Chapter 4

Sensory Perception and Communication in Electric Fish

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Contents

Introduction

Sensory Perception

Paramount to an adaptive behavioral response by an animal is the collection and filtering of information from its environment. Impinging on the limiting envelope of a living organism are an array of stimuli, some useful, some of little value, some actually harmful. Sensory cells are neural cells, marvels of cellular engineering, but delicate, easily destroyed by extremes of the environment which they have evolved to detect, and rarely capable of regeneration. As a consequence, the evolution of the limiting envelope has been a compromise between a rigid, tough integument for practical purposes and a small number of vulnerable "sensory windows" for reception of specific environmental stimuli. The windows include visual, chemical, tactile, acoustic, thermal, magnetic, and electric sensory modalities and are elegantly tailored to fit the environment in which the animal lives.

This exercise will use the extraordinary electric sense of several families of fish to illustrate the extreme adaptation of structure, physiology, and behavior of a species using a specialized sensory modality. Particularly remarkable is the fact that electric fish continuously generate a pulsed electric field around themselves for both electroperception as well as species and sex recognition in electrocommunication (Carr, 1990; Wu, 1984).

Electroperception and Electrocommunication

Electroperception depends upon the flow of negatively-charged electrons from an area of high negative charge to an area of low electron density. The electric field is created when electrons discharged from cells in an electric fish's tail flow along the lines of force to small pores along its head which detect the electron flow pattern. The pattern is changed when the electric field is distorted by a conducting or non-conducting object (Heiligenberg, 1977); by sensing the conductivity of the object, its size, shape, and location is determined (Figure 4.1). The sensitivity in the laboratory is great enough to detect glass rods down to 2 mm in diameter.

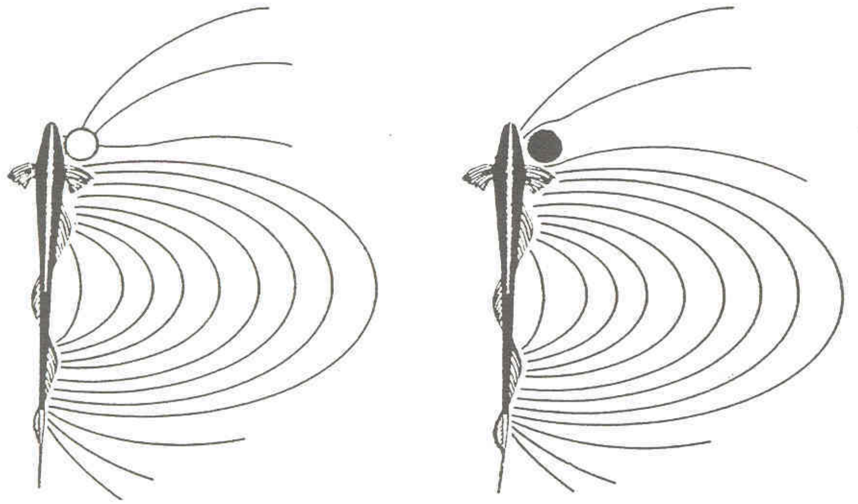


Figure 4.1. The electric field is distorted by objects in the fish's environment. A distortion is made by an object of high conductivity (left) or one of low conductivity (right).

In addition to electroperception, the signals clearly serve in electrocommunication. By differences in discharge pattern, some electric fish are able to communicate species, sex, and size (Hagedorn and Zelick, 1989). Some species such as Gymnotus also signal submissiveness by ceasing discharges altogether.

Electroperception and electrocommunication are uniquely suited to the turbid waters where electric fish live. Transmission, as in visual systems, is nearly instantaneous and is little affected by acoustic “noise” in a system, but fades out rapidly and thus is effective only over short distances. Like chemical and sound communication, an electric signal can also pass around objects.

Survey of Electric Fish

A brief survey of the habitats and life history of the three major electric fish groups will illustrate some of the features of the electric sense.

One group of closely related families, the gymnotids, or knife fish, are characterized by an elongate, laterally flattened body, typified by the Black Ghost, Apteronotus albifrons (Figure 4.2). Gymnotids are indigenous to the Amazon Basin of South America, where they live in the light-poor environment of turbid streams. Striking modifications for life in these muddy waters include reduced and nearly functionless visual and auditory senses. Swimming behavior is also specialized, presumably to minimize disruption of the electric field. The ventral fin of a gymnotid forms a ribbon-like structure along its ventral surface, and undulation of the fin propels the fish forward or backward.

Figure 4.2. The black ghost, Apteronotus albifrons (life size).

Highly modified muscle or nerve cells in the tail region, called electrocytes, operate like batteries in series to produce and discharge an electric field, while electroreceiver cells in the head or lateral line regions detect distortions in the field. Continuously discharging electrocytes create an electric field around the fish with a dipole effect of concentric rings of charge (Davis and Hopkins, 1988; Heiligenberg, 1989); the current strength decreases in intensity with distance from the fish (Figure 4.3).

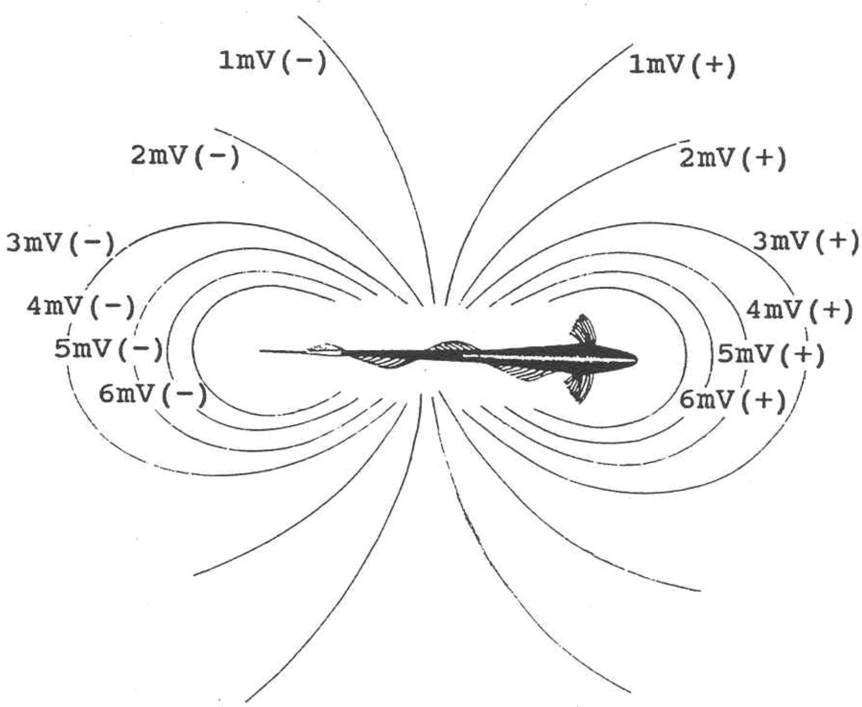


Figure 4.3. The electric field.

Most species produce a maximum voltage of a few millivolts, which serves well as a sensory field for a distance of approximately 1 m2 around an individual. One exceptional gymnotid in this group is the electric eel, a unique member reaching a length of over 1 meter and capable of a discharge voltage greater than 500 volts. The massive jolt of its shock is capable of killing a human or horse and is thus used in electrocution of its prey. In addition, this species uses its "weak," continuous pulse system for electroperception and electrocommunication.

A second taxonomically distant group of electric fish has evolved independently in muddy waters of the Nile Basin of Africa. About 300 species of fish in this group belong to the family Mormyridae or to a few other closely related families. Most have unusual shapes, giving rise to names such as "elephant-nose," or "baby whale;" they swim by means of myomorphic contractions and body undulations resembling more typical fish patterns. Mormyrid electric signals are far more complex than those of gymnotids; relatively little is understood about the function of their frequency-modulation (Bell, 1989; Moller and Serrier, 1986). As in the gymnotid group, one species of mormyrid, the electric catfish, has a powerful discharge used in predation as well as a weak system for electroperception and electrocommunication.

Finally, scattered around the world are a small number of other families of electric fish, a third group also capable of electroperception. Electric rays and skates of the family Rajidae live in marine waters and produce continuous weak electric signals (Belbenoit, 1986), and a small and inconspicuous minnow of the South Carolina coast, the "star gazer" of the Family Astrocopidae, is reported to produce weak electric signals as well.

Materials

The following list of materials specifies the quantities needed for five groups of four students each (20 students total):

5-gallon aquaria (5)
Aquarium supplies: pvc pipe for shelter, chlorine-free water, pH test kit, filter pump, thermometer, fish food, fish net, aquarium heater, gravel, plastic plants.
Oscilloscopes (5)
Preamplifiers (5, optional)
Carbon rod electrodes (10; 2 for each group)
Common goldfish (1 or more)
Well-cultured aquarium stocked with electric fish (1)

Consult your local aquarium shop for cost and detailed care of each species of electric fish. Since availability of the fish is seasonal and the fish are expensive, it is advisable to set up long-term aquaria, and maintain the fish until needed. They will live for a number of years in a well-designed and properly cared for aquarium. About 1 hour per week is required to maintain such a tank; regular tri-weekly checks of water pH, tank cleanliness, algae control, filter cleanliness, feeding, and prophylactic disease control are essential.

The most common types of electric fish readily available from pet and aquarium stores include:

Gymnotids

Black ghost (excellent choice, relatively easy care)
Brown ghost (rarer and less spectacular than the black ghost, very pH sensitive)
Carapo knife (very aggressive; must be maintained separately)
Glass knife (readily available and easy care)
Black knife (weak signal)

Mormyrids

Elephant-nose (spectacular, easy care)
Baby whale (easy care)
Electric catfish (easiest care)

False Electrics

Gray knife (Not electric, they are not even related to electric knife fish, which they superficially resemble; frequently sold by uninformed dealers as electrics)

Student Outline

Observations

Quietly observe the swimming behavior of all available species of electric fish and compare to that of a common goldfish. Do the gymnotids and morymrids move their fins? What is the shape and position of the fins? Describe the swimming motions. What do you suppose is the reason for the electric fish's relative rigidity of body? Which fish responds visually to stimuli such as a hand waved in front of the tank? Compare the relative size of the eyes in the different fish and suggest a reason for the difference. Also is there evidence for other obvious senses; for example, barbels, which would suggest a chemical sense? Finally, refer to the key below to identify all electric fish species available in your lab, both live and preserved specimens, and draw sketches of at least six species in Table 4.4.

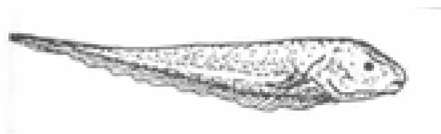
Identification Key for Electric Fish

1. If the fish has a relatively flattened body, rather knife-like in appearance with a ribbon-like ventral fin, it is from the Amazon Basin of South America. Freshwater. Most are weakly electric. See Table 4.1. Family Gymnotidae.

2. If the fish has a more typical fish-like body and fins (not ribbon-like), often with exaggerated snouts, it is from the Nile Basin of Africa. Freshwater. Most are weakly electric. See Table 4.2. Family Mormyridae.

3. If the fish does not resemble either 1 or 2, see Table 4.3 (Other).

Table 4.1. The Gymnotids.

	Black with sharp pointed ventral fin and a lengthwise pale gold stripe in adults only ... Black knife (Sternopygus sp.)
	Translucent with faint, longitudinal stripes ... Glass knife (Eigenmannia spp.)
	Large predatory mouth, mottled pattern ... Banded knife (Gymnotus spp.)

Brush-like tip of ventral fin. Dark color with white dorsal headband ... (A) or (B) below.

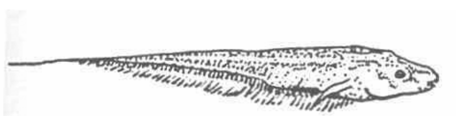
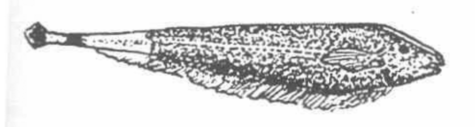
	(A) Muddy brown with rounded snout. Neurogenic ... Chocolate or brown ghost (Apteronotus leptorhynchus)
	(B) Intense velvety black with snow-white markings on tail. Neurogenic ... Black ghost (Apteronotus albifrons)

Table 4.2. The Mormyrids.

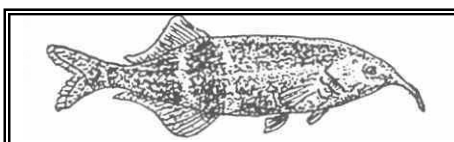
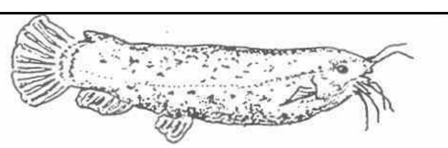
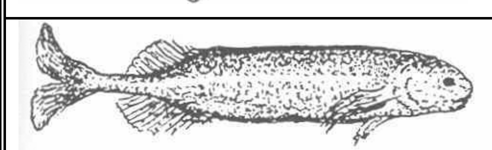
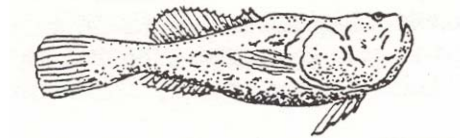
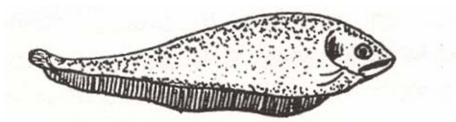
	Snout-like nose ... Elephant-nose (Gnathonemus spp.)
	Pronounced barbels on mouth. Chubby profile. Strongly electric ... Electric catfish (Malapterurus sp.)
	Chubby profile. No barbels ... Baby whale (Brienomyrus sp.)

Table 4.3. Other.

	Found in Western Atlantic (off the South Carolina coast). Eye on top of head. Discharge strength possibly strong ... Stargazer (Astroscopus sp.)
	Resembles one of the fish described above, but not electric ... False electric fish (i.e., Gray, African, or Peacock knives)

Equipment Orientation

Next familiarize yourself with the equipment that will be used (Figure 4.4). Connect the steel plates or carbon electrodes to the speakers and to the oscilloscope. Some of the oscilloscopes may need a preamplifier. One of the oscilloscopes may also be connected to an automatic scaling counter for read-out of the frequency. Observe the instructor's demonstration of the use of the oscilloscope and try adjusting the dials until you understand its principles and operation. Adjust the focus until the trace is clear and sharp. Most oscilloscopes have a sweep magnification or horizontal adjustment knob, and a sensitivity knob, often called the gain adjustment. The calibrations indicate the amount of deflection (in cm) per volt of signal. Other types of adjustment also will be demonstrated.

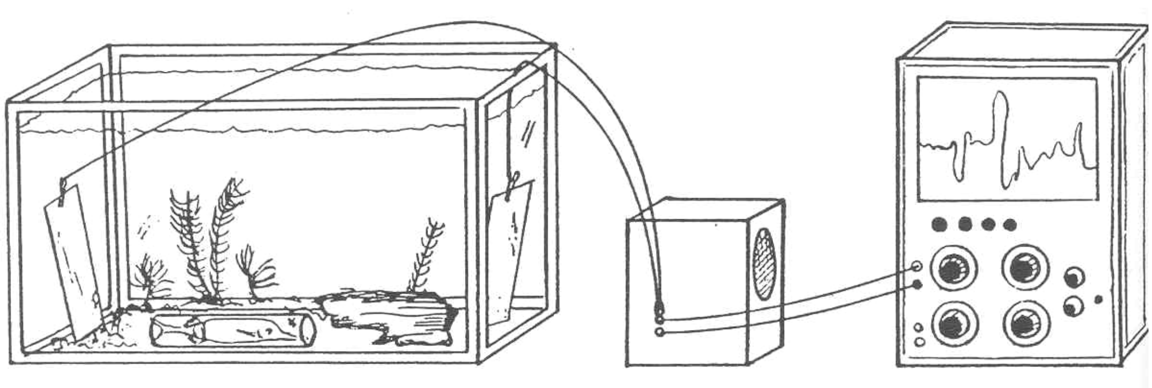


Figure 4.4. Apparatus for studying electric fish: elephant-nose in aquarium with electrodes (left), speaker (middle), and oscilloscope (right).

Table 4.4. Experimental observations.

Example	Geographic distribution	Sketch	Behavioral observations	Waveform	Frequency and modulation type
A – Gymnotidae and related families					
Gymnotus carapo Carapo knife	S. America				
Eigenmannia spp. Glass knife	S. America				
Sternopygus macrurus Black knife	S. America				
Apteronotus albifrons Black ghost	S. America				
A. leptorhynchus Chocolate or brown ghost	S. America				
B – Mormyridae and related families					
Gnathonemus spp. Elephant-nose	Africa				
Brienomyrus brachyistius Baby whale	Africa				
Malapterurus electricus Electric catfish	Africa				
C – Others					

Electric Fish Pulse Type, Waveform, and Frequency

Connect the electrodes to the oscilloscope and adjust dials until the signal appears sharply focused and centered on the screen with appropriate sensitivity. Photograph or draw the waveform, then calculate the frequency of the electric signal using the formula F = 1/P (where F is the frequency, and P is the period). Wait 5 minutes before measuring again. The audible signal you hear is a transduced sound. It is produced electronically by the speaker. The fish do not produce any sound, of course, but it is easier for humans to visualize sound pulses than electrical pulses.

Systematically test each fish for its pulse type, waveform, and frequency; record these on the chart provided. The signal of each species is characterized by these features. In the glass knife, Eigenmannia, for example, a simple sinusoidal waveform is found. Known as a "hummer type" of signal, the waveform and frequency create a species-specific pattern differing markedly from all other species (Figure 4.5).

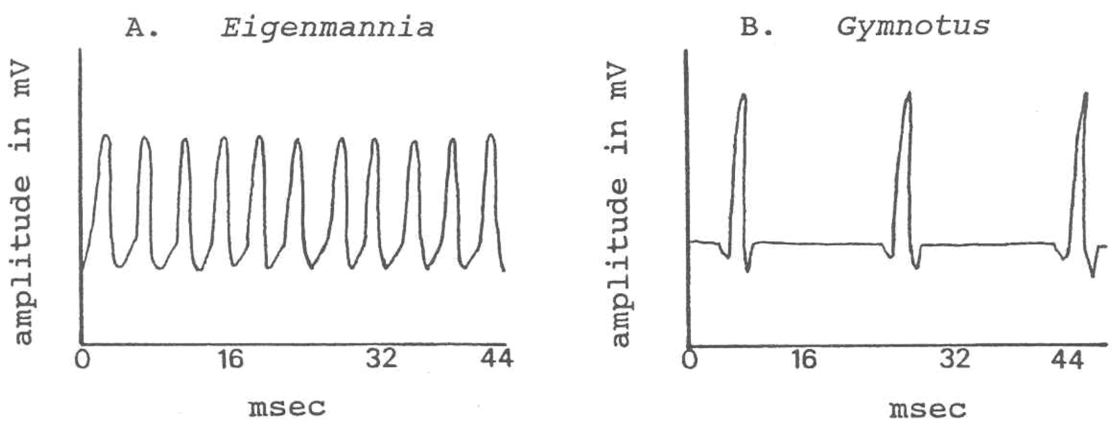


Figure 4.5. Species specific waveforms for a "hummer" (A) and a "pulse" type (B) electric fish.

Frequency in Eigenmannia may vary less than 10 percent during the lifetime of an individual; however, for different individuals, the frequency ranges from about 300 to 800 Hertz, with males possessing lower frequencies than females. The amplitude gives a clear indication in some species of the size of the individual, for the larger the fish, the greater the signal amplitude. A contrasting species, the carapo knife, Gymnotus carapo, has a pulse-type signal with a triphasic waveform, each pulse widely separated from the next, and a resultant frequency of only 60 Hertz (Figure 4.5). Are the fish you observe "hummers" (i.e, glass knife) or "pulse type" (i.e., carapo knife)? Approximately what pitch do the hummers produce? Why do you think the black ghost is a neurogenic electric fish? How could you demonstrate that the electric system is used in electrolocation? What information does the signal contain that could be used in communication? A simple experiment with a carapo knife will illustrate some of the subtle aspects of communication. Play back the pulses of Gymnotus carapo via a tape recorder to the same fish. What is the result when played back softly to the fish on his own territory? What is the result when intensity is increased? What is the significance of "interruptions" for communication?

Jamming

Whenever two electric fish of one species approach close to one another, a serious deterioration of their object-sensing abilities called “jamming” occurs due to the great similarity of their signal frequencies. To avoid jamming and to permit aggregation, each fish makes a subtle frequency change (Kramer, 1987). This “jamming-avoidance response” can be demonstrated by playing back an electric fish's own electric pulses, then quickly switching the oscilloscope to the recording mode to observe subtle changes in the electric fish's frequency. Try this experiment, and indicate your results.

Discussion

Write a lab report in which you discuss your results, and comment on the significance of several aspects of the electric fields generated by electric fish. The following ideas will guide you: Describe how pulses are produced by the electrocytes in the tail and perceived by the lateral line system (see Figures 4.1 and 4.2). Comment on the analogy between a series of batteries discharging and the muscles or neural cells that make up the electrocyte organ. Figure 4.3 illustrates the dipole effect; explain the distribution of charges of the field produced by the electrocytes.

Consider how interspecific waveforms differ. For example, contrast waveforms from the two species shown in Figure 4.5, as well as other oscilloscope traces you have viewed and/or photographed. Are these species-specific signals? Could they be used to distinguish one species from another? What kinds of information can the electric signals communicate? Can they convey information about gender, location, or territorial boundaries? Can they detect objects such as obstacles, food sources, mates, and rivals?

Finally, turn from electric fish to other types of highly specialized sensory systems in the animal kingdom, and comment on other animals in your experience possessing specialized sensory systems. Some species in light-poor environments, for example, have evolved highly specialized sensory receptors other than electroreceptors or eyes. Bats use echolocation or sonar to detect obstacles or flying prey at night. In this type of perception, pulses of high frequency sound are beamed out by the vocal chords of a bat, and the returning echoes give clues to the size and distance of an object (Griffin, 1974). If available, examine a live bat and notice teeth, eyes, and specialized ears including the tragus. Observe and listen to any movies available on bats. What type of living habits and activity patterns do bats have? Why has echolocation evolved in bats?

Two fascinating birds use sonar in their daily activities. The Oil Bird of Trinidad is related to our Whip-poor-will, while the Cave Swiftlet of India is related to our Chimney Swift.

Porpoises are still another group of animals living in a dimly-lighted habitat. Their sonar is adapted for prey catching and obstacle avoidance. Why would it be an advantage for porpoises to use sonar rather than vision? Find out about porpoise whistle “signatures,” vocalizations and “language.” Distinguish carefully between echolocation and communication in this group.

Can humans learn to echolocate? Read as much as possible about “facial vision” in blind humans. What hope does modern technology hold for sonar use by the blind in the future?

Echolocation is an active form of sensory perception, since the individual generates its own sensory probe and interprets the returning echoes. What advantages does an active perceptual system like this have over a passive system such as simple hearing? What are other examples of active sensory perception systems?

Acknowledgements

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APPENDIX A
Oscilloscope Technology

An oscilloscope is an electronic instrument capable of visual representation of the voltage difference between two points and capable of measuring changes in voltage with respect to time. Normally used with delicate and elaborate electrodes to measure nerve impulses in the central nervous system or sense organs, its basic operation can much more easily be learned with the macro-electrode plates or rods that suffice to pick up the relatively large signals of the electric fish. While complicated looking, oscilloscope operation can easily be mastered, and little possibility exists of damaging the instrument by turning the knobs.

The heart of an oscilloscope is the cathode ray tube whose screen is visible on the oscilloscope face. A cathode ray tube is the source of negatively charged electrons which can be accelerated, then aimed at the coated screen which phosphoresces when struck by the electron stream. The beam passes from its source towards the screen through two pairs of electromagnetically charged plates: a vertical deflection set of plates and a horizontal set of deflector plates (Figure 4.6). When a signal such as an electrical fish discharge is connected to the input of the oscilloscope, vertical deflection of the electron beam is proportional to the input voltage, and horizontal deflection reflects the time structure of the signal; by combining these, a graph of voltage amplitude versus time is drawn on the oscilloscope face. Using the calibrated dials of the oscilloscope, it is a simple matter to center each pulse of an electric fish, measure its voltage and period, and from this calculate its frequency. For a permanent record of the oscilloscope traces, photographs may be taken with a special camera.

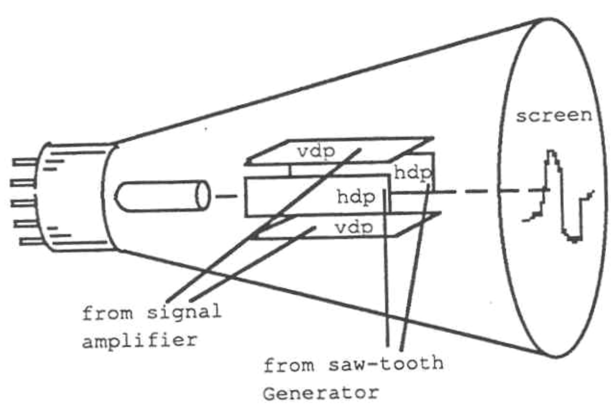

Figure 4.6. Diagram of the basic elements found in oscilloscopes. The electron beam from the cathode is deflected by the horizontal deflection plates (hdp) and the vertical deflection plates (vdp).