

Spatial Aspects of the Electric Fields Generated by Weakly Electric Fish

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Summary. 1. The electric fields of four species of wave type, gymnotid fishes were measured and mapped using a technique that allowed accurate assessment of small electric fields, free of unknown field compression and distortion artifacts.

2. Dipole moment values were calculated for each fish's electric field from measurements made at a sufficient distance (Table 1). A dipole moment is an absolute evaluation of the electric fish's field strength that can be used for quantitative, intraspecific and interspecific comparisons.

3. The electric fish, as a field source, represents a distributed rostral pole and a point-like caudal pole (Fig. 2). Deviations of a fish's electric field from that of a dipole field increase with fish size, decreasing water resistivity, and decreasing distance from the fish.

4. Apterodontid species maintain a constant current electric organ output (dropping less than 5%) in water of resistivity up to 15 kOhm·cm, whereas rhamphichthyid species maintain a constant current output only in water up to 10 kOhm·cm (Fig. 6). Within each family, the larger fish maintained their current output level in higher water resistivities than did smaller fish.

5. Electrocommunication distances for the individual fishes are predicted based upon their measured electric field magnitudes and the known electrosensitivities of these species (Table 2); consequences of the geometry of the fishes' electric fields on object detection and object resolution are discussed.

Introduction

Since Lissmann's first behavioral demonstration of the electric sense in a weakly electric fish (Lissmann, 1958), considerable evidence has accumulated for the functioning of the electrosensory system of electric fish in object detection and intraspecific communication (Lissmann and Machin, 1958; Black-Cleworth, 1970; Kastoun, 1971; Hopkins, 1972, 1974; Heiligenberg, 1973; Kalmijn, 1974). Spatial aspects of the electric fields generated by weakly electric fish are extremely important with regard to these functions. When considered together with existing behavioral and neurophysiological data, electric field measurements provide estimates of electrocommunication and object detection ranges, and explanations for certain observed behavioral patterns that are peculiar to these fish.

Electric field measurements from several species of electric fish have been made by numerous authors (Lissmann, 1958; Bullock and Chichibu, 1965; Granath *et al.*, 1968; Heiligenberg, 1973; Scheich and Bullock, 1974), but these studies were of limited scope and suffered greatly from electric field distortions imposed by the measuring techniques and the size of the measurement tanks

used. Consequently, quantitative data describing these fields are either unreliable or excessively restrictive.

In this study a new approach suggested by A. J. Kalmijn was used for accurately measuring and expressing dipole-like electric fields in a volume conductor, which allows a quantitative evaluation of the field source strength in terms of a simple dipole moment. At a sufficient distance, the field emanating from a current source and sink will appear as a dipole field regardless of the geometry of the field source; the field potential will fall off with the square of the distance and the field potential gradient will fall off with the cube of the distance. Measurements made at a sufficient distance yield a constant, dipole moment value which is independent of the measurement site. This value, when calculated for a fish, completely characterizes its electric field magnitude and geometry in this range, and provides an absolute measure of its field strength that can be used for intraspecific and interspecific comparisons.

The fields of four species of wave type gymnotid fish were measured and mapped in water of different resistivities: two species from the family Apterontidae with ectodermally derived electric organs, presumably from modified axonal processes (Couceiro and de Almeida, 1961); and two species from the family Rhamphichthyidae with mesodermally derived electric organs, from specialized muscle tissue (Bennett, 1971). All of these species are wave type electric fish; the discharge of the electric organ is long relative to its discharge interval (Scheich and Bullock, 1974). Current flows between the head and tail ends of the organ, periodically alternating in direction with a frequency that is characteristic of the species. The behavioral and physiological implications of the electric field characteristics to these electric fishes are discussed with respect to electrocommunication and object detection.

Methods and Materials

The electric fields of seven gymnotid fish were measured and mapped in the horizontal plane. They represented four species from two families: the rhamphichthyids *Eigenmannia virescens* (8.5 cm and 18.6 cm) and *Sternopygus macrurus* (19.2 cm), and the apteronotids *Apteronotus albifrons* (6.0 cm, 10 cm, and 22.0 cm) and *Adontosternarchus sachsii* (11.7 cm). The fish were maintained in individual tanks and were fed brine shrimp daily. All of the fish appeared healthy and showed good appetites for the duration of the experiments. The fishes were acclimated for two days to the water resistivities and temperature conditions under which their fields were to be mapped, except for the experiments measuring the effects of water resistivity on the fishes' voltage output that are described later. In all cases water resistivity was controlled using a salt mixture of CaSO_4 , MgSO_4 and KCl and in a weight ratio of 60:5:4 (recipe from W. Heiligenberg).

The fishes' electric fields were measured in "half-space" (ref. Appendix 1). Each fish was suspended at the surface of the test tank so that the top of its head and tail were submerged 1–5 mm. The voltages and voltage gradients were measured with electrodes located 3–5 mm below the water surface. The advantages of this procedure are that: (1) the electrode position relative to the fish can be easily recorded; (2) the depth of the tank does not have to be excessive in order to reduce interface field distortions to an acceptable level. The disadvantages of such a procedure include possible measurement errors due to field compression and the required extrapolation from "half-space" to "full space". This extrapolation assumes that the effective volume conductor resistance experienced by a fish when at the surface, is twice that which he would experience in mid-water (full space).

Field distortions imposed by the tank sides and the measurement procedure on a dipole of known magnitude were less than 5% at the water surface within a radius of 40 cm from the center of the tank.

Each fish was placed in the center of a round 300 cm diameter \times 90 cm deep test tank in a sock made of light nylon fish netting. The fish was sewn into the sock to prevent his movement, and the sock was stretched between two rods set 100 cm apart. A very thin ring of plexiglass was sewn into the sock at the head end to serve as a collar to allow for gill movement.

Two small frequency reference electrodes were placed at the head and tail of the fish. This frequency reference signal was amplified differentially with a nearby Grass P15 preamplifier (filter settings 1 Hz; 10 KHz), the output of which was FM transmitted to a distant E and M Instrument Company model FM 1100-7 receiver (Fig. 1A). The large volume of the measurement tank necessitated FM transmission of the signal to eliminate system ground loops. This signal was displayed on an HP 132 oscilloscope and then fed from the vertical output amplifiers of the oscilloscope into the "reference" terminal of a PAR Model HR-8 lock-in amplifier.

The recording electrodes were Ag/AgCl wire, insulated to 1 mm from the tip with glass capillary tubes. Electrode impedance was 125 kOhms at 1 KHz; no electrode polarization could be measured down to 5 Hz.

Field potentials (V) were measured with respect to a reference electrode placed 150 cm away at the zero equipotential plane of the fish's field. Voltage gradient (E) measurements were made with the electrodes spaced 1 cm or 5 cm apart, mounted on a movable turret (Fig. 1B). Amplification and transmission of this signal was identical to that of the reference signal, except that it was fed into the "signal" terminal of the lock-in amplifiers which measured and displayed the signal's root mean square (rms) value. The phase and frequency settings of the HR-8 were carefully adjusted for a maximal reading at each electrode position; the use of the lock-in amplifier enabled accurate measurements of small signals. The entire circuit was calibrated daily with a 1 mV sine wave placed at the input to the P15 preamplifiers.

Measurement electrodes were fixed to an x-y carriage system, which moved above the fish. A $1.5 \times 100 \times 100$ cm plexiglass plate was supported over the carriage system, functioning as a drawing surface. A prepared acetate grid consisting of a half circle of thirteen rays 15° apart (Fig. 1C) was placed on top of the drawing plate. Marks were placed at 5 cm intervals along each ray out to 40 cm, the maximum distance measured. The map was oriented so that the fish's head and tail lay along the 0° and 180° rays respectively, and so that the ray origins corresponded to the intersection of the fish's body axis and the zero potential plane of its field. Thus it was the left half of each fish's field that was mapped. The field potential was measured at each 5 cm mark; voltage gradient measurements were made on the 0° , 90° and 180° rays only. The field gradient vector direction was ascertained by first determining the zero gradient direction, and measuring 90° from this direction. The gradient vector magnitude was found by rotating the electrode turret until a maximum value was recorded. Field potential and voltage gradient data were recorded directly on the map for later tabulation. The distance along the fish between points of maximal potential (s) was also recorded.

A root mean square voltage (V_{rms}) to a peak to peak voltage (V_{pp}) conversion factor was computed for each field map by dividing the V_{pp} value of the largest field measurement, as detected and measured from the oscilloscope, by the simultaneous V_{rms} value from the lock-in amplifier. The recorded V_{rms} values were multiplied by this conversion factor to give the equivalent V_{pp} values used in the graphs and formulae.

The effect of various water resistivities (ρ_w) on the voltage output of the fishes was measured with each fish submerged to the center of a smaller aquarium ($30 \times 40 \times 90$ cm). The fish was restrained as in the mapping experiments, with pickup electrodes fixed at its head and tail. The signal was fed through a Grass P15 preamplifier and displayed on the oscilloscope. The fish's peak to peak discharge voltage recorded as ρ_w was gradually lowered from a high resistivity by adding salts directly into the tank.

Dipole Field Equations. The dipole moment predicted by the voltage or voltage gradient measurement at each measured point was calculated using the following equations modified from Bitter (1954). Appendix II presents a detailed explanation of these expressions.

Field potential measurements (V_{pp}):

$$P_f = \frac{4 \pi}{\rho_w} \frac{V_{pp} \cdot d^2}{\cos \Theta} \quad (4)$$

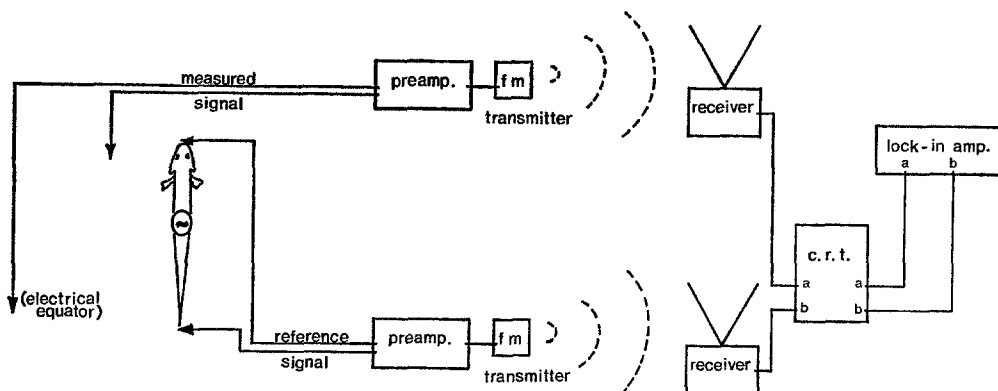
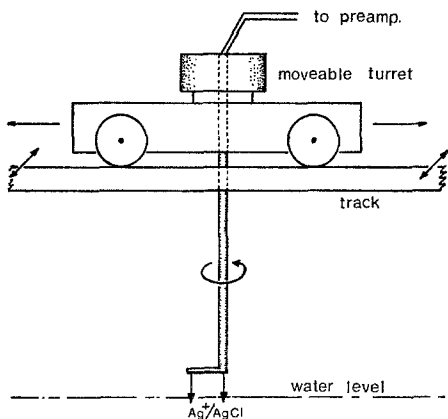
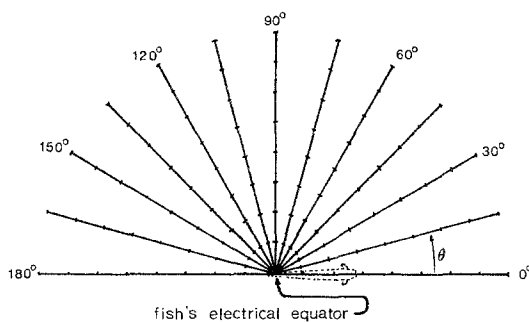
A**RECORDING CIRCUIT****B****ELECTRODE ASSEMBLY****C****GRID FOR FIELD MEASUREMENTS**

Fig. 1A-C. The recording circuit and equipment used in measuring the fishes' electric fields. *A* diagrams the basic recording circuit. V_{rms} values were read from the lock-in amplifier. *B* shows the X-Y carriage system with turret mounted electrodes used for picking up the measured signal. *C* depicts the acetate grid which was prepared for recording the measured electric field potentials and gradients. The rays were 15° apart with measurement sites placed every 5 cm. The fish was oriented on the 0° - 180° line as shown

Field gradient measurements along the axis of the dipole (E_{0° and E_{180°):

$$P_f = \frac{2\pi}{\epsilon_w} E \cdot d^2. \quad (9)$$

Field gradient measurements along the zero potential plane (E_{90°):

$$P_f = \frac{4\pi}{\epsilon_w} E \cdot d^2 \quad (10)$$

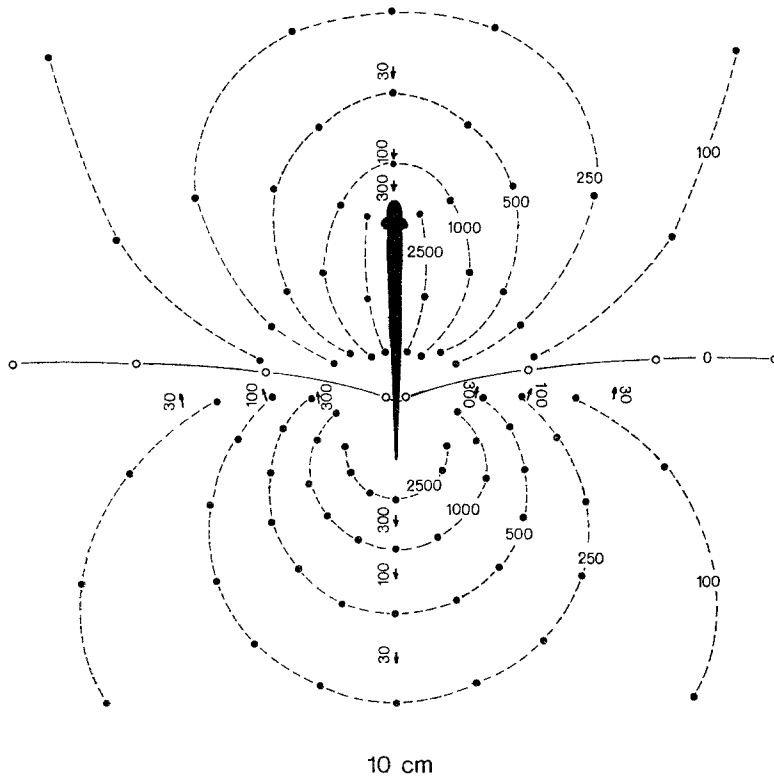
APTERONOTUS (22 cm)

Fig. 2. The electric field of a 22 cm *Apteronotus* in 3.8 kOhm·cm water. The field potential values in μV are written horizontally and in association with the appropriate equipotential line. Field gradient vectors in $\mu\text{V} \cdot \text{cm}^{-1}$ are shown along the axis of the fish and at right-angles to the fish. Field gradient magnitudes are written vertically, next to their corresponding vectors. Note the field asymmetry due to the distortive effect of the body

P_f refers to the dipole moment of the fish's field in $\mu\text{Amp} \cdot \text{cm}$, which is d cm away on a ray of angle θ from the dipole vector, chosen here to point from the tail to the head of the fish (see Fig. 3 inset). V_{pp} is the measured peak to peak voltage of the fish's electric organ discharge expressed in μV . E represents the measured field gradient and has the units of $\mu\text{V} \cdot \text{cm}^{-1}$; ρ_w is the water resistivity in Ohm·cm. P_f values for each fish at each ρ_w were placed in a matrix format for d and θ for data analysis.

Results

Electric field measurements made close to the fish's body on both the apteronotids and the rhamphichthyids revealed that their fields were far from dipole-like. Although the isopotential lines surrounding the tail region approximated a dipole field configuration, the field around the body region was produced by a distributed source of current (Fig. 2). The current distribution was not uniform, however, and a definite region of maximal current density along the body could be located. The distance from the fish's electrical equator to the point of maximal voltage was usually greater toward the head than toward the tail

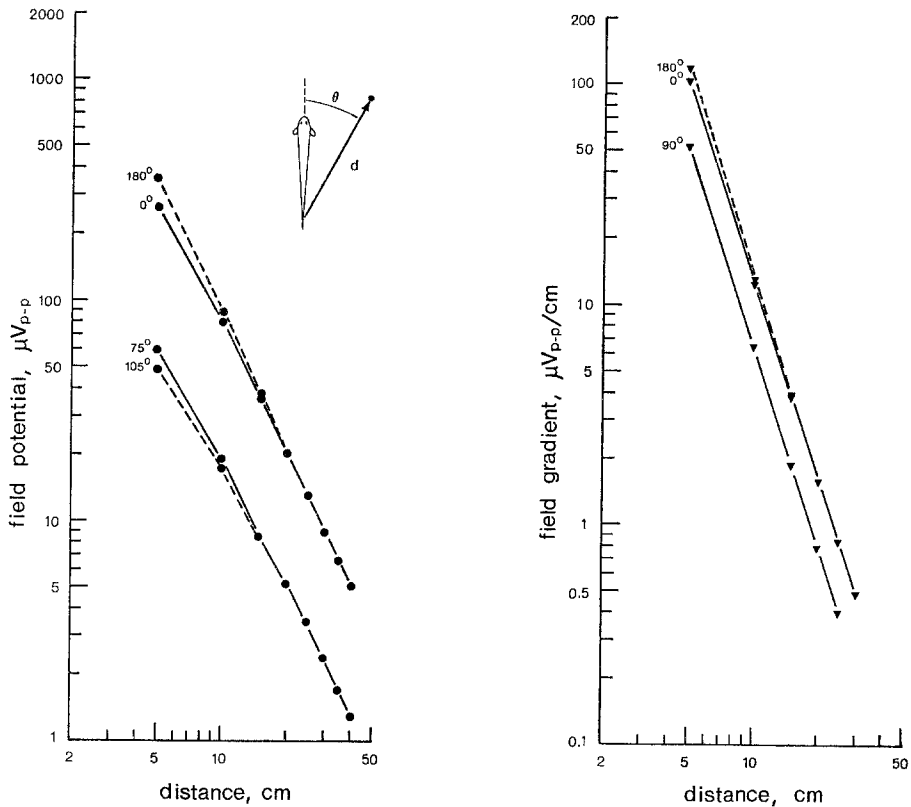
APTERONOTUS (6 cm)

Fig. 3. Field potential and field gradient plotted as a function of distance for a 6 cm *Apterotonotus* in 3.8 kOhm·cm water. For clarity only the field potentials along the 0° , 75° , 105° , 180° rays are plotted, although all rays were measured. The inset shows what θ and d represent. The plots for a dipole field would result in straight lines for each θ on both graphs: on the field potential versus distance graph the slopes would equal -2 , and on the field gradient versus distance graph the slopes would equal -3 ; the straight lines would shift up or down depending on the value of $\cos \theta$. As predicted by a dipole field, the field potential of this fish falls off with the square of the distance and its field gradient falls off with the cube of the distance (compare with Fig. 4)

especially in low resistivity water. This asymmetry of the field source was reflected in the geometry of the fish's electric field: equipotential lines in the head region ran nearly parallel to the fish's body thus projecting further forward in the head region than would have been predicted from a dipole source. In contrast, current emanating from the fish's tail was far more dense, concentrated at an apparent point source near the end of the tail. A further deviation from a dipole field geometry was a headward bending of the zero equipotential plane, which intersected the axis of the fish at a point 20% to 30% of the body length from the tip of the tail (Fig. 2).

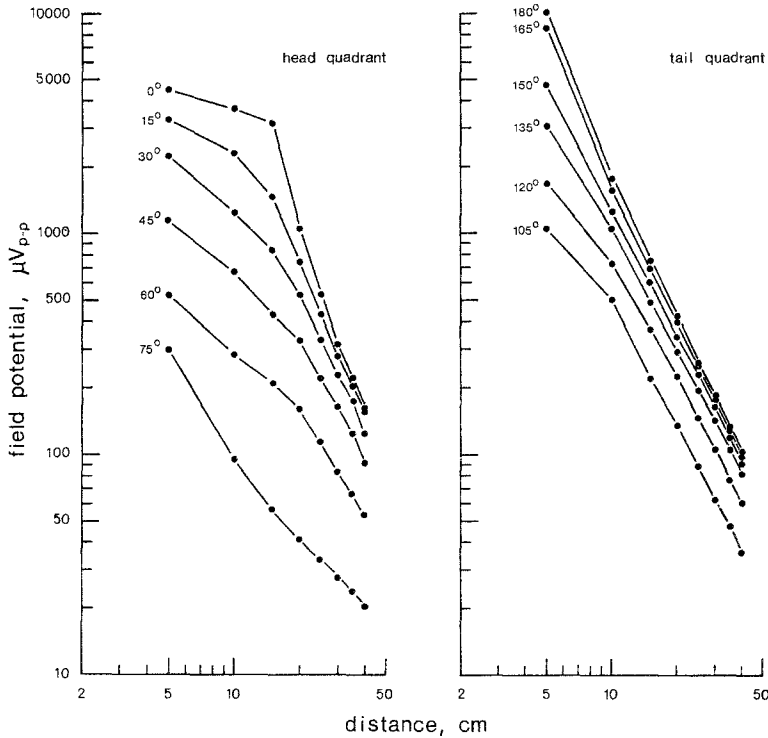
APTERONOTUS (22 cm)

Fig. 4. The electric field potential along each measured ray plotted as a function of distance for a 22 cm *Apteronotus* in 3.8 kOhm·cm water. Measurements in the head quadrant (rays 0°–75°) are plotted on the left graph; measurements for the tail quadrant (rays 105°–180°) are plotted on the right graph. While the tail quadrant field approximates dipole characteristics, the head quadrant field indicates a distributed current source (compared with Fig. 3)

The described deviations of the fish's field from that of a dipole field represent trends that increased as the size of the fish increased. The smaller the fish, the more closely did its field approach a dipole field (compare Figs. 3 and 4). This was a consequence of two factors: a decreased field distortion imposed by the body, and an increased d/s ratio, which is the ratio between the measurement distance and the source-sink separation distance that is assumed to be large in the dipole equations used (Ref. Appendix II). Thus, as shown in Table 1, the electric field of the 6.0 cm *Apteronotus* in 3.8 kOhm·cm water can be described as a dipole field with a moment (P_f) of 41.6 $\mu A \cdot cm$ to an accuracy of $\pm 5\%$ at a distance of 20 cm (Fig. 3). The electric field of the 10.0 cm *Apteronotus* under similar conditions approaches a dipole field to within $\pm 5\%$ at 25 cm, and the field of the 22.0 cm *Apteronotus* does not satisfactorily approximate a dipole field even at 40 cm (Fig. 4).

For any given fish these deviations of its electric field from a dipole field increased as a function of decreasing water resistivity (ρ_w). When ρ_w was high

Table 1. Dipole moments for electric fish fields

Genus	Length (cm)	ρ_w^a (kOhm·cm)	s (cm)	\bar{P}_f^b ($\mu\text{A}\cdot\text{cm}$)	P_f range at d cm distance
<i>Eigenmannia</i>	8.5	3.8	2.3	182.5	180 to 192 at 25 cm
		37	2.7	105.5	90 to 107 at 25 cm
		320	6.3	74.6	71 to 78 at 25 cm
<i>Eigenmannia</i>	18.6	3.8	5.4	948.7	903 to 1035 at 40 cm
		320	13.0	648.2	613 to 699 at 40 cm
<i>Sternopygus</i>	19.2	3.8	3.8	496.6	472 to 530 at 40 cm
		320	4.0	129.9	124 to 134 at 40 cm
<i>Apteronotus</i>	6.0	3.8	3.9	41.6	40 to 42 at 20 cm
		37	4.0	24.8	24 to 25 at 20 cm
		320	4.2	8.1	7.9 to 8.4 at 20 cm
<i>Apteronotus</i>	10.0	3.8	3.8	80.4	77 to 82 at 25 cm
		37	3.9	71.5	69 to 73 at 25 cm
		320	6.0	43.8	41 to 45 at 25 cm
<i>Apteronotus</i>	22.0	3.8	6.0	1237.7	850 to 1732 at 40 cm
		320	14.0	404.5	343 to 483 at 40 cm
<i>Adontosternarchus</i>	11.7	3.8	3.6	199.0	188 to 208 at 40 cm
		37	4.0	178.4	171 to 186 at 35 cm
		320	6.0	94.9	85 to 101 at 40 cm

^a Water resistivity with the fish in "full space".

^b Average of P_f values calculated from V_{pp} measurements taken at 40 cm distance using formula (4).

(320 kOhm·cm), the measured source-sink separation distance (s) was a fair approximation of the actual electric organ length. When ρ_w was low and the output of the electric organ was loaded to a greater extent, s decreased (Table 1), and the zero potential plane bent further headward and intersected the body closer to the tail.

Despite these deviations of the fishes' electric fields from dipole field geometries especially among the large fish, dipole moments based upon the average of the P_f values from the most distant measurements have been ascribed to each fish (Table 1). Although some of the dipole values are approximations, a definite correlation exists between the size of the fish and the magnitude of its dipole moment (Fig. 5). The correlation is linear with a slope of $75 \mu\text{A}\cdot\text{cm}$ per cm of fish length. This relationship generally applies even to interspecies comparisons with one noteworthy exception. The 19.2 cm *Sternopygus* had relatively low dipole moments of $496.6 \mu\text{A}\cdot\text{cm}$ in $3.8 \text{ kOhm}\cdot\text{cm}$ water and $129.9 \mu\text{A}\cdot\text{cm}$ in $320 \text{ kOhm}\cdot\text{cm}$ water. This fish also exhibited an unusually low source-sink separation (Table 1). Although these measurements indicate a comparatively small, low power electric organ for this species, more fish must be measured before any generalizations can be made.

Comparing the electric fields of the apteronotid species possessing ectodermally derived electric organs, with those of the rhamphichthyid species possessing

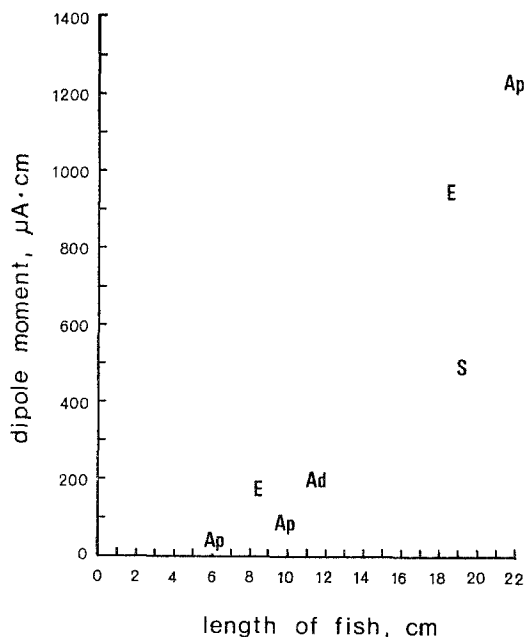


Fig. 5. Computed dipole moments plotted as a function of fish length. These are dipole moment magnitudes in $3.8 \text{ k}\Omega\cdot\text{cm}$ water for each of the fishes measured in this study. *Ap* *Apteronotus*, *Ad* *Adontosternarchus*, *E* *Eigenmannia*, *S* *Sternopygus*. A definite correlation exists between fish length and dipole moment magnitude, with the *Sternopygus* showing a distinctly weak electric field

mesodermally derived electric organs, revealed no fundamental differences. However when the voltage outputs from these two families of fish were monitored as the ambient water resistivity was lowered, a clear distinction appeared: apteronotids maintained a constant current output at higher water resistivities than did rhamphichthyids, as indicated by a linear voltage (V_x/V_{max}) increase with increasing ρ_w (Fig. 6). A fish's peak voltage in $350 \text{ k}\Omega\cdot\text{cm}$ water served as its reference voltage (V_{max}). In $15 \text{ k}\Omega\cdot\text{cm}$ water the current output from any of the apteronotid fish had not dropped more than 5%, whereas the current output from the rhamphichthyid fish had dropped 5% already between $8 \text{ k}\Omega\cdot\text{cm}$ and $10 \text{ k}\Omega\cdot\text{cm}$. Within each family of fish, the larger fish maintained their current output levels in higher water resistivities than did the smaller fish.

Discussion

A. Comparing the Fields of Electric Fishes

A dipole moment represents an absolute evaluation of the magnitude of an electric fish's field, with which quantitative intraspecific and interspecific comparisons of electric organ output capabilities can be made. However a fish, as a field source, is complex and does not approximate a dipole source at distances less than 20 to greater than 40 cm, depending upon the size of the fish. Conse-

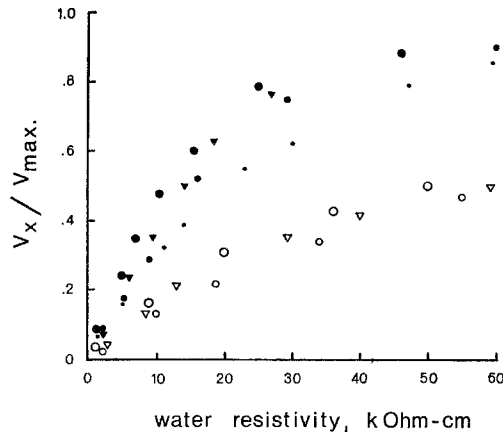


Fig. 6. The effect of water resistivity on electric fish voltage output. The ratio of each fish's head to tail voltage at a given resistivity (V_x) to its "unloaded" head to tail voltage at 350 kOhm·cm (V_{max}) is plotted as a function of the water resistivity. The closed symbols represent the apteronotid fishes; the opened symbols represent the rhamphichthyid fishes. The size of the symbol corresponds to the size of the fish. Notice the distinct groupings of the apteronotids and the rhamphichthyids, as well as the effect of fish size within each family. The relationship is linear ($\pm 5\%$) out to 15 kOhm·cm for the apteronotids, and out to 8–10 kOhm·cm for the rhamphichthyids. Closed circles = *Apteronotus*, closed triangles = *Adontosternarchus*, opened circles = *Eigenmannia*, opened triangles = *Sternopygus*

quently for an accurate estimation of a fish's dipole moment, a large aquarium must be used to avoid compression and distortion of the fish's electric field imposed by insulating interfaces.

Although too few individuals from any one species were measured in this study to draw specific comparative conclusions, two general trends were consistent throughout the selected population. One was the increase in dipole moment magnitude and rostrocaudal field asymmetry with increasing fish length. These two field characteristics could well indicate the size or age of the fish and thereby play a role in neighbor recognition and intraspecific dominance hierarchies. This correlation between fish length and electric field strength seems to apply also to *Electrophorus electricus* (Brown and Coates, 1952) and *Gymnotus carapo* (Black-Cleworth, 1970). The steepness of the slope of the dipole moment versus fish length plot (Fig. 5) is a significant point in this regard. At the rate of 75 $\mu\text{A} \cdot \text{cm}$ per cm of fish length, a doubling in fish length leads to a tremendous increase in dipole moment magnitude. Such a steep slope would allow an electric fish to make a fairly good estimate of another fish's size by virtue of that fish's field strength under standard conditions. The second trend was the grouping of the apteronotid plots as apart from the rhamphichthyid plots on the electric field voltage versus water resistivity graph (Fig. 6). If an electric fish were modeled as a *Thevenin* equivalent with its electric organ as the voltage source in series with a high resistance, and the surrounding water as the load resistance, then these plot groups indicate that the source resistances of apteronotid fishes are considerably higher than those of rhamphichthyid fishes. These fishes experience a wide

range of water resistivities in the course of a year; from a low of $2 \text{ k}\Omega \cdot \text{cm}$ during the dry season when shrinking pools are crowded with life, to a high of $100 \text{ k}\Omega \cdot \text{cm}$ during the rainy season when streams are constantly flushed of their salts. An average ρ_w of $6\text{--}15 \text{ k}\Omega \cdot \text{cm}$, however, is typical (Hopkins, 1972). Thus, while the current output levels of the rhamphichthyid fishes change over the range of water resistivities usually encountered in their environment, the apteronotid fishes with their higher source resistances simulate constant current sources; their output voltages increase linearly with the water resistivity and they expend a constant amount of energy to maintain their current output levels.

B. The Fish's Electric Field and Object Detection

In gymnotid fish the caudal end of the electric organ is tightly confined in the tail near the skin and is electrically isolated from the rest of the body by a high resistance barrier (Bennett, 1971). This causes the caudal end of the electric organ to channel current into the immediately surrounding water. The current density is extremely high at the tail, and radiates out as though arising from a point source. Surrounding the cephalic end of the organ, however, are low resistance body fluids, which tend to distribute current more or less uniformly over the entire forward body. As a result, the equipotential lines project forward in a geometry that to varying degrees follow the contours of the fish's body.

A gymnotid fish exploits this asymmetry in its field when it inspects objects in its environment. These fish often approach unfamiliar objects by swimming backwards toward the object, while moving the tail rapidly in the horizontal plane or in small circles. In this way a fish can bring an unknown object into the region of maximal current density, thereby maximizing the field distortions made by the object and possibly allowing for an estimation of the object's size and capacitative qualities (Scheich *et al.*, 1973; Bastian, 1973) without risking the loss of its head should the object prove to be a predator.

The field effects of the fish's long, conductive body probably optimizes its ability to resolve objects. Bennett (1971) demonstrated electrophysiologically that tuberous electroreceptors, which are distributed over the body surface and are responsible for sensing the fish's electric organ signal, only respond to changes in the perpendicular component of impinging current. Changes in the field strength experienced by an electroreceptor, as caused by nearby high or low impedance objects, will be most efficiently transduced where the current flows perpendicularly to the fish's body. The separation of the head and tail poles of the electric organ because of its elongate shape, and the almost uniform voltage distribution in the rostral body induces current to flow nearly perpendicular to the skin in this region of high receptor density, thus maximizing the resolving power of the fish's electroreceptive system.

C. The Fish's Electric Field and Electrocommunication

Knowing the dipole moment of an electric fish's field, besides being of comparative value, enables the calculation of its field strength at any distance where the fish's field conforms to a dipole field geometry. When coupled with behaviorally determined electrical sensitivities, such a calculation can estimate the

Table 2. Electrocommunication ranges for *Eigenmannia* and *Apteronotus*

Genus	Length (cm)	\bar{P}_f^a ($\mu\text{A} \cdot \text{cm}$)	ρ_w ($\text{k}\Omega\text{m} \cdot \text{cm}$)	Electrocommunication distance ^b (cm)	
				0°, 180°	90°
<i>Eigenmannia</i>	8.5	182.5	2	61	49
			10	83	66
<i>Eigenmannia</i>	18.6	948.7	2	107	85
			10	145	115
<i>Apteronotus</i>	6.0	41.6	2	38	30
			10	51	40
<i>Apteronotus</i>	10.0	80.4	2	47	37
			10	64	50
<i>Apteronotus</i>	22.0	1237.7	2	116	92
			10	158	125

^a The calculated \bar{P}_f in 3.8 $\text{k}\Omega\text{m} \cdot \text{cm}$ water (Ref. Table 1).

^b These distances assume the two fish to be in "full space" and that their electrical sensitivities are $0.25 \mu\text{V} \cdot \text{cm}^{-1}$ in 2 $\text{k}\Omega\text{m} \cdot \text{cm}$ water and $0.5 \mu\text{V} \cdot \text{cm}^{-1}$ in 10 $\text{k}\Omega\text{m} \cdot \text{cm}$ water (Knudsen, 1974).

range of electrocommunication for that fish. For both *Eigenmannia* and *Apteronotus* the appropriate behavioral measurements have been made (Knudsen, 1974). The electrical sensitivities to sine wave fields of both species decrease from $0.25 \mu\text{V} \cdot \text{cm}^{-1}$ in 2 $\text{k}\Omega\text{m} \cdot \text{cm}$ water, to $0.5 \mu\text{V} \cdot \text{cm}^{-1}$ in 10 $\text{k}\Omega\text{m} \cdot \text{cm}$ water. By approximating the constant current resistivity range for these fish as extending to 10 $\text{k}\Omega\text{m} \cdot \text{cm}$ (Fig. 6), the dipole moments calculated at 3.8 $\text{k}\Omega\text{m} \cdot \text{cm}$ should also apply at 2 $\text{k}\Omega\text{m} \cdot \text{cm}$ and at 10 $\text{k}\Omega\text{m} \cdot \text{cm}$. Substituting these values into equations 9 and 10, electrocommunication ranges of *Eigenmannia* and *Apteronotus* in 2 $\text{k}\Omega\text{m} \cdot \text{cm}$ and 10 $\text{k}\Omega\text{m} \cdot \text{cm}$ water were calculated (Table 2). These distance estimates are more accurate for the smaller fish, for which the dipole moments were more precisely measured.

Electrocommunication ranges change with the size of the fish, the relative positions of the fish, the presence of field distorting surfaces, and the resistivity of the ambient water. As shown in Table 2, the decrease in the fish's electrical sensitivity in 10 $\text{k}\Omega\text{m} \cdot \text{cm}$ water is more than compensated for by the increase in field strength due to the higher water resistivity. Keeping in mind that the electrocommunication distances given in Table 2 also assume that the two fish are in a large (nondistorting) body of water, and that these distances depend upon the relative angular positions of the fish, they are satisfactorily close to behaviorally determined electrocommunication distances of 30 cm for mormyrids (Moller and Bauer, 1973; Russell, Myers and Bell, 1974) and 7 m for *Electrophorus* (Bullock, 1969). Were these fish in shallow water, near the surface, or in a confined, insulating area their fields would compress and their electrocommunication ranges would increase.

Fig. 7 compares the range of object detection with the range of electrocommunication for the 18.6 cm *Eigenmannia* in 2 $\text{k}\Omega\text{m} \cdot \text{cm}$ water. The object

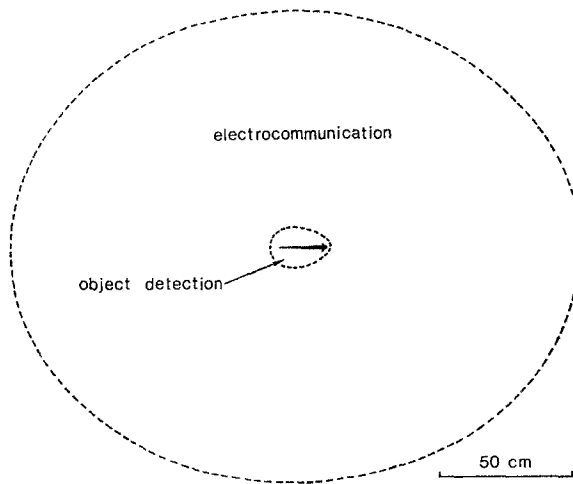


Fig. 7. The range of electrocommunication compared with the range of object detection for a 18.6 cm *Eigenmannia* in 2 kOhm·cm water. Values for electric field strength were measured in this study; electrical sensitivity values were taken from Knudsen (1974); object detection threshold distance was given by Heiligenberg (personal communication) for a 16 cm *Eigenmannia* sensing a 2 mm plexiglas rod in 2 kOhm·cm water

detection range was taken from values given by Heiligenberg (personal communication) who studied electromotor responses in a 16 cm *Eigenmannia* (Heiligenberg, 1973). Since there exists no absolute range for object detection without defining the size and resistive nature of the test object, the inner ring in Fig. 7 defines the area around the fish where the field distortion of a 2 mm plexiglas rod should be sensed. The measured threshold detection distance was 3 cm perpendicularly from the operculum of the fish, and was extrapolated for Fig. 7 to the surrounding regions which experienced at least an equivalent field gradient. The relative though not the absolute range dimensions illustrated in Fig. 7 most likely apply to fish of various sizes. Therefore, whereas gymnotid fish perceive each other at a distance as dipole sources, the asymmetry of their fields probably plays an important role in object detection and resolution.

Appendix I: Explanation of Half-Space Theory

A current source and sink in an infinite conducting medium is defined as being in “full-space”, and it experiences a load proportional to the resistivity of the medium. If this current source and sink are positioned at the surface of an insulating plane in an otherwise infinite volume, it is defined as being in “half-space”, and the load which it experiences will be one half the load experienced in full space. The magnitude of its halfspace electric field measured at this plane will thus equal the magnitude of its full space electric field in a medium of twice the resistivity.

Appendix II: Dipole Field Equations

Electrostatics theory states that the potential at any given point in a dipole field may be calculated from the following equation (Bitter, 1954):

$$V = \frac{q}{\epsilon_0} \frac{s \cdot \cos \Theta}{4 \pi d^2}. \quad (1)$$

The field source consists of equal and opposite charges (q), separated by a distance s . V is the voltage due to a dipole field measured with reference to an infinitely far electrode, at a distance (d) from the dipole, where d is much greater than s . Θ represents the angle subtended by a ray defined by the midpoint of the dipole and the designated point, and the dipole vector. ϵ_0 is the dielectric constant in a vacuum. V is expressed in volts, q in coulombs, ϵ_0 in coulomb ²/newton · meter, and s and d in meters.

In the case of a current source and sink in an infinite volume conductor, the term q/ϵ_0 (newton · meter ²/coulomb) is replaced by $I \rho_0$, where I equals the current flux in a medium of resistivity ρ_0 . Here I is expressed in amps and ρ_0 in Ohm · meters. The units of the quantity $I \rho_0$ may be reduced to volt · meters or its equivalent, newton · meter ²/coulomb. Thus, equation No. 1 becomes:

$$V = \frac{\rho_0 I}{4 \pi} \frac{s \cdot \cos \Theta}{d^2}. \quad (2)$$

Electrostatics defines the quantity $q \cdot s$ as the dipole moment (P_E) of the field. P_E has the units of coulomb · meters. If by analogy the quantity $I \cdot s$ is defined as the dipole moment (P_I) of a dipole field in a volume conductor, P_I will have the units of ampere · meters, and equation No. 2 simplifies to:

$$V = \frac{\rho_0}{4 \pi} \frac{P_I \cdot \cos \Theta}{d^2}. \quad (3)$$

Solving for P_I results in the form of the equation used in this study:

$$P_I = \frac{4 \pi}{\rho_0} \frac{V \cdot d^2}{\cos \Theta}. \quad (4)$$

When calculating the dipole moment of a fish (P_f), water resistivity (ρ_w) was entered in Ohm · centimeters, V was in microvolts, and d was in centimeters. This resulted in P_f being expressed in microamp · centimeters.

The same substitutions described above were made in arriving at the expressions given in terms of voltage gradient (E). The electrostatic equations from Bitter (1954) for the field gradient at points along the axis of the dipole,

$$E_{(0^\circ, 180^\circ)} = \frac{I}{4 \pi \epsilon_0} \frac{2 P_E}{d^3} \quad (5)$$

and for points in the plane that bisects the dipole at right angles,

$$E_{(90^\circ)} = \frac{I}{4 \pi \epsilon_0} \frac{P_E}{d^3} \quad (6)$$

transform into the following equations for a dipole in a volume conductor:

$$E_{(0^\circ, 180^\circ)} = \frac{\rho_0}{4 \pi} \frac{2 P_I}{d^3} \quad (7)$$

$$E_{(90^\circ)} = \frac{\varrho_0}{4\pi} \frac{P_I}{d^3}. \quad (8)$$

These equations were solved in terms of P_I for the calculations made in this study:

$$P_I = \frac{2\pi}{\varrho_0} E_{(0^\circ, 180^\circ)} \cdot d^3 \quad (9)$$

$$P_I = \frac{4\pi}{\varrho_0} E_{(90^\circ)} \cdot d^3. \quad (10)$$

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