A number of different types of fish are capable of producing appreciable electric currents in the water surrounding them. These currents are produced by special organs known as electric organs. The position of the electric organs in various electric fish is shown in fig. 15.1.

Electric organs are composed of columns of cells called electroplaques (sometimes called electroplates, electroplaxes or electrolytes), each of which is innervated by an excitor nerve. These electroplaques (with one exception - see p. 343) appear to be modified muscle cells which have lost their contractile function. In this chapter we shall examine the means whereby the electroplaques produce the electric currents constituting the discharge of the electric organs.

The electroplaques of the electric eel

The electric eel, Electrophorus electricus, is capable of producing an electric discharge of over 600 V (the record seems to be 866 V), consisting of about half a dozen pulses each lasting 2–3 ms. The gross structure of the electric organ is shown in fig. 15.2. Each electroplaque is about 100 μm thick (longitudinally), 1 mm wide (vertically) and 10–30 mm long (radially). The nerve endings are restricted to the posterior face. The anterior (non-innervated) faces are much folded, giving rise to numerous papillae. The high-voltage discharges are produced by the main organ; Sachs’ organ gives much smaller discharges. In the main organ, up to 6000 rows of electroplaques are arranged in series with each other. This series arrangement of the electroplaques leads to addition of the voltages produced by each one of them; for example, if a discharge of 600 V were produced by an organ containing 4000 rows of electroplaques, each electroplaque would have to produce a potential of 150 mV across it.

The electrical properties of the electroplaque were investigated by Keynes and Martins-Ferreira (1953), using intracellular electrodes. They used the electroplaques from the organ of Sachs for their experiments, since these electroplaques can be more easily isolated than can those of the main organ. In the resting condition, there is a resting potential of about −80 to −90 mV. Electrical stimulation of the electroplaque results in an all-or-nothing action potential appearing across the innervated (posterior) face, but there is no potential change across the non-innervated (anterior) face. The experimental evidence for this statement is as follows. In fig. 15.3, trace a is recorded from two microelectrodes placed just outside the innervated face; there is, of course, no potential difference between them either at rest or during activity. For trace b, one of the microelectrodes was inserted into the cell; this then records the resting potential, and, on stimulation, an ‘overshooting’ action potential of about 150 mV is observed. This means that the innervated face is electrically excitable, just as the cell membranes of nerve axons and vertebrate twitch muscle fibres are. In trace c, one of the electrodes is pushed right through the electroplaque so that the potential across the whole electroplaque is recorded. There is no steady potential at rest, indicating that the resting potential across the non-innervated face is equal to that across the innervated face. On stimulation, an action potential of the same size and shape as that across the innervated face appears across the whole electroplaque. This suggests that the non-innervated face is electrically inexcitable, and that the whole of the discharge is accounted for by the activity of the innervated face.

Confirmation of this view is provided by the experiment shown in fig. 15.4. Here, the potential across the non-innervated face (trace b) is not affected by stimulation (except for some small electrotonic changes), whereas the potential across
the whole electroplaque (trace c) shows the familiar action potential.

Thus the voltage produced by a stimulated electroplaque is caused by the asymmetry of the responses of its two faces, as is shown diagrammatically in fig. 15.5. In the complete electric organ, the electroplaques are arranged in series so that, as we have seen, their voltages are additive. Notice that the innervated face becomes negative to the non-innervated face during the discharge; this situation occurs in many other electric fish, and is sometimes known as ‘Pacini’s Law’ – but by no

Fig. 15.1. Diagrams showing the positions of the electric organs in some electric fish. Small arrows point to the electric organs. Large arrows show the direction of current flow through the electric organs during their discharge; for the three smaller species (Gnathonemus, Gymnotus and Sternarchus) the two or three arrows indicate successive phases of the discharge. (After Bennett, 1968, redrawn.)

STRONGLY ELECTRIC

Electrophorus

Malapterurus

Torpedo

Astroscopus

WEAKLY ELECTRIC

Gnathonemus

Gymnarchus

Raja

Gymnotus

Sternarchus
The electric organs of fishes

Fig. 15.2. The gross structure of the electric organs in the electric eel. (From Keynes and Martins-Ferreira, 1953.)

means all electric fish obey this rule. In Electrophorus, since it is the posterior face of the electroplaques that is innervated, the head end becomes positive to the tail during the electric discharge.

The ionic basis of the electroplaque action potential is much the same as that of the action potentials of nerve axons and twitch muscle fibres. Keynes and Martins-Ferreira showed that its size is dependent on the external sodium ion concentration, and Schoffeniels (1959), from radioactive trace measurements on isolated electroplaques, found that the sodium inflow across the innervated membrane increases greatly during activity.

Tetrodotoxin combines with the sodium channel protein and renders the electroplaques inexcitable. Antibodies to the tetrodotoxin-binding protein can be prepared. When these are allowed access to thin tissue sections, they bind entirely to the innervated faces of the electroplaques and not at all to the non-innervated faces (Ellisman and Levinson, 1982).

We have seen in chapter 6 that Electrophorus electric organ is one of the richest sources of sodium channel protein, from which it can be isolated (Agnew et al., 1978, 1983) and sequenced by isolating its messenger RNA followed by complementary DNA cloning (Noda et al., 1984).

Fig. 15.3. Responses of a Sachs’ organ electroplaque of Electrophorus to electrical stimulation. The position of the recording electrodes for each trace is shown in the lower diagram, in which the innervated face of the electroplaque is uppermost. (From Keynes and Martins-Ferreira, 1953.)
Fig. 15.4. Results of an experiment similar to that of fig. 15.3, but this time the non-innervated face of the electroplaque is uppermost. (From Keynes and Martins-Ferreira, 1953.)

![Graph showing electroplaque potentials](image)

Fig. 15.5. Diagram to show membrane potentials across the innervated (uppermost in the diagram) and non-innervated faces of electroplaques in the Sachs organ of the electric eel, at rest (a) and at the peak of the discharge (b). (From Keynes and Martins-Ferreira, 1953.)

![Diagram illustrating membrane potentials](image)
In the living animal, discharge of an electroplaque is not, of course, initiated by direct electrical stimulation, but by excitation via the efferent nerves innervating it. Altamarino, Coates and Grundfest (1955) found that stimulation of the motor nerves elicits an excitatory post-synaptic potential across the innervated surface of the electroplaque, which then induces the action potential (fig. 15.6). This system is biophysically similar to that whereby vertebrate twitch muscle fibres are excited, except that each electroplaque is innervated by a number of nerve fibres; if only a small proportion of these fibres is stimulated (as in fig. 15.6c), the resulting postsynaptic potential is not large enough to elicit an action potential.

**The electroplaques of some other electric fish**

Electric organs occur in a variety of different fish. They have probably arisen independently six times in evolution: in (1) the rajoid and (2) torpedoid rays among the cartilaginous fish, in (3) the electric catfish *Malapterurus* and (4) the stargazer *Astroscopus*, and in two large freshwater groups separated by the Atlantic ocean, (5) the six gymnotiform families of Central and South America and (6) *Gymnarchus* and the mormyrids of tropical Africa. Much detail is now known about the nature of their various electric discharges (see Bennett, 1971, and Bass, 1986); we shall here look at a few examples.

**Marine electric fish**

This group includes the electric rays *Torpedo*, *Narcine* and *Raia*, and the ‘stargazer’, *Astroscopus*. In all these fish, the innervated faces of the electroplaques are not electrically excitable, and the response to nervous stimulation consists solely of a depolarizing postsynaptic potential (Bennett and Grundfest, 1961a, b; Bennett *et al.*, 1961; Brock *et al.*, 1953), as is shown for *Raia* in fig. 15.7. Synaptic transmission is cholinergic, with large numbers of nerve endings and high densities of nicotinic acetylcholine receptors on the innervated face of the electroplaque. Ionic current flow across the innervated face occurs almost entirely via the channels of the acetylcholine receptors. Hence the maximum potential across the active electroplaque cannot be as large as it is in *Electrophorus*; it is usually less than 70 mV.

The electric organ of *Torpedo* has been much used as a rich source of acetylcholine vesicles (Whittaker, 1984) and acetylcholine receptors and their messenger RNA (Raftery *et al.*, 1976; Noda *et al.*, 1982), with the results that we have seen in chapters 7 and 8. Volta’s invention of the voltaic pile in 1800, a crucial step in the science of electricity, was described by him as ‘an artificial electric organ’ and may well have been inspired by the structure of the *Torpedo* electric organ (Wu, 1984).

Now why should the electroplaques of marine electric fishes be electrically inexcitable? If it were not for the existence of *Astroscopus*, we could assume that the situation was of no functional significance, since the marine rays and skates are phylogenetically distinct from the fresh-water teleosts; but *Astroscopus* is much more closely related to the fresh-water forms than to the rays, yet it too has electrically inexcitable electro-
plagues. There is no generally agreed answer to this question, but a possible explanation is as follows. We can regard the excited electroplaque membrane of a fresh-water fish as consisting of a battery $V_{Na}$ in series with a resistance $R_{Na}$. The current produced by the discharge flows through the resistance $R_{ex}$, which consists mainly of the resistance of the external medium in which the fish swims; the voltage produced by the membrane is $V$. This rather simplified scheme is shown in fig. 15.8a. In this circuit, it is evident that

$$V = V_{Na} \left( \frac{R_{ex}}{R_{Na} + R_{ex}} \right).$$

Thus if $R_{ex}$ is reduced, $V$ also falls. But we know that, in an electrically excitable system such as this one is, $R_{Na}$ rises as $V$ falls, which will itself produce a further fall in $V$, and so on. Hence it follows that an electrically excitable system, based essentially on a positive feedback relation between membrane potential and sodium conductance, is ineffective if the external resistance is sufficiently low. An analogous circuit for an electrically inexcitable electroplaque is shown in fig. 15.8b. In this system the resistance of the excited synaptic membrane ($R_s$) is independent of the membrane potential, hence the membrane potential during excitation is not disproportionately lowered if the external resistance is low. Since the external resistance is very much lower for fishes living in sea water, we might expect such fish to rely on

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**Fig. 15.7.** Responses of *Raia* electroplaques, as recorded by electrodes in various positions. (From Brock et al., 1953.)

**Fig. 15.8.** Simplified equivalent circuits of the electric organs in fishes whose electroplaques are (a) and are not (b) electrically excitable.
purely synaptic excitatory mechanisms for the discharge of the electroplaques, as indeed they do.

**Gymnusotus**

This is a South American fresh-water fish which produces weak electric discharges. The electroplaques lie in eight tubes, four on each side of the animal. Those in the dorsal pair of tubes are innervated on the anterior surface, whereas those in the other tubes are innervated on the posterior surface. The physiology of the discharge was investigated by Bennett and Grundfest (1959). They found that both faces of the electroplaques are electrically excitable, but, when the motor nerves are stimulated, the innervated surfaces are excited before the non-innervated surfaces, so that the potential change across the whole electroplaque is diphasic. During the natural discharge, the upper tube on each side (tube 1) fires first, and then the lower tubes (2 to 4) fire together. The result of this is that the potential change over the whole fish is triphasic (fig. 15.9), the sequence of events being: (a) excitation of the innervated faces in tube 1; (b) excitation of the non-innervated faces in tube 1 and of the innervated faces in tubes 2 to 4; and (c) excitation of the non-innervated faces in tubes 2 to 4.

**Malapterurus**

The strong electric discharge of *Malapterurus electricus* (the electric catfish) is of considerable interest in that it does not obey 'Pacini's law': the electroplaques are innervated posteriorly, yet the head becomes negative to the tail during activity. At one time it was thought that the electroplaques in this fish were derived from glandular tissue rather than muscle, and, in the absence of physiological observations, it was suggested that the innervated face became hyperpolarized during activity. Later observations showed both these ideas to be wrong.

The electroplaques of *Malapterurus* are rather unusual in that innervation occurs at the end of a stalk which is produced from the centre of the posterior face, as is indicated in fig. 15.11 (a somewhat similar arrangement occurs in mormyrids; see Bennett and Grundfest, 1961c). The sequence of events during discharge of an electroplaque has been determined by Keynes, Bennett and Grundfest (1961), using intracellular microelectrodes.

Excitation arises in the stalk and then passes into the electroplaque disc, where both faces are excited simultaneously. However, the action potential across the anterior ('non-innervated') face lasts only for about 0.3 ms (figs. 15.10 and 15.11). Hence, during the later stages of the response, only the anterior face is active, so that there is a net potential difference across the whole electroplaque.

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**Fig. 15.9.** Waveforms of a single pulse from the repetitive discharge of *Gymnusus carapo*, recorded at different positions near the body surface. Notice (a) that the potential is triphasic near the tail, rather more complex elsewhere, and (b) that the potentials are maximal near the tail and the head, suggesting that the electric organ acts as a dipole generator. (From Bennett and Grundfest, 1959.)
Fig. 15.10. Responses of a Malapterurus electroplaque to nervous stimulation, recorded across the whole electroplaque ($V_1$), across the anterior face ($V_2$) and across the posterior face ($V_3$). (From Keynes et al., 1961.)

Fig. 15.11. Schematic diagram showing the sequence of potential changes during the discharge of a Malapterurus electroplaque. (From Keynes et al., 1961.)

Fig. 15.12. The anatomy of the electric organ of Sternarchus. The middle diagram shows the course of one of the modified nerve fibres which constitute the organ and the lower one shows its structure. (From Bennett, 1971.)

Sternarchus

The electric organs of Sternarchus and its immediate relatives are unique in that they are composed of tissue derived from nerve axons rather than from muscle cells (Couceiro and de Almeida, 1961). The electromotor axons leaving the spinal cord are swollen distally to form ‘electrotubes’ which are analogous in function to the electroplaques of other electric fishes. Fig. 15.12 shows the structure of these swollen axons. After entering the electric organ each axon passes forwards for several millimetres, and then turns back on itself and runs backwards for an approximately equal distance. The diameter of the axon is about 100 μm in the swollen portions but only about 20 μm elsewhere. Each arm of the loop has three very large nodes (about 50 μm long) in the region just distal to the swollen portion (Waxman et al., 1972).

Waxman and his colleagues investigated the functioning of these remarkable axons (fig. 15.13). The greatly enlarged nodes on the distal side of each swollen portion are electrically inexcitable, whereas those on the proximal side behave in the normal manner. Thus inward current flow at the proximal nodes will pass outwards at the enlarged distal ones. The net external current produced by
The whole axon reverses in direction as the second arm of the loop is excited. The swollen portions will allow the internal current to pass along to the enlarged distal nodes without much attenuation, and the enlarged area of the distal nodes will facilitate its outward flow.

The functions and evolution of electric organs

The powerful electric organs of *Electrophorus* and *Torpedo* are used both offensively, in temporarily paralysing smaller fishes which can then be eaten, and defensively, in deterring predators. The discharges of *Astroscopus* and *Malapterurus* are also able to stun smaller fishes, and are probably used for offensive purposes.

However, it is clear that the low-voltage discharges of the mormyrids, *Gymnarchus* and the gymnotiformes cannot act as offensive or defensive weapon systems. Lissmann (1951) showed that *Gymnarchus* could detect the presence of electrical conductors and non-conductors in its environment, and was sensitive to weak electric currents. He suggested that the electric organs functioned as the ‘transmitter’ of a direction-finding system, the ‘receiver’ being electro-sensitive sense organs capable of detecting changes in the pattern of current flow around the fish. We shall examine these electro-receptors in a little more detail in chapter 17; suffice it to say, here, that Lissmann’s hypothesis is now well substantiated (Lissmann and Machin, 1958).

Electric signals are also used as methods of communication between individuals of the same species. The signals are species-specific, and in at least some species they may be involved in species identification, sex recognition, territorial or aggregational behaviour, the establishment of dominance hierarchies, and courtship (Hopkins, 1974;
Hopkins and Bass, 1981; Hagedorn, 1986). In the gymnotiform *Hypopomus*, the males have larger electroplaques than the females, but the difference disappears in females injected with male sex hormone (Hagedorn and Carr, 1985).

In discussing various objections to his theory of evolution by natural selection, Darwin (1859) mentioned the problem of the electric organs of fishes. At that time only the powerful electric organs (such as those of *Electrophorus* and *Torpedo*) were known, and it was impossible to see how these could have gradually developed through ancestors with weaker discharges, since such weak discharges would not be effective as weapons of offence or defence and would therefore give no selective advantage to a fish possessing them. Lissmann (1958) suggested that the offensive-defensive functions of strong electric organs are a development of the direction-finding function of weak electric organs. The first stage in the evolution of the direction-finding system must have been the development of electroreceptors; these may have been capable of detecting muscular action potentials, and the sensitivity and accuracy of the system could then have been increased by modification of the muscle cells to form electric organs.