Navigation, Touch, and Beyond

> When one flesh is waiting, there is electricity in the merest contact.
>
> —Wallace Stegner

Fishes need to move about to meet their needs, and they must be in certain places at certain times if they are to be successful at making a living and making more fishes. Like us, fishes return to specific places at different times of day, such as feeding locations, hiding and sleeping places, and cleaning stations. At certain times of the year they return to mating, spawning, and nesting sites. Living in a complex volumetric habitat, fishes face a challenging spatial milieu.

Fishes are excellent navigators, and they use a variety of methods to find their way around over both short and long distances. Blind cavefishes live in relatively small cave habitats, but most also live in total darkness, so having good navigation skills is important to them. These little fishes can learn the order of a sequence of landmarks en route to a destination by feeling the turbulence reflected off underwater obstacles. Swordfishes, parrotfishes, and sockeye salmons use sun compassing, setting their direction based on the angle of the sun. Yet others can use dead reckoning—taking wandering, novel outbound exploratory trips from a point of reference and then returning to home base using a direct path.

The navigation feats of salmons are the stuff of legend. Being able to return to their natal streams to spawn after spending years in the open ocean ranks these anadromous fishes (migrating to sea, homing to spawn) as having one of nature's finest built-in Global Positioning Systems. As far as we know, this system uses at least two and possibly three sensory tools to work at full capacity: geomagnetic sense, smell, and possibly vision.

Like sharks, eels, and tunas, these long-distance fishes plug into the Earth's magnetic field to aid their navigation. This manifests at the cellular level. Single cells containing microscopic magnetite crystals act like compass needles. By isolating cells from the nasal passages of trouts (very close relatives of salmons) and exposing these cells to a rotating magnetic field, a research team from Germany, France, and Malaysia found that the cells themselves rotated. The magnetite particles are firmly attached to the cell membrane, and by constantly pulling toward magnetic field lines, these particles generate torque on the cell membrane when the salmon changes direction. That torque must be directly transmitted to stress-sensitive transducers of some kind, because evidence shows that the salmons can feel it.

They also use their prodigious sense of smell. When heading downstream to the ocean, young salmons "record" the water chemistry along the way. Years later, they retrace their paths, following the distinctive odor signature of their home stream, like walking a trail in reverse. Anosmic salmons, whose noses had been experimentally plugged by biologists to eliminate their ability to smell, showed up in random streams, whereas unmolested fishes returned to their home streams to spawn.

In a less invasive experiment, the same research team, led by the late Arthur Hasler of the University of Wisconsin, split a group of young coho (freshwater) salmons into two groups, each of which was exposed to one of two different, innocuous but fragrant chemicals—morpholine and phenylethyl alcohol (PEA). After this exposure period, salmons from both groups were released together directly into Lake Michigan. During the salmon spawning migration one and a half years later, the researchers dripped morpholine into one stream, and PEA into another located five miles away. Nearly all of the recaptured salmons in the morpholine-scented stream were from the morpholine group, and nearly all of their PEA counterparts navigated up the other stream.

Might a salmon also use vision to aid navigation? A Japanese research team sought to find out in a study involving ocean release and recapture of sockeye salmons. The scientists blinded a sample of the fishes before release by injecting their eyes with carbon toner and corn oil. Upon recapture five days later, only 25 percent of these salmons, compared to 40 percent of the unaltered fishes, were caught in their natal stream. The authors suggested that these fishes are nevertheless using vision to reach the entrance to their natal stream, but I find this result unconvincing. I suspect that the pain, distress, and ensuing disorientation caused by blinding salmon with an injection of foreign substances might explain their lower success rate in finding their way home. To better control for that, they would need to have injected some salmons with a similar amount of solution that doesn't cause blindness. But I'm not recommending it.

Pressure Sensors

Not only do fishes navigate independently, they have another system of orientation that allows them to track closely the movements of their neighbors. Like flocking birds, who use vision and hair-trigger reflexes to coordinate their flight directions with their neighbors, large schools of fishes can change direction seemingly as one, as if there were some internal knowledge of the decision making of all others. It isn't clear who starts it, or if the chain reaction starts with whoever happens to make the first move.

Early naturalists ascribed this behavior to a form of telepathy, but analysis of slow-motion filmed sequences yields a no-frills explanation: minuscule delays in the propagation of movement through the school show that the fishes are reacting to each other's movements. Their sensory systems are operating on such a fine timescale that it gives the impression that they all change direction as one.

In daytime conditions, sharp eyesight helps schooling fishes move in unison as birds do. But unlike birds (or humans who dare try it), they continue to move as one even in darkness. How? It's thanks to a row of specialized scales running horizontally along their flanks, forming what is called the lateral line. The lateral line is usually visible as a thin, dark line because each scale has a depression that casts a shadow. The depression is populated by neuromasts, clusters of sensory cells each with a hair-like projection encased in a tiny cup of gel. Changes in water pressure and turbulence, including waves from the fish's own movement reflected back from its surroundings, cause deflections of the neuromast hairs, which trigger nerve impulses to the fish's brain. So the lateral line acts as a sonarlike system and is especially useful at night and in murky waters.

With the lateral line, fishes swimming in close proximity are virtually in physical contact, and the transmission of signals between them is comparable to that of visual information, giving rise to hydrodynamic imaging. It is hydrodynamic imaging that allows blind cavefishes to detect stationary objects such as rocks and coral by the distortion of the normally symmetrical field flow that surrounds a fish in open water. Blind cavefishes can form mental maps, a skill very useful for navigation by a creature lacking the means for visual orientation.

Lateralization of brain functions is now known to be widespread in fishes, and these clever little fishes also use their lateral lines nonsymmetrically when confronted with unfamiliar objects. When a plastic landmark was placed in their tank along the middle of one wall, blind cavefishes preferentially swam past it using the lateral line on their right side. This preference disappeared in a few hours as the fishes became familiar, and therefore comfortable, with the new landmark. Because visual and lateral line sensory systems operate independently in fishes, this finding suggests that lateralization of the brain is a deep-seated phenomenon. Sighted fishes were already known for a tendency to have a right-eye bias in emotional contexts, such as examining a new (and thus scary) object.

Like most biological designs, the lateral line comes with inevitable compromises. Water flow generated by swimming activates the neuromasts, and this "background noise" dampens the fish's reactivity to external movements. Experiments show that swimming fishes are only half as likely as stationary fishes to respond to the movements of a nearby predator. On the other hand, a fish can detect distortions in the bow wave formed in front of his own nose when swimming forward, and thereby avoid bumping into objects made invisible by darkness or transparency, such as an aquarium wall. It is unfortunate for fishes that this system seems unfit for detecting the presence of a fishing net.

Electrified

Having a sense that allows you to avoid bumping into a wall in the dark is useful, but imagine being able to detect the presence of something on the other side of the wall when you cannot see or hear anything. Enter the world of electroreception.

Electroreception is the biological ability to perceive natural electrical stimuli. It is nearly unique to fishes, the only known exceptions being monotremes (platypuses and echidnas), cockroaches, and bees. Electrical sensitivity is widespread in sharks, skates, and rays. Among the teleosts (the 30,000-plus species of bony fishes), more than three hundred species get a charge out of life, and it must have high value as a survival tool, for it has evolved independently at least eight times in fishes. Its predominance in aquatic habitats relates to water's strong electrical conductance properties as compared to air.

As the term implies, electroreception is a passive use of electrical information. The elasmobranchs are electroreceptive only; they can detect electric stimuli but they do not produce electricity themselves. They perceive it with a network of jelly-filled pores scattered strategically over the head. These pores are called the *ampullae of Lorenzini*, after Stefano Lorenzini, the Italian physician who first described them in 1678. Noting the concentration of black specks that surrounds sharks' snouts like a five-o'clock shadow, Lorenzini peeled away the skin to reveal tubular channels —some as wide as strands of spaghetti—leading to the brain, where they congregate in several large masses of clear jelly.

The function of the ampullae of Lorenzini in electroreception remained a mystery until 1960. They detect subtle electrical changes generated by nerve impulses of other organisms, which propagate efficiently through water. Such is the sensitivity of this system that just the heartbeat of a fish hiding six inches under the sand may be enough to betray its presence to a hungry shark or catfish.

Some bony fishes actively produce their own electrical charges. You have no doubt heard of electric eels. These South American river dwellers can grow to seven feet and forty-five pounds. They are named for their elongated shape and are not true eels, belonging instead to the knifefish family, close relatives of the catfishes. They use low-voltage discharges to help them navigate in their murky habitats by detecting the electric fields that bounce off solid objects. But they are better known for producing stunning electrical discharges up to 600 volts or more. The electric organs are housed in stacked cells within the tail musculature. As in the stacked cells of a battery, electricity can be stockpiled until needed, then, if the eel so chooses, released all at once. This built-in Taser gun can be used to stun or kill prey, or to repel unwelcome intruders.*

The voltage power of electrical discharges of electric eels and some other fishes, such as torpedo rays, have earned them the term *strongly* electric fishes. But for me the most interesting use of electricity is reserved for certain *weakly* electric fishes, who use it for the less violent purpose of communicating with others of their kind. Most of these fishes belong to two groups: the diverse elephantfishes of Africa—so-named for their elongated, downward-pointing noses—and the knifefishes of South America, named for their pale coloration and knifelike shape. Like so many fishes with stealth technologies, they inhabit muddy waters, which likely provided the adaptive basis for a novel nonvisual means of communication. They communicate with high-speed electric organ discharges (EODs) of up to 1,000 pulses per second, or 1 kilohertz (kHz), more than twice as fast as an electric eel's pulse rate.

They are adept at interpreting these signals, as illustrated by a species of elephantfish that lives in river and coastal basins of western and central Africa. When the biologists Stephan Paintner and Bernd Kramer from the Institute for Zoology at Regensburg University, Germany, presented them with simulated EODs, the fishes showed an "astounding" ability to discern pulse time differences down to a millionth of a second. This rivals echolocation by bats as the fastest form of communication in the animal kingdom.

By varying the rate, duration, amplitude, and frequency of their EODs, elephantfishes can exchange information about species, sex, size, age, location, distance, and sexual inclination. EODs also communicate social status and emotion, including aggression, submission, and mate attraction, for which signals are crafted into courtship "songs" to serenade potential mates using exotic patterns of chirps, rasps, or creaks. (When you communicate your desire with electricity, being "turned on" takes on added meaning.) They can identify other individuals by their EOD signatures, which are distinct and remain stable over time. Dominant individuals may chase trespassers off their territories when they detect the trespasser's EOD, which probably explains why fishes often deferentially turn off their EOD when swimming through a neighbor's territory. Pairs or groups of fishes also coordinate their EODs, producing "echoes" and "duets." Males will alternate EOD pulses with other males, whereas females will synchronize theirs with investigating males.

It could get confusing when a cluster of elephantfishes or knifefishes are chirping away in close proximity. They deal with it using a so-called jamming avoidance response: if two fishes' discharge frequencies are too similar and might interfere with discrimination, they adjust to enlarge the distinction. Fishes in a social group maintain a 10 to 15 Hz difference from neighbors, ensuring that each individual has a personalized discharge frequency.

Recordings of EOD-producing elephantfishes in the upper Zambezi River suggest that they also use their signals to cooperate. EODs produced by fishes threatened by a lurking predator induce neighbors to join in on what may be an early-warning alert. It benefits all fishes in the neighborhood if predators have low hunting success there. Signals exchanged by familiar neighbors can provide assurances that all is well, thereby avoiding the need for costly defense of territory. Such "dear enemies" also team up as shoaling partners when food gets scarce.

If all this sounds too sophisticated for a fish, it may be time to reassess your perceptions of fish intelligence. Consider also that the elephantfishes have the largest brain cerebellum of any fish, and that their brain-to-body-weight ratio—a highly touted marker of intelligence—is about the same as ours. Much of that gray matter is devoted to electroreception and communication.

There is a cost to using electricity to communicate. Electroreceptive predators could be tuning in. Such is the case with sharptooth catfishes, who hunt in packs during spectacular yearly migration runs up the Okavango River in southern Africa. Most of their diet during this time is a species of elephantfish called the bulldog. They locate the hapless bulldogs by eavesdropping on the bulldogs' EODs. But there's a further twist. Captive studies have found that the EODs of female bulldogs are too short for the catfishes to detect, whereas the males' EODs are ten times longer, and the catfishes can easily notice them. The size distribution of bulldogs found in catfish stomachs indicates that it is the males who are mostly being eaten. In the evolutionary arms race of avoiding being someone else's meal, we may expect male bulldogs to be shortening their EODs.

The Pleasure of Touch

While lateral lines and electric organ discharges are alien to our sensory systems, the sense of touch certainly is not. In exploring this familiar sensation in fishes, I want to connect it to another kind of sensation that we often derive from touch, and one that we rarely consider as being part of the lives of fishes. I am referring to the sense of pleasure.

In his iconic poem "Fish," D. H. Lawrence wrote:

> They drive in shoals.
>
> But soundless, and out of contact.
>
> They exchange no word, no spasm, not even anger.
>
> Not one touch.
>
> Many suspended together, forever apart.
>
> Each one alone with the waters, upon one wave with the rest.

I love these lines, and I can see what Lawrence means: to my airborne senses there is something lonely about fishes being forever suspended in their heavier, viscous medium.

But writing in the early 1920s, Lawrence didn't have the benefit of knowing what we know today about the lives of fishes. Fishes are not alone. They know each other as individuals and they have preferences for who they hang out with. They communicate through diverse sensory channels. They have sex lives. Contrary to the notion of their being separate, it turns out that fishes are highly sensitive to touch, and tactile communication enriches the lives of many.

While researching this book I was sent a video clip by a puzzled viewer who couldn't understand why a fish—in this case a bright-orange Midas cichlid who looks for all the world like a friendly character from *Finding Nemo*—would return repeatedly to be stroked, picked up, and playfully tossed back into the water by a man.

What would motivate a fish to do this?

The answer, I believe, is that it feels good. Fishes often touch one another in pleasurable contexts. Many court with rubbing or gentle nips. Cleanerfishes curry favor with their valued clients by caressing them with their fins as a means to strengthen the cleaner-client relationship. Moray eels and groupers approach familiar divers and receive strokes and chin rubs.

In an informal survey of public perceptions of fishes, I received unsolicited accounts from eight of a thousand random respondents who described behavior like that of the Midas cichlid we just met. These fishes would allow their humans to pet, touch, hold, and stroke them. The author Cathy Unruh later wrote to me about a Bahamian grouper she calls Larry. Whenever Cathy and other divers descend to his reef, Larry swims over to be petted. According to Cathy, Larry seems to enjoy making eye contact, and checking out the divers' bubbles. He even rolls side to side to be petted properly, as a dog or a pig will do. Today one can find videos of fishes cavorting and in some cases appearing to snuggle with divers, who stroke their bodies gently as if they were the family cat. There are also growing numbers of videos of aquarium fishes swimming repeatedly into the hand of a trusted owner to be lovingly stroked.

The other major group of fishes—sharks, rays, and skates—also show pleasurable responses to touch. The diver Sean Payne described an encounter he had with a juvenile manta ray off the Florida coast. The ray swam up to Payne and rubbed repeatedly against him, leading him in a circular tango that forced her body into his hands:

"As I ran my hands over her skin, her wing tips vibrated like a dog's leg during a particularly good belly scratch," said Payne.

Andrea Marshall, the founder of the Marine Megafauna Association, describes manta rays as strongly curious and interactive with humans. These massive elasmobranchs, who have the largest brains of all fishes, love getting bubble massages from Marshall. She swims beneath them and blows bubbles from her SCUBA regulator. If she stops, the rays swim away, but soon return for more. It's a similar story at the Shedd Aquarium in

Chicago, where two of the five zebra sharks in a 400,000-gallon tank like to swim among the staff divers. “I think they like the feel of the bubbles coming out of our regulators,” says Lise Watson, Wild Reef collection manager. “During our maintenance dives, if we put our regulators underneath them, they dance around while the bubbles tickle their bellies.”

Besides touch, there are many other ways that fishes may derive pleasure. Food, play, and sex spring to mind. And then there’s comfort for its own sake. Southern bluefin tunas in the waters of Australia spend hours rolling on their sides, catching the sun’s rays. It’s not known for sure why they do this. One possibility is that they are sunbathing to raise their body temperature, which in turn helps them swim and react faster, making them more efficient hunters. I expect the warmth of the sun also feels good to a tuna, for pleasure evolved to reward useful behaviors.

Ocean sunfishes are named for their fondness for sunbathing while lying on their sides just beneath the surface. These huge fishes are also parasite hotels, harboring as many as forty different species of external parasites, including large copepods that can reach six inches. The sunfishes queue beneath floating kelp beds, waiting their turn to be serviced by cleanerfishes there. The sunfish at the front floats onto its side to signal readiness.

But some of the parasites are too large to be removed by fishes, and this is when the sunfish turns to a specialist. Floating up to the surface, the giant fish invites gulls to surgically remove penetrating skin parasites with their powerful beaks. Sunfishes have been seen courting the birds, following them around and swimming sideways next to them.

Dare we think the sunfish knows the feeling of relief from a skin irritation, and understands the cause-and-effect of bird and parasite? It is the best-fit explanation I can think of for a wise old creature who may live a century and wander thousands of square miles of open ocean.

To know pleasure is to know pain. Or so it would seem. Yet, despite steady advances in our understanding of the full-bodied lives of fishes, the question of their capacity to feel pain remains a subject of debate. Should it? Let’s find out.