FEATURES

TALES OF THE TONGUE

Mammalian tongues are very maneuverable thanks to an intricate network of muscle fibers.

Since first evolving 350 million years ago, the tongue has taken myriad forms, unlocking new niches and boosting the diversity of life

By **Elizabeth Pennisi**

Twice, quarterback Patrick Mahomes has led the Kansas City Chiefs to victory in the Super Bowl, the pinnacle of U.S. football. Although most fans have their eyes on the ball as Mahomes prepares to throw, his tongue does something just as interesting. Just as basketball star Michael Jordan did as he went up for a dunk, and dart players often do as they take aim for a bull's-eye, Mahomes prepares to pass by sticking out his tongue. That may be more than a silly quirk, some scientists say. Those tongue protrusions may improve the accuracy of his hand movements.

A small but growing group of researchers is fascinated by an organ we often take for granted. We rarely think about how agile our own tongue needs to be to form words or avoid being bitten while helping us taste and swallow food. But that's just the start of the tongue's versatility across the animal kingdom. Without tongues, few if any terrestrial vertebrates could exist. The first of their ancestors to slither out of the water some 400 million years ago found a buffet stocked with new types of foods, but it took a tongue to sample them. The range of foods available to these pioneers broadened as tongues diversified into new, specialized forms—and ultimately took on functions beyond eating.

"The incredible variation in vertebrate tongue form is replete with astonishing examples of almost unbelievable adaptation," says Kurt Schwenk, an evolutionary biologist at the University of Connecticut. Salamanders whipping out sticky tongues longer than their bodies to snag insects; snakes "smelling" their environment with their forked tongue tips; hummingbirds slurping nectar from deep inside flowers; bats clicking their tongues to echolocate—all show how tongues have enabled vertebrates to exploit every terrestrial nook and cranny. In humans, still more functions crowded aboard the tongue. "I am amazed by everything we do with our tongue: eat, talk, kiss. It's a central part of what it is to be a human," says Jessica Mark Welch, a microbial ecologist at the Forsyth Institute.

Managing these functions spurred the expansion of brain capacity, paving the way not just for throwing touchdown passes, but perhaps also for thinking on our feet. "The idea is that if you can reach with your tongue, you can reach with your hands, and you can reach with your thoughts," says Ian Whishaw, a neuroscientist at the University of Lethbridge. "Intuitively, perhaps we know this," he adds, when we use phrases like "tip of the tongue," "slip of the tongue," and "biting my tongue."

Yet how tongues came about "is one of the biggest mysteries in our evolutionary history," says Sam Van Wassenbergh, a functional morphologist at the University of Antwerp. Like other soft tissues, tongues are rarely preserved in fossils. Hidden inside the mouth, they defy easy observation. In the past decade, however, new technologies have begun to reveal tongues in action in different groups of animals. That work is beginning to yield new insights about the tongue's evolutionary trajectories, and how its specializations fueled further diversification. Kory Evans, an evolutionary biologist at Rice University, says the more biologists learn, the more convinced they are that "tongues are really fantastic."

A TONGUE TURNS OUT to be a slippery thing to define. Although tonguelike structures exist in virtually all vertebrates, from lampreys to mammals, "There is no clear definition to what makes a 'true tongue,'" says Daniel Schwarz, an evolutionary biologist at the State Museum of Natural History

PHOTO: KICKERS/ISTOCKPHOTO

Stuttgart. We tend to think of tongues as soft, muscular, and flexible—like our own. The human tongue is a muscular hydrostat, which, like a water balloon, must maintain the same overall volume when its shape changes. So, when Mahomes sticks out his tongue, it gets thinner overall than when it's just bunched up in his mouth; the same is true for a giraffe's purple tongue when it stretches 46 centimeters to snag leaves from a spiny tree branch.

But murkier cases exist elsewhere in the animal kingdom. The palatal organ of fish such as minnows, carp, and catfish can also be a bundle of muscle, but biologists are split on whether it should be considered a tongue. "Instead of being at the bottom of the mouth, it's at the top," says Patricia Hernandez, a functional morphologist at George Washington University. And despite many ideas, no one really knows this organ's function, Hernandez adds.

That's because fish don't need tongues like ours to swallow their food. They can rely on suction. They open their jaws wide, expand their throats, and pump water through their gill slits to create currents that sweep in food.

But, "The moment animals stick their head out of the water, suction becomes useless," says Schwenk, who has devoted his career to the study of animal tongues. Once those creatures made landfall, "they needed something to take the place of water" to draw prey into their gullet—and air is not dense enough. For millions of years, early landlubbers likely wriggled back to the ocean to swallow prey snagged on land. A few may have held their heads up high and let gravity do the work, like many birds today.

But the makings of a new way of feeding were already present in fish anatomy: a series of curved bones called branchial arches and the supporting muscles. In fish the branchial arches form the jaws, the hyoid bone that supports the back of the jaw, and the skeleton that forms the throat and gill slits. When fish feed, muscles supporting these structures generate suction by depressing and retracting the hyoid and expanding the gill slits to draw water in. To tongue specialists those motions look familiar. "The hyoid's movement to generate suction is very similar to movement of the tongue back and forth to manipulate prey," Schwenk explains.

Schwenk and Van Wassenbergh think that in early land vertebrates the branchial arches and related muscles began to change to form a "prototongue," perhaps a muscular pad attached to the hyoid that flapped when the hyoid moved. Over time, the pad became longer and more controllable, and more adept at grabbing and maneuvering prey (see graphic, p. 789).

Based on experiments with newts, Schwarz thinks a prototongue became functional even before the transition to land. Like other salamanders, newts are aquatic when young but mostly terrestrial as adults. Their metamorphosis, and the change in feeding strategies that accompanies it, might be akin to water-to-land changes that occurred hundreds of millions of years ago. And it holds a clue to how those changes might have unfolded.

Schwarz and his team found that before newts transform into full-fledged adults, they develop a tonguelike appendage that presses food against sharp, needlelike "teeth" on the roof of their mouth. The finding, which he and his colleagues reported in 2020, suggests a tonguelike structure may have helped early tetrapods feed, even before they climbed onto solid ground.

THE DEMANDS OF FEEDING may have prompted the emergence of the tongue, but natural selection then tailored and honed it for myriad other purposes, sometimes creating "ridiculously crazy specialized systems," Schwenk says. For example, web-toed salamanders (*Hydromantes*) whip out a sticky tongue to nab insects or other small arthropods, shooting their entire throat skeleton out through their mouth. This feeding mode involved retooling throat muscles, with one set storing elastic energy that could be instantaneously released to shoot out the tongue, and another set reeling the tongue back in.

Other salamanders, at least 7600 frogs and toads, as well as chameleons and other lizards have independently evolved other extreme forms of this quick-fire "ballistic" feeding. Chameleons, for example, launch their tongues at almost 5 meters per second, catching crickets in less than 1/10th of a second.

Ballistic feeding required adaptations in tongue surfaces and in the spit coating them. Copious gooey saliva exuded from barely visible protrusions called papillae can help make some frogs' tongues so sticky they can snare prey 50% heavier than themselves. The saliva coats the papillae, which can act like tiny sticky fingers to help grip prey, David Hu, a biomechanics researcher at the Georgia Institute of Technology, and his colleagues reported in 2017.

Horned lizards (*Phrynosoma*) use saliva-coated tongues not just to grab prey, but also to protect themselves from it. The ants they eat are powerful biters and particularly venomous, but the lizards swallow them alive. In 2008 Schwenk and Wade Sherbrooke, former director of the Southwest Research Station of the American Museum of Natural History, discovered that thick strings of mucus secreted by tongue and throat papillae incapacitate the noxious prey. More recently, Schwenk found that in horned lizards, the muscles that usually make up the sides of the tongue are only attached at the back. Evolution has reconfigured the muscles' free parts into ridges along the tongue's sides, possibly to create a mucous pocket for binding the ants before swallowing.

Whereas many frog and lizard tongues became fine-tuned for catching prey and getting it down the hatch, snake tongues instead evolved to provide an exquisite sense of smell, an adaptation that enables snakes to detect and sneak up on distant or hidden prey. Differences in the concentrations of an odorant sensed by each tine of a snake's forked tongue help the snake home in on quarry it can't see. As stereotyped as the tongue's flicking seems to be, it's actually quite malleable. Snakes that track prey both in water and in air, such as the northern water snake (*Nerodia sipedon*), modify their tongue's movements depending on whether their head is underwater, at the surface, or in the air, Schwenk and his former graduate student William Ryerson reported last year in *Integrative and Comparative Biology*. They seem to adjust the flicking pattern to optimize the collection of odor molecules in different conditions.

After studying the morphology, physiology, and tongue movements of dozens of reptile species, Schwenk is awed by how much they reveal about an animal's lifestyle. "If you just show me the tongue, I can tell you a huge amount," he says.

TONGUE EVOLUTION helped reptiles and amphibians capture animal prey, but in birds, some of the most outlandish tongue adaptations reflect a taste for plants. Most avian tongues are a stiff sliver of keratin (think fingernails) or bone, with little muscle or other living tissue. They "are just a conveyor belt to move food from front to back," Schwenk says. But there are exceptions—most notably in hummingbirds and other birds that feed on nectar. "The tongue is probably the most vital component for nectar feeding in birds," says David Cuban, a graduate student at the University of Washington (UW) who works with behavioral ecophysicist Alejandro Rico-Guevara.

Nectar is packed with energy and easy to find. But each flower offers just a drop or so, often sequestered in a long, narrow blossom. Many nectar-eating hummingbirds, sunbirds, and other unrelated groups of birds cope with these constraints by being small—

Like some other reptiles and many amphibians, this panther chameleon (*Furcifer pardalis*) shoots out its tongue to catch prey.

PHOTO: ADRIAN DAVIES/NPL/MINDEN PICTURES usually less than 20 grams—and having long slender bills and highly specialized tongues.

Researchers used to assume these birds relied on capillary action—the tendency of a liquid to flow up a narrow tube—to take in nectar. And some of them do, including the pied honeyeater (*Certhionyx variegatus*), Rico-Guevara's student Amanda Hewes and her collaborators have found. In this species the tongue has a paintbrush-like tip for picking up nectar, which is then drawn inward along grooves that run the length of the tongue.

But for hummingbirds, which flick their tongues 15 times per second as they drain each flower and quickly move on, capillary action just isn't fast enough, Rico-Guevara says. His team captured high-speed videos as Anna's hummingbirds (*Calypte anna*), white-necked jacobins (*Florisuga mellivora*), sparkling violetears (*Colibri coruscans*), festive coquettes (*Lophornis chalybeus*), and other hummingbirds visited transparent artificial flowers loaded with artificial nectar. The movies revealed that the hummingbird tongue works like a tiny nectar pump.

Two grooves run from the tip about halfway back, lined with fringes that trap liquid. As the tip of the birds' flexible bill closes, it wrings nectar from fringes near the front of the tongue, pushing the liquid inward; then the bill opens at the base to help move nectar the rest of the way into the mouth, Rico-Guevara's team reported on 3 April in the *Journal of Experimental Biology*.

He and his collaborators have recently turned their attention to some of the oddest nectar-feeding birds: parrots. At

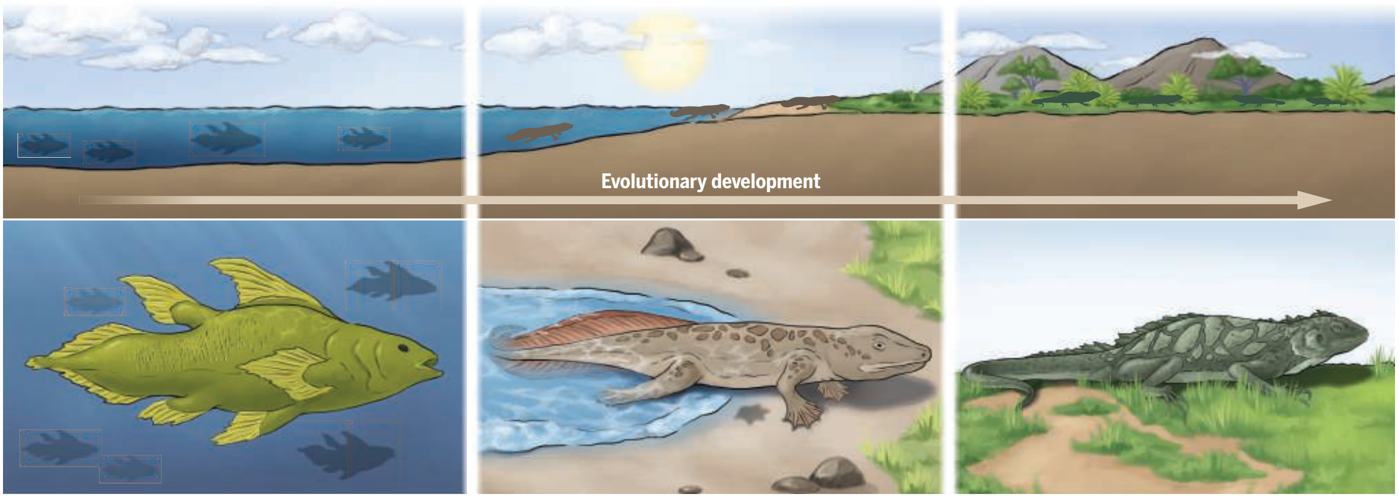
The dawn of the tongue

By making it possible to ingest food without suction, the evolution of the tongue some 350 million years ago was key to enabling vertebrates to move out of the sea and live on land. Skeletal structures originally used for opening gills had to evolve into the bones that could support a tongue and its movements.

Ancestral fish
By opening and closing their gills and throats, fish create water currents to suck in and swallow food.

First forays onto land
Lacking tongues, early tetrapods needed to return to the sea to swallow prey snagged on land.

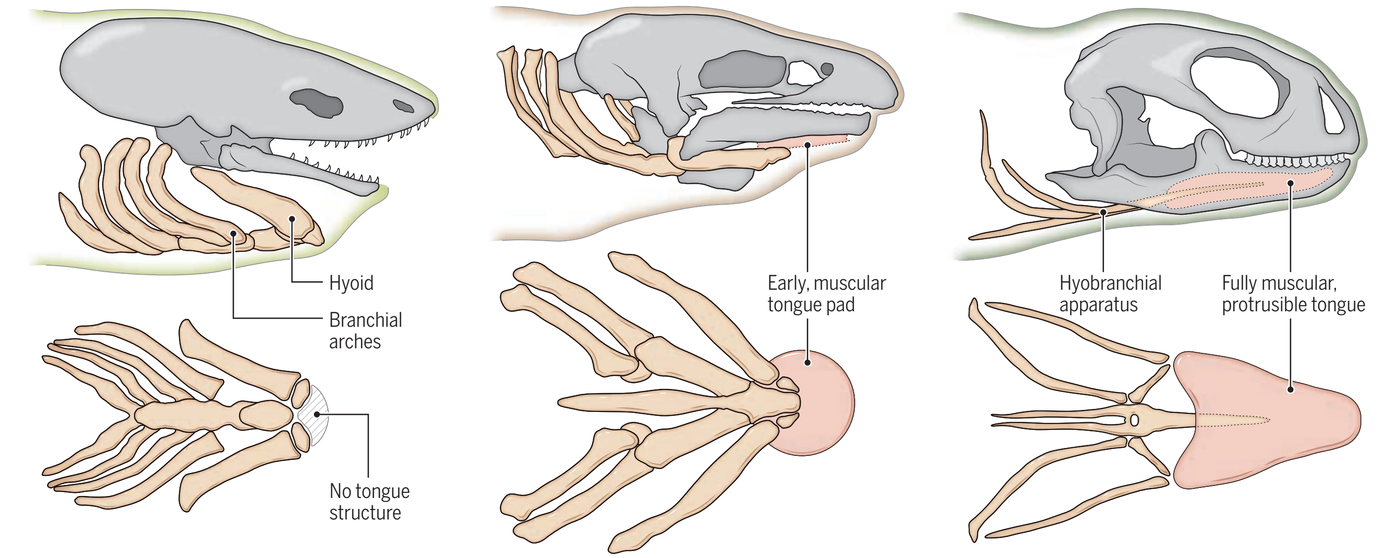
A life lived fully on land
Once animals evolved tongues, they could become fully terrestrial and exploit new foods.



The bare bones
Fish have a series of curved bones called the branchial arches. The bone closest to the mouth is the hyoid; the arches behind it support the gills.

A tongue's beginning
Over time, the hyoid of early tetrapods got more complex, with perhaps the first inklings of a tongue. Some arches disappeared as lungs replaced gills.

A completed transformation
With the skeleton and musculature to support and operate a protrusible tongue, land vertebrates finally became adept at feeding on land.



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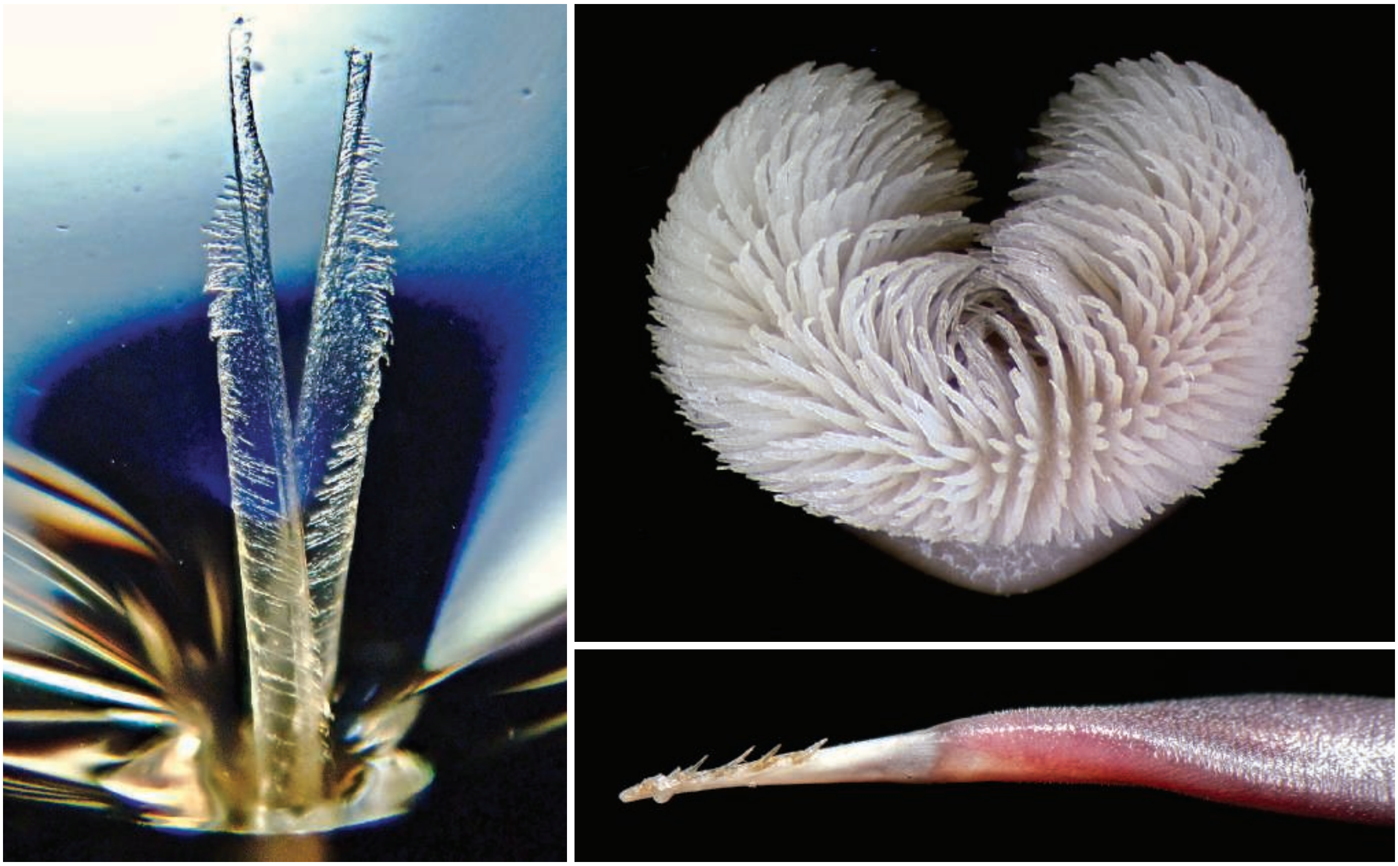


Bird tongues have specialized in many ways to take advantage of different food sources. To sop up nectar, the tongue tip unfurls with fringes in Anna's hummingbird (left), and opens up with paintbrush-like bristles in lorikeets (top right). Green woodpeckers have barbs to harpoon insects (bottom right).

PHOTOS: (CLOCKWISE FROM LEFT) KRISTIINA HURME; ALEJANDRO RICO-GUEVARA AND MAUDE BALDWIN; EMANUELE BIGGI/FLPA/MINDEN PICTURES

30 centimeters tall and 100 grams, the rainbow lorikeet towers over most nectarivorous birds and is utterly incapable of hovering in midair like a hummingbird. It has the typical short, stout, hooked parrot beak and a muscular tongue much like our own—all traits that make slurping nectar from long, thin blossoms impossible. But Rico-Guevara and Cuban have identified adaptations that enable these parrots to get the sweet stuff.

To start, the birds target flatter, more open blooms. And instead of hovering, they land on a nearby branch and contort their bodies around the flower. Then they open their beak and stick out their tongue, which undergoes an amazing transformation as it extends into a flower. The hard, scratchy tongue tip opens into a circular array of fine protrusions, Rico-Guevara recently discovered. "It looks like an anemone, almost," he says. These protrusions work like the bristles of a paintbrush to sop up nectar.

In one experiment, Rico-Guevara laced the test nectar solution with a barium compound, a diluted version of what doctors give patients to look for obstructions in the digestive tract, then took x-ray movies of lorikeet feeding. Once the tongue tip is saturated with a large drop of nectar, he found, the bird presses it against the top of the mouth, squeezing out the liquid. Then it closes its bill, nudging the nectar back toward the throat, and repeats the process until all the nectar goes down.

It's not the only way parrots consume nectar. Last year, Cuban filmed feeding in the more diminutive hanging parrots—so named because they sleep upside down. Instead of a bushy tongue tip like the lorikeet's, these parrots have a grooved tongue tip, and Cuban's videos reveal that they vibrate their tongues very quickly to pump tiny amounts of nectar back toward the esophagus and down the throat.

By describing in detail how these birds feed and calculating the energy they expend in the process, Cuban, Hewes, and Rico-Guevara hope to learn how their feeding strategies may have shaped their evolution—and that of the plants they feed on. Since evolving 22 million years ago, for example, hummingbirds have influenced how much nectar their partner plants produce and how deep their flowers are, and this in turn has influenced the length of the hummingbirds' beaks, their eagerness to monopolize flowers by chasing off competitors, and other traits. It's a coevolutionary dance of birds and flowers—mediated by their tongues.

IT'S IN MAMMALS, however, that the tongue displays its fullest versatility. The mammalian tongue has evolved into an intricate network of muscle fibers capable of moving in complex ways even without any bones, tendons, or joints. It contributes to suckling in most species, helps with thermoregulation in some (picture a panting dog), and takes on even more specialized tasks in a few, such as producing the sounds used for echolocation in bats and speech in humans. And it hosts the taste buds that help guide feeding in all these species. "The tongues of most mammals perform great feats," Hu says. "It's truly a multifunctional tool, and has only received less attention because it is less accessible than an animal's external appendages."

The tongue's most essential job in mammals is to position food to be chewed and swallowed. Depending on the species, that could mean shifting the food from one side to another with each bite or confining it to just one side, while the tongue itself stays safely away from chomping teeth. Then, with the addition of saliva it helps produce, the tongue shapes mashed food into a rounded "bolus" that can fit easily down the throat. Finally, it pushes that bolus back to be swallowed, making sure no food enters the airways. In a sense, the tongue has become a "hand of the mouth," says J.D. Laurence-Chasen, a biologist at the National Renewable Energy Laboratory.

All this processing enables mammals to digest food more rapidly and efficiently, so they get more from their diet than most other animals. That bounty has fueled other evolutionary advances, such as high metabolic rate and activity, prolonged pregnancies, and large brains. Indeed, Callum Ross, a biomechanist and neurobiologist at the University of Chicago, counts the origin of mastication as one the three course-changing evolutionary transitions enabled by the tongue, along with the shift from water to land and the origin of human speech.

Until recently, researchers couldn't get a detailed view of how the tongue maneuvers food because lips, cheeks, and teeth got in the way. But lately Ross's group has been using a technique called x-ray reconstruction of moving morphology (XROMM) that involves recording the movements of surgically implanted beads with x-rays and turning the results into 3D animations.

In their experiments with opossums and monkeys, cameras simultaneously capture images from different angles as an animal eats or drinks, and the reconstructed animation allows the researchers to see how the tongue moves in relation to the jaws and teeth. "We are able to see features of movement that were utterly hidden," explains Elizabeth Brainerd, a functional morphologist at Brown University and an XROMM pioneer who has advised Ross on how to adapt this technology for his studies. By comparing tongue movements in different species, researchers hope to learn how tongue specializations may have contributed to the evolution of each animal's lifestyle and food preferences.

More recently, Laurence-Chasen and Ross worked with Chicago colleague Nicho Hatsopoulos and Fritzie Arce-McShane, now a neurobiologist at UW, to combine XROMM analysis with recordings of neural activity in monkeys. Such studies, they hope, will reveal how the brain coordinates the complex tongue movements involved in feeding, drinking, and perhaps even vocalizations. In one experiment, an array of electrodes monitored a penny-size region of cortex located behind the temple as monkeys munched on grapes. This region contains both sensory neurons that receive input from the tongue and mouth and motor neurons that send signals back to help control tongue movement. The team found that the firing pattern of the motor neurons accurately predicted the tongue's shape changes, they will report soon in *Nature Communications*.

The work upends the once-prevalent notion that chewing, like walking, is mainly under the control of the brainstem. The cortex is very much involved as well, ensuring that the tongue "is capable of complex, asymmetrical deformations" that adjust on the fly to gummy bears, steak, even milkshakes, Laurence-Chasen explains.

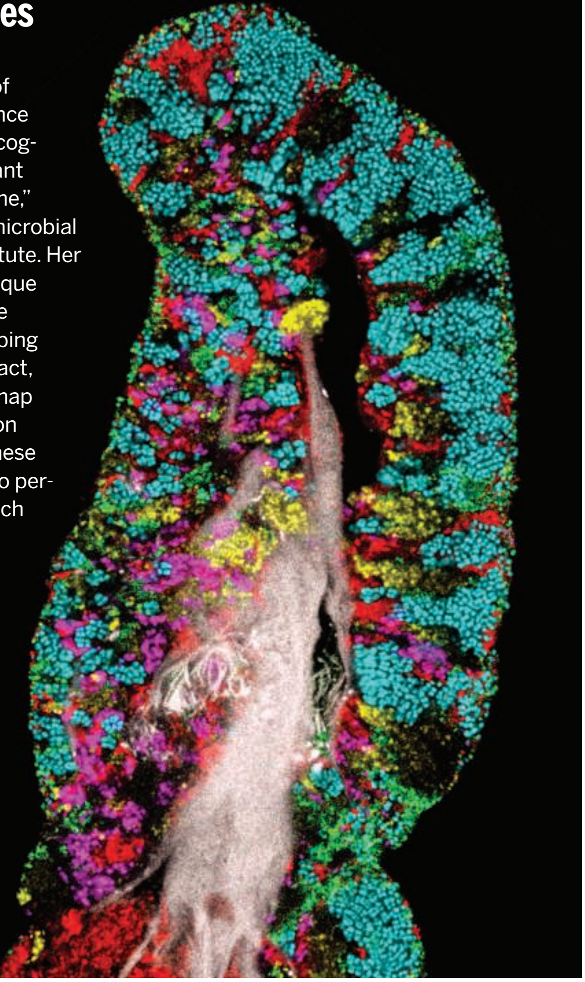
Whishaw wonders whether the human tongue's dexterity could have helped pave the way for our fine control of our hands and even our mind. His curiosity was piqued by an unexpected finding a few years ago. His team had taught mice to use their paws instead of their mouths to pick up fruit. They noticed that some animals stuck out their tongues as they reached with their paws, they reported in 2018.

In follow-up studies that have yet to be published, he, Duke University neurobiologist Xu An, and their colleagues have identified what they call the "oromanual" region of the cortex, a previously uncharted area that exerts control over both the hand and tongue. Whishaw thinks a similar brain region exists in humans and could help explain why so many people gesture as they talk, why children learning to write often twist their tongues as their fingers shape letters—a phenomenon noted by Charles Darwin—and even why Mahomes sticks his tongue out before a pass. He suspects many people move their tongue as they are about to use their hands—but because their mouth stays closed, no one is the wiser.

A common brain region for the hand and tongue makes evolutionary sense, Whishaw says. In early land animals, a dexterous tongue was essential for feeding; later, when some animals began grabbing food with their limbs, evolution might have coopted the same brain circuitry guiding the tongue to coordinate hand movements. He speculates that even more complex behaviors—such as thinking—could have arisen from the brainpower that initially evolved to coordinate the tongue. "I think it is the center of our being, as crazy as that might seem." ■

A home for microbes

The human tongue hosts a complex community of bacteria that can influence our health. "It's an unrecognized and really important part of the human microbiome," says Jessica Mark Welch, a microbial ecologist at the Forsyth Institute. Her team has developed a technique for labeling many of the more abundant bacteria while keeping the microbial community intact, allowing the researchers to map where each species resides on the tongue. Proportions of these microbes vary from person to person, Mark Welch says, but each may have a job. *Rothia mucilaginosa* (●), *Actinomyces* (●), *Neisseriaceae* (●), and *Veillonella* (●) convert nitrate to nitrite—something the human body cannot do—making nitrite available to help regulate blood pressure. Others may help prevent cavities or aid the immune system. "We don't know yet!" Mark Welch says. But seeing what's there is a first step toward finding out. —*E.P.*



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