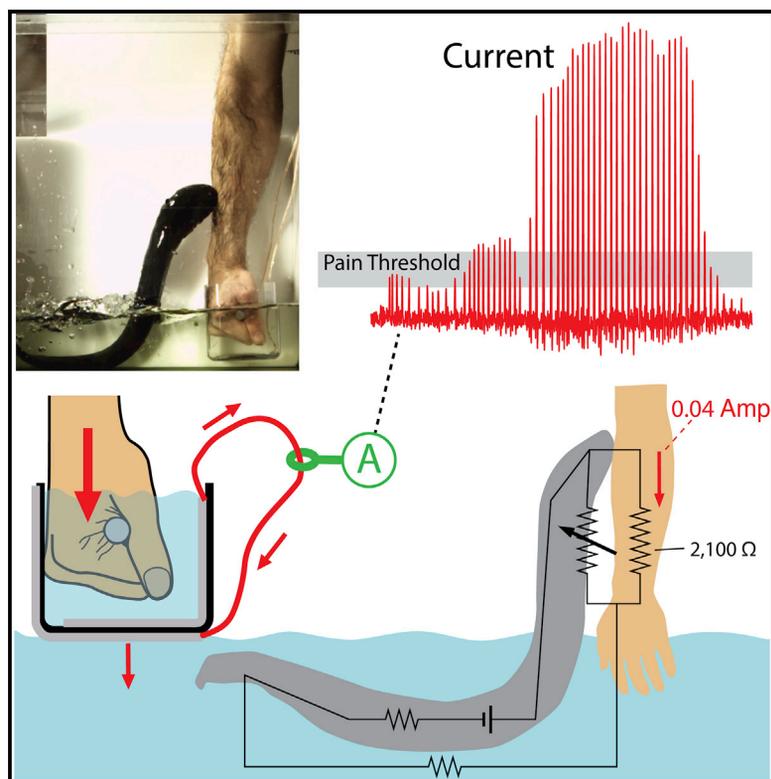


# Current Biology

## Power Transfer to a Human during an Electric Eel's Shocking Leap

### Graphical Abstract



### Authors

Kenneth C. Catania

### Correspondence

ken.catania@vanderbilt.edu

### In Brief

Catania tests the dynamics of the electrical circuit that develops when an electric eel leaps to electrify a threat. Even small eels use this strategy to direct the majority of their electric current through a target. Current levels and eel pulse rates efficiently activate nociceptors, providing a powerful deterrent to potential predators.

### Highlights

- Electric eels leap from the water to directly electrify threats, including humans
- Even small eels impart substantial electrical power to their target
- Currents greatly exceed thresholds for nociceptor activation in diverse species



# Power Transfer to a Human during an Electric Eel's Shocking Leap

Kenneth C. Catania<sup>1,2,\*</sup><sup>1</sup>Department of Biological Sciences, Vanderbilt University, VU Station B, Box 35-1634, Nashville, TN 37235, USA<sup>2</sup>Lead Contact\*Correspondence: [ken.catania@vanderbilt.edu](mailto:ken.catania@vanderbilt.edu)<http://dx.doi.org/10.1016/j.cub.2017.08.034>

## SUMMARY

Electric eels have been the subject of investigation and curiosity for centuries [1]. They use high voltage to track [2] and control [3] prey, as well as to exhaust prey by causing involuntary fatigue through remote activation of prey muscles [4]. But their most astonishing behavior is the leaping attack, during which eels emerge from the water to directly electrify a threat [5, 6]. This unique defense has reportedly been used against both horses [7] and humans [8]. Yet the dynamics of the circuit that develops when a living animal is contacted and the electrical power transmitted to the target have not been directly investigated. In this study, the electromotive force and circuit resistances that develop during an eel's leaping behavior were determined. Next, the current that passed through a human subject during the attack was measured. The results allowed each variable in the equivalent circuit to be estimated. Findings can be extrapolated to a range of different eel sizes that might be encountered in the wild. Despite the comparatively small size of the eel used in this study, electrical currents in the target peaked at 40–50 mA, greatly exceeding thresholds for nociceptor activation reported for both humans [9] and horses [10, 11]. No subjective sensation of involuntary tetanus was reported, and aversive sensations were restricted to the affected limb. Results suggest that the main purpose of the leaping attack is to strongly deter potential eel predators by briefly causing intense pain. Apparently a strong offense is the eel's best defense.

## RESULTS AND DISCUSSION

The first step in analyzing the circuit was to determine the electromotive force ( $\epsilon$ ) and internal resistance ( $r$ ) for the eel's summed electrocytes. For this study, a single relatively small (40-cm-long) electric eel was used for all measurements. Measurements from the eel are values taken from the peak of the high-voltage discharge. Electromotive force and internal resistance were determined using the same paradigm that is often used for batteries and that has been previously used for electric

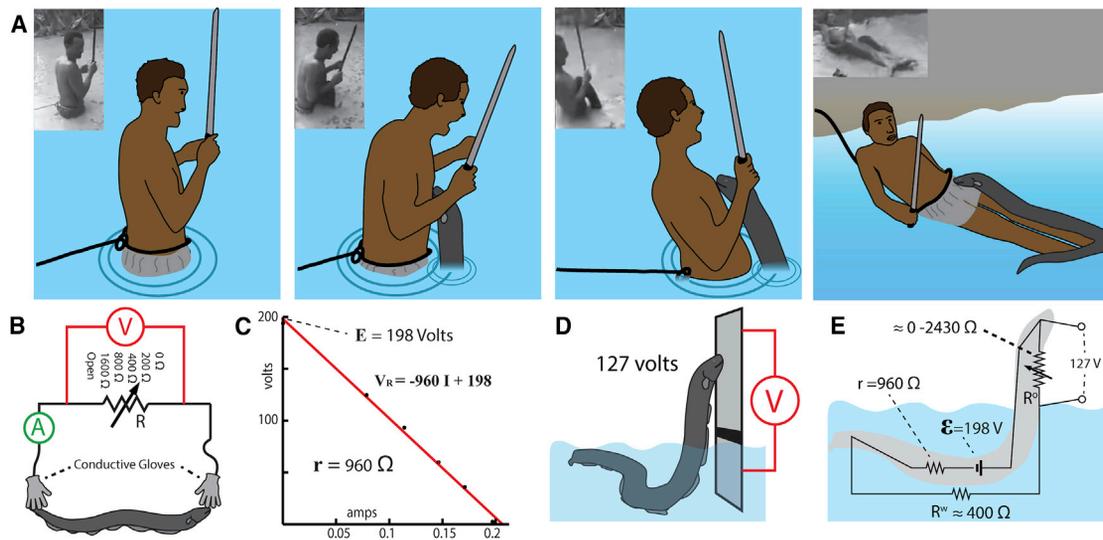
eels [12] and other electric fish [13, 14]. The method is illustrated in Figure 1. The eel was raised from the water in a non-conductive net and contacted at the head and tail with conductive gloves connected to wires. The wires led to a voltmeter and ammeter, as well as to relays that were sequentially introduced resistors into the circuit. Resistors had values of (approximately) 0 ohms, 200 ohms, 400 ohms, 800 ohms, 1,600 ohms, and (lastly) open circuit conditions (each condition lasting 200 ms). The resulting voltages and currents were simultaneously recorded (during the eel's high-voltage discharges) for each condition and then plotted (Figure 1C). A straight line was obtained ( $R$  squared 0.996,  $p < 0.0001$ ). The  $y$  intercept in volts indicates the electromotive force ( $\epsilon$ ), and the slope indicates the negative of the internal resistance ( $r$ ) for the summed electrocytes. The results show that the eel used in this study had an electromotive force of 198 V and an internal resistance of 960 ohms.

The equivalent circuit that develops during the eel's shocking leap has recently been proposed [5] and investigated [6]. In water, this circuit includes the electromotive force of the eel's electrocytes ( $\epsilon$ ), the internal resistance ( $r$ ), and the water resistance ( $R^w$ ). The water resistance was recently measured and was estimated to be approximately 400 ohms (for a 40 cm eel [6]) with water conductivity of 100  $\mu$ S at 25°C. When the eel emerges from the water during a shocking leap, a new resistance develops between the front pole of the animal and the main body of water. As the eel ascends to greater heights, the resistance of this return path from the head to the main body of water increases. The voltage drop across this resistance, relative to eel height, was measured using a split metal plate with one section protruding above the water [6] and a separate section below the water (Figure 1D). An insulator separated the plates, and voltage was measured between the plates while high-speed video was simultaneously recording at 1,000 frames per second. As the eel ascended, potential increased to 127 V.

From the peak voltage recorded in the experiment above, the range of the variable resistance for the return path to the water can be estimated. The total voltage ( $\epsilon$ ) for this eel was 198 V. Therefore, during the peak of the leap shown schematically in Figure 1D, the voltage drop across the summed internal resistance  $r$  and water resistance  $R^w$  was 71 V ( $\epsilon - 127$  V). The current in the circuit was then calculated as  $I = V/R$  or  $71/1,360 = 0.0522$  A. The peak resistance for the return path from the head is therefore estimated to be  $R = V/I$  or  $127/0.0522 \approx 2,400$  ohms.

Figure 1E illustrates the characteristics of the electric eel used in this study during one of its shocking leaps (in water of 100  $\mu$ S conductivity at 25°C). The proposed circuit can be considered an unloaded voltage divider. When the circuit is loaded by





**Figure 1. Attack on a Human and the Paradigm for Circuit Analysis**

Electric eel attack and procedures for investigating electromotive force ( $\epsilon$ ), internal resistance ( $r$ ), and electrical potential during eel shocking leap.

(A) Schematic and plates showing a fisherman being shocked by an electric eel (see [8] for movie link).

(B) Paradigm used to collect voltage and current measurements under six different resistance conditions, each lasting 200 ms. Relays cycled through the resistances as the eel was lifted from the water and contacted with conductive gloves.

(C) Plot of voltage versus current for each resistor condition indicating an electromotive force of 198 V and an internal resistance of 960 ohms.  $R$  squared was 0.996. SEs were too small to plot. For the x axis, SEs were 0.000, 0.006, 0.006, 0.005, 0.007, and 0.021 A for each data point from right to left, and for the y axis were 2.87, 9.19, 5.0, 2.7, 2.0, and 0.24 V for each data point from right to left.

(D) Schematic of the plate arrangement and voltmeter used to measure the electrical potential (127 V) as the eel ascended.

(E) Circuit showing electromotive force ( $\epsilon$ ), internal resistance ( $r$ ), water resistance ( $R_w$ ; from [6]), and the peak value for the variable resistor ( $R_o$ ) estimated from the peak voltage recorded in (D) (see main text).

electrifying a target, an additional resistance is added in parallel to the illustrated return path ( $R^o$ ). Without knowing the value of this added resistor in parallel with  $R^o$ , it is not possible to calculate the total current in the circuit or the voltage drop at each resistance when an eel electrifies a target.

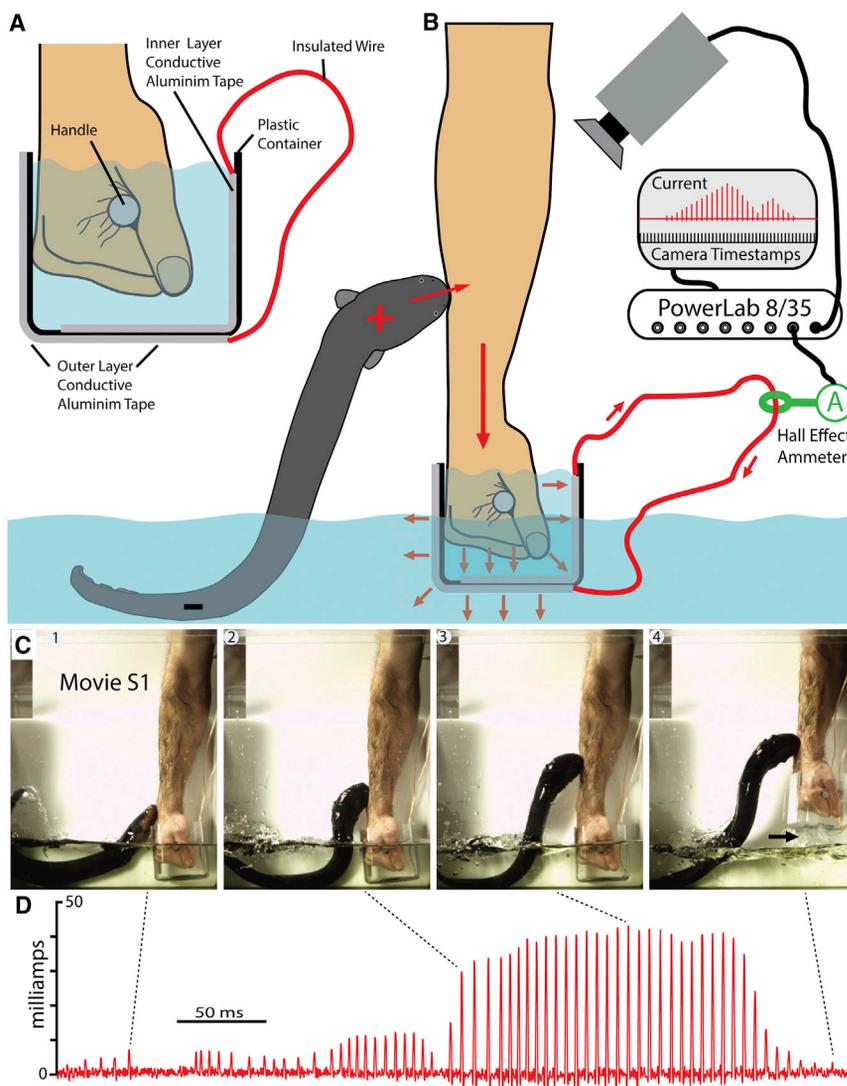
So that the value of this resistance could be determined, an apparatus was designed to measure current through the arm of a human subject as the eel made shocking leaps (Figure 2A). This apparatus consisted of a water-filled plastic chamber with a handle. The posterior and bottom portion of the chamber were covered with conductive aluminum tape such that no direct contact could be made between hand and tape. This paradigm preserved the eel-arm interface and the hand-water interface that normally exist. The chamber's internal layer of conductive tape was then connected, through insulated wire, to conductive aluminum tape on the bottom and front of the plastic chamber to complete the circuit. A hall-effect ammeter measured current through the wire as the eel leapt on the subject's arm (Figures 2B–2D; Movie S1). The trial in Figure 2 corresponds closely to the behavior exhibited in the trial used to measure voltage drop in the split-plate experiment and thus was used for analysis. The peak current through the subject's arm during this trial was 43 mA (Figure 2D).

From the peak current measured through the subject's arm at the top of the leap, combined with the estimation of an approximately 2,400 ohms return path resistance along the eel's body at the top of the leap (Figures 1D and 1E), the target resistance was determined to be approximately 2,100 ohms.

Figure 3 illustrates the complete circuit with corresponding currents and resistances for the small eel and the human arm used in this study. The values indicate that roughly 3.9 W of power was communicated to the arm during the peak of each high voltage discharge. These values provide a starting point for extrapolation to other eels, other target animals, and variable water resistances that might be encountered in the Amazon.

A human subject's arm was used in this study under the premise that directly recording data was preferable to making theoretical estimates of the complex interfaces between the eel, the arm, and the water. Additionally, it is clear that humans may be subjected to the eel's defensive behavior (Figure 1). For obvious reasons, a comparatively small electric eel was used for these experiments. Despite its small size, the juvenile eel was able to communicate 40–50 mA of current during each leap. In the trial documented in Figure 2, the eel's volley included more than 20 pulses, imparting 40 mA, at a rate of roughly 175 Hz. Figure S1 illustrates additional trials with currents that peaked closer to 50 mA.

Although 40–50 mA may not seem like much electrical current, it is far above the levels usually used to study pain and reflexive withdrawal reflexes. Most studies of withdrawal reflexes in humans stimulate with transcutaneous currents in the 5–10 mA range [9]. Withdrawal reflexes of horse forelimbs can be elicited with transcutaneous currents ranging from 1.7 to 5.5 mA [10, 11]. Likewise, in dogs, withdrawal reflexes are elicited with transcutaneous currents of 2–4 mA [15]. Moreover, trains of only five



**Figure 2. Current through a Human Subject during the Eel's Attack**

Paradigm for measurement of current through the subject's arm.

(A) Plastic chamber designed to preserve the hand-water interface while providing a low-resistance path (insulated 16G copper wire) back to the main body of water. Current was measured with a hall-effect ammeter independent of the circuit.

(B) Schematic of the eel, arm, and water, illustrating the circuit and current flow (red arrows). The ammeter was connected to a Powerlab data acquisition unit, which simultaneously recorded timestamps from the high-speed video camera.

(C) Frames from high-speed video documenting the eel and the subject's arm. Arrow marks break in circuit as arm was withdrawn.

(D) Current recording during the eel's shocking leap. Current increased as the eel ascended, as predicted from the equivalent circuit in Figure 1. Current peaks were approximately 43 mA. See also Figures S1 and S2.

the involuntary tetanus that occurs for prey [3] and people immersed in water (Figure 1) or when current from an electric eel passes through the trunk [19]. The eel used in this study invariably caused tetanus in submerged prey (fish). The lack of upper extremity tetanus in the present investigation is consistent with the more restricted, deeper, and proximal distribution of motor efferents compared to nociceptors. In one trial, the experimenter neglected to plug the leads from the hand chamber into the ammeter to complete the circuit. During this trial, the eel's discharges were completely undetected by the subject, confirming that the current path in this study was through

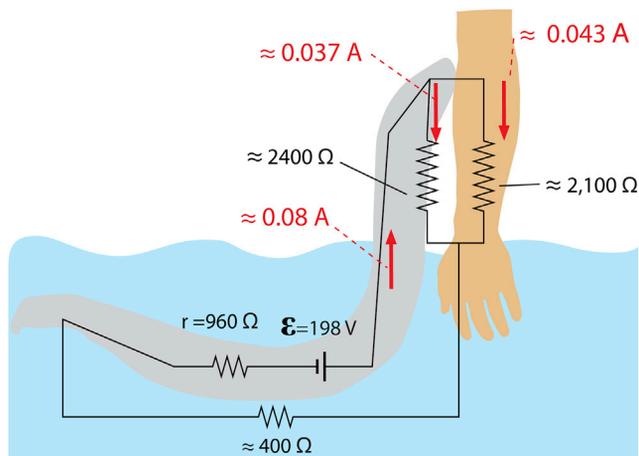
the chamber and that current does not flow through an ungrounded target that does not complete the circuit to water.

Given the comparatively small size of the juvenile electric eel used in this study, it is natural to wonder how the parameters measured in this investigation might apply to larger specimens. In a recent study, the electromotive force (EMF) and internal resistance of four different electric eels were examined using the methods described here [6]. The largest eel was 113 cm in length and had an EMF of 382 V and an internal resistance of 450 ohms. A larger eel could easily reach an EMF of 500 V [12] with a similar internal resistance. The return path resistance from lower jaw to the water for a large eel has been measured at over 5,000 ohms [6]. A human standing in water and contacted on the trunk by the comparatively large surface area of a large eel's lower jaw would be expected to have a considerably lower resistance (perhaps 1,000 ohms or less) than reported here. This follows from the larger surface area of a large eel's jaw, the much larger conduction volume of the human trunk compared to an arm, and the larger body-water interface that completes the circuit when a human stands in water. Electric eels in the Amazon

supra-threshold pulses are sufficient to elicit withdrawal reflexes and nociceptor activation in humans [9, 16, 17], horses [10, 11], dogs [15], and mice [18].

It is therefore not surprising that the subject reported that the eel's shocking leaps were strongly aversive. The subjective report was that involuntary arm withdrawal occurred on every trial during which a circuit was made by the eel (e.g., Movie S1 and Figure S1). Although a reflexive response cannot be confirmed without electromyogram (EMG) recordings and latency measures, it would be unusual if the withdrawal reflex had not been elicited. Greatly exceeding thresholds for the withdrawal reflexes in diverse species provides a convenient benchmark for rating the averseness of the eel's attack, and it is a testament to the potential effectiveness of the leaping defense.

Despite the reported efficiency of nociceptor activation in the present study, there was no subjective sensation of tetanus or restricted movement. Although it is possible the hand muscles were involuntarily activated, the biceps and shoulder were mobile throughout the experiment. This can be contrasted with



**Figure 3. The Complete Circuit**

Resistances and currents for each component of the circuit during the eel's leaping attack on a human arm. Resistances are shown in black, and currents are shown in red.

have been found in water with a conductivity of  $95 \mu\text{S}/\text{cm}$  [20], similar to the values used for the present experiments. With these assumptions applied to the circuit in Figure 3, the human target would experience a current of 0.25 A during each high-voltage discharge for a peak power transfer of 63 W. This is almost an order of magnitude greater than the 7.4 W imparted by the pulses of a law-enforcement TASER [21]. Clearly, electric eels can deliver substantial power directly to a threatening animal with this unique defensive behavior.

These findings raise a number of interesting questions for future study. For example, the juvenile eel used in this investigation projected a larger proportion of its body from the water than was observed for any of the large eels previously investigated [5, 6]. Typical examples for the largest eel are illustrated in Figure S2, during which the eel ascends for only about a third of its length. In contrast, the small eel often leapt to project almost its entire body above the water. It is possible that small eels, with greater internal resistance, shorter (absolute) leap heights, and less electromotive force [6], must leap to greater relative heights to divert sufficient current to their target. Alternately, any sized eel might need to reach a minimum absolute height to divert sufficient current to the target for deterrent effect. More study of a range of specimens and targets might shed light on this possibility. In addition, nothing is presently known about the predominant predators that led to the evolution of this behavior. It is possible that interposing fur or an epidermis of scales, typical of mammalian or crocodilian predators, respectively, have substantially greater resistance than human skin. If so, this would require the eel to reach greater heights to divert similar currents to the target.

Finally, although electric eels have been the subject of hundreds of years of “hands-on” study and there have been many shocking encounters between humans and eels in South America, the author is unaware of any documented lethal encounters from direct electrocution. Faraday famously conducted “hands-on” experiments with electric eels with no reported ill effects [22]. Even Humboldt, who seemed to relish a good fish story [7],

attributed the death of two horses in 1800 to exhaustion followed by drowning while trapped, rather than the direct result of electric shock. On the other hand, the effect of tetanus while in water would most likely pose a substantial danger; even an experienced swimmer might drown. An account from the 1600s describes a fisherman who was paralyzed by an eel and rescued by boat just before drowning [1]. This is presumably why, in Figure 1, the fisherman's comrades had him tied to a rope, obviously a wise precaution.

## STAR METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT INFORMATION AND RESOURCE SHARING
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
- QUANTIFICATION AND STATISTICAL ANALYSIS

## SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures and one movie and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.08.034>.

## AUTHOR CONTRIBUTIONS

K.C.C. conceived of the experiments, conducted the research, wrote the paper, and acquired the funding.

## ACKNOWLEDGMENTS

This work was supported by NSF grant 1456472 to K.C.C.

Received: July 9, 2017

Revised: July 27, 2017

Accepted: August 15, 2017

Published: September 14, 2017

## REFERENCES

1. Finger, S., and Piccolino, M. (2011). *The Shocking History of Electric Fishes: From Ancient Epochs to the Birth of Modern Neurophysiology* (Oxford University Press).
2. Catania, K.C. (2015). Electric eels use high-voltage to track fast-moving prey. *Nat. Commun.* 6, 8638.
3. Catania, K. (2014). The shocking predatory strike of the electric eel. *Science* 346, 1231–1234.
4. Catania, K.C. (2015). Electric eels concentrate their electric field to induce involuntary fatigue in struggling prey. *Curr. Biol.* 25, 2889–2898.
5. Catania, K.C. (2016). Leaping eels electrify threats, supporting Humboldt's account of a battle with horses. *Proc. Natl. Acad. Sci. USA* 113, 6979–6984.
6. Catania, K.C. (2017). Electrical potential of leaping eels. *Brain Behav. Evol.* 89, 262–273.
7. von Humboldt, A. (1807). Jagd und Kampf der elektrischen Aale mit Pferden. *Ann. Physiol.* 25, 34–43.
8. Hawkin, A. (2016). Would you act as bait for an electric eel? Brave fisherman wades into swamp to find creature - and gets the shock of his life. *Daily Mail*, May 24, 2016. <http://www.dailymail.co.uk/news/article-3606407/Would-act-bait-electric-eel-Brave-fisherman-wades-swamp-creature-gets-shock-life.html>.

9. Skljarevski, V., and Ramadan, N.M. (2002). The nociceptive flexion reflex in humans – review article. *Pain* 96, 3–8.
10. Spadavecchia, C., Spadavecchia, L., Andersen, O.K., Arendt-Nielsen, L., Leandri, M., and Schatzmann, U. (2002). Quantitative assessment of nociception in horses by use of the nociceptive withdrawal reflex evoked by transcutaneous electrical stimulation. *Am. J. Vet. Res.* 63, 1551–1556.
11. Spadavecchia, C., Arendt-Nielsen, L., Andersen, O.K., Spadavecchia, L., Doherr, M., and Schatzmann, U. (2003). Comparison of nociceptive withdrawal reflexes and recruitment curves between the forelimbs and hind limbs in conscious horses. *Am. J. Vet. Res.* 64, 700–707.
12. Brown, M.V. (1950). The electric discharge of the electric EEL. *Electr. Eng.* 69, 145–147.
13. Bell, C.C., Bradbury, J., and Russell, C.J. (1976). The electric organ of a mormyrid as a current and voltage source. *J. Comp. Physiol.* 110, 65–88.
14. Baffa, O., and Côrrea, S.L. (1992). Magnetic and electric characteristics of the electric fish *Gymnotus carapó*. *Biophys. J.* 63, 591–593.
15. Bergadano, A., Andersen, O.K., Arendt-Nielsen, L., Schatzmann, U., and Spadavecchia, C. (2006). Quantitative assessment of nociceptive processes in conscious dogs by use of the nociceptive withdrawal reflex. *Am. J. Vet. Res.* 67, 882–889.
16. Andersen, O.K., Sonnenborg, F.A., and Arendt-Nielsen, L. (1999). Modular organization of human leg withdrawal reflexes elicited by electrical stimulation of the foot sole. *Muscle Nerve* 22, 1520–1530.
17. Arendt-Nielsen, L., Sonnenborg, F.A., and Andersen, O.K. (2000). Facilitation of the withdrawal reflex by repeated transcutaneous electrical stimulation: an experimental study on central integration in humans. *Eur. J. Appl. Physiol.* 81, 165–173.
18. Kimura, S., Honda, M., Tanabe, M., and Ono, H. (2004). Noxious stimuli evoke a biphasic flexor reflex composed of A  $\delta$ -fiber-mediated short-latency and C-fiber-mediated long-latency withdrawal movements in mice. *J. Pharmacol. Sci.* 95, 94–100.
19. Ellis, M.M. (1913). *The Gymnotid Eels of Tropical America* (No. 77) (Carnegie Institute).
20. Crampton, W.G.R. (1996). Gymnotiform fish: an important component of Amazonian floodplain fish communities. *J. Fish Biol.* 48, 298–301.
21. Sinclair I.P. (2009) *TASER Model X26 Test Concepts*. Report from Electronics Test Centre, MPB Technologies, January 22, 2009, doc. no. ETC-CEW-0101201. Rev 7.
22. Faraday, M. (1832). Experimental researches in electricity. *Philos. Trans. R. Soc. Lond.* 122, 125–162.

## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
Electric Eel ( <i>Electrophorus electricus</i> )	Local Fish Store	N/A
Software and Algorithms		
LabChart 7 Pro v7.2.5	ADInstruments, Colorado Springs CO	N/A
JMP Pro 12 statistical program	SAS Institute, Cary, NC	N/A
Adobe Illustrator	Adobe Systems USA	N/A
Other		
MotionXtra NX7S1 camera	IDT, Tallahassee, FL	N/A
P4100 100:1 probe	Sainsmart, Lenexa Kansas	N/A
Model H1-ACDC-72 (hall effect) current sensor	BDW Enterprises	N/A
115 True RMS multimeter	Fluke	N/A
Conductive Therapy Gloves	Conductive Therapy Shop	N/A
Master 8 stimulator	A.M.P.I Jerusalem, Israel	N/A
PowerLab 8/35 Data Acquisition Unit	ADInstruments, Colorado, Springs CO	N/A
Tektronix TBS 2000 digital oscilloscope	Tektronix, Oregon, USA	N/A
TPP0100, 10x attenuating probe	Tektronix, Oregon, USA	N/A
Ohaus Starter 300C conductivity meter	Ohaus corporation, Parippany, NJ	N/A
RPS Studio CoolLED 100 RS-5610	Amazon.com	RS-5610

### CONTACT INFORMATION AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Kenneth Catania ([ken.catania@vanderbilt.edu](mailto:ken.catania@vanderbilt.edu)).

### EXPERIMENTAL MODEL AND SUBJECT DETAILS

All animal procedures were reviewed and approved by Vanderbilt's Institutional Animal Care and Use Committee. All human procedures were reviewed by Vanderbilt University's Institutional Review Board (IRB) and permission for procedures was given under IRB # 162051. The electric eel (*Electrophorus electricus*) was a single 40 cm length specimen of unknown sex. The human subject was a single male individual 51 years of age.

### METHOD DETAILS

A single 40 cm length electric eel (*Electrophorus electricus*) was used for this study. It was housed in a custom-made Plexiglas aquarium with aerated water, gravel bottom, plastic imitation branches and plants and fed earthworms and fish. Temperature was between 24 and 26°C and pH between 6.5 and 7.0, conductivity between 100-200  $\mu$ S/cm on a 12/12 light-dark cycle. To record voltage and current from the eel, it was lifted in a non-conductive net, and contacted at the head and tail with silver-thread conductive therapy gloves (Conductive Therapy Shop) worn over rubber gloves. The conductive gloves were connected to 16 gage, braided copper speaker wire to five relays controlled by a Master 8 stimulator (A.M.P.I Jerusalem, Israel) that sequentially activate the relays at 200 ms intervals (including 200 ms with no relay activated giving 6 conditions). The relays sequentially cycle through; open circuit, then approximately 1600 ohms, 800 ohms, 400 ohms, 200 ohms, and zero ohms. Voltage and current were simultaneously measured. The resistors were 5 W, 200 ohms ceramic resistors  $\pm$  5% accuracy that were added together by the relays to produce the values listed above during the experiment. Voltage was recorded with both a PowerLab 8/35 data acquisition unit (ADInstruments) through a P4100 100:1 probe (Sainsmart, Lenexa Kansas) using LabChart software (version 7, ADInstruments) and with a Tektronix TBS 2000 digital oscilloscope through a tuned TPP0100, 10x attenuating probe. Current was measured with a Model H1-ACDC-72 (hall effect) current sensor (BDW Enterprises). A known calibrating current (measured by a Fluke 115 True RMS multimeter) was passed through the current sensor and recorded prior to every trial. For all experiments in water, conductivity was 100 microseimens/cm (measured with a calibrated Ohaus Starter 300C conductivity meter accurate to  $\pm$  0.5%, Ohaus

corporation, Parippany, NJ) and water temperature was 25°C. Current through the subject's arm was measured from the wire connecting the hand chamber to the water using the same technique. For the split plate experiment, the electric organ discharges were recorded from the leaping eel by connecting a split aluminum plate to wires connected to a PowerLab 8/35 data acquisition unit and oscilloscope as illustrated in [Figure 1](#). Video was collected with a MotionXtra NX7S1 camera (IDT Inc, Tallahassee, FL) with 2 RPS Studio CoolLED 100 RS-5610 for lighting at 1000 frames per second. The high-speed camera's synchronization output was recorded on a separate PowerLab channel allowing coordination of video plates and voltage recordings. To illustrate the eel's output in relationship to eel behavior, data traces were copied at high-resolution from the LabChart 7 program into Adobe Illustrator and illustrated with vector graphics to allow scaling to variable final figure sizes.

### QUANTIFICATION AND STATISTICAL ANALYSIS

To convert recorded voltages from the Model H1-ACDC-72 current sensor into current measures, the relevant area of the LabChart 7 trace was selected, the "min-max" function was used to record the peak from each discharge using the Datapad function, and these values were exported to Microsoft Excel. The deflection from baseline was converted to current values (amps) based on the previously recorded calibration current. These data, in addition to the corresponding voltages from the oscilloscope, were imported into the JMP statistical program (SAS) to determine standard errors and standard deviations for each resistance value. The means for each value were plotted and linear fit determined using the "fit line" function, which was used to produce the graph, R squared value, and p value for the data illustrated in [Figure 1](#) and described in the text. Note that the standard errors in [Figure 1C](#) were too small to be visible on the figure and are instead listed in the figure legend.