SOUND PRODUCTION IN FISH

How do fish produce sounds?

Fishes produce different types of sounds using different mechanisms and for different reasons. Sounds (vocalizations) may be intentionally produced as signals to predators or competitors, to attract mates, or as a fright response. Sounds are also produced unintentionally including those made as a by-product of feeding or swimming. The three main ways fishes produce sounds are by using sonic muscles that are located on or near their swim bladder (drumming); striking or rubbing together skeletal components (stridulation); and by quickly changing speed and direction while swimming (hydrodynamics). The majority of sounds produced by fishes are of low frequency, typically less than 1000 Hz.

The Swim Bladder and Drumming

Some fish, such as the sand seatrout (*Cynoscion arenarius*), produce sound by using muscles on or near their swim bladder (also called gas bladder).

Among the best-known sounds produced by fishes are those made by drumming of the swim bladder with the sonic muscle. The swim bladder is a large chamber of air located in the abdominal cavity in most bony fishes. The swim bladder serves many functions. It is used primarily for regulating buoyancy. Air gets into the swim bladder in one of two different ways, depending upon the species. In some species, there is a duct between the swim bladder and esophagus (the pneumatic duct) – this sort of swim bladder is called "physostomous". These fish come to the surface and "gulp" air that is directed via this duct into the swim bladder. In other fishes, including all of those that live deep in the ocean, fishes have a special gas gland and rete mirabile, within the wall of the swim bladder, which is called a "physoclistous" swim bladder. The rete mirabile is made up of tightly packed capillaries, arranged so that those carrying incoming blood are adjacent to those carrying outgoing blood. This allows for filling of the swim bladder with gas from the circulatory system.Fishes such as drums and croakers (Family Sciaenidae) have sonic muscles attached to or near to their swim bladder. These muscles, the fastest contracting muscles known in vertebrates, cause the swim bladder to contract and expand at a rapid rate, thus creating drumming sounds. The majority of sounds produced in this way are short pulses with fundamental frequencies ranging from about 45 – 60 Hz (i.e., goliath grouper and black drum) to about 250 – 300 Hz (i.e., toadfish spp. and silver perch). Higher frequency harmonics produced by drumming are sometimes present above 1000 Hz (e.g., silver perch).

The sonic muscles of the toadfish are located along the lateral surfaces of the heart shaped swim bladder. Contraction of the sonic muscles produces a sound similar to a foghorn. In other species the muscles may be configured differently (such as anchored to the base of the skull) or may be attached to another anatomical feature, which is then triggered to vibrate the wall of the swim bladder. For example, some marine catfishes possess a modified swim bladder mechanism, called the "Springfederapparat" or "elastic spring apparatus." Thin elastic bones function in sound production. Specialized sonic muscles on the upper surface of this elastic spring cause the vibration of the swim bladder.

Drumming sounds have been described as thumps, purrs, knocks, and pulses all of which occur in different variations depending on the fish producing the sound. In this way fishes are able to produce species-specific sounds which can be used to identify them in recordings.

Stridulation

Stridulatory sounds are produced when hard skeletal parts or teeth are rubbed together, like the method used by crickets to make sounds. In fishes, stridulation often occurs during feeding when jaw teeth or pharyngeal teeth are gnashed together. Stridulation may be used intentionally to produce sound as a fright response or territorial display. Stridulatory sounds may be modified or amplified by the swim bladder. The component frequencies of stridulatory sounds range from < 100 to >8000 Hz, while predominant frequencies are generally between 1000 and 4000 Hz. Stridulatory sounds influenced by the swim bladder have predominant frequencies well below 1000 Hz.

Examples of fish species that produce sound by stridulation include marine catfishes and sea horses. In some species such as the grunts (Family Haemulidae), the swim bladder is hypothesized to function as a resonator to amplify stridulatory sounds.

Marine catfishes (*Arius felis* and *Bagre marinus*) have specialized pectoral fin spines that make a stridulatory squeaking sound. The base of the pectoral fin spine is modified in these catfish. A part of the base, known as the dorsal process, looks like a ridged potato chip. Sound is created when the dorsal process of the pectoral fin is rubbed against the pectoral girdle. This is commonly heard by anglers who catch a sea catfish.

The northern seahorse is also known for producing stridulatory sounds. In these fish, clicking and/or snapping sounds are produced when bony edges of the skull and coronet, a crown-shaped plate on the fish's head, rub together. These sounds are possibly amplified by the swim bladder.

Hydrodynamic Sound

Hydrodynamic sound production occurs when a fish quickly changes direction and/or velocity. These sounds are extremely low frequency. These sounds are simply a by-product of swimming. It is possible that hydrodynamic sounds may be important to predator and prey interactions and communication. For example, it has been postulated that sharks can detect the low frequency hydrodynamic sounds emitted by smaller fishes. Therefore, schooling fishes may inadvertently attract a shark simply by the sounds produced during swimming.

Weberian Ossicles

1. Meaning of Weberian Ossicles
2. Mode of Action of Weberian Ossicles
3. Functions

Weberian ossicles (Weberian apparatus) Structures found in bony fish belonging to the orders Cypriniformes and Siluriformes, and derived from the first four vertebrae. They form a link between the inner-ear region and the swimbladder, facilitating sound reception.

Meaning of Weberian Ossicles:
The perilymphatic sac and the anterior end of the swim-bladder are connected by a series of four ossicles (Fig. 2.40) which are articulated as a conducting chain. Of the four, the tripus, intercalarium and scaphium actually form the chain, while the fourth one, claustrum lies dorsal to the scaphium and lies in the wall of posterior prolongation of the perilymphatic sac.

The function of these ossicles is controversial. It is regarded that the Weberian ossicles either help to intensify sound vibrations and convey these waves to the internal ear, which help to understand the state of tension of air pressure in the bladder and transit changes of such pressure to the perilymph to set up a reflex action.

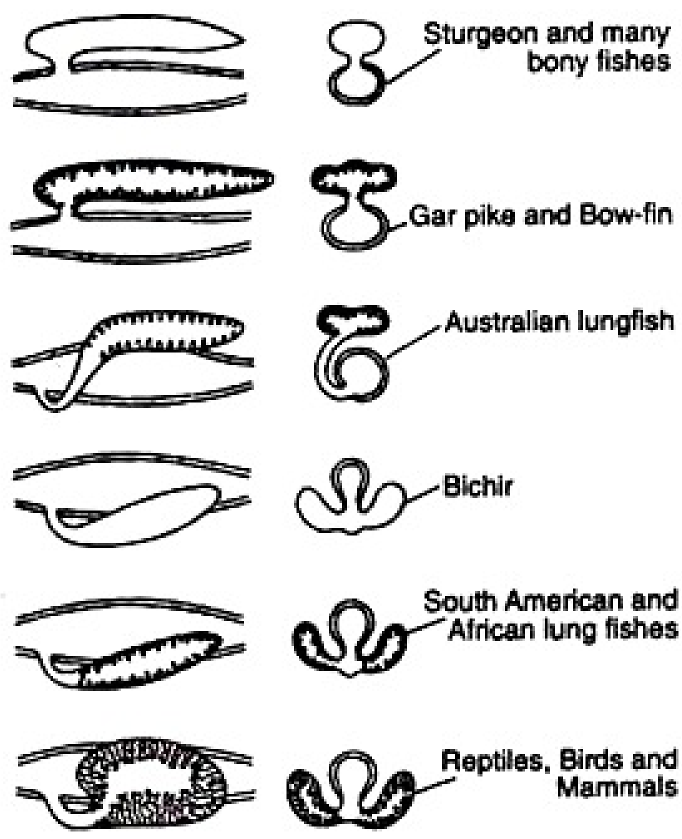


Fig. 2.40 : Showing the relationship between the swim-bladder and lung with the oesophagus in some fishes and tetrapods

There are various views regarding the actual process of derivation of these ossicles. It is believed that these ossicles are detached or modified processes of the first three anterior vertebrae. As regards the actual mode of origin of the four ossicles there are differences of opinion.

The claustrum is regarded to be modified inter-spinous ossicle or modified spine of first vertebra or modified neural arch of first vertebra or modified intercalated cartilage or modified neural process of first cartilage. The scaphium is considered to be the modified neural arch of the first vertebra or modified rib of the first vertebra or derived from the neural arch of the first vertebra and also from the mesenchyme.

The intercalarium is derived from the neural arch and transverse process of the second vertebra or from the neural arch of the second vertebra and also from the ossified ligament or from the neural arch of the second vertebra only.

The tripus is formed from the rib of the third vertebra and the ossified ligament or from the transverse process of the third vertebra along with ossified wall of the swim-bladder or from the transverse process of the third vertebra and the ribs of third and fourth vertebrae.

The ossicles are derived from the apophyses of anterior vertebrae

PART	LOCATION
TRIPUS	HINDMOST
SCAPHIUM	ATTACHED TO TRIPUS AND CLAUSTRUM
CLAUSTRUM	TOUCHES THE MEMBRANOUS WINDOW OF SINUS IMPAR
SINUS IMPAR	LIES IN THE BASSIOCCIPITAL BONE

Mode of Action of Weberian Ossicles:
There are two modes of action in different fishes:
1. Direct mechanical transmission of the vibrations.

2. Indirect system of transmission.

A change in the volume of the bladder causes its walls to bulge out of the opening and forces the ossicles forwards. In the indirect system of the cyprinoids, a backward movement of the posterior process of the tripus causes its anterior movement.

The movements of the ossicles cause an increase in the pressure of the perilymph in the sinus in-par, which is conveyed to the sacculus. Thus, the vibrations of the gas bladder wall are transmitted to the ear by changes in tension. In direct system (Siluroids), the swim- bladder is enclosed in a bony capsule and protrudes through an opening in it for attachment with the tripus.

Functions of the Weberian Ossicles:

The ossicles appear to perform a variety of functions:
1. As pressure register:
They are sensitive to changes in the volume of the swim-bladder due to variations in the hydrostatic pressure. Any change in the volume of the swim-bladder causes movements of the sinus impar. This is then conveyed to the sacculus through the endolymph of the transverse canal.

2. As barometer:

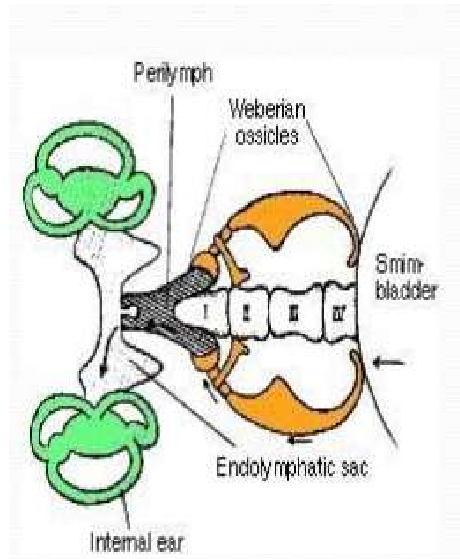
It is presumed that fish can detect variation in the atmospheric pressure through Weberian ossicles.

3. As auditory organ:
The ossicles transmit the vibrations of the bladder wall to the perilymph of sinus impar. The vibrations reach the saccular otoliths via endolymph.

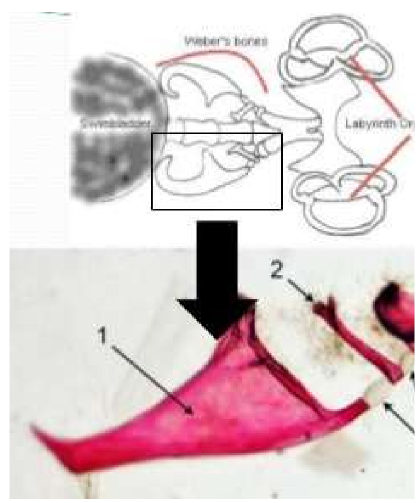
4. As sound locator:
The vibrations received on the side of the bladder nearest the source are stronger than the other side.

To summarize, Weberian ossicles are:

- Specialized auditory structure
- One of the most notable complex system in teleost fish especially in the order Cypriniformes
- It is a mechanical device improving audition, consisting of a double chain of ossicles joining to the air bladder to the inner ear
- It comprises of four bony elements
- From posterior to anterior, the Weberian ossicles are: the tripus, intercalarium, scaphium and claustrum



Volume changes of the gas bladder cause the Weberian ossicles to move in such a manner that pressure changes are transmitted to the perilymph and then to the sensory cells of the inferior portion of the labyrinth which is the seat of sound reception.



Luminous Organs or Photophore of the Fishes

Luminous Organs:
A number of fishes especially marine species are known to produce characteristic light through their special organs called luminous organs. These organs are commonly found in fishes living in deep-sea where the sunlight ceases to enter. The luminous organs are absent in freshwater fishes.
The most important function of bioluminescence is to illuminate surroundings for the purpose of camouflage, schooling and for recognition of movement of predators in the water. The luminous organs or photophores are special gland cells of the epidermis. Their distribution on the body type and adaptive value may vary in different species of fishes.

Structure of Luminous Organs:

On the basis of anatomy of photophores they may be categorized in two types:
1. Simple Photophore:
They are small in size, about 0.1 to 0.34 mm in width. It consists of light generating cells called as photocytes. Simple type may be provided with or without mantle of pigment. The lenses are formed by grouping of cells known as lenticular cells.

The distal part of photocyte is provided with acidophilic granules. A layer of melanophres surrounds the photophore. Simple type of photophores is present in sharks. In Stomias the luminous organs are logged in gelatinous corium of the epidermis.

2. Compound Photophore:
This type of photophores consists of additional structures like reflectors, pigmented mantle and sub-ocular organs. The latter one is a large organ deeply embedded in dermal tissue. The photocytes are arranged in the form of cords and bands.

Photogenic tissue, pigment and reflector layers are provided with nerves and blood vessels (Fig. 1). The photogenic tissues are found in the centre of the photophore and consist of two types of glandular cells.

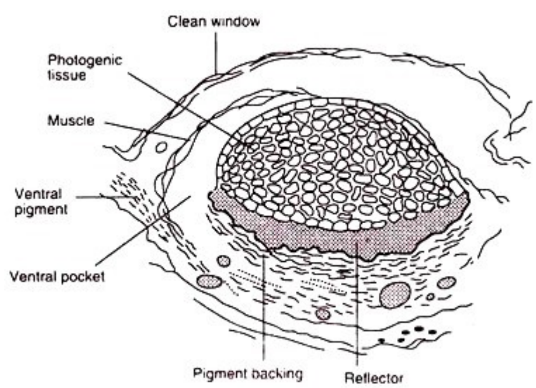


Figure 1: T.S. through a sub-ocular light organ of Astronesthes *richardsoni*
The mechanism of light production is peculiar in fishes and takes place the special sets of muscles present around the photocytes. When these muscles contract, they pull the outer surface of photophore downwards, causing brighter surface to be concealed.

In contrast the relaxation of these muscles exposes bright surface of the photophores. In some species, movement of pigmented layer carries out concealing and rotating of photophores.

Types of Luminous Organs:
On the basis of source of illumination it may be classified as follows:
1. Extra Cellular Luminescence:

Light may be generated by luminous secretion from the glandular tissues. Extra cellular luminescent organs are found in a very limited species of fishes. Certain fishes like rat tails emit light by secreting extra cellular slime. Rat tails possess special glands near its anus, which secretes slime of sufficient luminosity.

2. Intracellular Luminescence:
In this type the light is produced within the glandular cell or intrinsic photocyte. These luminous organs developed from the epidermis.

Fishes ornamented with this type of luminous organs belong largely to the family of teleosts, i.e., Sternoptychidae (hatchet fish), Myctophidae (lantern fish), Halosauridae (Halosaurid eel), Stomiatidae (scaly dragon fishes), Brotulidae (Brotulus), Lophiidae (anglerfish) and Zoarcidae (eel pouts).

3. Bacterial Luminescence:
In this type, symbiotic bacteria present in the photophore or luminous cell discharge light. Many different species are recognized particularly the genus photo-bacterium and achromobacterium have been isolated and grown in cultures. They are common on dead fish or spoiling meat.

The biochemical step in bacterial luminescence is linked to the electron transport chain of oxidative phosphorylation, in which flavin mononucleotide ($FMNH_2$) from the electron transport chain reacts with an aldehyde (RCHO) to form a complex (luciferin) that is oxidized to an acid (RCOOH) with emission of light.

$$FMNH_2 + RCHO + O_2 \xrightarrow{\text{luciferase}} FMN + RCOOH + H_2O + 0.1/hv$$

4. Chemical Luminescence:
It has been established that the glandular tissue secretes a chemical substance called as luciferin, which is an indole derivative consisting of tryptamine, arginine and isoleucine. Under the influence of the enzyme luciferase, this substance is converted into oxy-luciferin and emits blue or blue-green light. Apogon, the *Parapriacanthus* is known to possess luminous glands containing crude form of luciferin and luciferase.

Control of luminous Organs:
The function of light producing organs is controlled by the nervous or endocrine system.

1. Nervous Control:
Several workers have reported that light production by the luminous organs is controlled by the nervous system, probably by the peripheral sympathetic system. The nerves innervate the phagocytes. The efferent nerves enter the photogenic cells and activate them.

2. Hormonal Control:
It has been reported that some fishes have hormonal control on the photophores. Endocrine gland like supra renal activate them. Adrenalin or noradrenalin is known to control light emission from the photophores.

3. Mechanical Control:
The muscles present beneath the photophores contract and rotate the photophores in such a way that they get concealed. Thus fish is prevented from illumination specially when in danger.

In *Photoblepharon palpebratus* the ventral part of luminous organ has a fold of black tissue (Fig. 2). This fold can be drawn over the photophores and conceal the light. In some fishes the light production is also supposed to be influenced by the movement of pigment in the chromatophores.

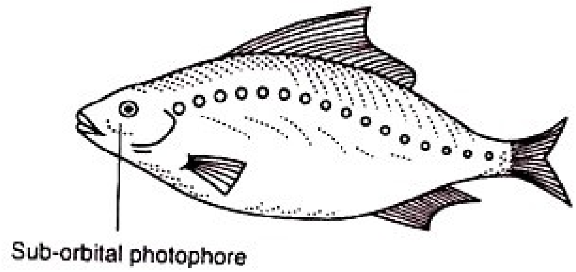


Figure 2: Light producing organs of *Photoblepharon*

Biological Significance of Luminous Organs:
This is useful in variety of ways in marine fishes specially in deep-sea fishes.

1. Illuminates Surroundings:
Some fishes utilize their luminous organs to illuminate their surroundings in the event of dimness. Thus they become able to search their prey in the dark waters. Some species (stomiatoid) are able to emit beam of light from the specially designed luminous cheek organ to catch the small creatures like planktons. The cheek organs of *Anamalops* produce light like a torch.

2. As Defensive Device:
Many fishes produce sudden flash of light from their luminous organs, which helps in diverting the attention of their predators. The emission of light facilitates an escape of fish by puzzling the enemy. *Alepocephalidae* produce a glowing spark, which confuses the predator for a spur of moment, and help the fish to escape.

However, some fishes use luminous organs to enable them inconspicuous. In doing so they illuminate their ventral surface that makes them inconspicuous against lighted background above.

3. As a Warning Signal:
A number of fishes use its luminous organ to warn the predators. For instance, the midshipman *Porichthys* that possesses, a toxic sign, flashes light when it is attacked by a predatory fish and avoids the danger (Fig. 3).

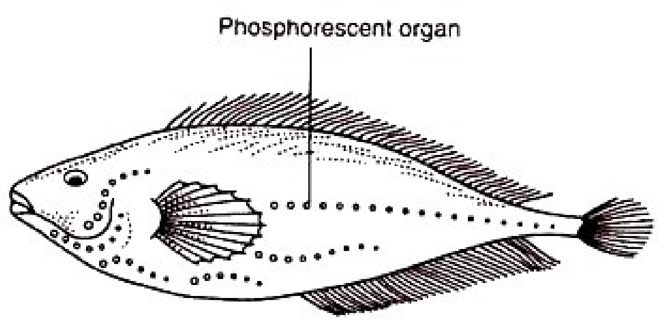


Figure 3: Light producing organs of *Porychthyes*

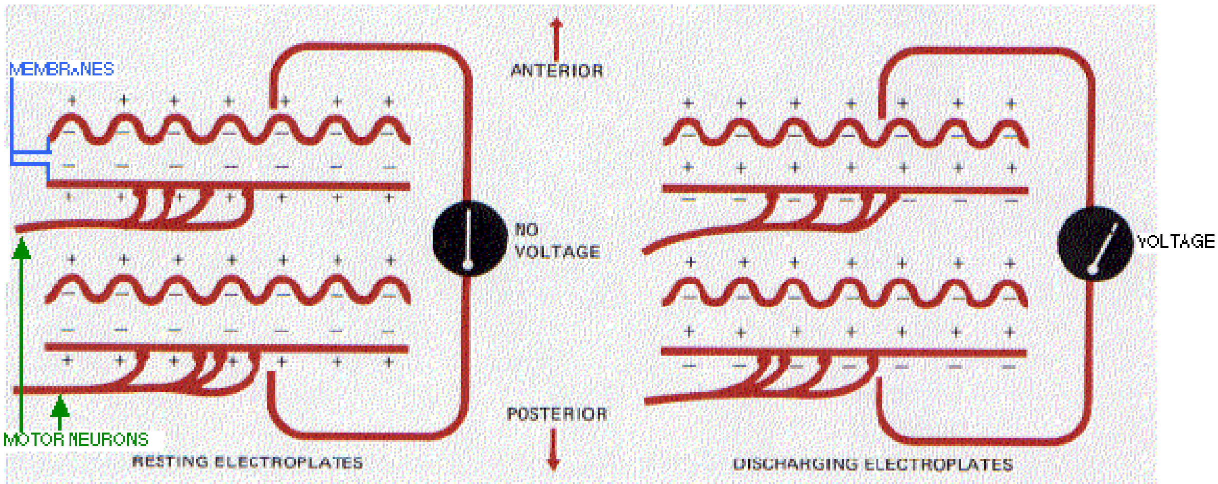
4. Recognizing Own Species:
Every species has a unique arrangement and distribution of photophores on their body, which help the fish to recognize species of same type and thus help in schooling behaviour. The luminous organs are also helpful in recognizing the mates for courtship, as the light organs may be different both in male and female.

Male lantern-fish has one or many photophores present above but in the female possess it below the caudal peduncle. In some species the size of luminous organ is different in both sexes. For example in many species of melanostommiatidae, the postorbital luminous organ is larger in the male and smaller in the female.

Electric Organs and Electroreceptors

Electric organs are masses of flattened cells, called **electrocytes**, which are stacked in regular rows along the sides of certain fishes, e.g., the electric eel of South America.

The posterior surface of each electrocyte is supplied with a motor neuron.



At rest, the interior of each electrocyte, like a nerve or muscle cell, is negatively charged with respect to the two exterior surfaces. The potential is about 0.08 volt, but because the charges alternate, no current flows.

When a nerve impulse reaches the posterior surface, the inflow of sodium ions momentarily reverses the charge just as it does in the action potential of nerves and muscles. (In most fishes, electrocytes are, in fact, modified muscle cells.)

Although the posterior surface is now negative, the anterior surface remains positive. The charges now reinforce each other and current flows just as it does through an electric battery with the cells wired in "series".

With its several thousand electrocytes, the South American electric eel (*Electrophorus electricus*) produces voltages as high as 600 volts. The flow (amperage) of the current is sufficient (0.25–0.5 ampere) to stun, if not kill, a human. The pulse of current can be repeated several hundred times each second.

Powerful electric organs like those of the electric eel are used as weapons - to stun prey as well as potential predators.

The Mechanism

While exploring its environment, the eel emits a continuous series of **low**-voltage discharges. Periodically it interrupts these with a discharge of 2 or 3 **high**-voltage pulses. These cause nearby prey, e.g. a fish, to twitch. Within a tiny fraction of a second (20–40 ms) of detecting the twitch, the eel unleashes a volley (~400 per second) of high-voltage discharges that stun the prey enabling the eel to capture it.

Remarkably, both the twitch response and the immobilization are triggered by the prey's own motor neurons. A pair of pulses induces a brief contraction while a volley of discharges induces **tetanus**.

Although action potentials in the prey's motor neurons were not measured directly, two pieces of evidence support this mechanism.

1. The responses remained intact even when the brain and spinal cord of the prey were destroyed thus eliminating the possibility that the prey was relying on a sensory→cns→motor reflex.
2. Curare, which blocks the transmission of action potentials across the neuromuscular junction did block the prey's responses.

Weak Electric Organs

The electric organs of many fishes are too weak to be weapons. Instead they are used as signaling devices.

Many fishes, besides the electric eel, emit a continuous train of electric signals in order to detect objects in the water around them. The system operates something like an underwater radar and requires that the fishes also have electroreceptors (which are located in the skin). The presence of objects in the water distorts the electric fields created by the fish, and this alteration is detected by the electroreceptors.

Electric fishes use their system of transmitter and receiver for such functions as

- navigating in murky water and/or at night
- locating potential mates
- defense of their territory against rivals of the same species
- attracting other members of their species into schools

Electroreceptors

Electroreceptors are also found in some nonelectric fishes and in some amphibians. Even the duckbill platypus, a mammal, has electroreceptors (located in its bill). With these it can detect the weak currents created by the muscle activity of its prey (e.g., small crustaceans) as it noses around in the muddy bottom where it feeds.

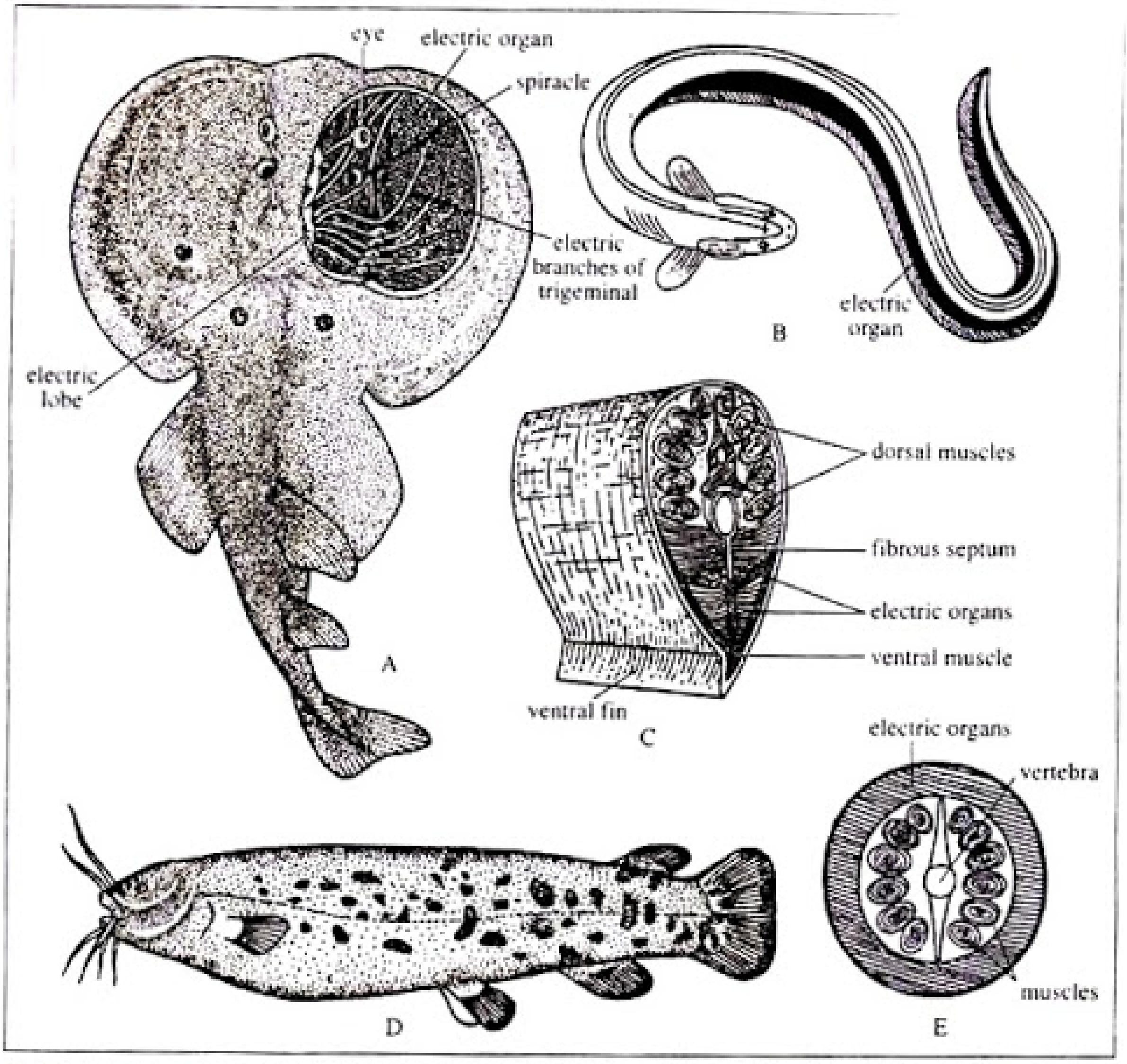
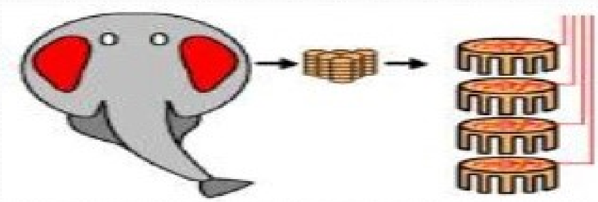


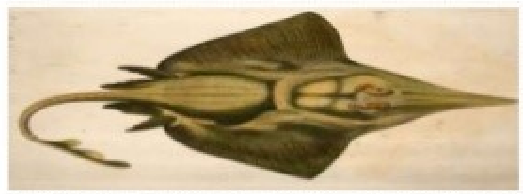
Fig. 6.98 : Electric organs in different fishes. A. *Torpedo*. A portion of the right dorsolateral side of the head region is removed to show the electric organ and its innervation. B. *Electrophorus electricus* showing the extent of the electric organ. C. Transverse section of *Electrophorus electricus* to show the position of the electric organ. D. *Malapterurus*. E. Transverse section of *Malapterurus*. Note the peripheral position of electric organ.

DISTRIBUTION OF ELECTRIC ORGANS

Name of fishes	Shape of electric organ	Location of electric organ
Torpedo	Flat kidney shape	On either side of mid-line
Malapterurus	Lozenge-shape	Located in skin
Raja (String ray)	Spindle-shape	Lying parallel to the spinal cord in the tail



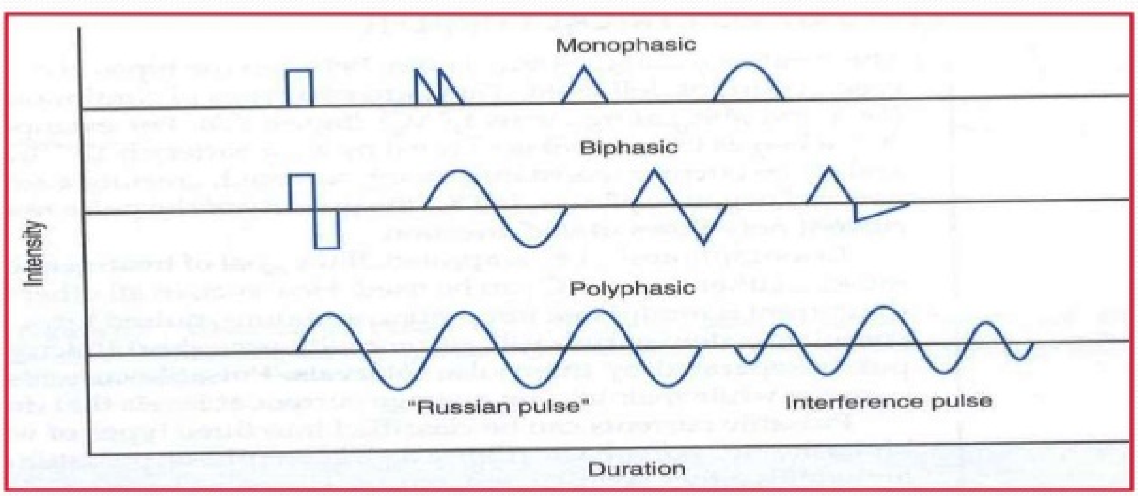
Torpedo



Raja

PATTERNS OF ELECTRIC ORGAN DISCHARGES

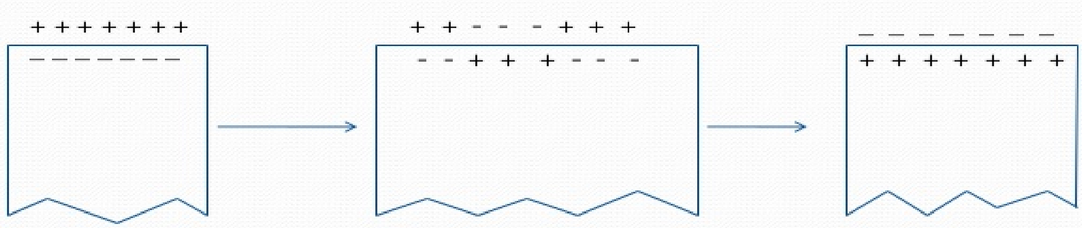
- Monophasic pulses
- Biphasic pulses
- Polyphasic pulses



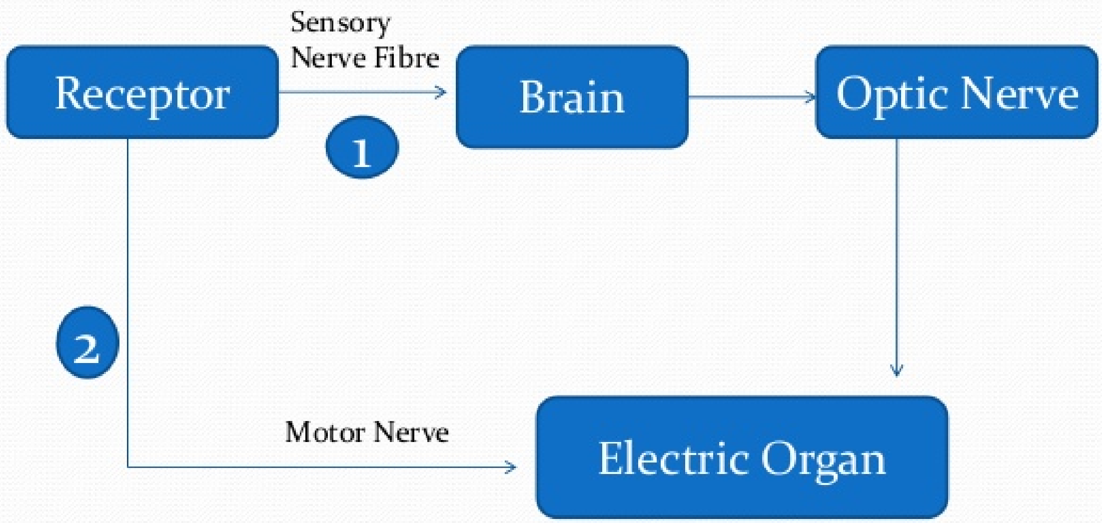
KINDS OF ELECTRIC ORGAN DISCHARGE

- Electrophorus: one small pulse followed by four large pulse.
- Electric shark: repetition of sequence of events.
- *Torpedo*: four large pulses which are continuously repeated.

MECHANISM OF ELECTRIC ORGAN DISCHARGE



Resting phase **Action Potential** **Spike stage**



Pathways of neural control of electric organ

FUNCTION OF ELECTRIC ORGAN

- Food procurement
- Defense
- Species and sex recognition
- Direction finding
- Communication
- Navigation