



On mating and function of associated electric pulses in *Clarias macrocephalus* (Günther 1864): probing an old puzzle, first posed by Charles Darwin

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Abstract The Asian broadhead walking catfish (*Clarias macrocephalus*) generates weak electric monopolar pulses during spawning. Males emit a single pulse when attracting a female, and while in amplexus, only females emit a single burst of similar pulses. This burst is a necessary component in the mating ritual of *C. macrocephalus*. Release of milt occurs about 5 s prior to the onset of a burst, which is immediately followed by the release of eggs. Following sperm release, the male remains in tight embrace with the female. Though both male and female could perceive each other's electric pulses via ampullary receptors (communication mode), we postulate that egg release can be facilitated by direct action of the female's burst on the male's neuromuscular system (contraction mode). Shedding light on the

function of weak episodic electric emission, we propose that the modification of electrogenic structures evolved towards increasing the efficiency of direct bodily impact. As extant clariids exhibit intermediate features between non-electric and strongly electric catfishes, *Clarias* should be considered a “serviceable transition,” which Charles Darwin deemed a possible intermediate form between these two groups.

Keywords *Clarias macrocephalus* · Spawning behavior · Electric fish · Episodic electric pulses · Mating ritual · Pulse-induced muscle contraction

Introduction

Writing about electric fishes in chapter 6 of the *Origins*, entitled “*Difficulties On Theory*”, Charles Darwin noted

“The electric organ of fish offers another case of special difficulty; for it is impossible to conceive by what steps these wondrous organizations have been produced. But this is not surprising, for we do not even know of what use they are” (Darwin 1872, p. 150).

Although our knowledge about electric fishes has vastly improved, this puzzle remains unsolved. Strongly electric fishes (*Electrophorus electricus*, *Malapterurus electricus*, *Torpedo* sp., *Astroscopus* sp.) use their electric organs to produce powerful electric discharges (EODs) serving in predatory behavior and in defense

We dedicate this paper to the memory of Hans Werner Lissmann (1909–1995).

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(review: Moller 1995; Finger and Piccolino 2011). The EODs of strongly discharging fish directly affect the target's motor neurons (Catania 2015). Strong electric discharges occur in episodic volleys of monopolar pulses with durations and pauses of about a few milliseconds (Bennett 1971; Bauer 1979; Belbenoit et al. 1979; Rankin and Moller 1986, 1992; Catania 2015).

A second functional group of electrogenic fishes with well-established behavioral functions includes all representatives of the Neotropical knifefishes (Gymnotiformes) and African elephant, or snout-fishes (Mormyriiformes). Both are nocturnal freshwater teleosts. Their electric activity is continuous in the form of either discharges with relatively short and almost constant inter-discharge intervals (wave-type fishes) or discharges with variable inter-discharge intervals (pulse-type fishes). Lissmann (1951, 1958) was first to record electric discharges from fish of both groups and demonstrated that the function of these discharges was to assist the fish in locating nearby objects and postulated a function in social communication. To play a role in social communication, EODs must not only be perceived by the target but also be responded to in an adaptive manner in the form of measurable physiological and/or overt changes in hormone titers (Carlson et al. 2000) and locomotor behavior and patterned EOD (Terleph and Moller 2003). These requirements distinguish the African mormyrids and Neotropical knifefishes from Rajidae, Uranoscopidae, and Siluridae (see below). Over the past 70 years, the function of EODs in object-location and communication was confirmed in numerous studies (reviewed in: Bullock and Heiligenberg 1986; Bullock et al. 2005; Kramer 1990, 1996; Heiligenberg 1991; Moller 1995; von der Emde 1998; Hopkins 1999; Ladich et al. 2006).

Addressing Darwin's difficulties, Lissmann (1958) suggested that the emergence of specialized electroreception preceded the origin of electric organs as evidenced by fish with electroreception but without electric organs. Lissmann's hypothesis was confirmed for many non-electric aquatic species (review: Bullock and Heiligenberg 1986). Initially, *Clarias* served as an example of such a highly sensitive, but non-electric fish (Lissmann and Machin 1963), but much later, surprisingly, *Clarias* was found to emit weak electric pulses, labeled discharges by Baron et al. (1994b).

Electrogenic fishes of a third group emit weak electrical pulses that differ markedly from typical myogenic activity (Bullock 1999). This group includes Rajiformes (Elasmobranchii) (Robin 1865; Ewart 1892; Bennett 1971), noted by Darwin as an example of weakly electric fish with unknown function. Other marine fishes with weak discharges are Uranoscopidae (Perciformes, Teleostei), (Baron and Mikhailenko 1976; Baron 1982, 2009), and Plotosidae (Baron and Orlov 2005). Among freshwater fishes, this electrogenic ability was found in several families of African and Asian Siluriformes (Hagedorn et al. 1990; Baron et al. 1994a, b, 1996; Morshnev and Olshansky 1997; Orlov et al. 2015b). Weak episodic electrical discharges have also been reported for Cladistia (Polypteriformes) (Baron and Pavlov 2003) and Dipnoi (Protopteriformes) (Orlov et al. 2015a) and even in Amphibia (giant Chinese salamander *Andrias davidianus*) (Olshanskii et al. 2016).

This third group is heterogeneous in terms of taxonomic affiliation, lifestyle, distribution, and electric manifestations. Within it are several species whose electric activity supports communication or object-location functions. In *Synodontis* (Mochokidae), the discharges are related to social interactions between individuals (Hagedorn et al. 1990; Baron et al. 1994a; Boyle et al. 2014); these fish also respond to external electrical stimulation (Orlov et al. 1993; Ol'shanskii and Morshnev 1996; Orlov and Baron 2005).

For most fish with episodic discharges, however, there is no conclusive behavioral evidence to support object-location or communication, although several hypotheses have been proposed addressing these functions (Baron et al. 1985; Baron 1994; Baron and Olshanskiy 2009). Nevertheless, such fish generate electrical discharges in response to mechanical stimulation; they precede attacks on prey and accompany subsequent aggression (Baron et al. 1994a, 2005; Olshanskiy and Kasumyan 2018). Discharges can occur both during aggression and hunting regardless of whether the targets were electroreceptive or not.

The fact that catfish and rays possess electroreceptors tuned to their electric discharge seems to provide a strong physiological basis for communication and electrolocation. However, if the function of the fish's discharges is object-location, why then are they emitted only episodically? If the function is in communication, why do we not see

noticeable electric responses to external electric stimuli in other fish? If long-lasting monopolar pulses of Rajiformes, Claridae, or Siluridae evolved through natural selection in concert with electroreceptive function, why then do Uranoscopidae that lack electroreception show very similar pulses as the aforementioned taxa? Thus, the behavioral function of weak episodic electric emission has remained largely enigmatic from Darwin's time on until now (Darwin 1872; Lissmann 1958; Baron 1994; Bullock 1999; Ol'shanskii et al. 2011). The answer to these questions requires a study of both the source of the discharge (sender), and the responsiveness of the target (receiver), and most importantly establishing how sender-receiver interaction benefits those fish possessing electrogenic structures.

Clarias macrocephalus, the broad- or bighead walking catfish, inhabits freshwaters in tropical Asia. It emits weak, irregular, and long-lasting monopolar pulses with a duration noticeably longer than a few milliseconds; similar to those recorded from Siluridae, Uranoscopidae, Rajiformes, and other fish with weak episodic pulses. The electric activity of *C. macrocephalus* has been recorded during social conflicts, hunting, and mating (Ol'shanskii et al. 2002, 2011; Baron et al. 2005; Olshanskiy et al. 2009, 2011; Kasumyan et al. 2013; Olshanskiy and Kasumyan 2018).

This study will focus exclusively on the spawning and mating ritual of *C. macrocephalus* with the following aims: (1) to describe in detail the locomotor events and concomitant electrical activity leading up to and during amplexus, and (2) to elucidate the functional significance of the exclusive male- and female-typical electric pulses. We assume that both male and female perceive each other's electric pulses via ampullary receptors (Lissmann and Machin 1963; Peters and Bretschneider 1981; Peters and van Ieperen 1989) so that they may serve in communication. But we further postulate that during amplexus, the female's electric pulses can directly affect the male's neuromuscular system, which results in tetanus-like axial muscle contractions, which in turn affect an even tighter sexual embrace, and all of which are instrumental in egg release. Our results demonstrate evidence for the behavioral significance of

episodic electric activity in the mating ritual of *C. macrocephalus*.

Some of the findings reported here were published previously in Russian journals as short communication and review (Olshanskiy et al. 2009; Ol'shanskii et al. 2011). Most of the data, however, were analyzed for the current study, and our hypotheses about the function of electric pulses are formulated and tested here for the first time.

Methods

Subjects

Clarias macrocephalus were caught in the Mekong River by local fishermen. Experiments were carried out in April–May of 2006, 2008, and 2009 in Vietnam when a majority of *C. macrocephalus* was sexually mature. Fish were identified, following Teugels et al. (1999) and Ol'shanskii et al. (2002), by identification of sexed-based differences in the shapes of their abdomen and urogenital papilla (De Graaf and Janssen 1996).

Fish were transported to a nearby field laboratory in Can Tho or to a stationary laboratory in Nha Trang where they were kept in 100-L tanks (water temperature 26–28 °C; 12:12 light:dark photoperiod, with lights on at 06:00, local time). Water was circulated through a biofilter and partly replaced every day. Water conductivity ("Econix-expert-001") in both common and experimental tanks varied between 70 and 1193 $\mu\text{S}/\text{cm}$, in the Mekong River delta between 200 and 4000 $\mu\text{S}/\text{cm}$. Commercial food pellets were used to feed fish daily.

We investigated 10 male-female pairs in over 800 matings in 10 spawning experiments (Table S1, see Supplementary Materials). A total of 203 h 33 min of video recordings and 320 h 21 min of electrical recordings were analyzed. Fish ranged in size from 200–300 mm (total length) and in weight from 100 to 210 g. There was no need to identify individual fish as they were used only once, except in experiments 9 and 10 when the same male was paired with different females.

Mating is defined here as the element of spawning behavior when fish are in amplexus, the specific posture where the male arches his body and tightly clasps the female's head with both fish remaining motionless for several seconds. A *spawning session* is defined as the

entire sequence of multiple matings following hormonal injection. It does not include the *pre-spawning period*, i.e., the time before hormonal injection, but includes both the *pre-mating period*, i.e., the period between hormone treatment and first courtship attempts, and the *mating period*, i.e., the period between the first and last mating observed in the spawning session. During spawning male-female attacks could be observed notably before and after a period of intense mating, a behavior common in clariids (Bruton 1979).

Induction of spawning

Fish were injected intramuscularly with 0.4 mL of human GnRH with a total dose 6000 IU/kg for females and 3000 IU/kg for males. Fish were injected twice at 7–10-h intervals; the first injection applied 70% of the total dose. Spawning occurred 12–14 h following the first injection. In the 2006 and 2008 experiments, prior to injection, males and females were placed in the experimental tank to record their motor and electric activity. In the 2009 experiments, several pairs were kept in closed plastic tanks prior to injection and again for 8 h following the first injection. The pair that displayed the first obvious signs of courtship behavior was chosen and placed into the experimental tank for video and electric recording.

Experimental setup

Most observations were made from a custom-built all-glass experimental tank (60 × 60 × 30 cm; wall thickness of 10 mm; water level adjusted at 25 cm). In exp. 9 and 10, a smaller tank (58 × 45 × 29 cm) was used. The tank was placed on a metal rack to permit observation and video recording through its transparent glass bottom. The tank was shielded with black cloth placed above and around its sides, and covered with a glass lid to prevent the fish from jumping, but leaving a 5-cm gap allowing air-breathing *C. macrocephalus* to take gulps of air at the surface. At night, the tank was dimly lit with luminescent lamps or LEDs mounted beneath the tank. Once the first mating had occurred, the fish continued to mate at any level of illumination, including bright direct sunlight. The first experiments were conducted at night under dim light; however, to ensure quality video recording, illumination was increased to

about 1000 lx (measured at water level) in later experiments.

The recording procedures of electrical activity in *C. macrocephalus*, which have elsewhere been described in detail (Olshansky 2010), required an adjustment to accommodate the fish's typical long-lasting weak monopolar electrical pulses. On average, we recorded no more than 50 pulses per hour, each lasting about 25 ms (see Table 1). To avoid recording long periods of "silence" to flash memory, we used a standby mode of recording.

The experimental tank was equipped with four carbon electrodes (1 × 1 × 25 cm) with an insulated wire-electrode junction affixed vertically. Electrodes were placed at the center of the tank's walls (exp. 1–3) or in all corners (exp. 7–10). Opposite placed electrodes were connected in pairs to differential inputs to two 2-channel autonomous microprocessor recording devices. In exp. 4–6, eight electrodes connected to two 2-channel devices were used. The hardware and software features were described in detail previously (Olshansky 2010). The chips in our equipment were obtained from Analog Device and Texas Instruments. Since the gain of the programmable amplifiers was recorded in a file, when viewing and analyzing the records, the data were automatically converted into absolute values of the potential difference between the electrodes. Signals were continuously digitized and sampled at 2.5 kHz. Examples of digitized signals are shown below (see Fig. 5). Only pulses with amplitudes larger than a set threshold obtained from at least one channel were recorded on flash memory together with the time of the electric event (accuracy 1 ms), the amplification coefficient, and the value of the threshold level. Threshold values were determined in preliminary experiments with pairs of catfish during aggressive-defensive behavior so as to capture all monopolar pulses, but at the same time as little myogenic activity and other electric interference. As a change in water conductivity (σ) affects the current to voltage ratio for both pulse and noise (Ohm's law), we set the thresholds as follows: for experiments 6 ($\sigma = 70 \mu\text{S/cm}$) and 8 ($\sigma = 88 \mu\text{S/cm}$), we set the threshold at $\pm 250 \mu\text{V}$; for exp. 4 ($\sigma = 1193 \mu\text{S/cm}$) at $\pm 100 \mu\text{V}$, and for all other experiments ($\sigma = 200\text{--}280 \mu\text{S/cm}$) at $\pm 125 \mu\text{V}$. Considering the much greater water conductivity than that in the other experiments, the threshold for exp. 4 seemed very high. However, the use of eight

electrodes allowed raising the threshold of the receiving equipment in standby mode.

We could connect and disconnect devices with the notebook computer at any time. This permitted real-time viewing of electrical events. Upon completion of the experiment, data were rewritten to a PC using a custom-made program. This program permitted viewing of the previously recorded events, automatically measuring the duration and amplitude thereof, building scatter charts to determine the direction of the current vector of the source, creating summary tables, and exporting these tables to MS Excel. In addition, the program automatically calculated and exported the amplitude and duration of each pulse to a table for each series, together with the count of pulses, amplitude and duration of the series, the relative amplitude and duration of each pulse, and the inter-pulse intervals. Pulse duration was measured at 10% amplitude level. Once a table was created, events were manually sorted for viewing in the following modes: single monopolar pulses, bursts of monopolar pulses, and other events, e.g., short electric pulses related to respiratory behavior, which were not further investigated in this paper (see Figs S1–S3 in Supplementary Material).

Video recording procedure and synchronization of video with electric events

In exp. 1–5, behavior was recorded using web cameras (Micro PAL-OV or Samsung 305i) mounted above the experimental tank. Exp. 6–10 required high-quality video recording with a Full HD SONY HDR-SR12E camera mounted underneath the tank. In some experiments, additional video recordings were made through the front wall of the tank. All video recordings were made with a frequency of 25 frames per second and, together with their timing, were stored automatically on the camera's hard disk.

For high-quality synchronization of the video recordings, a light-emitting diode (LED) was added to the setup. The presence of an electric pulse at the set threshold triggered a light flash that was recorded together with the fish's overt and electric behaviors. Thanks to the frequency of the video frames, it was possible to match frames with corresponding behaviors.

At the onset of each experiment, we submersed a functional dipole, a “catfish mimic” serving as a “calibrator,” into the tank to verify that the playback pulses (from a custom-made portable autonomous battery generator) exceeded the threshold at different positions and orientations, and that the waveform was displayed correctly on the computer screen. The dipole consisted of a Plexiglas cylinder (length 30 mm, diameter 40 mm). A pair of brass disks (electrodes) affixed to the end of the cylinder could deliver a series of three rectangular pulses (duration 20 ms, inter-pulse interval 30 ms; current in dipole 20 to 200 μ A). Following verification, the dipole was removed from the tank.

Determination of the source of electrical pulses

We will refer to *Clarias*' electrical activity as emission of electrical monopolar pulses. The electric pulse of *C. macrocephalus* is head negative (Ol'shanskii et al. 2002). While the precise biophysical nature of the electrogenic organ is yet unknown, its location is, i.e., in the anterior part of the body between the occipital process and the leading edge of the dorsal fin (Hagedorn et al. 1990; Baron et al. 2002; Boyle et al. 2014). Baron et al. (2002) measured potentials directly on the catfish's body and identified the location of maximum and minimum potentials on the fish's dorsal surface just behind its head.

Relying on this known location, we determined which fish (and thereby which sex) was the source of the pulse by comparing our synchronized electric and video recordings. During a mating embrace (amplexus), the values and polarities of electric pulses, monitored from two (or more) directions, allowed determination of the signal's source. Figure 1 illustrates the procedure. If we construct a scatter chart of the signals recorded by two channels, we will get the direction and polarity of the current source vector in the plane of the bottom of the aquarium. Using this vector, we determined the direction of the fish's head with reference to the signal source. Then, analyzing the video frame, we found that particular fish orientation which coincided with this direction. This procedure is applicable during mating, i.e., when the fish's heads were oriented opposite to one another, and therefore, only one of them corresponded to the calculated direction of the source. Thus, wherever

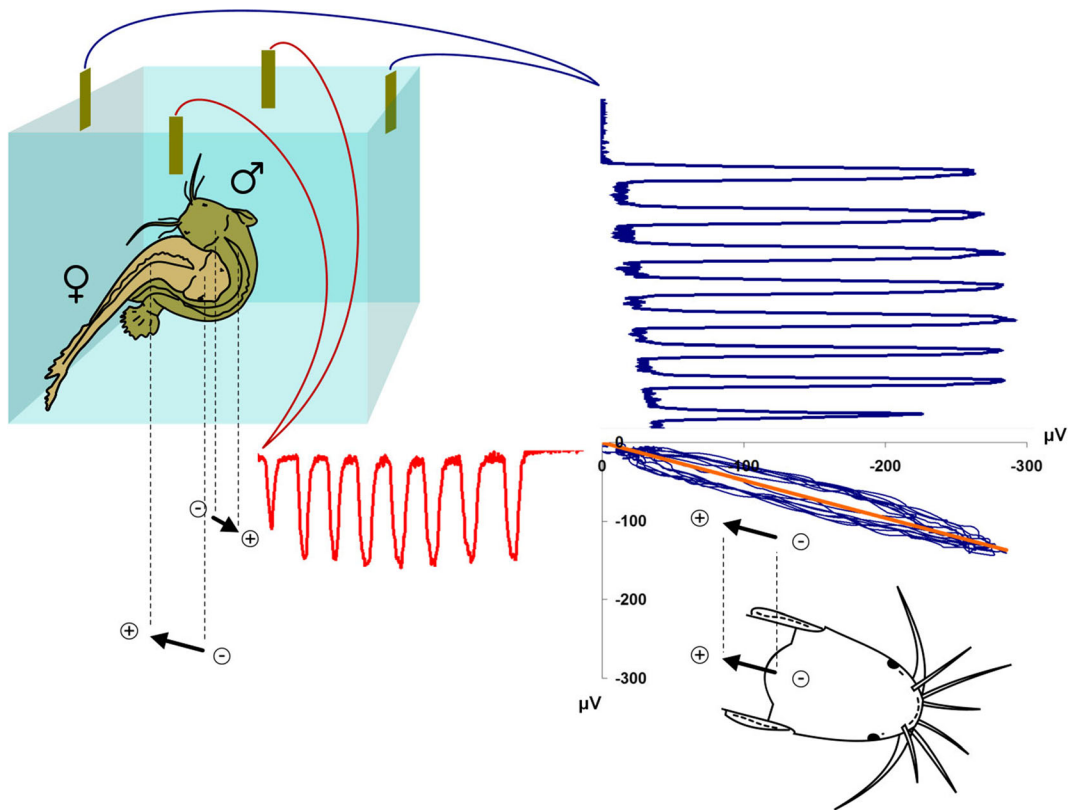


Fig. 1 Identification of a pulse-emitting fish. The electrogenic tissue is located between the caudal edge of the skull and the dorsal fin, and is oriented in the rostral-caudal direction. The orientation of the pulse vector can be determined using a scatter plot for two signals recorded by orthogonal pairs of electrodes. The source of the pulse is the fish whose head orientation

coincides with the orientation of the current vector. In this instance, the direction of the current vector corresponds to that of the female whose head is covered by the male. If the source of the discharge had been the male, the direction of the current vector would have been reversed

mating occurred, in the center of or near the tank's walls, because of the fish's typical opposite positions in amplexus, the source of the pulses was always unambiguously identified.

Comments on the use of animals

The experimental part of our work was carried out by staff of IEE RAS in 2006–2009 in collaboration with Vietnamese colleagues prior to the establishment of a Bioethics Commission (2017). At the time of our observations (2006–2009), neither Russian nor Vietnamese laws concerning the work with live animals (fish) required permission. Our work did not expose fish to surgical intervention, stress, or pain. We carried out

video recordings and remote electric pulse registrations; at the end of our experiments, fish were in good shape and were suitable for other studies. *Clarias macrocephalus* is not an endangered species. Moreover, specimens used in our experiments were obtained from local fish farms.

Results

Spawning behavior

During the pre-spawning period and for the first 8–12 h after hormone injection, males and females remained mostly motionless on the bottom of the tank and were

indifferent to each other (Fig. 2a). Typically, courtship behavior began after about 10 h following the first hormone treatment whereupon fish became active with the male more so than the female and both eventually moving closer to each other. The male attracted a female's attention by sporadically swimming in front of her head, prodding her barbels or rostrum with his own barbels and bending his body in a U-shaped posture in front of her head (Fig. 2b, c). When the female accepted the male's courtship display, she turned towards the male and thrust her head into the male's U-shaped bend (Fig. 2d). This elicited an immediate increase of the male's body-bend contractions. After several splashing movements, the male tightly embraced the female's

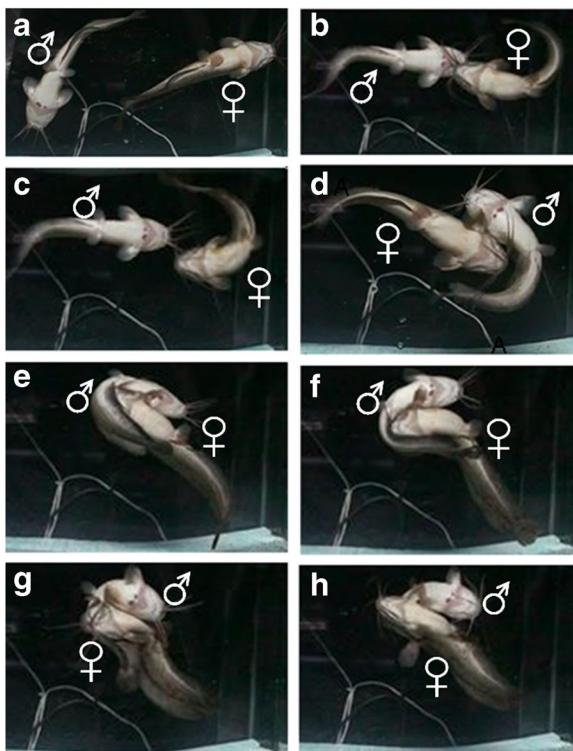


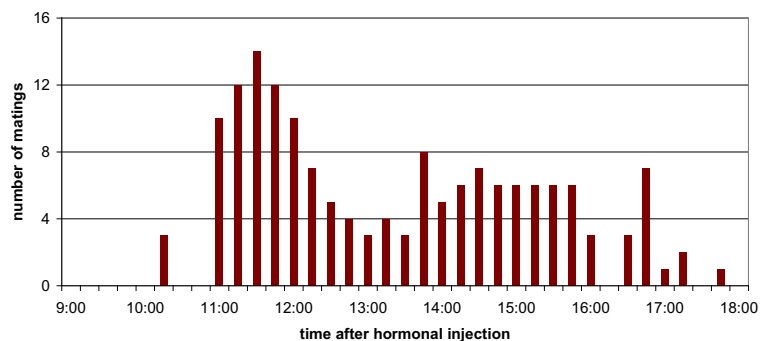
Fig. 2 Sequence of fish positions before and during courtship and mating. **a** Before first courtship attempts, male and female lying motionless and separated on the bottom of the tank. The female is easily identified by her large bloated stomach; **b** male attracted to female, but fish have not come into close contact; **c** male is slightly bending his body in front of the female's head; **d** male bending his body in a U-shaped posture and female entering into the male's U-shaped body bend; **e** position of fish entered into amplexus; **f** female turns to the front part of his body in the opposite direction from the head of the male; **g** position of fish at the moment of egg release; **h** position of fish at the end of amplexus

head in amplexus with both fish now remaining motionless (Fig. 2e).

Soon afterwards, the positions of the fish changed at a low pace with the female bending her body and turning her head to the left or right depending on the position of the male's head (Fig. 2f). The female then, with a slight wave of her tail and dorsal fin, lowered her head and slowly shifted it under the male's abdomen with the male still in tight embrace with the female pressing his head at the opercula level against the side of her body resulting in the combined girth getting even tighter (Fig. 2f). The fish then slid relative to one another such that the male's abdomen was now positioned over the female's head. When the rostral edge of the female's head emerged from underneath the male's abdomen, her maxillary barbels became free and stretched forward (Fig. 2g). The fish slightly rotated relative to each other with the male's operculum and tail gliding over and pressing down on the female's bulging abdomen resulting in the release of a single batch of eggs, which usually occurred 10–15 s after the fish had entered into amplexus. Male and female then straightened the anterior parts of their bodies while the male continued pressing his abdomen and tail against the female. The male eventually separated from the female as the female remained motionless (Fig. 2h). The male soon continued making renewed attempts to get the female's attention by swimming around and before her head, touching different parts of her head and body, and displaying his U-shaped courtship posture. Only a few of such renewed mating attempts were successful. Usually, the female remained motionless and ignored the male's activity.

Following the first mating events, their occurrence increased significantly with inter-mating intervals of only a few minutes and increased number of eggs released. (The abundance of released eggs was visually estimated by the size and density of the "egg cloud" as well as eggs found at the bottom of the tank). Eventually, towards the end of a spawning session, both the mating frequency and the amount of eggs released sharply declined. Nevertheless, the sequence of courtship events during each mating remained highly stereotypic. The time between first and last matings (mating period) could be several hours and might even exceed 2 days. Figure 3 illustrates the dynamics of the spawning activity observed in exp. 7.

Fig. 3 Spawning activity of *C. macrocephalus* (exp. 7)



Electrical pulses during spawning

In all 10 spawning sessions (Table 1), two types of electric monopolar pulses were recorded, single monopolar pulses (SPs) and bursts of such pulses (BPs). A comparison of the fish's pulse activity with the corresponding video data shows that SPs accompany male attacks on females. At the beginning of the mating period, the male usually generates SPs during a courtship behavior characterized by swimming briefly in front of the female and touching her with his barbels. As matings increased, SPs almost totally disappeared, and only increased in occurrence again as mating activity declined. The greatest number of SPs was recorded during the pre-spawning period. Males were always the source of SPs. In contrast, bursts of pulses (BPs) occurred exclusively during mating when fish were in amplexus, and without exception, only females emitted these bursts (Table 1). None of the matings occurred without a BP. Figure 4 highlights the time-dependent changes in SP and BP emissions during a spawning

session (exp. 5 had the largest number of SPs and exp. 7 had the largest number of BPs).

Characteristics of single pulses

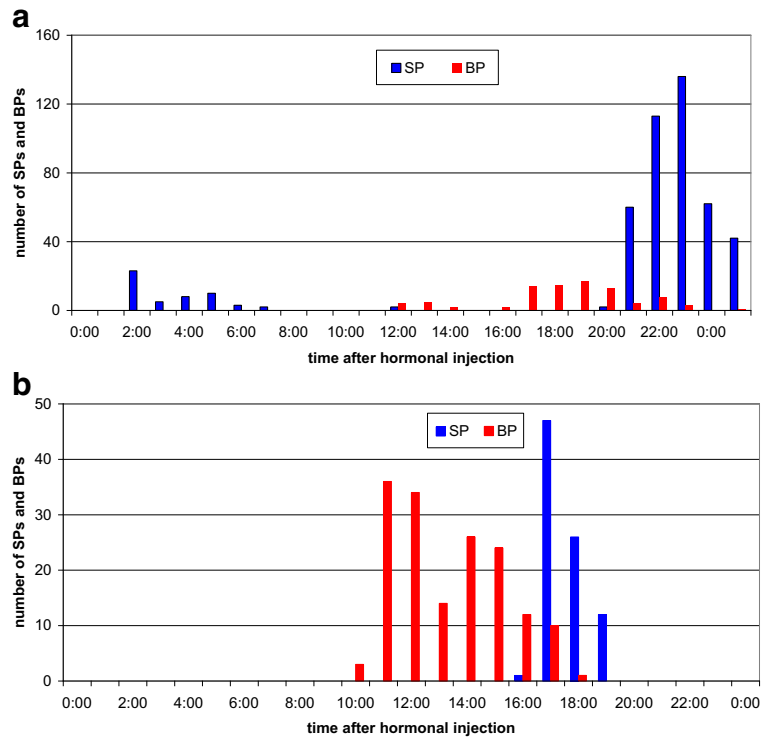
Single pulses lasted from 8–40 ms with means ranging from 16–23 and with more than 90% ranging from 16–30 ms; no SPs exceeded 40 ms. The shapes of SPs were variable and could change even during the same spawning session in the same pair of fish (Fig. 5a); the longer the duration, the greater the irregularity. When electric pulses were recorded with two or more pairs of electrodes, the pulse shape was identical for each of the channels, but differed in polarity and amplitude. Figure 6 illustrates the distribution of the amplitudes of all SPs and BPs recorded in experiments 7 and 10. Fish in these two experiments generated the largest number of SPs and BPs. The amplitude denotes the largest value of potential differences registered across recording channels.

Table 1 Total number and timing (hours:minutes) of single (SP) and burst pulses (BP) recorded in 10 spawning experiments

	Spawning experiments									
	1	2	3	4	5	6*	7	8	9	10
Pre-spawning period										
- Duration of electrical recording	11:28	21:20	9:22	-	50:40	-	-	5:03	-	-
- Number of SPs	137	283	51	-	1392	-	-	82	-	-
- Number of BPs	0	0	0	-	0	-	-	0	-	-
Spawning session										
- Duration of electrical recording	25:20	11:50	20:50	36:05	31:50	32:51	13:15	15:42	19:33	15:12
- Number of SPs	742	538	105	16	970	724	97	464	133	1188
- Number of BPs	56	30	74	91	88	9*	160	88	86	156

*Only the first nine bursts were recorded in exp. 6. "0"—no BPs were recorded; dashes—occurrence of placing male and female together following hormone treatment

Fig. 4 Time-depended change in single pulse (SP—blue) and burst of pulses (BP—red) emissions in exp. 5 (a) and 7 (b). (b Experiments were terminated at 20:00)



Characteristics of burst pulses

C. macrocephalus generated bursts in series with 2–9 monopolar pulses (Fig. 5b). Series with 5–7 pulses were the most common (68%). Bursts with only 2 or 3 pulses were rare (6%) and recorded mainly at the beginning of the mating period (Fig. 6). Burst duration ranged from 120 to 400 ms and differed between experiments (Fig. S1 in Supplementary Materials).

The mean number of pulses in bursts varied between spawning experiments and within the same pair of fish (Fig. S2 in Supplementary Materials). Pulse duration in a burst steadily increased from first to last pulse. The inter-pulse interval exhibited the opposite tendency and decreased over time. Pulses within bursts were smoother in form than typical single pulses. Within a burst, the first two pulses showed smaller relative amplitudes than the following pulses (Fig. S3 in Supplementary Materials). The duration of SPs within bursts (Fig. S3b, e) and the dynamics of the intervals between pulses (Fig. S3d, f) differed between spawning episodes. A comparison of BPs with SPs amplitudes showed that BPs amplitudes were about half those of SPs (Fig. 6).

Burst pulse emission: egg and milt release

The moment of BP emission strictly corresponds to the fish’s positions shown in Fig. 2g. While the burst continues (0.2–0.4 s), the fish remain almost motionless. The female, however, turns into the bend of the male’s embrace in such a way that its operculum presses the stretched side of the female’s abdomen along its gonads towards the genital pore (Fig. 7). About 0.1 s prior to emitting the BP, the female spread her ventral fins and released eggs 0.12 s following BP onset, followed by another batch 0.12 s later. Table 2 illustrates the stereotypic timing of the individual phases of a mating ritual.

At the end of the spawning sessions, large numbers of eggs were found at the bottom of the tank. To estimate their fertility, a portion of eggs was incubated in an aerated tank. The following day, most eggs had hatched to yolk-sac larvae at the bottom. Larvae eventually started feeding (cut pieces of *Tubifex*) and developed into freely swimming fry. Sperm and egg release were not completely synchronized as a small drop of milt typically appeared near the male’s genital opening about 5 s prior to the release of the first batch of eggs (Fig. 8).

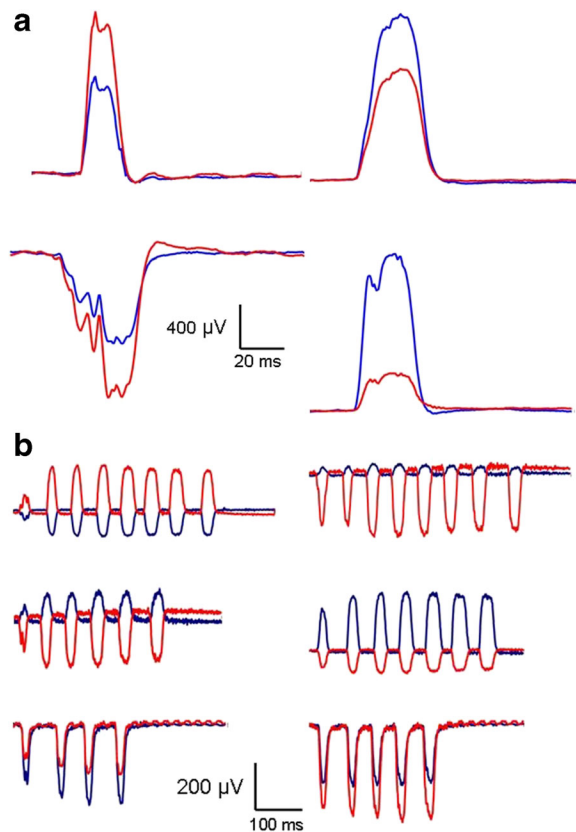


Fig. 5 Examples of single monopolar pulses (SPs) (a) and burst pulses (BPs) (b). Pulse waveforms registered on different channels coincide; amplitude and polarity are determined by the position and orientation of fish relative to recording electrodes

Discussion

We found a strong functional relationship between mating behavior and the associated electric activity in the Asian broadhead walking catfish *C. macrocephalus*. We have demonstrated that spawning is not only accompanied by electric pulses but that these pulses are a necessary component of the fish's mating behavior.

There were two pulse categories: single pulses (SPs) and bursts of SPs (BPs). Typically, SPs emitted by the male occurred at the beginning and at the end of a spawning session and accompanied the male's forceful attempts to mate. *C. macrocephalus*, however, can also generate SPs during aggressive-defensive encounters (Ol'shanskii et al. 2002; Baron et al. 2005; Kasumyan et al. 2013) as well as during hunting (Olshanskiy and Kasumyan 2018); BPs were observed only during amplexus when mating fish were in tight embrace. Functional sexual dimorphism in electric activity was

exhibited during spawning; only males generated SPs, while females were the sole source of BPs.

The mating ritual in *C. macrocephalus* is a rigid sequence of events and undoubtedly the result of natural selection. Bursts of electrical pulses have their exact place in this sequence of events. While generating BPs, fish are always strictly aligned in the same mutual pose. No matings were ever observed in the absence of BPs, and such bursts were never observed other than during mating behavior (Olshanskiy et al. 2011; Kasumyan et al. 2013; Olshanskiy and Kasumyan 2018). We submit that the emission of BPs during mating is a common, necessary feature in *C. macrocephalus* and very likely under genetic control.

Differences between SPs in clariids and electric organ discharges in mormyrids and gymnotids

Electric pulses generated by *C. macrocephalus* differ in several important features from electric organ discharges (EODs) in mormyrids and gymnotids. (a) The duration of clariid SPs is significantly longer and their shape is less stable than those of EODs. (b) In clariids as in some other weakly electric fish with episodic discharges, an SP reflects the added potentials of all electrocytes depolarizing with delays of a few milliseconds relative to each other (Bennett 1971; Baron 1982; Baron et al. 1994b; Orlov et al. 2019). The SP “probably involves the fused repetitive activity of many cells,” (Bennett 1971, p. 376) the sum total of which at a distant recording site appears as a monopolar pulse. Comparable delays in the depolarization of an array of electrocytes in strong electric fishes, mormyrids, and gymnotids last only fractions of a millisecond (Bennett 1971). (c) Each SP or BP in clariids corresponds to a complete behavioral act, e.g., attack or mating. Since the duration of EODs and inter-EOD intervals in mormyrids and Gymnotiformes is much shorter than the duration of any of the associated behaviors, a single behavioral act corresponds to multiple, patterned EODs as has been demonstrated for spawning behavior in species in both groups (e.g., Hagedorn and Heiligenberg 1985; Scheffel and Kramer 2006; Morson and Morrissey 2007; Wong and Hopkins 2007; Feulner et al. 2009).

The functions of EODs ascribed to mormyrids and Gymnotiformes (Morson and Morrissey 2007; Wong and Hopkins 2007; Feulner et al. 2009) do not apply to *C. macrocephalus* as they require that an electric pulse emitted by one partner precede the release of the

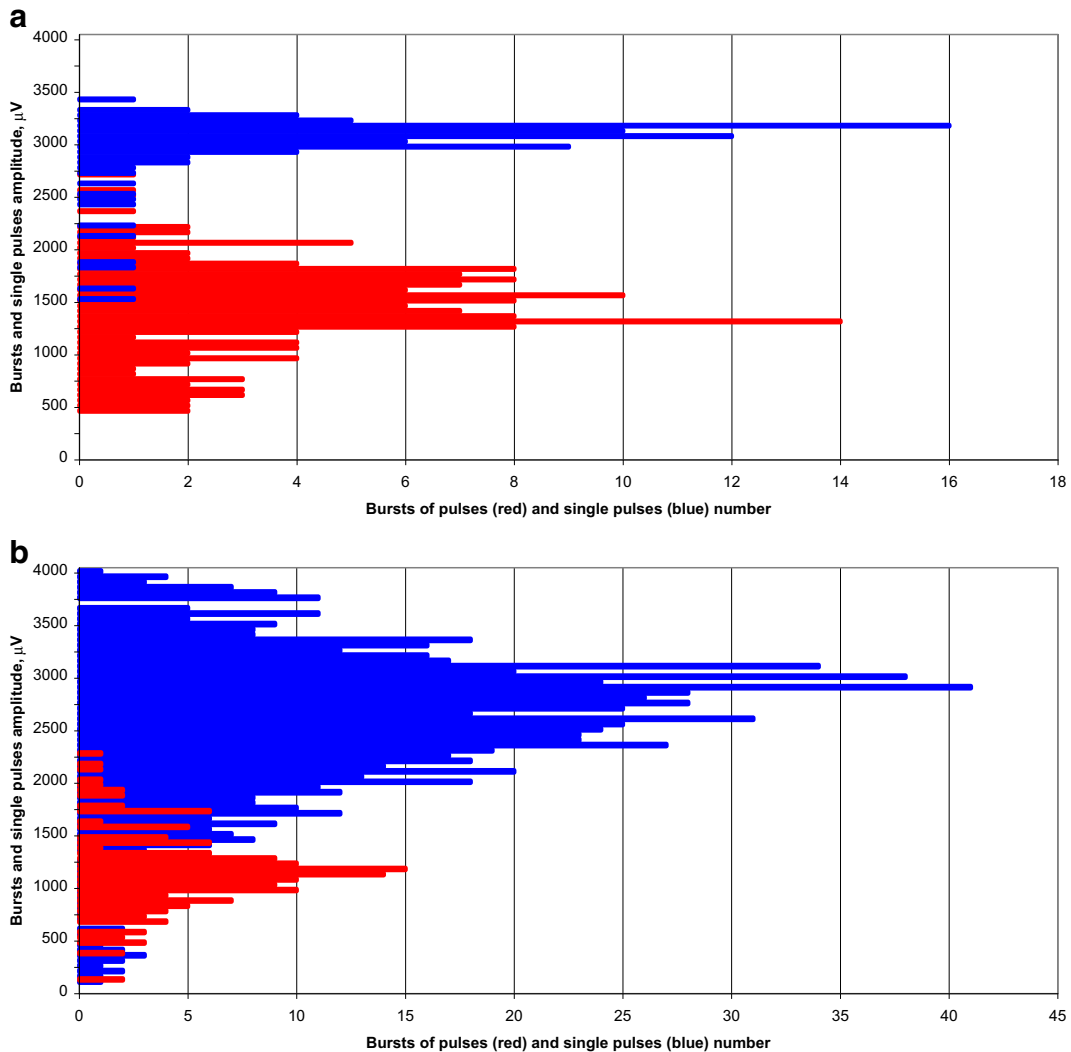


Fig. 6 Relationship between occurrence of single (blue) and burst pulses (red) and associated pulse amplitudes (μV). Representative data from two experiments (**a** exp. 7; **b** exp. 10)

reproductive products of the other. In *C. macrocephalus*, the release of sperm occurs a few seconds before the female generates the BP. Despite the fact that the male has already ejected sperm, his role in mating does not end there. He continues to tightly cover the head of the female even as she sharply arches her body. This suggested that the male acts as an “obstetrician,” and that his actions following sperm release help the female in releasing her eggs. Indeed, without the intimate embrace of a male, we have never seen the release of eggs in *C. macrocephalus*. Our observations have shown that an override female in the absence of a male can die from resorption of eggs. Egg release has never been observed outside amplexus or

in the absence of BPs. This suggests that the female’s BP triggers contractions of the male’s axial muscles, which in turn results in the male squeezing the female even more tightly, especially around the abdominal region of the convex side of her body.

To assess the strength of pulse amplitudes and receptor thresholds, voltages were measured directly on the fish’s body during its own pulse emission and those of a nearby conspecific (Ol’shanskii et al. 2002). Electrodes were mounted in the fish’s mouth and next to its dorsal fin. Its own pulses ranged in voltage from 25 to 40 mV. This was akin to the condition of BP emission when the male’s body (receiver) was in close contact with the anterior part of

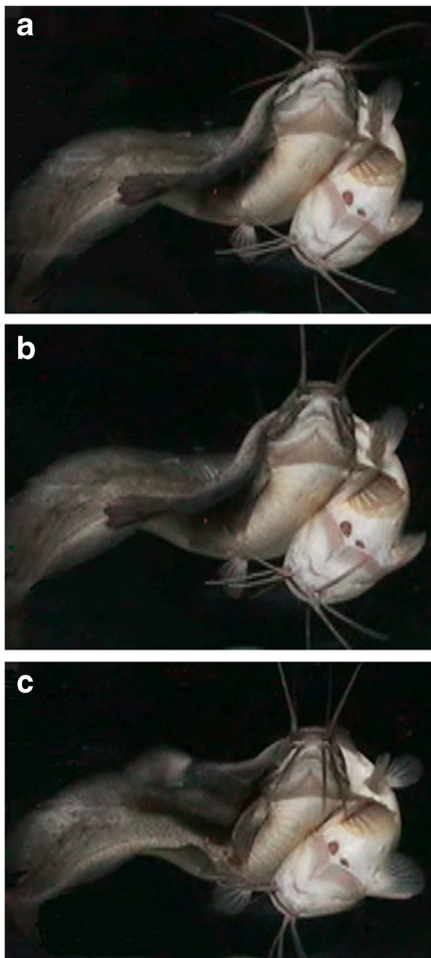


Fig. 7 Main position of fish during BP emission: **a** at the beginning, **b** at the middle, and **c** at the end of the burst. Video filmed through bottom of the tank

female (source). Voltages of pulses from the nearby conspecific (natural SPs) ranged between 1 and 10 mV.

The electrosensory threshold for *Clarias* was found to be less than 1 $\mu\text{V}/\text{cm}$ for pulses lasting about 20 ms (Lissmann and Machin 1963). Thus, the electric field gradient associated with electric pulses exceeds the electroreceptor threshold by several magnitudes. We noted earlier that the function of episodic electric pulses or discharges as a communication tool was enigmatic. If the fish's ampullary receptors are sensitive to SPs and BPs, the role of male SPs as a means of communication to attract females is a likely possibility.

On the other hand, while the female BP could also affect the male's behavior via electro-communication, we propose a more parsimonious role. A female-initiated BP may directly initiate axial muscle

contraction in the male without recourse to electroreception. The mutual entanglement of the fish maximizes this effect: the male's abdomen is in close contact with the area of the female's body where the "electric organ" is located. Thus, most of the current should not flow through the water, but through the male's body and affect axial muscle contractions, which in turn facilitate egg release. Increased current flow through the male's body compared with that through the surrounding water was indicated by the fact that BP amplitudes were 1.6–2.5 times smaller than those of SPs (see Fig. 6).

Spawning success; egg and milt release sequence

Sperm motility in *C. macrocephalus* and in other clariids does not exceed 2 min with mobility of 0.1 mm/s (Marchand et al. 2010; Wagenaar et al. 2012; our measurements). Thus, sperm may spread over a total distance of only 1–2 cm. How then is successful spawning achieved? The utility of the fish's position (see Fig. 2e), when the male arches around the female with the female's head resting on his belly, becomes clear in light of the fact that it is precisely in this position that the male emits sperm. How does sperm reach the eggs? We determined the distance between sperm and eggs to be 5–6 cm in a 30-cm fish. Small water turbulences, which inevitably occur with weak displacements of the fish, could facilitate the spreading of sperm. The most noticeable turbulence occurred when fish separated from amplexus, and 15 s is sufficient for all eggs to reach the sperm cloud. We propose that the female, with her highly developed olfactory sense (Resink et al. 1989), reliably detects the moment of sperm release, thereby ensuring fertilization of her eggs. Rapid detection is highly likely due to the close proximity of the female's olfactory organ to the male's genital pore, which is also the source of sex pheromones in male clariids (Resink et al. 1987, 1989).

Induced muscle contraction

Our hypothesis that the female *C. macrocephalus* compels a male to perform an obstetric function, i.e., asserts direct control of his muscles, needs further experimental and theoretical support (e.g., Babineau et al. 2006). Electric fish first became the object of research precisely because of their direct electric effects on humans and other animals (Moller 1995; Finger and Piccolino 2011).

Table 2 Fish positions and relative times for all phases of the mating ritual based on 15 consecutive matings observed in exp. 7

Burst time (h:min:s)	Number of pulses within burst	Code of mutual position of fish in seconds before burst onset						Time between position F and burst onset (s)	Time between position I and burst onset	Time between burst onset and position K
		<i>t</i> = 15 s	<i>t</i> = 12 s	<i>t</i> = 10 s	<i>t</i> = 1.5 s	<i>t</i> = 0.5 s	<i>t</i> = 0 s			
22:04:13	6	A-2	E	E	F	J	H	2.0	1.6	0.60
22:05:39	7	A-1	C-1	D	G	J	H	1.2	0.8	0.64
22:07:56	8	C-1	D	E	G	J	H	1.2	0.6	0.72
22:09:30	7	A-1	C-2	E	G	J	H	1.6	1.2	0.64
22:11:31	7	C-2	D	E	G	J	H	1.6	0.72	0.64
22:13:37	7	A-2	C-2	E	G	J	H	1.6	0.64	0.60
22:15:42	6	C-2	C-1	E	G	J	H	1.6	1.0	0.60
22:19:53	8	A-1	C-2	D	G	J	H	1.4	0.72	0.68
22:21:51	7	C-2	C-1	D	G	J	H	1.4	0.72	0.68
22:24:11	7	A-2	D	D	G	J	H	1.4	1.0	0.60
22:25:29	7	C-2	D	D	G	J	H	1.6	1.0	0.64
22:28:25	7	A-3	D	E	G	J	H	1.4	0.64	0.68
22:30:47	7	B-2	D	E	G	J	H	1.5	1.0	0.64
22:32:58	8	B-1	C-2	D	G	J	H	1.5	1.0	0.64
22:35:36	7	A-2	C-2	E	F	J	H	1.8	0.9	Not visible

A-1, fish apart (Fig. 2a); A-2, fish apart, heads parallel; A-3, fish separate, heads perpendicular; B-1, fish close, heads to head (Fig. 2b); B-2, fish side by side; C-1, male arc, but fish still apart (Fig. 2c); C-2, almost amplexus, but there is a noticeable gap between the female rostrum and the male abdomen (Fig. 2d); D, amplexus: female body straight, and besides a slight stirring of her tail both fish move only in relation to the aquarium; E, amplexus: female body straight, fish motionless (Fig. 2e); F, female begins to arc; G, female continues her arc; H, amplexus: female’s maxillary barbels are released and stretched forward; male’s body covers female’s back behind her head and presses tightly against her belly (Fig. 6a); I, female’s body bent, buries her snout in male’s belly (Fig. 2f); J, female’s head under male’s belly; and K, when burst ends, the lumen between the female’s belly and the male’s cheek is visible, and the female begins to straighten her head

Thus, the phenomenon of so-called induced muscle contraction is of interest to the current study. Carlo Matteucci discovered this effect in 1842 when he placed a “galvanoscopic frog,” i.e., the nerve of a frog’s leg (prepared following the method of Galvani) on the

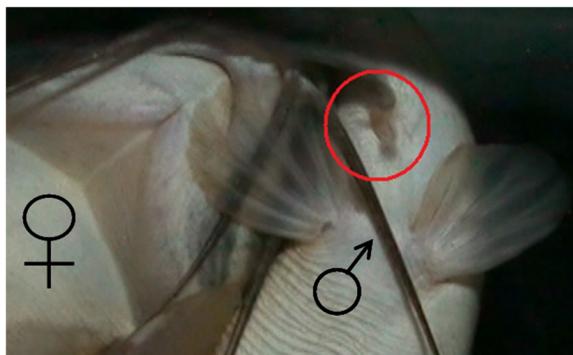


Fig. 8 Milt ejaculation in *C. macrocephalus*. Video recordings taken through bottom of the tank. Note sperm drop inside circle

surface of another muscle of a frog, pigeon, or rabbit. The electric excitation of this muscle led to excitation of the first frog’s muscle (Matteucci 1845, 1847a). In this context, it is worth noting that Darwin made reference to Matteucci’s work when he discussed the function of weak electric discharges in *Raja* (Darwin 1872, p.150), and Matteucci himself repeatedly emphasized qualitative similarities and quantitative differences of electrophysiological phenomena in electric fish and in neuromuscular structures, for example, in frogs (Matteucci 1847a, b; Moruzzi 1996).

In recent publications, Catania (2015, 2017) showed that the strong EOD emission of *E. electricus* acts directly on the motor neurons of its victims causing tetanus in prey. The stunning effect increases with shorter inter-discharge intervals not exceeding a few millisecond, which is the case in *Torpedo* and *Malapterurus* (Bennett 1971; Bauer 1979; Belbenoit et al. 1979; Rankin and Moller 1986; Catania 2015).

Comparable with strong electric fish, we surmise that in *C. macrocephalus*, the female-generated volleys cause a pulsating compression (tetanus) of the male's axial musculature and subsequently through his behavior contribute to egg release. In *E. electricus*, only a small part of the current passes through the victim's body while most of it passes through water (Catania 2015). In *C. macrocephalus*, with the male covering the female's electrogenic tissue during amplexus, most of the current should pass through his body. Future studies measuring the current densities near the electrogenic source must support these arguments. Raising a pertinent historical anecdote, narrated by Wu (1984), could vindicate the great Chinese pharmacist Li who in 1596 placed a catfish (*Parasilurus asotus*) in direct contact with the skin of his patients to cure ptosis and facial palsy; interestingly, *P. asotus* emits episodic weak electric pulses that resemble those of *C. macrocephalus* (Baron and Olshanskiy 2009).

Direct impact as a possible primary ethological function

We earlier asked why Uranoscopidae that lack electroreception show very similar pulses as members of Rajiformes, Clariidae, or Siluridae. A possible answer, and shedding some light on the enigma of the behavioral function of weak episodic electric emission, may lie in the modification of electrogenic structures towards increasing the efficiency of direct impact. We will therefore consider extant clariids analogues to ancient intermediate species that exhibited transitional features between non-electric and strongly electric catfish, and thus return and conclude with Darwin (1872, p. 150),

“beyond this we cannot at present go in the way of explanation; but as we know so little about the uses of these organs, and as we know nothing about the habits and structure of the progenitors of the existing electric fishes, it would be extremely bold to maintain that no serviceable transitions are possible by which these organs might have been gradually developed.”

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