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AN IMMENSE WORLD

How Animal Senses Reveal the Hidden Realms Around Us

ED YONG

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2.

Endless Ways of Seeing

Light

I AM STARING AT A JUMPING SPIDER, AND EVEN THOUGH ITS body is pointing away from me, it is staring back. Four pairs of eyes encircle its turret-like head, two pointing forward and two pointing sideways and backward. The spider has close to wraparound vision, and its only blind spot is immediately behind it. When I waggle my finger in its five o'clock, it sees my vibrating digit and turns around. As I move the finger, the spider follows. Jumping spiders "are the only spiders that will turn and look at you routinely," says Elizabeth Jakob, whose lab in Amherst, Massachusetts, I am currently visiting. "A lot of spiders spend a lot of time just sitting motionless on a web and waiting for something to happen. But these are active."

Humans are such a visual species that those of us with sight instinctively equate active eyes with an active intellect. In their flitting, darting movements, we see another curious mind investigating the world. In the case of jumping spiders, this is not unwarranted anthropomorphism. Despite their poppy-seed-sized brains, they really are surprisingly smart.* The *Portia* species are famed for planning out strategic

* I ask Jakob how much of a jumping spider's above-average intelligence (for a spider) is baked into its senses. Spiders that mostly sense vibrations along their webs don't have a huge amount of information to interpret, she says. "For the really visual spiders, the complexity of information they have to deal with is so much higher," she says. "I can't help but think it's valuable for them to be able to interpret it, and that seems like a good opening for evolution to

routes when stalking prey, or flexibly switching between sophisticated hunting tactics. The bold jumping spiders (*Phidippus audax*) that Jakob studies are less ingenious, but she still houses them in the company of stimulating objects—the kind of environmental enrichment that zookeepers might provide for captive mammals. Some have brightly colored sticks in their terraria. One individual, I note, has a red Lego brick. We joke about what it might build when our backs are turned.

Barely bigger than my smallest fingernail, the bold jumping spider is mostly black, except for white fuzz on its knees and vibrant turquoise splotches on the appendages that hold its fangs. It is unexpectedly cute. Its stocky body, short limbs, large head, and wide eyes are all rather childlike, and stir the same deep psychological bias that makes babies and puppies adorable. But its proportions didn't evolve to engender empathy. The short limbs power great leaps: Unlike other spiders that sit in ambush, jumping spiders stalk and pounce upon their prey. And unlike other spiders that mostly sense the world through vibrations and touch, jumping spiders rely on vision. That's why the eight eyes occupy up to half the volume of their large heads. They are the spiders whose Umwelten are closest to ours. In that similarity, I find affinity. I watch the spider, and it watches me back, two starkly different species connected by our dominant sense.

The late British neurobiologist Mike Land, described to me by one of his colleagues as "the god of eyes," pioneered the study of jumping spider vision. In 1968, he developed an ophthalmoscope for spiders, which he could use to observe the creatures' retinas as they, in turn, gazed at images. Jakob and her colleagues have refined Land's design; during my visit, they've placed a jumping spider in their device, which is currently trained upon the creature's central eyes. These point straight ahead and are the largest of the four pairs. They are also the sharpest. Despite being just a few millimeters long, they can see as clearly as the eyes of pigeons, elephants, or small dogs. Each eye is a

push them toward higher and higher cognitive skills. But I don't know. We have to factor in our own human bias toward being visual."

long tube, with a lens at the front and a retina at the back.[*] The lens is fixed in place, but the spider can look around by swiveling the rest of the tube inside its head. (Imagine gripping a flashlight by its head, and then aiming its beam by moving the tube.)[†] The female spider in the eye tracker is doing exactly that. Her body is still. Her eyes look still, too. But on the monitor, we can see that her retinas are moving. "She's really looking around," Jakob says.

For reasons that no one fully understands, the retinas of her central eyes are shaped like boomerangs. At first, on Jakob's screen, they seem separate (> <). But when she shows the spider a black square, the two retinas converge upon it, forming crosshairs (><). As the square moves, the retinas follow. After a while, though, the spider loses interest, and the retinas diverge. Jakob replaces the square with the silhouette of a cricket, and the retinas converge again. This time, they dance over the image, flitting between the antennae, body, and legs with the same jerky hops that our eyes make when taking in a scene. The retinas also rotate together, twisting clockwise and anticlockwise, perhaps because the spider is searching for specific angles that might help it identify what it's looking at. Mike Land once wrote that it is "an exhilarating but very weird experience to look into the moving eyes of another sentient creature, particularly one so far removed in its evolution from oneself." I couldn't agree more. At least 730 million years of evolution separate humans from jumping spiders, and it is hard to interpret the behavior of such a different creature. But on Jakob's monitor, I can watch a spider paying attention and losing interest. I can observe it observing. By watching its gaze, I can get as close as possible to glimpsing its mind. And, despite many similarities, I can see just how different its vision is from mine.

* Each central eye actually has two lenses, one at the top and one at the bottom. The top lens collects and focuses light, while the bottom one spreads it out. This arrangement enlarges images before they hit the spider's retina, which is why these tiny animals can see as sharply as small dogs. The telescopes that Galileo started using in 1609 work in the same way, using tubes with lenses at both ends to peer at distant objects. Unbeknownst to him, he was unwittingly plagiarizing a structure that jumping spiders had evolved millions of years prior, and which, on clear nights, they can use to see the moon.

† Baby jumping spiders are transparent. With good lighting, you can see their eye tubes moving about inside their heads.

For a start, it has more eyes. The central pair may be sharp and mobile, but their field of view is very narrow. If they were all the spider had, its vision would be like two flashlights sweeping around a dark room. The secondary eyes on either side of the central pair compensate for this shortcoming with a much broader field of view. And though they are themselves immobile, they are highly sensitive to motion. If a fly buzzes in front of the spider, the secondary eyes spot it and tell the central eyes where to look. And here's the truly bizarre part: If the secondary eyes are covered, the spider cannot track moving objects.

I find this almost impossible to imagine. As I write these words, I am focusing the sharpest parts of my eyes on the letters appearing on my screen. Meanwhile, in my peripheral vision, I can see the black shape of Typo, my corgi puppy, as he prowls around my living room in search of trouble. These tasks—sharp vision and motion detection—feel inseparable. And yet jumping spiders have separated them so thoroughly that they exist within *different sets of eyes*. The central ones recognize patterns and shapes and see in color. The secondary ones track movements and redirect attention. Different eyes for different tasks, and each set has its own distinct connections to the spider's brain.* Jumping spiders remind us that we share a visual reality with other sighted creatures, but we experience it in utterly different ways. "We don't have to look to aliens from other planets," Jakob tells me. "We have animals that have a completely different interpretation of what the world is right next to us."

Humans have two eyes. They're on our heads. They're equally sized. They face forward. None of these traits is the norm, and a cursory glance at the rest of the animal kingdom reveals that eyes can be as varied as the creatures that own them. Eyes can come in eights or hundreds. The eyes of the giant squid are as big as soccer balls; those of fairy wasps are the size of an amoeba's nucleus. Squid, jumping spiders, and humans have all independently evolved camera-like eyes, in which a single lens focuses light onto a single retina. Insects and crustaceans

* What about the other two pairs of eyes? One seems to detect motion behind the spider. The other is very reduced, and its purpose is unclear.

have compound eyes, which consist of many separate light-gathering units (or ommatidia). Animal eyes can be bifocal or asymmetric. They can have lenses made of protein or rock. They can appear on mouths, arms, and armor. They can accomplish all the tasks our eyes can perform, or just a few of them.

This smorgasbord of eyes brings with it a dizzying medley of visual Umwelten. Animals might see crisp detail at a distance, or nothing more than blurry blotches of light and shade. They might see perfectly well in what we'd call darkness, or go instantly blind in what we'd call brightness. They might see in what we'd deem slow motion or time-lapse. They might see in two directions at once, or in every direction at once. Their vision might get more or less sensitive over the span of a single day. Their Umwelt might change as they get older. Jakob's colleague Nate Morehouse has shown that jumping spiders are born with their lifetime's supply of light-detecting cells, which get bigger and more sensitive with age. "Things would get brighter and brighter," Morehouse tells me. For a jumping spider, getting older "is like watching the sun rising."

SONKE JOHNSEN OPENS HIS BOOK *The Optics of Life* by noting that vision "is about light, so perhaps we should start with what light is." And then, with admirable candor: "I have no idea." Though it surrounds us almost constantly, light's true nature is not intuitive. Physicists contend that it exists both as an electromagnetic wave and as particles of energy known as photons. The specifics of this dual nature needn't concern us. What matters is that neither guise is something living things should obviously be able to detect. From a biological perspective, perhaps the most wondrous thing about light is that we can sense it at all.

Look inside the eyes of a jumping spider, a human, or any other animal, and you'll find light-detecting cells called photoreceptors. These cells might vary dramatically from one species to another, but they share a universal feature: They contain proteins called opsins. Every animal that sees does so with opsins, which work by tightly embracing a partner molecule called a chromophore, usually derived from vitamin A. The chromophore can absorb the energy from a single photon of light. When it does, it instantly snaps into a different shape, and its contortions force its opsin partner to reshape itself, too. The opsin's transformation then sets off a chemical chain reaction that ends with an electrical signal traveling down a neuron. This is how light is sensed. Think of the chromophore as a car key and the opsin as an ignition switch. The two fit together, light turns the key, and the engine of vision whirs into life.

There are thousands of different animal opsins, but they are all related.* Their unity creates a paradox. If all vision relies on the same proteins, and if those proteins all detect light, then why are eyes so diverse? The answer lies in light's distinct properties. Since most light on Earth comes from the sun, its presence can hint at temperature, time of day, or depth of water. It reflects off objects, revealing enemies, mates, and shelter. It travels in straight lines and is blocked by solid obstacles, creating telltale features like shadows and silhouettes. It covers Earth-scale distances almost instantaneously, offering a fast and far-ranging source of information. Vision is diverse because light is informative in a multitude of ways, and animals sense it for myriad reasons.

The biologist Dan-Eric Nilsson says that eyes evolve through four stages of increasing complexity. The first just involves photoreceptors—cells that do little more than detect the presence of light. The hydra, a relative of jellyfish, uses photoreceptors to ensure that its stings fire more readily in dim light; perhaps it does this to save those stings for nighttime hours, when its prey is more common, or to deploy them when it senses the shadow of a passing target. Olive sea snakes have photoreceptors at the tips of their tails, which they will pull away from sources of light. Octopuses, cuttlefish, and other cephalopods have

* In 2012, evolutionary biologist Megan Porter compared almost 900 opsins from different species, and confirmed that they share a single ancestor. That original opsin arose in one of the earliest animals and was so efficient at capturing light that evolution never conjured up a better alternative. Instead, the ancestral protein diversified into a wide family tree of opsins, which now underlie all vision. Porter draws that tree as a circle, with branches radiating outward from a single point. It looks like a giant eye.

photoreceptors dotted throughout their skin, which might help to control their amazing color-changing abilities.*

In the second stage, photoreceptors gain shade—a dark pigment or some other barrier that blocks the light coming in from certain angles. Shaded photoreceptors can not only detect light's presence but also infer its direction. These structures are still so simple that many scientists don't even regard them as genuine eyes, but they are useful to their owners nonetheless. They can also show up anywhere. The Japanese yellow swallowtail butterfly has photoreceptors on its genitals. A male uses these cells to guide his penis over a female's vagina, and a female uses them to position her egg-laying tube over the surface of a plant.

In the third of Nilsson's stages, shaded photoreceptors cluster into groups. Their owners can now knit together information about light from different directions to produce images of the world around them. For many scientists, this is the point when light detection becomes actual vision, when simple photoreceptors become bona fide eyes, and when animals can truly be said to see.† At first, their vision is blurry and grainy, suitable only for crude tasks like finding shelter or spotting looming shapes. But with the addition of focusing elements like lenses, their view sharpens, and their Umwelt fills with rich visual detail. High-resolution vision is the fourth of Nilsson's stages. When it first appeared, it would have intensified the interactions between animals. Conflicts and courtships could play out over distances longer than touch or taste would allow and at speeds too fast for smell. Predators could now spot their prey from afar, and vice versa. Chases ensued. Animals became bigger, faster, and more mobile. Defensive armor, spines, and shells evolved. The rise of high-resolution vision might explain why, around 541 million years ago, the animal kingdom dramatically diversified, giving rise to the major groups that exist today. This

* There's always at least one person who writes in with a pompous and incorrect corrective, so let's get this out of the way: The word *octopus* is derived from Greek and not Latin, so the correct plural is not *octopi*. Technically, the formal plural would be *octopodes* (pronounced ock-toe-poe-dees) but *octopuses* will do.

† This distinction isn't universally agreed upon, and some researchers would argue that a stage-two eye—a photoreceptor plus a shading pigment—also counts as an eye.

flurry of evolutionary innovation is called the Cambrian explosion, and stage-four eyes might have been one of the sparks that ignited it.

Nilsson's four-stage model addresses a concern of Charles Darwin, who was unsure how complex modern eyes could have evolved. "To suppose that the eye, with all its inimitable contrivances . . . could have been formed by natural selection, seems, I freely confess, absurd in the highest possible degree," he wrote in *The Origin of Species*. "Yet reason tells me, that if numerous gradations from a perfect and complex eye to one very imperfect and simple, each grade being useful to its possessor, can be shown to exist . . . then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, can hardly be considered real." The gradations Darwin imagined do indeed exist: Animals have every conceivable intermediate from simple photoreceptors to sharp eyes. And different animal groups have repeatedly and independently evolved diverse eyes using the same opsin building blocks. The jellyfish alone have evolved stage-two eyes at least nine times, and stage-three eyes at least twice. Eyes, far from being a blow to evolutionary theory, have proved to be one of its finest exemplars.*

Darwin was wrong, though, in calling complex eyes perfect and simpler ones imperfect. Stage-four eyes are not some Platonic ideal that evolution was striving toward. The simpler eyes that preceded them are all still around and are well suited to the needs of their owners. "Eyes didn't evolve from poor to perfect," Nilsson emphasizes. "They evolved from performing a few simple tasks perfectly to performing many complex tasks excellently." As we saw in the introduction, a starfish has eyes on the tips of its five arms. These eyes can't see color, detail, or fast movements, but they don't have to. They only have to detect large objects, so that the starfish can slowly amble back toward the safety of a coral reef. A starfish has no need for an eagle's acute eye, or even a jumping spider's. It sees what it needs to.* The first step to understanding another animal's Umwelt is to understand what it uses its senses *for*.

* In 1994, Nilsson and Susanne Pelger simulated the evolution of a sharp stage-four eye from a simple stage-three one. The simulation began with a small, flat patch of photoreceptors. With every generation, the patch slowly thickens and curves into a cup. It gains a crude lens, which gradually improves. Assuming pessimistically that the eye improves by just 0.005 percent every generation, and that each generation lasts for a year, it would take just 364,000 years for the blurry stage-three eye to become something like ours. As far as evolution goes, that's a blink of an eye.

Primates, for example, probably evolved big, sharp eyes to capture tree-dwelling insects sitting on branches. We humans have inherited that acute vision, which sighted people now use to guide their dexterous fingers, to read symbols that they imbue with meaning, and to assess the cues hidden in subtle facial expressions. Our eyes suit our needs. They also give us a singular Umwelt that most other animals do not share.

IN 2012, WHEN AMANDA MELIN, a scientist who studies animal vision, met Tim Caro, a scientist who studies animal patterns, their conversation naturally turned to zebras.

Caro had become the latest in a long line of biologists to wonder why zebras have such conspicuous black-and-white patterns. One of the earliest and most prominent hypotheses, he told Melin, was that the stripes counterintuitively act as camouflage. They mess with the eyes of predators like lions and hyenas by breaking up the zebra's outline, or by helping it to blend in among the vertical trunks of trees, or by causing a confusing blur when it runs. Melin was dubious. "I had a look on my face," she recalls. "I said, 'I think most of the carnivores are hunting at night, and their visual acuity is going to be so much worse than humans'. They probably can't see the stripes.' And Tim went, '*What?*' "

Humans outshine almost every other animal at resolving detail.

* It's not the case, either, that advanced eyes always exist in advanced creatures and simple eyes always in simple ones. There are some microbes that consist entirely of single cells and which also double as surprisingly complex eyes. Consider the freshwater bacterium *Synechocystis*. Light that hits one side of its spherical cell becomes focused on the opposite side. The bacterium can sense where that light is coming from, and move in that direction. It is effectively a living lens, and its entire boundary is a retina. The warnowiids, a group of single-celled algae, also seem to be living eyes, and each cell has components that resemble a lens, an iris, a cornea, and a retina. What they see, and whether they see at all, are open questions.

Our exceptionally sharp vision, Melin realized, gives us a rarefied view of a zebra's stripes. She and Caro calculated that on a bright day, people with excellent eyesight can distinguish the black-and-white bands from 200 yards away. Lions can only do so at 90 yards and hyenas at 50 yards. And those distances roughly halve at dawn and dusk, when these predators are more likely to hunt. Melin was right: The stripes can't possibly act as camouflage because predators can only make them out at close range, by which point they can almost certainly hear and smell the zebra. At most distances, the stripes would just fuse together into a uniform gray. To a hunting lion, a zebra mostly looks like a donkey.*

An animal's visual acuity is measured in cycles per degree—a concept that, by happy coincidence, you can think of in terms of zebra stripes. Stretch out your arm and give a thumbs-up. Your nail represents roughly 1 degree of visual space, out of the 360 degrees that surround you. You should be able to paint 60 to 70 pairs of thin black-and-white stripes on that nail and still be able to tell them apart. A human's visual acuity, then, is somewhere between 60 and 70 cycles per degree, or cpd. The current record, at 138 cycles per degree, belongs to the wedge-tailed eagle of Australia.† Its photoreceptors are some of the narrowest in the animal kingdom, which allows them to be densely packed within the eagle's retinas. With these svelte cells, the eagle effectively sees the world on a screen with over twice as many pixels as ours. It can spot a rat from a mile away.

But eagles and other birds of prey are the only animals whose vision is substantially sharper than ours. Sensory biologist Eleanor Caves has been collating visual acuity measurements for hundreds of species, almost all of which are surpassed by humans. Aside from raptors, only other primates come close to our standards. Octopuses (46 cpd), giraffes (27 cpd), horses (25 cpd), and cheetahs (23 cpd) do reasonably well. A lion's acuity is only 13 cpd, just above the 10 cpd threshold at which humans are considered legally blind. Most animals fall below that threshold, including half of all birds (and surprising ones like hummingbirds and barn owls), most fish, and all insects. A honeybee's acuity is just 1 cycle per degree. Your outstretched thumbnail represents roughly one pixel of a bee's visual world, and all the detail within that nail would collapse into a uniform smudge. Around 98 percent of insects have vision that's even coarser. "Humans are weird," Caves tells me. "We're not the pinnacle of any sensory modality, but we're rocking it with visual acuity." And paradoxically, our sharp vision muddies our appreciation of other Umwelten, because "we assume that if we can see it, they can, and that if it's eye-catching to us, it's grabbing their attention," says Caves. "That's not the case."

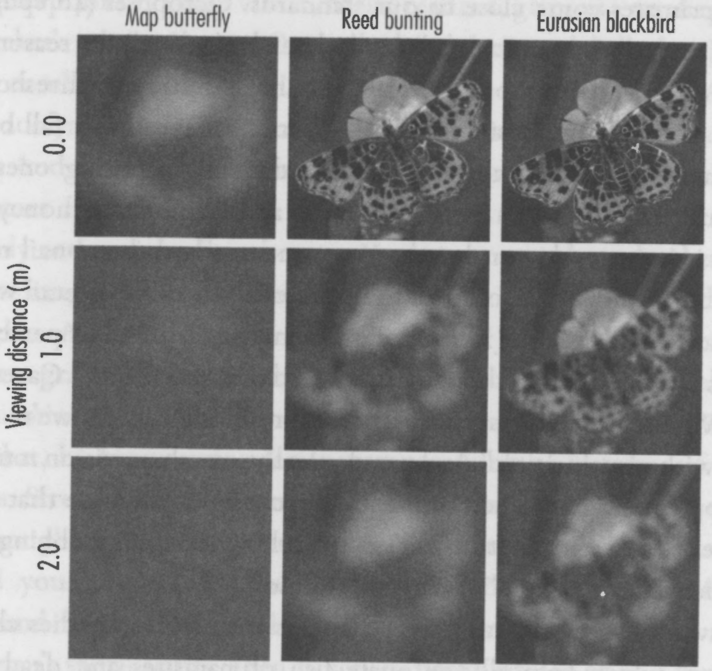
* So why are zebras striped? Caro has a definitive answer: to ward off bloodsucking flies. African horseflies and tsetse flies carry a number of diseases that are fatal to horses, and zebras are especially vulnerable because their coats are short. But stripes, for some reason, confuse the biting pests. By filming actual zebras, as well as normal horses dressed in zebra-striped coats, Caro showed that flies would approach the animals and then fumble their landings. It's not yet clear why this happens.

† One oft-quoted study from the 1970s suggested that the American kestrel has an acuity of 160 cpd, but other studies of the same bird have found much lower values on a par with humans.

Caves fell prey to this perceptual bias herself. She studies cleaner shrimps, which helpfully exfoliate fish of parasites and dead skin. "They're cleaning colorful coral reef fish, and they're colorful themselves, so I thought they'd have reasonable vision," Caves tells me. They do not. Their fish clients can see the vibrant blue spots on their bodies, and the bright white antennae that they wave about, but they themselves cannot. A cleaner shrimp's beautiful patterns are not part of a cleaner shrimp's Umwelt, even at very close range. "They probably can't even see their own antennae," Caves says.

Many butterflies also have intricate patterns on their wings, which might warn predators that these insects are toxic. Some scientists have suggested that the butterflies might recognize each other from these patterns, but that's unlikely when their vision isn't sharp enough. A blackbird can see the black spots that freckle the orange wings of a map butterfly, but another map butterfly probably just sees an orange blur. We've always looked at butterflies, cleaner shrimps, and zebras through the wrong eyes—ours.

Why, then, since animals are so frequently adorned with elaborate patterns, aren't sharp eyes more common? In some cases it's because eyes are constrained by their past. The curse of low resolution is baked



A map butterfly as viewed through the eyes of different species from varying distances

into the structure of a compound eye, and having started off with eyes of this kind, insects and crustaceans are now stuck. Robber flies manage 3.7 cycles per degree, but that's about the limit. For a fly's eye to be as sharp as a human's, it would have to be a meter wide.

Acute eyes also come with a hefty drawback. As the wedge-tailed eagle demonstrates, animals can achieve sharper vision by having smaller and more densely packed photoreceptors. But each receptor now collects light over a smaller area and is thus less sensitive. These qualities—sensitivity and resolution—seesaw against each other. No eye can excel at both. An eagle might be able to spot a far-off rabbit in broad daylight, but its acuity plummets as the sun sets. (There are no nocturnal eagles.) Conversely, lions and hyenas might not be able to resolve a zebra's stripes at a distance, but their vision is sensitive enough to hunt one at night. They, and many other animals, have prioritized

sensitivity over acuity. As ever, eyes evolve to suit the needs of their owners. Some animals simply don't need to see crisp images. And some animals don't need to see images at all.

DANIEL SPEISER NEVER THOUGHT he would spend his career trying to empathize with scallops. When he started graduate school in 2004, he thought about them the same way most people do—"as lumps of meat on a plate," he tells me. But those appetizing pan-seared lumps are merely the muscles that scallops use to close their shells. Look at a full, living scallop, and you'll see a very different animal. And that animal will see you, too. Each half of a scallop's fan-shaped shell has eyes arrayed along its inner edge—dozens in some species, and up to 200 in others. In the bay scallop, the eyes look like neon blueberries. Speiser finds them "funny and horrifying and charming," all at once.

It is strange enough that scallops have eyes when most other bivalves like mussels and oysters do not. It's even stranger that those eyes, as Mike Land showed in the 1960s, are complex. Each one sits at the end of a mobile tentacle. Each has a little pupil: "It's wild and creepy to see all of them opening and closing at the same time," Speiser says. Light passes through the pupil and hits the back of the scallop's eye, where it is reflected by a curved mirror. The mirror is a precisely tiled array of square crystals that collectively focus light onto the scallop's retinas. That's retinas, plural. There are two per eye, and they are about as different as two animal retinas could be.* Between them, they have thousands of photoreceptors, which gives them enough spatial resolution to detect small objects. "Their optics are really good," Speiser says.†

* There are two major groups of animal photoreceptors, known as ciliary and rhabdomeric. Both use opsins, but they function in very different ways. Scientists used to think that ciliary receptors were only found in vertebrates, and rhabdomeric ones were only in invertebrates. But that's not true: Both kinds of receptors are found in both groups. And both are found in the scallop, which has one retina full of ciliary photoreceptors and one full of rhabdomeric ones. Why? It's unclear, although one retina appears to be used to detect moving objects and the other is used for selecting habitats.

† It's not that scallop eyes are perfect. When light enters the eye, it must first get through the retina before the mirror can reflect and focus it. The retina gets two shots at absorbing that

But *why*? When scallops are threatened, they can swim away, opening and closing their shells like panicked castanets. Beyond these rare moments of action, though, they mostly sit on the seafloor, sieving edible particles from the water. They're "glorified clams," according to Sonke Johnsen. Why do they need such a complicated eye, let alone dozens or hundreds of them? What does a scallop use its vision for? To find out, Speiser ran an experiment that he called Scallop TV. He strapped their shells to small seats, placed them in front of a monitor, and showed them computer-generated movies of small, drifting particles. It was such a ridiculous setup that no one seriously thought that it would work. But it did: If the particles were large enough and moving slowly enough, the scallops opened their shells, as if ready to feed. "It was the craziest thing I've ever seen," Johnsen tells me.

At the time, Speiser thought that scallops must use their eyes to spot potential food. Now he thinks something else is happening. Interspersed between their eyes are tentacles that scallops use to smell molecules in the water. Speiser thinks they use smell to recognize predators like starfish and vision to detect things that are simply worth an investigative sniff. When they opened their shells in response to Scallop TV, they weren't trying to feed but were seeking to explore. "My guess is that we were seeing scallops being curious," Speiser says.

Speiser suspects that scallop vision works in a very different way than ours. Our brains combine the overlapping information from our two eyes into a single scene. A scallop *could* do the same across a hundred eyes, but that seems unlikely given how crude its brain is. Instead, each eye might simply tell the brain whether it has detected something moving or not. Think of the scallop's brain as a security guard watching a bank of a hundred monitors, each connected to a motion-sensing camera. If the cameras detect something, the guard sends sniffer dogs to investigate. Here's the catch: The cameras may be state-of-the-art, but the images they capture *are not sent to the guard*. All the guard sees on the monitors is a warning light for every camera that has spotted something. If Speiser is right about this bizarre setup, it means that even though each individual scallop eye has good spatial resolution, the animal itself might not have spatial *vision*. It knows when eyes in a certain region of its body have detected something, but it has no visual image of that object. It doesn't experience a movie in its head the same way we do. It sees without scenes.

light—once on its unfocused initial pass, and again in its more focused form. This means that the eye sees a focused image against a background of blurry haze.

This kind of vision is probably closer to our sense of touch than anything we experience with our eyes. We don't create a tactile scene of the world, even though we can feel with every part of our skin. Indeed, we largely ignore those sensations until something pokes us (or vice versa). And when we feel something unexpected, our most common reaction is to turn and look at it. Perhaps for a scallop, smell (not vision) is the fine-grained exploration sense and vision (not touch) is the crude, whole-body detection sense.*

But if that's the case, why does each individual eye have such good resolution? Why do sophisticated components like the mirrors and double retinas exist? Why are there so many eyes when just a few could cover the entire space around the scallop's shell? Why have such good eyes evolved in an animal whose brain can barely handle the information they convey?† No one knows. "Sometimes I feel like I can almost get my mind around it, and extend my empathy into scallops," Speiser tells me. "But a lot of the time I feel lost again."‡

* This idea is especially compelling because the eyes are actually modified chemosensory tentacles. It's a visual system jury-rigged from one originally used for smell and touch.

† In 1964, Mike Land, who was still a graduate student, looked into a scallop's eye and saw an upside-down image of himself. That's how he discovered that each eye contains a focusing mirror. He later showed that the mirror consists of layered crystals, and suggested (correctly) that the crystals are made of guanine—one of the building blocks of DNA. Guanine crystals don't naturally form squares, so the scallop must somehow control their growth. It's unclear how it manages this, or how it gets every crystal to the same exacting measurement—74 billionths of a meter thick.

‡ Scallops aren't the only animals with perplexing distributed vision. Chitons are mollusks that look like the disembodied forehead of a Klingon from *Star Trek*; their bodies are covered in armored plates, and those plates are dotted with hundreds of small eyes. Fan worms look like colorful feather dusters, extending from rocky tubes; those plumes are tentacles, which teem with eyes. Giant clams look like . . . well, very big clams; their meter-wide mantles contain several hundred eyes. Dan-Eric Nilsson likens all of these eyes to burglar alarms. They detect nearby movement and encroaching shadows, so their owners know when to take defen-

Some animals might have the scallop's distributed vision without possessing eyes at all. The brittle star *Ophiomastix wendtii* looks like a skinny, spiny starfish, or perhaps like five centipedes wriggling out of a hockey puck. It doesn't have any obvious eyes, but it clearly sees. It will scuttle away from light, crawl toward shady crevices, and even change color after sunset. In 2018, Lauren Sumner-Rooney showed that the brittle star has thousands of photoreceptors over the full lengths of its sinuous arms. It's as if the entire animal acts as a compound eye.* Weirder still, it's only an eye *during the day*.

When the sun is out, the brittle star expands sacs of pigment in its skin, which give it the deep red of a blood clot. At night, it shrinks these sacs, and becomes pale gray and striped. When expanded, the pigment sacs block light from reaching the photoreceptors at certain angles. This gives each receptor the directionality of a stage-two eye, and it gives the entire animal the spatial vision of a stage-three eye. But when the pigment sacs contract at night, the photoreceptors are fully exposed. Unable to tell the direction of incoming light, their spatial vision no longer works. "It knows when it's exposed to light, but doesn't know how to get away from it," Sumner-Rooney says.

It's anyone's guess what the brittle star itself makes of this change. Unlike a scallop, it doesn't even have a brain—just a decentralized ring of nerves surrounding its central disc. This ring coordinates the five arms but doesn't command them; they mostly act on their own. It's as if the brittle star has the same weird system of cameras as the scallop, but without the security guard. The cameras are just signaling each other. Do they do so across the entire animal? Is each separate arm its own eye? Is each arm a swarm of semi-autonomous eyes that happen to be linked? "It could be something so out there that we haven't even thought of it yet," Sumner-Rooney tells me. "Everything we know

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sive measures. The chitons clamp down onto rocks, the fan worms pull their fans back into their tubes, and the giant clams close their shells. It's likely that, like the scallops, none of these animals sees scenes.

* Like brittle stars, sea urchins also seem to use their entire bodies as a crude eyeball. Each urchin is a spiky ball that crawls around on hundreds of tube feet. Its photoreceptors are on those feet, and they are shaded either by the animal's spines or by its hard exoskeleton. Its vision may not be especially sharp, but it can certainly amble toward dark shapes.

about animal vision to date relies on having an eye. We're basing everything on a century's worth of research on contiguous retinas, with photoreceptors that are close together and grouped. [The brittle star] violates a lot of those assumptions."

With multitudes of eyes, no heads, and sometimes no brains, brittle stars and scallops all reveal how strange vision can be. "An animal doesn't have to see a picture to be able to use vision," Sumner-Rooney says. "But humans are such visually driven creatures that trying to conceive of these completely alien systems is very hard." It is easier to imagine the visual worlds of more familiar creatures with heads and two eyes. But even then, we might miss what is right in front of us.

RISING HIGH ON COLUMNS of warm air, griffon vultures soar over rolling landscapes in search of food. Since they can spot carcasses on the ground, they should easily be able to see large obstacles ahead of them. And yet vultures, eagles, and other large raptors often fatally crash into wind turbines. In one Spanish province alone, 342 griffon vultures collided with wind turbines over a 10-year period. How could birds that fly by day and have some of the planet's sharpest eyes fail to avoid structures so large and conspicuous? Graham Martin, who studies bird vision, answered this question by addressing another: Where exactly do vultures look?

In 2012, Martin and his colleagues measured the griffon vulture's visual field—the space around its head that its eyes can cover. They got each bird to rest its beak on a specially fitted holder, and then looked into its eyes from all directions with a visual perimeter. "It's the same device that an optician would use when you get an eye test," Martin told me at the time. "It's just a question of sitting the bird down for half an hour. One tried to grab at me and I did lose a bit of my thumb."

The perimeter revealed that a vulture's visual field covers the space on either side of its head but has large blind spots above and below. When it flies, it tilts its head downward, so its blind spot is now directly ahead of it. This is why vultures crash into wind turbines: While soaring, they aren't looking at what is right in front of them. For most of their history, they never had to. "Vultures would never have encountered an object so high and large in their flight path," Martin says. It might work to turn off the turbines if the birds are near, or to lure the vultures away using ground-based markers. But visual cues on the blades themselves won't work.* (In North America, bald eagles also crash into wind turbines for the same reasons.)

When I think about Martin's study, I'm suddenly and acutely aware of the large space behind my head that I cannot see and that I seldom think about. Humans and other primates are rather odd in having two eyes that point straight ahead. The left eye gets a very similar view to the right, and their visual fields overlap a lot. This arrangement gives us excellent depth perception. It also means we can barely see things to our sides, and we can't see what's behind us without turning our heads. For us, seeing is synonymous with facing, and exploration is achieved through gazing and turning. But most birds (except for owls) tend to have side-facing eyes and don't need to point their heads at something to look at it.

A soaring vulture that's scanning the ground can also see other vultures flying next to it, without having to turn. A heron's visual field covers 180 degrees in the vertical; even when standing upright with its beak pointing straight ahead, it can see fish swimming near its feet. A mallard duck's visual field is completely panoramic, with no blind spot either above or behind it. When sitting on the surface of a lake, a mallard can see the entire sky without moving. When flying, it sees the world simultaneously moving toward it and away from it. We use the phrase "bird's-eye view" to mean any vista seen from on high. But a bird's view is not just an elevated version of a human one. "The human visual world is in front and humans move into it," Martin once wrote. But "the avian world is around and birds move through it."†

* Why don't vultures just have wider visual fields that allow them to look ahead while flying? Martin thinks it's because their large, sharp eyes are vulnerable to dazzling glare from the sun. In general, he says, birds with large eyes tend to have larger blind spots. Birds with panoramic vision, like ducks, tend to have smaller and less acute eyes that can better tolerate the presence of the sun.

† Chickens and many other birds rely on frontal vision only at close range, when they want to accurately grab something with their beaks or feet.

Birds also differ from humans in where their vision is sharpest. Many animals have an area in their retinas where their photoreceptors (and the attendant neurons) are densely packed, increasing the resolution of their vision. This region goes by many names. In invertebrates, it's called an *acute zone*. In vertebrates, it's an *area centralis*. If that area is also inwardly dimpled, as it is in our eyes, it's a *fovea*. For all our sakes (except the vision scientists, to whom I apologize), I'm just going to stick with *acute zone*. In humans, it's a bullseye—a round spot in the center of our visual field. It's what you are training upon these letters as you read them. Most birds also have circular acute zones, but theirs point outward, not forward. If they want to examine objects in detail, they have to look sideways, with just one eye at a time. When a chicken investigates something new, it will swing its head from side to side to look upon it with the acute zone of each eye in turn. "When chickens look at you, you never know what the other eye is doing," says Almut Kelber, a zoologist who studies bird vision. "They must have at least two centers of attention, which is very hard to imagine."

Many birds of prey, like eagles, falcons, and vultures, actually have two acute zones *in each eye*—one that looks forward, and another that looks out at a 45-degree angle. The side-facing one is sharper, and it's the one that many raptors use when hunting. When a peregrine falcon dives after a pigeon, it doesn't plunge straight at its prey. Instead, it flies along a descending spiral. That's the only way it can keep the pigeon within its murderous side-eye, while also pointing its head down and maintaining a streamlined shape.*

The peregrine prefers to use its right eye to track prey. Such preferences are common to birds; when eyes see distinct views, those eyes can be used for distinct tasks. The left half of a chick's brain is specialized for focused attention and categorizing objects; the bird can spot food grains among a bed of pebbles if it uses its right eye (directed by its left brain), but not its left eye. The right half of the brain deals with the unexpected; many birds use their left eyes (directed by their right

* Turning the eyes is out of the question because birds of prey can barely move their eyes without turning their heads. Indeed, their eyes are so big that they almost touch each other inside the skull.

brains) to scan for predators, and are quicker to detect a threat when it approaches from the left.

An animal's visual field determines where it can see. Its acute zones determine where it sees *well*. Without considering both traits, we can seriously misinterpret an animal's actions. In a video that went viral on TikTok, a male argus pheasant displayed his dazzling plumage to a female, who seemed to look off to the side. Viewers laughed at her apparent disinterest, not knowing that she was looking right at him with her side-facing visual field. A seal's visual field is more similar to ours but with excellent coverage above its head and poor coverage below, presumably to spot fish silhouetted against the sky. A seal that swims upside down might look relaxed to a human observer, but is actually scanning the seafloor for food.

Cows and other livestock also have a somnolent air because their gaze is so fixed. They rarely turn to look at you in the way another human (or a jumping spider) might. But they also don't need to. Their visual fields wrap almost all the way around their heads and their acute zones are horizontal stripes, giving them a view of the entire horizon at once. The same is true for other animals that live in flat habitats, including rabbits (fields), fiddler crabs (beaches), red kangaroos (deserts), and water striders (the surface of ponds). Except for the occasional aerial predators, *up* and *down* are largely immaterial to them. There is only *across*, in every possible direction. A cow can simultaneously see a farmer approaching it from the front, a collie walking up from behind, and the herdmates at its side. *Looking around*, which is inextricable from our experience of vision, is actually an unusual activity, which animals do only when they have restricted visual fields and narrow acute zones.

Elephants, hippos, rhinos, whales, and dolphins have two or three acute zones per eye, possibly because they can't quickly turn their heads.* Chameleons don't have to turn because their turret-like eyes can move independently; they can look in front and behind at the same time, or track two targets moving in opposite directions. Other animals are steadier in their gaze. Many male flies focus upward: The large facets at the top of their compound eyes are called love spots, and allow them to detect the silhouettes of females flying overhead. Male mayflies have gone even further: The female-spotting parts of their eyes are so enormous that each eye looks like it is wearing a chef's hat. The fish *Anableps anableps*, which lives at the surface of South American rivers, also partitions its eyes. The top half sticks out of the water and is adapted for air vision, and the bottom half stays below the surface and is adapted for aquatic vision. It's also known as the four-eyed fish.

In the three-dimensional world of the deep ocean, above and below matter as much as in front and behind. Many deep-sea fish like barreleyes and hatchetfish have tubular eyes that point upward, allowing them to see the outlines of other animals silhouetted against the faint downwelling sunlight. The brownsnout spookfish, a kind of barreleye, has amended the upward eye of its kin with a downward-pointing chamber that has its own retina; with these two-part eyes, it can look up and down at the same time. So can the cock-eyed squid, whose left eye is twice the size of its right. It hangs in the water column with the small eye pointing downward to spot bioluminescent flashes and the big eye pointing up to spot silhouettes. Meanwhile, the deep-sea crustacean *Streetsia challengeri* has fused its eyes into a single horizontal cylinder, which looks like a corn dog. It can see in almost every direction circumferentially—above, below, and to the sides—but not ahead or behind.

It is almost impossible to imagine what it would be like to see like *Streetsia*, or a chameleon, or even a cow. The reverse-facing camera of my smartphone can show me what's going on over my shoulder, but that image still appears in my relentlessly forward-facing visual field. Again, as with the scallops, it helps to think about touch. I can simultaneously feel the sensations on the skin of my scalp, soles, chest, and back. If I concentrate, I can just about imagine what it might be like to fuse the omnidirectional nature of that sensation with the long range of sight. Vision can extend in any direction and every direction. It can envelop and surround. And it can vary in time as well as space. It can

* A whale's pupil doesn't constrict by shrinking into a pinhole, like ours does. Instead, it pinches in the middle, creating what looks like an awkwardly smiling mouth with two small openings at either end. Each of these openings is effectively its own mini-pupil, and admits light onto a separate acute zone.

fill not just the empty voids around us but also the fleeting gaps between moments.

THE MEDITERRANEAN IS HOME to a small, unassuming fly called *Coenosia attenuata*. Just a few millimeters long, with a pale gray body and large red eyes, "it looks like a standard housefly," Paloma Gonzalez-Bellido tells me. In fact, it is a killer. From its perch on a leaf, it will take off in pursuit of fruit flies, fungus gnats, whiteflies, and even other killer flies—"anything that's small enough for them to subdue," Gonzalez-Bellido says. During the chase, it stretches out its legs. As soon as one touches the target, all six clamp shut, forming a cage. Often, it will fly the victim back to its original perch. If you can coax a killer fly to crawl onto your finger, it will repeatedly launch itself from your digit and return with prey, like a (very tiny) falcon to its falconer. This experience can be unexpectedly magical for a human. It's less so for the prey. While a typical housefly has a proboscis that resembles a sponge on a stick, used for dabbing and sucking at liquids, a killer fly's proboscis is part dagger and part rasp, used for stabbing and scraping flesh. The fly shoves it into its victim and hollows it out while it is still alive. Gonzalez-Bellido has a video in which you can see a killer fly's mouthparts scraping away a fruit fly's eye from the inside, leaving nothing behind but a grid of transparent lenses. Farmers and gardeners frequently introduce this insect into greenhouses to take care of pests, and it has now spread all around the world.

For killer flies, speed is everything. "Their prey can come from anywhere, and the Mediterranean is so dry that it's rare for them to have prey," Gonzalez-Bellido says. They immediately take off after anything that could conceivably be a meal and, once airborne, catch their prey as quickly as possible so that they themselves aren't cannibalized by others of their kind. Their chases are near impossible for even well-trained human eyes to follow. By filming these pursuits with high-speed cameras, Gonzalez-Bellido showed that they typically take a quarter of a second. They might even be over in half that time. A killer fly can capture its target in the space of a human blink.

Their ultrafast hunts are guided by ultrafast vision. It may seem strange to talk about animals seeing at different speeds, because light is the fastest thing in the universe, and vision seems instantaneous to us. But eyes don't work at light speed. It takes time for photoreceptors to react to incoming photons, and for the electrical signals they generate to travel to the brain. In killer flies, evolution has pushed these steps to their limits. When Gonzalez-Bellido shows these insects an image, it takes just 6 to 9 milliseconds for their photoreceptors to send electrical signals, for those signals to reach their brains, *and* for their brains to send commands to their muscles.* By contrast, it takes between 30 and 60 milliseconds for human photoreceptors to accomplish just the first of those steps. If you looked at an image at the same moment as a killer fly, the insect would be airborne well before a signal had even left your retina. "We don't know of a faster photoreceptor than the ones from these flies," Gonzalez-Bellido tells me. She says it with something approaching pride.†

The fly's vision also updates more quickly. Imagine looking at a light that flickers on and off. As the flickering gets faster, there will come a point when the flashes merge into a steady glow. This is called the critical flicker-fusion frequency, or CFF. It's a measure of how quickly a brain can process visual information. Think of it as the frame rate of the movie playing inside an animal's head—the point at which static images blend into the illusion of continuous motion. For humans, in good light, the CFF is around 60 frames per second (or hertz, Hz). For most flies, it's up to 350. For killer flies, it's probably higher

* The photoreceptors in a killer fly's eye fire quickly and reset quickly. Both traits demand a lot of energy. Compared to the photoreceptors of a fruit fly, those of a killer fly have three times more mitochondria—the bean-shaped batteries that supply animal cells with power.

† Other predatory insects, like dragonflies and robber flies, have large, high-resolution eyes with distinctive acute zones. As they pursue their targets, they turn their heads to keep the prey within the sharpest part of their visual field. Killer flies "have to pay attention in all directions," Gonzalez-Bellido says, so they don't have an acute zone, and their visual resolution isn't especially high. Despite that, they seem to have a more demanding hunting strategy. Dragonflies hunt against the sky, spotting the silhouettes of prey that fly above them. But killer flies somehow "do the impossible thing of hunting against the ground," Gonzalez-Bellido says. They'll pick out prey moving in front of complex backgrounds, and then chase those targets through leaves and other cluttered environments.

still. To its eyes, a human movie would look like a slideshow. The fastest of our actions would seem languid. An open palm, moving with lethal intent, would be easily dodged. Boxing would look like tai chi.

In general, animals tend to have higher CFFs if they're smaller and faster. Compared to human vision, cats are slightly slower (48 Hz) and dogs slightly faster (75 Hz). The eyes of a scallop are positively glacial (1 to 5 Hz), and those of nocturnal toads are slower still (0.25 to 0.5 Hz). Those of leatherback turtles (15 Hz) and harp seals (23 Hz) are faster but still sluggish. Those of swordfish aren't much better under normal conditions (5 Hz), but these fish can heat up their eyes and brains with a special muscle, boosting the speed of their vision by eight times. Many birds have naturally fast vision; with a maximum CFF of 146 Hz, the pied flycatcher—a small songbird—has the fastest vision of any vertebrate that's been tested, perhaps because its survival depends on tracking and catching flying insects.* And those insects have eyes that are faster still. Honeybees, dragonflies, and flies have CFFs between 200 and 350 Hz.

It's possible that each of these visual speeds comes with a different sense of time's passage. Through a leatherback turtle's eyes, the world might seem to move in time-lapse, with humans bustling about at a fly's frenetic pace. Through a fly's eyes, the world might seem to move in slow motion. The imperceptibly fast movements of other flies would slow to a perceptible crawl, while slow animals might not seem like they were moving at all. "Everyone asks us how we catch the killer flies," Gonzalez-Bellido says. "You just move toward them slowly with a vial. If you're slow enough, you're just part of the background."

FAST VISION REQUIRES A lot of light, so killer flies can only be active during the day. Other animals are not so limited.

After the sun's golden fingers withdraw from the Panamanian rainforest and the understory's shade thickens into an even deeper darkness, a small bee emerges from a hollow stick. This is *Megalopta genalis*, a sweat bee. Its legs and abdomen are golden yellow. Its head and torso are metallic green. None of those beautiful hues are usually visible to human observers because the bee only emerges when there's too little light for humans to see, let alone see in color. But despite the darkness, *Megalopta* slaloms through a labyrinth of lianas and tracks down its favorite flowers. Having collected its fill of pollen, it somehow then returns to the very same thumb-width stick in which it nests.

Eric Warrant, who grew up collecting insects and now studies their eyes, first encountered *Megalopta* in 1999 on a research trip to Panama. He quickly confirmed, to his astonishment, that it uses vision to guide its nighttime flights. By filming the insect with infrared cameras, Warrant saw that when it first emerges from its stick, it turns around and hovers slowly in front of the entrance, memorizing the appearance of the surrounding foliage. Later, when it has finished foraging, it uses this visual memory to find its way home. If Warrant set up his own landmarks, like white squares, and moved them to another stick while the bee was away, it would return to the wrong place. The bee's feat would be hard enough in bright daylight: Rainforests are neither easy to navigate nor short of sticks. But *Megalopta* somehow finds its home "in the dimmest imaginable light," Warrant says. He has filmed the bee finding its nest on nights so dark that he couldn't even see his own hand in front of his face. He had to use night-vision goggles to see what the bee could with its own eyes. "They're no clumsier in the dark than a honeybee is in bright sunlight," Warrant tells me. "They come flying in quite rapidly, they don't hesitate, and they land incredibly quickly. It's one of the most amazing things I've ever seen."

Warrant suspects that *Megalopta*'s ancestors veered toward a nocturnal schedule to escape intense competition from daylight pollinators, including other bees. But life at night isn't easy for animals that rely on vision, for two major reasons. The first is obvious: There's much less light. Even the light of a full moon is a million times dimmer than full daylight. A moonless night that's illuminated by stars alone is a hundred times dimmer still. A night where starlight is obscured by clouds or tree cover is a hundred times dimmer again. These are the kinds of

* Traditional fluorescent lights flicker at 100 Hz—that is, 100 times a second. That's too fast for humans to see, but not for many birds like starlings, for whom the lights must be stressful and irritating.

conditions in which *Megalopta* can still navigate—starless darkness that offers barely enough light for an eye to collect. The second challenge is less intuitive: Photoreceptors can accidentally go off on their own, and at night, these false alarms can easily outnumber the real signals from actual photons. So nocturnal animals must not only detect the little light that's there but also ignore the phantom lights that aren't. They must overcome both the limits of physics and the messiness of biology.

Some animals have simply dropped out of the struggle. Like all sensory systems, eyes are expensive to build and maintain. It takes a lot of energy to even prep photoreceptors and their associated neurons for the arrival of light, so that they can react when needed. Even when animals aren't seeing anything, the mere possibility of sight drains their resources. This drain is significant enough that if eyes stop being useful or effective, they tend to diminish or disappear. Sometimes animals invest in other senses that aren't yoked to light. (We'll meet these later; many exceptional senses were discovered because scientists noticed animals doing amazing things in total darkness.) Others unsubscribe from vision entirely. In underground realms, in caves, and in other dark corners of Earth where vision cannot earn its worth, eyes are often lost.*

Other animals, instead of ceding their vision to the dark, have evolved ways of seeing in the dimmest of conditions. Some use neural tricks, including the sweat bee that Warrant studied. It pools the responses from several different photoreceptors, turning lots of smaller pixels into a few large megapixels. Its photoreceptors might also collect photons for more time before firing, like a camera whose shutter is left open for a longer exposure. These two strategies group the photons reaching the bee's eye in both space and time, increasing the ratio of signal to noise. Its vision is grainy and slow as a result but remains bright when brightness seems impossible. And "seeing a coarser,

* There are many ways to break an eye, and evolution has explored them all. Lenses have degenerated. Visual pigments have disappeared. Eyeballs have sunk beneath the skin or been covered by it. One species alone, the Mexican cavefish, has lost its eyes several times over, as different sighted populations moved from bright rivers to dark caves and independently abandoned vision. As Eric Warrant tells me, "Why Gollum in *The Hobbit* had extra-big eyes makes no scientific sense."

slower, brighter world is better than seeing nothing at all," Warrant says.*

Animals can also see in the dark by grabbing every last photon they can. Some species, including cats, deer, and many other mammals, have a reflective layer called a tapetum, which sits behind their retinas and sends back any light that gets past their photoreceptors; those cells then get a second chance to collect the photons they initially missed.† Other animals have evolved exceptionally large eyes and wide pupils. The tawny owl's eyes are so big that they bulge out of its head. The tarsiers—small primates from Southeast Asia that look like gremlins—have eyes that are each larger than their brains. And the biggest eyes of all evolved in one of the darkest environments in the planet—the deep ocean.

TO DIVE INTO THE OCEAN is to enter the largest habitat on the planet—a realm with over 160 times more living space than all the ecosystems on the surface combined. Most of that space is dark.

At 10 meters down, 70 percent of the light from the surface has been absorbed. If you were descending in a submersible, anything red, orange, or yellow on your person would now look black, brown, or gray. By 50 meters, greens and violets have largely vanished, too. By 100 meters, there is only blue, at just 1 percent of its surface intensity, if that. By 200 meters, the start of the mesopelagic or twilight zone, that intensity has fallen by another 50 times. The blue is now almost laser-like—eerily pure and all-encompassing. Through it, silvery fish dart about. Gelatinous jellyfish and siphonophores slowly snake past. At 300 meters, it's as dark as a moonlit night, and getting darker.

* This doesn't fully account for *Megalopta genalis*'s night vision, though. "I can't explain how they do it," Warrant tells me. "I've got clues about some of the mechanisms they use to enhance vision in dim light, but I can't see the whole picture."

† Reflections from the tapetum are responsible for the eyeshine of dogs, cats, deer, and other animals illuminated by car headlights or camera flashes. The structure of a reindeer's tapetum changes in the dark winter to reflect even more light. Coincidentally, this also changes the tapetum's color, and thus the color of reindeer eyes, from golden yellow in the summer to a rich blue in the winter.

Gradually, the fish get blacker, the invertebrates redder. Increasingly, they produce their own light, and their bioluminescent flashes paint the outline of your descending submersible. At 850 meters, the residual sunlight is so faint that your eyes can no longer function. At 1,000 meters, no animal eyes can. This is the beginning of the bathypelagic or midnight zone. The complex visual scenes of the surface are long gone and have been replaced by a living star-field of bioluminescence, twinkling in the otherwise total darkness. Depending on where you are in the world, there might be another 10,000 meters of ocean left to go.

The deep ocean's consummate darkness creates a problem for the scientists who want to study its denizens. Researchers can't see what's around them unless they turn on their submersible's lights, but doing so is devastating for creatures that have adapted to a lightless life. Even moonlight can blind a deep-sea shrimp in a few seconds. A submersible's headlights will do much worse. Some deep-sea animals end up doing kamikaze runs at subs. Startled swordfish ram them with their swords. Other creatures freeze or flee. "The way to think about ocean exploration is that we probably create a sphere a hundred yards wide that keeps away anything that can get away," says Sonke Johnsen. "Most of the time, we're seeing terror and blindness. We see how animals behave when they think they're being killed by some glowing god."

To be more respectful of deep-sea Umwelten, Johnsen's mentor Edith Widder created a stealth camera called Medusa. It films deep-sea animals with red light that most of them can't see, and attracts them with a ring of blue LEDs that resemble a bioluminescent jellyfish. "The only real innovation is that we turned off the lights," he says. "Once we do that, really big stuff shows up."

In June 2019, Widder and Johnsen took Medusa on a 15-day research cruise through the Gulf of Mexico. Under what seemed to be the only storm in the Gulf, they would manually lower the 300-pound camera to the end of its 2,000-meter line, and then haul it up again the next night. "Have you ever pulled up a fridge-sized object for a mile?" Johnsen asks me. "It took three hours every night." After every deployment, Nathan Robinson would pore over Medusa's videos. And over the course of the first four, "we saw a shrimp making a little bioluminescence," Johnsen says. "Yay?"

Then, on June 19, "I'm on the bridge, and all of a sudden, Edie's at the bottom of the stairs with a smile on her face that's practically cracking her ears off, and I thought: This can only be one thing." On its fifth outing, Medusa had filmed a giant squid.

The footage was unmistakable. At a depth of 759 meters, a long cylinder appears and snakes toward the camera before unfurling into a mass of writhing, suckered arms. It briefly grabs the camera with two long tentacles before losing interest and withdrawing back into the dark. The crew estimated that it was a 10-foot-long juvenile, which was nowhere close to the species' maximum size of 43 feet. Still, it was a *giant squid*—an almost mythic animal, and one with the largest and most sensitive eyes on the planet.

As I noted at the start of this chapter, the eyes of a giant squid (and the equally long but much heavier colossal squid) can grow as big as soccer balls, with diameters up to 10.6 inches. These proportions are perplexing. Yes, bigger eyes are more sensitive, and it makes sense for an animal in the dark ocean to have them. But no other creature, including those that live in the deep sea, has eyes that are even in the same ballpark as a giant or colossal squid's. The next-largest eyes, which belong to the blue whale, are less than half the size. A swordfish's eye, which is the largest of any fish at 3.5 inches, could fit inside a giant squid's pupil. The squid's eyes are not just big; they are absurdly and excessively bigger than those of any other animal. What does it need to see that it can't see with a swordfish-sized eye?

Sonke Johnsen, Eric Warrant, and Dan-Eric Nilsson think they know the answer. They calculated that in the deep ocean, eyes suffer from diminishing returns. As they get bigger, they cost more energy to run but offer little extra visual power. Once they get past 3.5 inches—that is, swordfish-sized—there's little point in enlarging them further. But the team found that extra-large eyes *are* better at one task, and one task alone: spotting large, glowing objects in water deeper than 500 meters. There's an animal that fits those criteria, and it is one that giant squid really need to see: the sperm whale.

The largest toothed predators in the world, sperm whales are the giant squid's main nemeses. Their stomachs have been found full of the squid's parrot-like beaks, and their heads often bear circular scars inflicted by the serrated rims of the squid's suckers. They do not produce their own light, but just like a descending submersible, they trigger flashes of bioluminescence when they bump against small jellyfish, crustaceans, and other plankton. With its disproportionately large eyes, the giant squid can see these telltale shimmers from 130 yards away, giving it enough time to flee. It is the only creature with eyes large enough to see these bioluminescent clouds at a distance, and also the only one that *needs* to do so. "No other animals are looking for things that are really large at depth," Johnsen says. Sperm whales and other toothed whales use sonar rather than vision to find their food. Large sharks tend to go after smaller prey. Blue whales subsist on tiny shrimp-like krill. Krill might benefit from seeing the bioluminescent cloud of a blue whale, but their compound eyes are too limited in resolution, and their bodies are too slow to do anything with that information. Giant (and colossal) squid are unique in being massive animals that need to see massive predators, and their singular need has led to a singular Umwelt. With the largest and most sensitive eyes that exist, they scan one of the darkest environments on Earth for the faint sparkling outlines of charging whales.*

TURN OFF THE LIGHTS, and our world becomes monochromatic. This shift occurs because our eyes contain two types of photoreceptors—

* The giant squid seems to be a global species that lives in every ocean. But for the longest time, it was known only from carcasses that washed ashore. The first photographs of this creature in the wild were only taken in 2004. The first natural footage was captured in 2012, when Widder and her colleagues deployed the then-new Medusa camera off the coast of Japan. Seven years later, the stealth camera proved its worth yet again, just 100 miles southeast of New Orleans. "That part of the Gulf is packed with oil rigs, and there are thousands of remotely operated vehicles there," Johnsen says. "Those pilots have never seen a giant squid, and we saw one on our fifth deployment. Either we are the luckiest people in the world, or it's that we turned our lights off." (They are pretty lucky. Half an hour after the crew saw the squid footage, lightning struck their ship, frying a lot of instruments but mercifully sparing Medusa's hard drive. Shortly after, the ship also dodged a waterspout.)

cones and rods. The cones allow us to see colors, but they only work in bright light. In the dark, the more sensitive rods take over, and a kaleidoscope of daytime hues is replaced by the blacks and grays of the night. Scientists used to think that all animals were similarly colorblind at night.

Then, in 2002, Eric Warrant and his colleague Almut Kelber did a pivotal experiment with the elephant hawkmoth. This beautiful European insect has a pink-and-olive body and a wingspan of almost 3 inches. It feeds entirely at night, hovering in front of flowers and drinking their nectar with a long, unfurled proboscis. Kelber trained hawkmoths to drink instead from feeders, which sat behind blue or yellow cards. Having learned to associate these colors with food, the moths could reliably distinguish them from equally bright shades of gray. And they kept on doing so as Kelber turned down the lights in her lab.

At light levels equivalent to a half-moon, Kelber's world turned black-and-white, but the moths were still going strong. At one point, "it took me 20 minutes sitting in my dark lab to be able to see the moth," she tells me. "I couldn't even see its proboscis," but it was still drinking from the right feeders. The lights then faded to the levels of dim starlight, and, though Kelber couldn't see at all, the elephant hawkmoth could still perceive the cards in all their glorious color. But those colors were probably very different from the ones we perceive.

48 **Adults vary so much** (Pain, 2001)
48 **And while smell can be put** (Yarmolinsky, Zuker, and Ryba, 2009)
49 **When a python swallows a pig** (Secor, 2008)
49 **Bees can detect the sweetness** (de Brito Sanchez et al., 2014)
49 **Flies can taste the apple** (Thoma et al., 2016)
49 **Parasitic wasps can use taste sensors** (Van Lenteren et al., 2007)
49 **But if that arm is covered with bitter-tasting DEET** (Dennis, Goldman, and Vosshall, 2019)
50 **Some have taste receptors on their wings** (Raad et al., 2016)
50 **Flies will start grooming themselves** (Yanagawa, Guigue, and Marion-Poll, 2014)
50 **The most extensive sense of taste** (Atema, 1971; Caprio et al., 1993)
50 **They have taste buds** (Kasumyan, 2019)
50 **They're exquisitely sensitive to amino acids** (Caprio, 1975)
50 **So in the mid-1990s** (Caprio et al., 1993)
50 **Cats, spotted hyenas** (Jiang et al., 2012)
50 **Vampire bats, which drink only blood** (Shan et al., 2018)
51 **Other leaf-eating specialists, like koalas** (Johnson et al., 2018)
51 **In 2014, evolutionary biologist Maude Baldwin** (Toda et al., 2021)
51 **Baldwin also showed that hummingbirds** (Baldwin et al., 2014)
52 **This is how all animals see** (Nilsson, 2009)

CHAPTER 2

53 **The *Portia* species are famed** (Cross et al., 2020)
54 **And unlike other spiders** (Morehouse, 2020)
54 **The late British neurobiologist Mike Land** Land wrote great accounts of his own work in Land (2018).
54 **In 1968, he developed an ophthalmoscope** (Land, 1969a, 1969b)
55 **"an exhilarating but very weird"** (Land, 2018, p. 107)
56 **And here's the truly bizarre part** (Jakob et al., 2018)
56 **The eyes of the giant squid** (Nilsson et al., 2012; Polilov, 2012)
56 **Squid, jumping spiders, and humans** A review of animal eyes is Nilsson (2009).
57 **Animal eyes can be bifocal** (Stowasser et al., 2010; Thomas, Robison, and Johnsen, 2017)
57 **They can have lenses** (Li et al., 2015)
57 **Jakob's colleague Nate Morehouse** (Goté et al., 2019)
57 **vision "is about light"** (Johnsen, 2012, p. 2)
57 **Every animal that sees does** (Porter et al., 2012)
58 **In 2012, evolutionary biologist Megan Porter** (Porter et al., 2012)
58 **Vision is diverse** The textbook *Visual Ecology* is a fantastic and very readable primer on vision and its many uses (Cronin et al., 2014).
58 **The biologist Dan-Eric Nilsson** (Nilsson, 2009)
58 **The hydra, a relative of jellyfish** (Plachetzki, Fong, and Oakley, 2012)
58 **Olive sea snakes have photoreceptors** (Crowe-Riddell, Simões, et al., 2019)
58 **Octopuses, cuttlefish, and other cephalopods** (Kingston et al., 2015)
59 **The Japanese yellow swallowtail butterfly** (Arikawa, 2001)
59 **This flurry of evolutionary innovation** (Parker, 2004)
60 **"To suppose that the eye"** (Darwin, 1958, p. 171)
60 **The jellyfish alone have evolved** (Picciani et al., 2018)
60 **In 1994, Nilsson and Susanne Pelger** (Nilsson and Pelger, 1994)
60 **As we saw in the introduction** (Garm and Nilsson, 2014)
61 **Consider the freshwater bacterium *Synechocystis*** (Schuergers et al., 2016)
61 **The warnowiids, a group of single-celled algae** (Gavelis et al., 2015)

61 **Caro had become the latest** (Caro, 2016)
62 **She and Caro calculated that** (Melin et al., 2016)
62 **Caro has a definitive answer: to ward off bloodsucking flies** (Caro et al., 2019)
62 **An animal's visual acuity** An excellent review of visual acuity in animals is Caves, Brandley, and Johnsen (2018).
62 **The current record, at 138 cycles per degree** (Reymond, 1985; Mitkus et al., 2018)
62 **One oft-quoted study from the 1970s** (Fox, Lehmkuhle, and Westendorf, 1976)
62 **Sensory biologist Eleanor Caves** (Caves, Brandley, and Johnsen, 2018)
63 **Octopuses (46 cpd)** (Veilleux and Kirk, 2014; Caves, Brandley, and Johnsen, 2018)
64 **Robber flies manage** (Feller et al., 2021)
64 **For a fly's eye** (Kirschfeld, 1976)
65 **Each half of a scallop's** (Mitkus et al., 2018)
65 **It's even stranger that those eyes** (Land, 1966)
65 **And both are found in the scallop** (Speiser and Johnsen, 2008a)
66 **He strapped their shells** (Speiser and Johnsen, 2008b)
67 **In 1964, Mike Land** (Land, 2018)
67 **Guanine crystals don't naturally form squares** (Palmer et al., 2017)
67 **Chitons are mollusks** (Li et al., 2015)
67 **Fan worms look like** (Bok, Capa, and Nilsson, 2016)
67 **Giant clams look like** (Land, 2003)
68 **In 2018, Lauren Sumner-Rooney** (Sumner-Rooney et al., 2018)
68 **Like brittle stars, sea urchins** (Ullrich-Lüter et al., 2011)
68 **Weirder still, it's only an eye** (Sumner-Rooney et al., 2020)
69 **In one Spanish province alone** (Carrete et al., 2012)
69 **In 2012, Martin and his colleagues** (Martin, Portugal, and Murn, 2012)
70 **A soaring vulture** See Martin (2012), which also reviews and cites Martin's many papers on bird visual fields.
70 **"The human visual world"** (Martin, 2012)
71 **Many animals have an area** (Moore et al., 2017; Baden, Euler, and Berens, 2020)
71 **When a chicken investigates** (Stamp Dawkins, 2002)
71 **Many birds of prey** (Mitkus et al., 2018)
71 **When a peregrine falcon** (Potier et al., 2017)
71 **The left half of a chick's brain** A wide range of experiments is reviewed in Rogers (2012).
72 **A seal's visual field** (Hanke, Römer, and Dehnhardt, 2006)
72 **Cows and other livestock** (Hughes, 1977)
72 **The same is true** An excellent review of regionalization in animal retinas is Baden, Euler, and Berens (2020).
72 **Elephants, hippos, rhinos, whales** (Mass and Supin, 1995; Baden, Euler, and Berens, 2020)
72 **A whale's pupil doesn't constrict** (Mass and Supin, 2007)
72 **Chameleons don't have to turn** (Katz et al., 2015)
73 **Many male flies focus upward** (Perry and Desplan, 2016)
73 **The fish *Anableps anableps*** (Owens et al., 2012)
73 **The brownsnout spookfish** (Partridge et al., 2014)
73 **So can the cock-eyed squid** (Thomas, Robison, and Johnsen, 2017)
73 **Meanwhile, the deep-sea crustacean *Streetsia*** (Meyer-Rochow, 1978)
74 **If you can coax a killer fly** (Simons, 2020)
74 **By filming these pursuits** (Wardill et al., 2013)
75 **Their ultrafast hunts are guided** (Gonzalez-Bellido, Wardill, and Juusola, 2011)
75 **Compared to the photoreceptors of a fruit fly** (Gonzalez-Bellido, Wardill, and Juusola, 2011)
75 **By contrast, it takes between 30** (Masland, 2017)

76 **In general, animals tend to have higher CFFs** (Laughlin and Weckström, 1993)
76 **Compared to human vision** Several values of animal CFFs can be found in Healy et al. (2013); Inger et al. (2014).
76 **Those of swordfish** (Fritsches, Brill, and Warrant, 2005)
76 **Many birds have naturally fast vision** (Boström et al., 2016)
76 **Traditional fluorescent lights flicker at 100 Hz** (Evans et al., 2012)
76 **And those insects have eyes** (Ruck, 1958)
77 **By filming the insect** (Warrant et al., 2004)
77 **The first is obvious** (O'Carroll and Warrant, 2017)
78 **The second challenge is less intuitive** (O'Carroll and Warrant, 2017)
78 **It takes a lot of energy** (Niven and Laughlin, 2008; Moran, Softley, and Warrant, 2015)
78 **Others unsubscribe from vision entirely** (Porter and Sumner-Rooney, 2018)
78 **There are many ways to break an eye** (Porter and Sumner-Rooney, 2018)
78 **Some use neural tricks** (Warrant, 2017)
79 **The structure of a reindeer's tapetum** (Stokkan et al., 2013)
79 **The tarsiers—small primates** (Collins, Hendrickson, and Kaas, 2005)
79 **To dive into the ocean** (Warrant and Locket, 2004)
79 **At 10 meters down** Two great reviews about vision in the ocean are Warrant and Locket (2004); Johnsen (2014).
80 **To be more respectful of deep-sea** (Widder, 2019)
81 **The footage was unmistakable** (Johnsen and Widder, 2019)
81 **But no other creature** (Nilsson et al., 2012)
81 **Sonke Johnsen, Eric Warrant, and Dan-Eric Nilsson** (Nilsson et al., 2012)
82 **The first natural footage was captured in 2012** (Schrope, 2013)
83 **Then, in 2002, Eric Warrant** (Kelber, Balkenius, and Warrant, 2002)

CHAPTER 3

84 **One textbook claimed that** (Tansley, 1965)
84 **And yet, very few species** (Neitz, Geist, and Jacobs, 1989)
85 **Dogs do see color** (Neitz, Geist, and Jacobs, 1989)
85 **Light comes in a range** For excellent primers on color vision, check out Osorio and Vorobyev (2008); Cuthill et al. (2017); and Chapter 7 of Cronin et al. (2014).
86 ***Daphnia* water fleas** A review of unusual color vision is Marshall and Arikawa (2014).
86 **Consider the story of the artist** (Sacks and Wasserman, 1987)
87 **Some, like sloths and armadillos** (Emerling and Springer, 2015)
87 **Others, like raccoons and sharks** (Peichl, 2005; Hart et al., 2011)
87 **Whales have just one cone, too** (Peichl, Behrmann, and Kröger, 2001)
87 **Surprisingly, the cephalopods** (Hanke and Kelber, 2020)
87 **The firefly squid** (Seidou et al., 1990)
87 **Physiologist Vadim Maximov suggested** (Maximov, 2000)
88 **Dogs have two cones** (Neitz, Geist, and Jacobs, 1989)
88 **This means that horses struggle** (Paul and Stevens, 2020)
88 **Color-blind people might be confused** (Colour Blind Awareness, n.d.)
89 **The first primates** (Carvalho et al., 2017)
89 **That's exactly what happened** (Carvalho et al., 2017)
90 **Each extra opsin increases** (Pointer and Attridge, 1998; Neitz, Carroll, and Neitz, 2001)
90 **Since the nineteenth century** (Mollon, 1989; Osorio and Vorobyev, 1996; Smith et al., 2003)
90 **More recently, some researchers** (Dominy and Lucas, 2001; Dominy, Svenning, and Li, 2003)
90 **In 1984, Gerald Jacobs** (Jacobs, 1984)