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= GENERAL BIOLOGY =

Electric Discharges and Electrogenesis Peculiarity in Two African Upside-down Catfishes, *Synodontis caudovittatus* and *S. eupterus* (Mochokidae, Siluriformes)

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Abstract—The paper reports spontaneous generation of weak electric discharges with an amplitude of 0.4– 1.0 mV and a frequency of $3-9 \text{ min}^{-1}$ by solitary *Synodontis caudovittatus* fish. When fish individuals were tested in pairs, their aggressive—defense interactions were associated with an increase in the amplitude of the discharges (up to 30-45 mV) compared to the discharges of individual fish, while the duration of the pulses increased up to 20-25 ms due to the prolongation of the second phase. In *S. eupterus*, electric activity was recorded only in the course of aggression—defense interactions, while spontaneous generation of discharges was not observed at all. The paper discusses the different aspects of electrocummunication between the catfish including the role of the reversion of polarity of the merged summated discharges with increased duration.

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Apart from strongly electric catfish belonging to the family Malapteruridae, the production of electric discharges by specialized electrogenerative systems was described in the representatives of three African catfish families: Mochokidae [1-4], Clariidae [5, 6], and Claroteidae [7, 8]. Among weakly electric catfishes, the structures responsible for the electrogenesis have been localized only for the representatives of the genus Synodontis belonging to the upside-down catfish family Mochokidae. Comparison of the typical muscle fiber in the lateral muscles of Synodontis with the modified muscle fiber in the acoustic muscles, which produce the electric discharge, revealed that the latter are significantly smaller in diameter and less densely (more loosely) packed [1]. Another study [4] performed on five Synodontis species demonstrated the negative correlation between the myofibril density in the modified muscle fibers and the ability of the species for electrogenesis, while for the sound production, the observed correlation was positive. It was hypothesized that the ability of these modified muscle fibers to produce electricity has not yet been fully established, and for this reason the representatives of the genus *Synodontis* may be considered as a transitive form between the species incapable of producing electric discharges and the electric ones [4]. In view of this hypothesis, comparative study of electric organ discharges (EODs) and the function of electrogenerative systems in different Mochokidae species is of particular interest.

The present work provides data on the electric activity of the two upside-down catfish species *Syno-dontis caudovittatus* and *S. eupterus*, which have not been studied in this respect to any detail so far.

The material for the study consisted of three specimens of S. caudovittatus with the standard length (SL) of 175–230 mm and five specimens of S. eupterus with SL of 107–116 mm. The material was obtained in the Baro River system in the White Nile basin in southwestern Ethiopia. The experiments were conducted in the field according to the previously used modified techniques [6, 7]. Fish were caught with cast and frame nets and transported in 40-L plastic containers to the field laboratory, where they were kept in the water obtained from the same river in which they were caught with constant aeration and active filtration. The experiments were carried out day and night at natural illumination. The acclimation period before the first record varied from four hours to several days. EODs were recorded from free-swimming fish in an aquarium ($40 \times 30 \times 20$ cm in size) using two rodshaped graphite electrodes placed on the short walls of the aquarium. The electric signals amplified in the Grass P15 differential amplifier (×100, 0.1 Hz to 10 kHz) were applied to the input of the analog-todigital converter (DAQ-card AI-16E-4, National Instruments) connected to the PCMCA port of the

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Fig. 1. Electric discharges of (a-d) *Synodontis caudovittatus* and (e-h) *Synodontis eupterus*. In all oscillograms, upward wave corresponds to electronegativity of the head. All oscilogramms are normalized for amplitude. Horizontal bar, 5 ms; vertical bar, (a) 0.2 mV and (b-h) 10 mV.

laptop and digitized (sampling rate 200 kHz, 12 bit). Fish signals were recorded and analyzed in real time mode by means of the custom-made software developed with the use of LabView 7.0 and adapted to the DAQ-card.

EODs of S. caudovittatus were two-phase signals with the short initial phase of 1-2 ms and the longer second phase of 3-12 ms (Figs. 1a-1d). In some cases, the duration of the second phase was as long as 20–25 ms. A solitary free-swimming fish in the aquarium repeatedly generated electric discharges of the type depicted in Fig. 1a at a frequency of $3-9 \text{ min}^{-1}$ (data obtained from three individuals for two 0.5-h intervals). The periods of electric activity of the particular fish were sometimes interrupted by pauses which could last for several hours. All other factors being equal, the amplitude of discharges of an individual depended from both the distance to the receiving electrodes and their position relative to longitudinal axis of fish. If to omit the strongest discharges, which account for 10% of all recorded signals and which were most probably obtained when the fish was in the immediate proximity to the electrode, the average signal amplitude values ranges from 0.4 mV to 1.0 mV.

When *S. caudovittatus* were tested in pairs within the restricted space of a small aquarium, the generation of discharges was mostly observed in the course of aggression–defense interactions, when one of the fishes, apparently the dominating one, launched series of attacks usually accompanied by EODs. The frequency of discharges in this case reached $6-8 \text{ min}^{-1}$. The amplitude of the EODs increased up to 30-45 mVcompared with the lower amplitudes of the EOD obtained from the solitary individuals, while the duration of the pulses increased due to the prolongation of the second phase of the discharge (Figs. 1b–1d).

The solitary freely swimming *S. eupterus* displayed no spontaneous electric activity. We did not even observe weak electric discharges within the microvolt range. EODs were generated only when catfish were tested in pairs with the frequency of discharges depending apparently on the behavioral status of the individual fish taken into the experiment. For example, in the case of the most active pair of *S. eupterus* catfish, 19 EODs were recorded during 0.5 h. As it was the case with *S. caudovittatus*, two-phase discharges differed significantly in their type; they varied from short (4–6 ms) discrete discharges (Fig. 1e) to a cluster of EODs merging into a single monopolar signal with the maximum duration reaching 30 ms and amplitude reaching 30 mV (Figs. 1f–1h).

Functional excellence of the electric organ (EO) is determined mainly by the two factors. The first factor is the optimal arrangement of electrocytes, i.e. their series-parallel connection, which makes it possible to match the internal impedance of the EO to the electroconductivity of the environment. The second one is the functioning of the command central neurons, which synchronize the activity of individual electrocytes so that the EOD form generated by each of them was absolutely the same as the form of the EOD generated by EO as a whole [9-12]. Assuming that short discrete discharges (Figs. 1a, 1e) are EODs generated by individual electrocytes, the long signals with the characteristic indented pattern (Figs. 1b–1d, 1f–1h) generated by catfish in the course of social interactions may appear to result from desynchronization of individual EODs due to imperfection of the controlling system.

However, the production of prolonged EODs with the characteristic indented pattern resulting from sequential temporal summation of discrete discharges has already been discussed for African catfish belonging to the genera *Clarias* [5] and *Auchenoglanis* [8]. The mechanism was described as well by which sequential dispersed discrete signals can merge into a single summated discharge (the examples of such merge may be the EODs provided in Figs. 1e, 1f, 1g, 1h). Since the electrosensory system in catfish consists of ampullary or slowly adapting (tonic) electroreceptors which are the most sensitive to electric pulses no shorter than 20–30 ms [13], then the generation of prolonged merged discharges in weakly electric catfish seems to be functionally justifiable as an attempt to match the frequency spectrum of EODs to the maximum sensitivity range of the electroreceptor.

In the representatives of all *Synodontis* species, including those studied by us, the first phase of the electric discharge always has negative polarity relative to the head. This is accounted for by individual electrocyte innervation, as well as by the orientation of electric cells along the rostro-caudal axis. As can be seen in Figs. 1d and 1h, the prolonged summated discharges of S. eupterus and S. caudovittatus have opposite polarity. Since the shortest discrete discharges of the catfish species under study (Figs. 1a, 1e) have different negative phase to positive phase ratios, then the quasimonopolar pulses resulting from arithmetic summation of the discrete discharges will have opposite charges. As soon as the short initial phase of the EOD of S. caudovittatus (Fig. 1a) cannot be detected by low frequency ampullary electroreceptors, then the opposite polarity of discharges may serve as an additional marker in the interspecies communication in Synodontis similar to what is observed in weakly electric Momyridae.

When muscle fibers transform into electrocytes in the acoustic muscles of Synodontis, the total number of electrogenerative units increases proportionally leading to an increase in the amplitude of electric discharges, which is the key criterion defining the place which the species occupies on the evolutionary tree in the course of development of the electric organ [4]. The amplitudes of discharges of S. caudovittatus and S. eupterus recorded in the course of aggressiondefense interactions were about the same. The only difference observed between the two species was weak periodical discharges in the µV range detected in S. caudovittatus, which are not adapted for electroreceptors because of their short duration, this finding suggesting that the electrogenerative systems of this catfish species being apparently at the lower stage of the development.

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