

Discrimination of objects through electrolocation in the weakly electric fish, *Gnathonemus petersii*

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Summary. Three weakly electric fish (*Gnathonemus petersii*) were force-choice trained in a two-alternative procedure to discriminate between objects differing in their electrical characteristics. The objects were carbon dipoles in plexiglass tubing (length 2.5 cm, diameter 0.6 cm). Their electrical characteristics could be changed by varying the impedance of an external circuit to which they were connected (Fig. 1). In one (the ‘capacitance dipole’) the resistance was very low ($< 3 \Omega$) and the capacitance variable. In the other (the ‘resistance dipole’) the resistance was variable and the capacitance low (< 50 pF).

Capacitances from several hundred pF (‘lower thresholds’, Fig. 2) to several hundred nF (‘upper thresholds’, Fig. 3) could be discriminated from both insulators and good conductors. In all cases the reward-negative stimulus was the capacitance dipole, which was avoided by all fish spontaneously. Thresholds were defined at 70% correct choices.

The fish were then tested for their ability to discriminate between one object with a given capacitance and another with resistances varying from 3Ω to 200 k Ω . The capacitance dipole continued to be the negative stimulus throughout. All 3 fish avoided it in at least 80% of the trials at each stimulus combination (Fig. 4). This result suggests that *Gnathonemus* perceives the capacitance and the resistance of objects differentially.

The effect of the dipole-objects as well as some natural objects on the local EOD was recorded differentially very close to the fish’s skin (Fig. 5). The amplitude of the local EODs was affected by all types of objects as they approached the skin. However, the waveform was changed only by capacitance dipoles and some natural objects (Figs. 6 and 7). It appears that the fish perceive not only intensity changes in the local EOD but waveform deformations as well and can thus distinguish objects of different complex impedances.

Abbreviations: EOD electric organ discharge; f_{\max} maximal spectral frequency; GP *Gnathonemus petersii*; LFS local filtered signal; PMA probing motor act, S+ positive stimulus, S– negative stimulus

Key words: Weakly electric fish – Electrolocation – Complex impedance – Detection threshold – Object discrimination

Introduction

African freshwater fish of the family Mormyridae emit brief pulses with an electric organ in their caudal peduncle. At each discharge (EOD) an electrical field builds up around the fish’s body and quickly dissipates. The pulses activate electroreceptors situated deep in the skin of mormyrids, enabling the fish to perceive both its own and also the discharges of nearby electric fish. The electroreceptors, distributed unevenly across its body, monitor local potential differences from the inside of the skin to the outside (Bennett 1971). If an object with an electric impedance different from that of the surrounding water comes close, the fish’s electric field is distorted during the approach of the object and the pattern of voltage gradients at the receptors changes. Thus the pulsed signal emitted by the electric organ and filtered by the object is perceived locally by each receptor. The filtered signal at the receptor level will be designated henceforth as the LFS (the local filtered signal). Mormyrids perceive changes in the LFS and thus detect objects in their vicinity, a process called electrolocation (Lissmann and Machin 1958).

Lissmann and Machin (1958) as well as other authors (e.g., Belbenoit 1970; Harder 1972; Heiligenberg 1973) have shown that mormyrids and also other weakly electric fish, can detect and discriminate between a poor conductor (plastic object) and a good conductor (metal).

In many objects, especially living tissues, the impedance is complex, consisting of both resistance and of capacitance components (Schwan 1963; Heiligenberg 1977). Harder et al. (1967) have shown that capacitive and inductive shunts elicited behavioral responses in mormyrids similar to those from purely resistive shunts. From their electrophysiological studies of electrorecep-

tors in gymnotoids, weakly electric fish from South America, Scheich et al. (1973) suggested that electric fish might be able to assess the capacitive and resistive components in the impedances of nearby objects. They proposed that this would be a useful additional way to discriminate objects, especially living organisms. In *Eigenmannia* (Gymnotiformes) they found one type of electroreceptor organ that responded differently to resistive and capacitive shunts of equal impedance. Feng and Bullock (1977) found the same phenomenon in two types of electroreceptors in *Eigenmannia*. Differential responses of mormyrid electroreceptors to different kinds of impedance have yet to be demonstrated.

Objects with a considerable capacitive component have two effects on AC electric signals, such as the discharges of weakly electric fishes: 1) There is a change in the intensity if the impedance of the object differs from that of the surrounding water. The impedance of a capacitive object is frequency-dependent in contrast to that of objects with purely ohmic resistances. Low-frequency components of an EOD are attenuated more strongly than high-frequency components. 2) There is a frequency-dependent phase shift of the signal: frequency components within a certain range, depending on the value of the capacitance, are phase-shifted more strongly than others. Objects with no capacitive components, on the other hand, do not cause any phase shift of the signal.

Both, frequency-dependent attenuation as well as frequency-dependent phase shift, lead to a change in waveform and timing of the LFS at receptors close to the object only. As electric fish have a substantial capacitance in their skin, the LFS seen by the electroreceptors is always distorted, even without any object nearby, compared to the emitted EOD. Capacitive objects cause additional alterations of the LFS whereas resistive objects do not.

Meyer (1982) demonstrated the importance of the frequency content of single EODs during electrolocation. He found that the behavioral response of different mormyrid species to capacitive shunts depended on the spectral composition of their EODs. Species with short, high-frequency discharges still responded with a spontaneous change of their electrolocation behavior to small capacitances, whereas species with long, low-frequency pulses did not. Both groups of fish responded to capacitive shunts of larger values. The response to pure resistive shunts of all values, on the other hand, was similar in all species. This result showed that the spectral composition of the EOD affects the detection of capacitive objects. Whether mormyrids can discriminate between resistive and capacitive impedances remained, however, an open question, although this was suggested by several authors (Scheich et al. 1973; Scheich and Bullock 1974; Feng and Bullock 1977; Heiligenberg 1977; Meyer 1982). Heiligenberg (1977) measured the electrical characteristics of water plants and found capacitances from 37 to 76 nF per 1 cm² leaf area in two plant species. The complex impedance of animal tissues was measured by Schwan (1963) for various tissues and frequencies. A cube of muscle for example, one cm on a side, ranged

from 5 to 90 nF for signals between 100 Hz and 10 kHz. Whole organisms were not measured but capacitive components may be anticipated in them, too.

The present study was designed to show whether electric fish can utilise capacitive and resistive characteristics of objects as distinct from each other during electrolocation. In the first part of this study the range of capacitances which can be discriminated both from insulators and good conductors by the mormyrid *Gnathonemus petersii* is determined. In the second part the question is examined whether fish can discriminate between a capacitance and a resistance of similar impedance. In both cases an operant conditioning technique was employed. In the last part, the LFS waveform and amplitude changes caused by various objects are described. Possible mechanisms for object-discrimination during electrolocation are discussed.

Methods

Animals. Three *Gnathonemus petersii* (GP1-3), obtained commercially from Nigeria, were used in this study. Their standard length was between 8 and 11 cm, hence they were all juveniles. They were housed individually in 100 l-tanks (75 cm · 40 cm · 32 cm) that were also used for training. Fish were subjected to an artificial light/dark cycle of 12:12 h; temperature, 27° ± 1 °C; water conductivity, 50 ± 5 µS/cm (= 20 kΩ · cm).

For analysis, the EOD of each fish was picked up by two carbon electrodes at each end of a ceramic tube in which the fish was hiding. The discharges were A/D-converted at a rate of 10 MHz for waveform analysis or at 156 kHz for spectral frequency analysis.

Experimental setup. The experimental tanks of 100 l (Fig. 1) were divided into two compartments by a dark plastic wall: one of about 60 l (50 cm · 40 cm · 32 cm), the other of about 40 l (25 cm · 40 cm · 32 cm). Between experiments, fish had to stay in their bigger home compartment with the heater and filter equipment. The home compartments were provided with a ceramic tube as a shelter during daytime and non-experimental hours.

The wall separating the two compartments had two gates (4 cm · 4 cm) with their centres separated by 19 cm, 7.5 cm above the aquarium bottom. The gates could be opened and closed by a thin thread from outside the aquarium by sliding their doors.

Just behind each gate, in the smaller compartment of the tank, an electrolocation object was placed (Fig. 1). It consisted of a dipole that was made of small carbon rods and plexiglass tubing, and had the form of an inverted T. The horizontal part of the T was oriented perpendicularly to the dividing wall pointing at the gate. The dipoles had two carbon poles, small cylinders with a height of 7 mm and a diameter of 6 mm, inserted inside the ends of the horizontal part of the tube (separation: 2.5 cm). They were pushed completely inside the plexiglass tube. Thus, the two carbon/water interfaces were also separated by 2.5 cm. Inside the tube, wires connected to each of the two carbon poles went up all the way the vertical part of the plexiglass tubing outside the water. There, the two wires of each dipole could be connected (i.e. short-circuited), or else various electronic elements (like resistors or capacitors) were introduced into the circuit.

In the case of a simple shunt the dipole-object was labelled a 'good conductor'. When the circuit was interrupted the object was called a 'non-conductor', or 'insulator'. With a resistor or capacitor inside the circuit, specific electrical features could be added to a dipole-object and it was labelled the 'resistance' or 'capacitance' dipole.

There is, of course, a difference between a real conducting object a fish might encounter in its natural habitat and our shunted

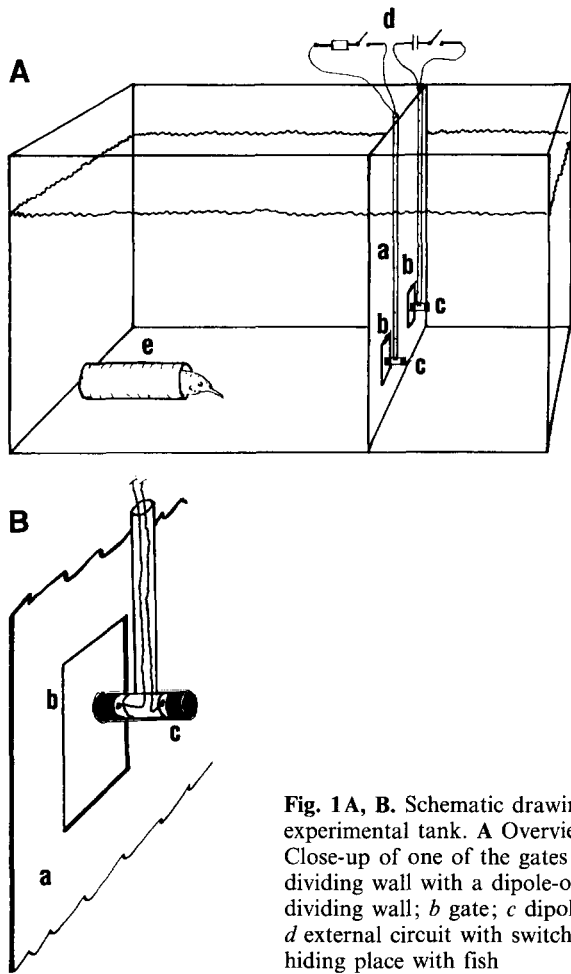


Fig. 1A, B. Schematic drawing of the experimental tank. **A** Overview. **B** Close-up of one of the gates in the dividing wall with a dipole-object. *a* dividing wall; *b* gate; *c* dipole-object; *d* external circuit with switches; *e* hiding place with fish

dipole-object. In the latter case, electric current enters and leaves the dipole-object at its two ends only, and not in-between where the plexiglass tubing provided insulation. Also, a true insulator would not have a small surface of conducting carbon at each end. In spite of these differences to objects of more homogeneous electrical properties, I regard our dipole-objects as an acceptable first approximation of real objects because both the distortions of the electric field around the fish as well as the waveform and amplitude changes of the LFS caused by the dipole-objects resembled those caused by natural objects (see Results).

The dipole-objects had a small capacitance even when no capacitor was present in the circuit. This was in the range from 40 to 50 pF and was mainly caused by wire capacitances. Polarization of the carbon electrodes, measured with square-pulses, was negligible up to a square-pulse duration of 250 ms. No differential attenuation or phase shifts of frequencies, measured with single-cycle sinewaves, were found between 4 Hz and 50 kHz.

Training procedure. Fish were trained in a two-alternative forced-choice procedure to discriminate between two dipole-objects differing only in their electrical features. Fish had to choose the object with electrical features previously defined as 'correct' (S+), by swimming through the gate opening to that object. A correct choice was rewarded by one or two chironomid larvae; fish then had to move back to their starting position. If the fish's choice was wrong it was chased back immediately without food reward. Presentation of S+ changed from left to right in a pseudorandom schedule (Gellermann 1933). Fish made 30 to 50 choices with constant stimulus parameters in one session per day, 5 days a week.

First, fish were taught to swim through the gates in order to obtain food. Both gates were left open with the wires of both

dipole-objects disconnected. Food was placed on the bottom of the smaller compartment of the experimental tank. Fish had to swim through the gates past the objects in order to find food. They usually did so within several minutes after the gates were opened, even at the first trial.

As a next step, one of the dipole-objects was given capacitive features by introducing a capacitance of 10 nF in the circuit. This object was defined as S- while the other one, which was left a 'non-conductor', was called S+. Even at the first trial all 3 fish spontaneously avoided the gate with the capacitance dipole and rather swam through the other one with the insulator mounted behind it.

Threshold determination. To establish the 'lower' detection threshold for capacitors (as distinct from insulators) a stimulus combination described as above was used: S+ was a non-conductor kept unchanged throughout the experiment, S- was a capacitance dipole. First S- had a capacitance of 10 nF that was reduced in steps during the course of the experiment, until the fish could no longer discriminate between S+ and S-. 70% correct choices was defined as the 'lower threshold'. Its value was interpolated from the psychometric function.

To find the 'upper threshold' for capacitors (as distinct from a short) the following procedure was used: S- again was the capacitance dipole while S+ was a good conductor (resistance: <3 Ohm), i.e., the wires of the two poles of a dipole-object were connected (pure short). The fish had to choose the gate with the conductor behind it, and should avoid the capacitance dipole. In the course of the experiment S+ was kept constant, while the capacitive value of S- was increased in steps from 10 nF to larger and larger values until the fish could no longer discriminate between S+ and S-. Again, 70% correct choices was defined as the threshold.

Discrimination between resistors and capacitors. In this set of experiments the fish had to discriminate between a capacitance dipole (S-) and a resistance dipole (S+). The fish had to swim through the gate with the resistance dipole. During one series of experiments the value of the capacitance of S- was kept constant, while the value of S+ decreased from 200 kΩ down to <3 Ω in at least 12 steps. For each stimulus combination the fish made at least 50 decisions. Each fish had to go through two series with a fixed value of S- at 1 nF or 10 nF (for *G. petersii* 3: 54 nF). Some additional experimental sessions were conducted around the resistance of S+ that was equal to the calculated impedance of the capacitance dipole at the frequency of peak power of the fish's EOD.

Control experiments. Several control experiments aimed at finding out whether the fish used other cues than the electrical features of the object, as might be detected by active electrolocation.

1) **Silenced fish:** After going through the complete training and testing procedure the electric organ of one fish (GP2) was surgically silenced. The fish was anaesthetised with MS222 (Sandoz) and its spinal cord cut just anterior to its electric organ located in the caudal peduncle. After 3 weeks of recovery the discrimination performance of the fish was tested again. In addition, a naive fish (GP4) was silenced in the same way; then training for discrimination between a capacitance dipole and an insulator was begun.

2) **Double blind test:** Several sessions for each fish were conducted as double blind tests. In addition to the experimenter who usually conducted the experiments, another person took part in the double blind tests. Before each trial, this person determined the location of S+ and S- in such a way that the experimenter did not know which one of the two gates was correct. Therefore, the experimenter could not guide the fish in some unconscious way to the correct object. The result of each double blind test was compared with the results of normal sessions with the same stimulus combination.

3) **Condenser-coupling:** When an object with no capacitive element in the circuit was used as a stimulus, DC currents could

not be excluded as an additional cue for discrimination. To prevent the fish from using such cues, a very big capacitor of $5 \mu\text{F}$ was placed in the circuit in about half of the trials. The results with and without condenser coupling were compared.

Electric field and LFS measurements. To measure the equipotential lines of the electric field around the fish and the distortions caused by an object, the following measurements were performed: In the middle of a $80 \text{ cm} \cdot 50 \text{ cm} \cdot 40 \text{ cm}$ tank a *G. petersii* was fixed in a thin sock of synthetic fibre. Perpendicular to the fish's skin a dipole-object was placed at a distance of 1.5 cm. The recording electrode was a silver wire, insulated except for the tip with a glass capillary tube. The tip was a small silver sphere with a diameter of about 1 mm. In order to reduce electrode polarization the silver tip was electrolytically covered with AgCl immediately before each measurement. Equipotential lines (peak-to-peak amplitude of the fish's discharge) were measured with respect to a reference electrode placed as far away as possible at the zero equipotential plane of the fish's field. The measurement electrode was fixed to an x-y carriage system above the fish.

The waveform of the LFS close to the electroreceptors was measured using a bipolar recording electrode, consisting of two thin carbon rods of 0.5 mm diameter that were insulated except for the tip, about 1 mm apart. An electrolocation object (a dipole-object as used in the behavioral experiments, or a natural object) was fixed at a distance of about 0.5 cm from the fish's skin dorsal of the fish's lateral line just behind the pectoral fins. At this part of the skin many electroreceptor organs could be identified visually. Between the object and the fish's skin the bipolar electrode was oriented perpendicularly to the equipotential lines, at a distance of 1 mm from the fish's skin.

For comparison, the fish's EOD was simultaneously recorded head-to-tail by a pair of carbon electrodes 10 cm in front of the nose and 10 cm behind the tail. The negative going main transient of the discharge (Fig. 5) pre-triggered the sweep of a digital oscilloscope (sampling rate = 10 MHz). On a second channel, the LFS, as recorded between object and skin, was displayed. Thus, the waveforms, amplitudes, and timing of the two signals that were simultaneously sampled could be compared. Additionally, both signals were A/D-converted at a rate of 156 kHz (8 bit) for later spectral analysis.

Results

Threshold measurements

All fish used in this study avoided the capacitance dipole spontaneously; thus no further training was necessary to start with the determination of the 'lower thresholds' (of a sufficiently small capacitor as discriminated from a circuit break). For 3 *G. petersii* the lower thresholds were interpolated from the psychometric functions (Fig. 2), which had a similar shape for all 3 fish. With capacitors bigger than about 1 nF the performance of the fish was around 90% correct choices. When smaller capacities were used the fish's performance deteriorated rapidly until it reached chance level at values between 250 and 400 pF. The lower thresholds for the three fish were 337, 286, and 486 pF.

The determination of the 'upper threshold' (large capacitor versus short) was more difficult because all fish tended to avoid both a good conductor (S+) and a capacitance dipole (S-). Training of about one week was necessary until the fish discriminated between a S- of 10 nF and a S+ that was a short ($< 3 \Omega$). With this

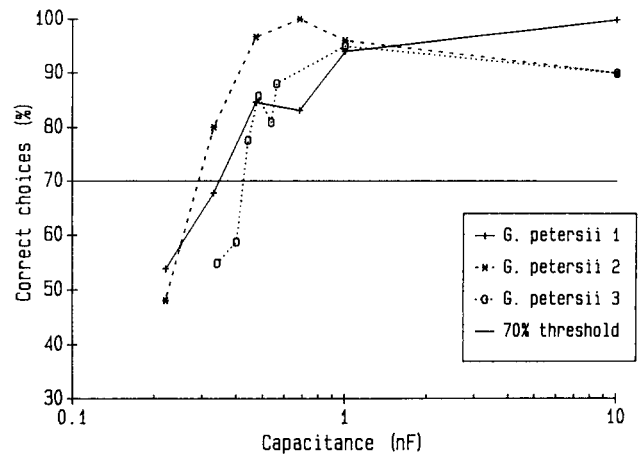


Fig. 2. Psychometric functions of three *Gnathonemus petersii* for determination of the 'lower detection thresholds' for capacitors. Percent correct choices plotted versus the capacitance of S-. S+ was a non-conducting dipole-object. Threshold is defined at 70% correct choices. Each point represents at least 40 decisions by a fish

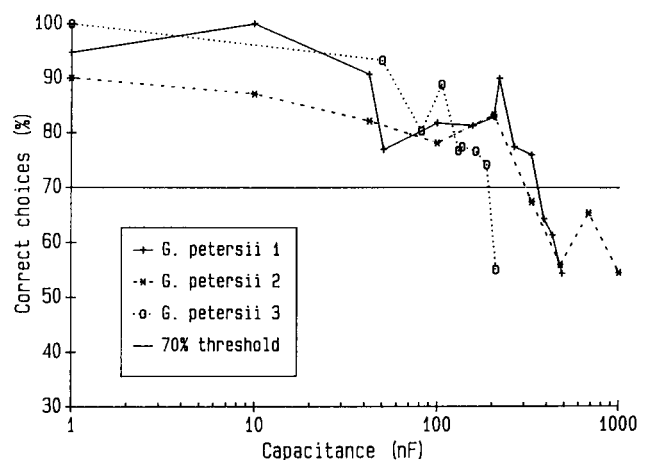


Fig. 3. Psychometric functions of GP1-3 for determination of the 'upper detection thresholds'. Abscissa capacitance of S-. S+ was a good conductor (shunted dipole-object) with a resistance of only 3Ω . Each point represents at least 40 decisions

association formed, the psychometric functions were measured without any problem (Fig. 3). Upper thresholds, interpolated from the psychometric functions, were 354, 308 and 191 nF for the 3 fish.

Discrimination between resistors and capacitors

For each fish two series of experiments were performed. The reward-negative stimulus was a constant capacitance during each series (for GP1 and GP2: 1 nF and 10 nF, for GP3: 1 nF and 53 nF). In each series the ohmic resistance of S+ decreased from very high (200 k Ω) to very low values ($< 3 \Omega$). All 3 fish showed the same results: they discriminated between the capacitance dipole and each resistance dipole used. Their performances were between 80% and 100% correct choices for each stimulus combination (Fig. 4A, B).

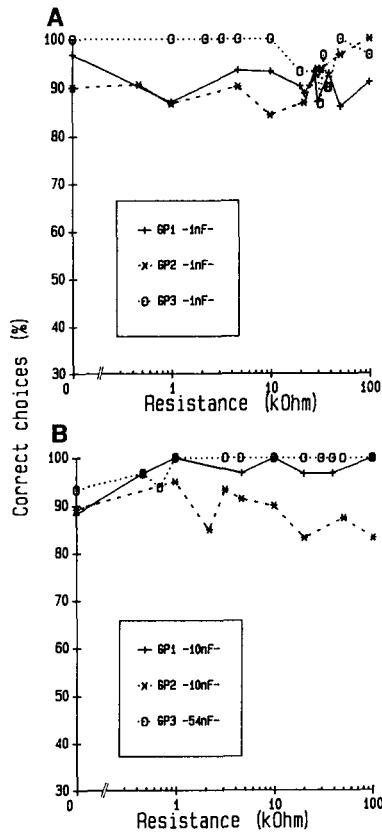


Fig. 4A, B. Performance of 3 fish (GP1–3) discriminating between a capacitance dipole-object (S^-) and a resistance dipole-object (S^+). For each curve the capacitance of S^- was held constant at 1 nF (A), 10 nF, or 54 nF (B). Abscissa gives values of S^+ . Each point represents at least 40 decisions of one fish

Behavior during discrimination

During the discrimination task the fish usually swam close to each of the two dipole-objects before choosing one. Close to an object they displayed some of the so-called 'probing motor acts' (PMA, Toerring and Belbenoit 1979). The most frequently shown PMAs were 'radial va-et-viens', 'chin probing' and 'stationary probing'. But also other types of PMAs mentioned by Toerring and Belbenoit (1979) were observed when the fish were exploring the electrical characteristics of the objects (except 'lateral probing' which was impossible with the set-up used).

At the beginning of the training many PMAs were observed and the fish repeatedly swam back and forth between the two objects. During this stage especially 'radial va-et-viens' were shown, i.e. the tail was directed towards the object after a 180° turn and the fish displayed several lateral tail strokes to the left and right while slowly approaching the object backwards, quite often swimming past the correct dipole-object. When the fish were more familiar with the training procedure, fewer 'va-et-viens' PMAs were performed, but instead 'chin probing' (fish approach the object and almost touch it with their chin) or 'stationary probing' (fish approach the object rapidly and suddenly stop when

the head is only a few centimetres away) were observed. Most of the time the fish now swam head-first through the gates. When during threshold determination the task became more difficult fish tended to display more 'radial va-et-viens' again, and more often swam backwards through the gates.

Control experiments

1) *Silenced fish*: GP2 was silenced after the completion of the discrimination tests, and GP4 was a naive fish. Neither fish was able to discriminate between two objects with different electrical characteristics after surgery. The

Table 1. Percent correct choices during double blind tests (A) and experiments with condenser coupling (B) compared with normal experiments. C: results of tests with silenced fish

A			
	GP1	GP2	GP3
	$S^- = 1 \text{ nF}$	$S^- = 10 \text{ nF}$	$S^- = 54 \text{ nF}$
	$S^+ = 22.1 \text{ k}\Omega$	$S^+ = 4.7 \text{ k}\Omega$	$S^+ = 470 \Omega$
Double blind test	90.0% $n = 30$	92.5% $n = 40$	95.1% $n = 61$
Normal test	88.9% $n = 27$	95.0% $n = 40$	96.7% $n = 60$
B			
	GP1	GP2	GP3
	$S^- = 1 \text{ nF}$	$S^- = 10 \text{ nF}$	$S^- = 54 \text{ nF}$
	$S^+ = 4.7 \text{ k}\Omega$	$S^+ = 3.2 \text{ k}\Omega$	$S^+ = \text{resistors between } 200 \text{ and } 0 \text{ k}\Omega$
Condenser-Coupling (5 μF)	88.9% $n = 36$	90.0% $n = 40$	98.5% $n = 195$
No Condenser-Coupling	92.3% $n = 26$	100% $n = 20$	98.9% $n = 197$
C			
	GP1	GP2	GP3
	$S^- = 1 \text{ nF}$	$S^- = 10 \text{ nF}$	$S^- = 100 \text{ nF}$
	$S^+ = \text{isolator}$	$S^+ = \text{isolator}$	$S^+ = \text{isolator}$
Silenced fish GP2	51.7% $n = 120$	53.5% $n = 86$	47.8% $n = 92$
Silenced fish GP4	46.7% $n = 90$	49.5% $n = 111$	50.5% $n = 103$

GP1–GP4, *G. petersii* Nos. 1–4; S^+ , positive stimulus; S^- , negative stimulus. Note that there is no significant difference between the control tests and the normal experiments in A and B. Silenced fish never learned the discrimination task; their performance always remained around 50% correct choices, or chance level

fish were trained to discriminate between a capacitance dipole (1, 10, or 100 nF) and a non-conductor, but even after 4 weeks of intense training their performance remained around chance level (50% correct; Table 1). This supports the hypothesis that the fish cannot solve the discrimination tasks without their EOD. Fish GP2 obviously had not relied on passive electrical cues during its original discrimination, but mainly on its own electric organ discharges.

2) *Double blind test*: During all double blind tests the performance of the fish closely resembled that of a normal test (Table 1). This shows that the experimenter did not unconsciously guide the fish to the correct gates.

3) *Condenser coupling*: The introduction of a big capacitor (5 μ F) in the circuit did not alter the performance of the fish at any stimulus combination tested (Table 1). Fish GP3 performed correctly in a whole series of discriminations between resistance dipoles and a capacitance dipole with and without condenser-coupling. It achieved almost exactly the same results for each stimulus combination whether the additional 5 μ F-capacity was used or not. This shows that there were no DC-currents developing in the circuits of the objects which could have served as additional cues for discrimination; or if there were, they were not used by the fish.

Electric field and LFS measurements

The electrolocation objects used in this study distorted the electric field of *G. petersii* in a similar way as reported for objects with impedances different from the surrounding water (e.g., Bastian 1986; Heiligenberg 1973). With the wires of an dipole-object connected (that is a short) the object resembled a good conductor causing a convergence of the equipotential lines upon it. With the wires disconnected the object electrically resembled a plastic object with diverging equipotential lines.

The LFSs recorded without any object present were very similar to each other at different locations along the body of the fish. They also resembled closely the EOD recorded head-to-tail both in waveform and spectral composition (Figs. 5, 6A, 7).

The LFS changed when an object was present. Its waveform and spectral composition were affected differently by the resistance and capacitance dipole (Fig. 5). The capacitance dipole differentially attenuated and phase-shifted certain spectral components of the fish pulse, thus causing a change of the LFS waveform. The LFS changed in several ways (Fig. 5): 1) A second head-positive phase of weaker amplitude developed, making the originally biphasic signal triphasic. 2) The duration of the P- and N-phase decreased. 3) The phase of the zero-crossing of the negative-going main transient was advanced. 4) The peak amplitudes of power spectra of single LFSs shifted to higher frequencies. 5) The amplitude ratio of the two main phases decreased to lower values (P/N-ratio).

A resistance dipole approaching the fish only altered the amplitude of the LFS, but left the waveform, timing, and amplitude spectrum almost unchanged (Fig. 5); that is the LFS resembled the LFS without any object and the head-to-tail EOD (Fig. 5).

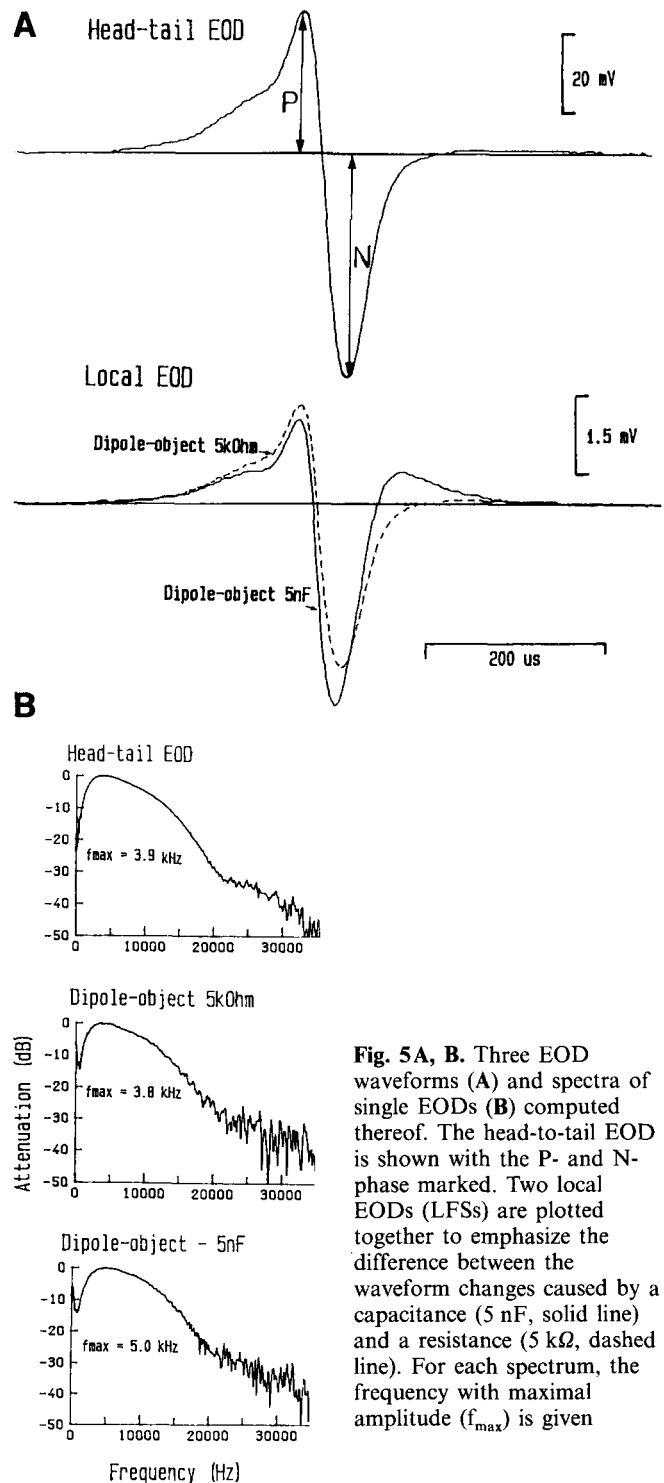


Fig. 5A, B. Three EOD waveforms (A) and spectra of single EODs (B) computed thereof. The head-to-tail EOD is shown with the P- and N-phase marked. Two local EODs (LFSs) are plotted together to emphasize the difference between the waveform changes caused by a capacitance (5 nF, solid line) and a resistance (5 k Ω , dashed line). For each spectrum, the frequency with maximal amplitude (f_{max}) is given

Figure 6A, B summarizes the effects of dipole-objects with different capacitors or resistors on the LFS. For demonstrating a waveform change caused by a capacitance dipole, I chose the P/N-ratio. It is the easiest and most reliable parameter to measure and reflects the waveform changes well. However, all of the other parameters mentioned above would lead to the same conclusions.

With the impedance increasing (increasing resistance or decreasing capacitance) the peak-to-peak amplitude of the LFS decreased (Fig. 6A, B). The P/N-ratio, as

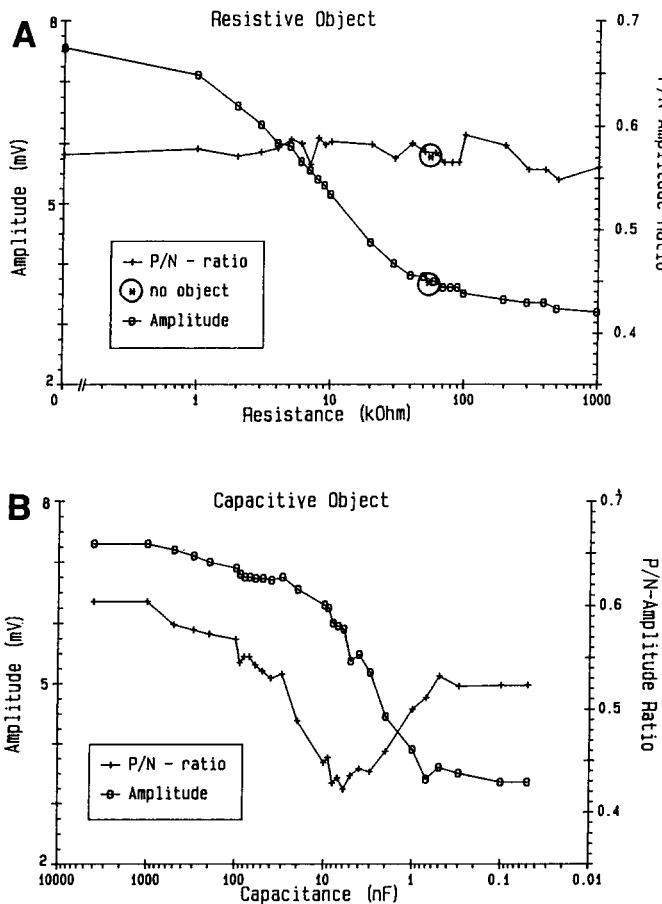


Fig. 6 A, B. LFS characteristics with a resistive (A) or a capacitive dipole-object (B) present. Peak-to-peak amplitude as well as P/N-amplitude ratio of LFS plotted versus resistance or capacitance of the dipole-object. In A, the results obtained without any object present (no object) are added (drawn at a resistance of 50 k Ω , which is approximately the resistance of the water-mass with the same volume as a dipole-object)

measure of waveform change, remained almost unchanged when the resistance dipole was used (Fig. 6 A). With the capacitance dipole this was not the case: The P/N-ratio decreased when capacitors between several hundred nF and several hundred pF were introduced in the external circuit of the capacitance dipole (Fig. 6 B).

In Fig. 7 the P/N-amplitude-ratio is plotted against the peak-to-peak amplitude of the LFS for the resistance and capacitance dipoles and for some natural objects. Within a certain range of amplitudes the capacitance dipole altered the waveform of the LFS. The resistance dipole, on the other hand, never caused any waveform deformations.

In Fig. 7, the results obtained with real objects are also plotted. Organic objects (plants and fishes) gave values which fall in between the two curves for the capacitive and resistive dipole-objects. This means that living tissues altered the waveform of the LFS (low P/N-ratio) and also changed its amplitude. The inorganic objects used (stones and metal rod) only slightly deformed the waveform of the LFS but altered the amplitude considerably. Their impedance was mainly composed of ohmic resistances, different from the surrounding water.

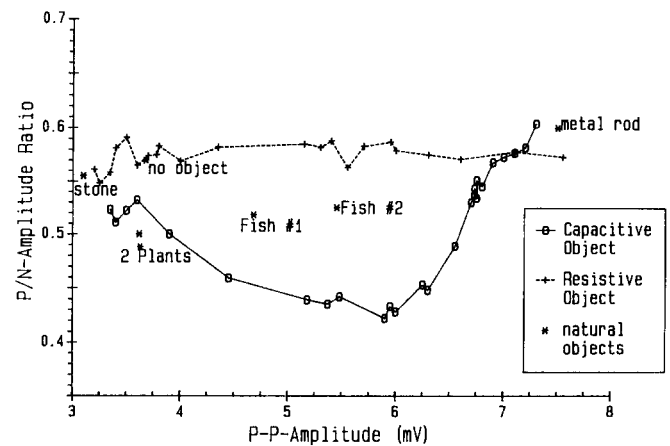


Fig. 7. P/N-amplitude ratio plotted versus the peak-to-peak amplitude of the LFS with either a capacitive or resistive dipole-object (data from Fig. 6) or some natural object present

Discussion

Previous studies have shown that electric fish respond spontaneously to capacitive shunts in their vicinity (Harder et al. 1967; Meyer 1982). Because capacitances have an impedance for alternating currents, the perception of this stimulus could be based on the same sensory mechanisms as that for resistive shunts: the receptors near the object detect a sudden change of peak intensity (ΔU) of the LFS (Heiligenberg 1975). Fish with high-frequency signals using this mechanism should detect smaller capacitances than fish emitting long, low-frequency signals (Meyer 1982) because the impedance of capacitances is lower for signals with higher frequencies ($Z = 1/(2\pi \cdot f \cdot C)$). Further, should the fish merely detect an amplitude change of the LFS (with one set of equally tuned receptors) they would not be able to discriminate between a capacitive and a resistive object causing the same change in ΔU . This study demonstrates that *G. petersii* can discriminate resistive from capacitive shunts, a capability which calls for an alternative explanation of the sensory mechanisms underlying the detection of capacitances versus resistances.

Threshold measurements

In the first part of this investigation the range of capacitances was determined that *G. petersii* discriminated both from a poor conductor ('lower threshold') and a very good conductor ('upper threshold'). If the capacitance shunting the dipole-object (width = 2.5 cm, diameter = 0.6 cm) was smaller than 300–400 pF (equivalent to a dielectric constant ϵ of about 480–650), its impedance became so high that the fish confused it with an isolator. If the capacitance used was greater than 200–400 nF (equivalent to a dielectric constant ϵ of $325 \cdot 10^3$ – $650 \cdot 10^3$) fish no longer were able to discriminate the object from a very good conductor. ϵ is the dielectric constant that would be needed to have the given capacitive values of a capacitor, given the area and separation of the two carbon electrodes of the 'object'.

These threshold values set a frame of interesting capacitive values of medium sized objects for the fish. As

the effect on the LFS varies with the size of the object (bigger objects cause stronger changes in ΔU ; Heiligenberg 1975) one would, within limits, expect somewhat different threshold values for different object sizes. On the other hand, the fish in our setup could freely choose their position and distance from the object for optimal detection. We therefore propose a range of detectable capacitances from several hundred pF (ϵ around 500) to several hundred nF (ϵ around $500 \cdot 10^3$) in *G. petersii* for objects in the cm-range.

Gnathonemus petersii should be able to detect the capacitances of natural objects like those of plants and animals, because they are inside the detectable range. This is shown by our LFS-measurements and also by previous studies. Heiligenberg (1973) measured the capacitances of water plants and got values of 37–76 nF per cm^2 leaf area. Schwan (1963) tested various animal tissues. In muscle tissue, for example, he measured 10–100 nF per cm^3 cube of tissue, equivalent to an ϵ between $50 \cdot 10^3$ and $1000 \cdot 10^3$.

LFS measurements

The LFS measurements of this study revealed that objects with capacitive impedances altered the waveform as well as other parameters of the LFS at the fish's skin (Figs. 5 and 6B). The range of capacitances (from several hundred nF to several hundred pF, as taken from Fig. 6B) that caused such changes approximately matches the range of capacitances that *G. petersii* discriminated from insulators and good conductors (Figs. 2, 3). It appears that the fish of this study used some of the same parameters I measured during the LFS measurements (there were 5 effects; see last section of Results).

A bipolar recording technique similar to the one of this study has been used to measure the local EODs without any object present in the gymnotoid pulse species *Hypopomus* (Bastian 1977) and *Gymnotus carapo* (Watson and Bastian 1979). In both species the shape of the LFS varied at different locations along the body of the fish. This was not the case in the *G. petersii* of this study. The LFS at any location along the body resembled the head-to-tail EOD both in waveform and spectral composition (Fig. 5). It is important for successful LFS measurements to orient the recording electrodes perpendicular to the skin at a location where the equipotential lines run parallel to the surface. As the body of *G. petersii* is laterally flattened, and since I determined the electric field geometry around the fish before the LFS measurement, this was not too difficult to achieve. Therefore, I am confident that I correctly measured the perpendicular potential gradient external to the receptor pores, which is the stimulus for the electroreceptors. Also the fact that the same range of capacitances that yielded good behavioral discrimination also caused significant alterations in the LFS waveform, suggests that the LFS reflect the local stimulus situation at the receptor organs.

I also determined the effect of natural objects on the LFS to see whether the dipole-object can serve as

a first approximation for real objects (Fig. 7). The organic objects used, two live fish (*Xiphophorus* sp., sword-tail) and 2 species of water plants (*Vallisneria* sp. and *Cryptocoryne* sp.), altered the amplitude and waveform of the LFS. The waveform changes at a given LFS amplitude, measured as changes of the P/N-ratio, differed from those caused by the capacitance dipole. They were stronger than those caused by the resistance dipole and by an inorganic object (stone or metal rod), both of which altered the LFS waveform only in a minor way. The organic objects had complex impedances with both capacitive and resistive components and so caused waveform and amplitude changes different both from a purely capacitive and a purely resistive dipole-object (Fig. 7).

Discrimination between resistances and capacitances

G. petersii was able to discriminate between a capacitance dipole and any resistance dipole, no matter which resistive value was used (Fig. 4). In each experimental series there must have been one combination of resistors and capacitors which caused a similar ΔU at the electroreceptor (Fig. 6). As the fish could discriminate between the two even if their impedance was equal, they perceived capacitances differently from resistances. Therefore, it is difficult to conceive that the fish measured the amplitude change of the LFS only. They must have used an additional cue for discrimination such as waveform-, spectral, or timing changes of the LFS caused by the presence of a capacitance but not a resistance dipole-object.

EODs of most mormyrids are brief, and their spectral composition is broad. The *G. petersii* used in this study emitted biphasic EODs of about 250 μs and a peak frequency, constant for each fish, between 3.9 and 6.7 kHz (Fig. 5). The spectral bandwidths of single pulses, measured 10 dB below peak intensity, were around 15 kHz for all 3 fish. This shows that the EODs contained a broad band of frequencies of considerable energy.

As a capacitive object differentially attenuates and phase-shifts the spectral components of the EOD, the LFS waveform close to the object is distorted (Fig. 5). Electroreceptors further away do not see any change of LFS waveform and so could be used as a synchronous reference. A purely resistive object, on the other hand, does not differentially alter the spectral components of the EOD, but only changes its amplitude (Figs. 5, 6, 7). If the electroreceptors of *G. petersii* were able to encode the changes of the LFS specific for capacitive as opposed to resistive objects, the fish had a means to discriminate between the two.

The receptor organs for electrolocation in mormyrids are the mormyromasts. The other type of high-frequency electroreceptors, the Knollenorgane, are not involved in active electrolocation because their input to the ELL (electrosensory lateral line lobe), the first brain structure receiving input from the electroreceptive periphery, is blocked by an inhibitory corollary discharge during each EOD (Bell and Grant 1989). Even though the ampullary

receptor organs are stimulated by an EOD, they do not play a major role during electrolocation (Bell and Russell 1978, but see Bastian 1987). The control experiments with silenced fish also indicate that passive, low-frequency detection by ampullary receptors was not involved.

The mormyromast receptor organs possess two types of sensory cells with afferent fibres projecting to two different somatotopic sensory maps in the ELL (Bell et al. 1989). Several physiological differences between these two fibre types concern their amplitude and frequency sensitivity (Bell 1990). One type of fibre (probably innervating the A cells) has a higher threshold and a smaller maximum spike number than the other fibre (probably arising from the B sensory cells). The 'A fibres' are tuned to slightly higher frequencies than the 'B fibres'. The tuning of both types of afferents is not very sharp, however, but shows broad regions of greater sensitivity. Bell (1990) speculates about the separate roles of the two sensory cells and fibre types but emphasizes that both types are intensity coders and not suitable for exact time-measurements (like the Knollenorgane).

How then can mormyrids discriminate between capacitive and resistive shunts if their electroreceptors for electrolocation are merely intensity coders? The LFS measurements of this study showed that it is not sufficient to measure the intensity of the local EOD to achieve that goal, because capacitances as well as resistances cause intensity changes of the same range (Figs. 6 and 7). For discrimination it is necessary to measure at least one additional parameter, like waveform cues (for example P/N-ratio), spectral cues (for example the maximal frequency f_{\max}), or timing cues (for example timing of zero crossings). One of these, together with intensity, would help to solve discrimination problems such as those *G. petersii* was able to solve in this study.

Possibly the additional parameters used were frequency cues. As mentioned above (Bell 1990), the two types of sensory cells of mormyromast organs have slightly different spectral sensitivity peaks, even though both are broadly tuned. With two types of differently tuned receptors it would theoretically be possible to detect the shift of the spectra of single EODs to higher frequencies when a capacitive object comes close (Fig. 5). It is also possible that receptors in different areas of the body surface are tuned differently. Since electric fish tend to 'scan' objects, they could compare inputs from receptors in different locations. Whether the mormyromasts encode for the frequency shift or some other waveform parameters, remains to be shown by future investigations.

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