Friedrich Max Müller, a former professor of philology and linguistics at Oxford University, United Kingdom, was a famous foe of Charles Darwin’s theory of evolution. In one of his public “Lectures on the Science of Language” in 1861, Müller claimed, “language is the Rubicon which divides man from beast, and no animal will ever cross it … the science of language will yet enable us to withstand the extreme theories of the Darwinians, and to draw a hard and fast line between man and brute.”

Darwin responded to Müller in a polite letter arguing “with cordial respect” that, although human language certainly surpasses that of other animals in complexity and scope, animal communication offers a vital window into the early origins of human language.

“With mankind some expressions, such as the bristling of the hair under the influence of extreme terror, or the uncovering of the teeth under that of furious rage, can hardly be understood, except on the belief that man once existed in a much lower and animal-like condition,” Darwin argues in his 1872 book The Expression of the Emotions in Man and Animals. “The community of certain expressions in distinct though allied species, as in the movements of the same facial muscles during laughter by man and by various monkeys, is rendered somewhat more intelligible, if we believe in their descent from a common progenitor.”

Contemporary science is showing that Darwin may have been right all along: The line between human and animal cognition may not be so clear-cut after all.

While rats, chimpanzees, monkeys, zebra finches, and fruit flies may be among the most-studied animals in science, researchers increasingly are turning to the rest of the animal kingdom to better understand the evolution and underlying mechanisms of human cognition. Although the study of these animal models has provided the backbone of our understanding of many cognitive processes, the study of wild animals also can provide tremendous insight into the mechanisms that shape human behavior.

**Beyond the Usual Suspects**
W. Tecumseh Fitch bridges the fields of linguistics, evolutionary biology, and cognitive science in his studies of animal cognition as a window into the evolution of human language. Fitch is a keynote speaker at the upcoming International Conference of Psychological Science in Vienna, Austria.

W. Tecumseh Fitch, the cofounder of the Department of Cognitive Biology at the University of Vienna, Austria, is one pioneer who is using the study of animal cognition to answer questions about the evolution of human language. Fitch’s integrative research bridges the divides among linguistics, evolutionary biology, and cognitive science. In order to learn how humans evolved complex cognitive processes — such as language — scientists can look to contemporary animals as a window into the evolution of our own animal ancestors, Fitch says.

A key challenge in studying cognition’s evolutionary history, Fitch argues in a 2002 paper coauthored with APS William James Fellow Noam A. Chomsky, is that unlike bones, “linguistic behavior does not fossilize.” Fitch, who will discuss his research in a keynote address next March at the International Convention of Psychological Science in Vienna, Austria, has collaborated with biologists, ethologists, neuroscientists, and psychological scientists to study the mechanisms of language across a broad range of animal species, from our closest primate relatives to koalas and crocodiles.

Fitch says that “the evolution of speech was closely tied to control over our sound production system: our vocal tracts”; thus, our impressive vocal repertoire must have evolved in tandem with the neurological and cognitive mechanisms required for making a wide array of sounds. Using comparative methods for examining contemporary species provides researchers with valuable tools for tracing the behavioral abilities of our evolutionary ancestors.

Humans are the only animals able to seamlessly integrate the necessary sensorimotor systems, cognitive systems, and computational mechanisms necessary for complex linguistic structures, allowing us a capacity for complex language through speech, gesture, and writing. Darwin proposed that human language is made up of many different components and mechanisms that evolved together over time; according to this “multicomponent” theory, many different motor, neurological, and cognitive mechanisms each play a part in speech and language. While some animals may have well-developed adaptations for some of these mechanisms, others may lack the necessary anatomy or cognitive development.
For example, primates — our closest evolutionary relatives — are largely incapable of mimicking human speech or other novel sounds in their environment. Even with the cognitive abilities of a human (e.g., some symbolic capacity and a desire to communicate), a bonobo or a chimpanzee lacks the voluntary vocal control necessary to produce human-like speech sounds. This is why chimpanzees and other primates can learn gestures or sign language but cannot speak. Parrots and other birds, on the other hand, are famous for their uncanny ability to mimic the sounds of human speech, but with a few exceptions don’t appear to attribute meaning to words. Thus, vocal control and vocal learning can evolve independently of the rich and complex semantics of human language.

Songbirds are some of the most commonly used animal models for studying vocal learning. Birds such as the zebra finch learn complex songs much as human infants learn language, making them excellent models for vocal learning in many ways. However, birds have dramatically different vocal anatomies and brain structures from mammals. Fitch and colleagues are looking beyond the usual suspects of songbirds and primates to help untangle some of the mysteries of human speech.

The Language of Seals

Most people have heard a parrot talk, but few realize that some seals can do so as well. As one of the only mammalian species capable of vocal learning that uses a human-like sound production system, with larynx, tongue, and lips, seals are some of the best nonhuman animals for research on complex vocal learning, Fitch and colleagues argue.

The last common ancestor of birds and humans lived approximately 300 million years ago; pinnipeds (the clade to which seals, sea lions, and walruses belong) shared a common ancestor with humans only about 65 million years ago. Not only do seals have vocal tracts and larynxes that closely resemble human vocal structures, but some pinnipeds appear capable of mimicking human speech with the same degree of skill as many parrots. Perhaps the most famous example of spontaneous vocal learning in a mammal is a male harbor seal named Hoover.

An orphaned pup raised by a Maine fisherman, Hoover was transferred to the New England Aquarium in Boston in 1971. As an adult, Hoover would mimic phrases such as “Hey! Hello they-uh!” and “Hey! Hoov-ah, come ovah hee-ah!” with an unmistakable New England accent, sounding like the very embodiment of a burly Maine fisherman.
Fitch, along with an international team of psychological scientists, cognitive biologists, and zoologists from Belgium, Germany, and the Netherlands, recently coauthored a paper extolling comparative pinniped research as a field ripe for further study. Not only are pinnipeds capable of vocal production learning (VPL), but new research suggests they also are capable of other forms of sophisticated auditory perception, including the use of rhythm and synchronization.

“We suggest that pinnipeds are ideal species to understand human speech, rhythm, and complex VPL at different levels (including physiology, behavior, neurobiology, and genetics). Pinnipeds’ vocal anatomy, brain evolutionary history, socioecology, and broad range of environmental conditions conveniently map to human biology,” Fitch and colleagues write in the article.

Hyenas Can Count

Seals aren’t the only wild mammals that might offer insight into how and why we developed the uniquely human adaptation of language.

Until recently, the largest colony of captive spotted hyenas in the world resided in Berkeley, California. Berkeley’s Field Station for the Study of Behavior, Ecology, and Reproduction (FSSBER) was started in the early 1960s to support the study of behavior in more natural settings than those provided by the typical laboratory cage. The FSSBER hyena colony was founded in 1985 by University of California, Berkeley, psychological scientist Stephen E. Glickman and wildlife biologist Laurence G. Frank as part of a research project examining sexual differentiation and the role of hormones in creating male and female phenotypes.

Hyenas live in highly hierarchical groups called “clans” that can include more than 90 individuals. Female hyenas are unique among other mammals for their highly masculinized biology; along with having very unusual genital development, female hyenas are typically larger than males and also hold the higher rank in the clan’s social hierarchy. They often hunt in groups, a strategy that allows them to bring down large prey such as wildebeest and zebras. The Berkeley hyena colony provided an exceptional array of diverse researchers with an unprecedented opportunity to study behavior and biology in highly social and intelligent nonprimates. Hyenas also can provide insight into another area of cognition: They have one of the richest repertoires of vocal communication of any mammal.

Although the FSSBER’s hyena facility shuttered in 2014 due to a lack of funding (the hyenas now are housed across several other wildlife parks), the 26-member hyena colony allowed scientists to study the cognitive mechanisms that eventually facilitated our evolutionary ancestors’ development of complex language.

Along with the ability to produce whoops, moans, and their famously human-like giggle, spotted hyenas possess a complex vocal repertoire that far surpasses most primates, providing researchers with an opportunity to study vocal communication in an animal more closely related to our highly social mammalian ancestors than zebra finches.

“Evolution of complex sound perceptions goes hand in hand with complex cognitive ability. Sounds need to be interpreted both socially and cognitively,” says Frédéric E. Theunissen, a University of
California, Berkeley, professor of psychology, in a video interview. “Hyenas aren’t primates, but they also have complex social structures and have a communication system that’s as sophisticated as those seen in nonhuman primates. [It] shows what is needed to evolve the capability of language.”

Just as humans communicate a wealth of information through tone, rhythm, pitch, and volume, hyenas are able to communicate an astounding amount of information through variations in sound.

A hyena’s giggle is actually more akin to a human’s nervous chuckle than to a belly laugh (a single giggle is composed of a several short bursts of sound, hence the common comparison to human laughter). In the wild, hyenas make this sound as a signal of submission during close social interactions, such as while feeding. Captive hyenas tend to giggle when they are frustrated, particularly when they are waiting for food.

An integrative team of researchers conducted a study on the Berkeley hyena colony in 2008 demonstrating that, much like human voices encode for distinctive individualizing information, hyenas use their individual “voices” to communicate startling amounts of information. The team included neuroethologist Nicolas Mathevon (Université de Saint-Etienne, France) and University of California, Berkeley, psychological scientists Aaron Koralek, Mary Weldele, Glickman, and Theunissen.

Using the same recording techniques traditionally employed to analyze vocal patterns in zebra finches, the research team visited the hyena habitat during feeding time to record the giggles of each of the 26 hyenas in the clan. To elicit giggles, the researchers kept food on the other side of the enclosure’s fence so the animals could see and smell it. They logged recordings for each animal across at least 4 different days. During the experiment, individuals being recorded were isolated from the other animals in their enclosure to prevent fights or injuries.

The scientists found that giggles not only were acoustically unique to each individual animal, they conveyed detailed information about the animal’s age, sex, and dominance position. Just as a human voice provides detailed personal information through tone, volume, accent, and prosody, hyenas rely on subtle elements of sound to communicate socially relevant information. The acoustic analysis focused on several features of each giggle, including the fundamental frequency (pitch), the energy distribution among the spectrum (vocal timbre), and the characteristics of the frequency modulation.

The results showing distinctive acoustical differences between individuals provide strong evidence that hyenas can identify individuals based on the sound of their giggles, similar to the way humans can identify each other by the sound of their voices. This ability to immediately identify which clan members are nearby becomes vitally important for bringing down prey. In the wild, lions regularly use their superior strength and numbers to steal kills away from hyenas. Giggles, which are quite loud and carry across great distances, allow hyenas to rally together to fend off such predators.

“It is known that a solitary hyena has no chance when confronted [by] a lion, whereas a hyena group often can ‘mob’ one or two lions and maintain or gain access to a carcass,” Mathevon and colleagues write. “Thus a lone hyena encountering a kill dominated by lions could use its giggle call to rally its clan.”
Studies conducted by Michigan State University behavioral ecologist Kay E. Holekamp have shown that hyenas can use these individually distinctive vocal cues to estimate how many interlopers are approaching. Holekamp and colleagues played recordings of hyenas made elsewhere in Africa to wild hyenas in Kenya and observed their reactions. When the hyenas heard the recordings in a group, they were likely to approach the source of the sound together. But playing the same recordings to single hyenas provoked very different behavior: When they perceived that they were outnumbered by strangers, they were unlikely to approach the source of the sound.

Holekamp’s colleagues in the Michigan State University Department of Psychology, Joseph Cesario and Carlos D. Navarrete, were intrigued by similarities between threat regulation in hyenas and their own research on threat responses in humans: When alone, humans tend to perceive threats as physically closer than they really are, but this distance bias seems to vanish when people are in groups.

Across two studies looking at more than 300 White participants, Cesario and Navarrete examined responses to racial bias and group threats. Whether participants were alone or in a group influenced their perceptions of the physical distance of an outgroup (in these experiments, Black males).

“Having one’s group or coalition around may change the perceived seriousness of the threat,” Cesario said. “In that situation, they may not see the threat quite so closely because they have their people around to support them in responding to the threat.”

Beyond race, similar studies conducted by APS Fellow Jay J. Van Bavel (New York University) have found that outgroup membership from Major League Baseball allegiances (New York Yankees fans vs. Boston Red Sox fans) to nationalities also can alter people’s judgements of proximity.

**Can Turtles Play?**

When it comes to animals playing, we might think of dogs fetching sticks or kittens tussling over a ball of string, but play has been described in all kinds of animals, from our nearest relatives (the great apes) to otters, crows, parrots, and even kangaroos. Researchers Sergio M. Pellis and Vivien C. Pellis have dedicated an entire book to describing such behavior in rats. But play may not be limited to mammals — or even to vertebrates.

APS Fellow Gordon M. Burghardt, a professor in the departments of Psychology and Ecology & Evolutionary Biology at the University of Tennessee, Knoxville, has spent decades researching reptiles. In his years of observation, Burghardt had never noticed any reptilian behavior reminiscent of a playful puppy — until he encountered a 50-year-old Nile soft-shelled turtle at the National Zoo in Washington, DC. The turtle, named Pigface, was acquired during the 1940s and kept in a solitary enclosure. When zoo staff added enrichment toys to the tank in the 1980s, Pigface began to interact energetically with them, pushing around basketballs and repeatedly swimming through colorful plastic hoops. A video analysis showed that Pigface spent about 31% of his time interacting with these objects when they were available.

The vast majority of animal taxa do not seem to engage in play behavior, which, until recent decades, was considered to be limited to mammals and some birds. However, just as human children suffer from a lack of play, many species of animals show signs of distress and dysfunction without adequate
opportunities for such engagement.

Pellis and Pellis suggest that social play provides numerous advantages for both animals and humans. In a 2007 review article published in *Current Directions in Psychological Science*, the researchers describe how play fighting in juvenile rats influences both social behavior and brain development. During play fighting, rats will nuzzle the nape of their partner’s neck; in contrast, during a genuine fight, rats will bite each other on the lower flanks and rump. Studies have shown that juvenile rats deprived of social play are more likely to end up with social, cognitive, and neurological deficits than are their well-socialized peers. Without adequate rat social skills, adult rats have difficulty coordinating the complex social behaviors needed for mating, defense of territory, and even getting food.

“If you saw a dog or an otter going around batting a ball, bouncing around and chasing it, and going back and forth and doing it over and over again, we’d have no problem calling it play,” Burghardt explained in a 2010 interview with *The Scientist* in commenting on Pigface. But identifying exactly what behaviors constitute play is a tricky question for comparative psychologists, even in well-studied animals such as rats and monkeys.

Although Burghardt is cautious to avoid anthropomorphism by labeling certain behavior “play,” he also thinks it’s important for researchers to keep an open mind about the possibility of play in “the so-called ‘lower’ vertebrates.” Identifying the variety of play behavior that might exist across species can provide insights into the mechanisms underlying the behaviors as well as the evolutionary history that led to these adaptations.

To help fellow researchers identify play behavior across species, Burghardt has suggested five minimal criteria for identifying an animal at play. The behavior should be incompletely functional for the context; spontaneous, pleasurable, rewarding, or voluntary; different from other, more serious behaviors in form or timing; repeated, but not in abnormal and unvarying stereotypic form (e.g., rocking or pacing); and initiated in the absence of severe stress.

“In a single sentence: Play is repeated, seemingly nonfunctional behavior differing from more adaptive versions structurally, contextually, or developmentally, and initiated when the animal is in a relaxed, unstimulating, or low stress setting,” Burghardt writes in a 2014 article on evolution and play. These criteria aren’t intended to be comprehensive or the final words on the matter, but Burghardt does emphasize that having basic guidelines can help researchers more accurately identify play in species that are less often studied.

Burghardt and colleagues have observed behavior matching this general definition of play in animals ranging from all classes of vertebrates to cephalopods, insects, and spiders: “Monitor lizards grab and push around all kinds of objects, shaking shoes and retrieving soda cans like dogs. A saltwater crocodile plays with a tethered ball. Dart poison frogs engage in social rough-and-tumble play. Mormyrid fish push around and manipulate balls, and the more social freshwater stingrays play keep-away with them. Octopuses manipulate Legos and play catch with balls using their jets. More recently it has been shown that such behavior does not readily habituate and is motivationally robust.”
Darwin’s Legacy

Darwin believed that animal models provided valuable opportunities to research not only the evolution of human biology, but also psychology.

Before publishing *The Expression of the Emotions in Man and Animals*, Darwin circulated a short psychology questionnaire on emotional expressions to his friends and family as well as to far-flung contacts living as far from England as Australia, Borneo, and South America. Inspired by the research on the musculature underlying facial expressions conducted by the neurologist Duchenne de Boulogne, Darwin theorized that not only are many facial expressions shared across human cultures, but that human emotions are the result of neurological mechanisms also present in other animals. “A scream, for instance, uttered by a young animal, or by one of the members of a community, as a call for assistance, will naturally be loud, prolonged, and high, so as to penetrate to a distance,” Darwin wrote. “When male animals utter sounds in order to please the females, they would naturally employ those which are sweet to the ears of the species; and it appears that the same sounds are often pleasing to widely different animals, owing to the similarity of their nervous systems, as we ourselves perceive in the singing of birds and even in the chirping of certain tree-frogs giving us pleasure.”

For more psychological science research on animal cognition, please see the Special Issue on Cognition in Dogs in the October *Current Directions in Psychological Science*.

W. Tecumseh Fitch will deliver a keynote address, “Cognitive Evolution: People are Animals Too,” at the International Convention of Psychological Science 2017, to be held March 23–25 in Vienna, Austria. For more information, visit www.icps2017.org.

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