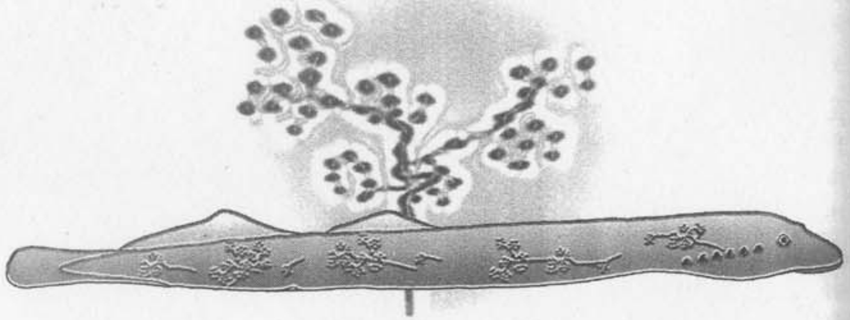

13

The Electoreceptor

Why was it so hard to identify the ampullae of Lorenzini with the sense of electroreception? Well, part of part of the difficulty lay in the fact that ampullae of Lorenzini are found in almost all fish—not just those that produce an electric discharge. Even the primitive lamprey has ampullae of Lorenzini. A close relative of the distasteful-looking hagfish, the lamprey is among the most primordial of all creatures. It has no skeleton, it has no jaw, it has no teeth. It does have a rapacious tongue armed with toothlike appendages on the end that serve as teeth. The lamprey attaches itself to another fish, using its tongue to burrow into the victim's flesh, eating as it goes. One of the earliest branches in the evolution of vertebrates, its only close relative is the hagfish. In any case, the lamprey has ampullae of Lorenzini. Interestingly, hagfish do not.

Perhaps the greatest testimony to the primeval origins of this sensory receptor is that it is found in the coelacanth, a creature so primitive that many thought it was extinct (figure 13.1). For a long time, the only known coelacanths were fossils that were estimated to be up to 400 million years old. Then, in 1931, a live coelacanth was caught in waters close to Madagascar. What an astonishing find! Catching a live coelacanth was considered about as likely as finding a live dinosaur.

Since that remarkable discovery in 1931, about 200 coelacanths have been caught, and it appears that their habitat is confined to the waters off the northern coast of Madagascar, near a small group of islands called the Cormoro Islands. "Coelacanth watchers" do not know how many

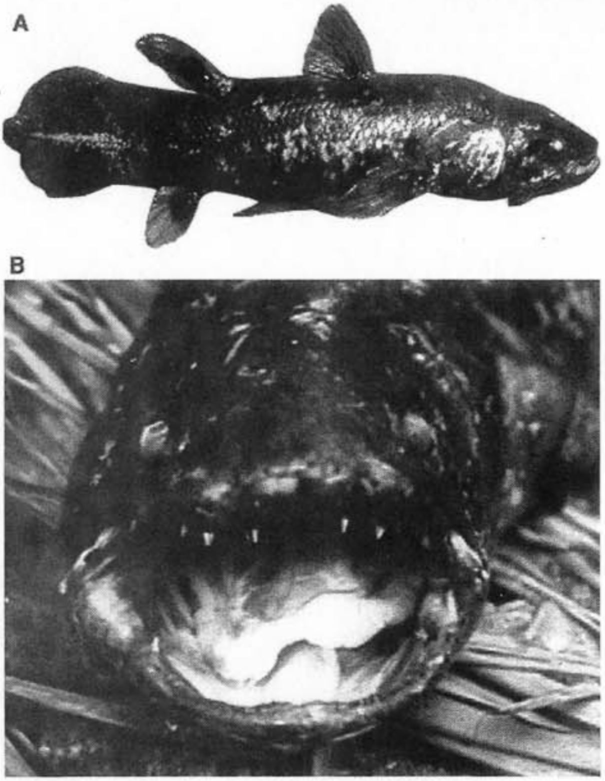

Figure 13.1
Perhaps the most primitive vertebrate known, the coelacanth is endowed with ampullae of Lorenzini, and is likely to be an electroreceptive species. Side view is shown in A. In B, many of the ampullae are distributed around this enormous mouth.

of the creatures remain, but there is concern that the species, which apparently has been perilously close to extinction for the last 100 million years, may now be on the verge of finally losing its fight for survival. By any standard of human aesthetics, the coelacanth is not an attractive beast. It has an enormous mouth filled with fiercely pointed teeth, very fleshy fins (it's sometimes called the fish with legs), and a somewhat corpulent body. But the ancient coelacanth has what appear to be ampullae of Lorenzini.

Sharks have them as well, and so do their close relatives the rays and skates (including of course, our now-familiar torpedo ray). The sharks and rays are members of elasmobranchs. They are distinguished from "bony fish" in part by the fact that their skeletons are made of cartilage rather than bone. But almost all of the bony fish have ampullae of Lorenzini, too. It was the ubiquity of these receptors that made their function so elusive. After all, if the ampullae are found in elasmobranchs and almost all bony fish, why would anyone think they had anything to do with an electric sense that was apparently specific to a restricted number of highly unusual African and South American freshwater species?

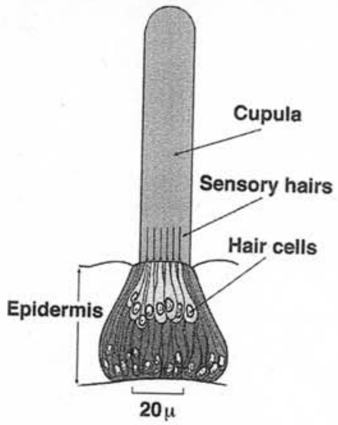

Figure 13.2
Anatomical structure of one type of sensory organ found in the lateral line system of fish. This one responds to water currents that touch the fish's skin (epidermis). Size calibration is specified in millionths of a meter.

Scientists did not yet appreciate certain key elements to complete the story. But that was soon to change, aided in large part by work that was begun during the early 1960s by a Dutch scientist named Sven Dijkgraaf, (the same Sven Dijkgraaf who had worked with bats 20 years earlier) and one of his students, Adrianus J. Kalmijn. Dijkgraaf did not start out with a specific interest in electroreception. He was, however, interested in an array of sensory receptors that is known as the lateral line organ. The lateralline organ is found on all aquatic vertebrates, and is really composed of a heterogeneous collection of receptor types.

One class of receptor cells has little hairs that protrude into the water. In some hair cell receptors, the hairs are embedded in the mucuslike coating that makes most fish feel slimy to the touch (figure 13.2). In

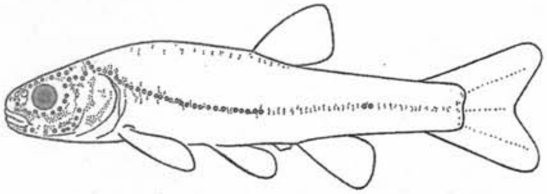

Figure 13.3
Distribution of sensory organs in the lateral line system of a minnow.

others, the hairs extend directly into the water. In addition to these hair cells, however, the lateral line contains ampullae of Lorenzini. These varied receptor cell types are widely distributed over the fish's body. They are found around the head, and extend in a line that runs the length of the animal's body (thus the name; see figure 13.3). When you look at most fish from the side, it is readily apparent that the top and bottom halves have distinctively different coloration. The change in coloring occurs right along the midpoint of the flank—where the receptors are.

The lateral line system provides the fish with what amounts to several different sensory modalities. The hair cells are sensitive to mechanical forces. These forces are produced by water currents and disturbances in the water initiated by movements of nearby objects. They bend the hairs, which in turn causes ionic currents to flow within the receptors. As in all sensory receptors, these current flows are converted into nerve impulses that are conveyed to the brain via sensory nerves. In some ways, these mechanical disturbances have the properties of underwater sound waves, although the receptors respond best to fairly low-frequency vibrations (less than 10 cycles per second, which is lower than normal human auditory sensitivity). In their physical details, these vibrations are not actually underwater sound waves, which are pressure waves that travel at a velocity of 1450 m/sec in freshwater. The stimulus that activates the hair cells is a little different. Rather than responding best to pressure waves, the lateral line organ responds to movements of the water that occur in response to movement of a nearby object. Thus, whereas the hair cells of the lateral line system are often compared with auditory receptors, the stimulus that excites them best is not truly an auditory pressure wave. In some ways, the hair cells of the lateral line organ are similar to a sense of touch. An apt analogy might be the feeling of a breeze moving across your face. You can hear the breeze, but the feel of it on your skin is a distinctively different modality. In any case, swimming motions of nearby fish can be sensed with this system.

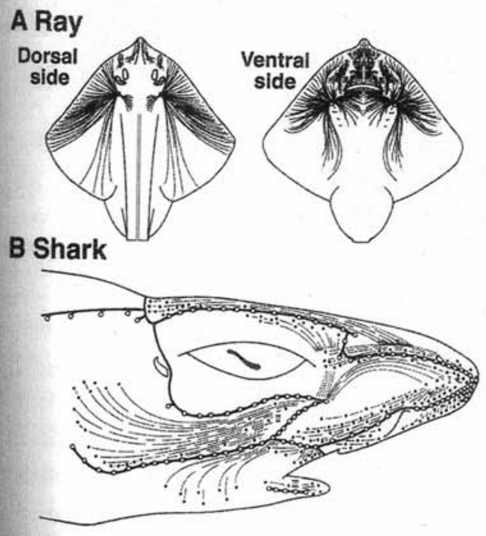

Figure 13.4
Distribution of ampullae of Lorenzini in rays and sharks.

The ampullary receptors are different. First of all, they look different—and as any good anatomist will tell you, form follows function—an adage that unfortunately is often easiest to see retrospectively. Rather than consisting of little hairs that protrude into the water, ampullae consist of receptor cells that are located at the base of a canal. The length of these ampullary canals can be as short as a millimeter, or can be quite long. Figure 13.4 schematically illustrates the location, orientation, and length of the canals found in sharks and rays. It is quite clear that sharks are well endowed with ampullae of Lorenzini, and while sharks have been accused of many things, they have never been accused of producing an electric discharge.

One might think that recordings of the bioelectrical responses of the sensory fibers that innervate the ampullae would establish the class of environmental energy they are designed to detect. After all, visual

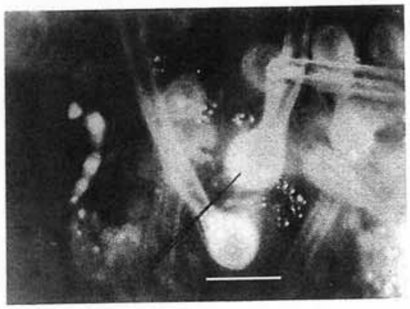

Figure 13.5
Photograph of ampullae of Lorenzini in a living specimen, taken through a microscope. In order to study the physiological properties of the organ, a microelectrode is being inserted into a sensory cell. The figure provides some appreciation for the technical skill this work requires.

receptors respond to light, touch receptors respond to touch. One might have thought it a simple matter to stimulate these receptors with different forms of energy and see which form produces a biological response. The problem was that when experiments of this sort were performed, the receptors were found to respond to a variety of stimuli. Touching them produces responses, and since they do indeed populate the skin, one might reasonably suggest that the ampullae function as a sort of touch receptor. Ampullae also respond to changes in water temperature (thermoreceptors?) and in the salinity of the water (chemoreceptors?). The variety of stimuli that can produce a response in the nerves that innervate the ampullary organs naturally caused some confusion. Which type of stimulus was the receptor actually designed to detect?

The first report that the ampullae were sensitive to electric fields appeared in 1962. Around the same time, Dijkgraaf and Kalmijn were studying the effects of galvanic fields in sharks. In experiments similar to those performed using catfish in 1917, it was found that sharks have a reflexive eye-blink response to very weak electric fields. The fields were about the same strength as the electric fields that Dijkgraaf had earlier found to be a natural consequence of the rhythmic gill movements that occur during breathing in fish. Dijkgraaf was clearly homing in on the solution to the puzzle. He reasoned that since all living fish produce these electric fields, predators like the shark may have evolved a mechanism that can detect them. The eye-blink reflex response to weak electric fields supported this conjecture—sharks always shut their eyes immediately before an attack. It's presumably a reflex designed to protect the eyes. Armed with the knowledge that the ampullae could respond to electric fields of the same strength as those that fish naturally produce, Dijkgraaf and Kalmijn tested the electric field sensitivity of sharks after the ampullary nerves had been surgically severed. They discovered that this operation abolished the eye-blink response to galvanic fields, and thus established an electroreceptive function of the ampullary organs.

In order to firmly establish the importance of electroreception in the daily lives of the shark, however, it was essential to demonstrate the way a shark normally reacts to these weak bioelectric fields. Kalmijn established a behavioral role of electric fields in a series of ingenious studies. First, a live flounder was placed in a shark's pool. The flounder quickly buried itself in the sandy bottom. Like chameleons, flounder are able to change their coloration to match that of their surroundings. All this camouflage was of little avail, however, for the shark, aroused by a delectable fish puree that had also been added to the water, began to search for food. Initially, the searching pattern of the shark was random, but when the shark passed within 15 centimeters of the "hidden" flounder, the attack was quick, accurate, and very effective: the flounder was immediately eaten.

Kalmijn next placed a flounder in an agar container. Agar is a gelatinous substance extracted from a type of algae. It is often used as a substrate in tissue cultures. Electrical currents can pass through it, but it is not transparent to light. The flounder was concealed in this chamber, through which water was pumped in order to keep the fish alive. This concealment was completely ineffective. The shark again searched, and when by chance it came close to the agar, the unsuspecting flounder was immediately attacked and devoured. Placing pieces of dead flounder in an identical chamber did not produce an attack directed toward the chamber. Instead, the shark attacked the end of the tube in which the ventilated water exited from the chamber; this evacuation tube was some distance from the chamber. This last observation proved that scent could provide a cue that would support a shark attack, since the water in this area had a high concentration of fish odor. If the agar experiment was repeated, again using a live flounder but a container wrapped in an electrically insulating plastic film, the shark ignored the chamber.

The final experiment in the series confirmed that electric fields were sufficient to provoke a shark attack. Following a procedure similar to that Lissman had used with *Gymnarchus* ten years earlier, Kalmijn placed electrodes in the sandy bottom of the shark tank. The shark viciously attacked the metal electrodes whenever currents that mimicked the electric fields of a flounder were emitted.

Kalmijn's behavioral experiments firmly established that sharks can detect prey on the basis of the weak electric fields living fish produce in seawater. Thus, two modes of electroreceptive senses have been established: an active mode and a passive mode. In the passive mode, fish can sense the electric fields produced by others. In the active mode, the fish detect disturbances in an electric field that surrounds their own body, a field that is created by their own EOD. Sharks employ only the passive mode. The weakly electric fish use both active and passive electroreception.