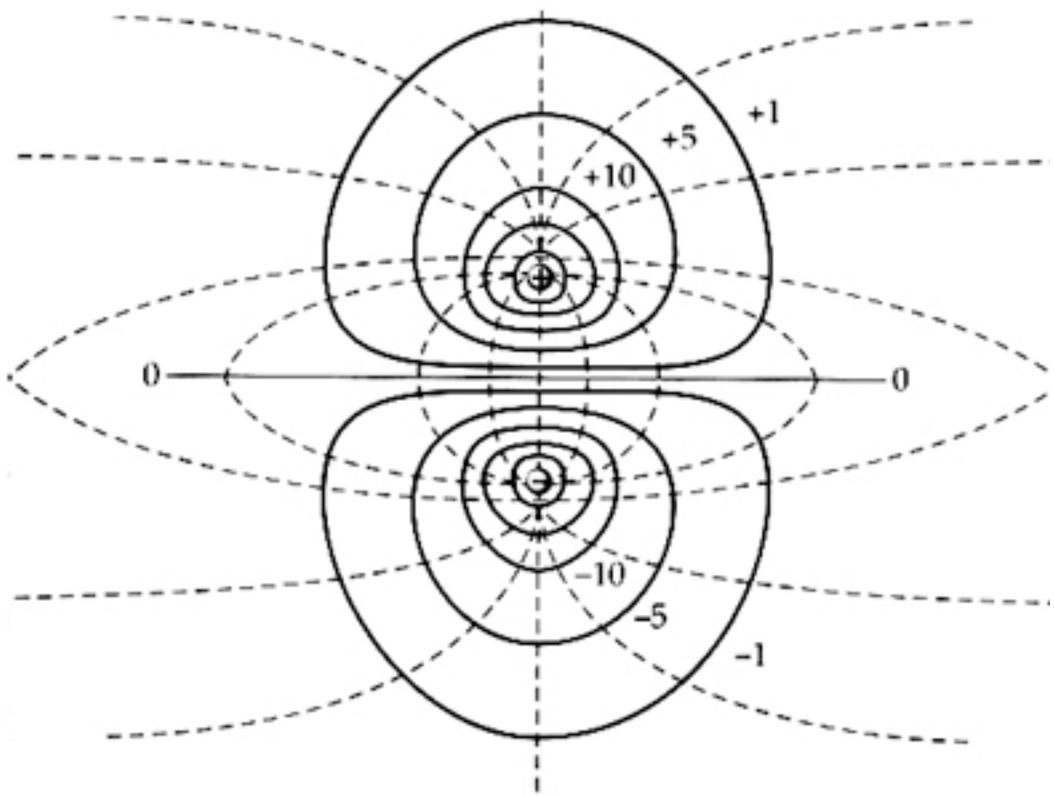
Electroreception

- Electric field properties
- Electroreception evolution
- Bioelectric field production
- Electrolocation
- Electrocommunication

Electric field



- Generated by separation of positive (electron deficit) and negative charges (e.g. a dipole such as a battery)
- Electric field lines (dashed) indicate direction and magnitude of force and electron flow
- Electric potential isoclines (solid) indicate strength of charge attraction or repulsion

Electric field properties

- Electric potential
  - measures the net attraction or repulsion of a charged particle at a specific location
  - measured in volts
  - always perpendicular to electric field
- Electric field
  - falls off with the cube of distance from a dipole
  - not useful over long distances
    - electrocommunication operates over a few meters
    - electrolocation over a distance of less than 1 m

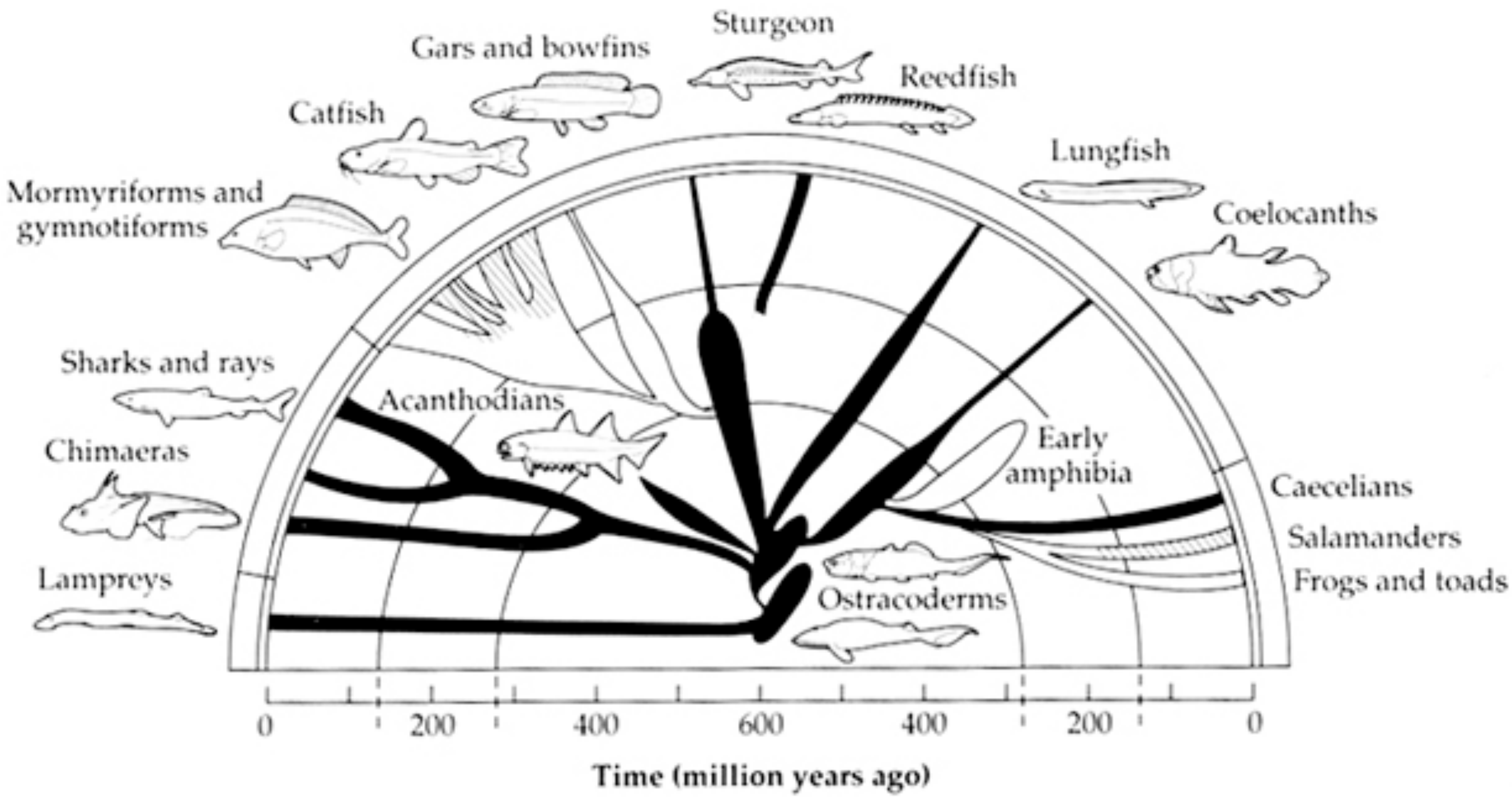
Effects of transmission media

- To detect an electric field there must be current, i.e. flow of electrons from + to -.
- Both vacuum and air act as insulators and do not conduct charges
- Water (with dissolved ions) does conduct charges
  - Salt water conducts better than fresh water
- Permits formation of electric currents that can be detected

Bioelectric fields

- Cells maintain an electrochemical gradient of -60 mV to -80 mV across the cell membrane
- Nerve cells generate an action potential that causes a change of 130 mV over a ms.
- Consequently, all living animals produce very weak electric fields
- These can be detected by a variety of predatory animals, such as sharks, rays, catfish, platypus, some salamanders

Electroreception evolution



Pattern suggests that electroreception evolved 600 MYA

Lungfish use bioelectric cues

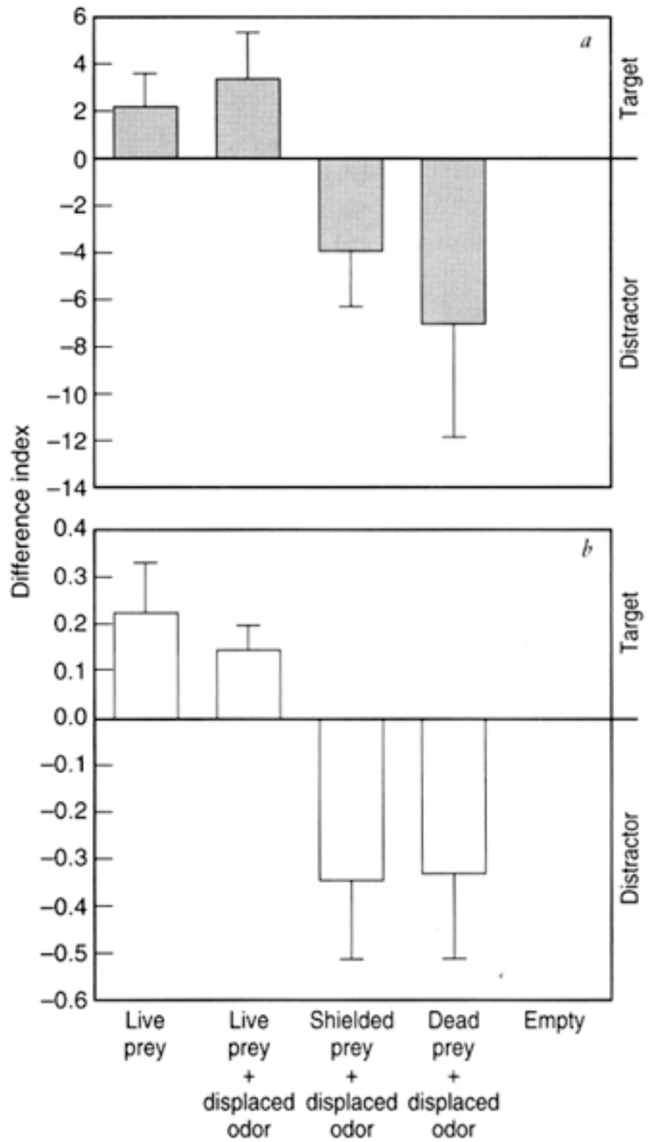
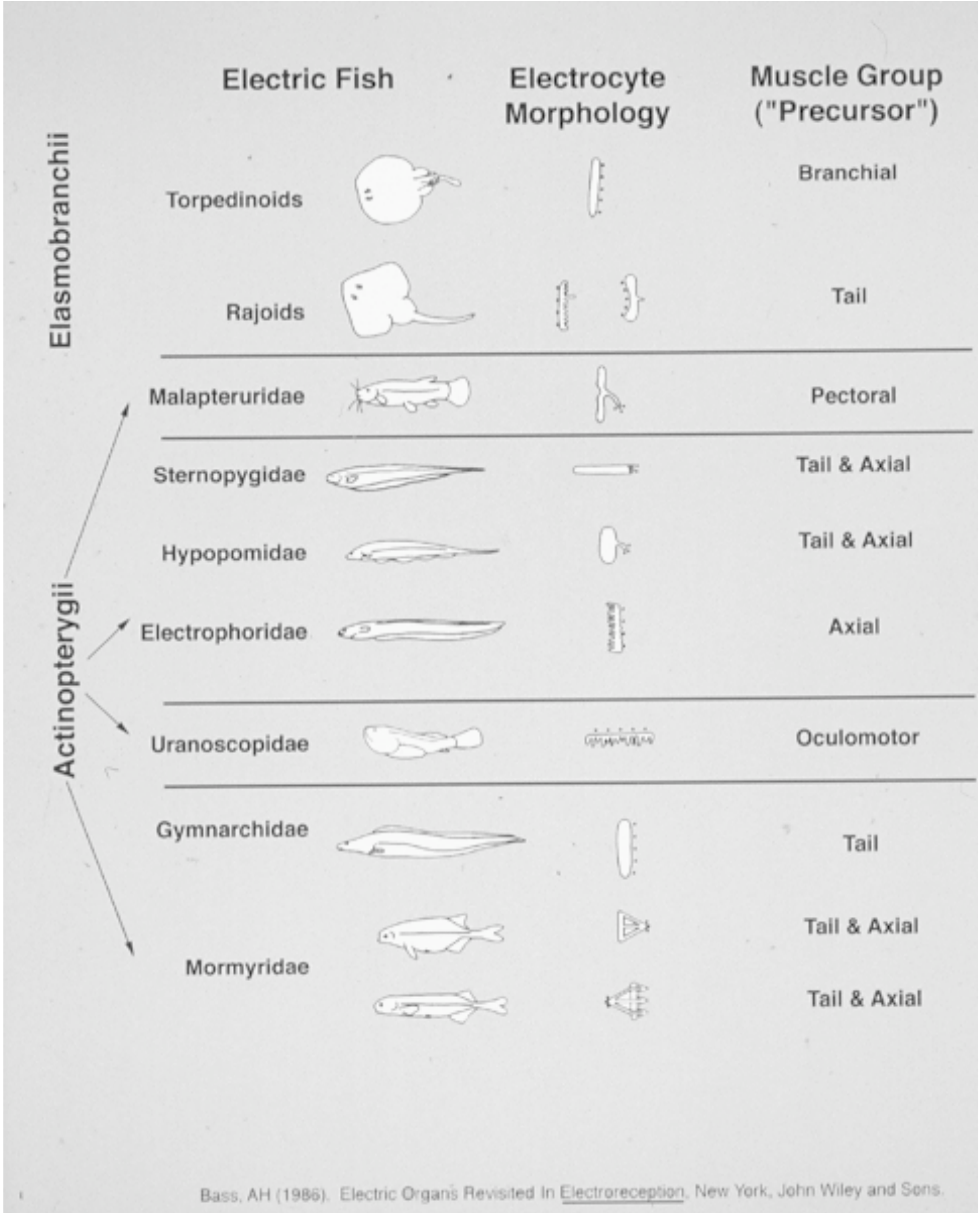


FIGURE 12.8 The results of experiments demonstrating that Australian lungfish can locate their prey by using the electrical field generated by any living organism in seawater. The results are shown as a difference index, which is the amount of foraging activity above the target, the hidden chamber where the prey was located, and the distractor, the region of the aquarium to which the prey's odor was displaced. A positive score indicates that the fish were foraging above the target; a negative score indicates that the fish were foraging over the distractor. The distractor indexes are shown for (*a*) the foraging intensity and (*b*) the foraging accuracy of each treatment. Although the lungfish can and do use chemical cues to locate prey, bioelectric cues are more important. (From Watt, Evans, and Joss 1999.)



Electric field production: electrocytes

- Electrocytes are modified muscle or nerve cells
- Produce higher voltages than simple nerve cells
- Have evolved independently in several fish families
  - Duplicate sodium channel gene is expressed only in electrocyte (Zakon 2006 PNAS)

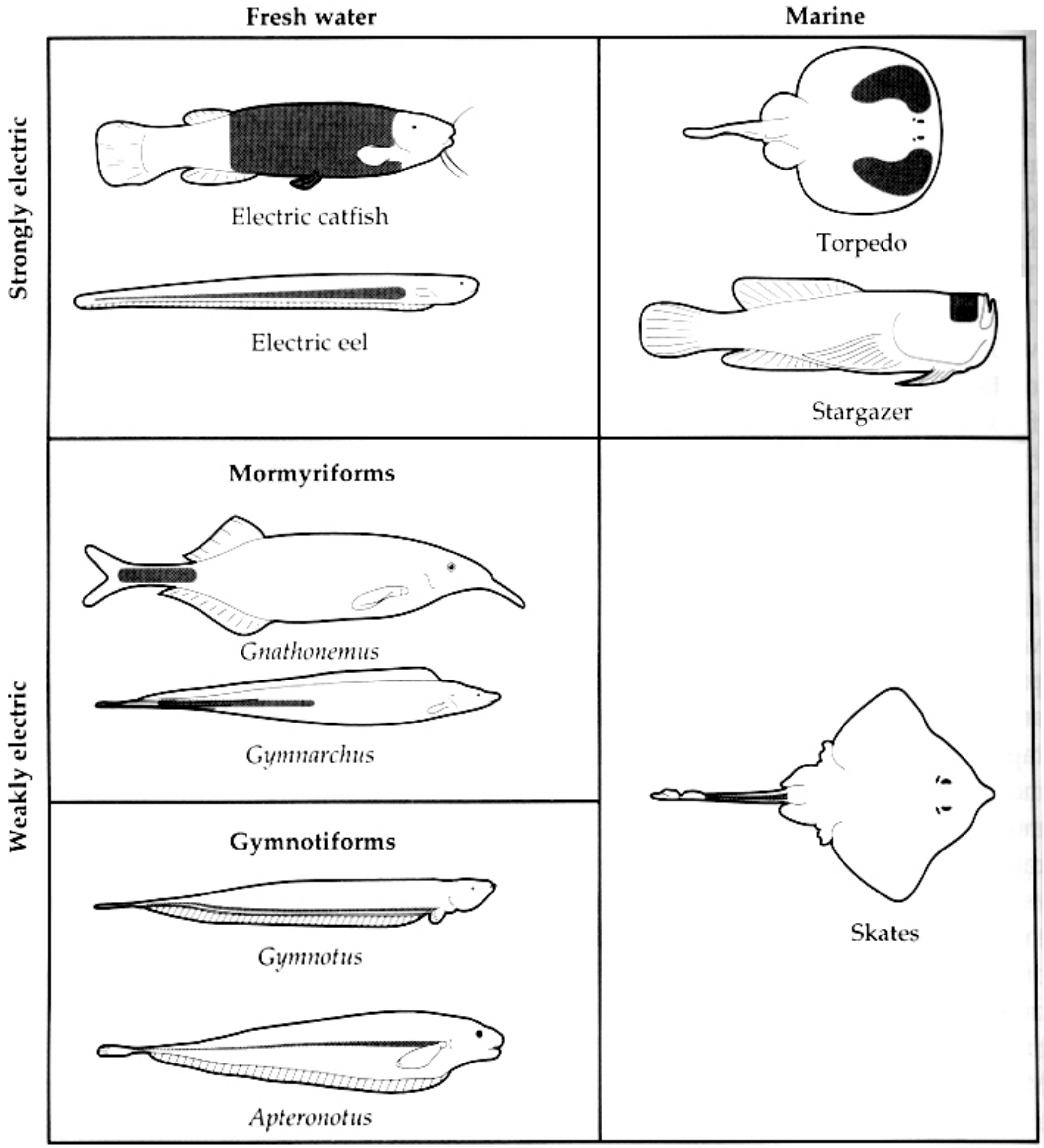


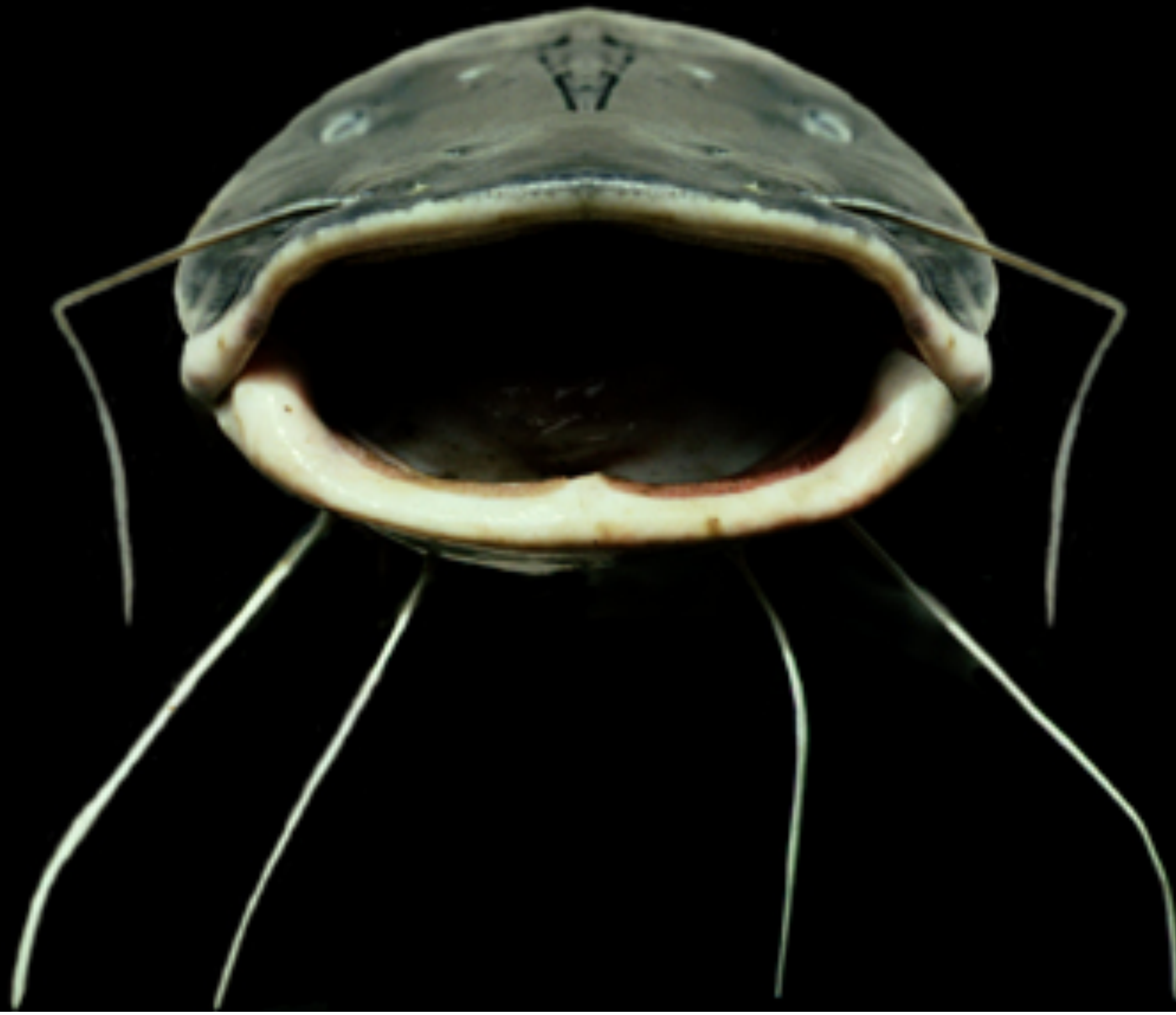
Figure 11.4 Shape and disposition of electric organs in fish. Electric organs are stippled or, if only thin rods, indicated by dotted lines. Taxa are divided according to strength of electric discharge (left axis) and habitat (top axis). Note the larger organ size in strongly electric species, and the long, thin shape of the electric organ in freshwater electric eel when compared to the short, fat shape of the organ in the marine torpedo. (After Bennett 1970.)

Electric field production: electric organs

- Electric organs contain tens to thousands of electrocytes arrayed in series
- Produce electric organ discharges (EODs)
- Voltage ranges from a few V to over 700 V

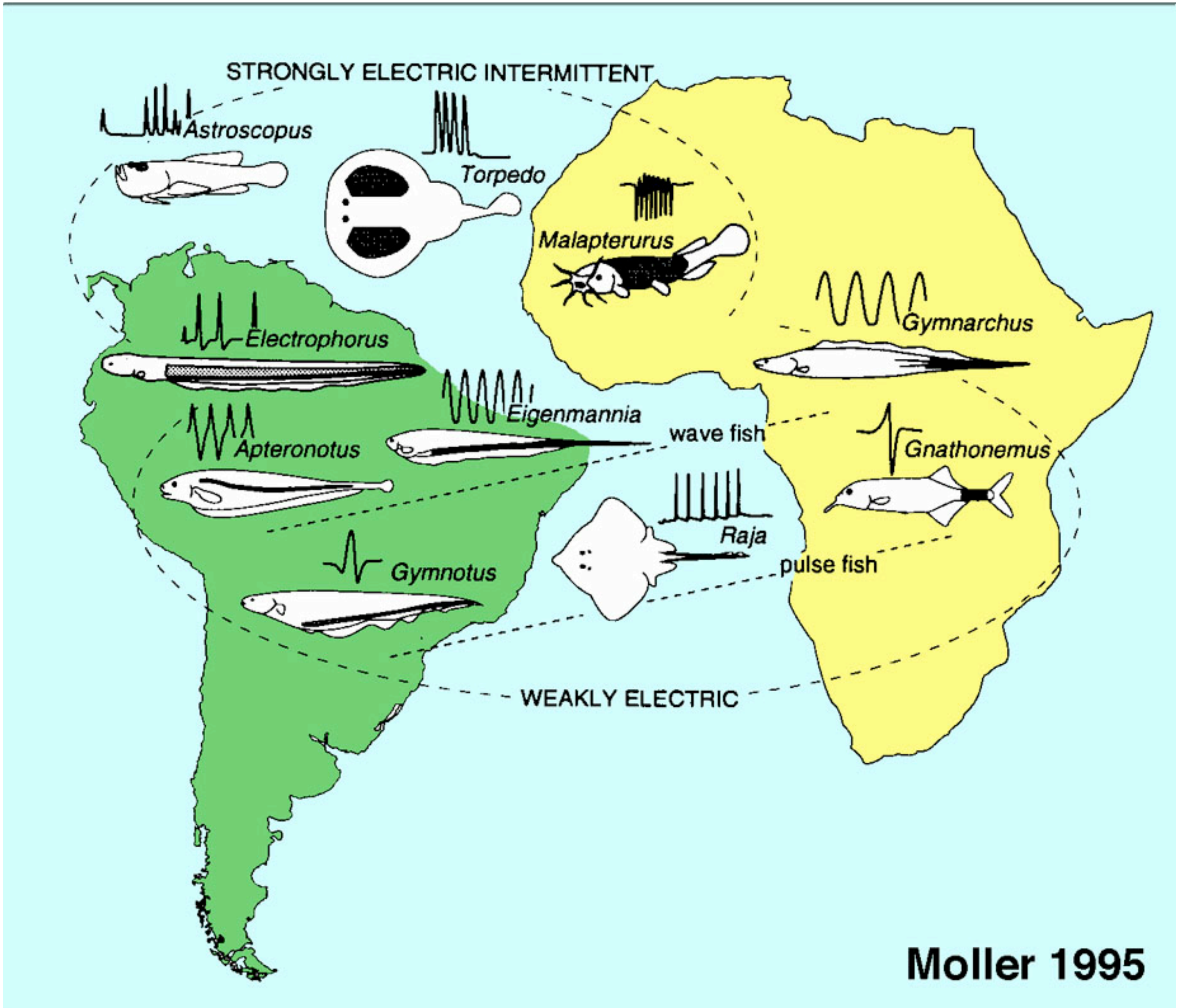
Electric catfish

Malapterurus



Electric eel
Electrophorus electricus

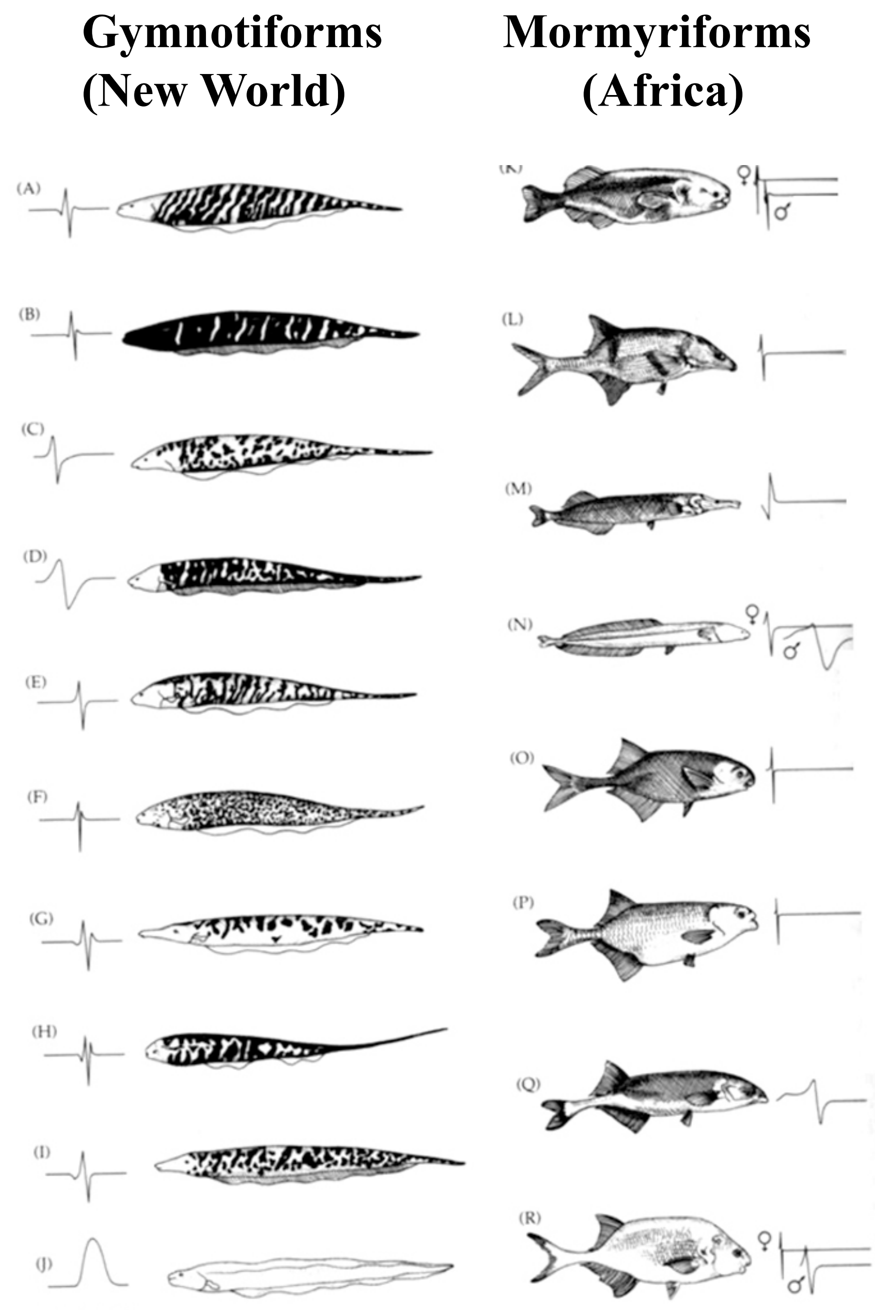
Electric organ has up to 6000 electrocytes and produces 720 volts
Can stop your heart, causing you to fall down and drown


STRONGLY ELECTRIC INTERMITTENT
Astroscopus
Torpedo
Malapterurus
Electrophorus
Gymnarchus
Eigenmannia
Apteronotus
wave fish
Gnathonemus
Raja
pulse fish
Gymnotus
WEAKLY ELECTRIC
Moller 1995

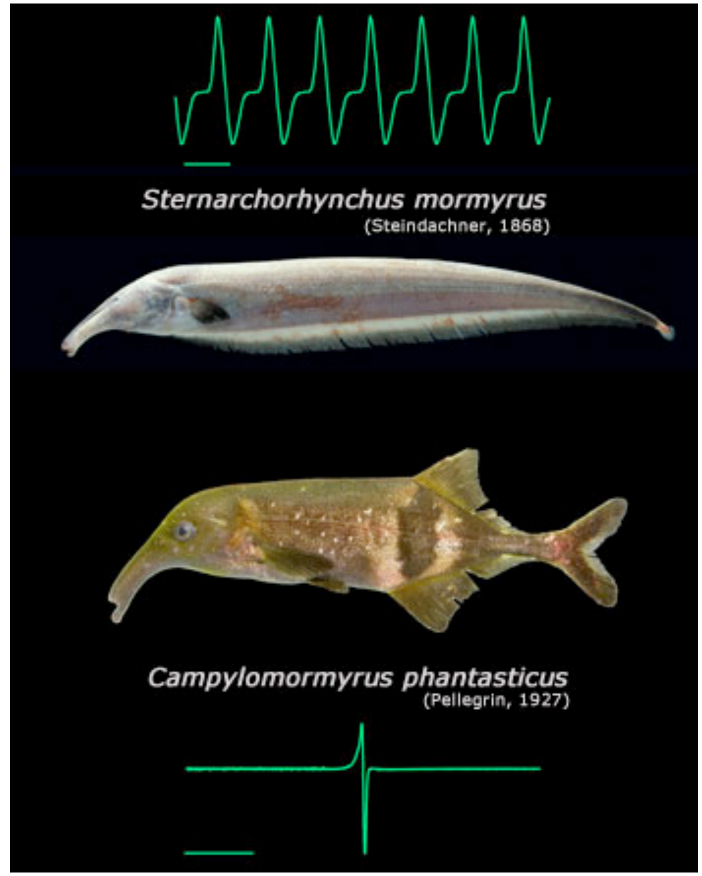
Freshwater electric fish

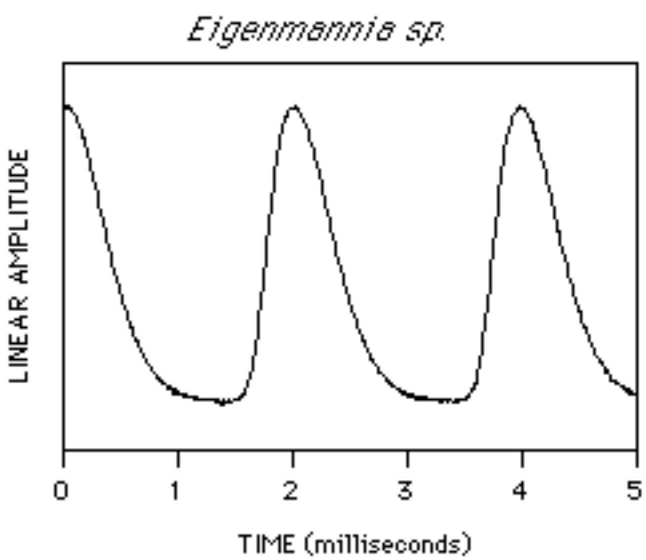
- Two separate lineages in tropics
  - found in muddy or dark water
  - often many sympatric species
- Wave EOD’s:
  - Includes Apteronotid and Sternopygid (Gymnotiform) and Gymnarchis (Mormyriform)
  - Long duration EOD
  - Steady discharge rate, AC
  - High maximal rates (300-1700 Hz)
- Pulse fish (most spp):
  - Short duration EOD
  - Variable rates, DC
  - Low maximal rates (50-100 Hz)

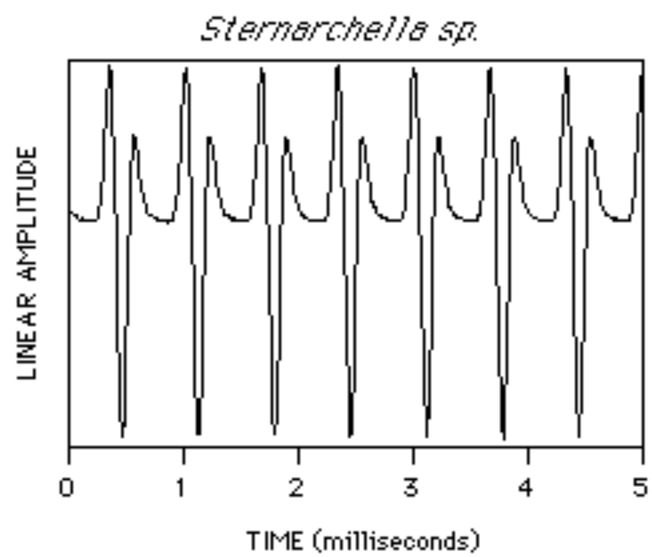
Today show video clip



Wave vs pulse EOD species







Electric field of an electric fish

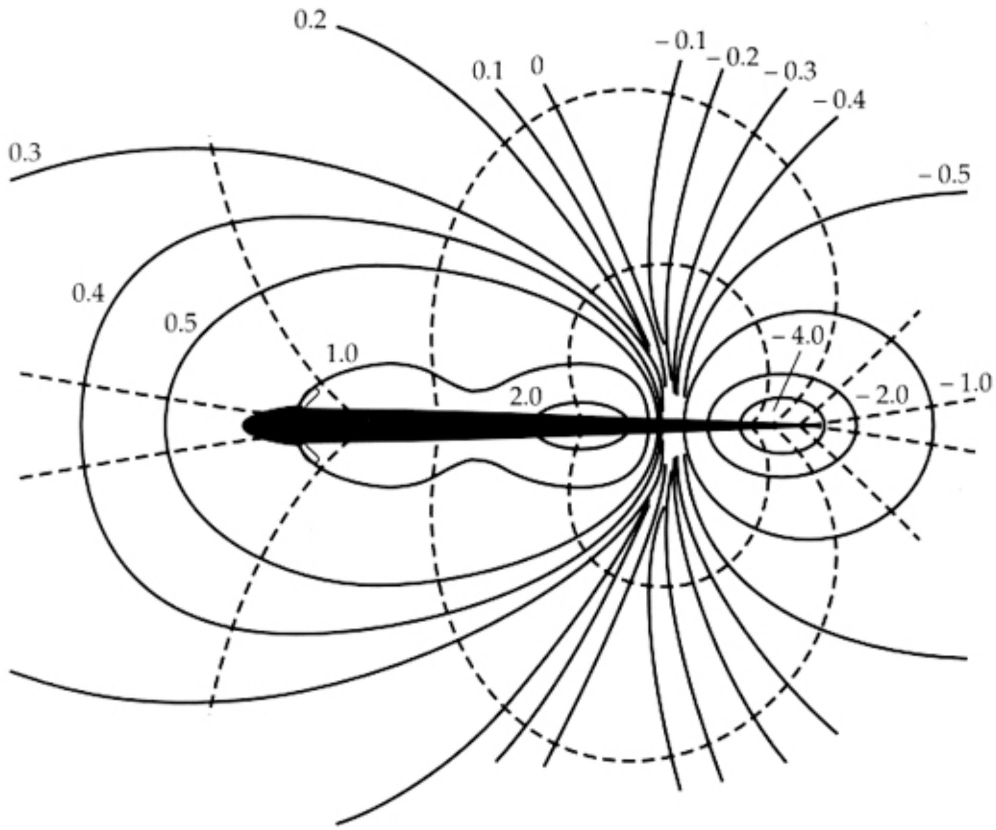
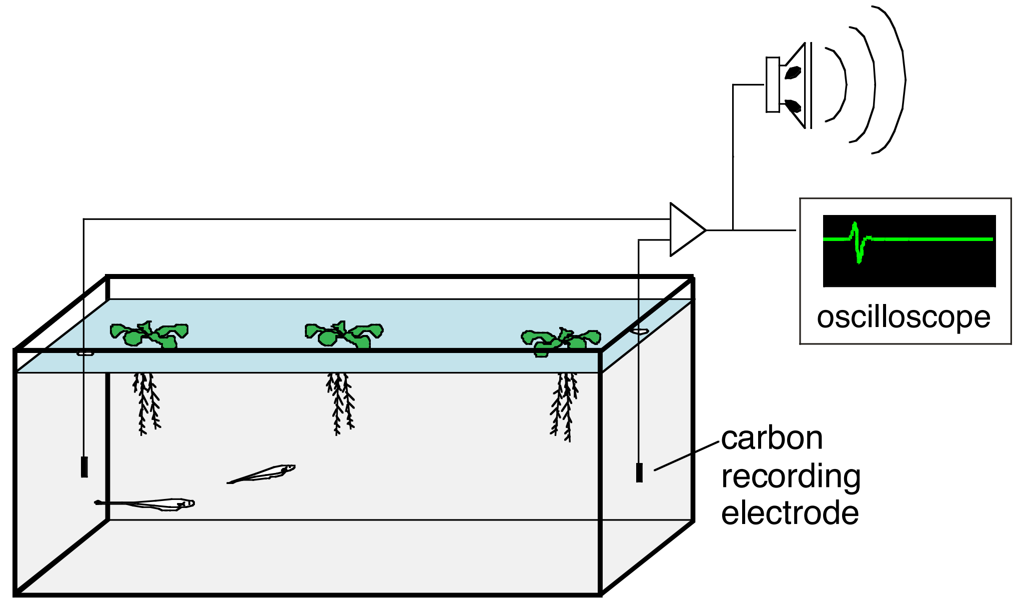


Figure 11.8 Electric field (dashed) and isopotential (solid) lines around weakly electric fish. Field shown with values of isopotential lines (V) at peak of EOD. Note the curvature of the 0 potential line away from the line perpendicular to the body that would be expected if the fish were a simple dipole. Note also the asymmetry in shapes and sizes of the isopotential lines at opposite ends of the fish's body. (From Heiligenberg 1977, © Springer-Verlag.)

Increasing tail length acts to increase charge separation in a dipole

This will extend isopotential lines further from the body

EOD movies

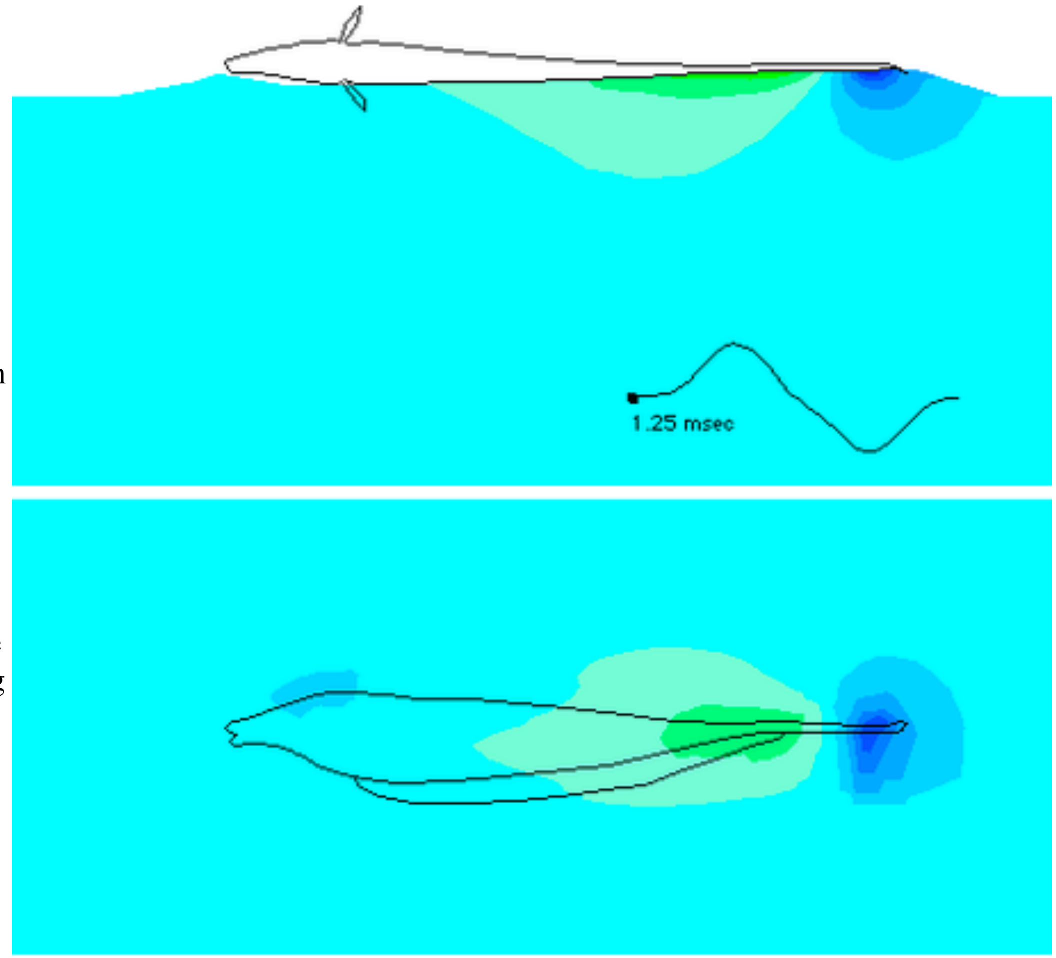


Weakly electric fish generate weak (<1 V/cm) high frequency (0.1-10 kHz) electric fields which they use to locate and identify nearby objects and to communicate with other electric fish

EOD measurements are represented as pseudocolor QuickTime movies, with light blue representing zero; green - yellow - red represent successively greater positive values; and blue - dark blue - violet representing successively negative values of the potential and field magnitude.

From http://www.fiu.edu/~stoddard/lab.html

Pulse EOD discharge of *Apteronotus leptorhynchus* (brown ghost knife fish)

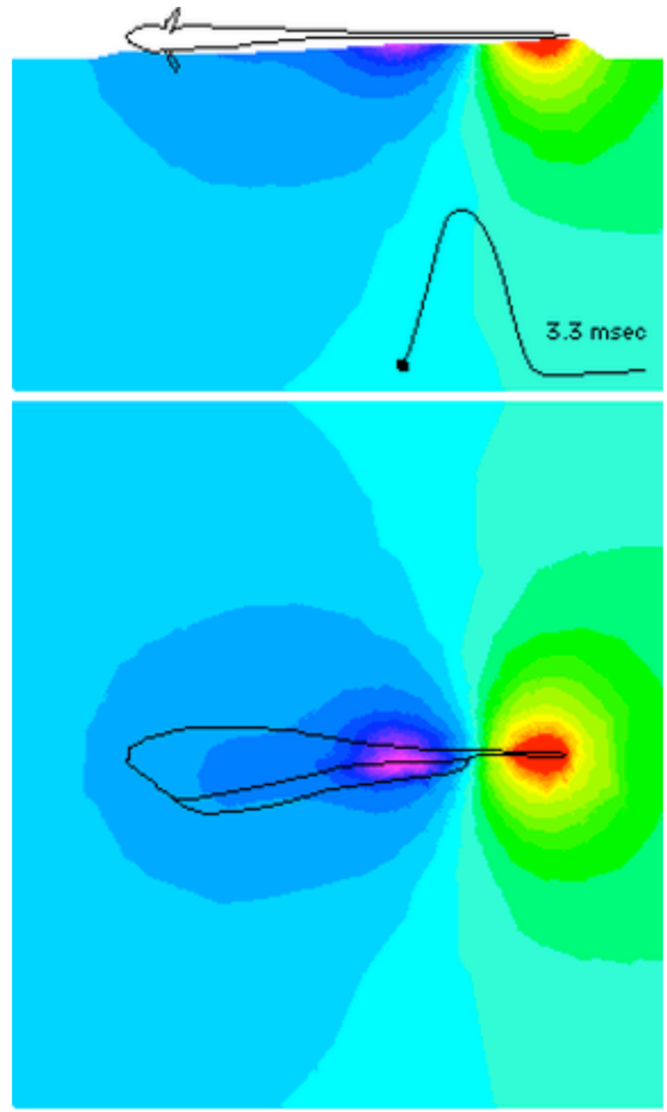


The top is a view looking down at the fish's midplane; bottom shows the potential in the vertical plane & on the fish's skin. The latter was measured with flexible electrodes. The asymmetry below the tail is an interpolation artifact due to low density of measurement points in this region. The inset shows the waveform recorded between two electrodes approximately 8 cm in front of the head and behind the tail, the dot shows the instantaneous phase. In contrast to a simple dipole, the peaks and zero crossings propagate caudally along the body, suggesting that segments of the electric organ are active sequentially instead of synchronously. The velocity of the peaks, approximately 5.10 cm/msec, is consistent with the expected conduction velocity of the spinal relay axons driving the electric organ. The fact that local peaks are present along the body suggests the electric organ "leaks" current radially out its sides, and is not perfectly insulated to just channel current out its ends.

Wave EOD discharge of *Eigenmannia virescens* (the glass knife fish)

Glass knife fish *(E. virescens)*

EOD: 250-500 Hz



Eigenmannia virescens is the only species we have mapped that has a simple EOD resembling an oscillating dipole. It is also the lowest frequency fish we have studied, with fundamental frequency of 300 Hz. Waveforms rostral to a stationary "zero plane" near the longitudinal midpoint of the electric organ are in phase with each other and are inverted or 180 degrees out of phase with caudal waveforms. Activation along the length of the electric organ is synchronized, implying the electrocytes fire in unison. Physiological and anatomical studies have shown that electromotor axons that project to anterior electric organ segments are thinner and slower than those projecting to posterior segments. Apparently path length compensation works well in this low frequency fish. The EOD amplitude peaks also reveal the ventral location of Eigenmannia's electric organ.

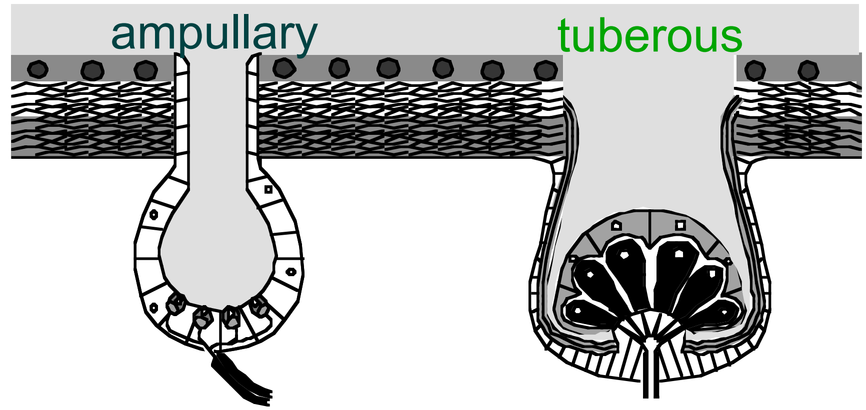
Amidst its uniform field, Eigenmannia exhibits an exceptional social behavior called the jamming avoidance response or JAR, which shifts the fish's frequency away from a superimposed jamming signal. The JAR requires detailed comparisons of spatio-temporal information across different regions of the body surface, with performance proportional to the surface area.

Ampullary organ

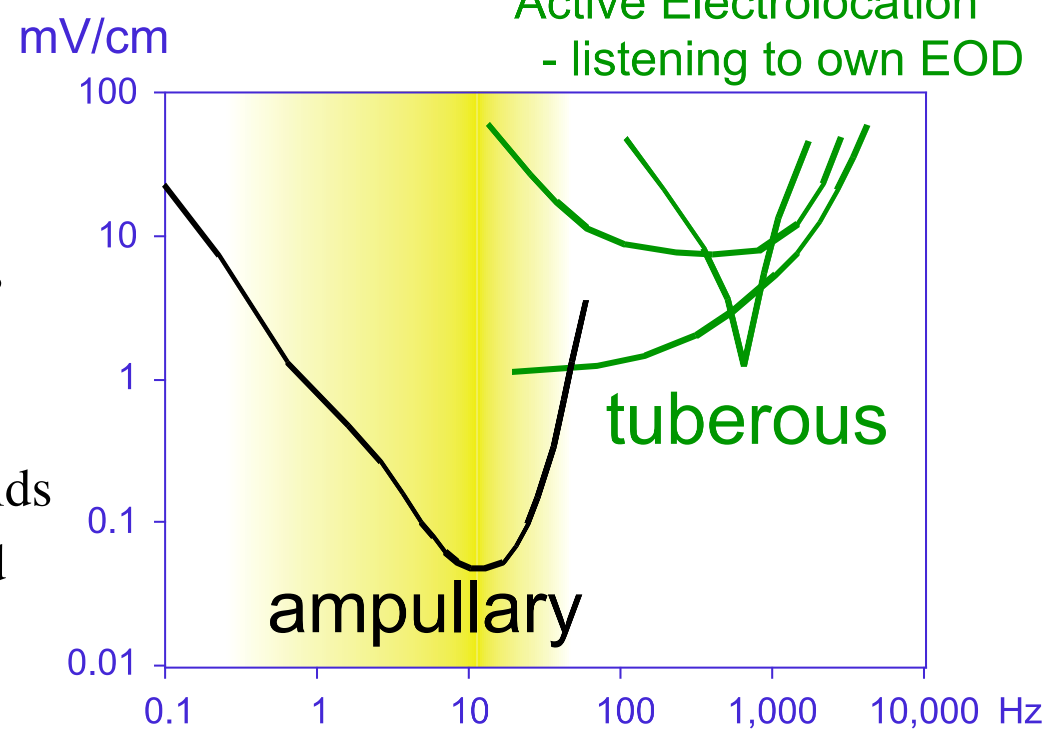
- Sensory cells at end of tubes sense current
- Longer tubes provide larger electric potential between medium and interior of body
- Tubes radiating from same source compare voltages between different surface points
- Allows formation of potential maps across the skin surface

Types of Electroreceptors

- Ampullary
  - all electroreceptive fish
  - detects weak electric fields
- Tuberous
  - Gymnotiforms & Mormyrids
  - used for electolocation and communication



Active Electrolocation
- listening to own EOD



Passive Electrolocation
- including predatory eavesdroppers

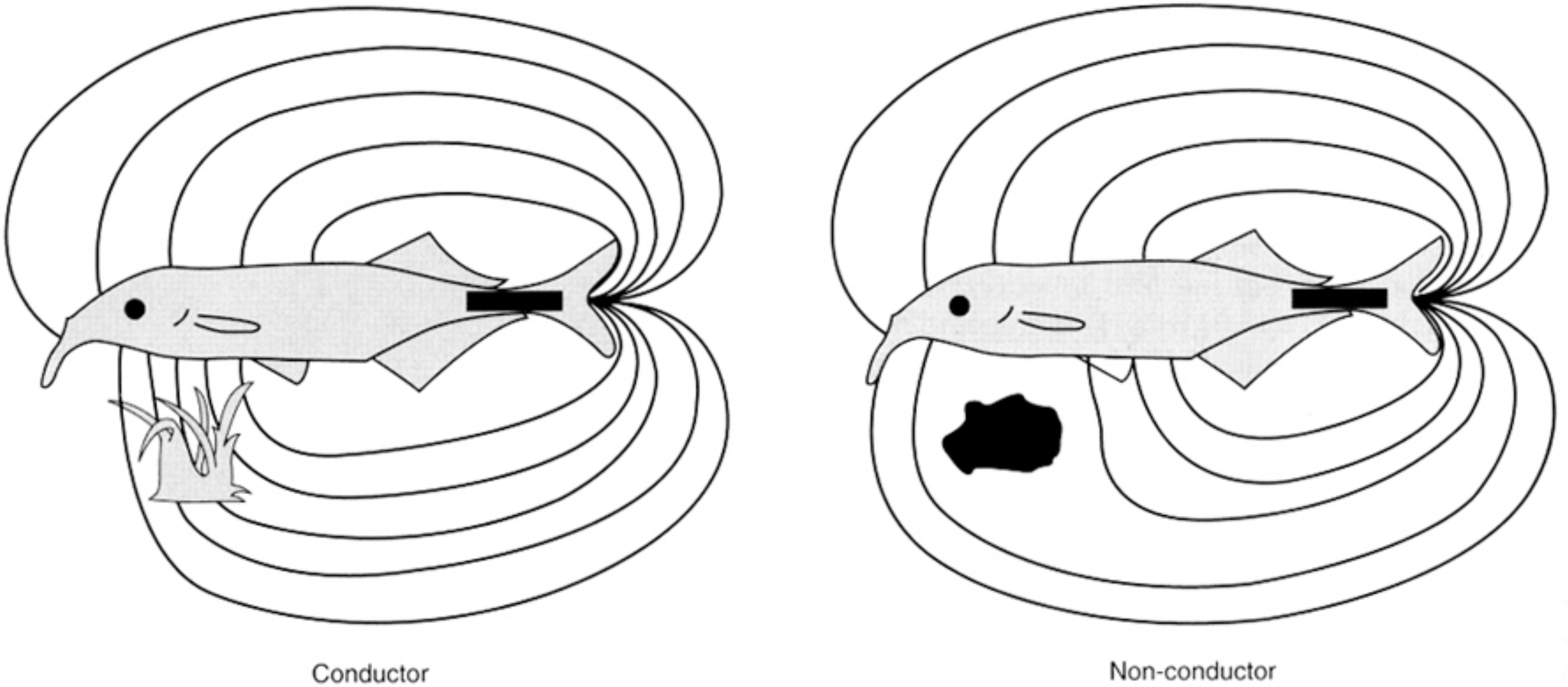
Physiology adapted from Dunning 1973
Shumway & Zelick 1988

Tuberous electroreceptor organs

Local perturbations are detected by electroreceptors on the fish's body surface. The body of *Apteronotus* is covered with approximately 15,000 specialized tuberous electoreceptor organs for detecting perturbations in it's own electric field. Each electroreceptor organ consists of a small (approx 0.1 mm diameter) pit in the skin with a cluster of sensory cells in the bottom of the pit. The receptor cells act like miniature voltmeters and monitor the voltage drop across the skin (the so-called transdermal potential). The figure to the right shows a cross-sectional view of a single tuberous electroreceptor organ. Each electroreceptor organ gives rise to a single afferent nerve fiber which conveys sensory information to the brain.

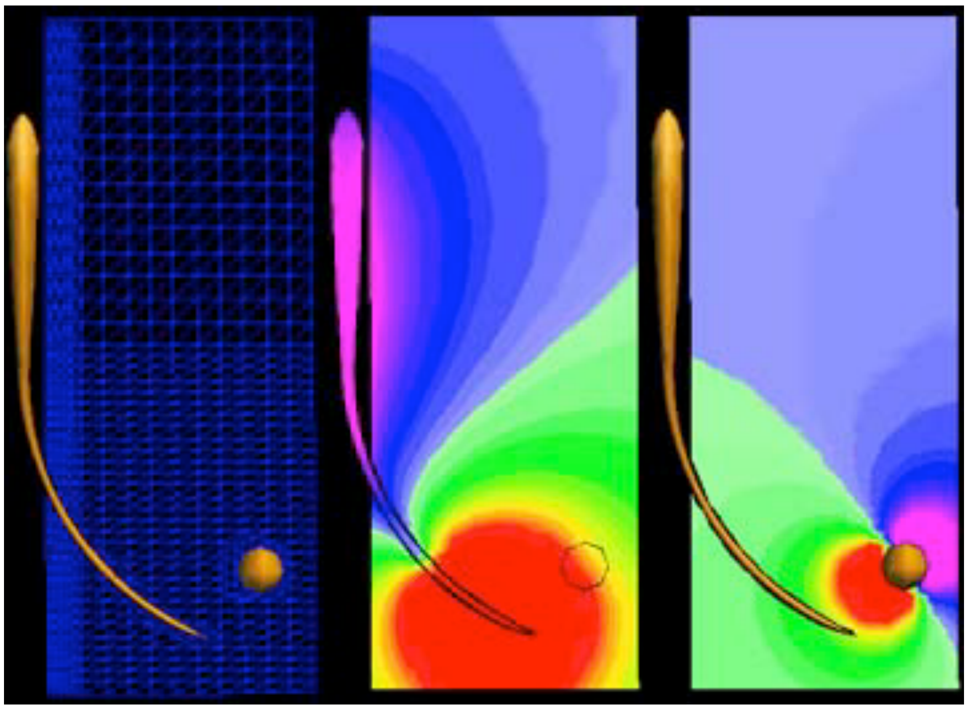
The electroreceptor organ density is highest in the head region of the fish (approx. 10-20 per mm2) and we sometimes think of the head as the "electrosensory fovea." The density is lower on the trunk (approx. 1-3 per mm2). On the trunk, the density is higher along the dorsal edge of the fish than on the lateral body surface. This turns out to be important because we find that prey detection typically occurs along the dorsal edge (Nelson and MacIver, 1999).

Electrolocation



- If object is more conductive than the water (e.g., grass, fish),
  - electric current will be shunted through the object because it represents a path of lower resistance.
  - Gives rise to "electrical bright spot" on the skin
- If object is less conductive than the water (e.g., a rock),
  - electric current will be shunted around the object
  - Gives"electrical shadow" on the skin

Electric field modification by objects



The left frame shows the 3-d fish body and object, as well as the points in the midplane at which the electric potential was simulated. The potential solution was linearly interpolated over the triangles shown in the blue mesh. The middle frame depicts the head-negative peak of the EOD, with the rainbow color scale ranging from purple (<= -10 mV) to red (>=10 mV), and the lightest blue at 0 mV. The rightmost frame shows the difference that the object makes: when we subtract the field simulated without the object from the field with the object present, the object's effect can clearly be seen as an induced dipole field. (The potential difference has been magnified by a factor of 100 to make it visible on this color scale.)

Electrical ranging of a sphere

Distance can be determined from the magnitude of the field distortion, and the size of the distortion.

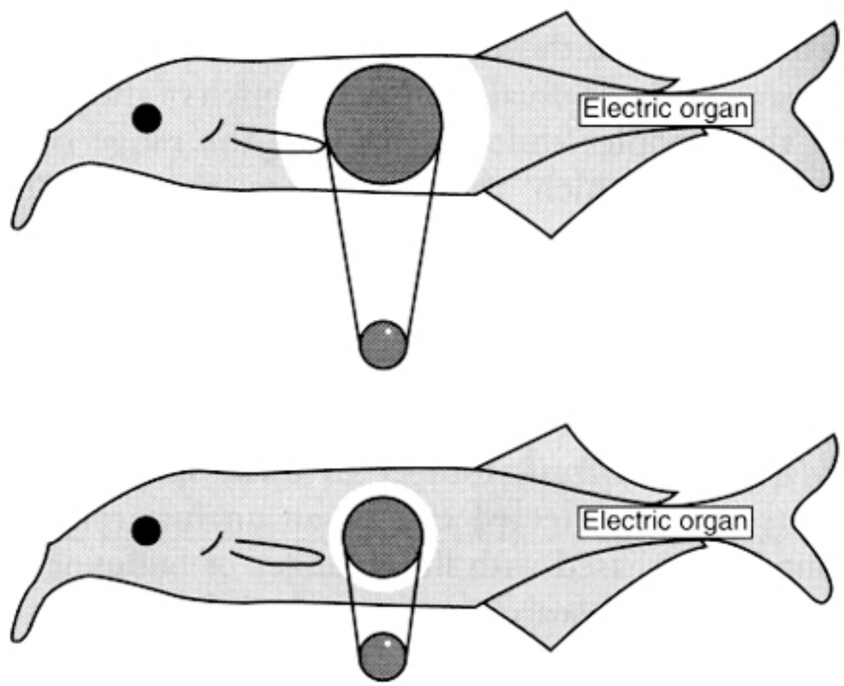


FIGURE 10.33 The electrical image of a metal sphere at different distances from the fish. The size (width) of the electrical image increases with distance. The amplitude differences in the degree of distortion of the electrical field between the center and the periphery of the electrical image decrease with increasing distance. (From von der Emde 1999.)

Electrical imaging and conductance

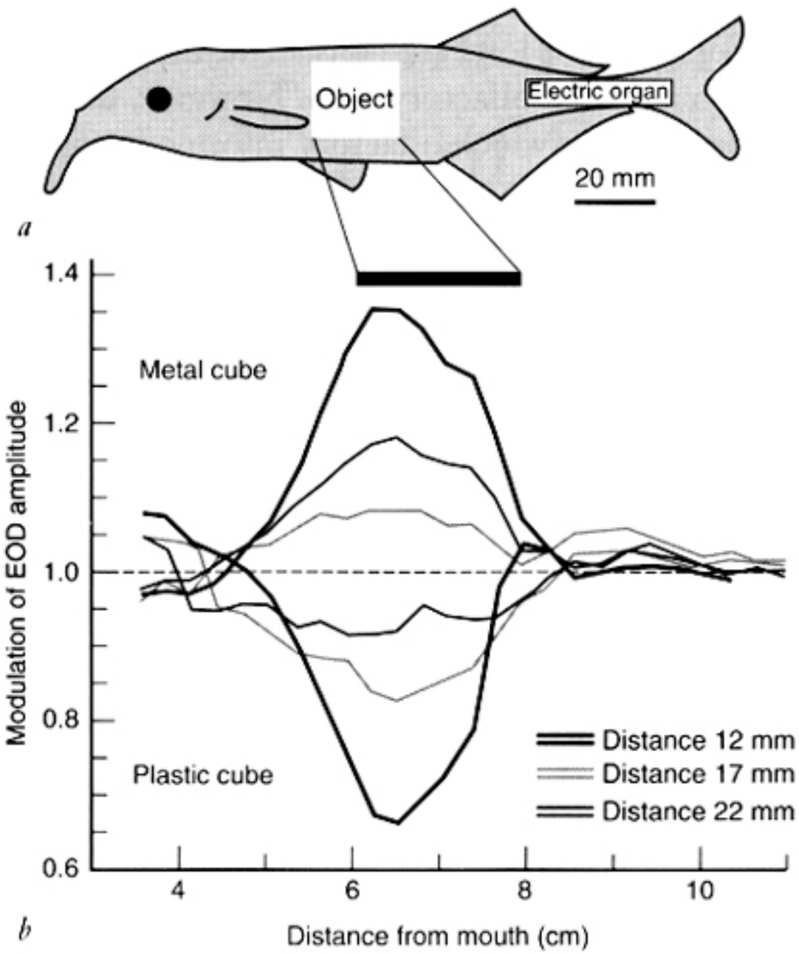
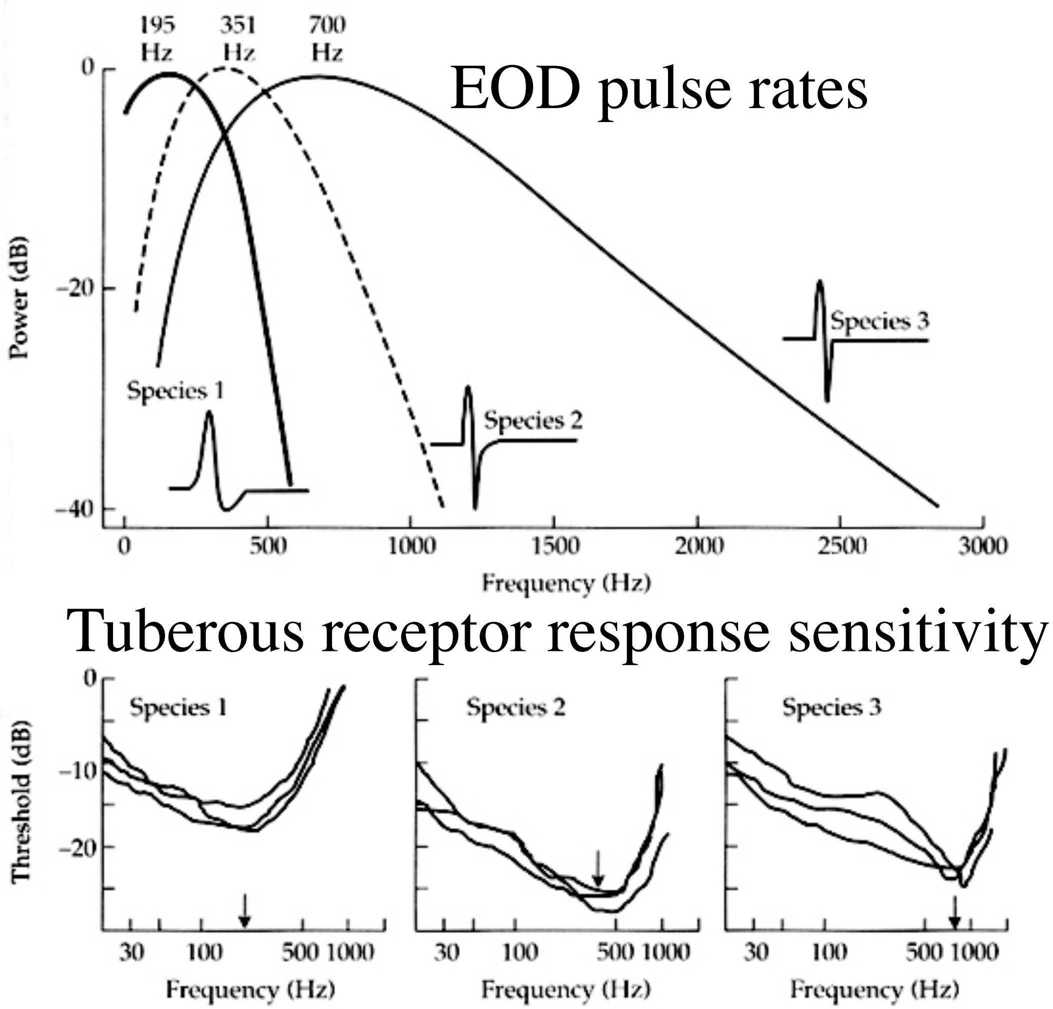


FIGURE 10.34 (*a*) A weakly electric fish, *Gnathonemus petersii*, with a 2-cm cube positioned for electrical image measurement. (*b*) The electrical images of a metal or plastic cube at three distances from the fish's surface, measured at the midline. The electrical image of the metal cube is shown as a peak and the image of the plastic cube is shown as a trough because metal (a conductor) pulls the lines of force together and plastic (a nonconductor) spreads them out. Regardless of the composition of the cube, the width of the electrical image increases with increasing distance. The difference in amplitude between the center and the periphery of the image gets smaller with increasing distance. The fish uses the ratio of two features of the image—size and the amplitude differences between the core and the rim—to determine the distance of an object (From von der Emde 1999.)

Social communication

- Used by nocturnal species or in murky habitats
- Used to defend territories, attract and court mates, recognize species, sex or individual ID
- Use modulation of discharge rate in aggression, courting, or to denote dominance hierarchies
- Jamming avoidance reflex - individuals will alter discharge rates to avoid overlapping neighbors
- Limited to about 1 m, often used in concert with acoustic signals

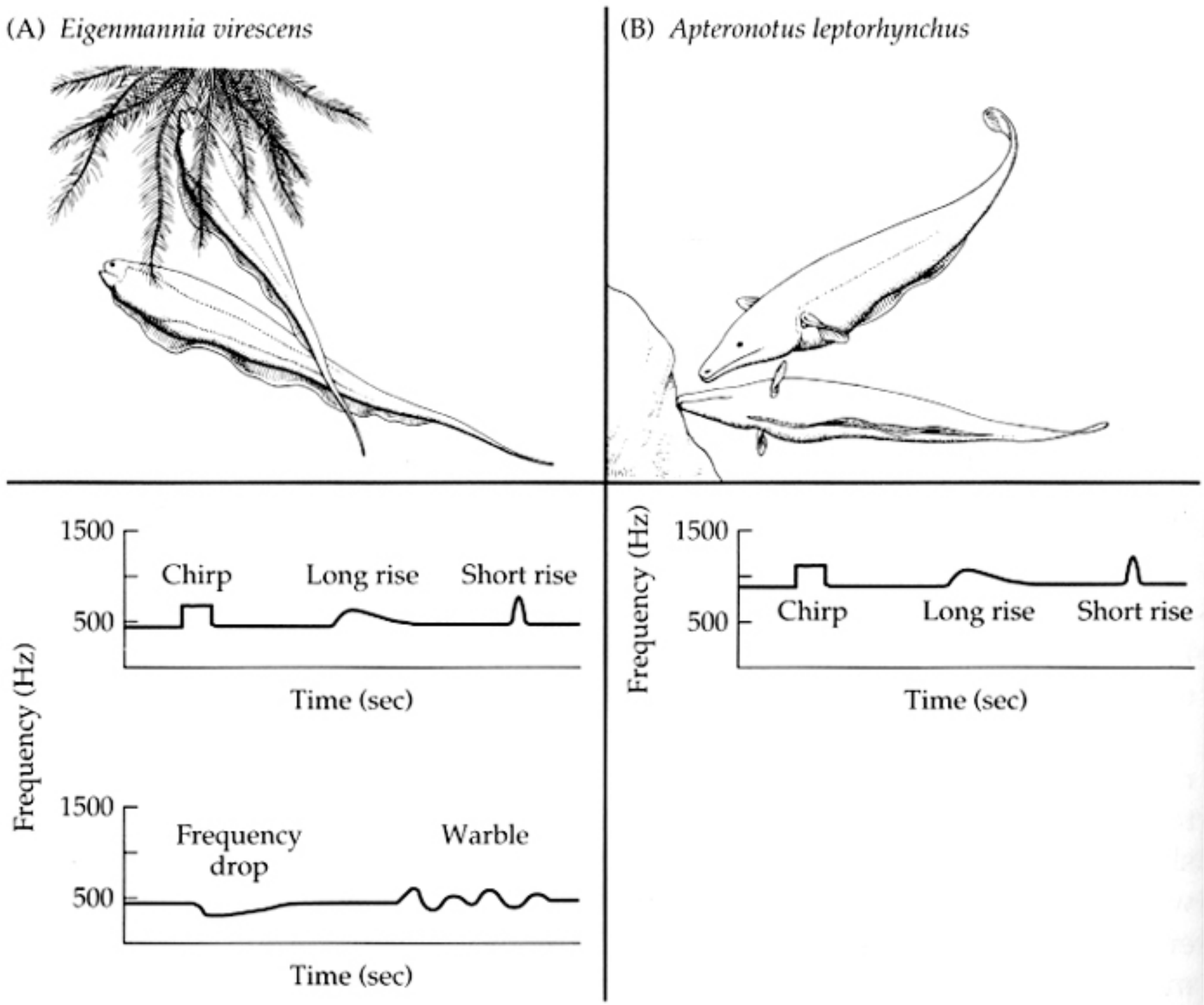
Tuberous receptors and species-specific tuning



- Occur in Gymnotiformes and Mormyriformes
- Cells respond only to higher frequencies of EOD
- In wave fish, receptors are tuned to own pulse rate or that of species
- In pulse fish more broadly tuned

[Hear sounds]

EOD courtship



Electrolocation of social signals

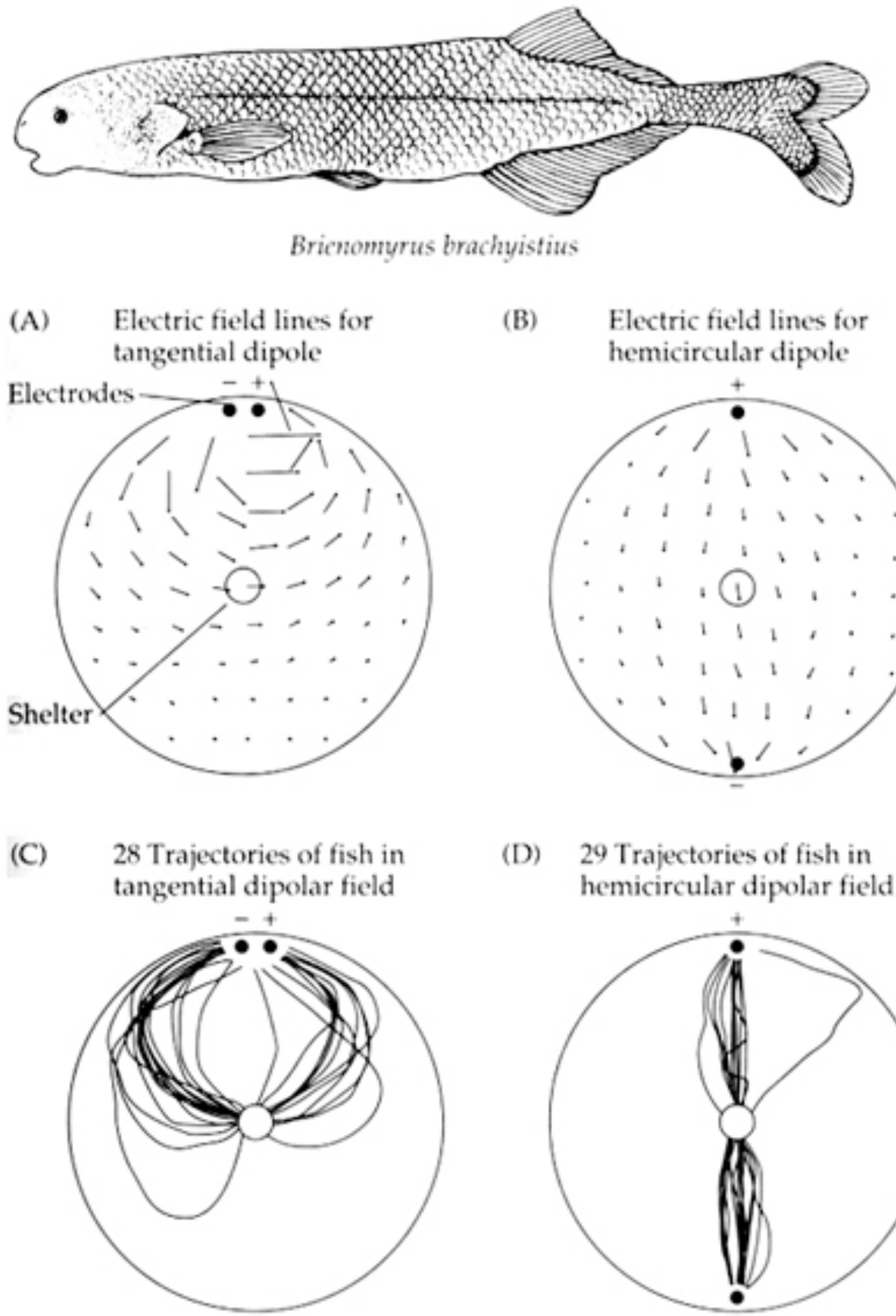


Figure 11.15 Location of the source of an electrical social signal. (A and B) Current and electrical field lines generated in two circular chambers by a pair of electrodes. Example A is a dipolar field (both electrodes close together near top of chamber) with elliptical force lines all passing through electrodes and extending into chamber. Example B is a linear field with electrodes on opposite sides of chamber. (C and D) Trajectories followed by mormyriform *Brienomyrus brachystitius* that leaves its shelter in the center of the chamber and approaches the source of the electrical field. In both cases, fish follow electric field lines to source of field. (From Hopkins 1988a, © Springer-Verlag.)