

PRINCIPLES *of* ANIMAL COMMUNICATION

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Chapter **11**

Electroreception

IN THIS CHAPTER, WE DISCUSS A FINAL MODALITY used in animal communication: electroreception. Whereas all of the other modalities discussed so far are available in both terrestrial and aquatic environments, electroreception can only be used in water. This limitation occurs because air is too effective an insulator to pass electric signals of biological magnitudes between senders and receivers. Even in water, the ranges over which electrical signals can be detected are quite limited. Although all of the other modalities are used by both invertebrates and vertebrates for communication, to date only aquatic vertebrates are known to use electroreception for this purpose. However, the ability to detect electrical signals is widespread among aquatic vertebrates with examples in fish, amphibians, and mammals, and the corresponding ability to produce electric signals appears to have arisen independently in both cartilaginous and bony fishes. Electrical communication exhibits certain properties that amplify and reinforce themes covered in prior chapters, and so we shall treat it in some detail below.

PROPERTIES OF ELECTRIC FIELDS

All of the matter on Earth is held together by the strong forces between electrons and protons. The total numbers of positively charged protons and negatively charged electrons are about the same and the world is largely neutral. However, within any piece of matter, there are often local regions of electron shortage that are spatially separated from regions of electron abundance. It is the attractive forces between these regions that hold them tightly together. The fact that most of the world is stable and structured is partly due to strong electrical forces.

Any piece of matter that contains a shortage or excess of electrons (relative to protons) is said to have a net **charge**: a shortage of electrons is said to confer a positive charge and an excess a negative one. The greater the excess or deficit of electrons, the greater the magnitude of the charge. Any other charged object near the first will experience a force on it due to the attraction or repulsion between the two charges. Charges of similar sign (e.g., both with electron excesses or both with electron deficits) will repel each other; opposite charges will attract. For two nonmoving objects in a vacuum with charges q_1 and q_2 , respectively, the force F experienced by each along the axis joining them is given by Coulomb's law:

$$F = \frac{1}{4\pi\epsilon_0} \cdot \frac{q_1q_2}{d^2}$$

where ϵ_0 is called the **permittivity constant**, and d is the distance between the two charged entities. When more than two charged objects are present within a given volume, the forces they generate combine vectorially at any location, and the direction and magnitude of the net force is likely to vary between locations. If we were to move a small unit charge to many locations around such an array of charges and measure the direction and magnitude of the force exerted on it at each point, the resulting map would describe the **electric field** around the charge array. As one moves further and further from the array, (i.e., as d increases), the magnitude of the electric field at each point will decrease. At an infinite distance, the force drops to zero. The magnitudes of electric fields are classically measured in **newtons/coulomb** (where a newton is a unit of force and a coulomb is a unit of charge equal to 6×10^{18} electrons).

Suppose we have such a group of charged objects localized near each other. Together they will generate an electric field around themselves that differs in magnitude and direction of force depending upon the location we sample. Suppose we then take a small unit charge located an infinite distance away from these objects (at which point the net force on it is zero) and move it to some location nearer to them. If the unit charge is repelled at most locations by the electric field around the objects, we shall have to do work to move the charge to its new location. If it is attracted, the electric field will help us move the unit charge and energy is released in the process (negative work). The overall work (positive or negative) expended to move the charge

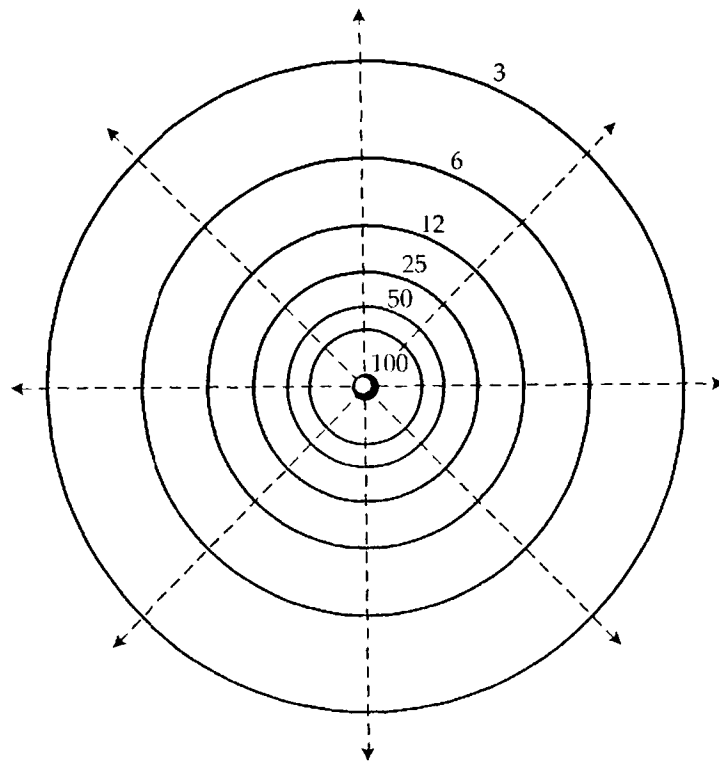
from infinity to a point closer to the array is called the electric potential at that point. As long as the charged objects are immobile, the work expended moving our unit charge to this point will be the same whatever path we take. Thus the electric potential at any point around a set of immovable charged objects is a fixed number. This is convenient, because if $\phi(a)$ is the electrical potential at point a , and $\phi(b)$ is that at point b , the work needed to move a unit charge between the points a and b is just the difference between their potentials: $\phi(a) - \phi(b)$. It is thus possible to make a plot of electric potential around our objects just as we can make a map of the electric field around them.

The electric potential and electric field maps are closely linked. If we select any point in the electric potential map, the corresponding electric field vector equals the gradient or slope in potential values at that location. Also, because the magnitude of the electric field decreases with increasing distance from the charged objects, less work must be done to move from infinity to locations distant from the charges and thus the map of potential, like the map of electric field, will show a decrease in magnitudes the farther away from the charges one samples. Electric potentials are usually measured in volts (a unit based on work/coulomb). The relationship between electric potentials and fields permits electric fields to be more practically measured in volts/unit distance (instead of newtons/coulomb).

Shapes of Electric Fields in a Vacuum

Let us examine the electric field and potential maps around some simple charged objects. Consider first a single charged particle with no other charged objects nearby. This is called a monopole situation (analogous to the acoustic monopole we discussed on page 76). The electric field and potentials surrounding a monopole charge are diagrammed in Figure 11.1. This plot may be envisioned as a topographic map in which solid lines connect locations of identical electrical potential: higher potentials constitute higher contours in the topography. Electric potential at a distance d from the charge is proportional to $1/d$; thus successively larger circles represent increasingly lower potentials. The electrical field in this plot is represented by dashed lines and indicates the trajectories down which a unit charge of the same sign would "roll" if allowed to move in this topography. Areas of high field magnitude are indicated by drawing adjacent lines closer together. For a monopole, the directions of the field at any location are pointed radially away from the point charge. Note that we have only drawn the electric field in one plane; in most situations, the field will be a three-dimensional one with lines of force radiating out of the point in all directions. Because the electric field equals the derivative of the potential with respect to location, and potential is proportional to $1/d$, the electric field at a distance d from a point charge will be proportional to $1/d^2$. In practice, we do not measure potentials or fields by moving tiny charges around, but instead by comparing the difference in electric force exerted on an instrument by potentials at two different locations. Since the locations are likely to differ in their distance from the monopole, the measured force will reflect the gradient in potential and thus the electric field. *Differences*

Figure 11.1 Electric field and potential around monopolar point charge. Dotted lines indicate direction of the electric field (convention is to draw arrows pointing away from a positive charge, toward a negative charge). Proximity of adjacent field lines indicates the strength of the electric field in that region (here highest strength is closest to the point charge). Solid circles indicate all locations around monopole with electric potential of a particular value. Relative values for individual isopotential circles are indicated, showing a rapid drop in potential with distance from the point charge.



in potential between two locations around a monopole thus tend to decrease with the square of the distance between them.

Now consider two small objects with equal and opposite charges. Suppose the two are separated by a distance δ , which is small relative to various distances d at which we sample the surrounding electric field and potentials. Such a charge array is called an **electric dipole**. The electric field and potentials surrounding a dipole are shown in Figure 11.2. Notice that this plot is not simply the sum of two monopoles. The electric field lines no longer radiate away from each charge in a radial fashion but are bent and distorted by the presence of the adjacent charge. This change in the electric field causes a corresponding change in the shapes of the equal potential lines around each charge: these are no longer circular, but are flattened on the side closest to the other charge. Unlike the situation with a monopole, we cannot characterize the potential around a dipole simply by specifying the distance to the sampling point d . Potential values vary with the relative angle between the line joining the two charges and that joining the sampling location to the midpoint between the charges. If we denote this angle by θ , and the absolute value of the charge on each point by q , then the potential around a dipole in a vacuum at location (d, θ) is

$$\phi(d, \theta) = \frac{1}{4\pi\epsilon_0} \cdot \frac{q\delta \cos(\theta)}{d^2}$$

The product $q \cdot \delta$ in the numerator is often called the **dipole moment** of the array and plays a major role in the magnitude of the potential at any point;

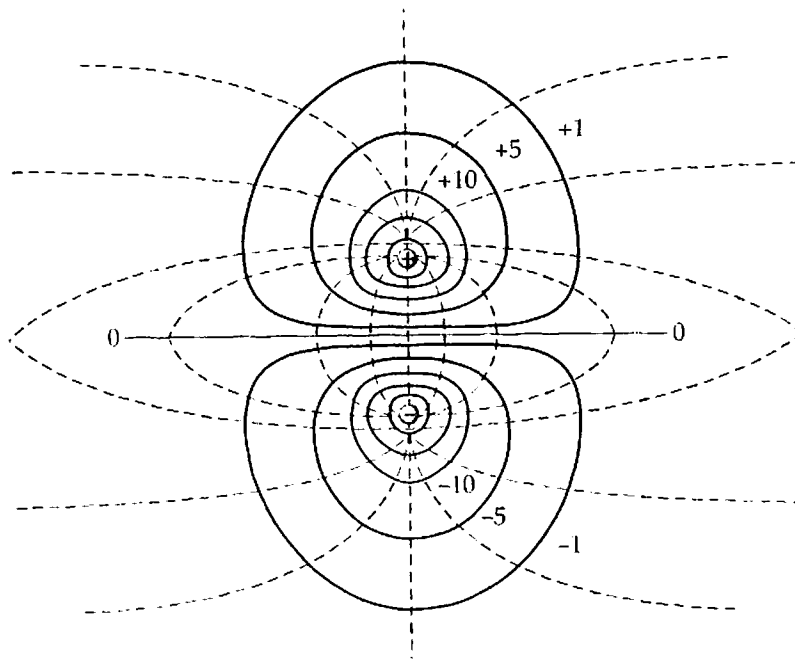


Figure 11.2 Electric field and potential around electric dipole. Conventions as in Figure 11.1. Positive charge is the top member of the pair, negative charge is the lower. Note that electric field lines are curved around the dipole, and lines connecting points of equal electric potential are distorted and no longer circular. Also, note the line midway between two points and perpendicular to the axis joining them along which potential is zero.

the farther apart the two charges are separated (δ), or the greater the charge at each point (q), the greater the potential at all d . The angle of the sampling point relative to the axis of the dipole is also important in determining the potential: $\phi(d, \theta)$ will be highest along the line joining the two charges [e.g., θ is zero and $\cos(\theta) = 1$], and zero at points perpendicular to the midpoint of the line joining the two charges [e.g., $\cos(\theta) = 0$]. As the equation indicates, the electric potential around a dipole is proportional to $1/d^2$ (and thus the electric field around a dipole, and the difference in voltage between two locations near a dipole, fall off with $1/d^3$).

The electrical fields generated by biological sources are rarely simple dipoles and are practically never monopoles. Instead, complex arrays of charges will have many axes around which the charges are distributed. The resulting field will be described by a sum of terms based on identifiable axes of charge distribution: a single axis contribution is called the dipole component, a second axis contribution is the quadrupole component, a third axis portion is the octupole component, and so on. The magnitude of each component's contribution to the overall electric field depends upon the distance between the sampling point and the charge array: the electric field of the dipolar component is proportional to $1/d^3$, that for an octupole is proportional to $1/d^5$. At very close distances to the charge array, all components of the field play significant roles in determining its shape and properties; at greater distances, all of the higher order components have such low magnitudes that only the dipole component is needed to describe the field. Just as with sound, we can thus speak of a near and far field around an array of electric charges. In the near field, all of the higher-order components of the field are required to describe the field; in the far field, only the dipole component is necessary.

Shapes of Electric Fields in Nonconducting Media

So far, we have discussed electric fields around an array of charges in a total vacuum (no surrounding matter present). Animals do not live and communicate *in vacuo* but live in some medium. How does the presence of a medium affect an electric field?

Media differ in how they respond to an applied electric field. **Conductors** (such as metals) have electrons that are relatively free to move. The moment an electric field is applied to a conductor, electrons begin moving within it to pile up on the side of the conductor facing the positive side of the field. The positive atoms that have given up their electrons are left behind on the side of the conductor facing the negative part of the field. This separation of charges inside the conductor generates an electric field exactly opposite to the external field. Eventually, this internal field balances the external one, there is no net force on any electron, and the magnitude of the net field (internal plus external) inside the conductor becomes zero. Because there is no remaining field within the conductor, it will take no work to move a point charge between any two points within this conductor. Thus the electric potential inside the conductor is the same everywhere. Note that there will still be an electric field outside of the conductor, and it will take work to bring a test charge from some point outside of the conductor to some point on or inside it.

Dielectrics are materials whose electrons have limited mobility. When placed in an electric field, dielectric electrons cannot move between atoms. However, many atoms permit their electrons to congregate on one side of the atom, or in a liquid, molecules that have one side slightly more positive than another (like water) will rotate until their positive sides face the negative side of the imposed field. This polarization of the atoms or molecules generates millions of tiny dipoles within the material with their dipole axes parallel to the lines of the electric field. Because the polarity of the dipoles is opposite to the imposed external field, the result is to reduce the net electric field inside of the dielectric. The stronger the polarization inside the material, the greater the reduction in internal field magnitude. The ability of a particular kind of matter to be polarized by an external electric field is characterized by its **dielectric constant** (k). The higher the value of k , the more easily a material is polarized and the greater the reduction of the electric field inside the material. For a vacuum (a perfect insulator), $k = 1$, whereas for a conductor, k is infinitely large. Some other sample values for k are given in Table 11.1.

The dielectric constant determines the permittivity of a medium and thus the size of an electric field at any point. Whereas for a vacuum, the permittivity constant is ϵ_0 , the permittivity for a medium, ϵ , is $\epsilon = k\epsilon_0$. (The dielectric constant k of a medium is thus seen to be the ratio of its permittivity to that in a vacuum.) Suppose we create an electric field inside a homogeneous nonconducting medium such as a liquid. Coulomb's law then becomes:

$$F = \frac{1}{4\pi\epsilon} \cdot \frac{q_1q_2}{d^2} = \frac{1}{4\pi k\epsilon_0} \cdot \frac{q_1q_2}{d^2}$$

Table 11.1 Dielectric constants for selected media

Material	Dielectric constant (k)
Vacuum	1.0000
Air	1.0004
Oil	5.0
Glass	10.0
Water	80.0
Metal	∞

This means that the magnitude of an electric field in a homogeneous medium with a dielectric constant k is reduced by a factor $1/k$ at all points relative to that expected in a vacuum. Since the electric field is reduced by this factor at all locations, so is the electric potential. For example, the electric potential around a dipole in a homogeneous nonconducting medium is

$$\phi(d, \theta) = \frac{1}{4\pi k \epsilon_0} \frac{q\delta \cos(\theta)}{d^2}$$

Electric Fields in Conducting Media

Suppose we place an electric dipole in a medium that is a worse conductor than a metal, but a better conductor than most dielectrics. Water is such an example. Water invariably has dissolved materials within it, and many of these, such as salts, break up in water into their component charged ions. The presence of an electric field in water will cause positive and negative ions to move in opposite directions. The ionic trajectories follow the electric field lines. This movement of ions in water (or of electrons in a metal) is called an **electric current**. The magnitude of an electric current between two points (measured in coulombs/second or amperes) is proportional to the potential difference or voltage between the points. The constant of proportionality between an applied voltage and a resulting current is called the **conductance** of the medium through which the current is flowing. More often, we use the reciprocal of conductance, called the **resistance**. If V is the voltage difference between two points and R is the resistance (in ohms), then the current I (in amperes) depends on these variables according to Ohm's law:

$$I = \frac{V}{R}$$

The convention in physics is that current flows from a region of positive voltage to one of more negative voltage. Note that this is opposite to the actual flow of electrons (from a negative to positive potential location).

Resistance in a particular context will be higher the greater the distance the current must flow, the smaller the cross-sectional area through which the current passes, and the worse the material as a conductor. The latter term is characterized by the material's intrinsic **resistivity**. Because of the resistance of the water in which we have placed our dipole, there will be a steady current of positive ions towards that part of the dipole of opposite charge to each ion. If there were no resistance, the initial current would quickly cancel the charge at each end of the dipole due to accumulations of oppositely charged ions. If the resistance is high enough, it may take some time before the dipole is fully neutralized. Alternatively, something may occur near the dipole to restore its charge. In either case, if the electric field is maintained for a sufficiently long period, we can measure the electric potential at various points around the dipole and the amount of current at each location. For a stable source of current in a conducting medium, the potential at location (d, θ) from the dipole is

$$\phi(d, \theta) = \frac{\rho_0 l}{4\pi} \cdot \frac{\delta \cos(\theta)}{d^2}$$

where the medium resistivity, ρ_0 and the current I have replaced the permittivity, ϵ , and the charge, q , used for nonconducting media.

Water and many other materials are both conductors and dielectrics. Some current will flow in them, but the resistance is high enough that electric fields are sustained, and their ability to be polarized and act as a dielectric permits some build-up of counterfields within the medium. For static electric fields, this may not be significant. If however, the electric field is changing in magnitude or direction, then the dielectric properties of the medium can become important. In a steady electric field, an electron in a conductor may move the entire length of the conductor. This is called a **direct current (DC)**. Now suppose we apply a sinusoidally reversing electric field to the conductor. Electrons will first move one direction and then back the other. This is an **alternating current (AC)**. The faster the frequency of the alternating field, the less distance any one electron can travel before it has to turn around and go the other way. In a nonconducting dielectric, electrons or polar molecules can move a bit, but they can never move far enough to sustain a steady DC current. However, if an alternating field is applied across such a material, the distance electrons have to travel per cycle may be within the polarizing limitations of the material. The higher the dielectric constant for the material, the lower the frequency of alternation which the material can track. The effective resistances of dielectrics may thus drop if the applied electric field varies sufficiently quickly. To keep this notion of resistance distinct from classical DC resistivity, the term applied to such dielectrics is **capacitive reactance**. Capacitive reactance decreases with the dielectric constant of the material and with the frequency of the electric field oscillation. Like resistance, it is measured in ohms. Remember that even if the waveform of the electric field variations is not sinusoidal, it can be considered as the sum of a number of differ-

ent sinusoids (see Chapter 3). Applying such a nonsinusoidal signal to a dielectric, we will find that the dielectric will act like a high-pass filter since it can more easily track the higher-frequency components than the lower-frequency ones. The overall impedance of a medium like water to a varying electrical field will thus depend on both the resistivity of the water and on the capacitive reactance of the water at the various frequencies making up the waveform of the changing field.

We have assumed so far that media are unbounded and homogeneous. The resulting electric fields can be called **free fields** (by analogy with sound). However, most media have boundaries and contain objects whose dielectric and/or resistive properties differ from those of the medium. The usual situation is thus not a free field. Boundaries and objects in the medium will distort and change the field shape from free field conditions. For example, suppose we place a monopole in a medium such as water and then place objects with resistivities greater or less than water near to the charge (Figure 11.3). Objects that have lower resistivities than the medium bend the electric field lines in the region between themselves and the charge closer together and towards the object. This region of enhanced electric field magnitude corresponds to a region of very closely spaced isopotential lines and thus a steep gradient in voltage. Objects that have higher resistivities than the medium bend the electric field lines away from themselves, lowering the field magnitude in the region between themselves and the charge, and flattening the potential gradient in this region. When many objects of differing conductivities are present, the shape of the field can become highly complex. Boundaries are also significant.

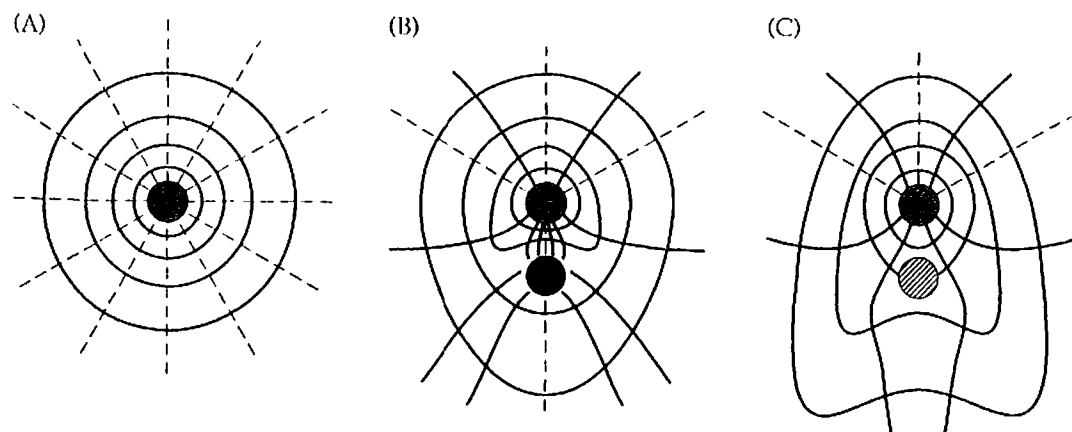


Figure 11.3 Distortion of electric field by neutral objects. (A) Simple monopole showing isopotential (solid) and electric field (dashed) lines. (B) Distortion of field and isopotential lines when an object (black) with resistivity lower than the medium is placed near the point charge (gray). Field lines between charge and object are close together, indicating a higher-magnitude field in this region, and isopotential lines are closer together, indicating a steeper potential gradient. (C) Distortion of the field due to proximity of an object (patterned) with higher resistivity than medium. Field lines are further apart in the region between charge and object, and more widely spread isopotential lines indicate a shallower gradient than elsewhere.

If we place our charge near to the air-water interface, or near a nonconducting bottom, the electric field magnitude and potential near to the charge will be twice as great as that for a charge suspended in an unbounded volume of water. This difference occurs because current can radiate in all directions in the unbounded case, but can only radiate away from the water's surface in the bounded example.

GENERATION OF BIOELECTRIC FIELDS

How might animals generate electrical fields? In fact, this is relatively straightforward since nearly all living organisms have electrical potentials across their cell membranes. Cells routinely use energy to pump potassium ions into their cytoplasm and pump sodium ions out. Both ions are missing an electron and thus are positively charged so the ion pump may not by itself generate any differences in net charge (although it does in some cases). The membranes of most cells are moderately permeable to potassium ions which tend to diffuse down their concentration gradients from the inside to the outside of the cell. The same membranes are relatively impermeable to sodium which cannot diffuse down its concentration gradient and enter the cell. Most negative charges inside the cell are large molecules (such as proteins) that cannot cross the membrane. Thus as potassium ions diffuse out, they generate a shortage of positive charges and an excess of negative ones inside the cell. This builds up an electric field across the membrane with the cell cytoplasm negative relative to the outside medium. Eventually, this electrical field becomes strong enough to draw the positively charged potassium ions back into the cell just as fast as they leave due to the concentration gradient. The result is a stable **electrochemical potential** of -60 to -80 mV across the cell membrane.

Many organisms have gone one step further by evolving excitable cells. When stimulated by a drop in the electrical potential across its membrane, an excitable cell suddenly makes its membrane much more permeable to sodium ions. These run down their gradient into the cell and generate a cytoplasmic potential with a polarity opposite to that generated by the potassium ions. In fact, the interior of the cell goes from -80 mV (relative to outside) before being excited to $+50$ mV at the peak of the sodium influx, a difference of 130 mV. After being depolarized by the sodium influx, the cell then changes its permeabilities back to normal and reestablishes the resting potential of -80 mV. This cyclic change in cytoplasm voltages can occur at slow or rapid speeds. Where it occurs quickly, it is called an **action potential** and is the basic mechanism of cellular stimulation in nerves and muscles.

Certain fish have evolved modified muscle cells (or in one family, the Apterontidae, nerve cells), called **electrocytes**, which are used to generate electrical signals larger than that due to a few nerves or muscles. Tens to thousands of electrocyte cells are arranged in columns within an **electric organ**. Each column is surrounded by insulating material and each electrocyte cell is supplied with nerves. When the fish's brain sends an appropriate signal, all of the electrocytes in a column are stimulated by their respective nerves and de-

polarize simultaneously. In freshwater fish, the depolarization is a rapid action potential; in marine species, it is slower and only goes from resting to zero potential. Because the cells are stacked in a column and prevented from shorting each other by the surrounding insulation, their voltages add up to produce a large net voltage between the two ends of the column. The more cells present per column, the higher the voltage produced. Since electric eels have over 6000 electrocytes in series, and each cell can produce a difference of 130 mV, these fish can produce discharges up to $6000 \times 130 \text{ mV} = 720 \text{ volts!}$ The amount of current that an electric organ can provide depends upon how wide each electrocyte is and how many parallel columns of electrocytes it contains—the more the number of columns, the greater the total current. A fish of a given size and a certain number of electrocytes could either organize those cells into a few long columns with many cells per column (giving high voltage but lower current capacity) or, alternatively, many columns but with fewer cells per column (giving a lower voltage but a higher current capacity).

Although electric organs are only known in fish, these structures appear to have evolved independently many times in this group. Some taxa have very large electric organs that produce high voltages and are used to stun prey and/or deter predators. Others produce much more moderate voltages and are used for intraspecific communication. Finally, some groups produce rapid trains of electric organ discharges for electrolocation: distortions in the induced electric fields due to nearby objects are used by the fish to detect and monitor their environment much as bats and cetaceans use sound to echolocate (see Chapter 26).

The size and shape of electric organs vary with the habitat of the fish and the function of the electric organ discharge (EOD). Most taxa produce EODs of only a few volts, which are used for either social communication, electrolocation, or both. Such weakly electric fish would include many marine skates, the freshwater Gymnotiformes of the New World tropics, and the freshwater Mormyriiformes of Africa. Organs in these species need not be very large and are usually located in the base of the tail with varying degrees of extension in the anterior (head) direction. As a general rule, species with voltages in the hundreds of volts use their organs for prey capture and self defense. Examples of such **strongly** electric fish are the freshwater electric eels of South America, the freshwater electric catfish of Africa, and the marine torpedo rays. Some torpedoes and the electric eel actually have two electric organs: one produces the high voltages for prey capture and defense, whereas the other is a low voltage organ used for social communication and/or electrolocation. The remaining electrogenic fish, the stargazer, is the only known bony marine fish with an electric organ. The function of its 5 volt EOD remains unknown. As a general rule, the higher resistivity of fresh water demands that these fish, whether weakly or strongly electric, generate somewhat higher voltages than for equivalent functions in sea water. Their electric organs thus tend to be long and thin, whereas many marine forms have shorter and fatter electric organs. The shapes and locations of the electric organs for these major taxa and EOD amplitudes are shown in Figure 11.4.

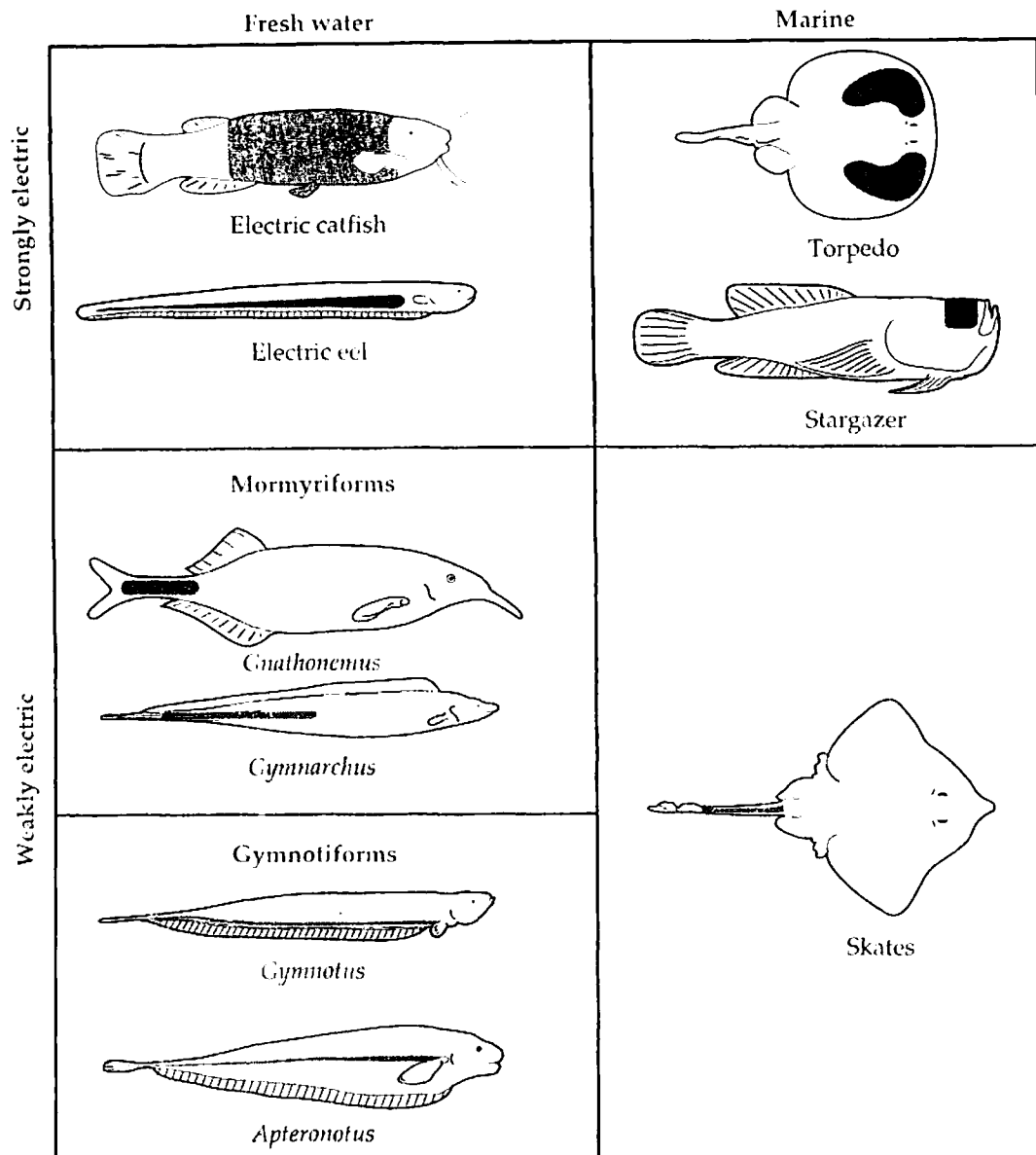


Figure 11.4 Shape and disposition of electric organs in fish. Electric organs are stippled or, if only thin rods, indicated by dotted lines. Taxa are divided according to strength of electric discharge (left axis) and habitat (top axis). Note the larger organ size in strongly electric species, and the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

In addition to differences in amplitude, the waveform of the EOD also varies widely among the electrogenic taxa (Figure 11.5). These varying waveforms result from a number of factors (Bennett 1970; Bass 1986). Electrocytes are usually flattened disks with enlarged anterior and posterior sides. In skates and the high voltage organ of the electric eel, only one side of each electrocyte can be excited and undergo depolarization. The polarity of the cell during the EOD depends upon which side of the cell is active. If the anterior

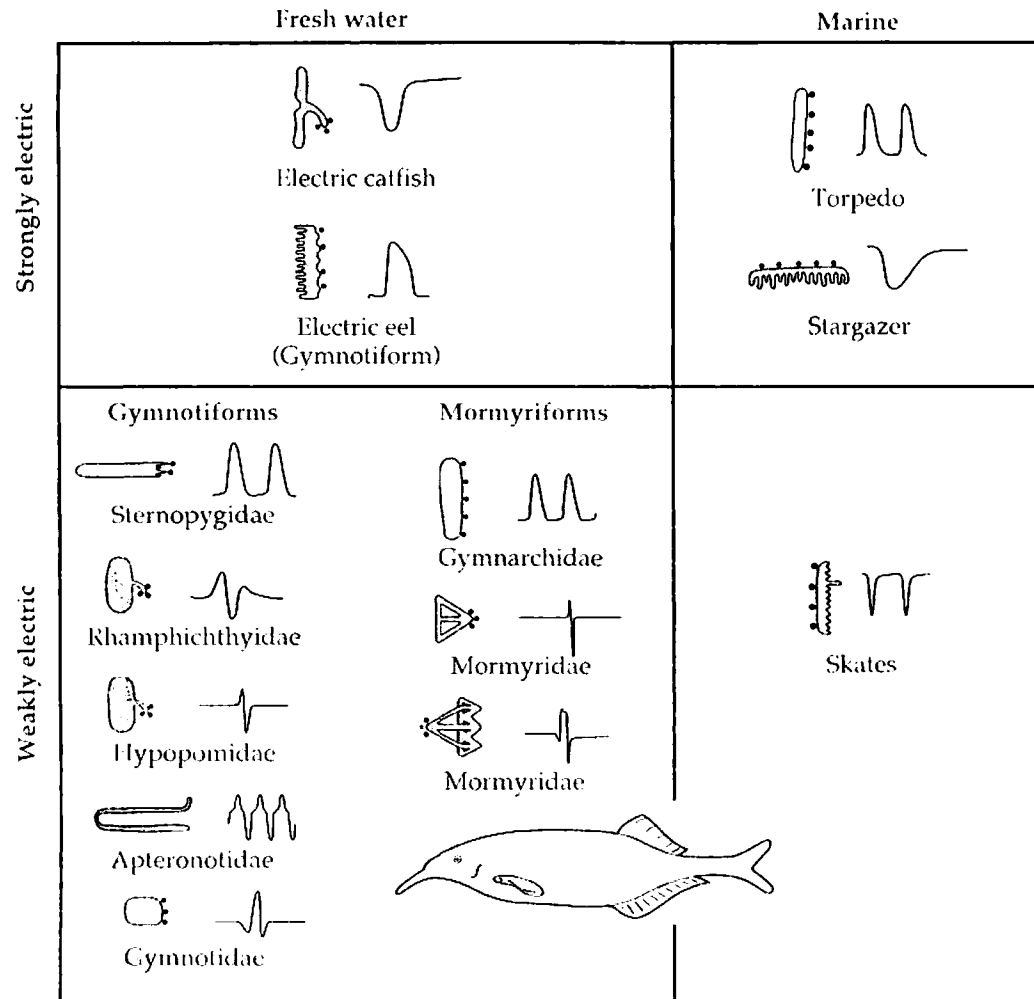


Figure 11.5 Electrocyte innervation and EOD waveform in electric fish. Each example shows disposition of electrocytes on the left and EOD waveform on the right. Electrocytes are shaded and dark dots represent contacts with stimulating nerves. Faces of electrocytes are oriented relative to position of fish shown at bottom of figure: anterior sides of cells are on the left and dorsal sides are on the top. Waveforms go upward when the anterior of the fish is positive relative to the tail, or downward when the anterior is negative. Note that electrocytes innervated on the posterior side (right side of figure) have an initial positive phase in waveform, whereas those innervated on the anterior go negative first. All electrocytes shown are derived from muscle cells, except in the gymnotiform family Apterotonidae where modified nerves are used. (After Bass 1986.)

side is the excitable one, then it is the positive membrane that is active, and current (which by definition moves from positive to negative) will flow through the animal to its posterior. Here it will emerge from the tail and flow through the water back to the head. Since the current in the external medium is flowing from tail to head, an external electrode close to the head will appear negative relative to one near the tail. Alternatively, if the electrocytes are stimulated on their posterior sides, then the external medium around the head of the animal becomes positive relative to that near the tail. In skates, in-

nervation is on the anterior side, and the EOD waveform shows a negative potential difference when the head is compared to the tail (Figure 11.6A); the opposite innervation and waveform is seen in the electric eel (Figure 11.6B). In both cases, the waveform is monophasic (has only one maximum or minimum) because only one side of the electrocytes is excitable.

Some gymnotiform fish have electrocytes that are excitable on only one side and thus produce monophasic EODs. In others, both sides of the electrocytes are excitable but only the posterior side is innervated. When stimulated, the posterior side of each cell fires an action potential, making the head of the fish positive relative to the tail just as in the high voltage organs of electric

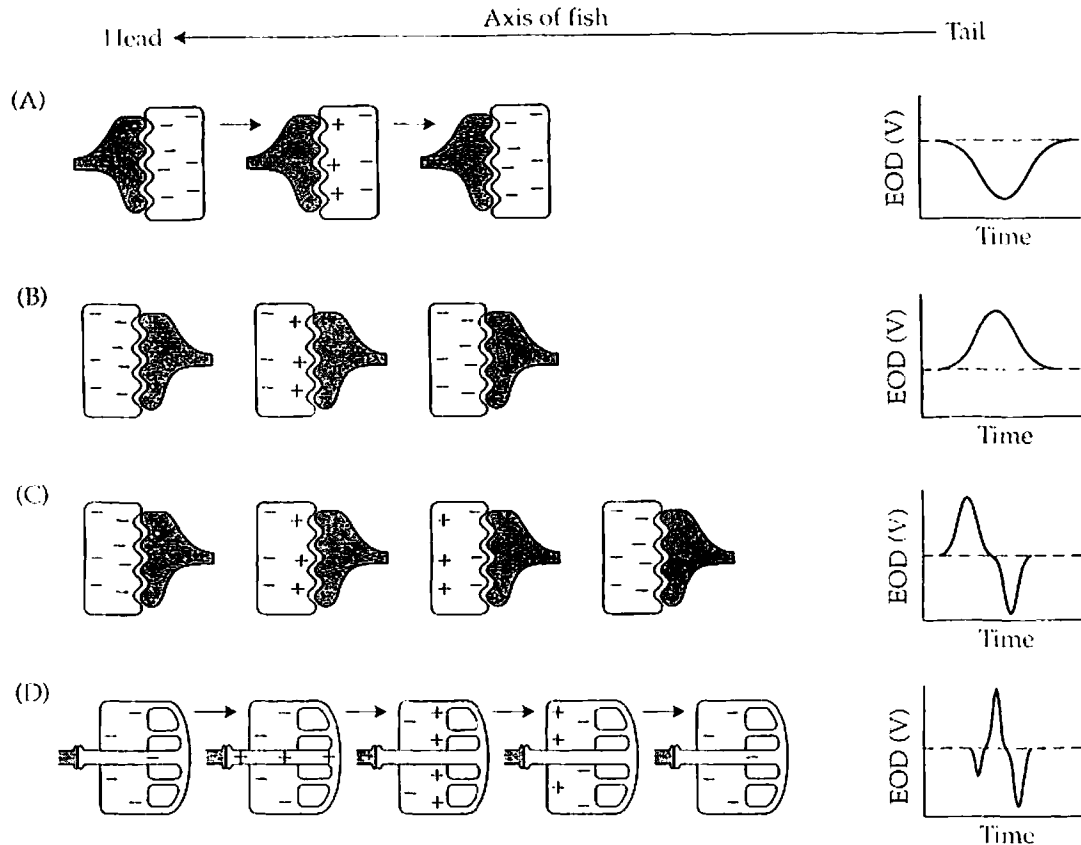


Figure 11.6 Mechanisms for generating varying EOD waveforms. The stippled cell is the innervating nerve; the empty cell is the electrocyte. (A) Skate electrocyte with innervation on the anterior face of the electrocyte and only the anterior face excitable. An EOD measured at the head relative to the tail shows a negative monophasic waveform. (B) An electric eel electrocyte with innervation on the posterior face of the electrocyte and only the posterior face excitable. The EOD near the head is a positive monophasic signal. (C) A gymnotiform electrocyte with posterior-face innervation and both faces excitable. Because the posterior face fires first, the waveform shows an initial positive phase followed by a negative phase. (D) Mormyriiform electrocyte with an excitable stalk connecting to the posterior face. The stalk extends through the electrocyte towards the anterior side where it is innervated. Excitation of the anterior stalk makes the head of the fish negative; subsequent excitation of the posterior face then adds a positive phase, and eventual excitation of the anterior side of the electrocyte generates a final negative phase.

eels. However, the depolarization of the cell soon stimulates an action potential in the anterior face as well. This action potential then generates an opposite voltage, with the head of the fish negative relative to the tail as in a skate. The waveform of these gymnotiforms, EODs is thus biphasic with a positive phase at the head followed by a negative phase (Figure 11.6C). A few gymnotiforms have additional electric organs in their heads. If the fish fires the main and additional organs biphasically but slightly out of synchrony, EOD waveforms with more than two phases or with highly distinctive shapes can be generated. Some examples are shown in Figure 11.7.

Finally, in mormyrid fish, the electrocyte is divided into three regions: an anterior face, a posterior face, and a stalk (Figure 11.6D). The stalk is a tube which connects to the posterior face and then penetrates through the electrocyte towards the anterior of the fish where it connects to the stimulatory nerve. All three regions of the electrocyte are excitable: the stalk fires first and being anterior generates a head-negative phase of the EOD. The posterior face fires next, generating a head-positive phase, and finally the anterior face fires, generating a final head-negative component. Depending upon the relative sizes of stalk and cell faces, and on the geometry and complexity of the stalk, very different EOD waveforms can be generated. Examples are shown in Figure 11.7.

Most weakly electric fish emit EODs continuously. The rate and pattern of discharges is controlled by a pacemaker in the brain. Two classes of discharge pattern are known: (a) pulse fish produce very short duration multiphasic EODs (1-3 msec) with variable rates and low maximal rates (50-100 Hz); (b) wave fish produce very steady rates of monophasic EODs with slightly longer durations (3-5 msec) and very high maximal rates (300-1700 Hz). All members of the Mormyridae except the single genus *Gymnarchus* are pulse fish; gymnotiforms in the families Aptereronotidae and Sternopygidae are wave fish, whereas all other families are pulse fish. As we shall discuss later in this chapter (pages 344-346), weakly electric fish apparently use both the shapes of the EOD waveforms and the patterns of discharge to identify electrical signals from conspecifics.

COUPLING OF ELECTRICAL SIGNALS TO THE MEDIUM

Weakly electric fish use electric organ discharges either to communicate with other nearby fish or for electrolocation. In either case, producing a signal with a large range is generally advantageous. Because electric fields of animals fall off with at least the cube of the distance, it would take an eightfold increase in EOD amplitude to double the range of detection by a receiver. Clearly, this increase is not feasible for most small species. The alternative is to maximize the coupling of each EOD to the medium. As we have seen, the magnitude of the electric field at any fixed distance from the fish will depend in part on the magnitude and geometry of the charge array within it, the dielectric and resistive properties of the medium relative to the fish, the presence of nearby boundaries, the nature of any objects in the medium, and the angle relative to the fish's effective dipole axis. Some of these factors the fish can control.

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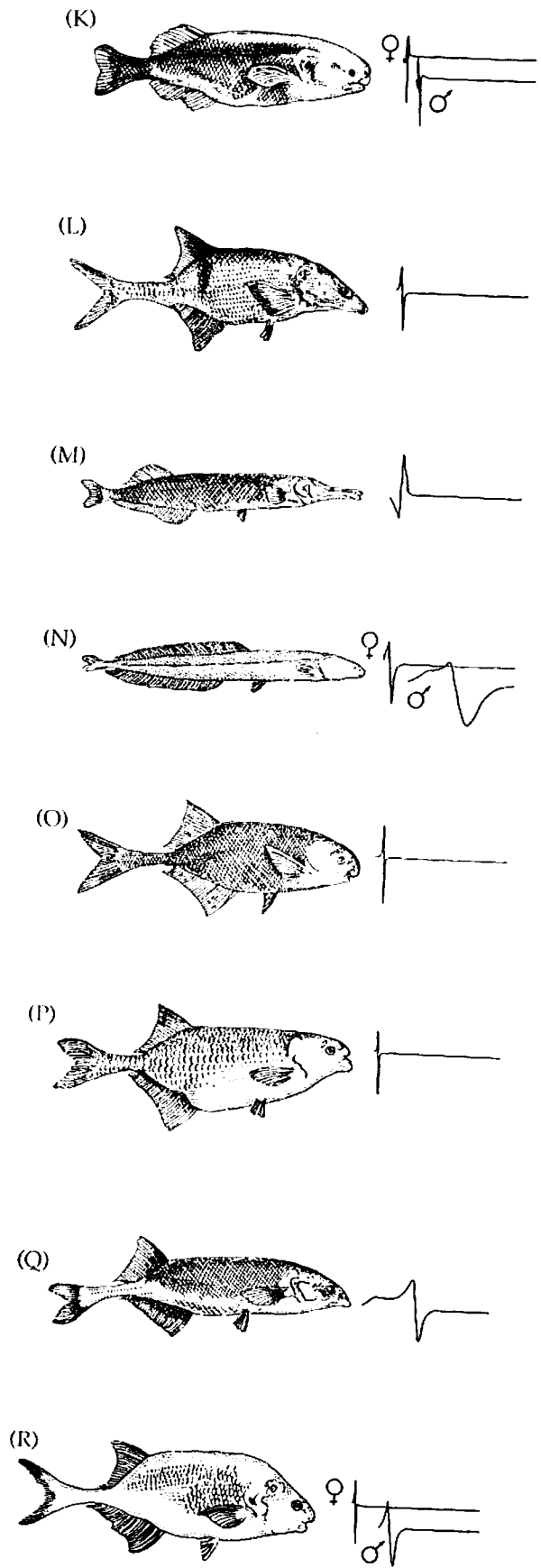
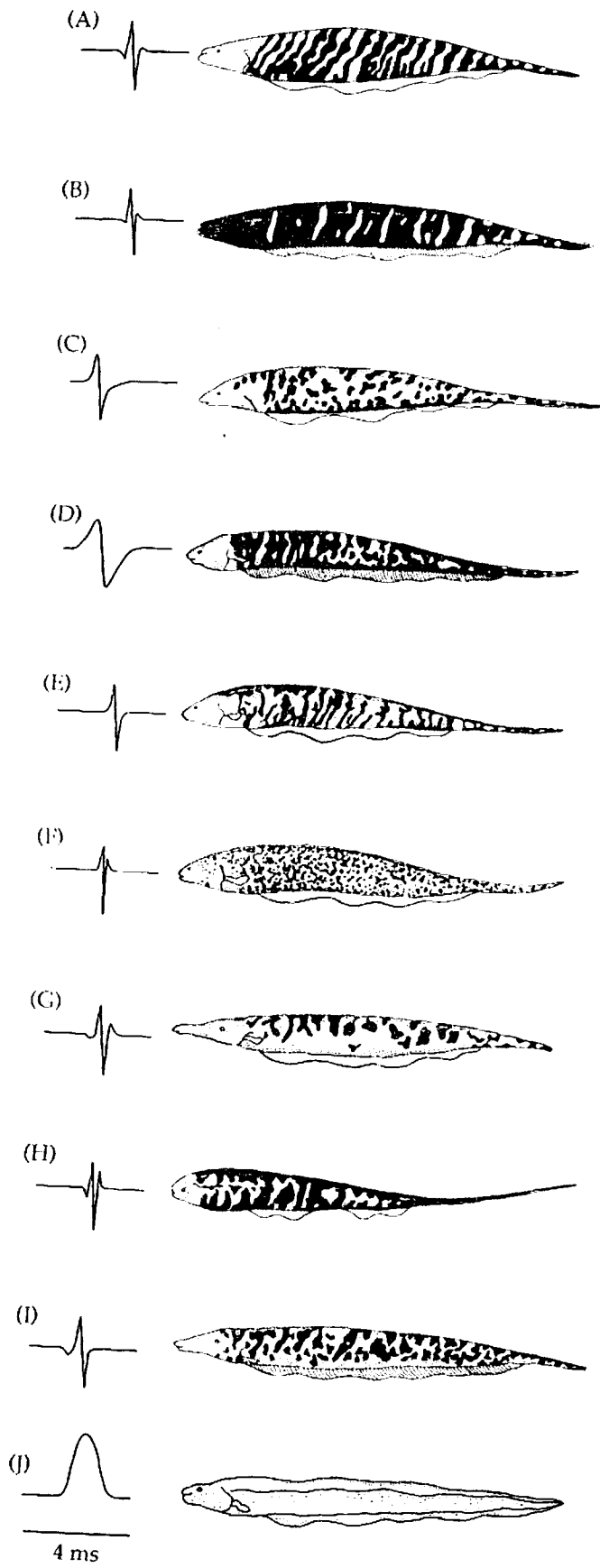
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◀ **Figure 11.7** Sample EOD waveforms for selected gymnotiforms (left) and mormyriiforms (right). The species of gymnotiforms shown all occur in coastal streams of the Guianas. The selected mormyriiforms all live in the Ivindo River or its feeder streams near Makokou, Gabon. It is common to find such high local species diversity of electric fish in tropical South America and Africa. Note the sexual differences in EOD for the first, fourth, and last mormyriiform species. Species names: (A) *Gymnotus carapo*; (B) *Gymnotus anguillaris*; (C) *Hypopomus artedi*; (D) *Brachyhypopomus brevirostris*; (E) *Brachyhypopomus beebei*; (F) *Brachyhypopomus sp.*; (G) *Gymnorhamphichthys hypostomus*; (H) *Hypopygus lepturis*; (I) *Rhamphichthys rostratus*; (J) *Electrophorus electricus*; (K) *Stomatorhinus walkeri*; (L) *Boulengeromyrus knoepffleri*; (M) *Mormyrops zancirostris*; (N) *Isichthys henryi*; (O) *Pollymyrus marchei*; (P) *Marcusenius paucisquamatus*; (Q) *Marcusenius conicephalus*; and (R) *Ivindomyrus opdenboschi*. (Fish based on drawings provided by Carl Hopkins.)

The electric field and corresponding isopotential lines for a typical weakly electric fish in a free field situation are shown in Figure 11.8. Although the fish roughly approximates a dipole, note the asymmetry of the isopotential lines when the two ends are compared. These plots were generated from a simplified model of such a fish by Heiligenberg (1975, 1977) and provide a good fit to observed measurements of actual fields (Knudsen 1975; Bastian 1986). The basic elements of the model are simple. An electric organ produces a voltage difference with the tail tip negative and the body tissues in contact with the anterior end of the organ positive. Ionic currents pass through the body tissues, across the skin, and then along the lines of electric field in the surrounding water. This simple circuit thus consists of a battery (the electric organ) and three resistors in series. The saline tissues of the fish are highly conductive and we can thus ignore this resistance. Because a fish's tissues are much more saline than the surrounding fresh water, water tends to move into the fish and cause it to swell. To prevent this, most freshwater fish have relatively impermeable skins to both ions and water, and thus the skin has a very high resistance. Two of the circuit resistors are thus the skin at the head and that at the tail. The third circuit resistance is that of the surrounding water which is higher than the fish's tissues, but generally lower than the skin.

By varying the geometry of model fish, Heiligenberg found that the longer the fish's tail, the farther a given isopotential line would lie from its body and the farther from such a sender a receiver would be likely to detect the signal (Figure 11.9). Increasing tail length is similar to increasing the charge separation distance, δ , in a dipole, a topic that we have discussed earlier. A quick glance at Figure 11.5 or 11.7 will show how many gymnotiform and mormyriiform fishes have long tails. The model also shows that if the resistivity of the fish's skin is very high relative to that of the medium, the electric field contracts around the anterior end of the fish, making the range of detection in the anterior direction poor. If the skin resistivity is very low relative to that of the medium, the field collapses around the tail, reducing signal range in that direction. The maximal field is thus achieved when the resistivity of the fish's skin and that of the medium are similar.

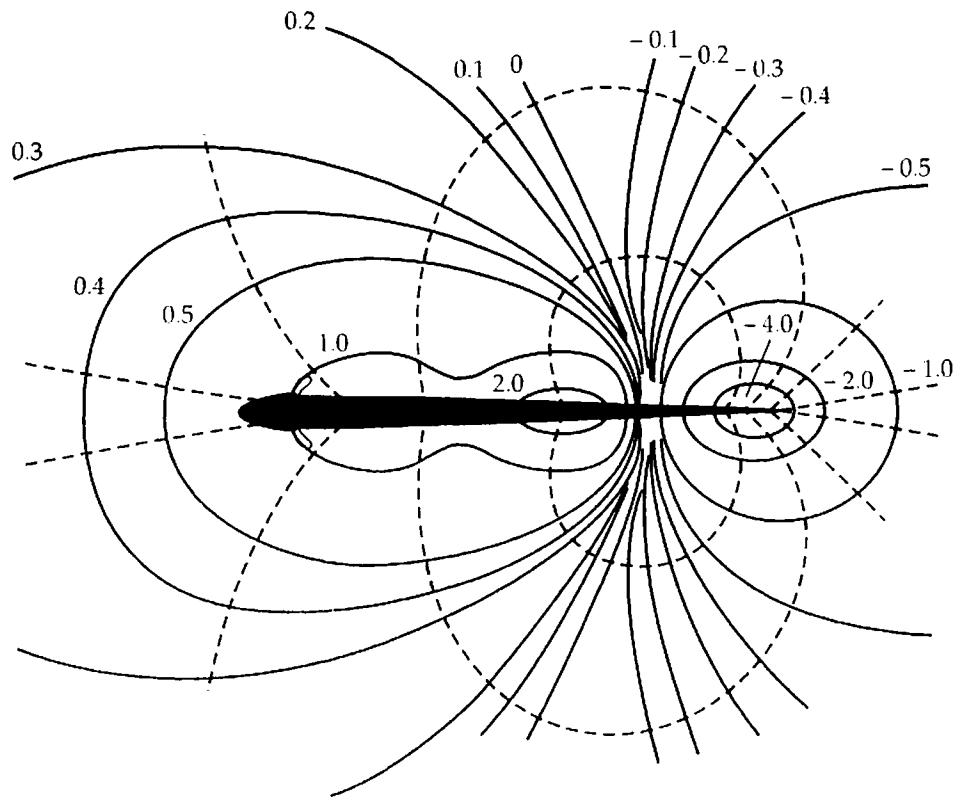
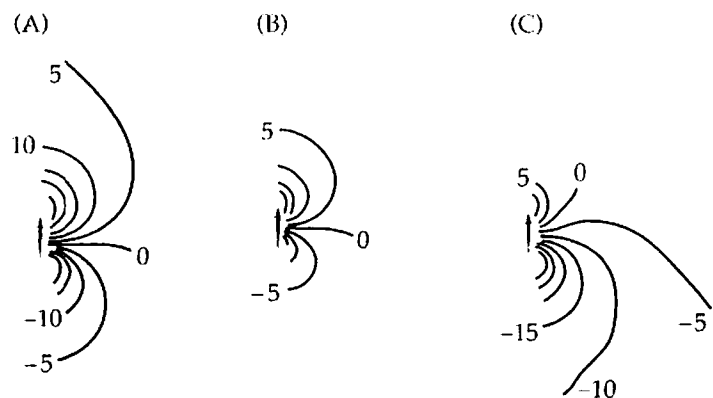


Figure 11.8 Electric field (dashed) and isopotential (solid) lines around weakly electric fish. Field shown with values of isopotential lines (V) at peak of EOD. Note the curvature of the 0 potential line away from the line perpendicular to the body that would be expected if the fish were a simple dipole. 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.)

Maximizing signal magnitude everywhere will help extend the range of electric signals. However, the ability of a distant receiver to identify and detect such a signal, or the ability of an electrolocating fish to interpret the distortions in its field induced by nearby objects, will depend very much on am-

Figure 11.9 Effects of fish shape and skin resistivity on an electric field. (A) Electric field around a fish with a long tail and resistivity similar to that of the medium. Values show relative voltages. (B) Field for a fish with a shorter tail. (C) Field for a fish with a long tail but high skin resistivity. Note that the field has collapsed around the head. The equivalent plot for a fish with a long tail but much lower resistivity than the medium would show a field collapsed around the tail. (After Heiligenberg 1975.)



bient electrical noise. Throughout the tropics in which weakly electric fish live, lightning is the major source of electrical noise (Hopkins 1973). Although storms may be far away, the magnitude of the lightning discharge is large everywhere and results in a noise bandwidth of 50 Hz to 50 kHz, with peak noise levels at about 2 kHz. Not surprisingly, noise voltages in the higher-resistivity fresh water are about two orders of magnitude greater than comparable marine habitats. In addition to lightning, many tropical freshwater habitats host a variety of sympatric electric fish. These add additional noise to the environment. It should be noted, however, that compared to sound in either air or water, the number of biological sources of electrical noise is significantly fewer, allowing different species considerable latitude to vary EOD waveform and discharge patterns in ways that make conspecific signals distinctive against the background.

RECEPTION OF ELECTRIC SIGNALS

The ability to detect electrical signals is much more widespread than is the ability to generate them. In fact, there is convincing evidence that electroreception evolved very early in the vertebrate line: the earliest fish fossils from the Devonian show indications of having electroreceptors, and electroreception remains widespread in the most primitive groups of fish (Bullock and Heiligenberg 1986). Lampreys, cartilaginous fishes (rays, sharks, and skates), sturgeon, paddlefish, and coelocanths all have electroreceptors. Among the bony fishes (Teleostei), electroreception is less common being found in catfish (Siluroidea), Gymnotiformes, Mormyriiformes, and the family Notopteridae. Adult aquatic salamanders and larvae of terrestrial ones have electroreceptors, and the bill of the duck-billed platypus (*Ornithorhynchus anatinus*), an aquatic mammal, appears to be electroreceptive (Scheich et al. 1986). Electroreceptors appear absent in both adults and tadpoles of frogs and toads. The distribution of known electroreception over the early vertebrate tree is summarized in Figure 11.10.

The functions of this widespread electroreception appear to be varied. Sharks and rays are highly sensitive to low-intensity DC and AC electric fields generated by their prey. Most living animals have regions of the body that are at slightly different resting potentials. In water, these generate weak DC fields that are detectable at short distances from the animals. If the animal is moving, the depolarizations of its muscles generate AC fields with frequencies in the range of 0.1–8 Hz. For example, Kalmijn (1988a) reports field strengths of 10^{-7} V/cm at a distance of 10 cm from the pulsating gills of marine fish. Since sharks and rays can detect fields as low as 10^{-9} V/cm, they should be able to locate prey using electroreception.

Electric fields appear to be used by a number of marine animals to navigate. Any time a conductor is passed through a magnetic field, a perpendicular electrical field is generated in the conductor. The flow of ocean currents through Earth's magnetic field generates electric fields on the order of 10^{-9} to 10^{-7} V/cm. Rays navigate by using these induced fields to identify topographic directions and possibly locations. The magnetic field of Earth has di-

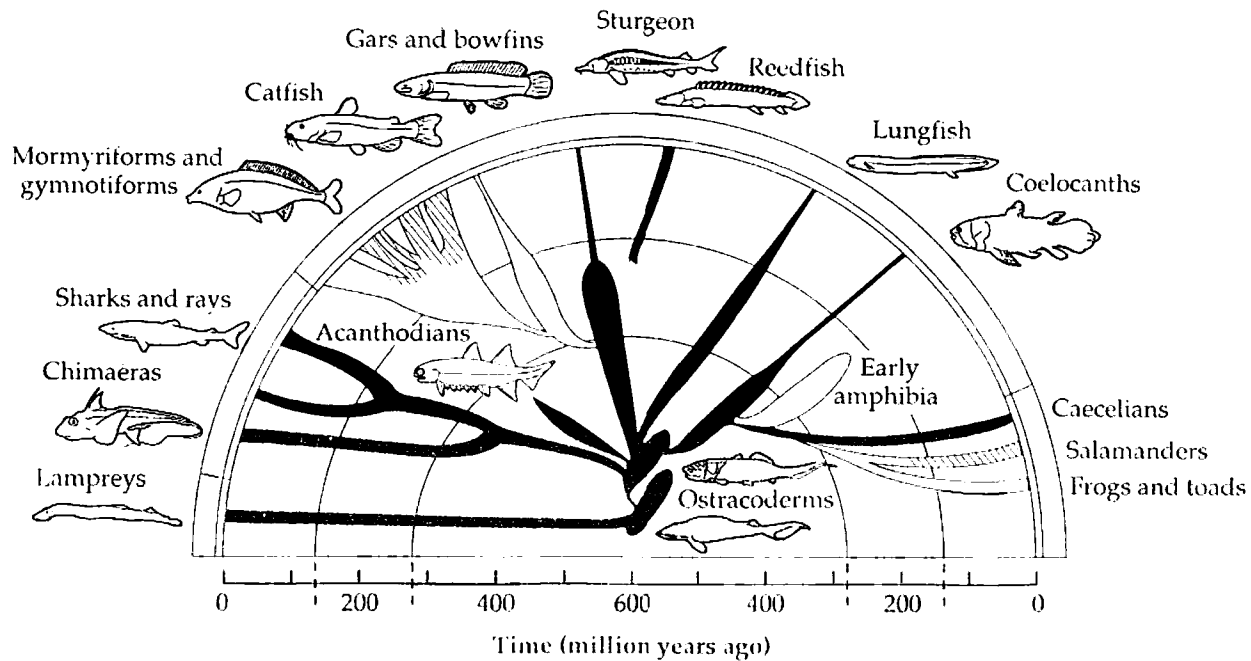


Figure 11.10 Electroreception in the early vertebrate evolutionary tree. Common names for major groups are indicated. Branches in black are those in which electroreception has been demonstrated or inferred from fossils and is the rule. Shaded branches are ones in which electroreception is present, but only in some taxa. (After Bullock and Heiligenberg 1986.)

rectional and locational properties. A shark swimming through the horizontal component of Earth's magnetic field experiences an induced electric field with an associated potential difference between its dorsal and ventral sides. The vertical component of the magnetic field generates a potential difference between its right and left sides. Both factors provide locational information that the shark might use to navigate over considerable distances. Freshwater fish do not have access to oceanic currents and thus experience 30% lower magnitudes of induced potentials as they move. However, the differential ionic compositions of the substrates over which fresh waters lie can generate electrochemical potentials that are location-specific and potentially available as navigational cues. Prey detection and navigation thus seem the likely selective forces favoring the widespread abilities of fish to detect electric fields.

Optimal Design of Electroreceptors

The sensory cells in fish electric receptor organs appear to be derived from the same kinds of sensory cells seen in the pressure receptors of the lateral lines of fish and in the equilibrium and hearing organs of all vertebrates. All electrosensory cells are stimulated when a sufficiently strong voltage difference is placed across their external and internal sides. Depending upon the voltage gradient in a particular field, the difference in voltages at any two locations may be small or large. To maximize this difference, the sensory organ needs to sample the field at points as far apart as possible (as in marine fish), or be located in that part of the field with the steepest gradient (as in freshwater fish).

In either case, it is easiest to see what is happening by treating the detecting fish as part of an electrical circuit made up of several resistors in series and connected to some voltage source that is generating the electric field. Consider a voltage V at the source applied to a chain of two resistors with resistances R_1 and R_2 , respectively. Current moves from one pole of the voltage source through the first resistor, then through the second, and finally back to the opposite pole of the voltage source (Figure 11.11). Because the same amount of charge must enter the circuit as emerges from it, the value of the current I through the circuit must be equal at all points and by Ohm's law is $I = V/(R_1 + R_2)$. Given that the current through the two resistors is the same, Ohm's law also requires that $I = V_1/R_1 = V_2/R_2$, where V_1 is the voltage experienced by the first resistor and V_2 that experienced by the second. If we combine these expressions, we find that the voltages experienced by R_1 and R_2 , respectively, are

$$V_1 = V \left[\frac{R_1}{R_1 + R_2} \right] \quad \text{and} \quad V_2 = V \left[\frac{R_2}{R_1 + R_2} \right]$$

Clearly, $V = V_1 + V_2$. If one imagines the trajectory of a test charge traversing this circuit, the charge will see the highest potential (e.g., be at the "top of the waterfall") as it emerges from the voltage source, will "drop" down by an amount V_1 as it emerges from the first resistor, and then will drop the remaining amount V_2 as it emerges from the second resistor and reenters the source.

Returning to the sensory cell of an electroreceptive fish, we can let R_1 be the resistance between the two sides of a sensory cell, and R_2 be all of the other resistances experienced by a current flowing from the voltage source, through the medium and the fish, and then back to the source. Clearly, the larger R_1 is relative to R_2 , the bigger the fraction of the overall V that the sensory cell will see, and the more likely the cell will detect the electric field. If the electric field is not static, but varying, then the receptor cells must also deal with capacitive reactance: the higher the frequency of the field variation, the lower the effective impedance (resistance and capacitive reactance combined) across the cell, and the less likely the cell is to be stimulated. If the cell is trying to detect low-frequency signals, then a simple resistive solution

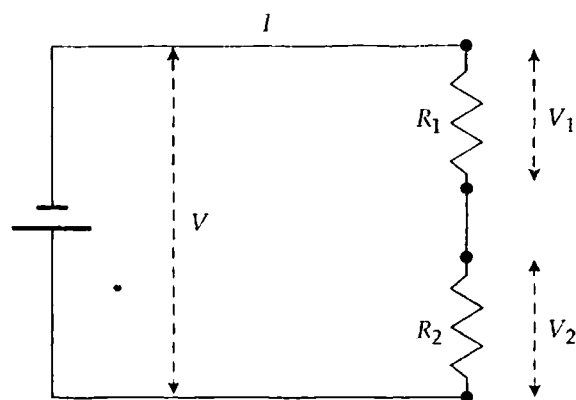


Figure 11.11 Simple circuit with two series resistances (R_1 and R_2) and voltage source (V). Ohm's law states that voltage drop across each resistor (V_1 and V_2 , respectively) is the total voltage (V) times the fraction of total resistance represented by that resistor [e.g., $V_1 = V(R_1/R_1 + R_2)$].

is appropriate. If, however, it needs to detect high-frequency field variations, additional adaptations are required. In electroreceptive fish, different sensory organs have evolved to deal with the different types of signals. We describe the major types in the next sections.

Ampullary Electroreceptors

The most widespread type of electroreceptive organ among fish is the **ampullary receptor**. This organ consists of a tube opening to the outside through the fish's skin, and extending to a small cavity lined with a few (in freshwater fish) or thousands (in marine fish) of receptor cells. In freshwater forms, the resistance of the fish's skin is very high (to protect against osmotic influxes from the medium). The interior of the fish is saline and thus has very low resistance; the medium resistivity is intermediate. This means that the major drop in a source voltage occurs across the skin, with much smaller drops occurring as current flows through the medium and the fish's body. If the fish places its sensory cells with one side facing the medium and the other facing the saline interior, e.g., as part of the skin, the cells will experience the maximal possible voltage difference across their two sides. For this reason, the tubes connecting ampullary receptors in freshwater fish are extremely short, just enough to expose the exterior side to the medium voltage and the interior side to the potential inside the skin.

In marine forms, the skin and interior of the fish are more similar in resistivity, whereas the medium represents a much lower resistance. To obtain a detectable potential drop, the ampullary tubes are usually much longer in marine forms. The tube itself has highly insulating walls and is filled with a conductive jelly that ensures that the potential near the exterior side of the sensory cells is very close to that near the tube opening. The potential at the interior side of the cells is determined by the amount of skin and tissue that any current has had to traverse to get to that point. By making the tubes long, the amount of tissue travelled is large, and the difference in potential on the two sides of a sensory cell is increased. In sharks, ampullary organ tubes are located on the head and are up to several cm long; in rays, the tubes open all over the ventral surface and may be as long as 20 cm.

Ampullary organs are present in all electroreceptive fish and amphibians and are used to detect DC or low-frequency electric fields of low amplitude. These are the kinds of fields encountered by fish when hunting for prey or navigating. Detection of such low intensity exterior fields is complicated because the fish's body is continuously generating its own internal fields as muscles and nerves depolarize, and as DC currents move from one part of the body to another. One sensory cell exposed to a given exterior voltage might thus be stimulated because its interior side was close to an internal voltage source, whereas another sensory cell exposed to the same exterior voltage, but located more distantly from the internal one would not. As a solution, therefore, many species such as rays have large numbers of ampullary organs together in clusters, even though the tubes for these organs open at very different places on the ray's body (Figure 11.12). This placement makes the internal

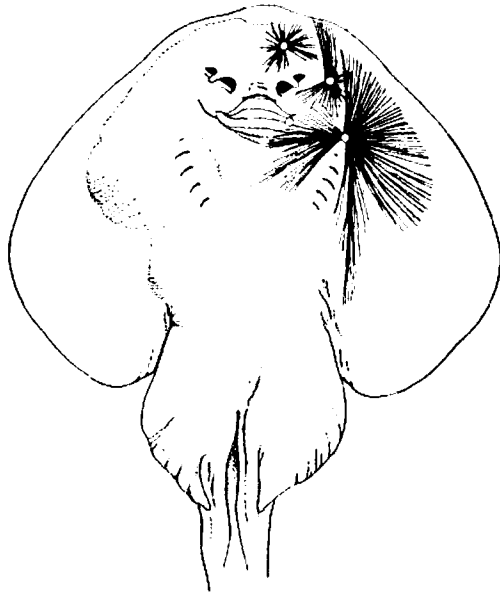


Figure 11.12 Ampullary organ canals in a ray. Each canal opens separately on the ventral side of the ray where it can be used to sense the low-frequency electrical signals of potential prey. Many different canals conduct samples to the same cluster of ampullary organs (open circles). Thus the different external voltages can all be compared to the same internal one. Such organs may also play a role in local navigation abilities.

voltages seen by all cells in a cluster similar, and any differences in voltage seen by different cells in a cluster are due only to differences in the external voltages at their tube openings.

The minimum field detectable by an ampullary receptor varies with the taxon and the habitat. Marine cartilaginous fishes can detect fields as low as 5×10^{-9} V/cm, whereas freshwater species require a minimum of 5×10^{-5} V/cm. Bony fish are all much less sensitive than sympatric cartilaginous ones: marine forms require about 5×10^{-4} V/cm, whereas freshwater forms need 5×10^{-3} V/cm. Given the much higher noise levels due to lightning in fresh water, the lower sensitivities in this environment may not be surprising. The polarity of a stimulating field also varies with taxon: in cartilaginous fish, it is the exterior side of the sensory cell that is excitable; these cells are thus stimulated when the exterior medium is negative relative to the fish's body. In bony fishes, it is the interior side of the sensory cell that is excitable, and these species respond when the medium becomes positive relative to the fish. Such organs act like rectifiers because they only respond when the current is moving in a given direction.

Although the direction and magnitude of electric field forces vary with location, it is very difficult for a receiver to use this information to extrapolate the location of a voltage source. The reason is that the field lines rarely point directly at or away from the source; instead, they form curved trajectories. Kalmijn (1988a) has suggested that sharks find prey that generate potentials by swimming in a way that keeps their bodies oriented with a fixed angle relative to the field lines. Any deviation from a fixed angle will change the potentials experienced on the two sides of the body. One such orientation is parallel to the field lines, which would allow the shark to track a given field line to its voltage source.

Tuberous Electroreceptors

Tuberous receptors occur only in the Gymnotiformes and Mormyriiformes where they are used for conspecific communication, electrolocation, or both. The electric fields that stimulate these receptors are EODs of the same fish or nearby fish. As we have seen, the EOD waveforms are highly time-variant and some modifications of the sensory organs are necessary to deal with frequency-dependent impedances.

Tuberous receptor organs also consist of a short canal opening at the skin and leading to a cavity lined with receptor cells. Unlike ampullary organs, the tuberous canal is partially filled with an epithelial plug, the walls of the canal are thickened with many cell layers, and the receptor cells are themselves encapsulated within other tissues. All of these features add to the resistances in the circuit other than the one across the sensory cell; they thus reduce that part of the voltage drop experienced by the sensory cell for DC and low-frequency signals. When the signal waveform is rapidly time-variant, then the plug and encapsulating tissues act as dielectrics, their capacitive reactances decline as the signal frequencies increase, and the contributions they make to the overall impedance of the circuit becomes small. Most of the voltage drop then occurs across the sensory cell. In short, the epithelial plug and encapsulations turn the organ into a high-pass filter so that the sensory cells can only respond to higher frequencies. The electrical properties of the sensory cell membranes are further modified to make them resonant at certain frequencies. Tuberous receptors are thus generally tuned to respond only within a fish's own specific range of electrical field frequencies.

In wave fish, (the Gymnarchidae within the Mormyriiformes, and the Apterontidae and Sternopygidae in the Gymnotiformes), the tuning of tuberous organs is very narrowly set to the specific pulse rate of the species' EOD. In some species, pulse rates differ between the two sexes, and within a sex, pulse rates of different individuals are slightly different. In all cases, the tuberous receptors of a given fish are tuned to the fish's own specific pulse rate (see review in Hopkins 1983b). In pulse fish, tuberous receptors are much more broadly tuned, but the majority of cells are best stimulated by the frequency with the largest amplitude in the power spectrum of the EOD waveform (Figure 11.13). Although the physics of tuberous receptors set an upper frequency limit of 12–15 kHz, the majority of species have EODs with major energy in the range of 200–1700 Hz.

Note that although most tuberous receptors are tuned, even in pulse fish, this does not mean that all signals are perceived only in the frequency domain. Hopkins and Bass (1981) have shown that holding the frequency spectrum of the mormyriiform *Brienomyrus brachyistius* EOD constant, but varying the relative phase spectrum results in quite different responses by attendant fish. Because the tuberous organs of these fish, like their ampullary organs, act like rectifiers, an organ is only stimulated when the external field is positive relative to the fish's interior. Any given field will generate opposite polarities on the two sides of a fish at any instant. When an EOD field rises to a positive value on one side, the organs on that side are stimulated, whereas those on

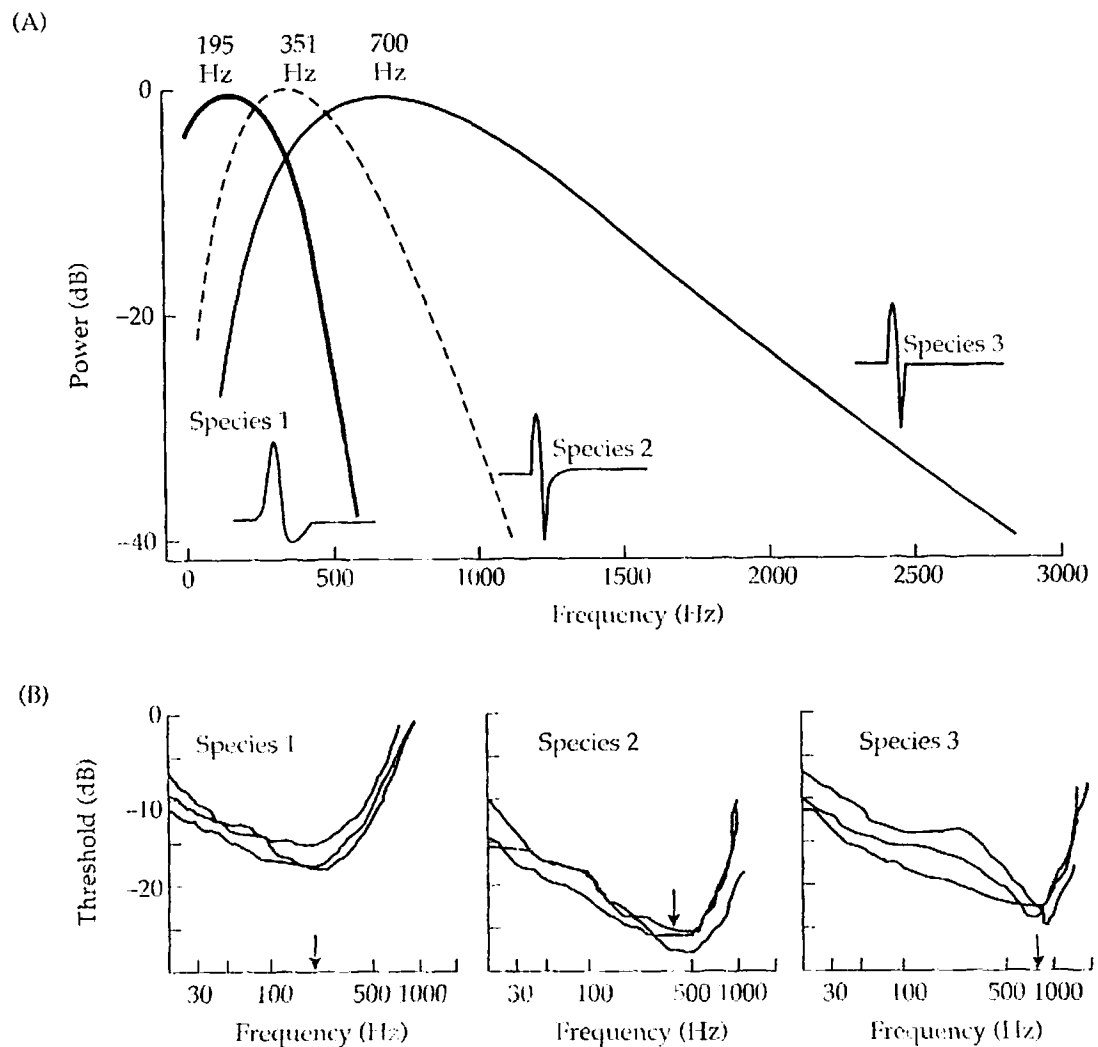


Figure 11.13 Matching of the EOD power spectrum to the best frequency of electric receptors. (A) Waveforms and power spectra of EOD waveforms for three species of the gymnotiform pulse fish, *Hypopomus*. (B) Corresponding tuning curves of receptor organs for each of the three species of fish. The reference value for the dB measure plotted on the y axis is here 90 mV/cm. In a tuning curve, the lower the threshold (y axis) for a given frequency (x axis), the more sensitive the unit is to that frequency. The best frequency is that with the lowest threshold and is marked in each plot with an arrow. In each case, best frequencies are very close to peak frequencies in power spectra. (After Heiligenberg 1977.)

the opposite side will be silent. By comparing the timing and pattern of tuberous organ stimulations on the two sides of its body, a *Brienomyrus* brain can basically reconstruct the successive maxima and minima in any received EOD waveform. It could thus perceive this signal in the time domain if both frequency and phase components were important.

In gymnotiforms, the same tuberous organs appear to mediate electrolocation and responses to the communication signals of other fish. However, there is a physiological division among organs depending upon which part of the EOD they encode in the nerves attached to them: some organs produce one nerve impulse per EOD received and thus reproduce the EOD pulse rate.

These are called **pulse markers**. Other organs produce bursts of impulses in which the number and rate of the impulses is related to the amplitude of the EOD field. These are called **amplitude coders**. In gymnotiforms, the amplitude coders are primarily used for electrolocation, whereas the pulse markers are used to identify the sex, species, or activities of nearby electric fish. Mormyriiform pulse fish have separated these functions between two distinct kinds of tuberous receptors: **knollenorgans** are pulse markers devoted solely to detecting communication signals between fish; **mormyromasts** are amplitude coders dedicated to electrolocation functions.

COMMUNICATION AND ELECTRIC SIGNALS

How are these various electrogenic and receptive organs combined to effect communication? Passive electroreception of prey is not a form of communication as we define it, and will not be discussed further. However, both the exchange of electric signals between fish and electrolocation can be considered as forms of communication. We take up each of these in turn.

Social Communication

Most gymnotiforms and mormyriiforms and probably many electric skates use electrical signals for social communication. Many of these species are either nocturnal or live in murky waters where visual communication is impossible or very limited. Some mormyriiforms use both acoustic and electrical communication to defend territories, attract and court mates, and to determine the species, sex, or individual identity of another fish. Most other members of these groups rely only on electrical signals.

As we have noted, the shape of the EOD waveform largely depends on species and may be perceived by a receiver in either the time or frequency domain (or both). Modifications of the EOD waveform evolved by varying the durations and times of discharges of various membranes in the electric organ, or by varying the synchrony of discharges of several adjacent electric organs. Wave fish tend to produce EODs with narrow bandwidths, whereas pulse fish produce quite wide bandwidth signals. In both mormyriiforms and gymnotiforms, there may be sexual differences as well, with male EODs generally being longer in duration than those of females. Playback experiments have shown that the two sexes are able to recognize each other's waveforms and males will court when played a typical female EOD.

Most social exchanges between weakly electric fish entail modulations of the EOD discharge rates. Such modulations include sudden rises in pulse rate with either abrupt returns or slow decays to normal, complete cessations of discharges, or continuous modulations up and down in wave species. The functional significance of these modulations appears to vary with the species and context. In several species, rapid increases and decreases in discharge rate are associated with aggressive interactions between fish, with subordinate individuals often responding by ceasing any discharge for some time. Dominance contests in wave fish such as *Eigenmannia virescens* result in hierarchies in which the dominant males have the lowest EOD rates, whereas the females controlling the

best spawning territories have the highest EOD rates. The opposite relation holds in the wave fish *Apteronotus leptorhynchus*. Most wave fish show an ability to shift their discharge frequency slightly when a nearby fish is using exactly the same discharge rate. This response is called the **jamming avoidance reflex** and presumably serves, in part, to prevent one fish's electrolocation signals from being confounded by those of a neighbor. However evolved, dominant wave fish often alter their discharge rates to overlap those of a neighbor. Subordinate fish so threatened immediately shift their discharge frequencies.

In several wave gymnotiforms such as *Sternopygus macrurus* and *Eigenmannia virescens*, males try to attract passing females and court those that approach by adding periodic modulations to the usual discharge rate. Examples of such modulations for two gymnotiform wave fish are shown in Figure 11.14. Long strings of modulations by wave fish have been likened to "songs" of advertising male birds. Many male mormyriiforms build nests and then seek to attract females who will mate with the male and lay eggs in his nest. Like some gymnotiforms, high-frequency bursts of pulses are used to advertise to nearby females and during courtship.

In fresh water, the range for electric communication is limited by the high resistivity of the medium and the size of the voltages that small fish can afford to produce repeatedly. As we have seen, it is also affected significantly by the shape of the fish: those fish with longer and thinner tails create electric fields with greater ranges. Nearly all weakly electric fish have a long thin tail. Several studies have shown that gymnotiform and mormyriiform fish can communicate only over distances of about a meter.

Fish that communicate with electric organ discharges face the same problem in locating the source of an electric signal which a shark faces in localizing a prey organism producing a DC electric field: lines of force rarely point towards the voltage source but instead are curved. Recent work on the mormyriiform *Brienomyrus brachyistius* suggests that individuals use the same rule of thumb to locate conspecifics that Kalmijn (1988a) has suggested for sharks homing in on prey, that is, the fish basically keeps its body parallel to ambient lines of force while swimming randomly (Hopkins 1988b). The result is a trajectory that roughly tracks the current lines to the source (Figure 11.15).

Electrolocation

As we shall argue in Chapter 26, electrolocation can be considered as a form of **autocommunication**: a fish emits and receives its own signal. Differences between the outgoing and returned signal are then used to extract information about the fish's immediate environment. What kinds of differences might be detected?

The EOD of an electrolocating fish generates currents emerging from the anterior of the fish, passing through the medium, and recentering near the tail. Because the tuberous receptors are only stimulated when the medium is negative relative to the fish's interior, it is only the anterior outgoing current that can be detected. As a consequence, most of the receptors are concentrated in the head region and become much less dense as one moves towards the electric organ. In the gymnotiform, *Apteronotus albifrons*, the density of organs is

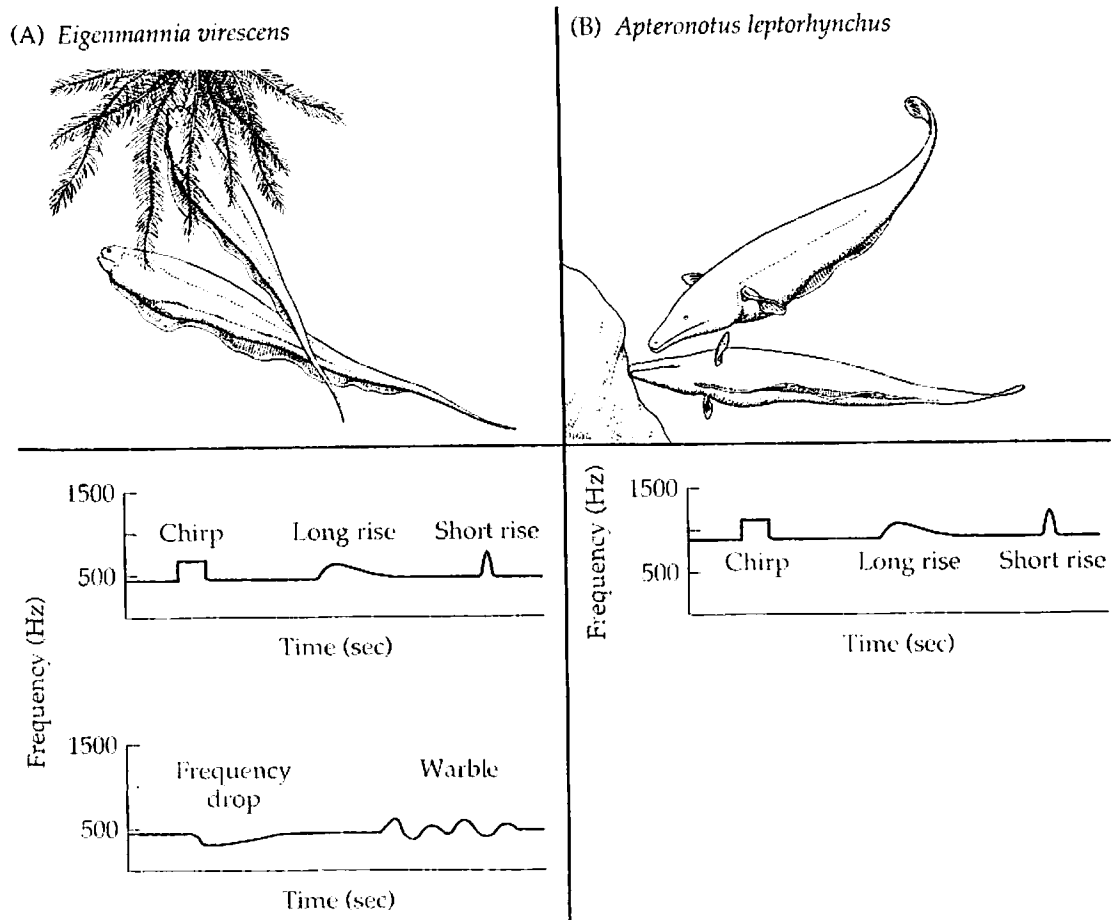


Figure 11.14 Electrical advertisement and courtship signals in a weakly electric fish. (A) Courting wave gymnotiform *Eigenmannia virescens*. The female is in the vegetation and the male below. The spectrograms show various frequency modulations in male electrical discharge rates seen during courtship. (B) Courting wave gymnotiform *Apteronotus leptorhynchus*. Male above and female below. The spectrogram shows several frequency modulations in male pulse rate during courtship. (After Hagedorn and Heiligenberg 1985.)

about $25/\text{mm}^2$ on the head and decreases to fewer than $1/\text{mm}^2$ in the region just anterior to the electric organ. We have already noted that it is the amplitude coders in gymnotiforms and the mormyromasts in mormyriiforms that are the major receptors for electrolocation. It is indicative of the importance of electrolocation that in the latter group mormyromasts are generally 10 times more common than knollenorgans.

The voltage drop across the sensory cells of tuberous organs depends on their resistance relative to the total resistance through which a given current line will flow. Where objects of resistivity lower than the medium are present near to the fish, the total circuit resistance through these objects will be lower than that through medium without an object, and the fraction of the EOD voltage seen across the sensory cells will be higher; where objects of higher resistivity are present, the voltage across the sensory cells will be less. In addition, the more dielectric the objects, the lower their effective impedance to the time-variant EOD signal. The voltage across any tuberous receptor will thus vary

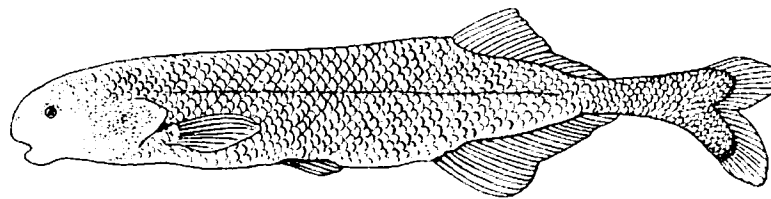
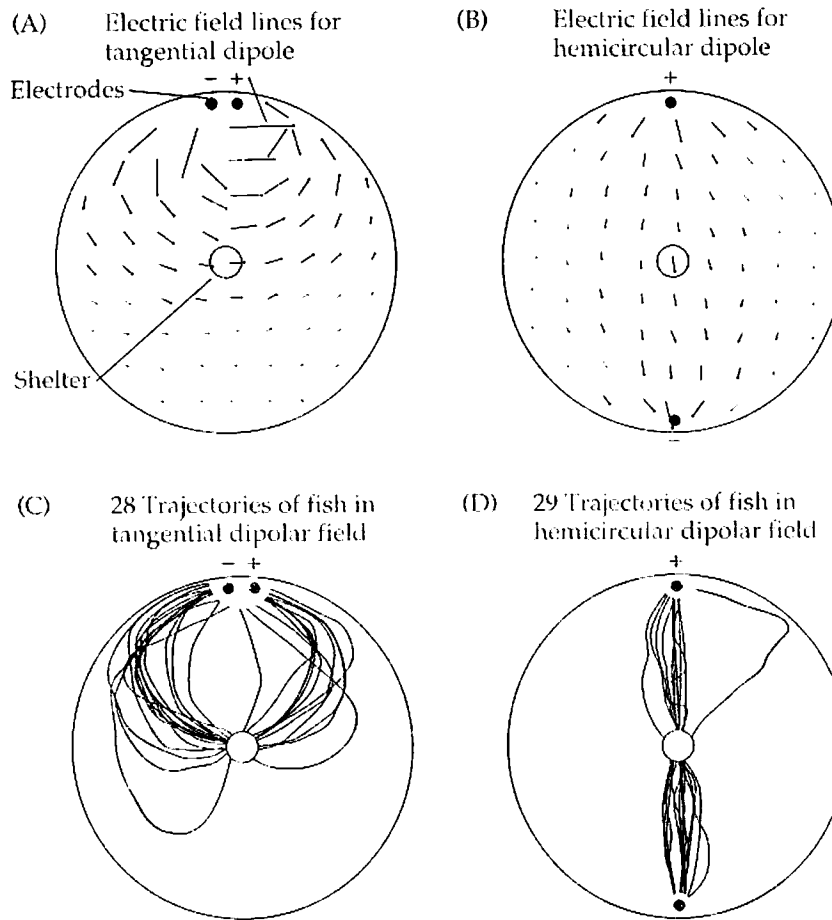
*Brienomyrus brachyistius*

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 mormyrid *Brienomyrus brachyistius* 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.)

with the resistance and capacitive inductance of objects in the nearby medium. Because current flows perpendicularly across the skin and sensory cells, only those receptors near the object will experience these changes in voltage. These changes create an electrical "image" of the object on the nearest parts of the fish's body (rather like the shadow on the fish that the object would cast were a light placed somewhat beyond the object). The relative locations of receptor organs in electric fish are preserved in the fish's brain to form an electrical body map. The size and location of any electrical image can thus be monitored by the brain. As the fish moves, the location of the electrical image will move along its body and the brain can use this to infer the approximate size and location of the object. Electric fish often approach novel objects, curl their bodies around them, and then make circling movements around the objects. This curling concentrates their electric fields on the objects and presumably gives them information about object shape and composition.

The size of the voltage differences between receptors within the image of an object and those outside of that image increases as object size is increased and as the object is brought closer to the fish. However, both effects vary in ways that greatly constrain the use of electrolocation. The rise in signal amplitude as object diameter is increased is very slow: a doubling of object diameter only increases signal magnitude by about 25% and it requires a 10-fold increase in object diameter to double signal magnitude (Bastian 1986). Electroreception is thus a crude discriminator of object size. By the same token, signal magnitude falls off very quickly with distance from the fish: a doubling of distance reduces signal amplitudes to 30% of the initial value, and a 10-fold increase in distance leads to a signal 2% of the initial one. This limits the effective range of electrolocation to only 2–5 cm from the fish (in contrast to over a meter for electrical communication).

Whereas passive reception of prey electric fields favors receptor cells with high impedances, electrolocation favors impedances more similar to the medium (Heiligenberg 1975). This difference occurs because passive reception is limited by the minimal absolute voltage that a sensory cell can detect; electrolocation is limited by the minimal difference in voltages between two cells that can be detected by the brain. These are quite different goals. It is easy to show that the difference in voltages between a cell exposed to pure medium and another exposed to medium with an object in it depends on the product of two ratios: the first is the fraction of the total circuit impedance represented by the skin and sensory cells (as with passive reception), and the second is the ratio between the change in circuit impedance introduced by the object's presence relative to the total impedance in the circuit. Whereas increasing the skin impedance increases the first ratio, it simultaneously decreases the second. Because of this tradeoff, the maximal difference between regions is attained when the impedances of the medium and the skin are about the same. This result is, in fact, what is generally found (Bell et al. 1976).

SUMMARY

1. Although the ability to use electrical signals for prey detection and navigation is widespread in lower vertebrates, only certain taxa of fish have evolved specific organs for generating electrical signals for communication.
2. The basis of electrical communication is the generation of an electrical field. This is a map of the direction and magnitude of electrical forces at any location. Electrical fields are usually generated by the short-term separation of positive and negative charges. In the vicinity of these separated charges, it takes work to move any test charge against the electrical field. The amount of work it takes to move a unit test charge between two locations is called the potential difference between those two points and is measured in volts.
3. A single charge is called a **monopole** and the field around it is fairly simple in shape; this is an unlikely biological configuration. Two separated charges constitute a **dipole** surrounded by a somewhat more complicated

electrical field. Even more complicated arrays of separated charges will generate fields with dipole, quadrupole, octupole, and more complex axes and shapes. The magnitude of the electrical field around a dipole decreases with the cube of the distance from the dipole, and the potential around the dipole falls off with the square of distance. Because higher-order fields fall off much faster than dipolar fields, we can divide the electrical field around a complex array of charges into a near field close to the array, (where all quadrupole, octupole, and other components are still important), and a more distant far field (where only the dipolar component is still important).

4. A conductor is a material in which electrons or ions can move freely when placed in an electric field. The flux of electrons through a conductor is called current and its magnitude depends upon the conductor's resistance and the potential difference applied across it (Ohm's law). If the electric field is unchanging, the current is unchanging and is called a direct current (DC). A dielectric is a material that cannot sustain a direct current. In a field that is time-variant, however, dielectrics may be able to conduct alternating currents (AC) if the frequency of alternation of the field is high enough relative to the physical properties of the dielectric. The effective resistance of a dielectric at a certain frequency is called its capacitive reactance. Many substances have both conductive and dielectric properties so that one must know both their resistivity and their capacitive reactance to know how much current they will carry when placed in a particular electric field. The combination of both resistance and reactance at a given frequency is called the impedance of a material.
5. Organisms generate electric fields for communication by ensuring differential diffusion of ions down their concentration gradients. This diffusion creates an electrochemical potential. Fish produce many modified muscle or nerve cells called electrocytes in series to form electric organs. The simultaneous discharge of all the electrocytes in an organ at once creates a brief electric field which may swing both positive and negative several times before it is over. The shape of this electric organ discharge (EOD) waveform depends on the species and is guaranteed by particular anatomical and timing adaptations of the electric organ.
6. Strongly electric fish use EODs with hundreds of volts to stun prey and protect themselves. Weakly electric fish produce electric signals of only a few volts, which they use for social communication or for the detection of objects close to their bodies (electrollocation). The range over which they can detect their own or another fish's signals depends upon the relative resistivity of the medium and the fish, and upon the levels of ambient electrical noise due to lightning. Weakly electric fish can be divided into wave fish, which maintain steady high rates of discharge, and pulse fish, which have much more erratic changes in EOD emissions.
7. Ampullary receptor organs are widespread in fish and the aquatic members of a few other vertebrate groups. They are very sensitive and respond only to the low frequency or DC potentials inadvertently produced by

prey and by Earth's magnetic field. Electrical communication is effected by **tuberous receptor organs**. These organs are usually tuned to respond to particular ranges of AC electric fields and only occur in fish that generate their own fields with electric organs. Some tuberous organs (**pulse markers**) respond to the rates of EODs, whereas others (**amplitude coders**) respond to the magnitudes of EOD fields. Pulse markers are usually used for social communication; amplitude coders are usually used for electrolocation.

8. Social communication between freshwater electric fish is limited to distances of about one meter. The waveform of the EOD and the rate of discharge, especially by a wave fish, provide important information about species identity. These same features may also vary, within species limits, according to sex, status, and individual identity. Aggressive and sexual interactions between fish are usually mediated by stereotyped modulations in the EOD emission rates.
9. Electrolocation entails emission of an EOD and careful monitoring of the consequent stimulation of sensory cells. Objects in the water near the fish change the external impedances and hence the voltage experienced by nearby tuberous receptors. Because receptor location is conserved as receptor signals travel to the fish's brain, the fish can place the location of a nearby object relative to a general body map. Different objects have different resistances, capacitive reactances, and sizes, and all of these can be used by the fish to infer information about the object. Electrolocation only occurs in the near electric field at distances of 2–5 cm (about 2% of the range for social communication by electric signals).

FURTHER READING

Good reviews of electrostatics and electric fields can be found in Feynman et al. (1964) and Paul and Sasser (1987). An early but classic review of electric signal generation and detection can be found in Bennett (1970). More recent reviews are found in Bullock and Heiligenberg (1986) and Hopkins (1974c, 1977, 1988b). An excellent comparison of electric-signal-generating organs can be found in Bass (1986), and Bell et al. (1976), Knudsen (1975), Heiligenberg (1975, 1977), and Kalmijn (1988a) analyze the shapes, ranges, and loading of fields generated by electric organs. The problems of ambient noise for both electrolocation and communication are treated by Brenowitz (1986) and Hopkins (1973). Electric reception organs are nicely reviewed and classified by Zakon (1986, 1988), and Scheich et al. (1986) describe electroreception by a primitive aquatic mammal. The process of electrolocation is discussed by Bastian (1986), Davis and Hopkins (1988), Hopkins (1983b), Heiligenberg (1977), and Meyer (1982), and electric social communication is the focus of papers by Black-Cleworth (1970), Hagedorn and Heiligenberg (1985), Hagedorn (1986, 1988), Hagedorn and Zelick (1989), Heiligenberg and Hopkins (1976), Hopkins (1972, 1974a,b, 1983a, 1986, 1988a), Hopkins and Heiligenberg (1978), Pimental-Souza and Fernandes-Souza (1987), and Westby (1975, 1988).