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Electrosensory prey detection in the African sharptooth catfish, *Clarias gariepinus* (Clariidae), of a weakly electric mormyrid fish, the bulldog (*Marcusenius macrolepidotus*)

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Abstract During their seasonal runs in the Okavango and other freshwater bodies in southern Africa, the sharptooth catfish, *Clarias gariepinus*, specialises on the bulldog, *Marcusenius macrolepidotus*, as its main prey. We examined whether the catfish can locate bulldogs by detecting their pulse-type electric organ discharges (EODs). The electrosensory threshold for single-cycle, monopolar square-wave pulses was exceedingly low (down to $13 \mu\text{V}_{\text{p-p}}/\text{cm}$ for 4-ms pulses) in trained, food-rewarded sharptooth catfish ($n=4$), confirming the results of Lissmann and Machin who were, however, unable to identify a biological function. Other stimulus pulse waveforms (single-cycle, monopolar as well as bipolar sine-wave pulses) were also effective stimuli according to their spectral low-frequency energy contents (0–30 Hz). Male bulldogs display an EOD pulse approximately $10\times$ the duration of female EODs (≈ 0.5 ms). The *C. gariepinus* threshold for field-recorded playbacks of a male bulldog EOD (of long duration) was $103 \mu\text{V}_{\text{p-p}}/\text{cm}$, whereas the brief female and juvenile EODs were not detected (using intensities of natural EODs). EODs of other mormyrids were detected when either monopolar or of long duration. Signal source amplitude increased linearly with standard length (SL) in bulldogs. Signal reach, as calculated from signal source amplitude and receiver sensitivity, is up to 150 cm for a large male bulldog (SL 27.5 cm), and 83 cm for a male that has just turned sexually mature (SL 12.6 cm). Therefore, most bulldogs eaten by catfish are probably male, in agreement with the size distribution of bulldogs found in catfish stomachs. These results suggest that sharptooth catfish rely heavily on their acute electrical sense during hunting, and an important function for electroreception in an African catfish has been identified.

Key words Electroreception · Prey detection · Electric organ discharge · Sexual dimorphism · Ampullary electroreceptor organs

Introduction

In the Okavango River (Botswana), the spectacular catfish runs are well-known and widely publicised. During their reproductive upstream migration, sharptooth (*Clarias gariepinus*) and bluntnose (*C. ngamensis*) catfish engage in pack hunting (Donnelly 1966; Pooley 1972), described in more detail by Bruton (1979).

A weakly electric, mormyrid fish species is the main prey: the bulldog, *Marcusenius macrolepidotus* (Peters, 1852) constituted 64% of the stomach contents of 363 sharptooth catfish dissected, with up to eight individuals in a single stomach (Merron 1993). The only other mormyrid eaten, the churchill [*Petrocephalus catostoma* (Günther, 1866)], represented only 26% of the diet. Mormyrid fish are both electroreceptive and electrogenic; they are endemic to Africa, and well-known for their sophisticated electrolocation (for reviews see Bastian 1990, 1994; von der Emde 1999) and electrocommunication systems (reviewed by Kramer 1990, 1994, 1996; Moller 1995; most recent progress: Turner et al. 1999).

Catfish are electroreceptive (Parker and van Heusen 1917; Lissmann and Machin 1963; Roth 1968; Peters and Bretschneider 1972) and possess ampullary electroreceptor organs in their skin (Roth 1969; Peters and Buwalda 1972; Szabo 1974; Finger 1986). Among all types of electroreceptor organ, the ampullary receptor is tuned to the lowest frequencies (reviewed by Zakon 1986, 1988; Andrianov et al. 1996); for *C. gariepinus*, 10–30 Hz (Peters and Bretschneider 1981). Therefore, catfish are insensitive to typical mormyrid electric organ discharges such as those of the genus *Marcusenius* (e.g. Scheffel and Kramer 1997) which are usually below 1 ms duration, and have their spectral peak amplitudes well beyond 1 kHz.

Therefore, the high predation pressure of the sharptooth and other catfish (Winemiller and Kelso-Winemiller

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1994) on the bulldog, but not on other mormyrid species, was paradoxical. This began to change with the observation of a marked sexual dimorphism in the bulldog's electric organ discharge (EOD) duration: on becoming sexually mature, the EOD of males increases about tenfold in duration (Kramer 1997a, 1997b). No similar phenomenon has yet been observed in any other of the sympatric mormyrid fauna.

We tested the hypothesis that the catfish detect the long-duration EODs of sexually mature males, since an EOD of long duration has a low spectral peak frequency. This hypothesis appeared reasonable in light of Lissmann and Machin's (1963) virtually forgotten short report on *Clarias* sp., demonstrating an electrosensory threshold for single-cycle square-wave pulses as low as 1 $\mu\text{V}/\text{cm}$ if of sufficient duration (10 ms). However, these authors were unable to identify a function for this keen electrical sense, and suggested (1) the detection of action potentials from predators or prey or (2) the detection of electric currents set up by the movement of water in the Earth's magnetic field.

We, therefore, examined in greater detail the dependency of catfish electrosensory threshold on the duration and waveform of stimulus pulses. Furthermore, we investigate which of the sympatric mormyrid species of the Upper Zambezi (that harbours the same mormyrid and catfish fauna as the Okavango with which it is interconnected; Skelton et al. 1985; van der Waal and Skelton 1984) possess EODs detectable by hungry catfish, and also the reach of EODs as relevant for the natural environment. Some of these results have been reported in short form in Hanika and Kramer (1999).

Methods

Animals

Four sharptooth catfish, *C. gariepinus* (Burchell, 1822) (Clariidae, Siluriformes, Teleostei) bred in the Netherlands (Utrecht University) were used in food-rewarded training tests. The fish, one male and three female, all had standard lengths (SLs) of about 25 cm (Zoologische Staatssammlung München; accession numbers, ZSM28577–ZSM28580). These fish are derived from stock originating in Bangui, Central African Republic (van der Walt et al. 1993). A single specimen of *C. theodorae* of Kenyan origin, obtained from a directly importing tropical fish dealer, was also tested.

Experimental set-up

Test trials were performed in tanks measuring at least 100×50×60 cm (Fig. 1). The water was filtered and aerated, the water level was maintained at 40 cm and water temperature at 26±1°C. Water conductivity during experiments was kept within 2 $\mu\text{S}/\text{cm}$ of 100 $\mu\text{S}/\text{cm}$. The test aquarium was divided into two compartments by fine plastic mesh, one compartment containing a porous pot as a shelter (outer and inner diameters, 20 cm and 17 cm, respectively). A door in the plastic mesh separation allowed the fish to pass to the other compartment where a feeding station was fixed above a stimulus dipole. At the feeding station the reward, a single *Chironomus* sp. (bloodworm) larva per positive response, was delivered.

Stimuli were delivered via a dipole, a pair of vertically oriented carbon electrodes (rod diameter 0.5 cm, length 1.0 cm, separation

3.0 cm) mounted on a horizontal plexiglass tube and connected to a stimulation device (DAM; see below). The dipole was positioned in parallel to the porous pot shelter, at a distance of 35 cm (centre to centre). The electric field strength generated by the dipole was set to 2.1 mV_{p-p}/cm as measured inside the porous pot (maximum value, determined using a 1-cm measuring dipole described further below). This field strength matches that generated by a bulldog of 13 cm SL replacing the dipole under otherwise identical conditions. Digitised stimulus pulse waveforms were transferred from hard disc to a microprocessor-controlled digital-to-analog converter with memory and differential output amplifier (DAM; details in Kramer and Weymann 1987). The device had an amplitude resolution of 8 bits (at each amplification step) and 2048 points per trace with a sampling rate of 500 kHz. A host computer, operated by the experimenter, gave the instructions necessary to select a waveform and to start and stop the stimulation (Fig. 1).

Field potentials of electric signals generated by the dipole were measured at the fish's resting position by a pair of glassy carbon electrodes (Sigradur G electrodes; rod diameter 1 mm, rod length, 60 mm; insulated except for 10 mm at the tips) with an inter-electrode separation of 1 cm. The maximum field potential was found by rotating the electrode at the desired position. Field potentials were measured at the maximum output of the DAM, that is, at 30–60 dB above threshold because actual threshold field intensities were too low to be measured. Step attenuation of the DAM output amplifier was linear, justifying extrapolation.

One trial for threshold determination consisted of a pulse train of 60 s duration, with a pulse rate of 3 Hz. A test session usually consisted of 30 trials per threshold, and mean values of one trained fish were averaged over ten test sessions. A trial was only started when the fish had assumed its resting position inside the shelter. Upon stimulus onset, fish had to swim through the open gate in order to obtain a reward. Following a correct response, that is, when the fish left the shelter on stimulus presentation, the stimulus amplitude was attenuated by 1 dB for the next trial. A trial was recorded as no-go when the fish did not leave its shelter within 5 s of stimulus onset. Following a no-go trial, the amplitude was increased by 3 dB. The lowest signal intensity at which 75% or more of the responses were correct was chosen as the threshold intensity. Inter-trial time intervals varied unpredictably from 5 to 90 s in steps of full seconds. They were calculated using Turbo Pascal's (Borland 7.0) RANDOM-function. Instances when a fish approached the reward without stimulus were not counted. To prevent this occurring too frequently, moderate punishment was used, i.e. a metal rod was waved in front of the fish without touching it. Otherwise, the experimenter was hidden behind a cloth to exclude stimuli other than the actual stimulus pulses tested. In every test session, three stimulus presentations of very low field intensities were included (min. 40 dB). Experimentally planned water conductivity changes were introduced 3–6 days prior to testing.

Stimuli

Three function-generator pulse waveforms (as opposed to playbacks of EODs) of variable duration were used: (1) single-cycle, bipolar sine-wave pulses representing one full period of a sine-wave, as did (2) single-cycle, monopolar sine-wave pulses in which the starting phase was delayed to 90° and (3) single-cycle, monopolar square-wave pulses (Fig. 2). These stimuli were calculated using a QuickBasic program (H. Knüttel) and downloaded to the microprocessor-controlled D/A device (see above).

EODs were also downloaded into DAM memory as computer files; however, their duration was the natural one for 26°C (that is, unmodified, natural EODs; EOD waveforms: Kramer 1996, p. 47). All EODs had been recorded during a field study of the Upper Zambezi System mormyrid fauna (detailed recording methods: Kramer 1997a). Briefly, EODs were recorded on a digital oscilloscope using a pair of low-impedance carbon electrodes and a wideband preamplifier (0.2 Hz–100 kHz), and stored on hard disc. Recordings were performed immediately after capturing the fish in the original river water, thus excluding conductivity-dependent

Fig. 1 Set-up used for food-rewarded training experiments with *Clarias gariepinus* (A differential amplifier, CRT oscilloscope, D stimulus dipole, DAM digital-to-analog converter with memory, E electrode, F feeding station, G gate, PC computer, R resting position of the catfish, SC plastic mesh wall)

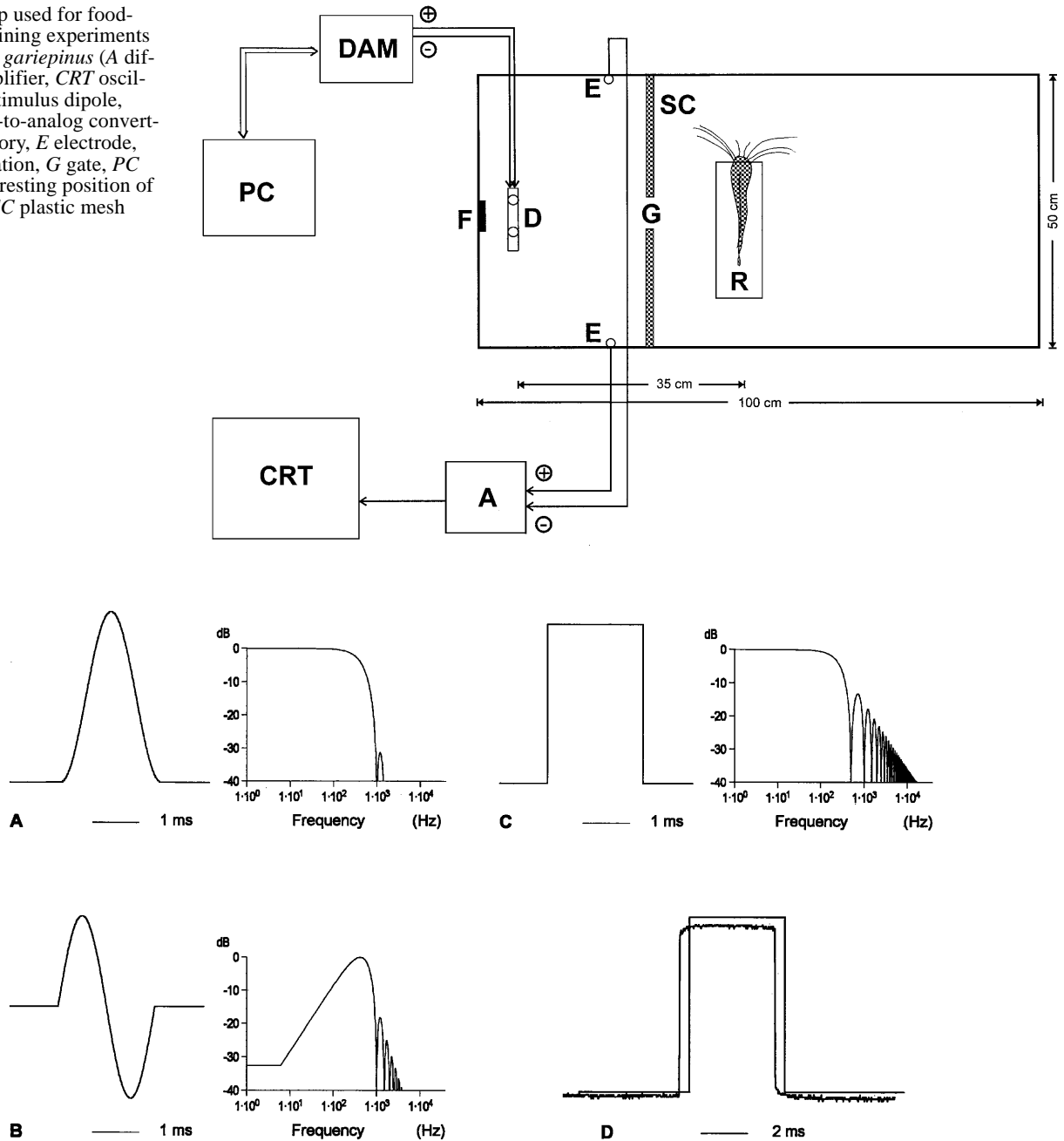


Fig. 2A–D Function-generator pulse waveforms. **A–C** Left panels waveform of stimulus pulses (voltage over time with baseline=0 V); waveforms as downloaded into DAM memory. Right panels spectral amplitudes (ordinate amplitude in decibels; strongest signal component=0 dB; abscissa frequency in kHz). Frequency window=5.09 Hz. **A** Single-cycle, monopolar sine-wave. **B** Single-cycle, bipolar sine-wave. **C** Monopolar square-wave pulse. **D** Comparison of generator (DAM) output (straight line square waveform) with waveform recorded from the water, at 35 cm distance from stimulus dipole (the catfish's resting position)

EOD waveform distortions (Kramer and Kuhn 1993). When necessary, discharges were temperature-corrected to 26°C using a Q_{10} of 1.5 (Kramer and Westby 1985). An estimate of EOD duration was obtained by going forward or backward in time from EOD peaks until the first crossing of the zero-line. Amplitude spectra were obtained by Fast Fourier Transform (8192 points, frequency

window 5.09 Hz) of digitised EOD samples using a routine provided by the signal analysis package FAMOS 3.2 (IMC, Berlin).

EODs of all mormyrid fish species living sympatrically in the Upper Zambezi River system were used (Fig. 3): *M. macrolepidotus* (Peters, 1852), *P. catostoma* (Günther, 1866), *Mormyrus lacerda* Castelnau, 1829, *Cyphomyrus discorhynchus* Myers, 1960, *Pollimyrus castelnaui* (Boulenger, 1911), *Hippopotamyrus ansorgii* (Boulenger, 1905) and the undescribed sibling species *Hippopotamyrus* sp. nov. (van der Bank and Kramer 1996; Kramer 1996; B. Kramer and F.H. van der Bank, unpublished data). For *M. macrolepidotus* with its sexually dimorphic EOD waveform, female and two male discharges of different durations were used because of the great variability in the male sex (Kramer 1997a, 1997b). *C. discorhynchus* Myers, 1960 is synonymous with *H. discorhynchus* (Peters, 1852). This species was placed into the genus *Hippopotamyrus* by Taverne (1971); however, van der Bank and Kramer (1996) reinstated its previous name *Cyphomyrus* because of the existing inconsistencies within the genus *Hippopotamyrus*.

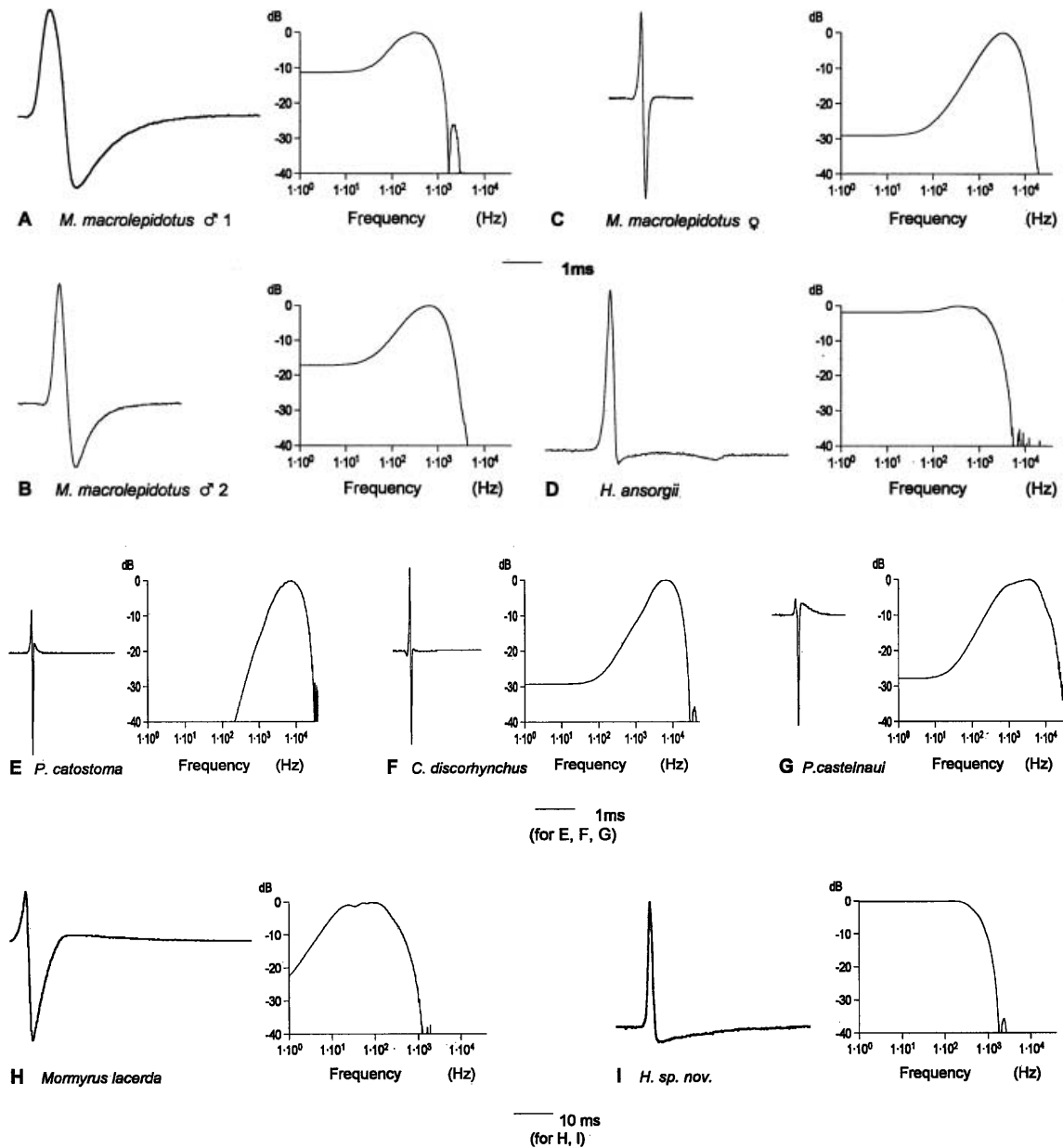


Fig. 3A–I Recordings of electric organ discharge (EOD) waveforms, as used for stimulation in the present experiments. *Left panels* voltage over time (baseline=0 V, head positivity is upwards) as downloaded into DAM memory. *Right panels* the associated amplitude spectra where the *ordinate* is amplitude expressed as dB attenuation relative to the strongest spectral component of an EOD; *abscissa* frequency in kHz (frequency window=5.09 Hz). EOD pulses are usually very short and show a broad-band spectral frequency content (e.g. the bulldog female, C). EODs of much more low-frequency content are emitted by sexually mature bulldogs (A,B), *Mormyrus lacerda* (H) and the two *Hippopotamyrus* species (D,I)

Reach: effect of water conductivity

Peak-to-peak amplitudes of EODs of *M. macrolepidotus* ($n=20$), *P. catostoma* ($n=1$), *C. discorhynchus* ($n=1$) and *Hippopotamyrus* sp. nov. ($n=4$) were measured. Unfortunately, not all of the species whose EODs we used for threshold estimations were available alive in the laboratory for amplitude measurements. For *M. macro-*

lepidotus ($n=20$), we used individuals originating from the Incomati River system, Kruger National Park, South Africa. All other species we used for amplitude measurements were exported from the Upper Zambezi River (Namibia, Katima Mulilo). Measurements were performed in a tank measuring 210×60×50 cm. During measurements, a fish was confined to a porous ceramic pot whose influence on recorded amplitude was negligible. (Measurement of field gradients, see above). The long axis of the pot was oriented perpendicular to that of the aquarium. Measurements were taken at distances of 10 up to 70 cm from a fish's side in steps of 5 cm with the measuring dipole oriented in parallel to the fish (see Squire and Moller 1982).

When determining the effect of water conductivity on field gradient amplitude, fish were habituated to a new conductivity for a period of 2 days prior to measuring (see Kramer and Kuhn 1993). Measurements always started at the lowest water conductivity; higher values were obtained by the addition of tapwater ($\approx 600 \mu\text{S}/\text{cm}$).

Linear regression was adequate to describe the dependency of log peak-to-peak field potentials generated by EODs on log distance from the signal-emitting fish. From these regression lines we

calculated maximum detection distances (reach) of *C. gariepinus*, using threshold field intensities of *C. gariepinus* for the various EODs. For some EODs, the associated threshold field intensities of *C. gariepinus* were below EOD field amplitudes actually measured at a distance of 70 cm. In these cases we linearly extrapolated from the regression line. Extrapolation was justified because log field potentials in water decreased linearly with log distance, also shown by Knudsen (1975) and Squire and Moller (1982).

For determining the dependency of reach on water conductivity we used values for EOD field amplitudes and catfish electro-sensory thresholds measured at the same water conductivity.

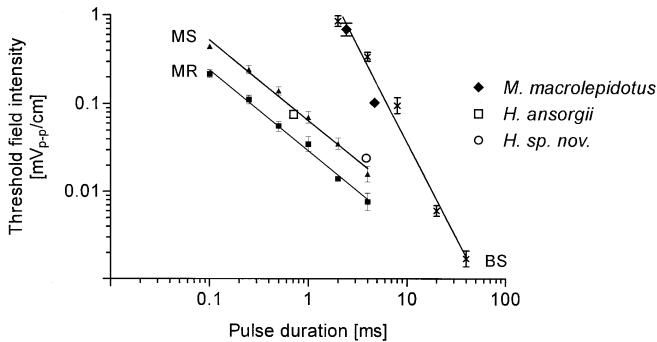


Fig. 4 Electro-sensory thresholds of *C. gariepinus* ($n=4$) conditioned to stimulus pulses, as a function of pulse duration and pulse waveform (mean values). Standard deviations are either shown or are too small to be drawn; $n=40$ for each threshold. *MR* single-cycle, monopolar square-wave pulse (closed squares); *MS* single-cycle, monopolar sine-wave pulse (closed triangles); *BS* single-cycle, bipolar sine-wave pulse (crosses). Abscissa stimulus pulse duration (ms); ordinate mean threshold (in mV_{p-p}/cm). Lines least-squares regression; thresholds decreased significantly ($P<0.001$) with stimulus pulse duration in each case. Note close agreement between the thresholds for *M. macrolepidotus* male EODs and bipolar sine-wave pulses, and between the thresholds for both *Hypopotamyrus* species EODs and monopolar sine-wave pulses

Results

Electrosensory thresholds for artificial stimulus waveforms

For all three artificial stimulus waveforms (monopolar square-wave, monopolar sine-wave and bipolar sine-wave pulses, Fig. 2), threshold intensity depended significantly on pulse duration (Fig. 4). In the range investigated, thresholds increased exponentially with decreasing pulse duration. Thresholds follow a straight line for data log-transformed on both axes, as shown in Fig. 4. Log-log plots of threshold versus stimulus duration yielded parallel lines for both kinds of monopolar pulses, of slope -1 . We confirm Lissmann and Machin's (1963) results in an "African *Clarias* species" (suggested species: *Clarias anguilloides*) that was stimulated with (apparently monopolar) square-wave pulses. In the present data, the difference in y-axis intercept between regression lines for both kinds of monopolar stimuli was significant (Table 1). A single specimen of *C. theodorae* proved just as sensitive as *C. gariepinus* (Table 1). For bipolar sine-wave pulses tested in *C. gariepinus*, the regression line slope was twice as steep (i.e. -2) compared to both monopolar pulses (Fig. 4).

The slopes of the regression lines were significantly different from zero in all cases (F -test, $P<0.0001$), and deviation from a linear relationship for log-log transformed data was not significant (runs test, $P>0.3$; Table 1). Within the range of pulse durations tested, no tuning was found (no "best" pulse duration), again confirming Lissmann and Machin (1963) for square-wave pulses. Thresholds for monopolar pulses were lower than thresholds for bipolar pulses of the same duration, and thresholds for monopolar square-wave pulses were the lowest

Table 1 Linear regression of the dependency of electro-sensory threshold on stimulus pulse duration (0.1–4 ms). (r^2 variance, P^* probability of mistakenly rejecting the null hypothesis of a re-

gression line slope equalling zero, P^{**} probability of mistakenly rejecting the null hypothesis that the data fall on a straight line

	Slope	y-Intercept	r^2	F	df	P^*	Test of non-linearity (runs test) P^{**}
Monopolar square-wave pulse							
Catfish I	-0.914 ± 0.04	1.57 ± 0.024	0.991	452.9	5	<0.0001	0.3 (n.s.)
Catfish II	-0.993 ± 0.022	1.61 ± 0.012	0.998	2008.9	5	<0.0001	1 (n.s.)
Catfish III	-1.037 ± 0.013	1.343 ± 0.008	0.999	6029.8	5	<0.0001	0.7 (n.s.)
Catfish IV	-0.948 ± 0.019	1.559 ± 0.011	0.998	2357.6	5	<0.0001	0.7 (n.s.)
<i>C. theodorae</i>	-1.025 ± 0.032	1.488 ± 0.018	0.996	1034.8	5	<0.0001	0.4 (n.s.)
Mean ^a	-0.970 ± 0.051	1.557 ± 0.066^b					
Monopolar sine-wave pulse							
Catfish I	-1.107 ± 0.017	0.95 ± 0.01	0.998	4041	5	<0.0001	1 (n.s.)
Catfish II	-0.955 ± 0.054	1.33 ± 0.03	0.987	312.4	5	<0.0001	0.3 (n.s.)
Catfish III	-0.936 ± 0.048	1.22 ± 0.027	0.989	369.6	5	<0.0001	0.4 (n.s.)
Catfish IV	-0.964 ± 0.055	1.15 ± 0.031	0.987	303.4	5	<0.0001	0.4 (n.s.)
<i>C. theodorae</i>	-1.030 ± 0.063	1.071 ± 0.035	0.985	265.9	5	<0.0001	0.7 (n.s.)
Mean ^a	-0.991 ± 0.085	1.163 ± 0.31^b					

^a Mean \pm SD with $n=10$ threshold estimations for every catfish (see methods)

^b Significant difference between mean y-intercepts (monopolar square-wave pulse vs monopolar sine-wave pulse; unpaired t -test, $t=7.862$, $df=78$, $P<0.001$)

(Fig. 4). Catfish were able to detect square-wave pulses of 4 ms duration down to a field gradient of $13 \mu\text{V}_{\text{p-p}}/\text{cm}$ whereas the less-effective monopolar and bipolar sine-wave pulses of 4 ms duration were detected down to $60 \mu\text{V}_{\text{p-p}}/\text{cm}$ and $800 \mu\text{V}_{\text{p-p}}/\text{cm}$, respectively.

Lissmann and Machin's (1963) threshold of $12.4 \mu\text{V}/\text{cm}$ for 1-ms square-wave pulses, as judged from their figures, agrees well with the lowest threshold determined in our most sensitive fish ($19.5 \mu\text{V}_{\text{p-p}}/\text{cm}$). Lissmann and Machin's generally somewhat lower thresholds may be explained by differences in methodological details. (1) These authors probably used local tapwater of high conductivity for their experiments, as was customary at that time. According to the Cambridge (UK) Water Authority, the conductivity of local tapwater in the early 1960s differed little from the present-day value of $530 \mu\text{S}/\text{cm}$ (November 1999). (As shown in Fig. 8, thresholds decrease with water conductivity). (2) Lissmann and Machin might have used a different threshold criterion; for example, the lowest single value observed rather than the mean value (as taken in the present study).

Why were monopolar sine-wave pulses less-effective stimuli than monopolar square-wave pulses of the same duration? When of identical peak-to-peak amplitude, the total energy content of the three artificial pulses differed according to a ratio of $1/8 : 3/8 : 1$ (bipolar sine-wave pulse:monopolar sine-wave pulse:monopolar square-wave pulse), as also observed in Postner and Kramer (1995). However, assuming energy content of the pulses as the critical factor for detection, one would expect thresholds for square-wave pulses to be 2.39 dB lower than those actually found in our behavioural tests (expected values based on behaviourally determined thresholds for sine-wave pulses). *C. gariepinus* was less sensitive to square-wave pulses than expected from the energy content of the stimuli. We suggest this result is due to "high-frequency reject" filtering, according to the low-frequency properties of the ampullary receptors. An amplitude spectrum of a monopolar square-wave pulse possesses relatively more energy in the high-frequency range than does a sine-wave pulse (Fig. 2), but catfish cannot detect high frequencies.

To test the hypothesis that in *C. gariepinus* only the low-frequency content determines the threshold for a given stimulus pulse, we integrated Fourier amplitude spectra from 0 to 30 Hz, which includes the frequency range of maximum sensitivity for sine-wave stimuli in *C. gariepinus* (Peters and Bretschneider 1981; their study species *C. lazera* is synonymous with *C. gariepinus*). When plotting the threshold field intensities versus the integrated low-frequency spectral energy of the test pulses used (rather than their duration as in Fig. 4), all threshold values fall on a single line, irrespective of pulse waveform (Fig. 5). The low-frequency energy content predicts the electrosensory threshold very well [as suggested by Lissmann and Machin (1963) for square-wave pulses]. When using an high-frequency cut-off of higher frequency (e.g. 0–100 Hz), the resulting relationship deviates from linearity.

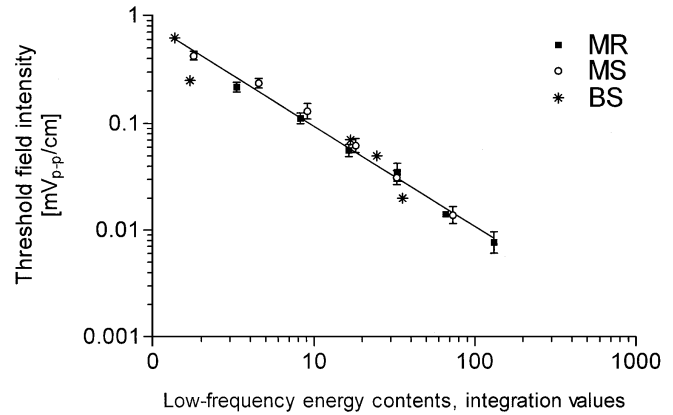


Fig. 5 Electrosensory threshold of food-rewarded *C. gariepinus* ($n=4$) as a function of the low-frequency energy contents of stimulus pulses of durations from 0.1 to 4 ms (bipolar sine-wave pulses: 2–8 ms), measured as Fourier spectra amplitudes integrated from 0 to 30 Hz. *MR* single-cycle, monopolar square-wave pulse; *MS* single-cycle, monopolar sine-wave pulse; *BS* single-cycle, bipolar sine-wave pulse. *Ordinate* threshold field gradient of an applied stimulus at which 75% of trials resulted in a fish responding; *abscissa* low-frequency energy contents (integration value) of the stimuli used (0–30 Hz). Thresholds shown are mean values ($\text{mV}_{\text{p-p}}/\text{cm}$) ($n=40$). SDs are either shown or are too small to be drawn. *Line* least-squares regression for pooled data of all waveforms shown in this figure

Electrosensory thresholds for EODs

C. gariepinus did not respond to very brief bipolar or tripolar EODs, as expected from the low sensitivity of their ampullary electroreceptors for stimuli of high-frequency content. Ineffective EODs included the bipolar discharges of female (or juvenile) *M. macrolepidotus* (0.49 ms duration; Fig. 3) and *C. discorhynchus* (0.47 ms, Fig. 3), as well as the tripolar discharges of *P. catostoma* (0.55 ms, Fig. 3) and *P. castelnaui* (1.2 ms, Fig. 3). The horizontal electric field gradient used for stimulation at the resting position of our catfish ($2.1 \text{mV}_{\text{p-p}}/\text{cm}$ at a distance of 35 cm from the stimulus dipole) is generated by a *M. macrolepidotus* of 12–13 cm SL, or maximum-sized individuals of *P. catostoma* ("standard" stimulus amplitude; see below). But even at a field gradient of $6.0 \text{mV}_{\text{p-p}}/\text{cm}$, that is, more than the EOD amplitude generated by our largest specimen of *M. macrolepidotus* ($5.19 \text{mV}_{\text{p-p}}/\text{cm}$ at 35 cm distance; SL=27.5 cm), *C. gariepinus* did not respond to these discharges of short duration. A field gradient of $6.0 \text{mV}_{\text{p-p}}/\text{cm}$ was reached at the decision point, at 25 cm distance from the dipole (open gate; see Fig. 1), when using the "standard" stimulus amplitude.

In contrast, all *C. gariepinus* detected the discharges of male *M. macrolepidotus* (of 4.7 ms and 2.4 ms duration; Fig. 3) down to $103 \mu\text{V}_{\text{p-p}}/\text{cm}$ and $688 \mu\text{V}_{\text{p-p}}/\text{cm}$, respectively (Table 2, Fig. 4). However, the catfish were also exceedingly sensitive to the discharges of *M. lacerda* ($28 \mu\text{V}_{\text{p-p}}/\text{cm}$) that are of exceptionally long duration (Kramer 1996, p. 47). The discharges of both *H. ansorgii* ($76 \mu\text{V}_{\text{p-p}}/\text{cm}$; Fig. 3) and *Hippopotamyus* sp. nov.

Table 2 Threshold intensities of *Clarias gariepinus* for the electric organ discharges used for stimulation in the present study, and their peak energy maxima. Threshold mean values \pm SD ($\text{mV}_{\text{p-p}}/\text{cm}$) are shown. EOD total duration of discharges. Fish A most sensitive *C. gariepinus* tested, $n=10$ test sessions. Fish I–IV mean threshold values, averaged for all *C. gariepinus* tested ($n=4$) (– threshold intensities were beyond $6.0 \text{ mV}/\text{cm}$, that is, above the field strength generated by a large mormyrid fish). Frequencies of spectral peak amplitudes were obtained by Fast Fourier Transforms

	EOD (ms)	Mean threshold fish A	Mean threshold fish I–IV	Frequency of spectral peak amplitude (Hz)
<i>Marcusenius macrolepidotus</i> ♂ 1 ^a	4.7	103 \pm 14	136.3 \pm 35.6	303
<i>Marcusenius macrolepidotus</i> ♂ 2 ^a	2.5	688 \pm 71	795.8 \pm 72.8	600
<i>Hippopotamyrus</i> sp. nov. ^b	3.88	24.2 \pm 1.9	30.8 \pm 6.1	82
<i>Hippopotamyrus ansorgii</i> ^b	0.71	121.3 \pm 13.3	125.3 \pm 24.7	346
<i>Mormyrus lacerda</i>	51.0	28.1 \pm 2.0	36.4 \pm 7.0	44
<i>Marcusenius macrolepidotus</i> ♀	0.49	–	–	2664
<i>Petrocephalus catostoma</i>	0.55	–	–	7558
<i>Cyphomyrus discorhynchus</i>	0.47	–	–	3738
<i>Pollimyrus castelnaui</i>	1.2	–	–	5442

^a In mature males pulse duration varies between 2 and 4.8 ms

^b The duration of the almost monopolar electric organ discharges of the two *Hippopotamyrus* species was measured for the positive phase only not including the weak negative postpotential (see Fig. 3)

($24 \mu\text{V}_{\text{p-p}}/\text{cm}$; Fig. 3) were also detected at very low field gradients (Table 2, Fig. 4). These discharges were almost monopolar, with head-positive phases lasting 0.7 ms and 3.9 ms, respectively (Table 2). *C. gariepinus* was more sensitive to discharges of long duration: for example, the discharges of *Hippopotamyrus* sp. nov. were detected at lower field gradients than those of *H. ansorgii*. Thresholds for the long male bulldog discharge (4.7 ms) were lower than those for the short one (2.5 ms; Table 2).

The relationship between low-frequency content and electrosensory threshold shown for function-generator pulse waveforms is also true for mormyrid EODs. Spectral amplitude peaks of single EOD pulses of different mormyrid species ranged from 44 to 7558 Hz (see Table 2). *C. gariepinus* still detected discharges with a spectral amplitude peak of 600 Hz (male *M. macrolepidotus*, 2.47 ms; Table 2); however, discharges with amplitude peaks above 2500 Hz were not detected (Fourier amplitude spectra, Fig. 3). We found close agreement between thresholds for male *M. macrolepidotus* discharges and bipolar, sine-wave pulses of almost the same duration that are similar in waveform (see Fig. 4); the threshold for the discharge was even lower because of its DC component. There was a similar agreement between the EODs of the two *Hippopotamyrus* species and monopolar sine-waves pulses of similar duration (see Fig. 4).

Reach of EODs

The reach of a signal depends on its amplitude at the source, attenuation over distance, and the sensitivity of the receiver.

The sensitivity of the receiver, *C. gariepinus*, increases with discharge duration, as shown above. For *M. macrolepidotus* ($n=20$), field amplitudes generated by EODs increased as a linear function of body size (SL; Fig. 6). *P. catostoma* ($n=1$) and *C. discorhynchus* ($n=1$) exhibited similar discharge amplitudes compared to *M. macrolepidotus* of similar size (Fig. 6). *Hippopotamyrus* sp. nov. ($n=4$) was an exception because its monopolar discharg-

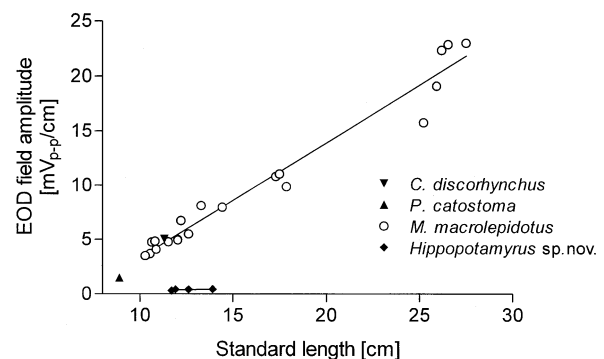


Fig. 6 Increase in EOD field potential with fish body size (standard length), measured at a distance of 20 cm from a fish's side with the electrode dipole oriented in parallel to the fish. Every point represents one individual fish; for *M. macrolepidotus* ($n=20$) and *Hippopotamyrus* sp. nov. ($n=4$), separate regression lines are shown

es of very low amplitudes barely varied between individuals (Fig. 6). For example, in a *Hippopotamyrus* sp. nov. of 13.9 cm SL we found an electric field potential of only $0.15 \text{ mV}_{\text{p-p}}/\text{cm}$ at a distance of 20 cm, compared to $8.13 \text{ mV}_{\text{p-p}}/\text{cm}$ for a *M. macrolepidotus* of almost the same size (13.3 cm) at the same distance.

The calculated signal reach for a *M. macrolepidotus* of 12.6 cm SL, as detected by a *C. gariepinus*, is 45 cm for our short male discharge, and 83 cm for the long male discharge. For a large *M. macrolepidotus* (SL 27.5 cm) that emits a long male discharge, the signal reach is 150 cm (Fig. 7).

Behavioural threshold intensities of *C. gariepinus* decreased with increasing water conductivity (Fig. 8), as studied over the naturally most relevant range of 50–150 $\mu\text{S}/\text{cm}$. For example, threshold intensities are $0.231 \text{ mV}_{\text{p-p}}/\text{cm}$ at 50 $\mu\text{S}/\text{cm}$ and $0.167 \text{ mV}_{\text{p-p}}/\text{cm}$ at 150 $\mu\text{S}/\text{cm}$. However, the reach of EODs is affected very little by this relationship because a threshold decrease due to an increase in water conductivity is compensated by a decrease in EOD field amplitude (for example, from a reach of 84 cm at 50 $\mu\text{S}/\text{cm}$ to 83 cm at 150 $\mu\text{S}/\text{cm}$).

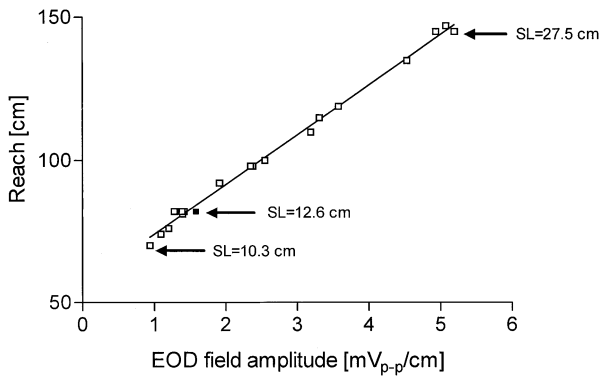


Fig. 7 The reach of EODs as detected by *C. gariepinus*, calculated from measured EOD amplitudes generated by *M. macrolepidotus* ($n=20$) of different sizes, and the electrosensory threshold of *C. gariepinus* for our male *M. macrolepidotus* EOD of long duration (4.7 ms). Reaches for our smallest and largest bulldog individual (standard length, *SL*) are indicated by arrows, as is the reach for an individual of a body size at which males have turned sexually mature and developed discharges of long duration (12.6 cm). Water conductivity, 100 $\mu\text{S}/\text{cm}$

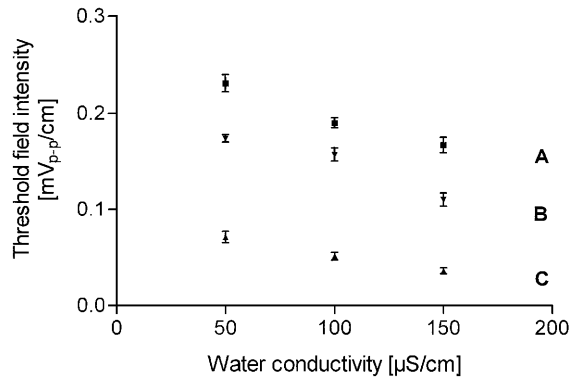


Fig. 8 Electrosensory thresholds as a function of water conductivity. *A* and *B*, mean thresholds for *C. gariepinus* ($n=2$) for our long-duration bulldog EOD (4.7 ms); *C*, thresholds for a square-wave pulse of 2 ms duration in *C. theodorae* ($n=1$). Mean values \pm SD ($\text{mV}_{\text{p-p}}/\text{cm}$)

Discussion

The present study shows that *C. gariepinus* catfish detect certain mormyrid EODs and other pulse signals despite the low-frequency tuning of their ampullary electroreceptors. This may explain Merron's (1993) observation of the at least temporary specialisation of *C. gariepinus* on the bulldog (we presume predominantly males) as its main prey.

Electrosensory thresholds for some EODs are remarkably low, even though these stimuli are not ideal for low-frequency receptors. The electrosensitivity maximum of the catfish *Ictalurus nebulosus* is 3–7 Hz as determined electrophysiologically (Peters and Buwalda 1972; Bretschneider et al. 1985, Andrianov et al. 1996), or between 1 and 3 Hz according to behavioural tests (Peters et al. 1988, 1995). In *Clarias lacera* (synonymous with

C. gariepinus), a maximum sensitivity of 10–30 Hz was found (Peters and Bretschneider 1981).

The present study found no evidence for tuning to a “best” stimulus pulse duration in the range investigated in *C. gariepinus*. In a log-log plot, electrosensory thresholds decreased linearly in the range of pulse durations studied, 0.1–4 ms; no minimum was reached (see Fig. 4). Similar results for a single individual of *Clarias* (presumably *C. anguilloides*) were described by Lissmann and Machin (1963): thresholds for single-cycle, as well as trains of square-wave pulses decreased with increasing pulse duration. This contrasts with high-frequency electroreception (which is based on tuberous electroreceptors) in weakly electric, mormyrid fish which are (weakly) tuned to their own pulse-like EODs (as behaviourally determined: Postner and Kramer 1995; as suggested by electrophysiological data: Hopkins 1981).

C. gariepinus was more sensitive to monopolar square-wave pulses than to monopolar sine-wave pulses of the same duration: parallel regression lines differed only in their y-intercept (see Fig. 4). This is because *C. gariepinus* only detects the low-frequency energy contents of pulse-like electric signals [as shown by Lissmann and Machin (1963) for square-wave pulses]. Considering only spectral amplitudes from 0 to 30 Hz (“low-frequency content”), thresholds for artificial pulses of different waveforms fell on the same straight line (see Fig. 5). These results indicate that thresholds do not depend on the waveform of a stimulus (unlike *Pollimyrus adspersus* larvae: Postner and Kramer 1995), but rather on its low-frequency content (an infinite number of waveforms satisfy a given amplitude spectrum, see general physics textbooks). A log-log plot of threshold versus integrated low-frequency spectral energy shows a linear relationship (see Fig. 5).

As revealed by behavioural experiments, catfish can electrically locate live prey or conspecifics (Peters and Meek 1973; Kalmijn 1974). Electrosensory prey detection has mainly been investigated in marine sharks that detect the individual electric fields of non-electrogenic prey fish that are associated with e.g. homeostasis of body fluids and muscle contractions; attack distances of up to 40 cm were found (Kalmijn 1978). In electrosensory freshwater teleosts only distances of up to 5 cm have been recorded (Roth 1972; Kalmijn 1988). This contrasts with the surprisingly long reach of certain mormyrid EODs for *C. gariepinus* as determined in the present study, even though catfish in general possess only the non-specialised but extremely sensitive ampullary electroreceptors. On the basis of the present study, a maximum reach of 1.50 m for an almost maximum-sized bulldog prey fish with a long-duration EOD is calculated. For a bulldog of 12.6 cm [close to the median 12.5 cm *SL* of bulldogs found in the stomachs of *C. gariepinus* dissected by Merron (1993)], a maximum reach of 0.83 m was calculated on the basis of catfish electrosensitivity and measured EOD amplitude. For *Brienomyrus niger* that, like all mormyrids, possesses tuberous electroreceptor organs that are co-adapted to the species-spe-

cific EOD, a similar reach was found (135 cm; Squire and Moller 1982).

Signal reach depends on source amplitude and the sensitivity of the receiver. As shown here, catfish sensitivity for an EOD increases with its duration and strength of the low-frequency content (0–30 Hz). EOD amplitude increased with fish size (Fig. 6; as also observed in gymnotids: Knudsen 1975; Caputi et al. 1989; Hopkins et al. 1990). Even though the electromotive force of an electric organ is species specific and independent of fish length, measured field amplitude associated with an EOD increases with fish length because the internal resistance of the whole fish body is an inverse function of its length (Caputi and Budelli 1995; Caputi 1999). An almost maximum-sized *M. macrolepidotus* generated a field potential of 5 mV/cm as measured at a distance of 35 cm. Water conductivity affects both the recorded peak-to-peak voltage of the EOD (which decreases with water conductivity in the range used; as demonstrated for *Gnathonemus petersii*: Bell et al. 1976) and the sensitivity of the catfish's electroreceptors (which increases with water conductivity, as also observed for high-frequency, electric gymnotiforms: Knudsen 1974). Therefore, the effects on the reach of electric signals largely cancel each other out.

This study shows that for an adolescent male bulldog, an increase in EOD duration and strength of the DC component of its EOD increases the probability of being detected by a catfish. Three factors suggest sex-selective electrosensory predation in catfish. (1) The long reach of some pulse-like EODs (e.g. the male bulldog's) and the observation that *C. gariepinus* can easily be trained to such signals suggests catfish detect some mormyrids also in nature. (2) Merron (1993) found size-selective predation on *M. macrolepidotus*: the median SL of prey fish was 12.5 cm. At that size, all males ($n=30$) of Kramer's (1997a, 1997b) field study had reached sexual maturity, and displayed an EOD of long duration. (3) The same study (Kramer 1997a, 1997b) demonstrated the presence of male EODs of the longest duration among males around an SL of 12.5 cm having just turned sexually mature, and not among larger and older individuals that emitted discharges of, within the male population, relatively short duration. This suggests a higher predation pressure on individuals with EODs of the longest durations that are detected by *C. gariepinus* from a greater distance. Whether reproductive success is related to male EOD duration is unknown.

In contrast to EODs of *P. catostoma*, *P. castelnaui* and *C. discorhynchus*, *C. gariepinus* detected the discharges of *M. lacerda*, *H. ansorgii* and *Hippopotamyrus* sp. nov. at natural stimulus intensities. *M. lacerda* and the *Hippopotamyrus* species were not represented in the diet of *C. gariepinus* as determined by Merron (1993), even though their EODs are more effective stimuli than those of the male bulldog. This absence of certain mormyrids from the catfish diet may be attributable to the lower abundance, more solitary habits or concealed life of these species. For example, the two *Hippopotamyrus* species hide in rock holes where they are safe from catfish at-

tacks during the day (B. Kramer, personal field observation). They also do not occur in shoals like bulldogs, as they are extremely intolerant of conspecifics (Scheffel and Kramer 2000).

Most mormyrid fish do not display discharges of long duration or monopolar waveform ("low-frequency" pulses). A possible reason for the predominance of "high frequency" pulses among mormyrids is the increased predation pressure from electroreceptive predators like certain catfish (as suggested by Kramer 1997a). In our study area, these comprise *Clarias* and *Schilbe* (*Eutropius*) species (see also Winemiller and Kelso-Winemiller 1994), and also the less common *Parauchenoglanis ngamensis* (B. Kramer, personal observation). However, even though *C. gariepinus* does not detect EODs of the churchill (*P. catostoma*), this species still constitutes 26% of its diet (Merron 1993), presumably due to the churchill's high abundance and shoaling habits when not reproducing (Skelton 1993).

A similar situation may apply for the weakly electric gymnotiform fish of South America. From its stomach contents, the bagrid catfish *Pseudoplatystoma tigrinum*, but not *Pseudoplatystoma fasciatum*, seems to prey mainly on gymnotiforms (Reid 1983). Reid (1983) suggests that *P. tigrinum* feeds opportunistically on the kind of prey that is most common during its nocturnal period of activity, that is, gymnotiforms; no suggestion of electroreception is made (this would resemble predation of the African churchill by the sharp-tooth catfish, see above). South American gymnotiforms exhibit a wide variety of mono-, bi- and triphasic EOD pulses or continuous waves, most of which have their energy peak in the high-frequency range (e.g. Kramer 1990; again, similar to our churchill example). Therefore, in light of the present study, the great majority of gymnotiform EODs (i.e. short bi- and triphasic pulses and continuous waves) are probably not detected by catfish; however, even these species must watch out for the electric eel, a gymnotiform that possesses tuberous (high-frequency) electroreceptors in addition to ampullary (low-frequency) electroreceptors. Westby (1988) reported a chance field observation of an electric eel (*Electrophorus electricus*) that apparently located and probably caught a *Gymnotus carapo* by electrical eavesdropping. Westby (1988) also demonstrated the efficiency of weak "high-frequency" electrical pulses in attracting a captive electric eel and evoking its attack response. There is no equivalent of the electric eel among African mormyrids.

Stoddard (1999) suggested avoidance of detection by electroreceptive predators such as catfish (based on Reid 1983) and the electric eel as a driving force towards more complexity and a shift to higher spectral frequencies in the EODs of gymnotids. Regarding the eel that was tested by Stoddard, a shift of prey gymnotiforms to higher spectral EOD frequencies may, however, not noticeably reduce the risk of being detected (see Westby 1988). Electrosensory thresholds have not been determined in the eel. Apparently without knowledge of the work of Hanika and Kramer (1999) and Kramer (1997a,

1997b), Stoddard (1999) speculated about the possibility of a parallel situation for mormyrids and catfish in Africa. Whether the South American situation is parallel to the one presented here (catfish detect certain weakly electric fish by electroreception) remains a matter of speculation.

The present study confirms Lissman and Machin's (1963) result that an ampullary electroreceptive system, such as that of *C. gariepinus*, can detect brief stimulus pulses, especially when monopolar, very well. This was puzzling for Lissman and Machin (1963) who could not identify a function: "It is in any event, almost inconceivable that this great electrical sensitivity is fortuitous, and not used by the fish in any way." In the Okavango, Upper Zambezi, and surely many other African river systems as well, *C. gariepinus* encounters mormyrid EOD pulses it can detect easily. For example, West and also Central Africa possess several mormyrid species displaying EODs of long duration (e.g. Kramer and Kuhn 1994; Hopkins 1999; B. Kramer, unpublished data). Signal reach, as calculated from catfish electrosensory thresholds for bulldog EODs and bulldog EOD source amplitudes, competes with that for mormyrid intraspecific communication. The reach of the sexually dimorphic EOD of the male bulldog is so long it can explain Merron's (1993) observation of bulldogs as main prey of *C. gariepinus*. To be sexually mature, these bulldogs must be of sufficient size (Kramer 1997a); at that size, catfish eat them in greatest numbers (Merron 1993).

Electroreception and sensitivity for mormyrid EODs must now be regarded as a major sense in the predatory behaviour of certain African catfish, rivalling the gustatory sense (Hara 1992) that is better studied in catfish.

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