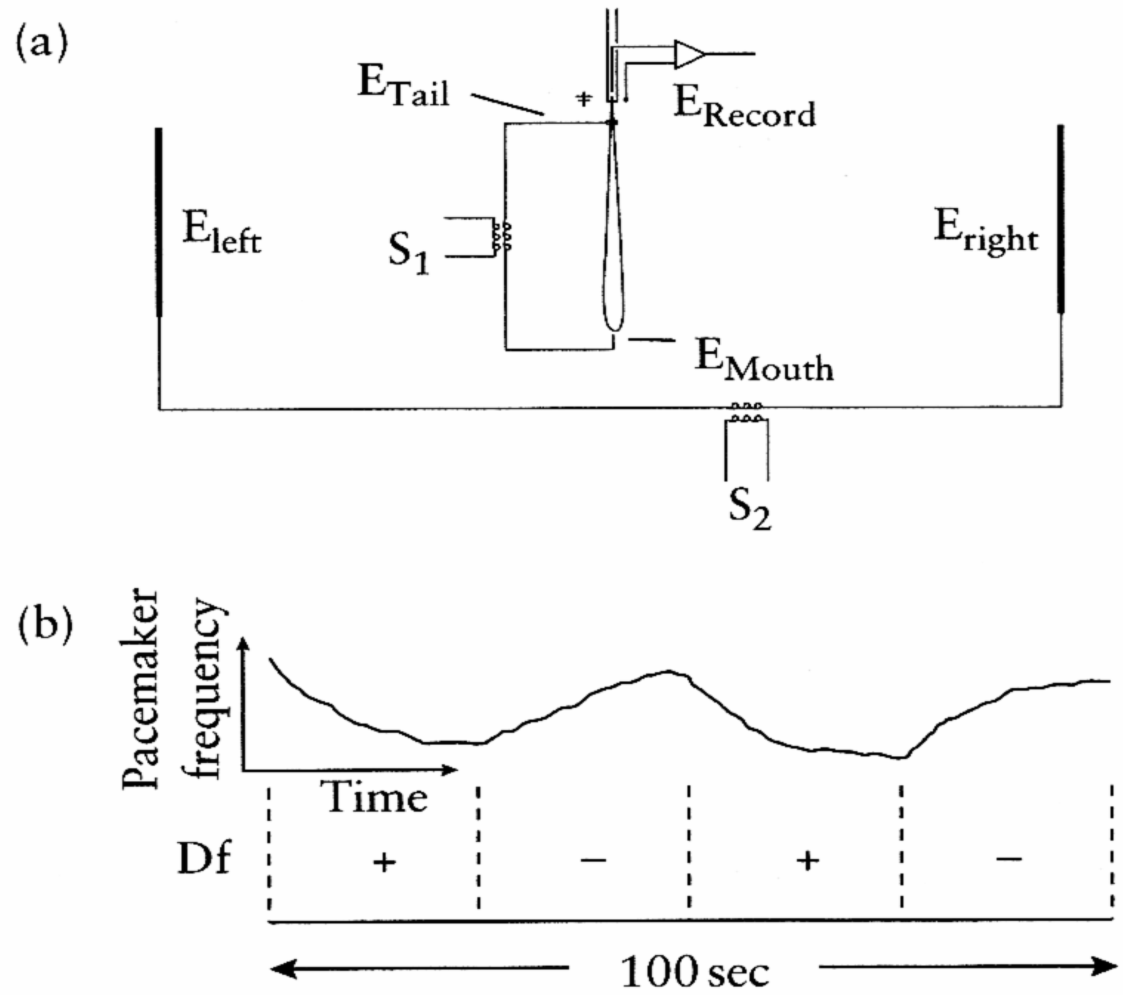
EOD
(Electric Organ Discharge)

(remove any objects)

Objects in the environment:
Distortions in electric field =
Net Electric Field

Experimenter’s control:
Artificially-produced
Electric Fields

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

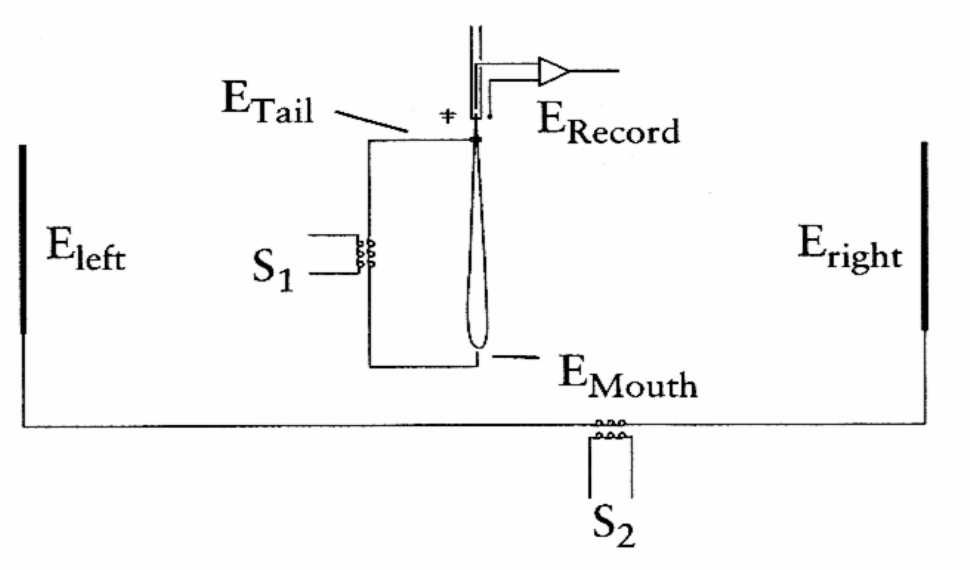


JAR is still present after blocking the EOD with curare and replacing it with artificial "self-produced" signal → hence, JAR is purely <u>sensory</u>-based.

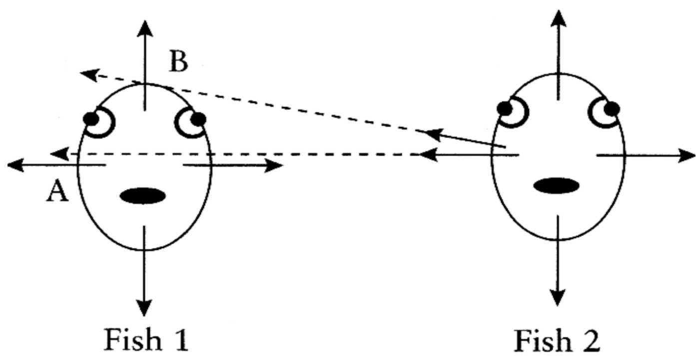
↓

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

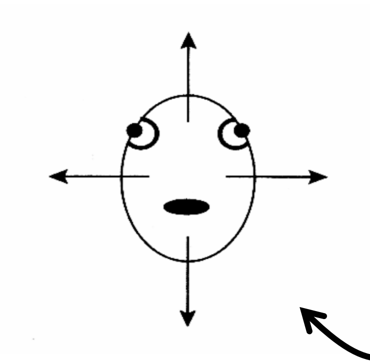
Natural geometry (two separate sources) is important for JAR



- If the two signals, S1 and S2, are spatially separate sources – JAR is normal.



- If the two signals are added S1+S2 but this sum is presented from one location – no JAR occurs.



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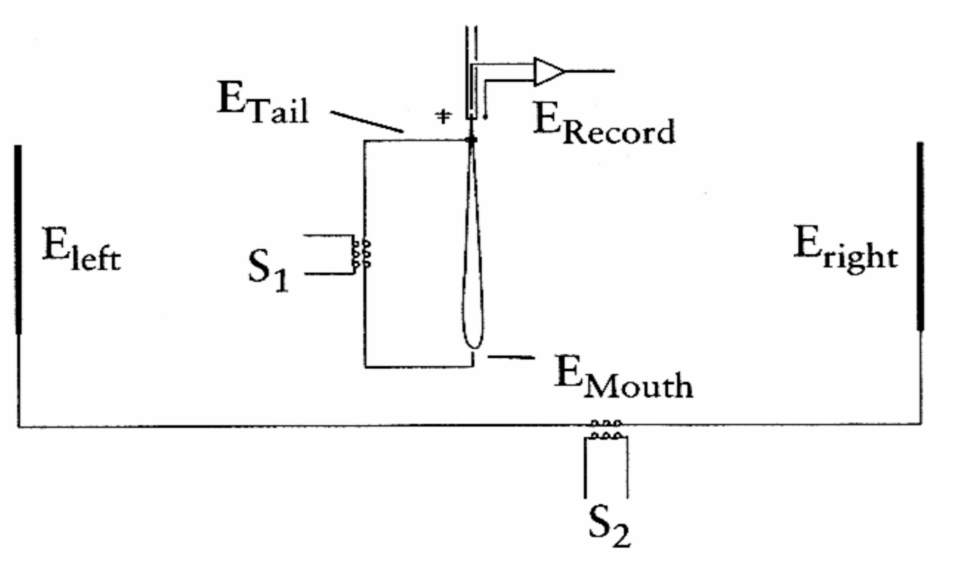
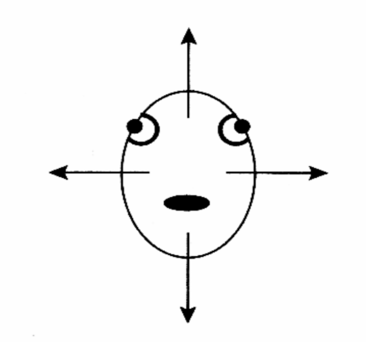
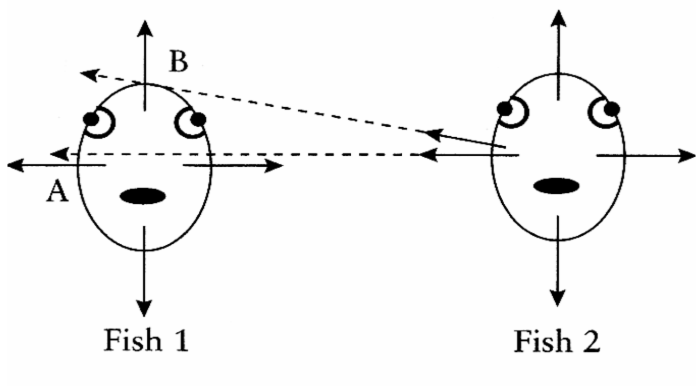
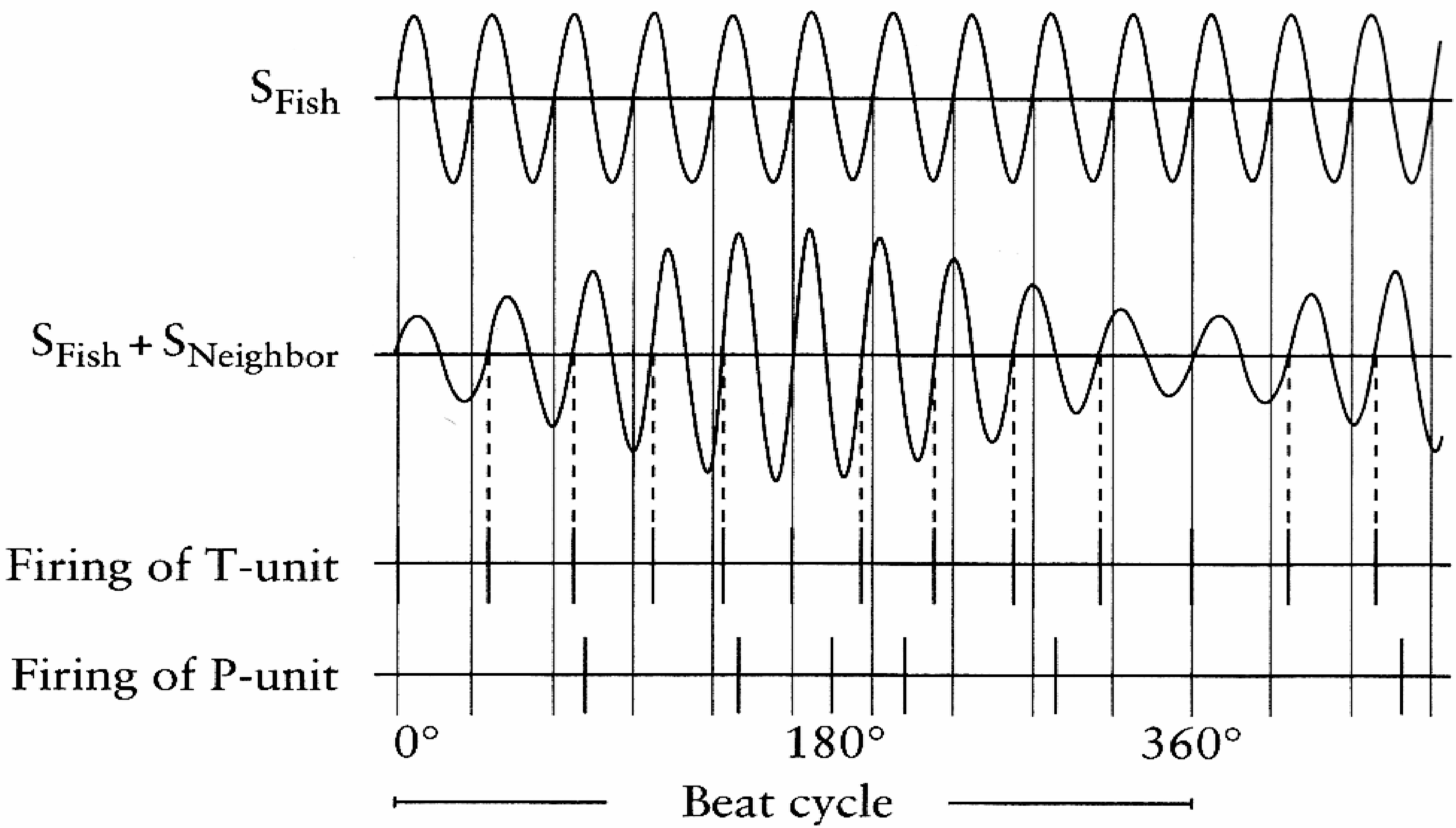




Hence: Variation of relative amplitudes S1/S2 across the body surface is important for JAR



How does the fish knows the sign of Δf ? That is, to shift ↑ or ↓ ?



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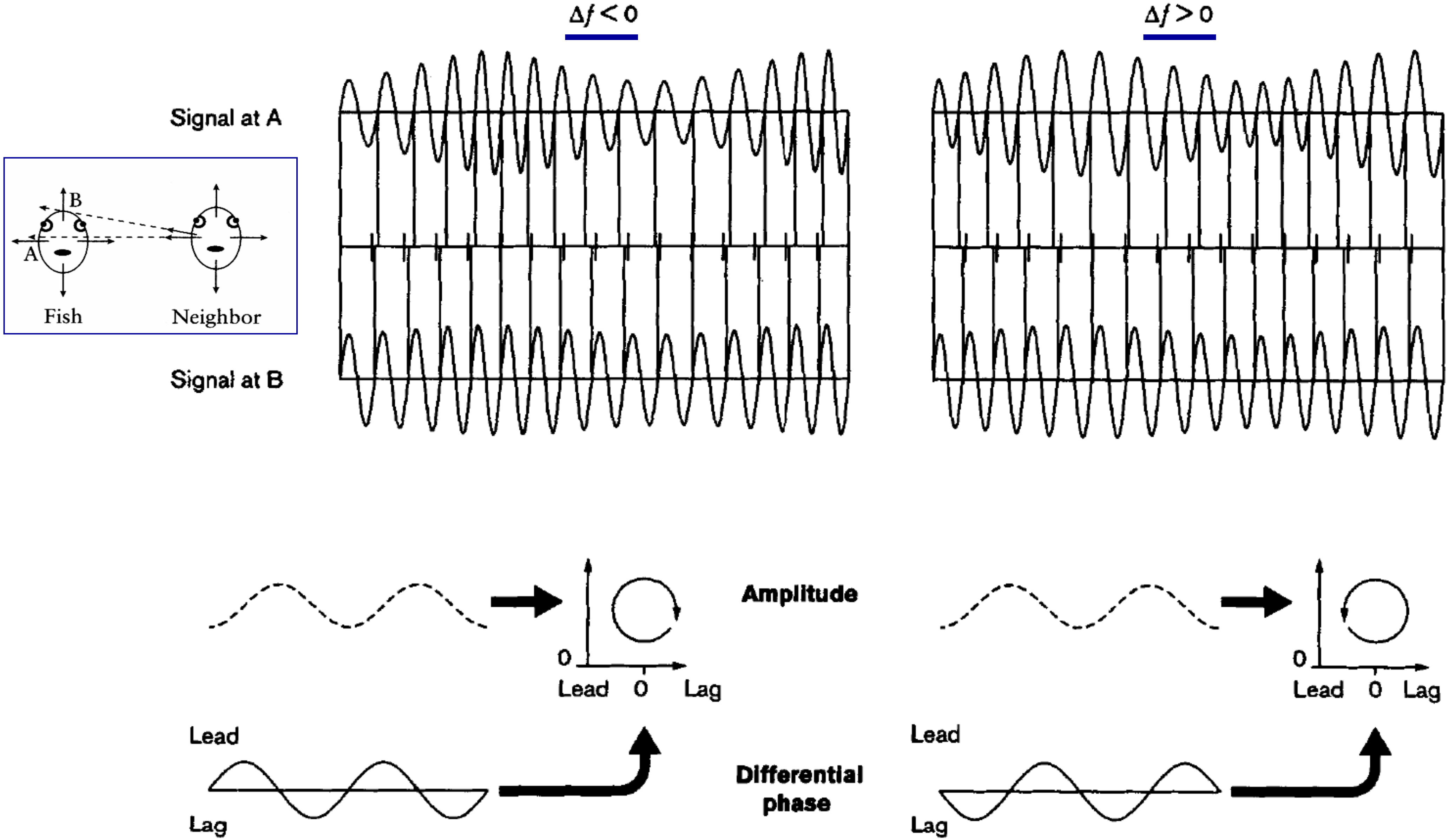

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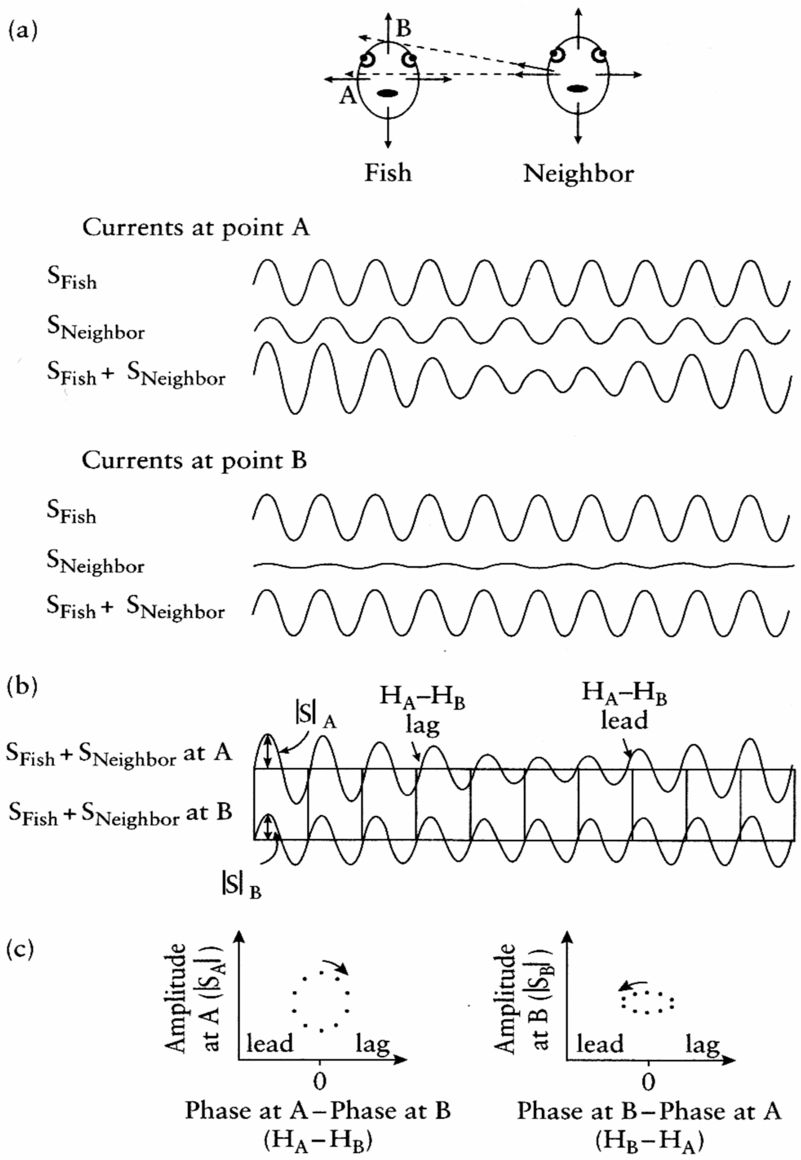
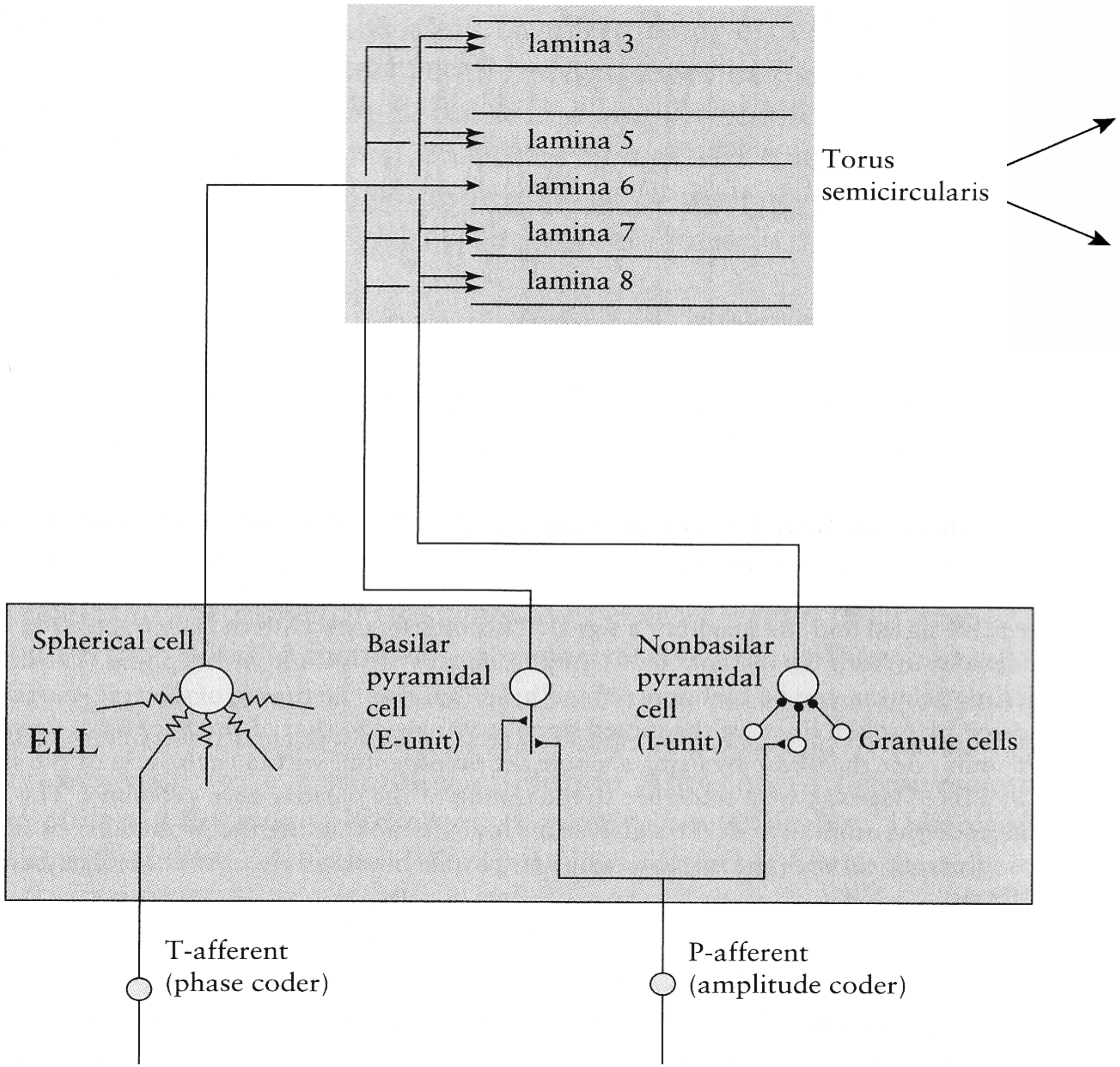


Neural circuits mediating JAR

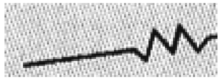


Lamina 6: Differential phase computation

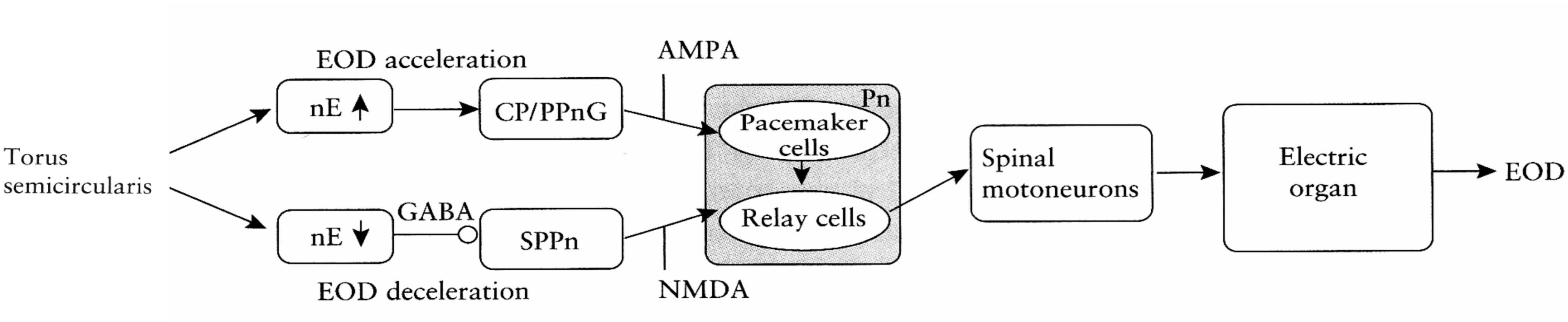
Laminas 5,7: Amplitude modulation computations

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

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

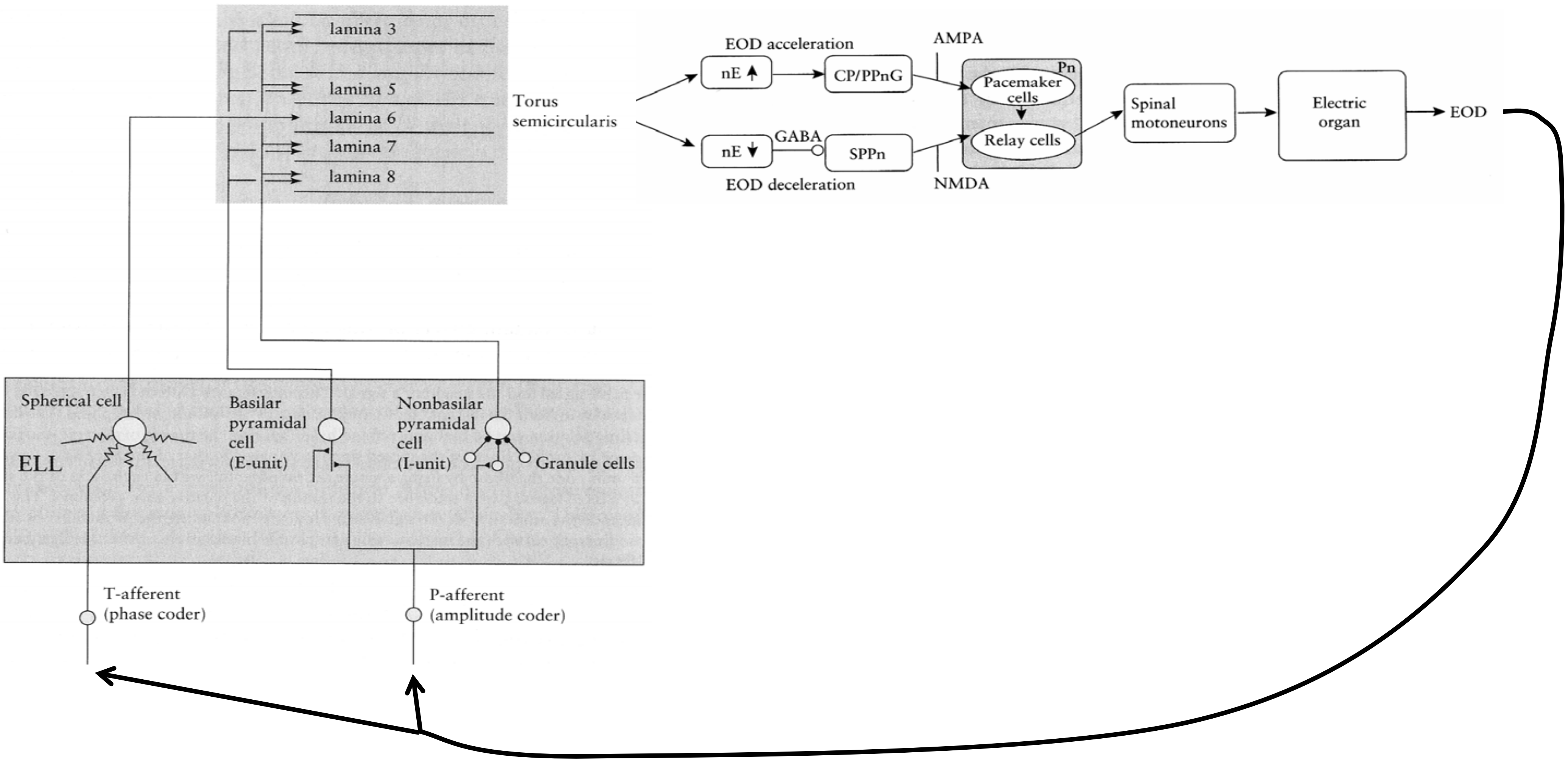

Electrical synapse

Neural circuits mediating JAR

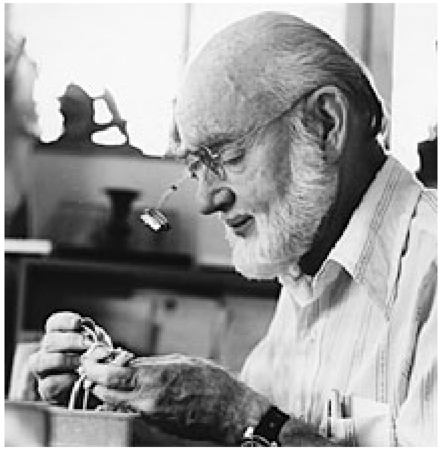


nE: *nucleus electrosensorius*: The first station where neurons are found that code for Δf irrespective of the geometric spatial arrangement of the jamming signal (i.e. no ambiguity)

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)