Electroreception of catfish *Ictalurus nebulosus* in uniform and non-uniform DC fields: detection threshold and body length

Lonneke B.M. Eeuwes, Robert C. Peters, Franklin Bretschneider and Wim J.G. Loos

Utrecht University, Comparative Physiology, Neuroethology
Padualaan 8, NL-3584 CH Utrecht, The Netherlands

ABSTRACT. Catfish are able to detect electric fields with their electroreceptor organs. It goes without saying that the electrodetection threshold depends on the sensitivity of the electroreceptor organs. The sensitivity in turn depends on a variety of extrinsic factors such as water temperature, conductivity, and electric field frequency. The aim of this study was to determine the effect of an intrinsic characteristic, namely body length, on the electrodetection threshold. In a two-alternatives forced-choice experiment, catfish of different sizes were tested in uniform or non-uniform direct-current fields. The results show no significant relation between body length and electrodetection threshold. The electrodetection thresholds are lower in uniform fields than in non-uniform fields. From this it is concluded that other factors than body size alone determine the electrodetection threshold.

KEY WORDS: electroreception, body length, catfish, behaviour, threshold.

INTRODUCTION

In the history of electrophysiology much research has been done to investigate if there exists a correlation between specimen size and the behavioural responses of fish to galvanic stimuli. In a variety of species, both electrosensitive and non-electrosensitive, the lowest current density that still elicited a response was found to increase with decreasing body length (ABE, 1935; SCHEMINZKY & SCHEMINZKY, 1931). Today, specimen size still plays a prominent part in research on electric fishing (STERNIN et al., 1972; ZALEVSKI, 1985). Surprisingly enough, in electroreception studies of the last five decades specimen size has not been taken into account, whereas a number of other factors on which the electrodetection threshold was thought to depend, such as ionic composition of the environment (PETERS et al., 1991; PETERS & WESTERINK, 1999; ROTH, 1971) electric field frequency, and temperature (PETERS et al., 1995a), were studied profoundly.

As catfish grow, the physiological properties of the electroreceptor organs change. Both the number of receptor cells and the number of ampullae per afferent nerve fibre increase, which causes not only an increasing signal-to-noise ratio and a sharpening of the bandpass filter but also an increase in the absolute sensitivity of the electroreceptor organ (PETERS et al., 1997; PETERS & IEPEREN, 1989, PETERS & MAST, 1983; TEUNIS et al., 1990; ZAKON, 1987). Moreover, a large specimen spans a larger area in the electric field and thus is able to perceive a higher potential difference than a small specimen (KALMIJN, 1974). On those grounds, a correlation between body length and the electrodetection threshold may be expected; a large specimen presumably has a lower electrodetection threshold than a smaller specimen.

Hence, behaviour that depends largely on the electric sense could differ between catfish of different sizes. Distances to prey at the initiation of an attack for instance, could, as in dogfish (KALMIJN, 1982), decrease with decreasing body length. The aim of the present study was to investigate in a psychophysical experiment if the sensitivity of catfish in direct current fields is size-dependent.

Corresponding author: R. Peters, e-mail: R.C.Peters@bio.uu.nl

MATERIAL AND METHODS

Animals

Twenty-four specimens of freshwater catfish (*Ictalurus nebulosus*, LeSueur, 1819), eleven females and thirteen males, with weights ranging from 13 to 270 g and lengths of 95 to 280 mm, were subjects of this experiment. Juvenile catfish were obtained from Visplant (Numansdorp, The Netherlands). Several years prior to the experiments, adults were obtained from Van de Put (Zonhoven, Belgium). They were kept in glass tanks filled with tap water at Utrecht University until the experiments began. During the experiments the fish were kept in a glass aquarium, 91 x 30 cm, water height 10 cm. This aquarium was connected to a buffer tank, from which water was circulated and filtered. The total water volume was 180 litre. The tanks were placed in a climate-controlled room, and the temperature of the water was kept at 17 ± 2°C with a cooling device. Initially the tanks were filled with water, conductivity 0.31-0.38 mS/cm. The conductivity increased by approximately 0.01 mS/cm during the course of the experiments due to excretions of the fish and feeding. Once a week the water was partly refreshed. The fish were tested during the dark period of a 12h dark, 12h light regime. During the experiments the fish were fed minced beef with gelatine and agar-agar from peristaltic tubes on either side of the tank.

Working with small specimens (< 150 mm) required some adjustments: Water height was decreased by 2-4 cm to improve detection by the sensors used; the stimulus strength was adjusted. A small amount of Trouvit Elite response 1.6 mm (Paling, Putten, The Netherlands) was added to the food to make it more attractive for the juveniles, which were not used to eating beef. To avoid novelty stress, two juveniles were kept together in a test tank for a week before they were separated at the beginning of shaping.

Protocol

The electrodetection threshold was determined for each fish in a number of threshold sessions. The catfish were subjected to two sessions a night. A single session consisted of 100 or more trials. For the juveniles a single session consisted of 30 trials, because at that point they lost their appetite and motivation. At the beginning of each trial a light bulb above the test tank was switched on, which caused the fish to seek shelter underneath a PVC strip, approximately the same size of the fish, attached to the wall of the tank (Fig. 1A,B). If the fish stayed underneath its shelter for two seconds, the light was switched off and a weak uniform or non-uniform direct current field was presented. Each series of trials solely consisted of uniform field presentations or non-uniform field presentations. Each fish was subjected to only one form of field presentations.

In uniform fields, the side at which the anode was located was alternated pseudo-randomly. If the fish interrupted the infrared bundle nearest to the cathode, food was dispensed through the feeding tubes and 30 s of dark feeding time was offered. If the fish interrupted the infrared bundle nearest to the anode, the light bulb above the tank was switched on immediately and no food was offered.

In non-uniform fields the stimulus was presented either on the right or the left side. If the fish crossed the decision point at the side where the stimulus was presented, food was dispensed through the feeding tubes and 30 s of dark feeding time was offered. If the fish crossed the decision point at the opposite side, the light was switched on immediately and no food was offered.

At all times, the light above the test tank was operating as a negative reinforcer. After a correct choice, the strength of the following stimulus was decreased by 1 dB. After a false choice the following stimulus was increased by 3 dB (Fig.2). The steps up and down were not equal (respectively 3 dB and 1 dB) because if so, the stimulus would stay undetectable for a long period near the threshold value and the fish would become less motivated. This so-called staircase method eventually reveals the electrodetection threshold in orientation in catfish (Peters et al., 1995a).

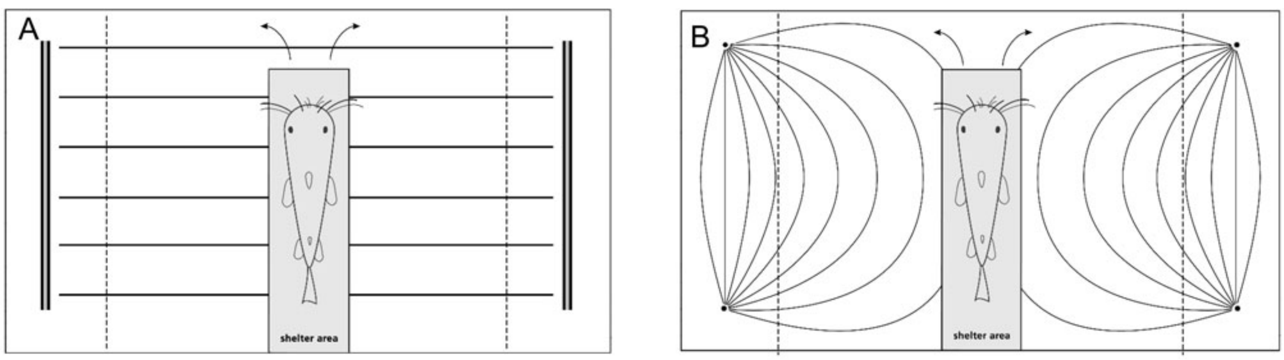

Fig. 1. – Schematic drawings of the experimental tanks used in uniform field presentation (A) or non-uniform field presentation (B), top view. The shelter area (grey) provides protection for top lights (not shown) and serves as a dwelling space between trials. Several centimetres from the electrodes infrared detectors are placed on the outside of the tank. At the same position a plastic bar (dotted line) is placed at the bottom of the tank to provide a tactile stimulus for the catfish. These bars are the decision lines. If the fish crosses a dotted line, it has made a choice. Food dispensers are placed between the dotted lines and electrodes. (A) Thick lines represent the strip electrodes. Parallel solid lines between electrodes represent the field lines during a trial. The polarity of the electrodes changes between trials. (B) Dots in the corners of the tank represent the steel bar electrodes. Solid lines between electrodes represent the field lines during a trial. The stimulus presentation is either on the left or the right side.

Fig. 2. – An original recording of the electrodetection threshold during a single session. At false choices the stimulus rises by +3 dB. The solid line without markers represents the running average over 12 successive trials. During analysis of data stimulus attenuation (dB) is converted into stimulus strength (µV/cm) and corrected for resistivity. In this example the electrodetection threshold is reached at -45 dB, which equals 0.72 µV/cm.

Stimulation

Since catfish can localise prey and orientate by means of their electroreceptor organs, dc dipole fields were used to mimic prey, and uniform direct-current (dc) fields to imitate environmental fields (PETERS & BRETSCHNEIDER, 1972). Stimuli were generated by a LAB-PC data acquisition card (National Instruments). The stimulus was fed into a home made voltage-to-current-converter (VCC), powered by floating power supplies. To generate uniform fields the VCC was connected to a pair of electrodes made of a strip of Perspex (15 x 30 cm) and silver wire. Creating a non-uniform field was achieved by means of two pairs of stainless steel bar electrodes with a diameter of 3 mm.

Shaping

Before the actual testing started, the fish was subjected to a period of shaping. In this period the stimulus protocols differed. In non-uniform fields the stimulus was presented right and left alternately, and in uniform fields the anode location was switched from one side to the other after each trial. The field strength (200-1000 mV/cm) was certainly within the perceptive range. As soon as the fish performed at a 90% level, the alternating left and right stimulus presentation in non-uniform fields and the anode location in uniform fields were randomised with a maximum of three in succession at the same side. When the level of correct choices was 90% or over, threshold determination was initiated. For the shaping period no particular skills are required, because the fish spontaneously orients to electric dipole sources, or to cathodes, and thereby autoshapes itself.

Statistics

Threshold has been defined as the minimum stimulus strength that could be detected by the fish for a certain period of time. As the steps up and down were unequal, every false choice had to be compensated for by three correct choices in order to maintain the same overall stimulus strength. To determine whether or not the catfish had reached its threshold or was still changing its performance, the running average over twelve successive trials was calculated. If the running average stayed the same for four successive calculations, this value was accepted as the threshold value. This means that the false-correct-correct-correct sequence had to be repeated at least three times, in which the order of the false and correct choices is irrelevant as long as the initiation point of the sequence is proceeded by more than three correct choices. If a single session yielded more than one threshold value, only the lowest was used in further analysis. Sessions that did not yield threshold values were left out. Kruskal-Wallis' non-parametric, distribution-free test for more than two independent samples was applied to detect differences in thresholds between catfish of varying size. A sample consisted of all threshold values found for a particular fish (with a certain body length). A regression analysis was also conducted.

RESULTS

Literature

Before the experiments were initiated a literature search was carried out to investigate what was already known about electrodetection thresholds. Over the years, all kinds of species have been subjected to research on detection of electric stimuli. To reduce the amount of information it yielded, the literature search was restricted to data of behavioural studies concerning fish. As shown in Fig. 3 and Table 1, a wide range of electrodetection

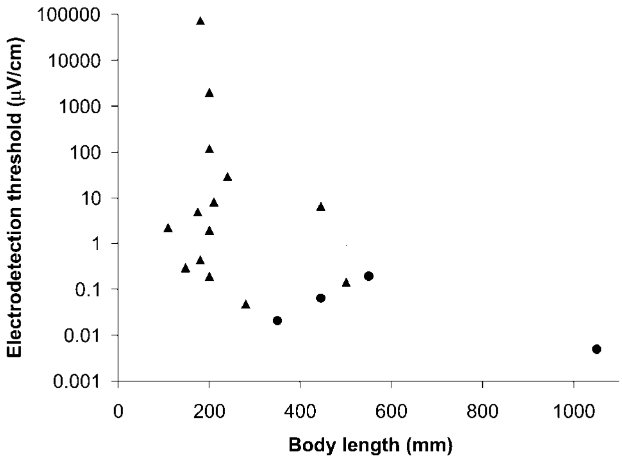

Fig. 3. – Relation between body length and electrodetection thresholds of 12 different electrosensitive species of fish. Freshwater species are represented by triangles, marine species by circles.
All values are taken or calculated from literature. Only data of behavioural studies is used. Although the experimental methods differ, almost all electrodetection thresholds are determined by a trained response. For three data points body length has been estimated by the author based on the average size of particular species and experiment devices used (open markers). For *Parasilurus asotus* the value given by ASANO & HANYU (1987) represents the real electrodetection threshold. See also Table 1.

thresholds ($5*10^{-3}$ to $7.5*10^4$ µV/cm) is covered by a relatively small range in body length (11-105 cm). In general, electrodetection thresholds are lower in marine species than in freshwater species. It should be noted, however, that most electrodetection thresholds published were the best ones found. Only rarely, body length of the particular specimen that produced this threshold was mentioned. If it was not mentioned, average body length of all specimens subjected to a certain study has been used.

TABLE 1

Relation between body length and electrodetection thresholds of 12 different electrosensitive species of fish. Freshwater species are represented by triangles, marine species by circles. See also fig. 3.

Body length (cm)	Species	Freshwater or Marine	Threshold (µV/cm)	Author
11	*Ictalurus nebuolosus*	F	2.25	Baranyuk (1981)
14.8	*Apteronotus albifrons*	F	0.3	Knudsen (1974)
17.5	*Ictalurus nebuolosus*	F	5	Peters et al. (1991)
18	*Parasilurus asotus*	F	75000	Abe (1935)
18.1	*Apteronotus albifrons*	F	0.45	Knudsen (1974)
20	*Ictalurus nebulosus*	F	2	Peters & Van Wijland (1974)
20	*Parasilurus asotus*	F	2000	Kokubo (1934)
20	*Potamotrygon*	F	120	Szabo et al. (1972)
20	*Sternarchus albifrons*	F	0.2	Granath et al. (1967)
21	*Ictalurus nebuolosus*	F	8.5	Peters et al. (1995b)
24	*Ictalurus nebuolosus*	F	30	Dijkgraaf (1968)
25	*Urolophus halleri*	M	0.005	Kalmijn (1982)
28	*Parasilurus asotus*	F	0.05	Asano & Hanyu (1987)
30	*Scyliorhinus canicula*	M	0.1	Dijkgraaf & Kalmijn (1962)
35	*Mustelus canis*	M	0.021	Kalmijn (1982)
44.5	*Anguilla rostrata*	F	6.7	Rommel & McCleave (1972)
44.5	*Anguilla rostrata*	M	0.067	Rommel & McCleave (1972)
50	*Clarias*	F	0.75	Lissmann & Machin (1963)
50	*Gymnarchus niloticus*	F	0.15	Machin & Lissmann (1960)
55	*Hydrogalus colliei*	M	0.2	Fields et al. (1993)
105	*Mustelus canis*	M	0.005	Kalmijn (1982)

General performance

Occasionally, a fish just did not respond during a trial or failed to make a decision in time. These so-called ”nogo” measurements are left out from the determination of the electrodetection threshold, because they rendered an artificial stabilisation of field strength. Reaction times, viz. time between onset of stimulus and choice, were measured during the entire experimental period. Both the number of “nogo” measurements and the reaction times were of use in the evaluation of the well-being of the fish.

Some of the catfish used in experiments with non-uniform field presentations were transferred to a second experimental tank, tested, transferred back to the first experimental tank and tested again. This was done to ensure that the differences between thresholds of the subjects were not due to the specific tank in which they were tested. No significant differences between tanks were detected, although in general, the catfish improved their performance over time.

Uniform fields

Electrodetection thresholds of six subjects are plotted against their body length in fig.4 (circles). Each data point is the average threshold calculated over at least seven and at most thirty-four threshold values found. Kruskal-Wallis' test proved the smallest specimen used (110 mm) to have a significant higher threshold than only one of the larger catfish (240 mm). A second specimen of medium length (210 mm) was found to have a higher threshold than all specimens used except the smallest. No other significant differences were found. The correlation between electrodetection threshold and body length is not significant.

Non-uniform fields

Electrodetection thresholds of eighteen subjects are plotted against their body length in Fig.4 (open markers). Each data point represents the average threshold calculated over at least eleven and at most 180 threshold values found. Statistical analysis confirms the observation that although electrodetection thresholds of subjects differ from each other, there is no significant correlation between electrodetection threshold and body length.

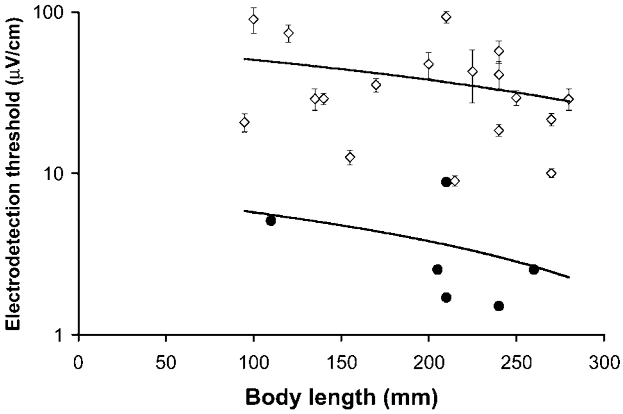

Fig. 4. – Electrodetection thresholds in relation with body length for catfish, *Ictalurus nebulosus*, in uniform fields (circles) and non-uniform fields (open markers). Each point corresponds with the mean threshold value plus S.E.M. of a specimen. For some specimens in uniform fields the S.E.M. falls within the marker. Thick solid lines are linear trendlines. The variation between the different individuals might mask a weak correlation between electrodetection threshold and body length. There is no significant correlation or regression.

DISCUSSION

In both uniform and non-uniform field presentations no significant correlation between body length and electrodetection threshold was found. It should be noted however, that threshold values in uniform fields were, on average, about ten times lower than threshold values in non-uniform fields. In part, this can be explained by the efficiency of the stimulus. In uniform fields the catfish moves parallel to the field lines, whereas in non-uniform fields the catfish moves in a certain angle with respect to the field lines. Therefore, in non-uniform fields, the potential cannot be measured across the entire body length. Thus, stimulation in uniform fields will be more effective than stimulation in non-uniform fields.

Although it does not show in the final data, occasionally it was observed that even the smallest specimen used in uniform fields could detect gradients as weak as 1 μV/cm. As the convergence of the electroreceptor organs onto afferent nerve fibres increase during growth, small specimens have a lower signal-to-noise ratio. As a consequence, the electrodetection threshold could show more variability in small specimens. This could result in an overall higher threshold for small specimens, as changes in stimulus strength after each choice (steps up and down, Fig. 2) were biased.

In the experimental set-up, one major imperfection occurred. Although the side at which the presentation of stimuli was located alternated pseudo-randomly within a single session, every single session was exactly the same as the preceding. In theory, the fish could have learned the successive turns it had to make. This could explain the improvement of all catfish during the first days of the experimental period. On the other hand, when the session was initiated with a very low stimulus strength (well beyond the electrodetection threshold) the catfish made almost hundred percent false choices until the stimulus strength exceeded a certain level.

As the results indicate that total body length is not correlated with electrodetection thresholds, the expectations mentioned in the introduction have to be reconsidered. Information of the electroreceptors throughout the body might not be integrated in the higher order neurones as expected. Furthermore, the internal body of the catfish might not be as electrically uniform as assumed. In that case the internal reference potential cannot be considered as the mean potential between two equipotential lines perpendicular to the body axis of the fish. As a result, the actual internal reference potential(s) might be independent of the body length.

From this it is concluded that the relation between electrodetection threshold and body size is more complex than initially expected. Perhaps the temporal interactions between fish and electric field, as well as neural processing, are more important determinants for the electrodetection threshold than body length.

REFERENCES

ABE, N. (1935). Galvanotropism of the catfish: *Parasilurus asotus* (Linné). *Sci. Rep. Tôhoku Univ. Biol.*, 9: 393-406.

ASANO, M. & I. HANYU (1987). Sensitivity to electricity in the catfish *Parasilurus asotus*. *Comp. Biochem. Physiol. A*, 86: 485-489.

BARANYUK, G.V. (1981). Orientation of the catfish in uniform and nonuniform electric fields. *Neurosci. Behav. Physiol.* 11: 459-63.

DIJKGRAAF, S. (1968). Electroreception in the catfish, *Amiurus nebulosus*. *Experientia*, 24: 187-188.

DIJKGRAAF, S. & A.J. KALMIJN (1962). Verhaltensversuche zur Funktion der Lorenzinischen Ampullen. *Naturwiss.*, 49: 400.

FIELDS, R.D., T.H. BULLOCK & G.D. LANGE (1993). Ampullary sense organs, peripheral, central and behavioral electroreception in chimeras (*Hydrolagus*, Holocephali, Chondrichthyes). *Brain Behav. Evol.*, 41: 269-289.

GRANATH, L.P., H.G. SACHS & F.T. ERSKINE III (1967). Electrical sensitivity of a weakly electric fish. *Life Sci.*, 6: 2373-2377.

KALMIJN, A.J. (1974). The detection of electric fields from inanimate and animate sources other than electric organs. In: *Electroreceptors and other specialized receptors in lower vertebrates*, vol. III/3 (ed. A.E. FESSARD), pp. 147-200. Berlin etc.: Springer-Verlag.

KALMIJN, A.J. (1982). Electric and magnetic field detection in elasmobranch fishes. *Science*, 218: 916-918.

KNUDSEN, E.I. (1974). Behavioural thresholds to electric signals in high frequency electric fish. *J. comp. Physiol.*, 91: 333-353.

KOKUBO, S. (1934). On the behaviour of catfish in response to galvanic stimuli. *Sci. Rep. Tôhoku Univ. Biol.*, 9: 87-96.

LISSMANN, H.W. & K.E. MACHIN (1963). Electric receptors in a non-electric fish (*Clarias*). *Nature (Lond.)*, 199: 88-89.

MACHIN, K.E. & H.W. LISSMANN (1960). The mode of operation of the electric receptors in *Gymnarchus niloticus. J. exp. Biol.*, 37: 801-811.

PETERS, R.C., J. BRANS, F. BRETSCHNEIDER, E. VERSTEEG & A. WENT (1997). Convergence of electroreceptor organs improves sensitivity and tuning. *Neurosci.*, 81: 297-301.

PETERS, R.C. & F. BRETSCHNEIDER (1972). Electric phenomena in the habitat of the catfish, *Ictalurus nebulosus* LeS. *J. comp. Physiol.*, 81: 345-362.

PETERS, R.C. & S. VAN IEPEREN (1989). Resting discharge and sensitivity of ampullary electroreceptors in *Clarias gariepinus* related to convergence ratio during ontogeny. *Brain Behav. Evol.*, 34: 43-47.

PETERS, R.C., W.J.G. LOOS, F. BRETSCHNEIDER & P.S. HEIJMEN (1995a). Psychophysical assessment of catfish electro-sensitivity versus temperature and electric field frequency. *Neth. J. Zool.*, 45: 3-4.

PETERS, R.C., W.J.G. LOOS, M. HOBBELEN, F. BRETSCHNEIDER & L.M. HERMENS (1995b). Lindane raises catfish electrodetection threshold. *Belgian J. Zool.*, 125/1: 185-191.

PETERS, R.C., W.J.G. LOOS, F. BRETSCHNEIDER & I.S.A. NEUMAN (1991). Electro-reception and Aquatic Biomonitoring. In: *Bioindicators and Environmental Management* (eds. JEFFREY, D.W. & MADDEN, B), pp. 427-435. London: Academic Press.

PETERS, R.C. & F. MAST (1983). Information transmission by ampullary receptors: parallel convergent inputs. *Comp. Biochem. Physiol.*, 76A: 143-151.

PETERS, R.C. & R.H.S. WESTERINK (1999). Catfish electroreceptor organ functioning during five days exposure to different calcium environments. *Fish Physiol. Biochem.*, 21: 81-88.

PETERS, R.C. & F. VAN WIJLAND (1974). Electro-orientation in the passive electric catfish, Ictalurus nebulosus LeS. *J. comp. Physiol.*, 92: 327-28.

ROMMEL, S.A. & J.D. MCCLEAVE (1972). Oceanic electric fields: perception by American eels? *Science*, 176: 1233-1235.

ROTH, A. (1971). Zur Funktionsweise der Elektrorezeptoren in der Haut von Welsen (*Ictalurus*): Der Einfluss der Ionen im Süsswasser. *Z. vergl. Physiol.*, 75: 303-322.

SCHEMINZKY, F. & F. SCHEMINZKY (1931). Körpergroße und Empfindlichkeit gegen den galvanischer Strom. *Pflügers Archiv ges. Physiol.*, 228: 548-564.

STERNIN, V.G., I.V. NIKONOROV & U.K. BUMEISTER (1972). *Electrical Fishing. Theory and Practice*. Israel Program for Scientific Translations, Jerusalem, pp. 315.

SZABO, T., A.J. KALMIJN, P.S. ENGER & T.H. BULLOCK (1972). Micro-ampullary organs and the submandibular sense organ in the fresh water ray, *Potamotrygon*. *J. comp. Physiol.*, 79: 15-27.

TEUNIS, P.F.M., F. BRETSCHNEIDER & R.C. PETERS (1990). Convergence ratio and transduction in catfish electroreceptive organs. *Comp. Biochem. Physiol. A*, 97: 405-410.

ZAKON, H.H. (1987). Variation in the mode of receptor cell addition in the electrosensory system of gymnotiform fish. *J. Comp. Neurol.*, 262: 195-214.

ZALEWSKI, M. (1985). The estimate of fish density and biomass in rivers on the basis of relationship between specimen size and efficiency of electrofishing. *Fisher. Res.*, 3: 147-155.