What a Fish Hears, Smells, and Tastes

> The universe is full of magical things,
> patiently waiting for our wits to grow sharper.
>
> —Eden Phillpotts

Just as water influences the dynamics of vision, so it does for hearing, smell, and taste. Water is a superb conductor of sound waves, where they are almost five times longer than in air, as sounds travel five times faster in water. Fishes have benefited from this since the dawn of bones and fins, using sound for both orientation and communication. Water is also an excellent medium for diffusing water-soluble chemical compounds, and is well suited for the perception of smells and tastes. Fishes have separate organs for smelling and tasting, although the distinction is blurred because all substances are encountered in a water solution.

As they did color vision, fishes probably invented hearing. Despite the common assumption that fishes are silent, they actually have more ways of producing sounds than any other group of vertebrate animals. None of these methods involve the main method of all the other vertebrates: the vibration of air against membranes. Fishes can rapidly contract a pair of vocal muscles to vibrate their swim bladder, which also serves as a sound amplifier. They have the options of grating their teeth in their jaws, grinding additional sets of teeth lining their throat, rubbing bones together, stridulating their gill covers, and even—as we'll see—expelling bubbles from their anuses. Some land-dwelling vertebrates get creative in producing nonvocal sounds, such as the drumming of woodpeckers and the chest pounding of gorillas, but fishes' terrestrial cousins possess just two types of vocal apparatus—the syrinx of birds and the larynx of all the rest.

With their versatile acoustic portfolio, fishes produce a veritable symphony of sounds, especially in the percussion section. Among the descriptors we have assigned to them are hums, whistles, thumps, stridulations, creaks, grunts, pops, croaks, pulses, drums, knocks, purrs, brrrs, clicks, moans, chirps, buzzes, growls, and snaps. So notable are the sounds of some fishes that we have named the fishes accordingly: grunts, drums, trumpeters, croakers, sea robins, and grunters. Having ears evolved for processing vibrations in air and not water, we were until recently deaf to most of the sounds fishes were making. It was only in the past century, as underwater sound-detecting technology improved, that the list of acoustic fishes began to grow.

And yet, as recently as the 1930s, scientists believed that fishes were deaf. This prejudice probably arose from the fact that fishes lack an external hearing organ. With our human-centric view of the world, such a lack could only mean one thing: no hearing. Now we know better: fishes don't need ears, thanks to water's incompressibility, which is why water is an excellent conductor of sounds. It is not until we peer inside a fish that we find structures modified and recruited for producing and processing sounds.

Karl von Frisch (1886–1982), the Austrian biologist famous for his discovery of the dance language of honeybees, was also a devoted student of fish behavior and perceptions. Decades before he became the corecipient of the Nobel Prize in 1973 for his contributions to the emergence of ethology (the science of animal behavior), von Frisch was the first to demonstrate hearing in fishes. In the mid-1930s, he devised a simple but ingenious study in his lab with a blind catfish named Xaverl. He did this by lowering a piece of meat on the end of a stick into the water near the clay shelter in which Xaverl spent most of his days. Having an excellent sense of smell, Xaverl would soon emerge from his hiding place to retrieve food. After a few days of this routine, von Frisch began to whistle just before delivering the food. Six days later, he was able to lure Xaverl from his lair just by whistling, thereby proving the fish could hear him. This experiment, and others that followed, were critical to advancing our appreciation for the fish's umwelt.*

Xaverl belongs to an evolutionarily successful group called the Otophysi, which number about 8,000 species (including carps, minnows, tetras, electric eels, and knifefishes). They have evolved a specialized hearing apparatus called the Weberian ossicles, named for its discoverer, the nineteenth-century German physician Ernst Heinrich Weber. The ossicles are a series of small bones derived from the first four of a fish's vertebrae behind the skull. These bones have become separated from their parent bones, forming a chain linking the gas-filled swim bladder with fluid-filled spaces surrounding the inner ear. The apparatus aids hearing by acting as a conductor and amplifier of sound waves, in a manner similar to the middle ear ossicles of mammals.

There are ways in which fish hearing surpasses our own. Most fishes hear in the range of 50 hertz (Hz) to 3,000 Hz, which is within our own range of 20 Hz to 20,000 Hz. But careful studies in captive and wild settings have now documented sensitivity to ultrasounds in the upper range of bat hearing: up to 180,000 Hz in American shad and Gulf menhaden. That is well above the upper human limit. It is believed to be an adaptation for eavesdropping on the ultrasonic sounds produced by dolphins, who prey on these fishes.

At the other end of the hearing spectrum, fishes such as cods, perches, and plaices are responsive to infrasounds as low as 1 Hz. Nobody knows for sure why these fishes have evolved the ability to tune in to super-low sound, but the vast aquatic environments they live in provide clues. Water does not move randomly in oceans and large lakes. Global climate patterns generate currents, local weather patterns produce waves, and our moon's gravitational pull drives the constant heave-ho of ocean tides. Moving water also bumps up against cliffs, beaches, islands, reefs, coastal shelves, and other submerged barriers. All of these forces combine to create ambient infrasound. Biologists from the University of Oslo, Norway, think that fishes use this acoustic information for orientation during migrations. Think of it as a fish's equivalent of birds' use of celestial cues. Pelagic (open ocean) fishes may also detect changes in the surface wave patterns caused by distant land formations and different water depths. Sensitivity to infrasound has also been reported in some cephalopods (octopuses, squids, and others) and crustaceans—further evidence of its utility.

Fishes' hearing sensitivity makes them vulnerable to human-generated underwater noise. For instance, the delicate hair cells lining the inner hearing apparatus become severely damaged by high-intensity, low-frequency sounds produced by air guns used in marine petroleum exploration. Intense noise produced by seismic air-gun prospecting off the coast of Norway decreased the abundance and catch rates of cods and haddocks in the adjacent area.

Some fishes can also detect rapid pulses of sound, discerning as individual beats what we hear only as a constant whistle. And they are proficient at sound directionality, distinguishing sounds from directly ahead versus directly behind, and from directly above versus directly below—perceptual tasks that our brains are less able to manage.

That said, 99 percent of airborne sound energy is reflected off the water surface, so fishes—even if they're congregating close to the shore—are not likely to hear, say, a group of humans talking on a beach. However, airborne sounds transmitted through a solid object, such as an oar bumping against the side of a boat, are easily detected by fishes. This is why anglers sitting in a boat learn to be quiet, and why experienced shore fishermen wander a few yards inland before moving to a new spot; they know that the fish they're after may detect vibrations transmitted through the ground.

With ingenuity, we can hear *them*, too. Fishermen along the Atlantic coast of Ghana use a special paddle as a sort of tuning fork. By placing his ear against a paddle immersed in the water, an experienced practitioner can hear the grunts and whines of nearby fishes, and by rotating the flat plane of the paddle he can locate their whereabouts. A fish's keen hearing may also work in the angler's favor, for many fishes may not realize that the worm they hear up ahead is, unfortunately for them, wriggling on a hook.

Whereas migration and predator avoidance are useful functions for fishes' listening, most sound production has a social function. Here's an example from piranhas. When the biologists Eric Parmentier from the University of Liège, Belgium, and Sandie Millot from the University of Algarve, Portugal, placed hydrophones in a tank holding captive red-bellied piranhas, they recorded a variety of sounds, three of which are common enough to have been ascribed possible functions. One, a repetitive grunt or bark, appears to signal a challenge to others. Another, a low thud, is usually made by the largest fish in the group during aggressive behavior and fighting. These two sounds are produced by a fast-twitching muscle next to the swim bladder that contracts 100 to 200 times per second. A third sound occurs when a piranha grinds or rapidly snaps her teeth while chasing another fish. These descriptors hint at a mean-spirited animal, befitting the piranha's pugnacious reputation as a savage devourer of living victims. In fact, piranhas are mostly scavengers, and pose little danger to humans.

Given that fishes use sounds to communicate with one another, might they also use sound to communicate with us? I know of no scientific study to test this, but there are many anecdotes. Karen Cheng, a computer scientist from the Washington, D.C., area, has four rescued goldfishes in a twenty-gallon tank who, she claims, communicate with her at mealtimes. Around feeding time, when Karen or her husband is in the room but not paying attention to them, their goldfishes rise to the surface and make loud smacking sounds with their mouths. They will also hurl their bodies and bang their tails against the aquarium wall, apparently to get their humans' attention. The sounds produced can be heard from the other side of the room. They stop doing it when someone approaches the tank: "They seem aware of us," says Karen. "Whenever we come up to the tank they abort their activities and swim over to the glass. They don't ignore you like the aquarium fish at the doctor's waiting room."

Sarah Kindrick, a clinical protocol administrator with the National Institutes of Health, saw similar behavior in an eight-inch pinktail triggerfish who lived with her for about three years. Furchbar, as she named him, would take a pebble in his mouth and rap it on the glass wall of his tank around the time she would normally feed him. This is not just an example of interspecies communication by a fish, it is tool use (we'll see more on tool use soon).

Concerto in D Major for Fish

A further testament to fishes' acute hearing is their ability to discriminate tonal patterns of sound—specifically, music. Ava Chase, a research scientist at Harvard University, was interested to see if fishes could learn to categorize sounds as complex as music. She conducted an experiment using three pet store–bought koi named Beauty, Oro, and Pepi. Chase set up a sophisticated apparatus in the fishes' tank that included a speaker at the side for presenting sounds, a response button on the bottom that fishes could push with their bodies, a light that signaled to the fish that his response had been recorded, and a nipple near the surface that dispensed a food pellet when the fish swam up and sucked it after a "correct" response. She then trained the fishes by rewarding them (with a food pellet) when they responded to a certain genre of music and not rewarding them for responding while another genre emanated from the speaker. She found that the koi were not only able to discriminate blues recordings (John Lee Hooker guitar and vocals) from classical recordings (Bach oboe concertos), but that they could generalize these distinctions when presented with new artists and composers for each genre. For example, once familiar with the blues of Muddy Waters, the koi recognized its commonality with blues artist Koko Taylor, as they did for the classical music of Beethoven with that of Schubert. One of the three fishes, Oro, had an especially good ear, able to discriminate melodies in which timbre cues had been removed; that is, all the notes had the same quality except their pitch and timing.* Chase concludes: "It appears that [koi] can discriminate polyphonic music [playing multiple notes simultaneously], discriminate melodic patterns, and even classify music by artistic genre."

Despite their skill as music connoisseurs, neither koi nor goldfishes were known by scientists to communicate using sounds. (Let Karen Cheng's observations serve as preliminary evidence to the contrary.) So it remains a mystery why a mute fish would have such discerning acoustic skills, though as we saw earlier there are benefits to being able to tune in to ambient sounds in one's environment.

Being able to discriminate subtle (and not so subtle) qualities in music is one thing, but it makes me wonder: What psychological effect might it have on a fish? Do fishes appreciate music, or is it just a neutral stimulus?

A research team from the Agricultural University of Athens decided to investigate. They divided 240 common carps among twelve rectangular tanks and randomly assigned them to three different treatments: no music (the control group, for comparisons with the music groups), Mozart's "Romanze: Andante" from *Eine Kleine Nachtmusik*, and the anonymous nineteenth-century "Romanza: Jeux Interdits," a name it got from its use in the 1952 French film *Forbidden Games*. The track duration for these pieces was 6:43 and 2:50, respectively, and the assigned fishes were exposed to four hours of it a day for 106 days. Music exposure was done on weekdays only; like office workers, the fishes got the weekends off (probably because the scientists did).

Fishes in both music groups grew faster than the control group. Feeding efficiency (growth per unit of food), growth rates, and weight gains were higher with either of the two romantic music recordings than without, and intestinal function appeared to be improved. When these fishes were presented with noise or with nonmusical human sounds, the research team found no such changes.

It is a central challenge of animal studies that the subjects cannot report to you in plain language (that we understand) how they are feeling. With these data we can only speculate that carps are responding positively, or negatively, to the music. For instance, a skeptic might suggest that the fishes grew stronger from trying to *escape* the incessant sound of violins and oboes. I must say that, much as I enjoy classical music, hearing the same track over and over is not my idea of acoustic heaven.

We should also consider the possibility that the fishes' growth was no reflection of any subjective experience, but a mechanical response to a physical stimulus. An earlier study by the same Greek scientists noted favorable responses (raised appetites and digestive function) in response to Mozart (the only composer used) by gilthead sea bream, a species with very limited, lo-fi hearing. We also should be wary of anthropomorphism, for there may be little basis for assuming that what we perceive as pleasant music is perceived that way by a fish. Perhaps they prefer *any* sound to none at all. On that score, a better control than silence would be a recording of nonmusical sounds.

There are studies dating back a century that find human patients reporting improved relaxation and reduced pain when exposed to music that they enjoy. A 2015 review of 70 clinical trials involving more than 7,000 patients concluded that music was an effective therapy before, after, and even during surgery, and that it reduces patient anxiety and the need for painkillers. My point here is that music—or more generally, patterned, tonal sounds—may tap deeply into our biology with therapeutic results. The implication is that music appreciation might be widespread in nature.

When I asked one of the authors of the Greek studies, the biologist Nafsika Karakatsouli, she expressed uncertainty that carps enjoy music: "I am not at all convinced that music may have substantial positive effects for fish. There is no music underwater! However, there are plenty of other natural sounds, more relevant to fish living underwater, that may have some meaning to fish and may have produced better results. Nonetheless, some of the fish species we examined, especially carp (a species with excellent hearing abilities), did perform better when music was transmitted." Karakatsouli agrees that a better approach would be to see if carps would choose by themselves an environment with music or not.

There isn't anything musical about the sounds that herrings make, but their innovative method might warrant a fish Grammy Award. One paper describes the first example of what might loosely be termed *flatulent communication*. Both Pacific and Atlantic herrings break wind by releasing gas bubbles from the anal duct region, producing distinctive bursts of pulses, or what the research team playfully named Fast Repetitive Ticks (FRTs). A bout of FRTs can last up to seven seconds. Try that at home! The gas probably originates in the gut or the swim bladder. It isn't clear how these sounds function in herring society, but since per capita rates of sound production are higher in denser schools of herrings, a social function is suspected. So far there is no evidence that herrings ever beg your pardon.

I couldn't think of a better segue from fishes' sense of hearing to their sense of smell than herring FRTs. So let us have a sniff at their smell and taste.

A Good (Sense of) Smell

You may think that a dead fish smells bad, but living fishes have a good sense of smell. They use chemical cues (we'll just call them "smells") for finding food, finding mates, identifying danger, and homing. Smells are especially useful in aquatic environments, where murky conditions make vision unreliable. Some fishes can recognize others of their own kind by scent alone. Sticklebacks, for example, use smell to identify mates of their own species, where proximity to another stickleback species might otherwise present the risk of mating with the wrong kind.

The sophistication of the smelling organs of fishes varies greatly, but the basic design is shared among all the bony fishes (the 30,000 or so fish species that are separate from the sharks and rays group). Unlike those of other vertebrates, fishes' nostrils do not do double duty as organs of smell and openings for breathing; they are used exclusively for smell. Each nostril is populated by layers of specialized cells composing the olfactory epithelium, which is folded upon itself to save space, forming a rosette. Some fishes expand and contract their nostrils, and thousands of tiny cilia pulse in sequence to propel water into and out of the sense organ. Signals from the epithelium are sent to the olfactory bulb at the front of the brain.

Smell is an extremely useful sense for some fishes, as evidenced by their legendary sensitivity. A sockeye salmon can sense shrimp extract at concentrations of one part to a hundred million parts water, which translates in human terms to five teaspoons in an Olympic-size swimming pool. Other salmon can detect the smell of a seal or sea lion diluted to one eighty billionth of water volume, which is about two-thirds of a drop in the same pool. A shark's sense of smell is about 10,000 times better than ours. But the champion sniffer among all fishes (as far as we know) is the American eel, which can detect the equivalent of less than one ten millionth of a drop of their home water in the Olympic pool. Like salmons, eels make long migrations back to specific spawning sites, and they follow a subtle gradient of scent to get there.

One of fishes' most useful adaptations is the production of an "alarm chemical" in the presence of danger, such as a predatory fish or a spearfisherman. Once again, we owe it to Karl von Frisch for discovering yet another phenomenon in the world of fish senses. When he accidentally injured one of his captive minnows, von Frisch noticed that other fishes in the tank began darting back and forth and freezing in place—classic predator-evading behavior. Experiments by von Frisch and others showed that injured minnows (among other fish species) release a pheromone—a secreted or excreted chemical factor that triggers a social response in members of the same species. Detecting this particular pheromone causes agitated reactions by the minnows. Von Frisch coined the term *schreckstoff* (which translates literally to "scary stuff") for these pheromones.

The cells that release schreckstoff are located in the skin, and are fragile enough that they will rupture and release the substance if a fish is placed on moist paper. And it is potent stuff: a thousandth of a milligram of chopped skin is enough to elicit a fright reaction from another fish in a 3.7-gallon aquarium. That's like chopping a marshmallow into 20 million pieces, dropping one piece (if you can still see it) into a sink full of water, then trying to taste the sweetness. Schreckstoff must have evolved long ago, for it is produced by several families of bony fishes.

As a freely available signal, schreckstoff acts like a fire alarm that can be used by other nearby fishes, including different species that may also recognize it. Case in point: fathead minnows. When they smell the poop of northern pikes who have fed on other fathead minnows or on brook sticklebacks—both of which produce schreckstoff in their skin—they immediately flee to hiding places or form tighter shoals. But if the pikes have been fed only on swordtail fishes—which do not produce schreckstoff—the minnows show no signs of fear. Thus, it is not the smell of the pike that the minnows are reacting to. Instead, they detect and react to the schreckstoff from the pike's victims. It is probably due to olfactory skills like the minnows' that pikes refrain from defecating in their own hunting grounds.

The schreckstoff reaction illustrates how fishes can extract subtle clues from waterborne chemicals. But schreckstoff is not the only way to detect a fish foe by fragrance. There is the old-fashioned way of simply recognizing the smell of the predator. Juvenile lemon sharks react to the odor of American crocodiles, who sometimes prey on them. If you are an Atlantic salmon, it depends on what your predator has been eating. In a study conducted at Swansea University in Wales, predator-naive juvenile salmons were presented with water containing traces of dung from one of their natural enemies, the Eurasian otter. The salmons only showed a fear response if the otter had been dining on salmon. In those cases they fled the smell, then remained still, and they breathed faster. Salmons exposed to blank water or to dung from otters on a non-salmon diet were unfazed. The scientists concluded that Atlantic salmons apparently do not innately recognize otters as a threat—they perceive them as a danger only if salmon is on the menu. This generalized mode of predator detection works well because it does not require learning the smell of different predators. Instead, one may just learn to recognize who has been eating one's own kind.

If avoiding predators has a rival in the survival game, one candidate is the quest for sex. Just as aromas have been found to play an important role in human sexual attraction, so, too, do sex pheromones get a fish's juices flowing. For one, they help fishes identify who else is in a mating mood.

Fishes have the ability to tease out subtle sex cues and use them for personal gain. Experiments from the 1950s showed that male frillfin gobies will start their courtship displays when a sample of water from a tank holding a sexually receptive female frillfin goby is added to their own tank. Later studies show that females are no less perceptive or active in the mating game. Female sheepshead swordtails from Mexico can discriminate the smell of well-fed males from hungry males of their species—two- to three-inch denizens of tropical rapids—and you can probably guess which they prefer: all else being equal, a well-nourished fish is a more resourceful one, which makes him the better sperm donor. Female swordtails do not discriminate the odor of well-fed females from hungry females, suggesting they are responding to male sex pheromones and not merely to food-based excretions.

So far, we've been examining fish sensory systems as separate units, but they need not work in isolation. Male deep-sea anglerfishes illustrate the interplay of senses. They have the largest nostrils relative to head size of any animal on Earth, according to Ted Pietsch, the world's go-to guy on anglerfishes. His book *Oceanic Anglerfishes* is an astonishingly detailed and lavishly illustrated source for everything currently known about these bizarre fishes.

The male anglerfish's nostrils are not his only well-developed senses; his eyes are also well put together, and Pietsch believes the two senses, smell and vision, function in tandem to help males find females in the dark abyss. A female releases a species-specific pheromone, and a male's fine sense of smell helps guide him toward her species-appropriate perfume. This is important because there are at least 162 known species of anglerfishes cruising about in the world's largest habitat, and you don't want to mate with the wrong one. When he gets close enough to the female, the male angler can confirm that she is his type by the signature of light she emits with the aid of glowing bacteria living in her filamentous lure. One can almost imagine a time in the deep past when the god of deep-sea anglerfishes proclaimed, "Let there be light!" and a lot of the guesswork was taken out of finding a mate.

One last note on the olfactory behavior of fishes: it has been widely assumed by the conservative-leaning scientific establishment that fishes' release of chemicals for communication is passive and not consciously controlled, since they lack external scent glands or scent-marking behavior. That's a shaky presumption. Consider a 2011 study of our friends the sheepshead swordtails. In their fast-flowing habitats, males use at least two tactics to make females aware of their pheromones: (1) they urinate more often when they have an audience of females, and (2) when courting they situate themselves just upstream of females.

For better or worse, that implies that in addition to being able to smell a male's sexual readiness, female sheepshead swordtails can also taste it. What else might a fish be tasting?

Tasteful Fishes

For fishes, the sense of taste is used mainly for food recognition. As for all the other main vertebrate groups—amphibians, reptiles, birds, and mammals—the primary organs of taste are taste buds. Fishes also display a range of teeth types, eight in all, including incisors for snipping, canines for stabbing, molars for grinding, flattened triangular teeth for slicing, and teeth fused into beaks for scraping algae off corals.

Like us, fishes have tongues, and gustatory receptors connected to specialized nerves that relay taste signals to the brain. Not surprisingly, most of a fish's taste buds are located in the mouth and throat. But because fishes are quite literally immersed in the medium they smell and taste, many also have taste buds on other parts of their bodies, most often the lips and snout. Taste buds are also more numerous in fishes than in any other animal. For instance, a fifteen-inch channel catfish had approximately 680,000 taste buds on his entire body, including fins—nearly 100 times the human quota. These and other fishes of murky waters taste their way around their environments. (Try as I might, I cannot imagine what it would feel like if my entire body could function as a tongue, but I'm quite sure I would want it to include an "off" switch.) Cavefishes also benefit from a bonanza of taste buds, which provide a high-definition flavor sensing system to aid food finding in the darkness. Many bottom-feeders, including catfishes, sturgeons, and carps, are equipped with barbels, whiskerlike feelers usually located around the mouth, which serve as taste sensors.

In case you're wondering why fishes would need a sense of taste—well, they need it for the same reasons we do. Fishes have food preferences that may be distinctive to species and even individuals. It can take a fish a while to ascertain the palatability of a food item; if you've watched fishes in aquariums you might have seen how they will sometimes take a morsel into their mouth, spit it out, then re-ingest it several times before either swallowing or rejecting it. Overall taste preferences within a fish species, and within different populations of the same species, generally do not vary much, as is the case for human ethnic groups. The same does not hold true of individual preferences. In our case, think Brussels sprouts, spicy versus mild, and the dizzying array of present-day variations on a cup of coffee. Studies of rainbow trouts and carps find that finicky eaters are not rare.

Fishes' reactions to unpleasant tastes are reminiscent of our own. Just as we will quickly eject a mouthful (as gracefully as possible if in public) when we bite into a surprisingly rotten piece of fruit or meat, a Dover sole expresses her distaste for a food item by violently turning and rapidly swimming away from it, shaking or nodding her head. Stéphan Reebs, the author of *Fish Behavior in the Aquarium and in the Wild*, describes a fish's reaction to the taste of toad tadpoles—a toxic and particularly foul-tasting item in its environment: "It must be said that a very hungry bass, its back to the wall, will stoop to eat toad tadpoles. But if the reaction of other fishes that mistakenly take tadpoles in their mouth is anything to go by—they violently shake their head and you can almost see the grimace on their face—having tadpoles on the menu is no great culinary experience for a fish."

Living in a relatively dense aqueous medium imposes some limitations, but it also provides fishes with sensory opportunities unavailable to land-dwelling beasts. Can you imagine chatting with your neighbor using electric pulses? In the next part of the book, we'll get beyond the mainstream senses into some less familiar ways fishes use to perceive their environments.