Efficient high-voltage protection in the electric catfish

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ABSTRACT
For thousands of years, starting with detailed accounts from ancient Egypt, the African electric catfish (Malapteruridae) has been renowned for its ability to hunt and to defend itself with powerful electric shocks. Surprisingly, the degree to which electric catfish are protected against their own or external electric shocks, how specific any protection would be to the species-specific waveform and whether a discharging catfish has to actively prepare for the onset of its high-voltage discharges has never been analysed. Here, we used digital high-speed video to record catfish during their own discharges or as they were exposed to external discharges, employing goldfish to carefully calibrate the efficiency of all discharges. Electric catfish show a remarkable degree of protection against high voltages: both self-produced and external electric shocks that heavily affected control goldfish failed to evoke involuntary muscle contraction or to affect sensorimotor processing. Even a commercial electrofishing device, set to efficiently immobilise and narcotise fish, has to actively prepare for the onset of its high-voltage discharges has never been analysed. Here, we used digital high-speed video recordings to examine to what extent these remarkable fish are protected against their own and external electric shocks.

KEY WORDS: Electronarcosis, Strongly electric fish, Electric shock, Predator, Novelty response

INTRODUCTION
Starting with the remarkably detailed accounts of the ancient Egyptians (Gamer-Wallert, 1970; Westendorf, 1999), the African electric catfish (Malapteruridae) has been renowned for its ability to generate powerful electric shocks. These are emitted by a specialised electric organ which is composed of a thin layer of electrolytes located directly below the skin that covers nearly the whole body (Fig. 1A,B) (Johnels, 1956). Each electric organ discharge produces a strong monophasic pulse with a duration of 2–3 ms and an amplitude of up to 300 V (Bauer, 1968; Remmler, 1929). Similar to other strongly electric fish, such as the electric eel, electric catfish use their high-voltage pulses as a defensive and offensive weapon (Bennett, 1971). During prey capture, electric catfish emit volleys of electric organ discharges (Fig. 1C) with an initial high-frequency phase (up to 500 Hz) and up to 500 pulses (Bauer, 1968; Belbenoit et al., 1979) that paralyse the muscles of prey fish. These volleys can last for several seconds and stop when the immobilised prey is snapped up and swallowed (Bauer, 1968). Electric catfish are also able to produce brief discharges composed of several high-voltage pulses (Fig. 1D–F) (Ballowitz, 1899; Bauer, 1968) that are thought to be emitted during defensive behaviour against predators (Bauer, 1968; Belbenoit et al., 1979; Rankin and Moller, 1992) or to stir up prey fish (Bauer, 1968; Belbenoit et al., 1979). Such defensive discharges can be elicited by mechanically stimulating the skin of electric catfish (Ballowitz, 1899; Bauer, 1968; Bennett, 1971). In addition, electric organ discharges may also play a role in social interactions between conspecifics (Rankin and Moller, 1986) or in intraspecific communication (Kastoun, 1971; Rankin and Moller, 1992).

High-voltage electric shocks have massive effects on the nervous system (Beaumont, 2016; Nordgreen et al., 2008; Robb and Roth, 2003; Sharber and Sharber Black, 1999) as well as the skeletal muscles of fish (Beaumont, 2016; Catania, 2014, 2015). However, up to now it has only been speculated whether electric catfish are self-protected against their own high-voltage electric shocks (Babucchin, 1877; Bilharz, 1857; Du Bois-Reymond, 1887; Norris, 2002; Rankin and Moller, 1986). Despite centuries of interest, the extent to which skeletal muscles or other electrically vulnerable tissues of electric catfish are affected by their own high-voltage discharges has not been analysed. Moreover, it is unknown whether a discharging catfish prepares for the high voltages similar to the way in which echolocating bats avoid deafening by their intense calls (Suga and Jen, 1975). In this study, we exposed electric catfish to different types of high-voltage electric shocks and used digital high-speed video recordings to examine to what extent these remarkable fish are protected against their own and external electric shocks.

MATERIALS AND METHODS
Animals
We used two electric catfish (Malapterurus beniensis Murray 1855, Malapteruridae) and five goldfish [Carassius auratus (Linnaeus 1758), Cypriniformes]. All fish were obtained commercially from an authorised specialist retailer (Aquarium Glaser GmbH, Rodgau, Germany). The electric catfish (6 and 16 cm) were kept individually in 120 l glass aquaria and the goldfish (5–16 cm) were kept in a 240 l glass aquarium under a 12 h:12 h light:dark cycle (lights on at 07:00 h and off at 19:00 h). The size range of electric catfish and goldfish was chosen so that we could have control goldfish that matched the experimental catfish in size. Temperature (22–24°C), pH (6.5–7.0) and conductivity (250–300 μS cm⁻¹) of the water [based on 50% tap water and 50% demineralised water, enriched with 7% (w/v) NaHCO₃, 4% (w/v) CaSO₄ and 1% (w/v) marine salt] were kept constant during the experimental period. Animal care and all experimental procedures were conducted in accordance with the German Animal Welfare Act (Tierschutzgesetz) as well as the German Regulation for the protection of animals used for experimental purposes or other scientific purposes (Tierschutz-Versuchstierordnung) and were approved by the government of Lower Franconia (Regierung Unterfranken, Würzburg, Germany).

Natural and artificial defensive discharges
Defensive high-voltage discharges can be elicited by touching the electric catfish as described previously (Bauer, 1968; Bennett, 1971). In this study, all defensive discharges of the electric catfish
were elicited by slight mechanical stimulation of the tail with a paint brush as described by Bauer (1968). Additionally, the effect of artificial high-voltage defensive discharges was tested. The artificial discharges consisted of monopolar square wave pulses (99 V) delivered at frequencies of 200 Hz (4 pulses of 3 ms duration each), 300 Hz (5 pulses of 1.5 ms duration) or 600 Hz (10 pulses of 1 ms duration) by an isolated stimulator (DS2A, Digitimer) driven by a pulse generator (TGP-110, TTI).

**High-speed video analysis of the effect of defensive discharges**

To analyse the impact of natural and artificial high-voltage defensive discharges, two fish (either 2 electric catfish or 1 electric catfish and 1 goldfish) swam in an oval custom-made Plexiglas channel. The channel was separated into two halves by plastic mesh. In the centre of one half, a paddle wheel powered by an electric motor created a water current against which the two fish swam in the other half of the channel (12 cm diameter and 90 cm long). A porous filter pad in the channel separated the two fish. The fish were monitored from below at ≥1000 frames s⁻¹ using a high-speed digital video camera (HotShot 2300cc, NAC Image Technology; 20 mm f/1.8 EX DG lens, Sigma). To optimise the contrast, the tank was illuminated from below with two LED floodlights (IP FL-50 COB 6400K, Eurolite). Four control goldfish (5–10 cm) and two electric catfish (16 cm) were monitored while exposed to either defensive discharges generated by the electric catfish or artificially generated discharges delivered by a pair of stimulation electrodes (silver wire) that were positioned 60 cm apart and perpendicular to the longitudinal axis of the Plexiglas channel. As the exact field strength and spatial properties of the defensive discharges within our setup were unknown, special care was taken to ensure that the positions of the test fish were similar in each experiment. More precisely, the discharging electric catfish was always positioned behind (at 5–10 cm distance) the receiving goldfish or catfish, respectively. Additionally, only experiments in which the discharging catfish and the receiving fish swam in line (with a tolerated maximal deviation of about 5 deg) were included in the analysis. All electrical discharges were recorded using two carbon electrodes in the water placed at opposite ends of the test aquaria. Each electrode was first fed into a voltage divider to reduce the output voltage to a quarter of the input voltage and connected to a differential amplifier (EXT 02F-2, npi electronic). Its output was used to trigger the high-speed video system so that it recorded the catfish 100 ms before and for another 100 ms after onset of its discharges.

We analysed the pectoral fin angle relative to the body, body bending and apparent body length using ImageJ software. Body bending was defined as the angle between the tip of the fish’s snout, the ventral midline between the pectoral fins and the caudal peduncle. Body length was defined as the distance between the tip of the fish’s snout and the caudal peduncle (Fig. 2A) and was determined by using the line selection tool in the ImageJ toolbar. The pectoral fin angle and body bending were determined by using the angle tool in the ImageJ toolbar. It was sufficient to determine all parameters every 5 ms in a period from 50 ms before (control interval) to 50 ms after the beginning of a discharge. Body length was normalised to the mean value before the discharge. Movie 1 illustrates the effect of high-voltage defensive discharges on an electric catfish and a goldfish.

**Effect of high voltages on acoustically elicited electric startle responses**

The novelty response in electric catfish was discovered and analysed in a test tank (60×30×25 cm) filled with 15 l of water. To produce an acoustically elicited electric startle response, we used an intense auditory stimulus that consisted of 300 Hz sine waves of 16.66 ms duration. The stimulus was generated using a function generator (DS345, Stanford Research Systems) and delivered by a large loudspeaker (112 MA, Thomann) placed next to the tank. The maximum sound pressure level was 190 dB re. 1 µPa, as measured with a hydrophone at the position of the fish (hydrophone: Brüel and Kjær, type 8106; amplifier: Brüel and Kjær, type 2610). Latency of the defensive discharges generated by the fish in response to the acoustic stimulus was defined as the time between onset of the acoustic stimulus and onset of the discharge. To avoid habituation, acoustic stimuli were delivered at intervals of at least 5 min. In the tests, artificial defensive discharges (5 pulses, 1.5 ms, 99 V, 300 Hz) were delivered simultaneously to the acoustic stimulus and the effect of pairing on latency of the acoustically induced startle response was examined. The artificial discharges were delivered by a pair of stimulation electrodes (silver wire, length 30 cm) that were positioned 60 cm apart and perpendicular to the longitudinal axis of the aquarium and the test fish. Efficiency of the...
Two electrofishing electrodes (each a braided copper strip connected to plate aluminium electrodes; 10×30 cm) were positioned 70 cm apart and perpendicular to the longitudinal axis at the ends of the tank covering the whole surface at each end. One goldfish (15 cm in length) and one electric catfish (16 cm in length) were exposed to a homogeneous electric field (100 Hz pulsed direct current, peak voltage gradients of 3 V cm$^{-1}$) generated by an electrofishing device (ELT61NGI, Hans Grassl GmbH). In all experiments shown in this study, the electric catfish and the goldfish swam in parallel to the electric field lines (tolerated maximal deviation ∼5 deg) at the onset of the electric shock.

First, the fish were exposed to electric shocks for about 1 s to identify any involuntary muscle contractions in the electric catfish. The responses of the fish were recorded from below at 1000 frames s$^{-1}$ using a high-speed digital video camera (HotShot 2300cc, NAC Image Technology; 20 mm f/1.8 EX DG lens, Sigma). To illustrate the normal swimming of the electric catfish during the electric shocks, we analysed the pectoral fin angle relative to the body every 10 ms in a period from 1 s before (control interval) to 2 s after the beginning of an electric shock by using the angle tool of the ImageJ software.

Additionally, the responses of the fish to longer (3–4 s) electric shocks that usually narcotise fish were recorded from the side at 30 frames s$^{-1}$ using a video camera (Blackmagic Cinema Camera MFT, Blackmagic Design; 16 mm f/2.2 lens, Walimex Pro). The swimming speed of the fish was measured every 200 ms in a period from 30 s before to 100 s after the electric shock by determining their position every 200 ms using ImageJ software. The timing of mouth or opercula opening was defined as the timing of respiration. The recovery time of the narcotised goldfish was defined as the period from the end of the electric shock until respiration started again. The effect of the narcotising electric shocks is shown in Movie 2.

**Data analysis and statistics**

Statistical analyses were carried out using Graph Pad Prism version 5.01 (Graph Pad Software) and Excel (Microsoft). Normal distribution of data was tested using the D’Agostino–Pearson normality test. Pairwise comparisons were performed using the paired two-tailed $t$-test. The effect of high voltages on startle response latency and startle response probability was tested by using the Mann–Whitney $U$-test and two-tailed Fisher’s exact test, respectively. Pearson’s correlation was used to test the

**Fig. 2. High-speed video showing the absence of any muscle twitches in discharging electric catfish.** (A) Experimental approach with fish swimming stationary against a water current to closely examine involuntary muscle contractions that might accompany the firing of discharges in the electric catfish. The electric catfish was always positioned behind the goldfish at a defined distance. Discharges were elicited by touch and their detrimental effect was calibrated using similar-sized goldfish. Pale red lines schematically indicate the electric dipole field produced by the discharging electric catfish. (B) Time course of the pectoral fin angle velocity and (C) the body length of an electric catfish ($n=10$ trials, $N=1$ fish) compared with goldfish ($n=18$ trials, $N=3$ fish). Body length was normalised to the mean value of the control interval (50 ms interval before the discharge). The defensive discharges started at time zero. In every trial, they induced involuntary muscle contractions in goldfish within the first 20 ms (red areas). Pectoral fin angle and body length were determined every 5 ms. Each line represents the mean±s.e.m. (D) Effect of the discharges on maximal pectoral fin angle velocity and (E) minimal body length before (control interval) and during electric shocks (yellow warning signs) in catfish ($n=10$ trials) and goldfish ($n=18$ trials). The decrease in goldfish body length was the result of whole-body muscle contractions but not a change in body bending (Fig. S1). Red points represent the mean. ***$P<0.001$; ns, not significant; paired two-tailed $t$-test.
relationship between body length and body bending. Values of $P<0.05$ were considered statistically significant. All data are presented as means±s.e.m. $N$ and $n$ denote the number of animals and trials, respectively. Movies were edited using Adobe Premiere Pro 2.0 (Adobe Systems Incorporated).

RESULTS

**Electric catfish do not twitch in response to their own defensive discharges**

We first explored whether high-voltage pulses fired by an electric catfish might cause any involuntary contraction of its own skeletal muscles. We used digital high-speed video to closely monitor an electric catfish that swam steadily in a countercurrent arrangement and that could reliably be induced to fire defensive discharges (4–7 high-voltage pulses of about 250 Hz; Fig. 1E,F) by mechanical stimulation. These defensive discharges had massive effects on goldfish that swam in the same countercurrent setup. We identified the two most reliable effects of the defensive discharges on the control goldfish (Fig. 2; Movie 1). First, the defensive discharges caused the fast spreading of the pectoral fins (increase in pectoral fin angle velocity: paired $t$-test: $P<0.001$; Fig. 2B,D). Second, whole-body muscle contractions (see Fig. S1) caused a typical and significant body shortening (paired $t$-test: $P<0.001$; Fig. 2C,E). However, neither of these effects could ever be detected in the electric catfish that fired the discharges (Movie 1). A close analysis based on digital high-speed videos failed to show any significant changes in pectoral fin angle velocity (paired $t$-test: $P=0.413$; Fig. 2B,D) or in body length (paired $t$-test: $P=0.500$; Fig. 2C,E).

**Insensitivity to electric shocks does not require any preparedness**

The electric catfish that fired a defensive discharge in the preceding experiment controlled the timing of its discharges and the number of pulses and could thus potentially have prepared in some way for the expected effects of the high-voltage discharge, much as a bat must prepare for its intense echolocation calls (Suga and Jen, 1975) or an elephantnose fish must prepare the processing of its exquisitely sensitive ampullary electroreceptors for its own discharges (Bell, 1981). Perhaps similar mechanisms are essential for the apparent insensitivity of a discharging electric catfish. To test this, we simply confronted two electric catfish using the same experimental approach as described in Fig. 2. By touching one electric catfish of the pair, it could be induced to fire its defensive discharges with arbitrary timing. Hence, the non-discharging test fish, whose response we then evaluated, had no control over the timing and number of pulses that it received (Fig. 3A). However, again we did not observe any twitches of the skeletal muscles or any other reactions caused by the defensive discharges emitted by the conspecific (Fig. 3B–D). Neither pectoral fin angle velocity (paired $t$-test: $P=0.559$) nor body length (paired $t$-test: $P=0.401$) was affected by the discharges that all strongly affected the control goldfish (see Fig. 2).

We next replaced the discharges of a conspecific catfish with artificial discharges from a generator (Fig. 4A). These discharges differed in slope, duration of the individual pulse and rate from those of the electric catfish (see Fig. 1) and all had demonstrable effects on goldfish: all artificial discharge mimics induced whole-body muscle contractions in the goldfish (Fig. 4). Again, in each experiment, the artificial discharges induced a significant increase in pectoral fin angle velocity (paired $t$-test: $P<0.001$), resulting in a fast spreading of the pectoral fins (Fig. 4B,F–H) and caused a typical and significant body shortening (paired $t$-test: $P<0.001$; Fig. 4D,I–K).

Fig. 3. Electric catfish are insensitive to electric shocks of conspecifics. (A) Experimental approach with catfish swimming stationary against a water current to detect involuntary muscle contractions in an electric catfish (receiver) after touch-elicited defensive discharges of a conspecific (sender). The discharging electric catfish was always positioned behind the receiver at the same distance as used in the goldfish experiments. Pale red lines schematically indicate the electric dipole field produced by the discharging electric catfish. (B) Time course of pectoral fin angle velocity and (C) body length of the non-discharging electric catfish ($n=5$ trials). Body length was normalised to the mean value of the control interval (50 ms interval before the discharge). The defensive discharge started at time zero. The red areas indicate the time interval in which the involuntary muscle contractions in goldfish were induced. Pectoral fin angle and body length were determined every 5 ms. Each line represents the mean±s.e.m. (D) Effect of the electric shocks on the maximal pectoral fin angle velocity and (E) the minimal body length before (control interval) and during the electric shocks ($n=5$ trials). The red points represent the mean. ns, not significant; paired two-tailed $t$-test.
Nevertheless, the electric catfish skeletal muscles were insensitive to the tested artificial discharge mimics (Fig. 4B–K). These findings suggest that electric catfish not only need not prepare for high-voltage discharges but that they also tolerate at least some deviation from their species-specific discharges.

**Sensorimotor processing in electric catfish remains unchanged during exposure to high voltages**

The above experiments only monitored the effect of high-voltage discharges on muscle contractions. However, the discovery of a robust novelty response allowed us to also test whether the
transduction of sensory signals, the subsequent integration and processing of sensory information in the brain as well as the production of an appropriate motor output were equally immune to high-voltage electric shocks (Fig. 5A). The electric startle response could be reliably elicited by intense acoustic stimuli to which the fish respond with a defensive discharge (Fig. 5B,C), fired at a low latency of 12.40±2.78 ms (mean±s.d., n=200 trials; Fig. 5F). Producing this response requires the functioning of mechanosensory cells of the inner ear and the lateral line system (Higgs and Radford, 2013), and circuits that can elicit the response, perhaps similar to the well-known escape response of teleost fish (Mirjany et al., 2011; Zottoli, 1977). If high voltages interfered with any component of the process, one would predict a decrease in startle response probability or an increase in latency. To test these predictions, we presented the acoustic stimuli while the electric catfish were simultaneously exposed to high-voltage discharges. These experiments could be run by using the artificial discharges introduced in Fig. 4 that all had strong effects on similar-sized control goldfish (Fig. 4) and that could easily be paired with the acoustic stimuli (Fig. 5D,E). Our results clearly show that the electric shocks neither changed response latency (12.46±2.90 ms; P=0.979, Mann–Whitney U-test; Fig. 5F) nor affected the capacity of the acoustic stimulus to cause the usual behavioural response (P=0.888, two-tailed Fisher’s exact test; Fig. 5G).

Electric catfish are neither immobilised nor narcotised by electrofishing

The above findings demonstrate that electric catfish are insensitive to short high-voltage discharges. But electric catfish additionally emit high-voltage volleys that can last for seconds (Fig. 1B) (Bauer, 1979). Therefore, we next examined whether electric catfish can also resist electric shocks with an increased duration and intensity by challenging the fish with a commercial electric fishing device (Fig. 6A). This was set as in electrofishing operations (100 Hz pulsed direct current, peak voltage gradient of 3 V cm⁻¹) to cause an immediate immobilisation following whole-body muscle contractions, loss of consciousness (Beaumont, 2016; Robb and Roth, 2003; Schwartz and Herricks, 2004) and cardiac arrest in fish (Schreer et al., 2004) (Fig. 6A). As in our previous experiments (Figs 2–4), we first used high-speed videos to analyse whether we could identify any involuntary muscle contractions at the beginning or during an electric shock of 1 s duration delivered by the electrofishing device. However, instead of being immobilised instantaneously as a result of tetanic muscle contractions, the electric catfish showed undisturbed swimming behaviour and normal movements of their fins (Fig. 6B,C; Figs S2 and S3).
Impressively, there was also no electronarcosis even after longer electric shocks (3–4 s) that always instantaneously narcotised the control goldfish (Fig. 6E,G; Fig. S3 and Movie 2). Goldfish immediately stopped moving (Fig. 6D,F; Fig. S3 and Movie 2) and breathing (Fig. 6H), and resumed breathing only 24.0±3.2 s (n=6) after the discharges had ended. In summary, these results demonstrate that the electric catfish is immune to high-voltage electric shocks from a commercial device that reliably immobilises and narcotises other fish.

**DISCUSSION**

Our results demonstrate for the first time that electric catfish are completely immune not only to their own high-voltage electrical shocks but also to external shocks delivered by a commercial electrofishing device. We show that the catfish’s skeletal muscles are not activated by discharges that induced massive muscle contractions in goldfish. In none of our experiments did we see any involuntary muscle twitch in electric catfish, either in response to their own discharges, generated by their own electric organ or that of another electric catfish, or after strong artificial discharges from an electrofishing device. Moreover, the findings obtained in our experiments using the novelty response suggest that the nervous system and sensorimotor processing within the brain were also unaffected by the high-voltage electric shocks used in this study. These findings confirm the centuries-long speculation that electric catfish are protected against their high-voltage discharges. They also exclude several mechanisms that have been proposed for this and show that the protection is far more powerful and extends even to external high voltages.

Although we simply used the novelty response as a tool to assess the effects of external discharges on sensorimotor processing, we would like to briefly comment on the conspicuously short latency of only 12.40±2.78 ms. This latency is in the range of latencies known for mechanically induced Mauthner neuron-driven escape C-starts of teleost fish (e.g. Korn and Faber, 2005). In the electromotor system of the catfish, two large electromotorneurons command the high-voltage discharges (Bennett et al., 1967; Schikorski et al., 1992) and so these neurons might either directly receive at least mechanosensory information or, more plausibly, be directly driven by the Mauthner neurons. A connection between the Mauthner neuron and an electromotor pathway has been suggested in the South American weakly electric fish Gymnotus carapo (Falconi et al., 1995).

In fish, electric shocks of increasing intensity elicit the startle response, complete muscle tetanus and finally electronarcosis (Beaumont, 2016). High-intensity shocks are used in electrofishing operations to immobilise and catch fish. Depending on fish size, species, water conductivity or duration of the electric shock, field strengths of 0.5–1.0 V cm⁻¹ (pulsed direct current, as used in this study) are sufficient to immediately cause whole-body

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Fig. 6. A commercial electrofishing device fails to narcotise electric catfish. (A) Experimental approach to analyse the response of an electric catfish (N=1) and a goldfish (N=1) to stronger and longer lasting (1–4 s) electric shocks (100 Hz pulsed direct current, peak voltage gradient of 3 V cm⁻¹) that are typically used in electrofishing operations. Pale red lines schematically indicate the homogeneous electric field produced by the electrofishing device. (B) Representative examples of pectoral fin movement in goldfish and electric catfish before and during an electric shock. The duration of the electric shock (1 s) is indicated by the red area. For additional examples, see Fig. S2. (C) The electric shocks had no effect on the electric catfish but immediately caused spreading and subsequent immobilisation of the fins of the goldfish. Solid lines represent the mean±s.e.m. (n=4 trials). (D) Swimming speed of a goldfish and (E) an electric catfish before, during (red area) and after a narcotising electric shock (3–4 s). Swimming speed was determined every 200 ms. (F,G) Distribution of swimming speed for (F) goldfish and (G) electric catfish before and after the narcotising electric shock (n=6 trials). (H) Timing of respiration of goldfish (n=6 trials) and electric catfish (n=4 trials) before and after the electric shocks. Each vertical line indicates the timing of respiration events. The red areas indicate the duration of the electric shocks.
muscle tetanus (Beaumont, 2016). To affect the nervous system of fish (Beaumont, 2016; Norgreen et al., 2008; Robb and Roth, 2003; Sharber and Sharber Black, 1999) and subsequently induce electronarcosis, field strengths of 0.5–2.0 V cm⁻¹ are necessary (Beaumont, 2016; Gaikowski et al., 2001; Taylor et al., 1957; Walker et al., 1994). It is therefore remarkable that even stronger electric shocks (3 V cm⁻¹) caused neither involuntary muscle contractions nor any changes in the processing within the central nervous system of the electric catfish. During the last 150 years, many suggestions have been made on how strongly electric fish could potentially avoid shocking themselves. The ideas range from simply tolerating the self-induced contractions (Babucchin, 1877; Sachs, 1879) to a size-dependent dilution of the current (Caputi, 2006), or wrapping of evolvable organs such as the muscles or the brain in insulating tissues (Bilharz, 1857; Nelson, 2011; Norris, 2002). Our findings clearly eliminate the idea that electric catfish simply tolerate getting shocked each time they emit high-voltage electric organ discharges. Our results also exclude another idea that has been suggested based on the typically large size of strongly electric fish, in which current would be diluted over their large volumes (Caputi, 2006). However, in our electrofishing experiments, we selected the catfish to match the control goldfish in size and still only the goldfish but not the catfish was shocked. Most importantly, our findings exclude mechanisms in which the discharging catfish prepares for the effects of its electric shocks, similar to how an echolocating bat prepares before emitting a potentially deafening high-intensity echolocation call (Suga and Jen, 1975): electric catfish are equally well protected against external discharges whose timing and waveform they cannot control. Because generating high voltages does not affect the discharging electric catfish, the idea of employing some type of active compensation might seem attractive; here, the electric organ would be fired in response to an external high voltage so as to reduce the resulting overall voltage. Such an active compensation would, however, only account for our findings if it were capable of somehow being adjusted; it would have to work not only for the species-specific fields but also so as to match the time course, amplitude and geometry of the artificial pulses from our electrofishing device. Importantly, we never saw any indication that the catfish discharged in response to our external high-voltage stimuli.

Taken together, the easiest explanation of our findings is probably that electric catfish achieve immunity by highly resistive tissues that shield the whole animal or, individually, its muscles, heart and nervous system. Alternatively, or perhaps additionally, some tissues might have evolved some intrinsic tolerance. Electric shocks as used in our study readily induce cardiac arrest (Schreer et al., 2004) and arrhythmias (Biswas and Karmarkar, 1979; Schreer et al., 2004) in the hearts of other fish. Given that cardiac damage and arrhythmia are the most serious and most common injuries following electrical shock in humans (Waldmann et al., 2017), the present findings make the powerful high-voltage protection of the electric catfish a promising subject to explore further.

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Competing interests
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Author contributions

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