THE SENSING OF ELECTRICAL CAPACITANCES BY WEAKLY ELECTRIC MORMYRID FISH: EFFECTS OF WATER CONDUCTIVITY

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Summary

Weakly electric fish can perceive electric properties of objects by monitoring the responses of their epidermal electroreceptors (mormyromasts) to their own electric organ discharges (EOD), a process known as active electrolocation. Mormyrid fish can distinguish capacitative from resistive properties of objects. It is mainly animate objects that possess capacitative properties. Water conductivity is a critical environmental factor that varies widely from season to season and has strong effects on the emitted EOD.

The two goals of this study were: (1) to investigate the ability of *Gnathonemus petersii* to detect the properties of capacitative objects in waters of different ion content and (2) to test a recently formulated hypothesis which states that the detection of the features of a capacitative object depends on a comparison of the inputs from the two types of mormyromast primary afferents. Individuals of *G. petersii* were tested in a conditioned electrolocation procedure.

With increasing water conductivities from 50 to $1100\,\mu\mathrm{S\,cm^{-1}}$, EOD amplitude decreased and the detection threshold for small capacitances increased. At $50\,\mu\mathrm{S\,cm^{-1}}$, the smallest detectable capacitative value was below 0.5nF; this increased to about 20nF at $800\,\mu\mathrm{S\,cm^{-1}}$. When conductivity approached about $1000\,\mu\mathrm{S\,cm^{-1}}$, fish were no longer able to electrolocate, probably because of the reduction in EOD amplitude at high conductivities.

The fish's ability to discriminate a capacitative object unequivocally from every resistive object was also tested at different conductivities. Below about $800\,\mu\mathrm{S\,cm^{-1}}$, all fish could do so. Above that conductivity, however, fish could no longer discriminate between capacitative and resistive objects of similar impedance, although they could still discriminate between objects of different impedances. The two types of receptor afferents (from the 'A' and 'B' cells) of mormyromast electroreceptor organs have different thresholds, with the B afferents being more sensitive. I suggest that only the B receptor cells remain active at about $800\,\mu\mathrm{S\,cm^{-1}}$, when the EOD amplitude is much reduced. With input from B afferents only, an unambiguous capacitance detection was no longer possible. This supports the hypothesis that capacitance detection is achieved by comparing inputs of A and B electroreceptor cells.

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Introduction

African weakly electric fish use active electrolocation to detect, localize and evaluate objects in their near surroundings (Lissmann, 1958; Heiligenberg, 1977; Bastian, 1990; von der Emde, 1990). The discharge of the electric organ in their tail creates an electric field around the fish's body that is measured by epidermal electroreceptor organs (mormyromasts) (Szabo and Wersäll, 1970; Harder, 1972; Bell, 1990).

Nearby objects with electric properties differing from those of the surrounding water influence the locally measured electric organ discharge (EOD) (Bullock, 1982; von der Emde, 1990). Because fish electrolocate by measuring the difference between the impedance of objects and that of water, water conductivity probably has a strong effect on the fish's electrolocation abilities. Moreover, water conductivity has a marked influence on EOD amplitude (Bell *et al.* 1976; Squire and Moller, 1982). Rising water conductivities reduce the peak-to-peak voltage of the EOD and impair the afferent responses of the electroreceptors (Bell and Russell, 1978). From Bell and Russell's (1978) study it can be predicted that electrolocation should be impossible in water conductivities greater than about 400–$500 \, \mu\text{S cm}^{-1}$ because the responses of mormyromast electroreceptors disappear at this point. This prediction is tested in this study.

Living objects, such as water plants, other fishes or food items, possess capacitative components besides resistive components (Schwan, 1963; Heiligenberg, 1973). The possible importance of capacitative objects during electrolocation was first suggested by electrophysiological studies of electroreceptor afferents of weakly electric gymnotiform fish (Scheich *et al.* 1973; Scheich and Bullock, 1974). In these experiments, T-type receptor afferents responded differently to capacitative and resistive shunts in the water. The behavioural experiments of Meyer (1982) showed that mormyrids are sensitive to capacitative shunts in the water. Later, von der Emde (1990) demonstrated that *G. petersii* and other mormyrids (von der Emde and Ringer, 1992) can unambiguously discriminate between resistive and capacitative objects. These authors showed that mormyrids could distinguish a capacitor from any resistor even if both caused the same EOD amplitude change, indicating that mormyrids were not responding only to a simple change in EOD amplitude during capacitance detection.

The present study has two goals. The first is to test behaviourally the abilities of the mormyrid *Gnathonemus petersii* to detect capacitative objects in waters of different conductivities. At each water conductivity, the detection threshold for capacitative objects was determined and the ability of *G. petersii* to discriminate unequivocally between resistive and capacitative objects was tested.

The second goal of the paper is to test a hypothesis about the central mechanism of capacitance detection. This hypothesis states that capacitance detection requires the comparison of the responses in the two types of mormyromast afferents (from the A and B cells of Szabo and Wersäll, 1970). Mormyrids recognize capacitances not only by measuring local EOD amplitude but also by measuring a second variable. This second variable is probably the distortion of the EOD waveform that occurs only in the presence of a capacitative object (von der Emde, 1990). Electrophysiological recordings of

electroreceptor afferents have revealed that only one type of primary afferent from each mormyromast electroreceptor organ (the B afferents) responds very strongly to the EOD waveform distortions. A-type afferents, in contrast, respond only to EOD amplitude changes (von der Emde and Bleckmann, 1992*a,b*). The hypothesis to be tested is that the fish need the afferent inputs of both the A and B receptor cell populations to discriminate between capacitative and resistive objects that have the same impedance and therefore cause the same local EOD amplitude changes.

A and B afferents have different thresholds to EOD stimuli (Bell, 1990; von der Emde and Bleckmann, 1992*b*), with the B afferents being more sensitive than the A afferents. By raising water conductivity, it should be possible to reduce the EOD amplitude to a point where most A cells are no longer responding while the B cells are still excited. This would block the input of only one type of receptor cell to the brain. The hypothesis stated above predicts that fish will not recognize capacitative object features when only one type of afferent input remains.

Materials and methods

Animals

Eight individuals of the African mormyrid species *Gnathonemus petersii* (Günther) (GP1–GP8), obtained commercially from Nigeria, were used in this study. Fish had a mean standard length of 12.4±1.5cm. They were housed individually in 100l tanks (75cm×40cm×32cm) which were also used for training. The light:dark cycle was 12h:12h. Experiments were carried out during the light period (170lx). During training and testing, the lights were dimmed to about 10lx, which rendered the fish more active and usually improved electrolocation performance. Temperature was kept constant at 27±1˚C.

Water conductivity was measured by a digital conductivity meter (LF92, WTW). It was kept within $20\,\mu\mathrm{S}\,\mathrm{cm}^{-1}$ of the indicated value by adjusting its value daily. It was raised by adding a certain amount of water of high conductivity, which was produced by adding synthetic sea salt (wimex, Wiegandt GmbH) to aged, ion-exchanged water that was almost free of ions ($0.5\,\mu\mathrm{S}\,\mathrm{cm}^{-1}$). For individual fish, experiments were always started at $50\,\mu\mathrm{S}\,\mathrm{cm}^{-1}$, which was the conductivity of the animals' stock tank. Conductivity was raised in steps of at most $30\,\mu\mathrm{S}\,\mathrm{cm}^{-1}\,\mathrm{day}^{-1}$ by adding water of higher conductivity. When the desired conductivity value had been reached, fish were allowed to acclimate to it for at least 3 weeks before testing.

Experimental arrangement

Experiments were performed in a glass tank divided in two compartments (65l and 35l) by a plastic mesh wall (Fig. 1A). The larger compartment was the fish's home compartment during non-experimental hours and was equipped with a ceramic tube as a shelter, a filter and heater equipment.

The dividing wall had two gates (4cm×4cm) with their centres separated by 19cm, 7.5cm above the aquarium bottom. By sliding the doors, the gates could be opened and closed by the experimenter by pulling a thin thread. An electrolocation object was placed
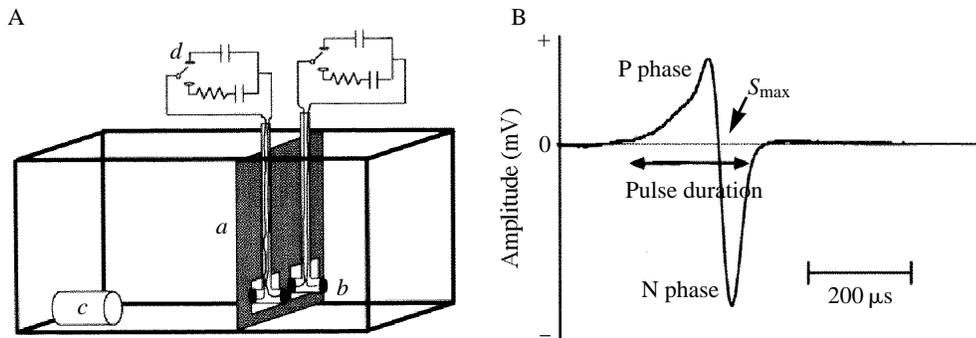
Fig. 1. (A) Aquarium showing the experimental arrangement. *a*, dividing wall with two gates; *b*, electrolocation objects with passive electrical circuit; *c*, fish resting in shelter tube; *d*, device for switching between resistive and capacitative electrical properties of the objects. A is not drawn to scale. (B) Example of an EOD recorded from *Gnathonemus petersii*. The signal duration and the positive (P) and negative (N) phases are indicated. The point where the maximal slope (S_{max}) occurs is marked.

behind each gate in the smaller compartment of the tank. It consisted of Plexiglas tubing in the shape of an inverted T. The horizontal part of the T (length 2.5cm) was oriented perpendicular to the dividing wall. One of its ends protruded through the gate into the larger compartment for about 0.5cm (Fig. 1A). At the two ends of the horizontal part of each object, a cylindrical carbon electrode (diameter 0.6cm; height 0.8cm) was inserted into the Plexiglas tube so that it sealed its ends. Inside the tube, a wire was connected to each carbon pole and travelled up the length of the vertical part of the tube outside the water.

The passive electrical properties of the dipole objects could be changed by introducing various electrical elements into the circuit between its poles (Fig. 1A). For example, when the two wires were shunted, the object resembled a good conductor. When the wires were completely separated, the electrical properties of the object were like those of a nonconductor. A purely 'capacitative object' was created by placing a capacitor between the poles. For a discussion of the differences between natural objects and the dipole objects, see von der Emde (1990).

Training

Fish were trained to discriminate between two dipole objects with different electric properties in a two-alternative forced-choice procedure. When the gates opened, the fish had to swim towards the objects, investigate them by electrolocation and choose one object with electric properties previously defined as correct (S+) by swimming through the corresponding gate. If it chose the correct gate it received a food reward (one or two chironomid larvae), if not it was mildly punished by the experimenter gently knocking against the glass tank wall and no food reward was given. After having eaten the food reward, the fish had to swim back through one of the gates into its home compartment and a new trial was started. The inter-trial time was 2min. Presentation of S+ changed from

left to right in a pseudorandom schedule (Gellermann, 1933). Fish were subjected to 30–60 trials in one session per day, 5 days a week.

Threshold determination

For water conductivities between 50 and 1100 μS cm^{-1}, the discrimination thresholds for capacitative objects were measured, i.e. the smallest capacitative value that could just be discriminated from a nonconductor was determined. *G. petersii* produces biphasic EODs with a total duration of about 200–300 μs (Fig. 1B). The impedance of a capacitative object to this a.c. current is the complex impedance *Z*. The smaller the capacitative value of the object, the higher is its impedance. For a purely capacitative object, *Z* can be calculated using the formula:

$$Z \text{ (in ohms)} = 1/2 \; fC \text{ ,}$$

where *f* is the frequency of the a.c. current and *C* is the capacitative value of the object. It follows that objects with very small capacitative values have a high impedance similar to that of a nonconductor and the fish cannot discriminate between the two.

To determine thresholds, the descending method of limits was used. The positive stimulus (S+) was a nonconducting dipole object that was kept constant throughout the experiment. The negative stimulus (S−) was a capacitative object. During training its value was high, usually 100nF. When a fish could discriminate this stimulus combination with more than 90% correct choices, the value of the S− was reduced in steps until the fish could no longer discriminate between the two objects. At that point its performance fell to chance level (50% correct). The capacitative value of S− that a fish discriminated correctly in 70% of the trials was defined as threshold, because at this point the psychometric functions usually had their steepest slopes. The threshold value was interpolated from the psychometric function of each fish (see Fig. 2).

Discrimination between resistive and capacitative objects

The ability of the fish to discriminate between resistive and capacitative objects was tested at water conductivities between 50 and 1000 μS cm^{-1}. Fish were trained to discriminate between a capacitative object and a nonconductor as described above. During tests, a subthreshold capacitative object (S−) of a fixed value had to be discriminated from a resistive object (S+) whose value changed in the course of the experiment from very high (1 M) to very low (<3) values. The value of S − was 100nF, 80nF or three times the threshold value previously determined at the same water conductivity.

With each stimulus combination at least 40 trials were conducted. The method of constant stimuli was used, i.e. all the values of the S+ were determined in advance and then one was chosen randomly. To prevent d.c. currents from serving as an additional cue, a relatively high-value capacitor of 12 μF was placed in the circuit of the resistive object in series with the resistor.

EOD measurements

To determine the mean peak-to-peak amplitude and other EOD characteristics (Fig. 1B)

at different water conductivities, a carbon electrode was fixed at each of the two ends of a ceramic tube (diameter 4cm; length 15cm) in which the fish was hiding. The signals picked up by the electrodes were differentially amplified, A/D converted at a rate of 156kHz or 2MHz, and stored on a computer for later calculation of various EOD variables: peak-to-peak amplitude, amplitude ratio of the positive and negative main phases of an EOD (P/N ratio), EOD duration (the beginning and end of the EOD were taken as the points where the signal departed from the baseline by 3% of the peak-to-peak amplitude), duration of single EOD phases, peak power spectral frequency (F_{peak}), relative spectral bandwidth (Q_{10dB}, i.e. F_{peak}/the range of frequencies with an amplitude not less than 10dB below that of F_{peak}) and maximal slope between the P and N phases (S_{max}). Fast Fourier Transformation (FFT) amplitude spectra were calculated from single discharges by using a Pascal version of the subroutine FFT842 of the package FAST (Bergland and Dolan, 1979). S_{max} was determined by setting the peak-to-peak amplitude of the pulse to 100% and then finding the maximal amplitude difference between two consecutive sample points. It was expressed in percentage amplitude change per microsecond. EODs of each individual were sampled at least 15 times under identical conditions.

Local EOD measurements

The adequate stimulus for the electroreceptors is the fish's own signal emitted by its electric organ, filtered by the surrounding water and possibly by an electrolocation object. This perceived signal is called the local filtered signal, LFS (von der Emde, 1990). To measure the LFS at different water conductivities, the fish was fixed in a thin silk sock in the middle of a circular tank (diameter 1.5m). Two thin carbon rods (diameter 0.5mm), insulated except at the tips and about 2mm apart, were used as differential electrodes to record the LFS. They were positioned at an angle of 90° relative to the fish' skin, very close (<1mm) to the pore of a mormyromast electroreceptor organ located dorsal of the fish's lateral line just behind the pectoral fins. An electrolocation object identical to the ones used in the behavioural experiments was fixed at a distance of about 5mm from the recording electrodes.

In addition to the LFS that was influenced by the object, the fish's EOD was simultaneously recorded head-to-tail by a pair of carbon electrodes 10cm in front of the mouth and 10cm behind the tail. Both signals were A/D converted (8-bit) at a rate of 156kHz (or 2MHz) and stored for later analysis.

Results

Threshold determination

For two fish the smallest capacitative value of an object that could just be discriminated from a nonconductor was determined at water conductivities between 50 and 1000 μS cm^{-1}. At each conductivity, a psychometric function was determined (Fig. 2). Below 800 μS cm^{-1}, all fish discriminated between large capacitors and a nonconductor with more than 70% correct responses. When the capacitative value of the S− was reduced, the discrimination performance deteriorated and finally reached chance level (50% correct). The threshold values (70% correct) at each conductivity were interpolated
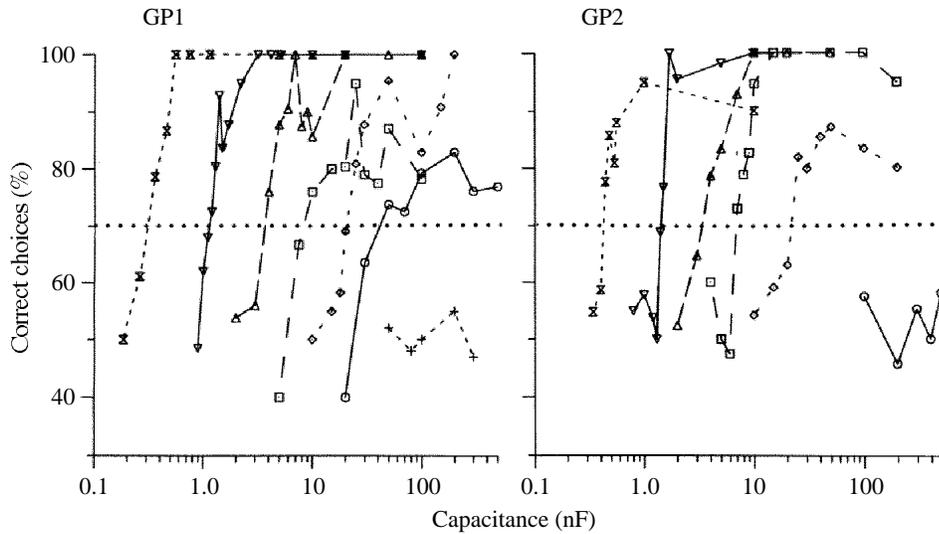
Fig. 2. Psychometric functions of two fish (GP1 and GP2) discriminating between a nonconductor (S+) and a capacitative object (S−) whose value is given on the abscissa. Each curve depicts the results at a different water conductivity. Hour glasses, $50\,\mu S\,cm^{-1}$; ∇, $200\,\mu S\,cm^{-1}$; $\triangle$, $400\,\mu S\,cm^{-1}$; squares, $600\,\mu S\,cm^{-1}$; diamonds, $800\,\mu S\,cm^{-1}$; circles, $1000\,\mu S\,cm^{-1}$; crosses, $1100\,\mu S\,cm^{-1}$. Threshold values were interpolated as the capacitative value where the curves crossed the dotted 70% line. Each point represents at least 40 decisions by a fish. Note that at $1000\,\mu S\,cm^{-1}$ (GP2) or $1100\,\mu S\,cm^{-1}$ (GP1) the fish's performance never exceeded chance level (50% correct choices) and no threshold values could be determined.

from the psychometric function. In both fish they increased logarithmically with water conductivity (Fig. 3). At conductivities above $800\,\mu S\,cm^{-1}$ (GP2) or $1000\,\mu S\,cm^{-1}$ (GP1) threshold determination was no longer possible because the fish's performance never exceeded 60% correct choices even when very large capacitors were used.

At water conductivities above $600\,\mu S\,cm^{-1}$ the general electrolocation performance of the fish started to deteriorate. Fish made more mistakes at the beginning of testing compared with their performance at lower conductivities, even if S− was a large capacitor. Further training usually improved the fish's performance and eventually a threshold value could be determined. At $1000\,\mu S\,cm^{-1}$ (GP2) or $1100\,\mu S\,cm^{-1}$ (GP1), fish could no longer discriminate between the objects even if S− was very large (Fig. 2).

Discrimination between resistive and capacitative objects

Four fish were tested to determine whether they could discriminate unequivocally between a capacitative and a resistive object at different water conductivities. Fig. 4 shows that all fish could do so when the water conductivity was below about $800\,\mu S\,cm^{-1}$. At low conductivities, the fish's performance always stayed above 70 % correct choices no matter what object combination was used.

At a certain conductivity, usually around $800\,\mu S\,cm^{-1}$ (Table 1), fish could no longer
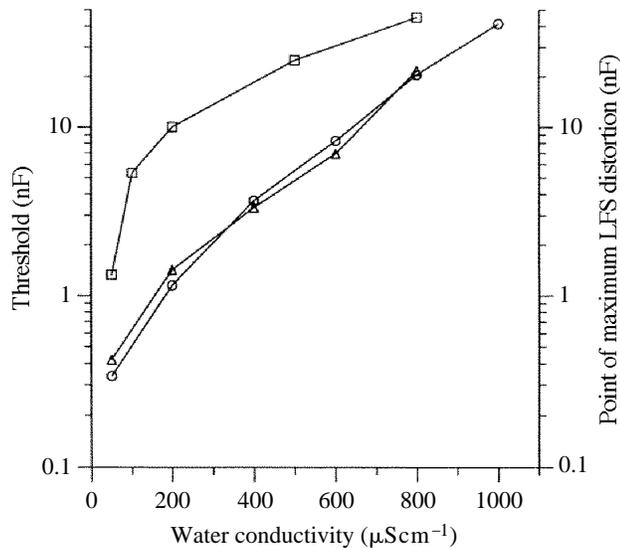
Fig. 3. Threshold values for two fish taken from Fig. 2 plotted *versus* water conductivity. Circles, GP1; triangles, GP2. The capacitative values where maximal LFS waveform distortions occurred (taken from the experiment illustrated in Fig. 6) are also plotted (squares). All curves rise in a similar way with water conductivity, suggesting that fish might have used waveform cues to detect capacitative objects.

discriminate between a capacitative object and every resistive object (Fig. 4). Fish could discriminate between the two objects if their complex impedance was different but not if it was similar. When the resistive object (S+) had a value smaller than 1–4 k and the capacitative value of the alternative object (S−) was 100nF, the performance of all fish deteriorated and reached chance level. In only one fish (GP4) did the discrimination performance improve again when the resistive value of S+ dropped to 10 (fish's performance 70% correct). Like all other fish, this fish was not able, however, to discriminate between a resistive object of between 100 and 1000 and a 100nF capacitor (Fig. 4).

EOD measurements

The EODs of the fish showed a reduction in peak-to-peak amplitude as water conductivity increased (Fig. 5). The relationship between amplitude and water conductivity can be expressed by a power function very similar to the one determined by Squire and Moller (1982).

Apart from amplitude, the other pulse variables measured showed no significant correlation with conductivity (Table 2). After a 3-week acclimation to changed water conditions, neither the spectral variables, F_{peak} and Q_{10dB}, nor S_{max}, the P/N amplitude ratio, and the total pulse duration, was affected by conductivity.

Local EOD measurements

Higher water conductivities decreased the peak-to-peak amplitude of the LFS in a

Table 1. *Discrimination between resistive and capacitative objects*

Fish	Water conductivity (μS cm^{-1})	S− (nF)	Impedance of S− (Ω)	Point of no discrimination (70% correct)
GP3	50	1	33900	–
		54	627	–
	400	10	3386	–
		100	339	–
	600	25	1355	–
		100	339	–
	800	100	339	<1.74 kΩ
	1000	100	339	No more electrolocation
GP4	400	10	3423	–
		100	342	–
	600	25	1369	–
	800	100	342	–
	920	100	342	<4.17 kΩ
			342	>10 Ω
	1100	100		No more electrolocation
GP5	200	10	3460	–
	315	10	346	–
	460	10	3460	–
		100	346	–
	600	25	1384	–
		100	346	–
	720	100	346	<1.41 Ω
	1000	100	346	No more electrolocation
GP6	350	25	1201	–
	450	25	1201	–
		100	300	–
	550	50	601	–
	650	50	601	–
	750	60	500	–
	825	80	375	<1.51 kΩ
	1000	100	300	No more electrolocation

The last column gives the range of resistive values that were not discriminated from the capacitative object depicted in the third column.

–, all object combinations used were discriminated; no more electrolocation, at this water conductivity the fish could not discriminate between any two objects.

At low water conductivities, where both A- and B-type receptor cells were functional, the fish could unequivocally discriminate between all resistive objects and a fixed capacitative object. At higher water conductivities, ranging from about 800 to 1000 μS cm^{-1}, where presumably only the B-type receptor cells were functional, fish failed to discriminate between resistive and capacitative objects of similar impedances. At very high conductivities, where both A- and B-type receptor cells were no longer functional, all fish were unable to discriminate between any resistive and capacitative object.
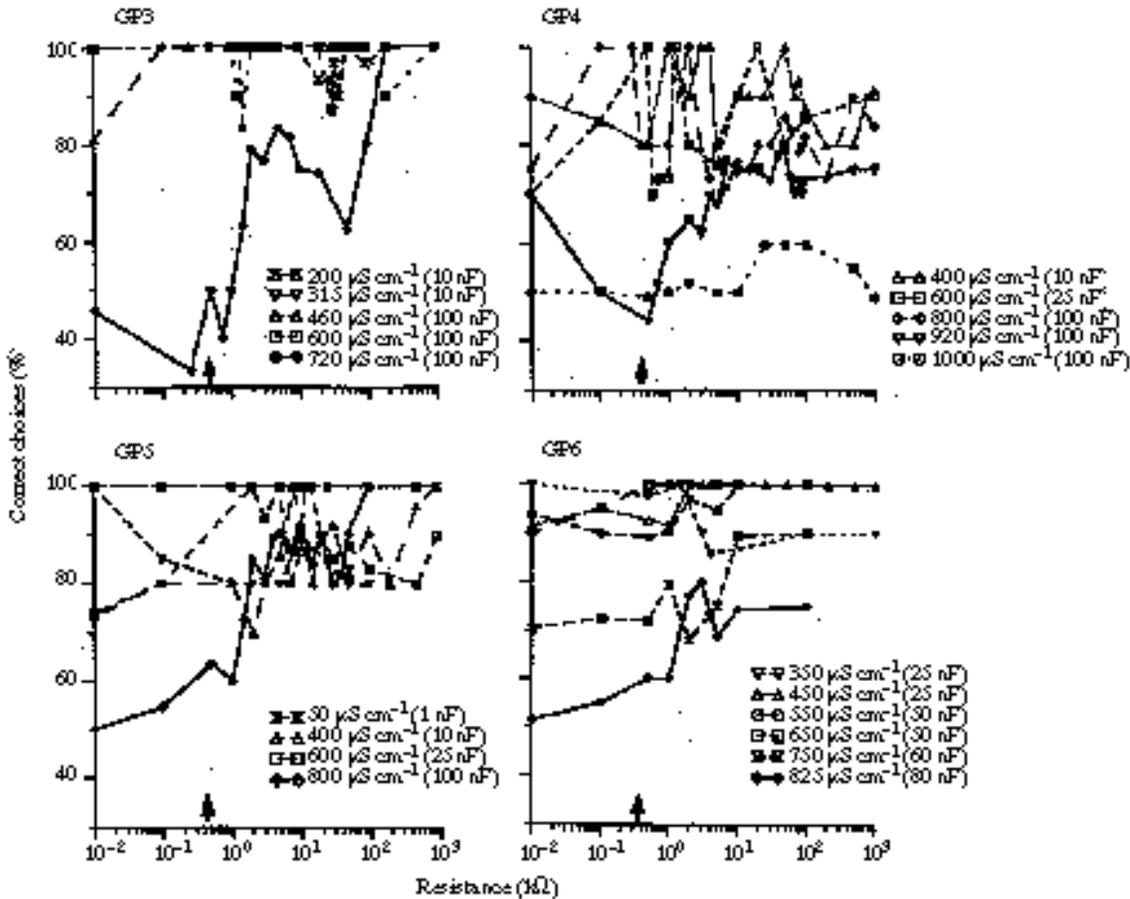
Fig. 4. Discrimination between a capacitative object (S−) of a fixed value (indicated in parentheses for each curve) and various resistive objects by four *G. petersii* (GP3–GP6). The values of the resistive objects are given on the abscissa, and the percentage of correct choices of the resistive object are indicated on the ordinate. Each diagram shows the performance of a single fish. Each curve in a diagram represents the results from that fish at a different water conductivity. The arrows are positioned at the *x*-value that depicts the impedance of the capacitative object (S−). Curves drawn in bold type show the results obtained at water conductivities where discrimination only occurred when the two objects had different impedances. When their impedances were similar (near the arrows), performance dropped to chance level (about 50% correct choices). At lower water conductivities (thin lines), fishes' performances always stayed above 70% correct choices, even when object impedances were similar. For one fish (GP4), the performance curve at a conductivity of $1000\,\mu S\,cm^{-1}$ is also shown (circles). At that high conductivity, the fish never performed better than at chance level.

similar way as the peak-to-peak amplitude of the head-to-tail EOD. In addition, the range of capacitances that influenced the LFS differed at different water conductivities.

Objects with small capacitative values (i.e. with a high impedance) caused a reduction in the LFS amplitude whereas those with large capacitative values (i.e. low impedance)
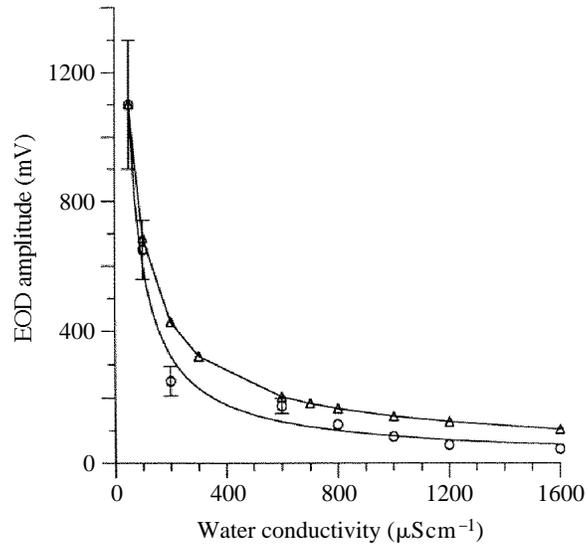
Fig. 5. Mean peak-to-peak amplitude ± S.D. of the EOD of GP1 at different water conductivities (circles). The triangles show amplitudes calculated using the formula given in Squire and Moller (1982), normalized to the amplitude measured in this study at a conductivity of $50 \mu S\,cm^{-1}$, $N \geqslant 15$.

Table 2. *EOD variables at different water conductivities*

Water conductivity ($\mu S\,cm^{-1}$)	F_{max} (kHz)	S_{max} (% μs^{-1})	Q_{10dB}	P/N ratio	Pulse duration (μs)
1650	4806.5±191	3.067±0.1	0.425±0.02	0.681±0.02	181.5±16.5
1250	4947.9±92	3.121±0.01	0.431±0.01	0.665±0.01	172.9±2.5
1000	4893.5±223	3.016±0.09	0.435±0.03	0.665±0.02	175.6±5.9
775	5025.8±209	3.13±0.08	0.44±0.02	0.688±0.01	168.5±4.8
600	5083.0±223	3.045±0.05	0.442±0.02	0.674±0.01	170.4±2.4
400	4882.8±246	2.98±0.06	0.433±0.02	0.665±0.02	175.0±5.0
275	5070.0±137	3.05±0.05	0.439±0.02	0.671±0.01	171.1±2.5
142	5149.6±201	3.125±0.04	0.45±0.01	0.680±0.01	173.8±5.8
50	4965.7±120	3.121±0.04	0.44±0.01	0.672±0.01	171.4±1.3
Correlation coefficient	$r=-0.18$ ($P>0.2$)	$r=-0.02$ ($P>0.8$)	$r=-0.19$ ($P>0.2$)	$r=0.12$ ($P>0.4$)	$r=0.19$ ($P>0.2$)

increased it. A sigmoid curve results when amplitude is plotted against the capacitative value of the object. This curve shifts to larger capacitances at higher water conductivities (Fig. 6).

Capacitative objects of a certain range also distorted the LFS waveform. This was not so with very large or very small capacitative values. With those objects, the LFS waveforms were similar to the waveform of the head-to-tail EOD. Intermediate capacitative values, however, changed several waveform variables: (1) the last positive
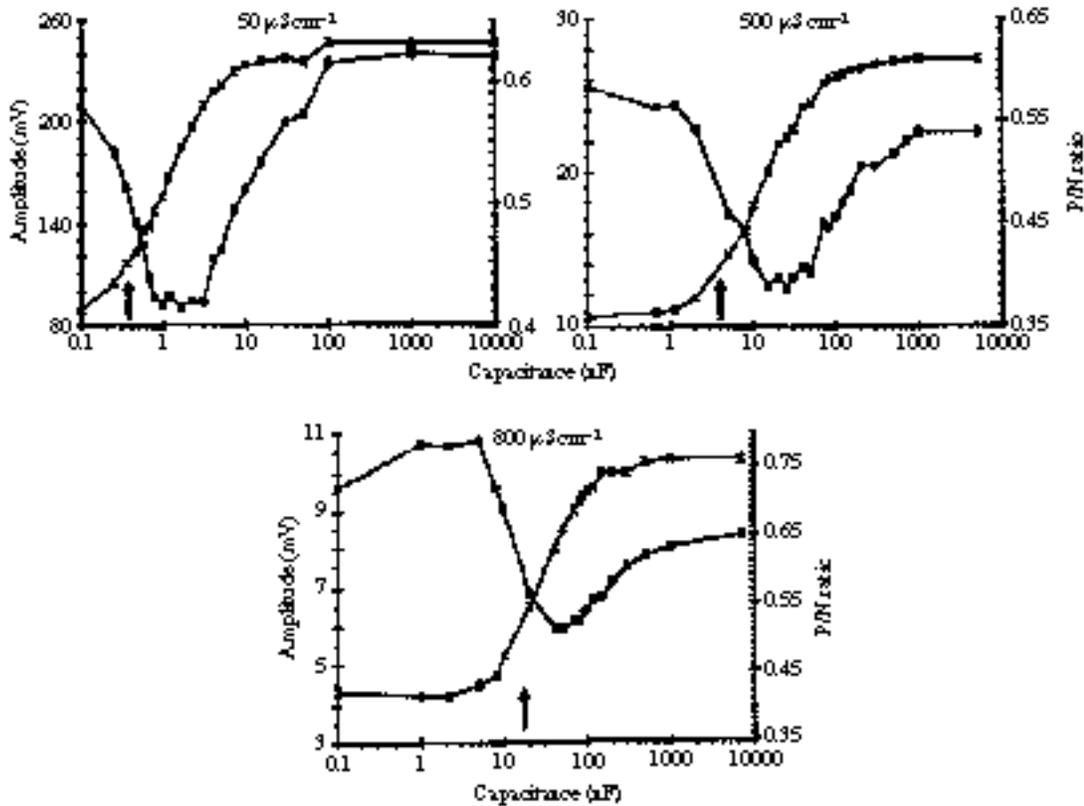
Fig. 6. LFS amplitude (crosses) and LFS waveform distortions (circles), measured as P/N amplitude ratio, in the presence of capacitative objects whose values are given on the abscissa. Each diagram depicts the results at a different water conductivity. Each point is the mean of 10 consecutive measurements. Arrows show mean values of the behaviourally determined detection thresholds (interpolated from Fig. 2) at the respective water conductivity.

phase of the pulse became larger; (2) the P/N amplitude ratio became smaller because the N phase amplitude increased relatively to the P phase amplitude; (3) S_{max} increased; (4) F_{peak} also increased. All these pulse variables were affected maximally at a certain capacitative value depending on water conductivity. At smaller or larger capacitative values they were less affected. I chose the P/N amplitude ratio as a measure of pulse distortions because it was the easiest to measure.

A plot of P/N ratio *versus* capacitance gives a U-shaped curve (Fig. 6). Smallest P/N values correspond to maximal pulse distortions. At higher water conductivities, the P/N curves of Fig. 6 shift so that the minimum occurs at larger capacitative values. This shift corresponds to the shift in the amplitude curves. The capacitative value that caused maximal pulse distortion (Fig. 2) and the smallest capacitative value that just caused pulse distortion are shifted to larger capacitative values at higher water conductivities (Fig. 6).

Discussion

In this paper I show that water conductivity strongly influences the detection threshold of capacitive objects during electrolocation. At low conductivities around $50\,\mu\mathrm{S\,cm}^{-1}$, thresholds have small values and mormyrids can detect very small capacitative objects, perhaps even food items such as chironomid larvae (von der Emde and Ringer, 1992). Fish can no longer detect these small capacitative values at higher water conductivities because thresholds increase sharply with conductivity (Fig. 3).

Several authors have measured water conductivities between 5 and $120\,\mu\mathrm{S\,cm}^{-1}$ in the natural habitat of mormyrids (Gosse, 1963; Moller *et al.* 1979; Hopkins, 1980). Higher conductivities may also occur temporarily during the dry season, for example. Mormyrids usually live in waters of low conductivity where electrolocation (and also electro-communication, Squire and Moller, 1982) functions optimally and permits the detection of objects of low capacitance that might be important for the fish.

There are three possible reasons why capacitance detection thresholds increased at higher water conductivities. (1) The amplitude of the EOD decreases dramatically at high conductivities (Bell *et al.* 1976; Squire and Moller, 1982). This restricts the distance at which objects can be detected by electrolocation and finally leads to the cessation of active electrolocation because electroreceptors are no longer excited. With a lower EOD amplitude, the fish's electrolocation ability might show a general deterioration leading to higher detection thresholds. (2) Fish detect an object if its impedance differs by a certain amount from that of the surrounding water. When the impedance of the water surrounding the fish decreases, the impedance of an object also has to decrease to be detectable. In the case of a capacitative object, a decrease in object impedance corresponds to an increase in its capacitative value. Thus, threshold values should be higher at higher water conductivities. (3) Fish probably detect capacitative objects by the EOD waveform distortions that they cause. The capacitative value at which waveform distortions begin to occur depends on water conductivity. If it is higher, the capacitance has to be larger to cause a waveform distortion (Fig. 6). This leads to higher threshold values in fish that use waveform cues.

Whether the fish used amplitude or waveform cues or both, one would always expect higher thresholds at higher water conductivities. Both the amplitude and the pulse-distortion curves are shifted towards larger capacitances at higher water conductivities and the threshold values follow that shift (arrows in Fig. 6). At each conductivity level, threshold values occur at the point where the LFS amplitude begins to increase and waveform distortions begin to occur.

EOD amplitude was affected by conductivity, but other EOD variables were not (Table 2). The reason for this might be that conductivity was changed slowly and fish were allowed to acclimate to each new water conductivity for at least 3 weeks. Former studies have shown that the EOD waveform was affected by water conductivity, but mainly if it suddenly fell below $50\,\mu\mathrm{S\,cm}^{-1}$ (Bell *et al.* 1976; Bratton and Kramer, 1988). A recent study showed that fish could actively adapt to water of low conductivity so that the waveform distortions induced by a sudden change were largely reversed after 2 days (Kramer and Kuhn, 1992). Fish can apparently keep the EOD waveform approximately

constant. This seems to be necessary for the discrimination between capacitative and resistive objects that is possibly based on EOD waveform cues (von der Emde and Bleckmann, 1992*b*).

In addition, the fish could possibly adjust the sensitivity of their electroreceptors. Two former studies predicted that the fish should not be able to electrolocate at the high conductivities observed in this study. (1) Bell and Russell (1978) found no mormyromast afferents that still responded to the natural EOD amplitude above 400–500 μS cm^{-1}. (2) Primary afferents from mormyromast electroreceptor cells have a small dynamic range: between 5 and 11dB in A afferents and between 5 and 7dB in B afferents (von der Emde and Bleckmann, 1992*b*). An 11dB reduction in EOD amplitude occurs when water conductivity increases from 50 to about 200 μS cm^{-1} (Fig. 5). This means that mormyromasts should no longer be able to respond to the EOD of the fish above 200 μS cm^{-1}. The fish in this study could electrolocate up to a water conductivity of about 1000 μS cm^{-1}, however, which corresponds to a 23dB reduction in EOD amplitude relative to the amplitude at 50 μS cm^{-1}. Therefore, it is possible that receptor cell sensitivity is somehow enhanced during the acclimation process to a higher water conductivity.

Alternatively, fish in highly conductive water might rely on a small population of receptor cells with low thresholds. Threshold measurements revealed that mormyromast afferents have very different thresholds to EOD stimuli, spanning a range from 15 to 1100mV (transepidermal voltage) in A fibres and from 9 to 175mV in B fibres (von der Emde and Bleckmann, 1992*b*). The brain of the fish might still receive some input from the most sensitive afferents at a high water conductivity. Because of the narrow dynamic range of the receptor cells, however, the high-sensitivity cells would be driven to saturation and would therefore be of limited use for electrolocation at low water conductivities.

Squire and Moller (1982) also found that conductivity affects both signal intensity and receptor sensitivity of the *Knollenorgane* that respond to pulses of other fish. In their study, however, receptor sensitivity decreased at higher conductivity levels. The reason for this difference from the present study is not known.

G. petersii can unequivocally discriminate between resistive and capacitative objects (von der Emde, 1990) as long as water conductivity is no higher than about 800 μS cm^{-1} (Table 1, Fig. 4). Von der Emde and Bleckmann (1992*b*) proposed a mechanism to explain how mormyrids might discriminate between resistive and capacitative objects. The fish might compare the inputs of the two types of afferents (from the A and B cells, Szabo and Wersäll, 1970) of mormyromast electroreceptor organs. A fibres only convey information about EOD amplitude and do not change their firing pattern when waveform distortions occur. B fibres, in contrast, respond both to amplitude changes and to waveform distortion. The sensitivity to EOD distortions is very high in these fibres and waveform cues can override amplitude cues if they change in different directions (von der Emde and Bleckmann, 1992*b*). With a purely resistive object present that does not distort the EOD, both fibre types will report the same amount of amplitude change to the brain of the fish. If, however, a mismatch between the inputs of A and B fibres occurs, then the object under investigation must have

distorted the local EOD waveform and therefore must have a capacitative component. The fish might detect this mismatch and thus recognize capacitative object properties. According to this hypothesis, fish need both types of afferents for the identification of a capacitative object.

At $800\,\mu\text{S cm}^{-1}$, fish could discriminate between resistive and capacitative objects only if the impedance of the resistive object was greater than 1.5–$4\,\text{k}\Omega$ and in one case when it was smaller than $100\,\Omega$ (Table 1, Fig. 3). The capacitative objects (S−) used in this study had a value of 100 or 80nF. This value corresponds to an impedance of between 300 and $450\,\Omega$ at the peak power spectral frequency (F_{peak}) of a single EOD (Table 1). Accordingly, fish failed to discriminate when the two objects had similar impedances at $800\,\mu\text{S cm}^{-1}$. They could discriminate, however, between two objects having clearly different impedances. In that case, they presumably performed an object discrimination based only on amplitude cues and could not detect the EOD waveform distortions caused by the capacitative object (Fig. 6).

I suggest that the fish did not recognize waveform distortions because only the most sensitive receptor afferents were still providing input to the fish brain. All other afferents were already subthreshold because of the low EOD amplitude at $800\,\mu\text{S cm}^{-1}$ (Fig. 5). If water conductivity rose just a little bit more, to about $1000\,\mu\text{S cm}^{-1}$, signal amplitudes became too low to excite any electroreceptors and the fish were no longer able to electrolocate. Peripheral recordings of mormyromast afferents revealed that the most sensitive receptor afferents are B afferents (Bell, 1990; von der Emde and Bleckmann, 1992*b*). With only B afferents left active, a central comparison of the two types of afferents was no longer possible and the fish had to rely solely on cues provided by the B cells. This might be the reason why they failed to discriminate between the capacitative and resistive objects.

The B afferents respond to a change in waveform in a similar way as they do to an increase in local amplitude (von der Emde and Bleckmann, 1992*b*). If LFS waveform distortions occur in the presence of a capacitative object, B afferents 'report' a higher amplitude to the brain than they do in the presence of a resistive object of the same impedance. This might be the reason why all but one fish (GP4) failed to discriminate between a resistive object of very low resistance ($10\,\Omega$) and the 100nF object at conductivities greater than $800\,\mu\text{S cm}^{-1}$ (Fig. 4). Another reason might be that the impedances of a 100nF (about $400\,\Omega$) and a $10\,\Omega$ object were still too similar to be discriminated by the fish.

This study provides evidence that the electrolocation system of *G. petersii* is best suited for waters of low conductivity, such as those found in its natural habitat. Higher water conductivities impair electrolocation and raise detection thresholds for capacitances. Under these conditions, fish can no longer detect objects with small capacitances, such as insect larvae (von der Emde and Ringer, 1992). At certain high water conductivities, just below those where electrolocation comes to a halt, fish can no longer discriminate between objects of similar complex impedance. They can probably no longer detect LFS waveform distortions because only B-type receptor cells are active at this point. These findings support the hypothesis that mormyrids need the afferent input of both their A- and B-type sensory cells to identify a capacitative object unequivocally.

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