LEMON SHARK chomps down on an unlucky fish.

THE SHARK'S ELECTRIC SENSE

An astonishingly sensitive detector of electric fields helps sharks zero in on prey

By R. Douglas Fields

A menacing fin pierced the surface and sliced toward us. A great blue shark—three meters in length—homed in on the scent of blood like a torpedo. As my wife, Melanie, and I watched several large sharks circle our seven-meter Boston Whaler, a silver-blue snout suddenly thrust through a square cutout in the boat deck. "Look out!" Melanie shouted. We both recoiled instinctively, but we were in no real danger. The shark flashed a jagged smile of ivory saw teeth and then slipped back into the sea.

We had drawn the sharks by ladling blood into the ocean, but we were not interested in their well-known attraction to blood. Rather we were investigating the hunters' mysterious "sixth sense." Laboratory research had demonstrated that sharks can sense extremely weak electric fields—such as those animal cells produce when in contact with seawater. But how they use that unique sense had yet to be proved. We were on that boat to find out.

Until the 1970s, scientists did not even suspect that sharks could perceive weak electric fields. Today we know that such electroreception helps the fish find food and can operate even when environmental conditions render the five common senses—sight, smell, taste, touch, hearing—all but useless. It works in turbid water, total darkness and even when prey hide beneath the sand.

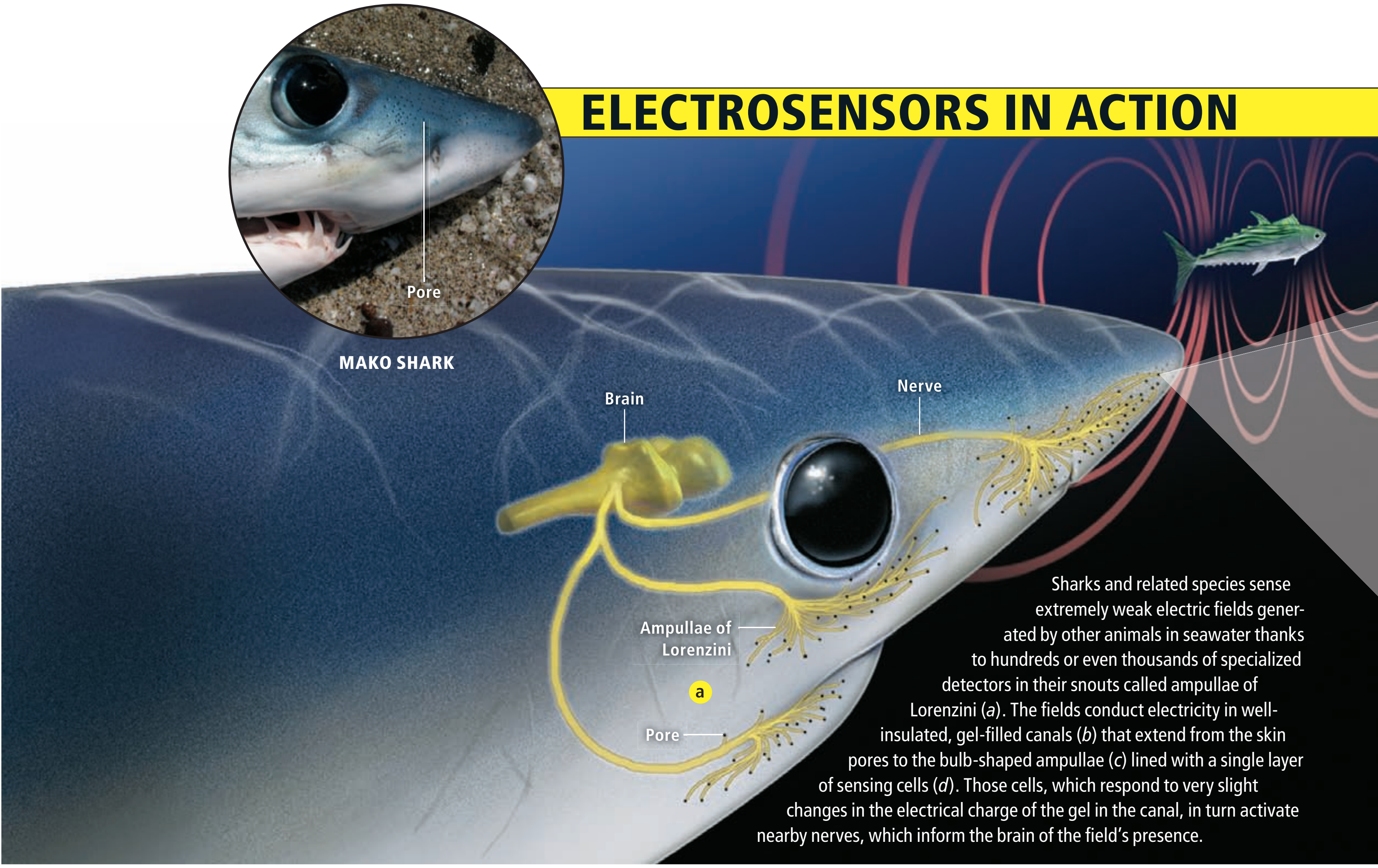
My research colleagues and I are now exploring the molecular basis for this ability, while others pursue such questions as how the sensing organ forms during development and whether our own vertebrate ancestors once could detect electric fields before they left the sea. All this work is still

KEY CONCEPTS

- Sharks and related fish can sense the extremely weak electric fields emitted by animals in the surrounding water, an ability few other organisms possess.
- This ability is made possible by unique electrosensory structures called ampullae of Lorenzini, after the 17th-century anatomist who first described them.
- The author and his colleagues have demonstrated that sharks use this "sixth sense" to home in on prey during the final phase of an attack. Other potential uses for electroreceptors remain to be determined.

—The Editors

ELECTROSENSORS IN ACTION



Sharks and related species sense extremely weak electric fields generated by other animals in seawater thanks to hundreds or even thousands of specialized detectors in their snouts called ampullae of Lorenzini (*a*). The fields conduct electricity in well-insulated, gel-filled canals (*b*) that extend from the skin pores to the bulb-shaped ampullae (*c*) lined with a single layer of sensing cells (*d*). Those cells, which respond to very slight changes in the electrical charge of the gel in the canal, in turn activate nearby nerves, which inform the brain of the field's presence.

quite preliminary, though. Here I describe how investigators first discovered electroreception in sharks and how we demonstrated its importance to successful hunting—a fascinating, little-known tale that spans centuries.

ONE MILLIONTH OF A VOLT ACROSS A CENTIMETER OF SEAWATER can be distinguished by a shark. This is equivalent to a voltage gradient created by a 1.5-volt AA battery with one pole dipped in the Long Island Sound and the other pole in waters off Jacksonville, Fla.

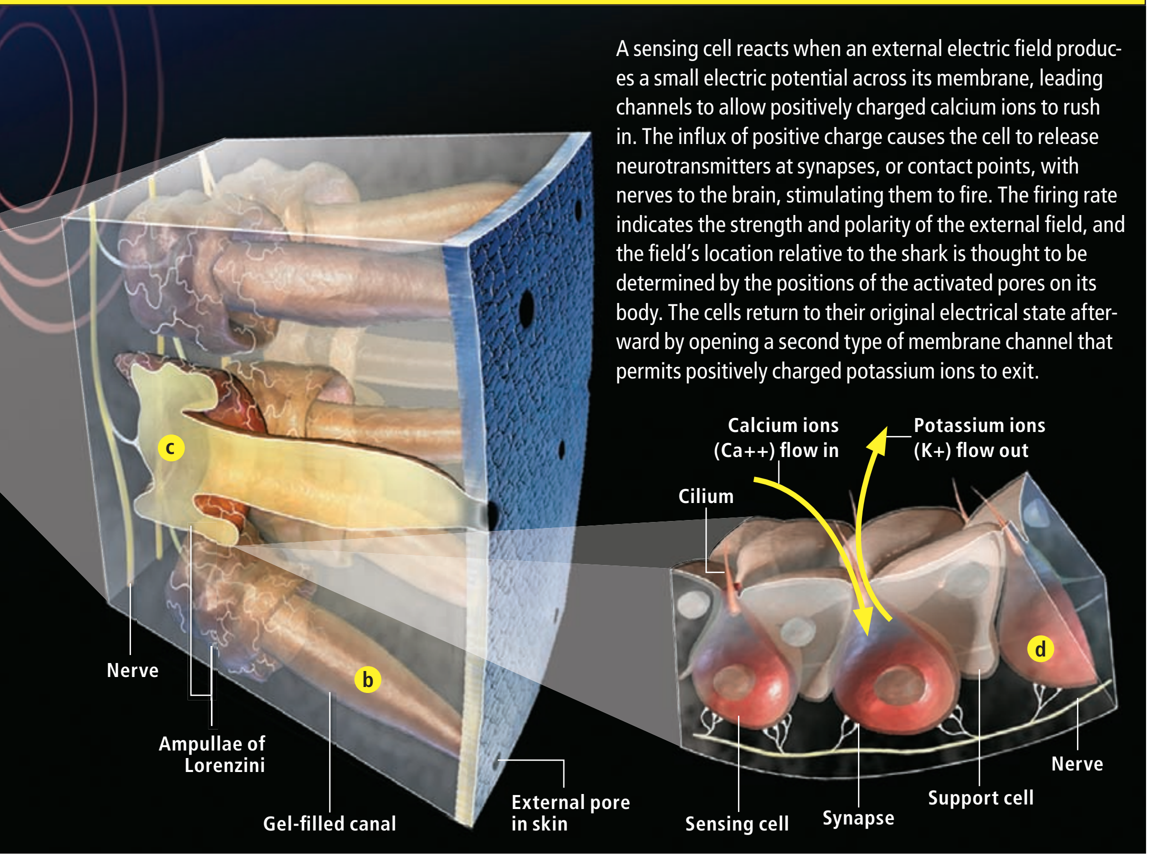
Hidden Sense

The story begins in 1678, when Italian anatomist Stefano Lorenzini described pores that speckled the forward part of the head of sharks and rays, endowing them with something resembling a bad five-o'clock shadow. He noted that the pores concentrated around a shark's mouth and found that if he peeled back the neighboring skin, each opening led to a long transparent tube that was filled with a crystalline gel. Some of the tubes were small and delicate, but others were nearly the diameter of a strand of spaghetti and several inches in length. Deep within the head, Lorenzini discovered, the tubes congregated in several large masses of clear jelly. He considered and then rejected the possibility that these pores were the source of fish body slime. Later, he speculated that the pores might have another, "more hidden function," but their true purpose remained unexplained for hundreds of years afterward.

The pores' purpose started to become clear in the middle of the 19th century, when researchers began to glean the function of the so-called lateral line, an organ that shares some similarities with Lorenzini's pore-and-tube system. The lateral line, a stripe extending down the sides of many fish and amphibians from gills to tail, detects water displacement. In fish, it consists of a specialized row of perforated scales, each of which opens into a tube lying lengthwise just under the skin. At swellings along the length, specialized sensory cells called hair cells extend slender, brushlike projections (or cilia) into the tube. Slight water movements, such as those caused by fish swimming a few feet away, bend the microscopic hair masses like wind-driven waves rippling through a field of grain. This reaction excites nerves, whose impulses inform the brain about the strength and direction of the water displacement. We retain the descendant of this lateral line in our ear cochlea.

By the late 19th century the newly improved microscope revealed that the pores on a shark's snout and the unusual structures underneath them, today called ampullae of Lorenzini, must be sensory organs of some kind. Each tube was

BRANDON COLE (*preceding pages*); AMADEO BACHAR (*photograph and illustration of mako shark snout*)



seen to end in a bulbous pouch, or ampulla. A thin nerve emerged from the ampulla and joined branches of the anterior lateral line nerve. Scientists traced these nerve fibers to the base of the skull, where they enter the brain through the dorsal surface of the medulla, a destination characteristic of nerves that carry sensory information into the brain. Observers discerned a single tiny hair cell, similar to those of the human inner ear and of a fish's lateral line system, inside each ampulla. The type of stimulus they might detect remained unknown, however.

Electroreception Confirmed

Researchers found themselves faced with a dilemma: How could they determine the function of this entirely foreign sense organ? The eventual solution came down to the combination of good instrumentation and a fertile imagination.

In 1909 biologist G. H. Parker of Harvard University removed skin from around the ampullar openings of a dogfish to eliminate any tactile receptors in the area. He then observed that the fish nonetheless reacted when the exposed tubes were touched gently. This response suggested that the organs might sense water motion or perhaps water pressure, but he could not be sure. After all, a reflex reaction to a poke in the eye does not necessarily mean that eyes had evolved to perceive sudden jabs.

Just as microscopes had opened up new research avenues a century before, the just-devised vacuum-tube amplifier advanced the study of brain function in the second quarter of the 20th century. In 1938 Alexander Sand of the Marine Biological Association in Plymouth, England, succeeded in amplifying and recording nerve pulses running from ampullae of Lorenzini to the brain. He saw that impulses shot down the nerve in a steady stream but that certain stimuli caused the rate to increase or decrease suddenly. Sand noticed, as Parker had, that the organs responded to touch or pressure, but he found that the firing rate also rose when cooled. Indeed, the ampullae were so sensitive to temperature that they could detect external changes as small as 0.2 degree Celsius. Such fine discrimination, together with the well-known importance of water temperature to migration and other fish behavior, seemed strong evidence that the organs were temperature receptors.

In the early 1960s biologist R. W. Murray of

TIMELINE: UNDERSTANDING ELECTRORECEPTION

1678: Italian anatomist Stefano Lorenzini describes the structure of the electroreception system of sharks and rays. Its function remains a mystery.

Late 1800s: Scientists explain the function of fish's lateral line, an organ that detects water displacement and in some ways resembles the electroreception system. Examination with microscopes delineates the details of what soon become known as ampullae of Lorenzini.

1909: G. H. Parker finds that the ampullae respond to touch. He speculates that they might sense water motion.

1938: Alexander Sand records nerve impulse output from ampullae of Lorenzini in response to various stimuli. He notices that they react to tiny temperature changes.

1950s: H. W. Lissmann and others describe "tuberous receptors" in weakly electric fish that sense their own fields. The discovery adds electroreception to the list of known animal senses.

Early 1960s: R. W. Murray finds that ampullae of Lorenzini are sensitive to slight salinity variations and weak electric fields.

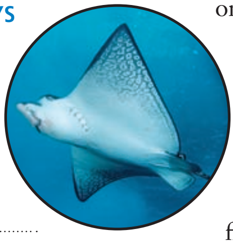
1970s: Adrianus Kalmijn determines that in seawater animal bodies produce electric fields. He also demonstrates that captive sharks can locate and attack buried electrodes that emit similar electric fields.

1990s to present: Researchers show that electroreception is an ancient sense that is widespread among aquatic animals.

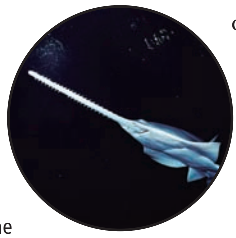
FISH WITH A SIXTH SENSE

Beyond sharks, several well-known fish have similar ampullary electroreceptors, including:

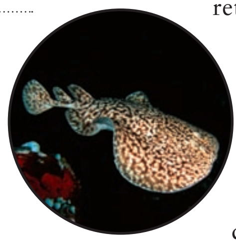
COMMON RAYS AND SKATES, which glide on enlarged pectoral fin "wings" close to the bottom to feed.



SAWFISH, which have sawlike snouts covered with motion-sensitive and electrosensitive pores that allow them to detect prey buried in the ocean floor.



ELECTRIC RAYS, which have organs that can deliver an electrical discharge to stun or kill prey.



STURGEONS, which use their wedge-shaped snouts and sensitive, whiskerlike barbels to find food in the bottom sediments.

LUNGFISH, which can breathe air and are adapted to fresh, often muddy, water.

the University of Birmingham in England repeated Sand's experiments with modern electrophysiological instruments and confirmed the responses to temperature changes, pressure differences and touch, but he also observed that the organs were sensitive to slight variations in salinity. Moreover, when he happened to switch on an electric field near the opening of a tube connected to an ampulla, the firing pattern changed. Further, the pattern altered according to the intensity and polarity of the field. When the field's positive pole neared the opening of an ampulla, the firing rate declined; when the negative pole came near, firing increased.

Astonishingly, Murray determined that the organs could respond to fields as weak as one millionth of a volt applied across a centimeter of seawater. This effect is equivalent to the intensity of the voltage gradient that would be produced in the sea by connecting up a 1.5-volt AA battery with one pole dipped in the Long Island Sound and the other pole in the waters off Jacksonville, Fla. Theoretically, a shark swimming between these points could easily tell when the battery was switched on or off. (Later measurements of brain response indicate that sharks can discern 15 billionths of a volt.) No other tissue, organ or animal exhibits such extreme sensitivity to electricity. Indeed, engineers have difficulty measuring such weak fields in seawater using modern equipment.

The Search for a Function

What could fish gain by detecting weak electric fields? Hints to the answer came from earlier studies of "bioelectricity"—electric field emissions—by other fish. Electric eels, for example, can stun prey with strong shocks generated by a specialized organ. Certain other fish, however, seem to purposely produce much weaker electric fields too faint to serve as weapons. The evolution of such apparently useless organs puzzled even Charles Darwin, who grappled with this biological riddle in *On the Origin of Species.*

Searching for the function of that weak bioelectricity, zoologist H. W. Lissmann of the University of Cambridge and others in the 1950s found that fish that produced it were able to detect their own electric field. Their sensors, known as tuberous receptors, are very different from ampullae of Lorenzini: they lack the long tubes and are not nearly as sensitive to electric fields. Nevertheless, at the time, their discovery added electroreception to the familiar list of five senses.

Together, weak electric organs and tuberous electroreceptors form the emitter and receiver of a radarlike system that is extremely useful for tasks such as navigating the muddy Amazon River or feeding at night. As objects distort the shape of the emitted electric field, tuberous receptors detect the change, thereby revealing the location of the objects.

Sharks and rays lack dedicated organs for emitting fields, however. Researchers speculated that the acutely sensitive ampullae of Lorenzini might work as a passive "radar" system, detecting feeble electric fields occurring naturally in the environment—much like some night-vision goggles reveal a nighttime battlefield by amplifying starlight.

What, then, were these animals detecting? Possibly they were sensing very brief, weak forms of bioelectricity such as brain waves and heart muscle contraction potentials. But it seemed unlikely that sharks could use their ampullae of Lorenzini to detect electric field pulses that last only a few thousandths of a second. On the contrary, these organs are tuned to sense only the slowest-changing electric fields, such as those generated by electrochemical batteries.

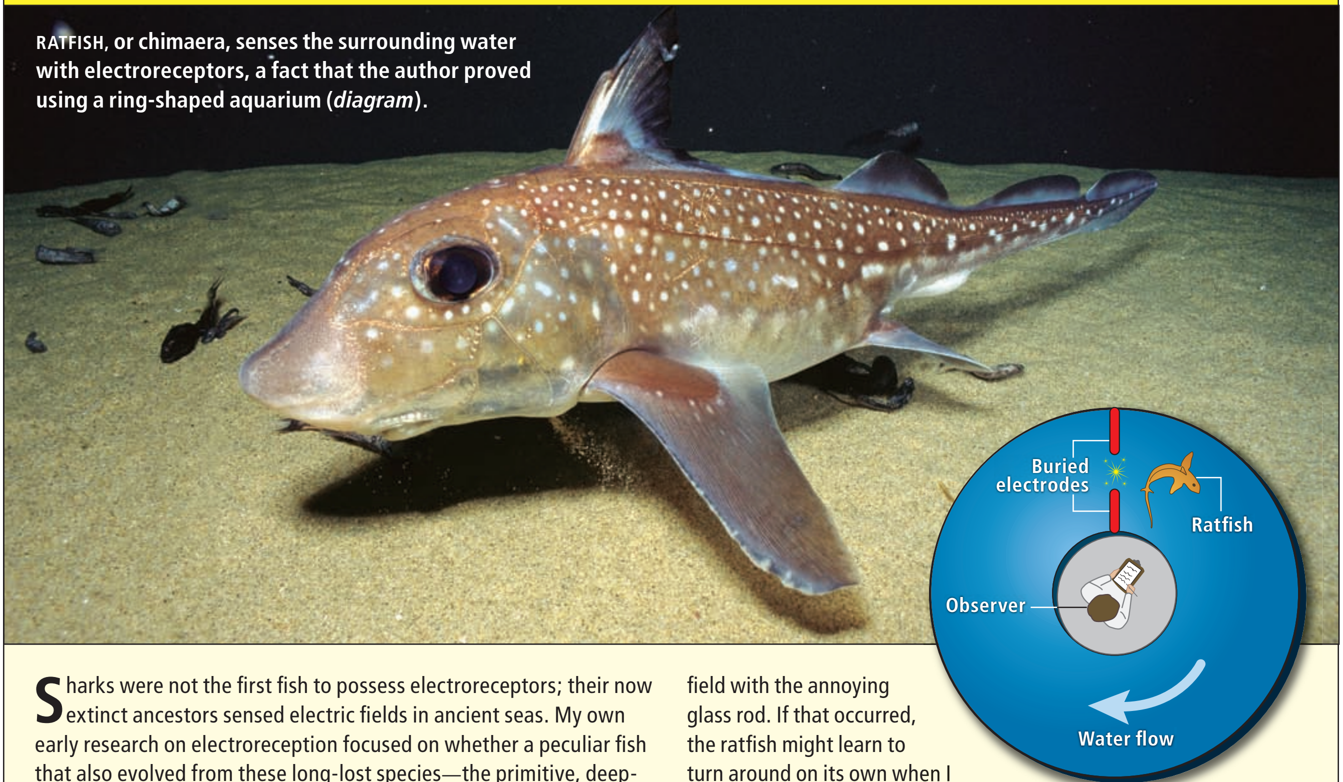
This detection ability would make sense because all biological cells in the body function as batteries as a consequence of their structure. A typical battery produces a voltage when two salt solutions with different net electric charges are separated inside an electrochemical cell. Opposite charges attract, and the resulting movement of charge creates an electric current. Likewise, living cells contain a salt solution that differs from seawater, causing a voltage to arise at the interface. Consequently, a fish's body in seawater operates as a weak battery that emits an electric field around it. The field produced by this battery changes slowly as the fish pumps water through its gills.

By using an electronic amplifier in the 1970s biologist Adrianus Kalmijn, then at the University of Utrecht in the Netherlands (and now at the Scripps Institution of Oceanography), showed that animals produced bioelectric fields in seawater. These very weak fields changed little (or not at all) over time, exactly the type of electric signature ampullae of Lorenzini are equipped to detect. Kalmijn also demonstrated that a captive shark would locate and attack electrodes he had buried in the sand of an aquarium if the elec-

FRED BAVENDAM *Minden Pictures (ray)*; NORBERT WU *Minden Pictures (sawfish)*; STEPHEN FRINK *Corbis (electric ray)*; WIL MEINDERTS *Foto Natura/Minden Pictures (sturgeon)*; JEAN-PAUL FERRERO *Auscape/Minden Pictures (lungfish)*

[EXPERIMENTS]

INVESTIGATING AN ANCIENT SENSE



RATFISH, or chimaera, senses the surrounding water with electroreceptors, a fact that the author proved using a ring-shaped aquarium (*diagram*).

Sharks were not the first fish to possess electroreceptors; their now extinct ancestors sensed electric fields in ancient seas. My own early research on electroreception focused on whether a peculiar fish that also evolved from these long-lost species—the primitive, deep-ocean dweller called chimaera—has electroreception.

I first encountered one of these bizarre-looking creatures in the late 1970s on a commercial fishing trawler when I was a graduate student at Moss Landing Marine Labs in California. The chimaera had large incisors that prevented its mouth from fully closing. This feature and its big eyes made it resemble a bunny or a rat—which is why it is commonly called a rabbitfish or ratfish.

Because the ratfish had no commercial value, the captain allowed me to take it home for study. I soon noted that the bulk of the head between the skin and underlying muscle was filled with a transparent gelatinous mass. When I shone a light through the jelly at an angle, I saw a tangle of transparent, gel-filled tubes that radiated out to pores on the surface of the head, which resembled ampullae of Lorenzini in sharks. I suspected that ratfish also possess these organs, but to confirm this conjecture, I needed to catch a ratfish unharmed and keep it alive long enough for experimentation.

To this end, I enlisted the help of the crews of the commercial fishing boats that ply the seas around Monterey Bay. One foggy morning the *Holiday II* brought in a live ratfish, and the skipper radioed me to pick it up at the dock. Back at my lab, I placed the fish in a ring-shaped aquarium in which seawater circulated constantly (*diagram*). The center of the ring was just large enough to allow me to observe the fish as it swam against the water current (its preferred direction).

I soon realized that the ratfish's tendency to swim against the flow might help to answer my questions. First, I buried electrodes under the sand. When the ratfish swam over the hidden electrodes, I switched on the electric field and simultaneously gently tapped the fish with a glass rod, coaxing it to swim with the water current. The ratfish soon reversed course, returning to its favored route. I assumed that if the fish could detect the weak electric field, it would come to associate the field with the annoying glass rod. If that occurred, the ratfish might learn to turn around on its own when I flipped the switch only. If the animal never learned to do this, the failure would mean either that it could not sense weak electric fields or that it was untrainable.

After considerable effort, I finally got the result I sought. I hit the switch, and the chimaera reversed direction instantly. It had sensed the electric field and figured out the routine. From then on, every time I applied the electric stimulus, the ratfish turned around, but it passed over the electrodes without hesitation if I did not engage the field. By adjusting the field's intensity and frequency, I found that the fish easily detected fields as weak as those emitted by fish in seawater.

Although the experiment showed that ratfish can detect weak electric fields, it did not prove that the fish use the structures resembling ampullae of Lorenzini for that purpose. Electrophysiologist David Lange of the Scripps Institution of Oceanography and I set out to address this issue with the same ratfish. Taking the approach employed by Alexander Sand in 1938, we recorded the activity of the nerves connected to these organs. When a nerve impulse raced from the mystery organ to the brain, a green phosphorescent wave trace swept across our oscilloscope screen and a loud crack resounded from a speaker.

As the fish slept peacefully under anesthesia, the nerve firing pulsed gently in rhythm with its respiration. When we placed an electric field near the opening of one of the skin pores, though, the laboratory instantly filled with noisy cracks, reflecting a stream of nerve impulses shooting to its brain. Next, we pulsed the electric field, and the impulses followed in lockstep, like Marines on the march. And when we reversed the field's polarity, we demonstrated that the negative pole excited the organ, whereas the positive pole inhibited its function, just as R. W. Murray observed with the ampullae in sharks. There was no doubt that the chimaera had electroreceptors. Later examination revealed that the ratfish's electrosensors are identical to those in sharks. —***R.D.F.***

NORBERT WU *Minden Pictures* (*ratfish*); MELISSA THOMAS (*diagram*)

MAGNETIC REPELLENTS?

Inventors are attempting to drive sharks away from fish baits and maybe even swimmers by zapping their sensitive electroreceptors with strong magnets. The idea is to confuse a shark's electrosensors by inducing an internal voltage as its body passes through the magnet's field, say researchers and entrepreneurs Samuel Gruber, Eric Stroud and Mike Herrmann.

"The focus is on saving sharks, not humans," explains Gruber, a marine biologist at the University of Miami. The World Wildlife Fund estimates that 20 percent of shark species are endangered. If fixed to commercial longlines, such devices might save 50,000 sharks a night from being caught by fishers worldwide, Gruber claims.

With support from the World Wildlife Fund, the team is developing a baited fishhook with a powerful magnet (*black cylinder, above*) attached to the leader. Commercial and game fish, which do not have electroreceptors, would bite the hook unawares. Preliminary tests are encouraging, but don't swim in the ocean with suits stuffed with magnets just yet; no peer-reviewed scientific studies have shown if magnets have any effect whatsoever on shark behavior. —***R.D.F.***

trodes emitted fields mimicking those produced by the shark's typical prey. (My own early work in electroreception paralleled Kalmijn's research, except that I focused on a relative of sharks called chimaera [*see box on preceding page*].)

Electroreception in the Wild

Showing that fish with ampullae of Lorenzini respond to electric fields in the controlled conditions of the laboratory is one thing, but determining if and how they use this sense in their own environment is another. This task proved challenging in part because weak electrical signals from prey can be accompanied by electrical noise generated by other natural phenomena—salinity, temperature, water motion, acidity, and so on. In the ocean, even a metal wire creates a voltage that any shark can easily perceive.

To test how fish use this sensory ability in nature, such as while hunting, we had to observe them doing so in the sea—which is how we ended up on the small fiberglass (nonmetallic) boat with the square hole cut into its deck. In 1981, hoping to see if large oceangoing sharks relied on electroreception during normal feeding, Melanie and I, as well as Kalmijn and his associate Gail Heyer of the Woods Hole Oceanographic Institution, developed a T-shaped apparatus with sets of electrodes positioned at each end.

Later that summer, out at sea, we lowered the device through the cutout in the deck and pumped ground-up fish into the water through a port located at the join between the electrodes. We then energized the electrodes to produce electric fields mimicking those emitted by sharks' typical prey fish. One person activated one electrode at a time in a random sequence while a second person (who did not know which electrode was activated in any instant) observed the effect on the sharks. If the animals preferentially attacked the activated electrode, we would know they used their electric sense to catch prey.

Crouching on the boat deck during the first night of our experiment, we peered into the hole as a great blue shark circled and then zeroed in on the scent of ground fish flowing from the apparatus. It swam straight toward the odor and at the last instant veered sharply to the right, snapping the right leg of the T in its jaws. The shark shuddered and thrashed and abruptly released the apparatus. In the final moment of the attack the predator had ignored the odor source and instead turned to bite the activated electrode. Throughout the summer we witnessed many attacks in which the animals strongly preferred the activated electrode over the inactive electrode and the source of food odor.

The finding that electroreception can override even the strong sensory cues of taste and smell in the final moments of attack might explain puzzling anecdotal accounts of shark attacks on humans. People have reported instances in which a human victim of a shark attack was repeatedly assaulted while being towed to safety by another swimmer whom the shark ignored during the rescue. Although a shark might be expected to lose track of its initial victim when blood obscured vision and smell, it seems that its electroreception sense enables it to locate the strong electric field originating from the bloody salts pouring from the wounds of the victim.

Sharks use all their senses when they hunt, but each one has special advantages and different sensitivities [*see box on opposite page*]. Smell and hearing would be most useful for locating prey from great distances. Vision, lateral line senses and taste would become more important at closer ranges. During the terminal phase of an attack, when a shark comes within a meter of its prey, however, electroreception becomes the most useful way to precisely locate the prey and correctly orient its jaws. Such an insight may one day inform the development of a device that could decoy sharks away from swimmers.

My colleagues and I have focused on feeding behavior because it is relatively easy to elicit in sharks, but these fish undoubtedly wield their electric sense for other purposes as well. We can only imagine what it must be like to see the world through this strange and altogether unfamiliar sense. ■

[THE AUTHOR]

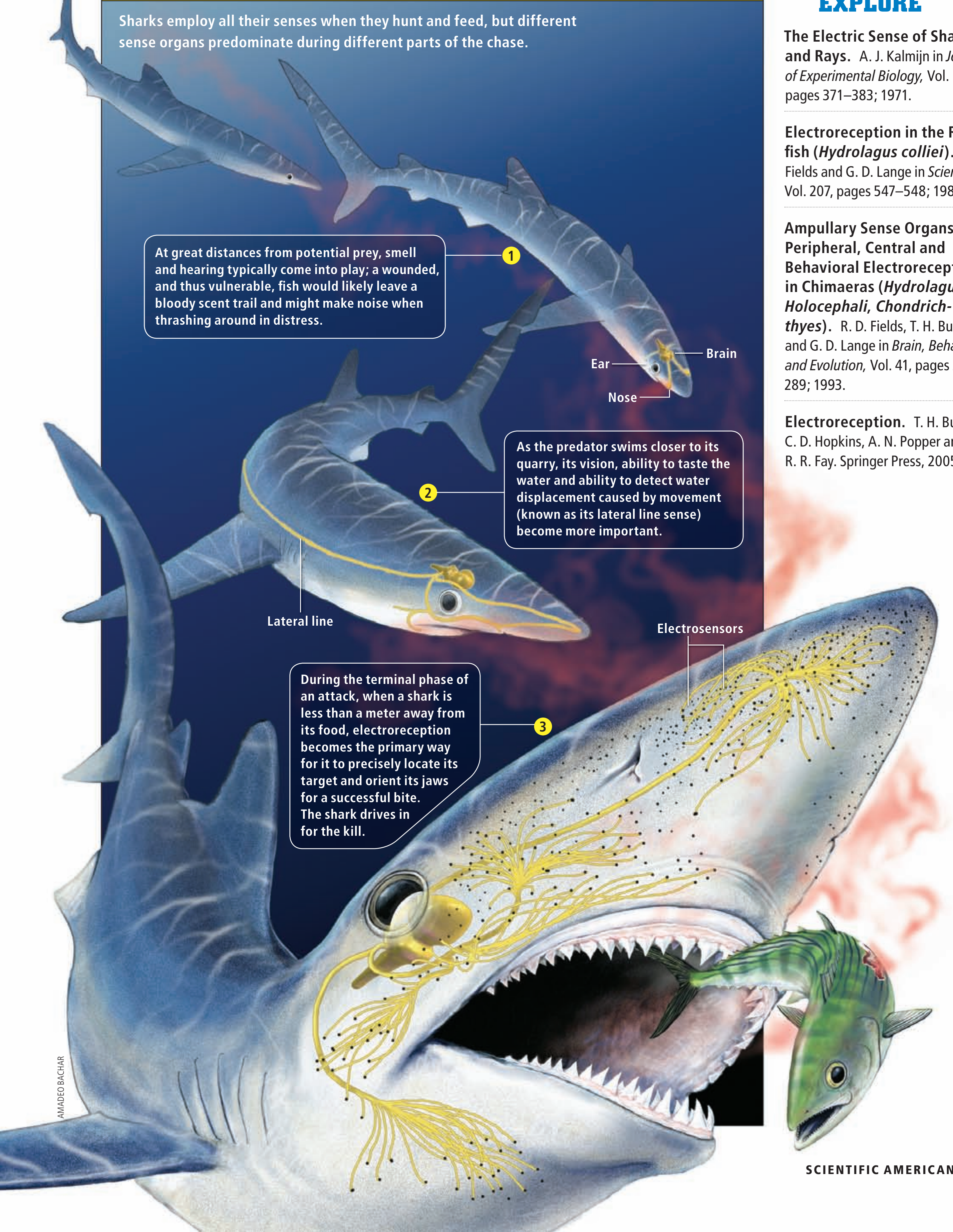
R. Douglas Fields, who holds an M.A. from Moss Landing Marine Labs in California and a Ph.D. in biological oceanography from the Scripps Institution of Oceanography, is a neurobiologist at the National Institutes of Health. For his shark studies, he collaborates with his wife, Melanie Fields, a high school biology teacher. Outside of work, Fields spends time rock climbing, scuba diving and guitar making. This is his third article for *Scientific American.*

ERIC STROUD AND MICHAEL HERMANN *Shark Defense* (*top*); COURTESY OF R. DOUGLAS FIELDS (*bottom*)

[SCENARIO]

SHARK SENSES ON THE HUNT

Sharks employ all their senses when they hunt and feed, but different sense organs predominate during different parts of the chase.



AMADEO BACHAR

MORE TO EXPLORE

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