Animal Behavior: Electric Eels Amp Up for an Easy Meal

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The high voltage discharge generated by electric eels is a powerful predatory weapon. A new study shows that eels exploit basic physics to increase the voltage delivered to prey, inducing muscle fatigue that turns challenging prey items into easy targets.

Electric eels (*Electrophorus electricus*) can deliver powerful jolts of electricity to immobilize prey and defend themselves from possible threats [1,2]. These discharges are generated by a specialized organ containing thousands of excitable cells, whose individual electrical potentials summate to generate an external field as large as 600 V [3–7]. Despite longstanding fascination with these creatures [8,9], we are just beginning to understand exactly how this weaponry works to subdue prey. In 2014, Kenneth Catania [10] revealed that the eel's discharges remotely activate prey motor neurons, resulting in whole-body muscle contractions that cause temporary immobilization. What's more, eels use this remote control to 'ping' hidden prey by inducing involuntary twitches that betray the prey's location [10]. Now an exciting new study by Catania [11], reported in this issue of *Current Biology*, shows that eels take advantage of the physics of electric fields, precisely bending their bodies in such a way as to more than double the voltage delivered to prey. This allows for reliable overstimulation of the prey's muscles, causing extreme muscle fatigue that prevents escape and buys the eel some extra time to handle especially large or poorly positioned prey items before ingesting them.

Electric eels are freshwater fish from northern and central South America, where they are quite common. Human deaths from eels are extremely rare, due to the low levels of current (~1 amp) and short duration (~1 ms) of each discharge. Nevertheless, the high voltage can pack quite a punch, causing involuntary muscle contraction and a painful numbing sensation, which has been likened to the effects of law-enforcement tasers [12]. In some cases, numbness, tingling, and pain can persist for several hours after the initial shock. Thus, they are well known to locals who frequent the water, many of whom refer to them as 'trembler' ('temblador' in Spanish, or 'tremedor' in Portuguese). Early European explorers provided written accounts of the eel's special powers as far back as the early 1500s [8]. Yet, it was not until the mid-1700s that electricity was even hypothesized as the underlying mechanism, and it took until 1776 for convincing evidence to be obtained [8]. As research subjects, electric eels proved useful in deciphering how electricity works, and they were critical to the discovery that electricity plays a

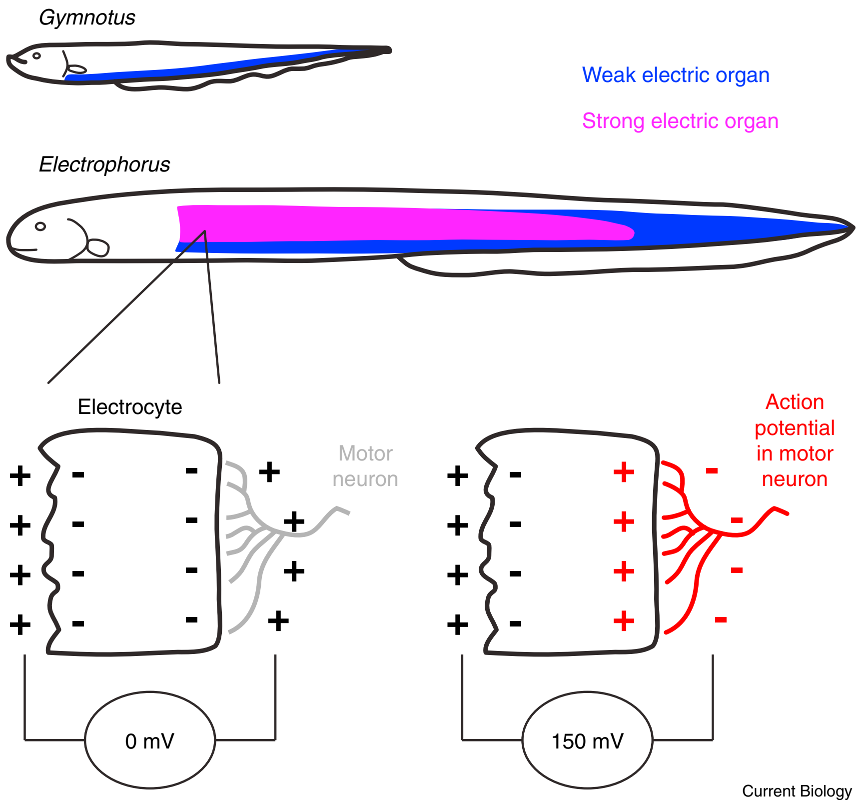

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Figure 1. Electrical discharges are generated by biological batteries called electrocytes.
Weakly electric fish, such as those in the genus *Gymnotus*, generate electrical discharges using the same kinds of cells as the strongly electric eel (*Electrophorus*). At rest, these electrocytes maintain a negative resting potential (inside is negative relative to outside). In response to an action potential from a spinal motor neuron, positive ions flow into one side of the electrocyte, causing its potential to reverse. As a result, the voltage difference across the electrocyte increases by ~150 mV. All of the electrocytes within the electric organ are excited simultaneously so that their voltages summate, like batteries in series. The eel is larger and devotes more of its body to electrocytes, thus resulting in a much larger summated voltage than in weakly electric fish.

fundamental role in the nervous systems and muscles of all animals [8].

There is a large gap, however, between the feeble electricity generated by muscle and the painful shocks generated by the eel, one of many observations that troubled Charles Darwin [13]. According to his theory of natural selection, evolving a powerful electric organ from muscle would require functional intermediates. But how could an electric organ that is too weak to cause shocks be of any use? The answer came ~100 years later, when weak electric organs were shown to mediate electrical communication and active electrical sensing of the environment [14]. The main difference between weak and strong electric organs is simply the number of electrically excitable cells, called electrocytes, housed within the organ [4–7]. In fact, the electric eel has both strong and weak electric organs. Further, the electric eel is not actually an eel at all, but a knifefish in the order Gymnotiformes [15]: given that all gymnotiforms possess weak electric organs, it is clear that the eel's strong organ evolved from weak precursors (Figure 1). Indeed, the eel's genome was recently sequenced, and this helped to identify fundamental genetic changes underlying the evolution of electric organ from muscle [16].

With such longstanding, widespread fascination with electric eels among both scientists and the public at large, one would expect that details of how the eel's shock incapacitates prey would have been discovered long ago. Yet, remarkably, this question was not addressed until recently. Catania [10] observed that eels preceded attacks on prey by discharging high-frequency (~400 Hz) volleys from their strong electric organ, resulting in complete immobilization of prey in just 3 to 4 milliseconds. In an elegant series of follow-up experiments, Catania demonstrated that this resulted from whole-body muscle contractions caused by direct electrical stimulation of motor neurons. Remarkably, the patterning of the eel's high-voltage discharge matches patterns of intrinsic motor neuron activity that most reliably induce rapid and powerful muscle contraction [10,12].

Nevertheless, predation can be a tricky business. Just as predators have evolved an array of specialized predatory adaptations, so too have prey evolved a number of defense and escape tactics. And the scales are not exactly balanced in this arms race: prey are fighting for their life, but predators are only fighting for a meal [17]. Thus, it should come as no surprise that even the stealthiest of predators can be quite bad at catching prey [18]. Large prey might provide an especially filling meal, but they are more difficult to handle, and therefore more likely to escape. And prey positioning can also be an issue: it is much easier to ingest a fish if it is swallowed head first, especially if it has defensive spines. The handling time required to reposition prey so that they can be swallowed creates extra opportunity for escape.

So how might electric eels prevent prey from escaping in such situations? One obvious solution would be to increase the voltage of their discharge, thereby increasing its effectiveness. But the only way to do this would be to increase the voltage produced by each electrocyte. The weakly electric cousins of the eel are indeed able to adjust the amplitude of their discharge in this way, but it requires making new proteins, shuttling existing proteins around the cells, or triggering intracellular signaling pathways to modify existing proteins [7,19]. These all take time, time that the eel does not have when it is dealing with prey trying desperately to escape. Catania [11] has now discovered that, rather than adjusting the *source voltage* coming from the organ, the eels instead perform a behavior that exploits basic physics to increase the *effective voltage* delivered to prey without any change in the actual output of the organ.

As their common name implies, electric eels have long, flexible bodies. Catania [11] observed that when eels capture prey they are not able to swallow immediately, they respond reliably with a precise behavioral sequence. While holding the prey in their mouth, they bend their body so as to position their head close to their tail, and then follow this with a high-frequency, high-voltage volley before releasing the now immobilized prey and repositioning it

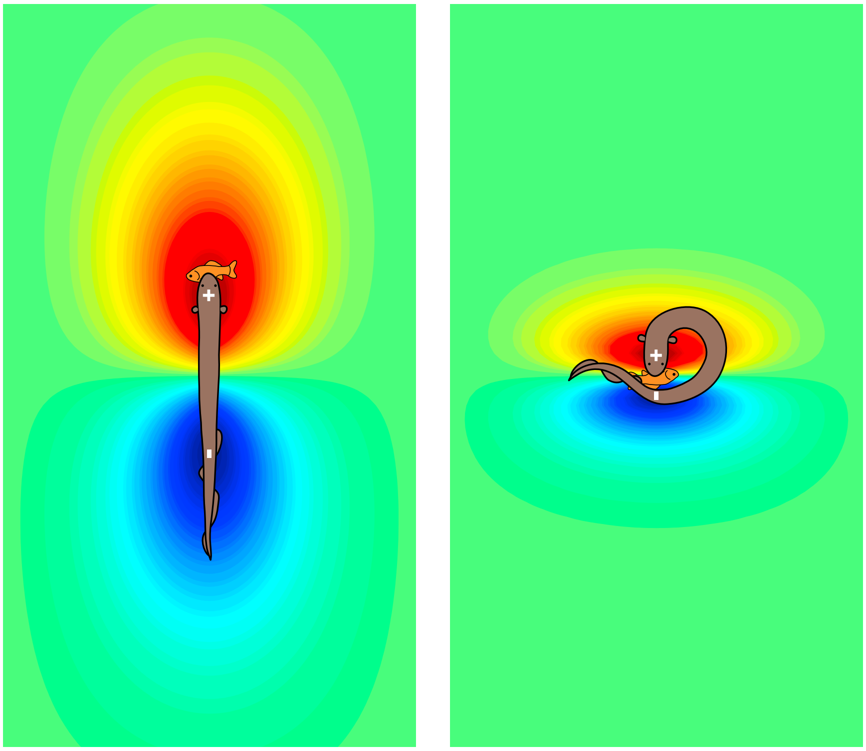

Figure 2. Electric eels bend their bodies to increase the voltage delivered to prey.
When dealing with large or struggling prey that are difficult to handle, the eel bends its body so as to bring the positive and negative poles of its electric organ closer together [11]. This simplified simulation of a dipole electric field shows how this increases the voltage delivered to prey, with different colors representing regions of equal voltage. The voltage gradient (range of colors) imposed on the prey item increases substantially when the eel bends its body.

so that it can be swallowed head first. The high reliability of this behavior suggested it was an adaptation for prey capture, and the physics of electric fields provided a likely answer. The electric organ makes up a whopping ~80% of the eel's body length. When the eel is straight, this means that the positive and negative poles of their internal battery are widely separated in space. But when the eel curls its body, these poles are moved much closer together. In theory, this should lead to a dramatic increase in the voltage experienced by prey (Figure 2). Direct measurements confirmed this theory: the voltage measured at the prey's location more than doubled after the eel curled its body. Catania [11] then went on to show experimentally that the high-frequency, (extra) high-voltage volleys delivered when eels were in this position were extremely effective at inducing muscle fatigue in their prey. This effect lasted long enough to give the eel sufficient time to reposition the prey before it could recover and escape.

Catania's [11] discovery represents a remarkable example of animal behavior exploiting physics of the natural world. Although this behavior is seen in young eels, it remains unknown if it has been innately specified through natural selection or if it results from trial-and-error learning by the eel about what works best at successfully capturing prey. Electric eels have been reported to feed on other gymnotiform species [2,20]. One intriguing question is whether the eel's strong discharge interferes with the electrosensory systems of their weakly electric brethren at a greater working distance than its immobilizing effects. And how does the behavior of the eel compare to that of other strongly electric species such as the torpedo ray or African electric catfish? The surprisingly nuanced and sophisticated electrical predatory behavior of the eel suggests there is still much to be learned about the evolution of behavioral interactions between predator and prey.

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Entomology: A Bee Farming a Fungus

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Farming is done not only by humans, but also by some ant, beetle and termite species. With the discovery of a stingless bee farming a fungus that provides benefits to its larvae, bees can be added to this list.

Farming, the active cultivation or production of useful organisms for nourishment or other benefits, is a kind of mutualistic symbiosis. Typically, the farmed species benefits from protection or improved growth conditions provided