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African *Clarias* catfish elicits long-lasting weak electric pulses

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Abstract. The African catfish *Clarias* is generally considered to possess electroreceptors but not electric organs. It is reported here that at least one species of the genus, *C. gariepinus*, can produce weak monophasic discharges during aggressive interactions with conspecifics. These irregular pulse discharges are substantially longer than the electric organ discharges (EODs) of all other pulse-generating freshwater electric fishes. It is also shown that the optimal sensitivity of *Clarias*' ampullary receptors just corresponds to the modal pulse duration. The *Clarias* catfish, with its very specific EOD, may be of special interest in the evolution of the electrogenic system in the siluriforms, comprising many electroreceptive but nonelectrongenic catfish species.
Key words. Catfish; *Clarias*; electric fish; electric organ discharge; electroreception.

The possession of electric organs is characteristic of only a few fish taxa[1,2]: three marine groups and three freshwater ones, including some catfish. For a long time the study of electrocommunication and electrolocation systems was restricted to the two groups of weakly electric fish – African Mormyriformes and South American Gymnotoidei[3]. The electrosensory system in these fish consists of two classes of receptors: ampullary and tuberous organs, tuned to detect weak low and high frequency electric signals, respectively. The biological significance of ampullary electroreceptors in these and some other fish species in which there are no electric organs (EOs) has been associated with so-called passive electroreception, the detection of electric fields including the bioelectric fields of living things[4] in aquatic environments. The electrolocation and electrocommunication functions are provided only by the tuberous electroreceptors.

The discovery in African Synodontid catfish (Mochokidae) of EOs which can generate weak electric discharges with a duration of about 4 msec[5] challenged the generally accepted notions in this field. Such short discharges lie outside the frequency range associated with perception of electric fields by ampullary electroreceptors of investigated catfish species[6–8], complicating the assignment of a biological role to these discharges. However, one of the Synodontid species has been shown to be sensitive to weak electric impulses in the range of 5–100 ms[9] including the ones whose duration is close to that of its own electric organ discharges (EODs). These data and those of Hagedorn et al.[5], suggest that this group of fish as well as the two other groups mentioned earlier could also possess the systems of active electroreception. In this work we present data of a study of the electrogenic ability of the African *Clarias* (the Old World airbreathing catfish family Clariidae). Our preliminary field observations have shown unusually long-lasting EODs, which appear during the characteristic social behavior of these fish.

Methods

In our study, catfish individuals identified as *Clarias gariepinus* in accordance with the recent revision of the genus[10] were sampled from two natural populations inhabiting Lake Awasa and Koka Reservoir in the Ethiopian Rift Valley. The fish were maintained in laboratory tanks for up to six months. They retained the ability to produce electric signals during this period. Recordings were taken from 16 individuals of 12–18 cm in total length in preconditioned tap water at 26 °C (1–2 kΩ cm). The experimental arena was an aquarium partitioned longwise with plexiglass to allow the size of compartments to be adjusted for recording. It was fitted with two stainless steel electrodes (10 × 14 cm) attached to the partition and to the opposite wall of the aquarium. All of the data on amplitude presented here were obtained from a 20 × 20 × 30 cm compartment. The discharges were detected with a low noise differential amplifier (gain 10^4, frequency band $0–10^4$ Hz). In the field, EOD visualization and recording were made with a portable oscilloscope and a Bruel & Kjaer FM magnetic tape recorder 7007 (0.3 Hz–20 kHz). In the lab, EOD storage and analysis were carried out with a PC supplied with a 12 bit analogic digital convertor (sampling rate up to 10 kHz). Videorecording was used to correlate particular behavior with EOD emission.

Drawings were made from video records containing both a view of the experimental tank and the oscilloscope screen displaying fish EODs. All discharges were recorded from different pairs of *Clarias* catfish placed simultaneously in the experimental tank.

Results and discussion

The discharges that we recorded from *Clarias* were monophasic pulses of positive polarity with respect to the head. Their duration varied in the range 5-260 ms, that is generally greater than the upper limit of pulse duration in most electric fish[2,11]. The discharge amplitude that we observed was nearly an order of magnitude greater than the maximum action potentials of muscles in the same fish during a chase (fig. 1). It was rather difficult, however, to obtain an accurate estimate of the discharge amplitude because it depended on the relative positions of the fish and electrodes, and the discharges only occured while the fish were moving. Our best estimate of the electric field strength at 10 cm from the presumed electric organ was roughly 150 μV/cm. Thus, the amplitude of the *Clarias* discharge was of the same order as in the mochokid catfish *Synodontis obesus*[5] and fell within the wide range of discharge characteristics typical of weakly electric fish. From the wave form and discharge amplitude we believe that the *Clarias* catfish possesses an electric organ though the anatomical location is uncertain.

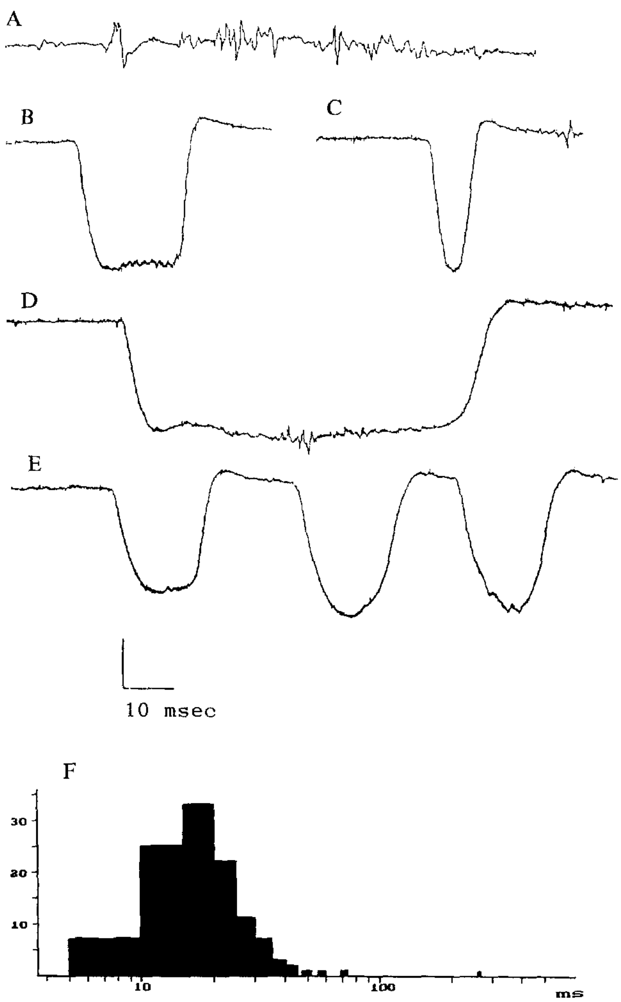

Figure 1. The electrical activity of *Clarias gariepinus* individuals. *A* The action potentials of muscles. *B–D* Examples of EODs with variable duration. *E* The catfish elicited single discharges or irregular series of up to four pulses. Vertical scale bar is 200 μV for *A* and 1 mV for *B–E*.
F Time-duration histogram based on data obtained from 6 individuals (114 discharges in total). Abscissa: time duration of EODs (msec) on a log.scale. Binwidth 5 msec. Ordinate: number of EODs per bin.

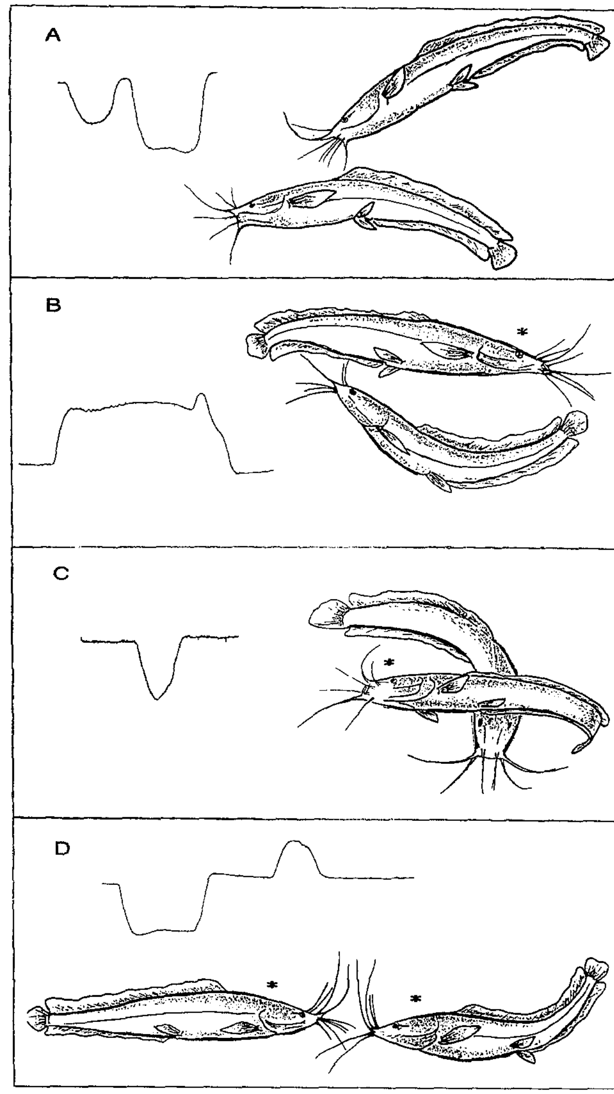

Figure 2. Drawing from videorecords containing in the same frame a view of experimental tank and a screen of oscilloscope displaying fish EODs. The individual marked with an asterisk is discharging.

It is noteworthy that no EODs were registered from solitary individuals. We also failed to provoke discharges by mechanical stimulation. *Clarias* emitted discharges exclusively in the course of aggressive interactions with conspecific individuals (fig. 2). When two fish were placed into the small experimental tank, a short latent period of accommodation was usually followed by repeated fights interspersed with pauses of different lengths. The determination of EOD polarity is easily done while two fish are placed unidirectionally (fig. 2A). If the dominant-subordinate relationship between individuals was established, the subordinate fish sometimes emitted discharges in response to an attack by the dominant as shown in figure 2B. Most frequently single or serial discharges accompanied attacks by the dominant individual while it attempted to bite its escaping opponent. Such attacks were usually confined to a chase and discharge by the dominant without real biting (fig. 2C). Particular conditions (small size difference between individuals, a period of food deprivation preceding the experiment, and a reduced volume of the test aquarium) provoked especially severe agression in both fish (fig. 2D). In these cases we observed virtually constant fighting, associated with persistent electric organ activity. The intervals between discharges produced by the different fish were greatly reduced. The same fish were more likely to produce series instead of single pulses in such situations.

We also observed nonaggressive interactions between pairs of well fed larger individuals. They were characterized by a certain 'intertwisting' mode of swimming and might be related to sexual behavior. EODs did not accompany this behavioral pattern, nor did we observe any EODs from catfishes engaged in feeding behavior, including those catching fish prey.

These data led us to a hypothesis about the possible role of electric signals in *Clarias* communication.

The use of ampullary receptors for detection of electric fields from inanimate and animate sources in catfish has been widely discussed[7,8,12], as well as a possible role of the catfish passive electrosense in social interactions[8,12]. The peak sensitivity of *Clarias* electroreceptors falls in the range of 10–30 Hz under alternating current stimulation as determined by electrophysiological experiments[13]. The behavioral threshold in *Clarias* stimulated by rectangular current pulses of duration 20–30 ms was found to be around 1 $\mu V/cm$[6]. Taking into account the fact that duration of the *Clarias* discharges overlapped with the peak sensitivity range of its electroreceptors, EODs of the amplitude characteristic of this fish could be perceived by conspecific individuals at a distance of at least 20–30 cm. Consequently, both the electrogenic and electroreceptive systems permit electrocommunication in *Clarias*.

The EOD duration distinguishes *Clarias* not only from other electrogenic catfish[5,9], but from most other electric fish as well[2]. There are only two marine groups of electric fish, skates (Rajoidei) and one of the stargazer species, *Uranoscopus scaber* (Uranoscopidae), that produce EODs of similar duration to those in *Clarias* catfish. Their EODs however, may be even longer than in *Clarias*, up to 200 ms[14] or 1 s[15] in skates and up to 800 ms in stargazer[16].

Similarities between these two marine groups on the one hand, and the *Clarias* catfish on the other hand, lead us to some interesting speculations. The fundamental electrophysiological differences between freshwater and marine fish groups have been considered to be determined by their electrocyte membrane properties. The electrocytes of all marine electric fish, including skates and stargazers, are equipped with a postsynaptic membrane, while the electrocytes of all previously studied freshwater electric fish have spike-generating membranes[17–19]. It is suggested that the long-lasting pulses of skates 'involve fused repetitive activity of many cells[1]'. There are two possible explanations for the presence of long lasting pulses in *Clarias*.

If the same mechanism of long pulse emission occurs both in *Clarias* and in skates, the former would be the only freshwater fish known to possess the postsynaptic electrocyte membrane. On the other hand, if like all other freshwater electric fishes the *Clarias* catfish have spike-generating electrocyte membranes, the mechanism of the *Clarias* electric organ action should be quite distinct. This is because EODs of all previously known pulse-generating freshwater electric fish involve a highly synchronized response of all electrocytes[3] that results in a relatively short pulse duration. We are faced with two hypotheses concerning the evolution of the *Clarias* electrogenic system.

The first is as follows: the catfish represents a primitive stage in the evolution of the electric organ and its long lasting discharge results from the poorly synchronized and fused activity of many cells. The other possibility would be that this catfish evolved from an ancestor posessing a short EOD typical for all other freshwater electric fish. Evolutionary changes might be caused by the necessity to adjust the characteristics of electric signals to the peak sensitivity of electroreceptors.

In any case, siluriform fish appear to be a unique taxon containing a wide spectrum of electroreceptive but non-electrogenic species and weakly electric forms, as well as a strongly electric catfish. This group seems to display different stages of the evolution of electrogenic ability in fish. Such a group has been a sweet dream of fish electrophysiologists since the pioneering work of Lissmann[20]. The question of whether the *Clarias* catfish represents a primitive stage of electric organ evolution in siluriforms or whether it is a highly specialized advanced form will be the subject of future studies.

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