PART II

WHAT A FISH PERCEIVES

There is no truth. There is only perception.

—Gustave Flaubert

What a Fish Sees

> … red-gold, water-precious, mirror-flat bright eye
>
> —from “Fish,” by D. H. Lawrence

We are taught that there are five senses: vision, smell, hearing, touch, and taste. In truth, this is a restricted list. Think how dull life would be if you did not have a sense of pleasure! And while the idea of life without pain is appealing, how dangerous would it be if you didn’t realize you were resting your hand on a burning hot stove? Without a sense of balance, we’d have no success walking, let alone bicycling. Without the ability to detect pressure, handling a knife and fork adeptly would become tasks requiring herculean feats of concentration. As we might expect for creatures who have had a lot of time to evolve, fishes have diverse, advanced modes of sensory perception.

One of my favorite concepts learned as a student of animal behavior is *umwelt*—a term created early in the twentieth century by the German biologist Jakob von Uexküll. You can think of an animal’s umwelt as its sensory world. Because their sensory apparatus varies, different species may have different perceptions of the world even if they inhabit the same environment.

For instance, owls, bats, and moths all fly in the nighttime, yet differences in their biology predict differences in the umwelt for each. Owls rely mainly on vision and hearing to catch their prey. Bats also depend on hearing but in a way that is quite different from the owl: they interpret echoes of their own high-pitched calls, hunting and navigating by echolocation. Moths, as invertebrates, may be the least relatable of the three from the perspective of our own umwelt, but we do know that they have good vision and that they can find mates over long distances with their superb perfume detectors. How a species' senses work goes some way toward understanding the mysteries of its felt experiences.

We can expect fishes' umwelts to differ from ours since they evolved in water and not air. But evolution is a conservative designer with a tendency to hang on to a neat idea. Case in point: fish eyes. Apart from their obvious lack of eyelids, fishes' eyes resemble our own. Like most vertebrate eyeballs, including humans', a fish's eyeballs are served by three pairs of muscles that swivel the eye on all axes, as well as a suspensory ligament and retractor muscles that help the fish focus on those bubbles dancing up from the aerator, or that upright creature staring intently from the other side of the glass. As the evolutionary forebears of land-dwelling animals, early fishes originated this system of seeing. It is not easy to spot the swiveling eye movements of most small fishes, but peer closely next time you visit an aquarium and you should be able to detect eye movements in the larger individuals as they shift their gaze to look at different parts of their surroundings.

With a spherical lens of high *refractive index*—defined as the ratio of the speed of light through a medium (in this case, the lens) to its speed through a vacuum—a fish can see as clearly underwater as we can see in air. Needless to say, fishes have neither lacrimal glands nor tear ducts, nor eyelids to moisten the eyes' delicate surface; they don't need them, since the eyeball is kept constantly clean and moist by the water they swim in.

Seahorses, blennies, gobies, and flounders have further upgraded their eye musculature to allow each eye to rotate independently, as in chameleon lizards. I can only conclude from this that a creature thus endowed is able to process two visual fields at a time. That seems just so radically different from what human brains do, and when I try to imagine the mental experience of two independent visual fields, each under my conscious control, it exceeds my umwelt no less than trying to imagine a limit to the universe. Although a team of scientists from Israel and Italy have simulated the visual system of chameleons by building a "robotic head" with two independently moving cameras, I am not aware of any attempts to understand how a single brain processes them. Is a chameleon having two thoughts simultaneously as one eye focuses on a juicy grasshopper on the neighboring twig while the other eye searches the branches overhead for a better approach route? Can a seahorse ogle a potential mate with one eye while tracking the movements of a lurking predator with the other? My single-track brain can't. If I read the newspaper while the radio plays *This American Life*, my mind can toggle back and forth between the two, but try as I might I cannot stream both stories at the same instant.

I also have trouble getting my head around the visual experience of flounders, especially during their early childhood. Baby flounders look like any other normal fish, swimming upright with one eye on each side. Then, in preparation for adult life, they undergo a bizarre transformation: one eye migrates to the other side of the face. It's like facial reconstructive surgery, only in slow motion, and without scalpels and sutures. It isn't even always slow. The entire migration takes just five days if you're a starry flounder, and less than one day in some species. If a fish can have an awkward adolescence, this one qualifies.

In exchange for the indignity of having both eyes nestled next to each other on one flank, flounders have fabulous binocular vision. Like proud neighbors, the two eyes protrude from the body, and each can swivel independently. (Could it be that flounders are the only fishes able to startle themselves by looking themselves in the eye?) Binocular vision is a useful adaptation for a lifestyle of lying in wait on the sandy or stony bottom, exquisitely camouflaged against the substrate, watching for an opportunity to snatch an unsuspecting shrimp or other unfortunate passerby with a lightning-fast lunge. With refined depth perception, a flounder can better judge the timing and wisdom of her ambush.

Ocular migration has obviously proven an effective survival strategy for flounders and related flatfishes, of which there are more than 650 species, including soles, turbots, halibuts, sand dabs, plaices, and tonguefishes. Some species are referred to as "righteye flounders," always lying on their left side after their left eye migrates to the right side of the body. Others are lefteye flounders. Despite their fine adaptations, many Atlantic flounder and sole species are now threatened by overfishing.

The four-eyed fish—which inhabits fresh and brackish waters along the Atlantic coast of Central and South America—enhances its visual field in a different way. Nature's inventors of the bifocal lens, these relatives of the guppy sport a discrete demarcation between the upper and lower portion of their retina. The fish swims so that the demarcation aligns exactly with the plane of the water surface, the airborne portion of the eyes providing ideal air vision while the submerged portion accommodates the aquatic medium. Flexible genetic coding makes the upper eyes sensitive to green-light wavelengths that predominate in air, and the lower eyes more sensitive to the yellow wavelengths found in muddy waters. This is a valuable visual tool kit when you want to search for a tasty morsel below without being surprise-attacked by a hungry bird from above.

Most larger, faster, open-ocean predatory fishes, including swordfishes, tunas, and some sharks, rely on speed and keen vision to catch prey. The eyes of a twelve-foot swordfish can measure nearly four inches across. Yet hunting underwater presents a set of special visual challenges. If you've ever entered a cave without a flashlight, then you'll have a sense of what fishes experience as they dive deeper below the surface, where there is less light available to see with. There's another problem: water temperatures drop with greater depth, and cold retards brain and muscle function, delaying response times.

To surmount the sluggish effects of cold, some fishes have evolved an ingenious means of improving the functioning of their brains and eyes: they harness heat generated by their muscles, which powers their sensory organs to perform at higher capacity. Swordfishes can heat up their eyes twenty to thirty degrees Fahrenheit above the water temperature. The heat is generated by a countercurrent exchange between the incoming and outgoing blood vessels surrounding the eye muscles. Arteries bringing cold blood from the heart and veins are warmed by a special heat-generating organ in one of the eye muscles. These arteries form a tight, latticed network, enhancing the exchange of heat between them. Studies of eyes removed from recently caught swordfishes suggest that this warming strategy improves by more than tenfold the fish's ability to track rapid changes in prey movements.

Unlike swordfishes, many sharks prefer to hunt at nighttime, when light levels are exceedingly low. Supremely adapted to their realms, sharks' eyes have a layer of reflective cells called the *tapetum lucidum* (Latin: “bright tapestry”) next to the retina. Light hitting this layer bounces back through the shark’s eye, striking the retina twice and effectively doubling the shark’s night vision. This effect is what creates the familiar “eyeshine” of cats and other terrestrial night stalkers. If sharks walked on land, you would see them in the headlights at night by the eerie glow of their eyes.*

Avoiding predators is no less a priority than is catching prey. Be it in an ocean, lake, or stream, fishes use a variety of visual techniques to get the upper fin. For those living in the shallows, for example, the underside of the water surface acts as a mirror. This enables a fish to see the reflection of objects that are not in direct view. A bluegill—a saucer-size fish that lives in the shallows of North American lakes, ponds, and slow-moving streams—may be able to spy on a predatory pike lurking on the far side of a rock or thicket of pondweeds by gazing up at the surface reflection. What’s good for the goose is also good for the gander, and I’d expect that predators may also use this technique to spy on their prey. I believe this could be studied quite easily in a temporary captive setting.

The mirror technique that the bluegill uses only works in calm waters, and in such conditions fishes can also see quite well what is going on above the surface, allowing them to take evasive action when a diving bird approaches. The fact that wavy water impairs the ability to resolve objects above the surface might explain why seabirds hunt more often and catch more fishes in wavy than in calm waters. The refractive properties of calm water also enhance fishes’ ability to see objects on the shoreline. Fishermen armed with this knowledge sometimes stand farther away from the water’s edge to reduce the likelihood of detection by their quarry.

Color Badges and Flashlights

There are times, of course, when being detected is the goal. Coral reefs present diverse opportunities for visual innovation. Corals grow in tropical seas at shallow depths, where temperatures and light levels are high. Light does magical things with color, which accounts for the mesmerizing kaleidoscope displayed on the bodies of reef fishes. In fact, when scientists in 2014 discovered evidence of rods and cones in a fossilized sharklike creature that lived 300 million years ago, they concluded that color vision was invented underwater.

In the ages since, fishes have evolved visual capacities beyond our own. For example, most modern bony fishes are tetrachromatic, allowing them to see colors more vividly than we do. We are trichromatic creatures, which means we possess only three types of cone cells in our eyes and our color spectrum is more limited. Having four types of cone cells, fishes' eyes provide four independent channels for conveying color information. Some fishes also see light in the near ultraviolet (UV) spectrum, where light's electromagnetic wavelengths are shorter than what we can see in the so-called "visible spectrum." This helps explain why about one hundred known species from twenty-two families of reef fishes reflect large amounts of UV light from their skin. It all makes me wonder whether a fish gets more excited to see a diver whose wetsuit has blue and yellow racing stripes compared to one wearing a plain black wetsuit.

In 2010, scientists made a discovery that illustrates the value of having a wider visual spectrum than someone else has. Their work focused on visual communication in damselfishes—a colorful and diverse group of reef denizens. They studied two species—the ambon damselfish and the lemon damselfish—which inhabit the same reefs in the western Pacific, and which, to humans, look identical. Ambon damselfishes defend their territories most vigorously against members of their own species. But how do they know an intruder isn't merely a lemon damsel? The researchers had a hunch that vision was still somehow playing a role. It turns out each species has a different facial pattern visible only in the UV light spectrum. When researchers shone a UV light on them, the damsels' faces revealed attractive patterns of dots and arcs resembling a fingerprint, which differed between species in a subtle (to humans) but consistent way. Tested for their recognition skills in captivity, the fishes could reliably indicate correct choices by tapping a picture of their own species with their mouths in return for a food reward. When the researchers used UV filters to eliminate this visual information, the fishes started failing the tests. Furthermore, because the predators of damselfishes appear blind to UV light, the damselfish's face recognition system operates covertly without compromising the camouflage that helps them avoid being seen by their finned foes. It's like being the only one to know who's behind that alluring mask at the masquerade ball.

Fishes' bodies have a variety of ways of expressing themselves through color. In addition to species identification, the coloration of many fishes conveys information to their species-mates about gender, age, reproductive status, and mood. Pigmented cells in the skin contain carotenoids and other compounds that reflect warm colors: yellow, orange, and red. White coloration is not produced passively, by a lack of pigment, but actively, by light reflected from crystals of uric acid in *leucophores* (from the Ancient Greek: leukos = white) and guanine in *iridophores* (iridescent *chromatophores*). Greens, blues, and violets are mostly produced by structural patterns in a fish's skin and scales, and further varied by the thickness of these tissues. Think of a very colorful "clownfish" (such as the Disney character Nemo), whose coloration identifies him as a particular species of anemonefish, and signals a conspicuous warning to other fishes that it would not be a good idea to follow him into the stinging tentacles of his home anemone.

If wearing bright clothes is useful, being able to change them may be even better. By expanding or contracting their melanophores—clusters of cells containing black granules—fishes like cichlids and boxfishes are able to quickly turn darker or lighter in color. Some fishes, such as flounders and cornetfishes, have remarkable control over which cells expand or contract, while colorful coral-reef fishes in particular can usually control the intensity of their so-called "poster coloration." They can ramp up their beauty to lure a potential mate or intimidate the competition, or tone it down to mollify an aggressive competitor or go undetected by a predator.

I think of the flatfishes (the ones with the migrating eyes we visited earlier) as the champions of pigment manipulation. They use their skin to melt chameleonlike into the background. I remember flipping through a biology textbook when I was in high school and encountering a jaw-dropping photo of a flounder who had been placed on a checkerboard in his tank. Within minutes, the flatfish had produced a fine rendition of a checkerboard across his back. From a distance, the flounder effectively disappears. This ability to mimic backgrounds by changing the distribution of skin pigments is a complex and poorly understood process that involves vision and hormones. If one of the flounders' eyes is damaged or covered by sand, they have difficulty matching their colors to their surroundings, which hints at some level of conscious control by the flounder rather than a cellular-level mechanism.

Surrounded by friends and enemies, fishes face a compromise between being detected and not being detected. Near the surface in the Sunlight Zone, practically everything is visible. But light penetration in water decreases exponentially with depth. Being seen is a high priority for a fish, for 90 percent living in the Twilight Zone between 100 and 1,000 meters (0.6 miles) have light-emitting organs (*photophores*) that serve as beacons in the darkness. The proportion is even higher for fishes living in the Midnight Zone, the vast abyss at depths of 2,000 meters and beyond, where no light reaches. Fishes who live here include bristlemouths, lanternfishes, and the famous anglerfishes.

Down here, most of the light is produced by luminous bacteria that coexist with the fishes in an ancient symbiosis. In return for room and board, the light-producing bacteria provide a range of benefits to their hosts. Deep-sea anglerfishes are experts when it comes to light displays. They emit light from the fishing lure that protrudes from their head, and in some species also from a treelike structure suspended from the lower jaw. These glowing adornments enhance their attractiveness to potential prey who, drawn like moths to a candle, swim to their deaths in the jaws of these ambush predators. On the flip side, sudden bursts of light cast from the same structures can be used to startle would-be predators. Body lights can also provide camouflage by casting a faint glow across the fish's lower side, making her less visible against the dim light filtering down from above. And when fishes want to spend some time with companions, the distinctive light patterns produced by these organs can help in recognizing others of their own kind.

Ponyfishes have a peculiar method of luminescence. The *photophore*, or package of light-producing bacteria, carried by males around their throat is shone inward toward a specialized swim bladder (a gas-filled organ that helps control buoyancy) with a reflective coating. The light bounces off this coating and out through a transparent patch of skin. By controlling a muscular shutter in the body wall, the ponyfish creates a flashing display. Schools of males sometimes coordinate their flashing to create a dazzling show, which scientists believe is a strategy to get females into a mating mood.

Flashlight fishes—one of the few bioluminescent fishes generally not found in deep waters—take a more direct approach to illumination, using a multifunctional light consisting of a semicircular organ just below each eye. This pair of organs contains luminescent bacteria whose continuously emitted light can be turned on and off by the fish using a muscular lid. Like ponyfishes, flashlight fishes gather in nighttime shoals, where their combined light helps attract, as well as illuminate, zooplankton prey. These fishes also use the light to evade predators. When the danger approaches, the targeted fish keeps his light on until the last moment before switching off and changing direction. (That must take some nerve.) Mated pairs of flashlight fishes maintain territories over a reef, and if an intruding flashlight fish approaches, the female of the pair will swim up and flash her light literally in the interloper's face, as if to say: "Get lost!"

These deep-sea light shows happen in the blue-green spectrum, which is the color of most bioluminescence, probably because aquamarine light travels farthest through water. But there is one group of fishes that breaks the color rule: the loosejaws. Named for a capacious lower mandible whose flexible hinge allows an enormous gape, these fishes might as well have been called the stoplight fish (actually, one of them is), for the powerful beam of light they shine from a concentrated photophore beneath each eye is red. The color is achieved by a unique fluorescent protein in some species and by a simple gel-like filter over the photophores in others. Naturally, evolution has seen to it that loosejaws can see red, thanks to a small change in a gene responsible for eye pigment structure.

The advantage is huge: a flashlight beam that only the bearer can see. Thus endowed, these hunters of the abyss can spy on others without being seen. Whereas other deep-sea fishes use their lights intermittently, flickering and flashing lest they be discovered and eaten, loosejaws audaciously keep their lamps lit full-time, invisible to their predators and to the prey they stalk with impunity. It is the deep-sea answer to night-vision goggles.

Fooled You!

Clearly, fishes have a diverse and innovative visual repertoire. Their tools are used to enhance their seeing ability, to make themselves more or less visible, to declare their identities, to lure and repel, and to manipulate.

But how do fishes perceive what they themselves see? What is the mental experience of a fish, and how might it compare to our own?

One way of probing this question is by considering optical illusions. If an animal is unaffected by a visual image that fools us, then it would seem that that animal perceives visual fields in a mechanical way, as a robot might "perceive" them. If, however, they fall for the illusion as we do, it suggests that they have a similar mental experience of what they are seeing.

In *Alex & Me*, Irene Pepperberg's touching memoir of thirty years with an African Grey parrot, one of the many captivating findings reported is that these intelligent birds perceive optical illusions as we do: they are fooled by them. The implication, as Pepperberg remarks, is that parrots *literally see the world as we do*.

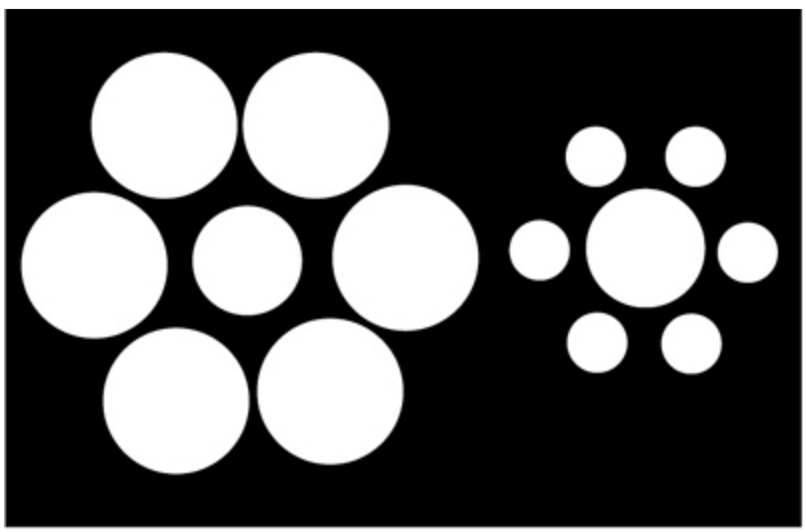

Figure 1: The Ebbinghaus illusion.

Are fishes fooled by optical illusions? Well, in a captive study of redtail splitfins—small fishes that originate from highland Mexican streams—they learned to tap the larger of two disks to get a food reward. Once they had mastered the task, the scientists presented them with the Ebbinghaus illusion, which consists of two disks of the same size, one of which is surrounded by larger disks, making it appear smaller (at least, to human eyes) than the other, which is surrounded by smaller disks (see Figure 1). The splitfins preferred the latter disk.

This result showed the scientists that redtail splitfins do not perceive things in a mindless, stimulus-response way. Rather, they form mental concepts—sometimes fallible ones—based on their perceptions. Similarly, an earlier study found that redtail splitfins also fall for the more familiar Müller-Lyer illusion, in which two identical horizontal lines appear to have different lengths (see Figure 2). Trained to choose a longer line, they chose the line labeled B.

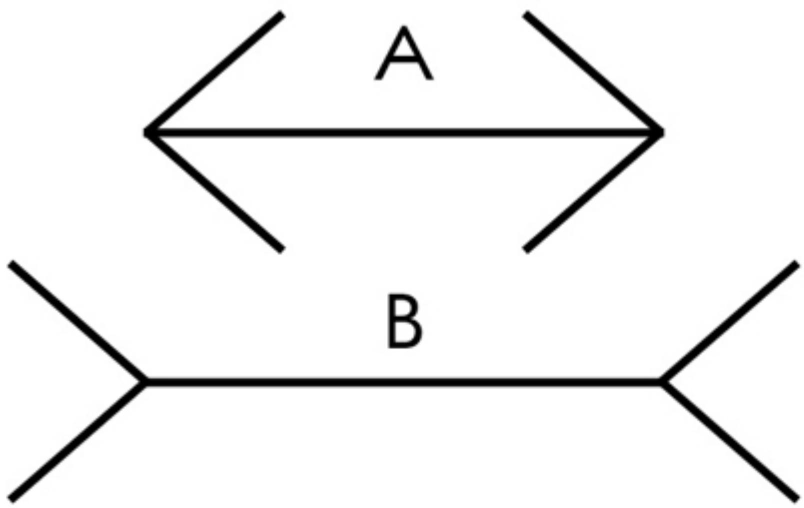

Figure 2: The Müller-Lyer illusion.

Studies of goldfishes and bamboo sharks show that they, too, respond to visual illusions. You can train goldfishes to discriminate black triangles from black squares on a white background. Then if you present them with a Kanizsa triangle or a Kanizsa square, they perceive a triangle and a square, respectively. Kanizsa illusions were developed in the 1950s by the Italian psychologist Gaetano Kanizsa. When humans regard these figures we see a white triangle (or a white square) that looks slightly brighter than the background, even though no triangle is actually drawn (see Figure 3). So what the goldfish brains are doing is the same as what ours do—completing an incomplete picture.

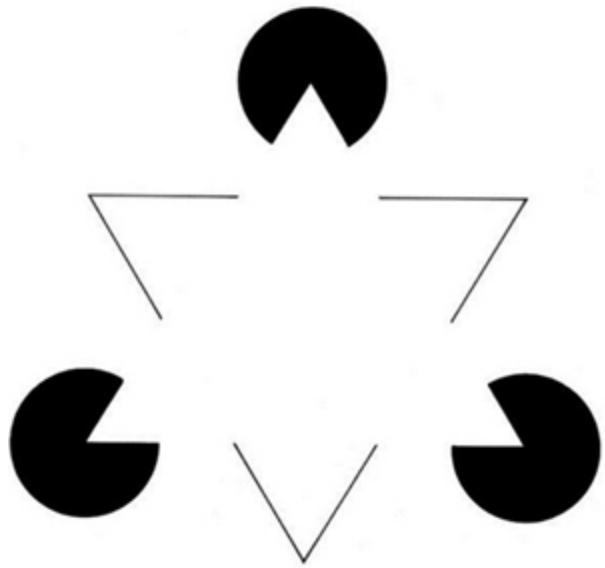

Figure 3: A Kanizsa triangle.

That splitfins, goldfishes, and bamboo sharks can complete an incomplete picture isn't meant to imply that they are unique among fishes in falling for optical illusions. They were simply the species chosen for these studies. Splitfins and goldfishes are only distantly related, so it seems likely that many other fishes would be fooled by optical illusions. These species are studied for the mundane reason that their care in captivity has been well worked out, so using them is a matter of convenience. It takes time and effort (and money) to conduct meticulous studies of animals. So, what we know about fishes is only a tiny slice of what *they* know.

In the survival game, fishes may exploit the visual perceptions of other fishes with illusions of their own. One way to do this is to deflect a predator's attack away from the important parts of one's body. For the fairly obvious reason that it is more likely to be lethal, predators usually direct an attack at the head end of their prey. That many aquatic predators tend to aim for the eyes is evidenced by the evolution of deceptive eyespots on many fishes. Examples of fishes who benefit from this deception include cichlids, butterflyfishes, angelfishes, pufferfishes, and bowfins. The deception may be enhanced in various ways. Like us, fishes are more likely to notice bright colors, so those deceptive eyespots tend toward conspicuous brilliance, while the real eye at the other end may be relatively obscure. The pattern of a young emperor angelfish doesn't include an eyespot, but a bull's-eye surrounded by concentric rings of alternating white and neon blue looks just as effective, while the real eye is obliterated by a maze of meandering lines. A predator rushing in for the kill won't have time to make fine assessments, and these color tricks might tip the scales in the prey's favor.

A further enhancement is having a tail end shaped to resemble a fish's head. The rear end of a comet fish is so arranged to resemble the face of a parrotfish, and the actual eye is virtually lost amid a constellation of white spots covering the entire body, including the eye itself. A behavioral manipulation can enhance these effects even further. Scientists have observed two species of butterflyfish who switch gears and swim slowly backward at the first sign of trouble, then suddenly lurch into forward overdrive if a predator darts in. If they move fast enough, the predator may be snapping at empty water. Otherwise, a butterflyfish is more likely to live on if the chunk of missing flesh came from the tail than if it came from the head.

I find it endearing that fishes perceive optical illusions as we do, and that they are tricked by the visual deceptions of their intended prey. It says something special about the perceptual world—the umwelt—of another being that her mind should construct something that isn't actually there. It suggests the capacity for belief. Beliefs and perceptions can be exploited, and as we've already seen (and will see ahead), fishes use a range of deceptions—visual and otherwise—to improve their chances at success.

As highly visual creatures, we may be able to relate to the importance of having the keen vision that most fishes have. From childhood games we know the disorientation of being blindfolded, and we look on with admiration at how well blind humans learn to cope with the challenges. It is doubtful that a blind fish would live long, even if he inhabits the Midnight Zone, where built-in lights rule supreme. But fishes are not solely dependent on seeing to make their livelihoods. Like us, they have evolved other senses to help them navigate life's demands.