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THE EFFECT OF ENVIRONMENTAL FACTORS ON COMMUNICATION AND SPACING IN WEAKLY ELECTRIC FISH

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THE EFFECT OF ENVIRONMENTAL FACTORS ON COMMUNICATION AND SPACING IN WEAKLY ELECTRIC FISH

by

Ann Odmark Squire

A dissertation submitted to the Graduate Faculty in Psychology
in partial fulfillment of the requirements for the degree of
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TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

GENERAL INTRODUCTION

Communication among animals is a subject which has interested animal behaviorists for years and about which volumes have been written. Human communication is accomplished overwhelmingly by means of a verbal language. Indeed, it is only in recent years that the study of non-verbal human communicative modes such as "body language" has been undertaken. No animal species has yet been found to possess anything comparable to human language, although recent work with primates, porpoises, and bees indicates that their communication systems are much more complex than was previously thought. Perhaps it is this gulf between human and animal communicative behavior that has led many people to regard animal communication as qualitatively different from human communication. This has made it difficult to reach an overall definition of communication that includes both human and animal types.

Some authors have solved this problem by defining communication very broadly. Brown (1975) considers communication to be "the processes by which an animal influences others in a social context." A similar definition is given by S. A. Altmann (1967): " . . . social communication is a process by which the behavior of an individual affects the behavior of others." Burghardt brings in the notion that for communication to have evolved, it must benefit the signaller. He states that communication occurs "when one organism emits a stimulus that, when responded to by another organism, confers some advantage (or the statistical probability of it) to the signaller or its group" (Burghardt 1970b).

Marler approaches the problem of definition by listing some criteria for communicative behaviors. Behaviors involved in communication give evidence of "evolutionary specialization of stimulus production and design for evoking particular responses from another organism." What distinguishes true communication from cases where an animal simply emits a signal to deter predators is that communication "implies evolutionary specialization of a mutualistic, cooperative nature" (Marler 1977).

All of these definitions are useful as general descriptions of communication. When one is interested in specifying the factors which influence communication among animals, however, it is necessary to take into account the environment in which the animals live and communicate. It is clear that communication does not occur in a vacuum. Any communication signal, whether it be chemical, accoustical, visual, or electrical, will be affected by the conditions of the animal's environment. Indeed, characteristics of the environment may play a major role in determining what modalities are used for communication in the first place.

For example, the lemurs of Madagascar are arboreal and some species are nocturnal as well. Since both of these characteristics limit visual contact among lemurs, one would not expect vision to be the major sensory modality employed for intraspecific communication. In his field studies of lemurs, Petter (1965) lists vocalizations and scent-marking behavior as the two primary means of communication. This is not surprising. Auditory communication is well suited to the lemur's environment, since vocal signals are not impeded by dense forests as visual signals would be and they are not dependent on ambient light for their transmission. Scent-marking complements auditory communication by providing a more long-lasting form of communication.

Hopkins (1977) recognizes the importance of environment in his discussion of communication:

> Communication among animals is a complex and highly refined process by which one individual's behavior, acting as a stimulus or signal, effects a change in the behavior of another. *Mediated by the environment through which the stimulus must be transmitted*, signals and the responses they elicit have evolved to the mutual benefit of both participants. *But with each of the diverse energy modalities used for encoding stimuli, the problems associated with the creation, transmission, and final detection of communication signals are unique*. . . . (Emphasis added.)

Not only does the animal's environment help determine what modalities will be used for communication, but once a modality has been chosen, environmental fluctuations will affect the efficacy of signal transmission and reception. Communication among animals which rely primarily on vocalizations will be affected by the ambient noise level of the environment. When the background noise level is high as a result of natural events such as wind and rain or biological noise such as the vocalizations of other animals, auditory communication will be hampered. If environmental conditions are extreme (as in a severe storm, for example), auditory communication may be impossible, forcing animals to use another mode of communication.

Weakly electric fish, which have been found to communicate at least in part by means of electric signals, should be greatly affected by environmental conditions. The presence of background electrical noise (low frequency electromagnetic radiation from lightning, magnetic storms, earthquakes, or water movement through the earth's magnetic field; and noise resulting from electrical discharges of other electric fish) will help determine the range at which an electrical signal from another fish is detectable. Environmental variables such as the presence of nearby non-conducting objects and the conductivity of the water will determine the effective range of an emitted electric signal.

It is evident that its environment exerts both ultimate and proximate influences on an animal's communicative behavior. On both ultimate and proximate levels, the environment will help determine what modalities are selected for communication. On a proximate level, environmental fluctuations will affect the efficacy of signal transmission from moment to moment.

Although the communicative behavior of a species may rely primarily on one sensory modality, it is usual for a communication system to be based on several modalities. Hearing the vocalizations of others is certainly a predominant mode of communication in humans, but it would be hard to deny that vision, touch, and even smell are important factors in communication as well. The use of a multitude of sensory systems in communication has an obvious adaptive value. If an animal can communicate through several modalities, it is more likely to be able to adapt to environmental changes which limit the effectiveness of one sensory system. If a sensory system is damaged or lost, the animal may be able to get along on information gained through other systems.

The weakly electric fish is a particularly intriguing subject for the study of sensory integration in and environmental influences on communication because, in addition to the "standard" senses, it possesses an addition one--an electric sense. It has been established that weakly electric fish communicate, at least in part, by means of electric signals.

As has been discussed, fluctuations in an animal's environment may influence the usefulness of one or another sensory modality. However, the extent to which these environmental fluctuations influence communication and communication-related behaviors depends directly on the extent to which the animal employs the affected modalities in communication. For instance, the turbid water typically found in the natural habitat of weakly electric fish limits visual contact among individuals, but if the fish do not use visual signals in communication, then the effect of water turbidity on communication will be negligible.

In the present experiment, I was interested in the effect of water conductivity fluctuations--which specifically affect the electrosensory system--on behaviors related to communication. Clearly, the impact of conductivity fluctuations on communication may be expected to vary with the degree to which the fish communicate electrically. The experiment was designed, therefore, to assess conductivity effects (1) when the fish were forced to communicate electrically, and (2) when they could use both electric and non-electric senses in communication.

The Electrosensory System

Electric organs and electroreceptors have been found in many species of both marine and freshwater fish. To show that a species does indeed possess an electric sense, it is necessary to demonstrate that it responds to imposed electric fields. Three possible sources of natural electric fields have been described by Kalmijn (1974):

1) inanimate electric fields of physical or chemical origin,
2) bioelectric fields from electric organs,
3) bioelectric fields from sources other than electric organs, such as the "incidental" electric fields which emanate from all living plants and animals.

An electric signal is perceived when current flows through the electroreceptors. Electroreceptors are specialized, low-resistance, cutaneous sensory organs which are innervated by the lateral line nerve. Two major classes of electroreceptor have been described: ampullary receptors, which have been found in both electric and non-electric fish, and tuberous receptors, which occur only in electric fish. The two types of receptor differ in their anatomical structure and in the type of electrical signals to which they are sensitive (Bennett 1971; Szabo 1974; Fessard and Szabo 1974).

In the ampullary receptor, several sensory and accessory cells lie at the and bottom of a jelly-filled canal which connects them to the exterior. Several such ampullae are innervated by a single branching afferent nerve fiber and together make up one functional ampullary electroreceptor. The length of the jelly-filled canal varies among species, sometimes reaching several centimeters in length. Ampullary receptors respond to low-frequency a.c. as well as d.c. electrical stimuli. Also known as tonic receptors, they produce a spontaneous emission of spikes which is enhanced or depressed by changes in the local electric field produced by objects in the environment. Ampullary receptors have also been found to respond to electric organ discharges, but only under conditions where the water contains very little dissolved ionic material--at conductivities of less than 100 micro Siemens/centimeter (µS/cm) (Bell and Russell 1978).

Tuberous, or phasic, receptors consist of several sensory cells lying in a cavity covered by layers of epithelial cells--there is no canal to the surface. Innervation is through a single afferent fiber which penetrates the basement membrane, branches between supporting cells, and comes in contact with the basal part of the sensory cells. Tuberous organs are sensitive to high-frequency (> 50Hz) stimuli, and respond phasically to stepwise changes in stimulating voltage--thus they are responsive to electric organ discharge (EOD)-like stimuli.

Two types of tuberous receptor may be distinguished on the basis of their responses to electrical stimulation (Fessard 1974). In the common tuberous receptor or "knollenorgan," each electrical stimulus produces an all-or-none receptor potential, which is followed by a nerve impulse. This one-to-one stimulus-response relationship holds up to stimulus frequencies of 150-200 Hz, after which further increases in stimulus frequency produce a proportional increase in frequency of receptor response. The knollenorgan is thought to be the receptor which is sensitive to the EODs of other electric fish.

The specific tuberous receptor, or mormyromast, does not show the one-to-one stimuls-response activity of the knollenorgan. Rather, the mormyromast shows graded receptor potentials, and responds to an increase in stimulus intensity with an increase in number and decrease in latency of nerve impulses. The mormyromast is thought to function in the active electrolocation process, in which the fish detects distortions in its electric field produced by objects which differ in impedance from the surrounding water.

The two principal groups of freshwater electric fish--the African mormyrid and the South American gymnotid fish--possess both ampullary and tuberous receptors. In mormyrids, the electroreceptors are distributed over the head and the dorsal and ventral surfaces of the body, but are absent on the sides of the body and the tail (Bennett 1971).

The electric generating organ is derived from either muscle or nerve tissue, with muscle-derived organs being the more common type. The organ consists of four columns of multinucleated cells known as electrocytes, with each column containing 100-200 electrocytes in series (Bennett 1971). Each electrocyte is innervated by a separate motor neuron. When a nerve discharge excites the electrocyte, a spike is generated. The discharges of many electrocytes summate to produce a voltage. In mormyrid fish the electric organ is derived from tail muscle and is located in the caudal peduncle.

The electric organ discharges emitted by strongly electric fish such as the electric eel (Electrophorus electricus), electric catfish (Malapterurus electricus), and marine torpedo ray serve a predatory function. However, the EODs of weakly electric fish are insufficient for this purpose, reaching a maximum of only a few hundred millivolts. What then is the adaptive significance of the weak electric discharge?

One function that has received experimental support is that of electrolocation, which may be divided into passive and active types. In passive electrolocation, the fish detects electric fields which are imposed on it from external sources. These sources may include "incidental" bioelectric fields emanating from aquatic plants or animals, which would be detected by the ampullary receptors, as well as the electric organ discharges of other electric fish, which would be detected by the knollenorgans.

In active electrolocation, the fish generates an electric field around itself by emitting electric organ discharges. An object which differs in impedance from the surrounding water will produce characteristic distortions in the electric field. The fish detects a distortion as a change in the current flow across the mormyromasts. The intensity of the field distortion and the particular receptors affected provide the fish with information about the distance and location of the distorting object in the environment (Kalmijn 1974; Bullock 1974).

Electric organ discharges have also been shown to serve a communicative function. In electrocommunication, the EODs of one fish may excite the knollenorgans of a conspecific, thus serving as a form of social communication. Changes in the temporal patterning of EOD activity during social encounters are evidence of a communicative role. In response to the presence of another electric fish, pulse-type fish (whose discharge is much shorter in duration than the inter-discharge interval) have been found to: cease discharging briefly (Moller and Bauer 1973); decrease the variability of interpulse intervals ("regularization" of EOD rate--Moller 1970); show brief accelerations in EOD rate (Bauer 1972); and synchronize their discharges with those of another fish (echo response--Russell et al. 1974). Wave-type species (whose discharge duration is long compared to the inter-discharge interval) show a jamming avoidance response, where they shift their EOD frequency away from the EOD frequency of another nearby fish

(Heiligenberg, 1977). Hopkins (1977) reviews evidence which suggests that EODs serve in species and individual recognition, and as sexual, age class, and motivational signals among gymnotid and mormyrid fish. The amplitude of perceived EODs may provide information on the distance and/or size of another fish. Moller (1976) has shown that EODs play a role in schooling behavior in the mormyrid fish Marcusenius cyprinoides. Electrically silent M. cyprinoides showed less locomotor activity than did intact fish. Parallel lineup and single-file swimming were not observed in operated fish. Moller suggested that the EOD plays a role in schooling by keeping the individuals spaced and reducing physical encounters. This would serve a valuable function in the natural environment of the fish, where visibility is limited as a result of turbid water.

Because the electric sense is unique, most studies of electric fish have focused on it. Most, however, have not paid sufficient attention to the potential effects of environmental variables on the functioning of the electrosensory system. The researcher must keep in mind that in its natural habitat, the weakly electric fish lives in murky, electrically noisy waters, where environmental conditions may have a marked influence on the efficacy of signal transmission and reception. The first part of the present research is a controlled study of the effects of one potentially important environmental variable--water conductivity--on the range of electrocommunication in mormyrid fish which were deprived of most non-electric cues they might normally utilize in communication. During the experiments in Part I, the fish were confined within ceramic shelter tubes which prevented them from using visual or mechanical cues in detecting each other. Since the shelter tubes were porous, it is possible that the fish could have detected chemical stimuli which diffused through the walls of the tube. In all probability, however, such stimuli, as well as any acoustic stimuli, were greatly attenuated by the walls of the shelter tubes. Because the fish were forced to rely primarily on electric signals from each other, it was expected that the influence of conductivity changes--which specifically affect the electric modality--would be intensified.

Another point which has sometimes been overlooked in the "physiological and ethological enthusiasm" over Lissmann's (1958) discovery of the electric sense is that it is but one of the fish's sensory systems. Mormyrid fish may also use chemical, acoustic, mechanical, and, under certain circumstances, visual cues in their communicative behavior (DeFazio 1979; Teyssedre and Moller in preparation). The second part of the present research examines the effects of conductivity changes on the communication and spacing behaviors of groups of free-swimming mormyrids. The fish in Part II were able to use both electric and non-electric cues in detecting and communicating with each other.

INTRODUCTION TO PART I

EFFECTS OF WATER CONDUCTIVITY ON ELECTROCOMMUNICATION AND SPACING

Investigators have examined the effects of such variables as light (Harder et al. 1964; Lissmann and Schwassmann 1965; Dewsbury 1966a, b; Moller et al. 1979), temperature (Moller et al. 1979; Toerring and Serrier 1978) and shock (Gallon, Mandriota, and Thompson 1967) on electric fish behavior, but water conductivity has traditionally been a parameter that has been held as constant as possible, or even neglected, rather than varied experimentally.

Conductivity of water is determined by the number of charged particles or ions in the water The more ions the water contains, the higher the water's conductivity. Conductivity is the reciprocal of resistivity ($C = \frac{1}{R}$), and is measured in microSiemens per centimeter ($\mu S/cm$). Thus, the higher the conductivity, the lower the resistivity of the water to flow of electric current. Because the ionic content of the water affects the flow of current, it should affect transmission of electric signals. Therefore, the distance at which a fish can detect electric signals emitted by another fish should be affected by water conductivity.

There are ample data concerning conductivity conditions in the natural habitats of weakly electric fish. Researchers have reported extreme fluctuations in water conductivity in the natural habitats of both mormyrid and gymnotid fish. Gosse (1963) found that waters in the

Congo Basin containing Gnathonemus petersii varied between 5 and 76 µS/cm (equivalent to a resistivity of 180-13 kOhm.cm), depending on exact location and time of year. Hopkins (1972) stated that gymnotids in the wild survive conductivity fluctuations between 10 and 500 µS/cm (100-2 kOhm.cm), with 50-150 µS/cm (15-6 kOhm.cm) being typical. Moller, Serrier, and Belbenoit (1976) reported a water conductivity of 106 µS/cm (9.4 kOhm.cm) in the Chari River (Chad Basin). Moller et al. (1979), working in an inlet of the Swashi River (Lake Kainji, Nigeria), found that water conductivity depended on depth of the water, varying from 65 µS/cm (15.4 kOhm.cm) at the surface to 110 µS/cm (9.1 kOhm.cm) at the river bottom (the increase in conductivity caused by larger amounts of sediment at the bottom). A few systematic attempts have been made to relate changes in water conductivity to changes in behavior. It is known that both African mormyrids and South American gymnotids breed during the rainy season (Ellis, in Hopkins 1974; Blache 1960; Okedi 1969). Kirschbaum (1975) created an artificial rainy season in the laboratory by continuously decreasing pH and conductivity levels while simultaneously increasing water level. These manipulations resulted in gonad growth and spawning in Eigenmannia virescens. It has been reported that several mormyrid species begin migrating at decreasing conductivity levels (Okedi 1969) and that mormyrids leave Lake Chad for the Chari River when water conductivity in the lake is very high (Moller pers. comm.).

Interestingly, laboratory investigators who study electric fish behavior often pay little attention to conductivity conditions in their experimental tanks. Past laboratory investigations of electrocommunication have generally reported high, unnatural values or large fluctuations in conductivity, or have failed to report conductivity data altogether. The few experimenters who have been interested in the effects of conductivity have not focused on its effects on behavior. Rather, they have examined the effect of water conductivity on the form of the electric organ discharge (EOD) and on the responses of afferent fibers of the electroreceptors.

Bell, Bradbury, and Russell (1976) studied the battery-like properties of the electric organ of G. petersii by varying water conductivity and measuring the peak-to-peak voltage of the diphasic EOD. When recording electrodes were placed directly on the electric organ, and water conductivity varied, the following changes were seen: as conductivity was decreased, the voltage of the first phase of the EOD rose smoothly. The voltage of the second phase rose sharply, reached a peak at about 33 µS/cm (30 kOhm. cm), and then fell steeply. When these measurements were combined, it was found that peak-to-peak voltage rose as conductivity was decreased, reached a maximum at about 30-33 µS/cm (33-30 kOhm.cm), then fell and levelled off at conductivities lower than 20 µS/cm (50 kOhm.cm).

When peak-to-peak voltage was measured at points on the skin of the fish several centimeters anterior to the electric organ, the 30 µS maximum EOD peak was not as pronounced. Instead, peak-to-peak voltage rose as conductivity was decreased, levelled off at about 50 µS/cm (20 kOhm.cm), and remained roughly constant as conductivity was further decreased.

Thus, in the natural habitat of the fish, where conductivities are often quite low, the amplitude of the EOD may remain fairly constant. Bell et al. suggest that the relative insensitivity of peak-to-peak voltage to conductivity fluctuations below 50 µS/cm could simplify the analysis process in electrolocation.

However, changes in conductivity at values above 50 µS/cm can have drastic effects on the amplitude of the EOD. For example, at 250 µS/cm (4 kOhm.cm), a typical conductivity in many laboratory aquaria, the peak-to-peak voltage of the EOD is only one-third as great as it is at 25 µS/cm (40 kOhm.cm).

In studying electrolocation or electrocommunication, both of which depend critically on the strength of the electric signal, it would seem invalid to generalize from lab to field or even from lab to lab unless conductivity conditions were carefully matched.

Bell and Russell (1978) studied the effect of water conductivity on the response of ampullary electroreceptors of G. petersii to a playback of electric organ discharges. They recorded from ampullary afferent fiber bundles while stimulating the fish with its own EODs, which were delivered through nearby electrodes. Ampullary receptors had not previously been found to respond to EOD-like stimuli; however, this may have been due to the fact that earlier experiments were carried out at high water conductivities.

Bell and Russell found that at conductivities lower than 100 µS/cm (10 kOhm.cm) most ampullary afferents (as well as tuberous afferents) responded to the EOD. As water conductivity was raised, ampullary responses decreased in amplitude and finally ceased altogether. At 500 µS/cm (2 kOhm.cm), no ampullary fibers responded to the EOD.

The responses of tuberous (mormyromast) afferents also fell with increasing conductivity: the number of spikes per EOD decreased, and latency to fire increased. In four out of eight cases, the mormyromast afferent response to the EOD was abolished when conductivity was raised to 250-500 µS/cm (4-2 kOhm.cm).

In sum, at high water conductivities, the functioning of the entire electrosensory system is impaired. Raising the conductivity lowers the amplitude of the EOD, which in turn causes a reduced response in both ampullary and tuberous afferents.

Knudsen (1975) measured the strength of the electric fields of several species of gymnotid fish at various water conductivities and found a greater field strength at low conductivities. Using this information in conjunction with the known electrical sensitivities of the fish to sine wave fields (determined behaviorally by Knudsen in 1974), he was able to estimate the electrocommunication ranges for Eigenmannia virescens and Apteronotus albifrons. He predicted larger communication ranges at lower water conductivities; however, no behavioral experiments were made to test these predictions.

An experiment on electrocommunication behavior was done by Moller and Bauer (1973), using the mormyrid fish Gnathonemus petersii. In studying EOD interaction in pairs of fish confined to ceramic shelter tubes, these investigators found that when one fish was moved toward the other, there was a point at which an EOD frequency increase in one member of the pair resulted in a temporary EOD cessation in the other. EOD cessation by the non-dominant member of a pair of mormyrids has been reported by Cleworth (1969) and has been interpreted as a "hiding" response (Bennett and Steinbach 1969), by which the submissive fish makes itself electrically undetectable. The interfish distance at which this occurred, approximately 30 cm, was defined as the threshold communication distance for this species. In the present study, however, the more neutral term "EOD cessation distance" will be used, since it is not clear that this is the point at which the fish first detect one another.

A determination of an "electrocommunication" distance, however, would appear to be incomplete in the absence of information on the environmental conditions under which it was measured. It has been shown that water conductivity affects the range of the fish's emitted electric field and, by extension, the size of the communication field as well. In the Moller and Bauer study, the range of water conductivities was large: from 500-1000 µS/cm. Furthermore, behavioral data were not taken at low conductivities, where one would expect each fish to be maximally sensitive to the other's EOD activity.

Thus there have been gaps in both types of experiment reported so far. In the first type of experiment, conductivity was very carefully controlled and manipulated, but no attempt was made to assess the effect of these manipulations on the electrocommunication behavior of the "whole fish."

In the one behavioral experiment on electrocommunication, conductivity was not controlled carefully enough to permit a reliable estimation of communication range. In Part I, I attempted to fill the gaps left by both types of experiment by conducting a behaviorally-oriented study of electrocommunication in which conductivity conditions were carefully controlled.

EXPERIMENT

THE EFFECT OF WATER CONDUCTIVITY ON EOD CESSATION DISTANCE IN *BRIENOMYRUS NIGER*

When two electric fish are moved close to each other, the electric fields created by their EODs begin to overlap. One fish can detect another's EODs before it can detect the fish itself (Scheich and Bullock 1974). Thus the EODs serve as a kind of "early warning system" which alerts one fish to the presence nearby of another fish. The possibility of an agonistic encounter or competition for food or shelter may make it advantageous for the fish to act on the early warning afforded by the EODs and retreat to a "safe" distance.

Another effect of the electric field overlap which occurs when fish are very close together is that each fish's EODs may interfere with the other's electrolocating system. As was discussed previously, electric fish have developed ways of dealing with this interference: discharge synchronization (the echo response) and the jamming avoidance response. Another tactic could be to maintain an interfish distance at which the EODs of other fish are not detectable. It is clear that water conductivity, which has a direct effect on the effective range of the fish's emitted electric field, could influence interfish distances. In the experiment in Part I, most cues other than EODs that a fish could use to detect the presence of a conspecific (such as visual, mechanical, chemical, and acoustic cues) were eliminated in order to focus on the effects of water conductivity. Fish were confined to shelter tubes so that they could not flee when moved close to one another. Because of this, discharge cessation was chosen as the criterion to indicate when the fish had been moved "too close" together. Water conductivity was varied, and the effect on the interfish distance at which EOD cessation occurred was assessed.

Methods

The experimental animals were African weakly electric fish, Brienomyrus niger. The mean length of the fish was 11.0 cm ± 1.0 cm For a period of three to four days prior to testing, the fish were housed individually in 7.5 liter aquaria in a glass-roofed greenhouse. Water conductivity in these tanks was kept within 15 µS/cm of the value at which the fish were tested, and water temperature was kept at 23°C ± 1.3°C. The fish were exposed to an L:D cycle corresponding to the natural day:night cycle during the months of October through May.

Experiments were performed in a cement tank measuring 400 cm by 70 cm by 63 cm, with the water level maintained at 40 cm, and water temperature the same as in the tanks where the fish were housed. Between 4 and 8 pairs of fish were tested at each conductivity. In cases where fish were used more than once at a particular conductivity, a period of at least two weeks elapsed between the first and second tests.

Measurement of EOD cessation distance

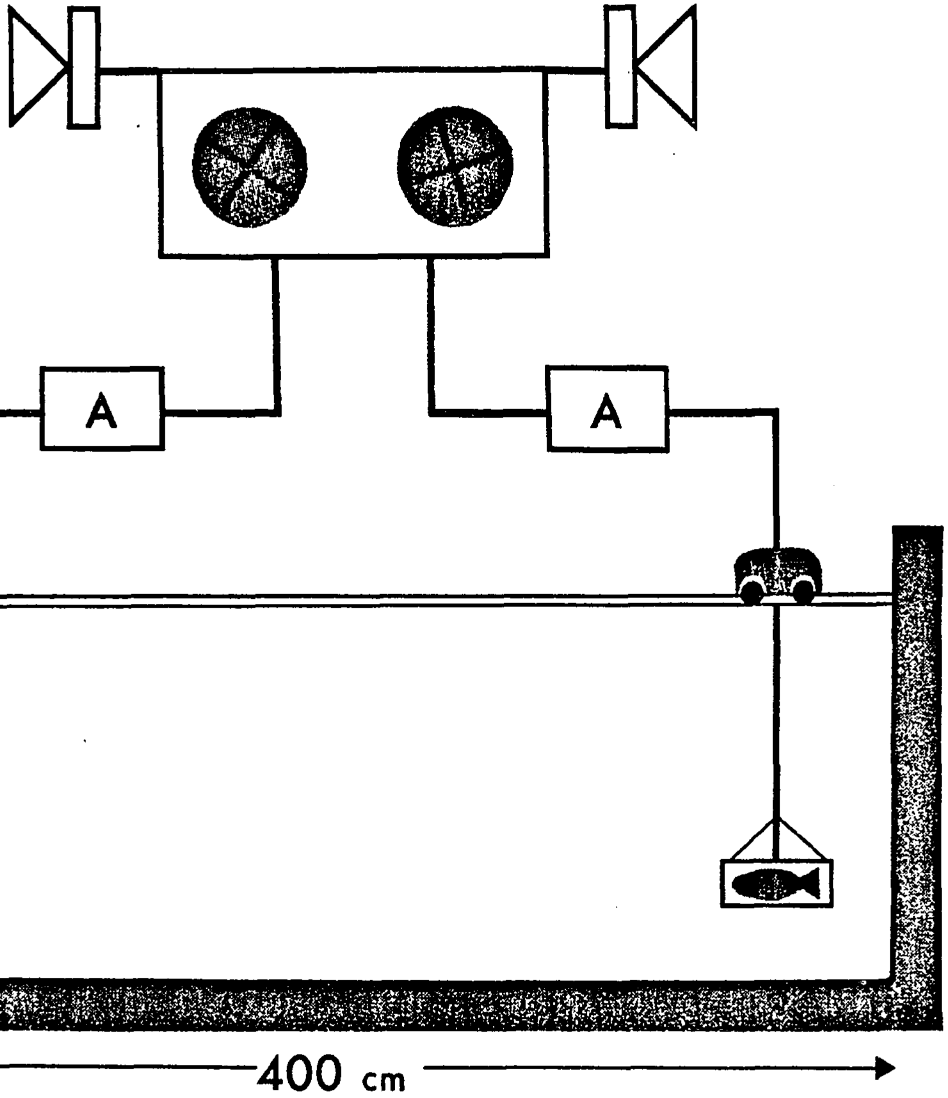
The technique used in this experiment is an adaptation of one developed by Moller and Bauer (1973) to measure EOD cessation distances in pairs of weakly electric fish. Two parallel plastic-coated rods running the length of the tank formed a track 25 cm above the surface of the water (Figure 1). At each end of the track was a wheeled carriage, from which a 15 x 5 cm porous ceramic shelter tube was suspended 10 cm above the tank floor by means of a rigid hollow plastic rod. Each tube had an opening at one end. During experiments a fish was confined within the tube by a sliding plastic partition which covered the open end. A motor-driven system of pulleys allowed one carriage/tube assembly to be moved back and forth along the track at a speed of 1.9 cm/sec while the other carriage/tube assembly remained stationary.

During the experiments, one fish was confined to each tube, thereby excluding mechanical and visual interactions between the fish and significantly reducing any chemical or acoustic interactions. The electric organ discharges (EODs) of both fish were monitored with a pair of carbon electrodes affixed to each tube (interelectrode distance = 10 cm). The EODs were differentially amplified and recorded on separate channels of a two-channel Sony tape recorder (Model TC-270). In addition, EODs were monitored by loudspeakers throughout the experiments.

The experimental procedure was as follows: the tubes were positioned at opposite ends of the tank, at an intertube distance of 380 cm. Intertube distances were measured from the center of one tube

Figure 1

Experimental set-up. Two mormyrid fish were confined to porous shelter tubes which were suspended from an overhead track. The fish on the right was moved from its original position (intertube distance: 380 cm) towards its conspecific on the left and back again. The electric organ discharges emitted by both fish were monitored from a pair of electrodes affixed to each shelter, differentially amplified, and recorded separately on tape.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400 cm

to the center of the other. After one minute of EOD recording with the tubes in this position, one tube was moved toward the other until one of the fish ceased discharging for at least 500 milliseconds, at which time tube movement was stopped. The intertube distance at which EOD cessation occurred was defined as <u>EOD cessation distance</u>. Following one minute of recording at the EOD cessation distance, the movable tube was returned to its original position. One minute of stationary recording plus one forward and back excursion of the tube constituted a trial. Each pair of fish was given 5 to 10 such trials during an experiment.

The electric field emanating from a discharging fish approximates a dipole shape at points distant from the fish (Knudsen 1975). Because of this, the distance at which the fish are able to detect each other may vary depending upon how they are oriented toward each other. Accordingly, each pair of fish received half of the trials with the tubes oriented end-to-end and half of the trials with the tubes oriented parallel to each other. Current generated by the EOD flows almost exclusively parallel to the body of a distant recipient fish in the parallel orientation and perpendicular to the body of a recipient fish oriented end-to-end with respect to the sender fish. The effective stimulus for electroreceptors, however, is transepithelial <u>voltage</u> (Bennett 1971b; Viancour 1979). Since voltage lines run perpendicular to current lines, parallel orientation should result in maximum potential across the skin of the receiver and, therefore, optimal electroreceptor response. It was expected that the fish would respond to each others' EODs at larger distances in the parallel orientation.

In order to determine whether EOD cessation was actually a reaction to the other fish or merely to movement of the tubes or to some other extraneous disturbance, two types of control trial were done: (1) with the movable tube occupied and the stationary tube empty, and (2) with the movable tube empty and the stationary one occupied. It should be noted that these control trials allowed me only to test for differences in a fish's response to a discharging conspecific versus an empty tube. I cannot be certain whether a response on an experimental trial represented a reaction to the EODs of a conspecific or to the conspecific's physical presence.

Each pair of fish received four control trials, two of each type. To control for changes in responding that may have taken place during the experiment, two control trials were done before the experiment began, and two were done at the end.

Along with the EOD recordings, the following data were gathered during each trial: the intertube distance at which EOD cessation occurred; the intertube distance at which discharging resumed; and which fish stopped discharging (smaller vs. larger). At the end of the experiment the standard length of each fish was determined, and both fish were placed in a 375-liter communal tank.

This procedure was repeated at five different water conductivities: 2.0 ± 1.4, 52.0 ± 5.4, 153.0 ± 4.8, 314.0 ± 17.5, and 678.0 ± 40.9 µS/cm (500, 19.2, 6.5, 3.2 and 1.5 kOhm.cm). Conductivity was varied by the addition of appropriate quantities of sea salts ("Instant Ocean") to aged, aerated tap water. Water of the lowest conductivity was obtained by passing tap water through a deionizer (Barnstead High

Capacity Hose Nipple Cartridge). Conductivity was measured using a conductivity meter (Yellow Springs Instrument Corp. S-C-T Meter Model 33).

Amplitude measurement of individual EOD

The peak-to-peak EOD amplitudes of three fish were measured at eight different water conductivities (10, 50, 120, 300, 700, 3900, 10000, and 36000 µS/cm). A fish was confined to a shelter tube as described previously and its EODs were recorded through the electrodes affixed to either end of that tube. Individual EODs were displayed on a Tektronix 502A oscilloscope and photographed.

Electric field gradient measurements

In order to estimate electric field conditions, the peak-to-peak EOD amplitudes of three fish were measured as a function of distance from the fish. Measurements were made at each conductivity level used in the behavioral experiments (except at the lowest, since water of this low a conductivity was not found to be conducive to continued survival of the fish). A fish was confined to one of the shelter tubes and the strength of the electric field gradient (peak-to-peak EOD amplitude/interelectrode distance) was measured between the two electrodes attached to the second, empty tube. Measurements were made first with the tubes adjacent to each other, and then repeatedly as the intertube distance was increased in 5 cm steps. Measurements were made with tubes in both end-to-end and parallel orientations.

Data Analysis

As described above, both tape recorded electric organ discharge data and behavioral data were collected during this experiment. Most of the behavioral data, such as the effects of water conductivity and of tube orientation on EOD cessation and EOD resumption (rebound) distances were assessed by means of one-way and two-way analyses of variance and t-tests. A Z-test for significance of a proportion was used to test for effects of fish size.

Sections of the tape recorded EOD data were analyzed in a sequential mode on a Synex interval histogram computer by displaying the EOD frequency of each fish at 500 millisecond intervals throughout the trial. In this way it was possible to compare the EOD activity of the two fish at any intertube distance.

Error Estimation

The electric field of a discharging fish emanates from the electric organ which is located in the caudal peduncle. The position and orientation of the fish inside the shelter tube will determine the location of the source of the field and, by extension, the strength of the field at any distance from the electric organ.

Because both fish were able to move around somewhat inside the tubes, it is necessary to estimate the amount of error this might have introduced into the measurements. Although it would have been possible to restrain the fish so that no movement was possible, it was judged that such a manipulation would prove too disruptive of the fish's normal EOD behavior.

Since different degrees of error are possible in the end-to-end and parallel tube orientations, each orientation will be considered separately.

Figure 2

Possible sources of error due to variation in orientation and position of fish.

Figure 2

POSSIBLE SOURCES OF ERROR DUE TO VARIATION IN ORIENTATION AND POSITION OF FISH

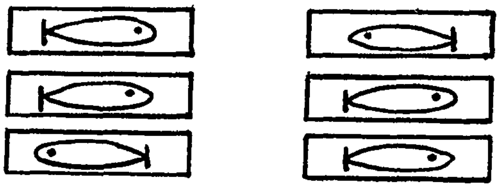
I END TO END TUBE ORIENTATION

A. POSSIBLE FISH ORIENTATIONS

1) Head to head

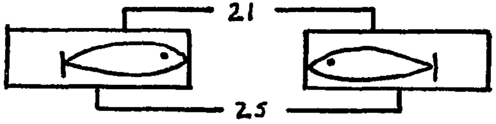
2) Head to tail

3) Tail to tail

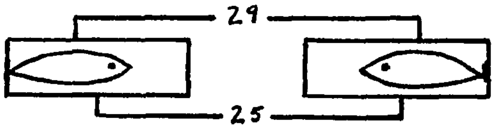


B. POSSIBLE FISH POSITIONS

1) Fish are as close together as possible



2) Fish are as far apart as possible

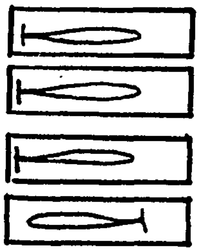


II PARALLEL TUBE ORIENTATION

A. POSSIBLE FISH ORIENTATIONS

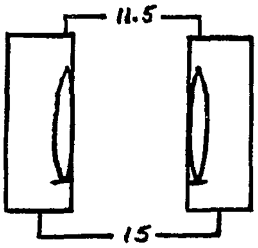
1) Parallel

2) Antiparallel

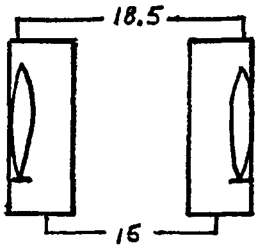


B. POSSIBLE FISH POSITIONS

1) Fish are as close together as possible



2) Fish are as far apart as possible



I. End to end tube orientation (see Figure 2)

A. Orientation of fish inside tubes--One source of potential error is the orientation of each fish inside its tube. The two fish could assume the following orientations:

1) head to head
2) head to tail
3) tail to tail

As was mentioned previously, the electric organ is located in the tail. The greatest concentration of electroreceptors is found near the head, with a sparser distribution of electroreceptors over the rest of the body. Thus the perceived strength of the EODs of one fish as detected by the other would vary depending upon which of the above orientations each fish assumed. Perceived EODs would be weak for both fish in the head to head orientation; they would be slightly stronger for both in the tail to tail orientation. The strength of perceived EODs of the conspecific would be strongest for the fish on the left (in Figure 2) in the head to tail orientation, because this fish's greatest concentration of electroreceptors is closest to the other's electric organ. They would be weakest for the fish on the right, because its greatest concentration of electroreceptors is farthest away from the other's electric organ.

B. Position of fish inside tubes--Another potential source of error stems from the fact that the tubes at 15 cm are several centimeters longer than even the largest fish. This raises the possibility that the fish may have stayed closer to one of the ends of the tube, thereby displacing the source of the electric field. Consider two fish of average length--11 cm--inside tubes that are 25 cm apart:

1) Fish are as close together as possible. As is shown in Figure 2, the centers of the tubes are 25 cm apart, but the centers of the fish are 21 cm apart.

2) Fish are as far apart as possible. In this case, the tube centers are 25 cm apart, while the fish centers are 29 cm apart.

Thus there is a possibility of an average error of up to 4 cm in either direction in the reported intertube distances in end-to-end trials attributable to the positions of the fish inside the tubes.

II. Parallel tube orientation--when the tubes were in the parallel orientation, the possibility of error was smaller than in the previous case.

A. Orientation of fish inside tubes--Again, the first potential source of error is the orientation of each fish inside its tube. The fish could assume the following orientations (Figure 2 gives an overhead view of the tubes):

1) Parallel

2) Antiparallel

The perceived EODs of the conspecific would be stronger in the antiparallel orientation, where each fish's greatest concentration of electroreceptors is closest to the other's electric organ, and weaker in the parallel orientation, where each fish's electroreceptors are farther from the other's electric organ.

B. Position of fish inside tubes--This too was a source of error in the parallel orientation trials, though smaller than in the end-to-end trials. Consider two fish confined to tubes whose central axes are 15 cm apart. The tubes were 5 cm in diameter, and the average fish was 1.5 cm in diameter.

1) Fish are as close together as possible. As is shown in Figure 2, the central axes of the tubes are 15 cm apart, while the central axes of the fish are 11.5 cm apart.

2) Fish are as far apart as possible. In this case, the central axes of the tubes are 15 cm apart, while the central axes of the fish are 18.5 cm apart. Thus, there is the possibility of an average error of up to 3.5 cm in either direction in the reported intertube distances in parallel trials. It should be noted, however, that because of the curvature of the walls of the shelter tubes, it is unlikely that a fish would stay at the extreme edge of the tube.

In addition, it is likely that the fish's position in the tube would change as the fish swam along with the moving tube. Thus all the error estimates calculated herein represent upper limits.

III. Error resulting from experimental procedure.

Another source of error derived from the methodology used in the experiment. As was mentioned in the Methods section, tube movement was stopped when one fish ceased discharging. Although every effort was made to stop the tube as soon as discharge cessation occurred, there were occasionally trials on which up to two seconds elapsed between discharge cessation and tube movement cessation. At a tube movement rate of 1.9 cm/second, this translates into a maximum potential error of 3.8 cm in the reported EOD cessation distances. It should be noted that this error would be in one direction only--EOD cessation distances could be up to 3.8 cm larger than those reported, but they could never be smaller.

Results

EOD Cessation and Rebound

Forward Tube Movement. In this section I will present data collected during the first half of each trial, as one tube was being moved toward the other. These data, therefore, were obtained as the distance between the tubes was decreasing.

EOD cessation response. A response that occurred during the forward tube movement phase was the EOD cessation response (Figure 3). As the distance between the two caged fish was decreased, there came a point at which one fish (Fish B in Figure 3) ceased to emit electric organ discharges for a period ranging from several seconds to several minutes. The EOD cessation response occurred on 156 of the 168 experimental trials (92.9%).

EOD cessation was not a response to tube movement. In control trials (with one tube empty), EOD cessation was observed on only 3 of the 83 trials (3.6%). A Z-test for significance of a difference between two proportions revealed a highly significant difference ($p < .001$) between the proportions of EOD cessations seen on experimental and control trials.

Effect of water conductivity on EOD cessation distance. Water conductivity had a marked effect on EOD cessation distance. As conductivity was increased, EOD cessation distances decreased.

Figure 3

Electric organ discharge (EOD) cessation and rebound EOD activity from two fish (A and B) during successive 500 ms intervals. B was moved toward A; the movement was stopped when B ceased discharging (cessation distance). Following a 60 sec stationary period, fish B was returned to its starting position.

Note: Fish B's EOD rebound caused a brief EOD cessation in A. The associated rebound distance was larger than the initial cessation distance.

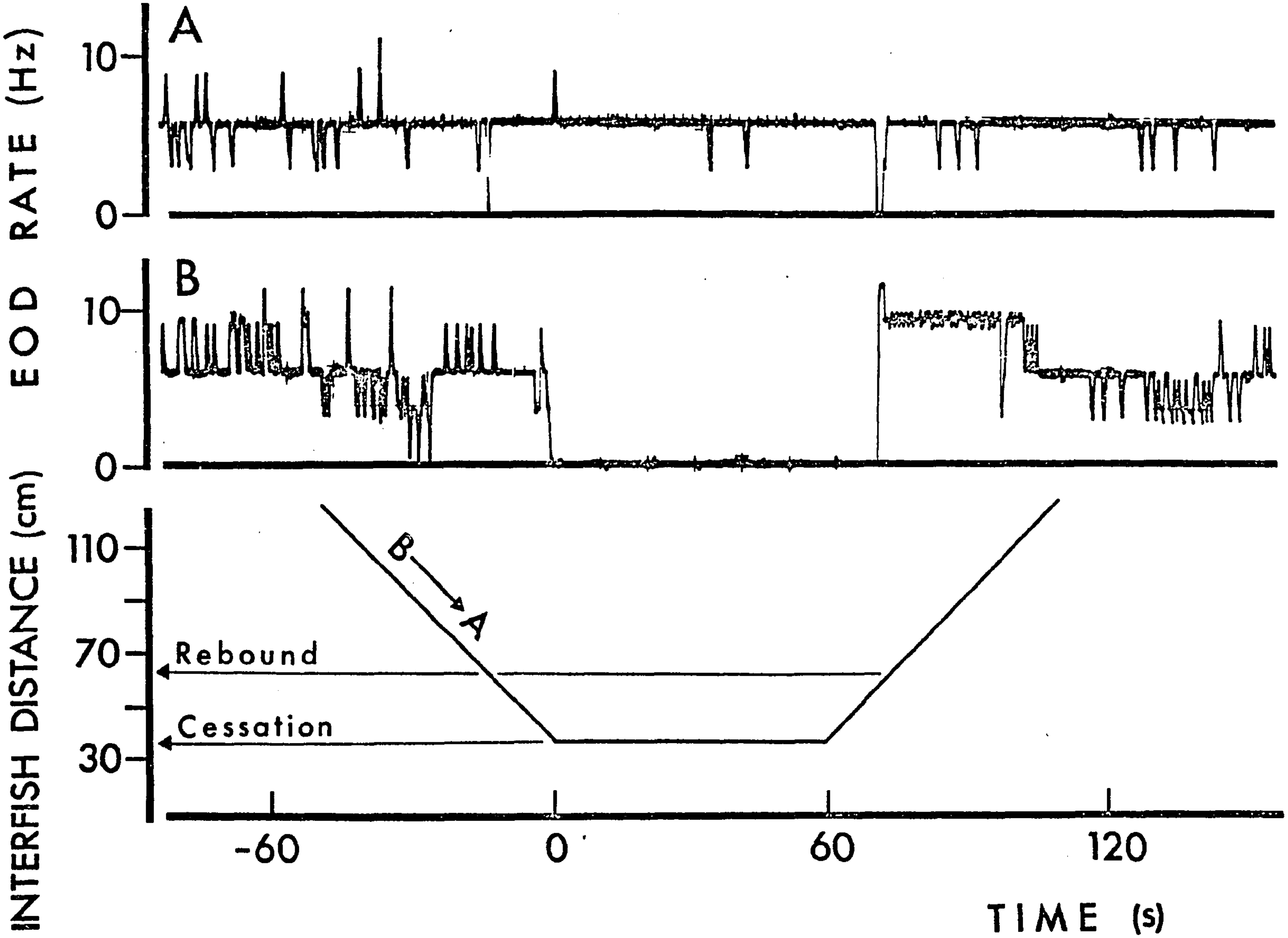

A
B
EOD RATE (Hz)
10
0
10
0
INTERFISH DISTANCE (cm)
110
70
30
B
A
Rebound
Cessation
-60
0
60
120
TIME (s)

Figure 4

Electric organ discharge cessation distance as a function of water conductivity. (a) linear representation of combined tube orientations (end-to-end and parallel); (b) log-log representation of combined tube orientations. Dashed line: best-fitting line as determined by least-squares linear regression ($\log y = -0.56 \log x + 2.97$); (c) linear representation of data according to tube orientation (triangles: end-to-end; squares: parallel); (d) log-log representation of data; dashed lines: best-fitting lines as determined by linear regression (end-to-end: $\log y = -0.58 \log x + 2.93$; parallel: $\log y = -0.63 \log x + 3.22$). Dashed lines in (a) and (c) represent cessation distances as predicted by linear regression equations.

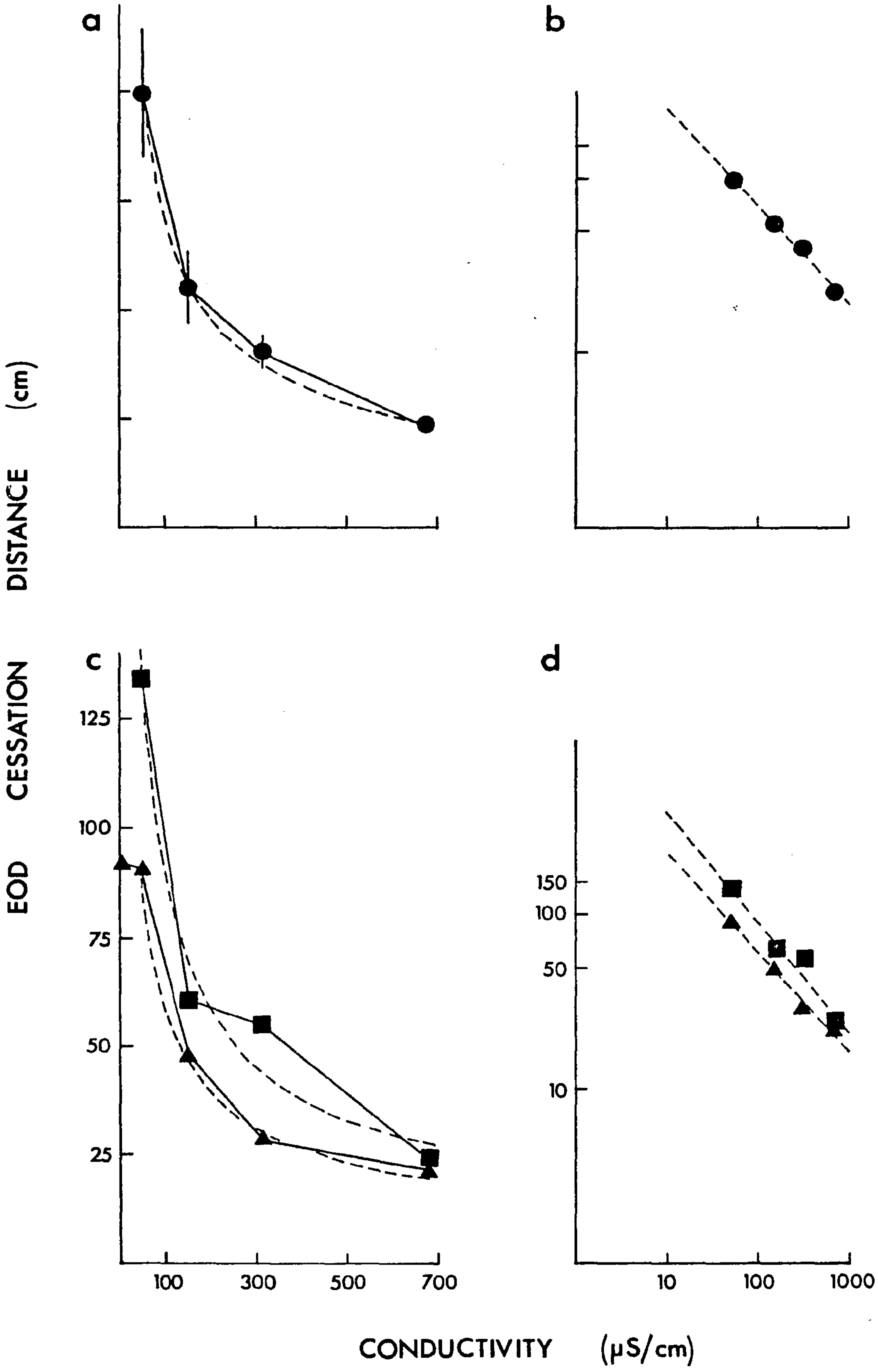

a
b
c
d
DISTANCE (cm)
EOD CESSATION
125
100
75
50
25
150
100
50
10
100
300
500
700
10
100
1000
CONDUCTIVITY (µS/cm)

Figure 4a shows EOD cessation distances plotted as a function of water conductivity for combined end-to-end and parallel tube orientations. (Data taken at the lowest conductivity are not included here, since only end-to-end orientation trials were run at that conductivity.) At 52 µS/cm, the mean EOD cessation distance was 99.6 cm; as water conductivity was raised in steps, the mean EOD cessation distance decreased until, at 678 µS/cm, EOD cessation did not occur until the fish were a mean distance of 22.5 cm apart.

In Figure 4b, the same data are plotted logarithmically. A least-squares linear regression was used to compute the best-fitting line using the logarithmic values of the data points. It is described by the equation: $\log y = -0.56 \log x + 2.97$, where y represents EOD cessation distance and x represents conductivity. The correlation of the points to the best-fitting line, $r = 0.995$. The regression equation makes it possible to predict EOD cessation distance at a given water conductivity. The dashed curve in Figure 4a is a plot of such predicted EOD cessation distances.

Figure 4c shows EOD cessation distances plotted separately according to tube orientation. At all conductivity levels the mean EOD cessation distances were larger when the tubes were oriented parallel to each other. Fish in the parallel orientation reacted to each other a mean of 21.2 cm farther apart than they did in the end-to-end orientation.

Figure 4d illustrates the corresponding logarithmic functions which are described by the equations: $\log y = -0.58 \log x + 2.93$ for the end-to-end orientation, and $\log y = -0.63 \log x + 3.22$ for the parallel orientation. Correlations of data points with the best-fitting linear functions are $r = 0.994$ and $r = 0.971$ for end-to-end and parallel orientations respectively. The dashed curves in Figure 4c are linear plots of predicted EOD cessation distance values, which are valid for conductivities in the middle range exceeding 50 μS/cm. EOD cessation distance remained constant at 2 and 52 μS/cm. A t-test revealed no significant difference between EOD cessation distances measured at 2 and 52 μS/cm ($p > .20$).

The effects of water conductivity on EOD cessation distance were highly significant. One-way analyses of variance performed on combined, parallel, and end-to-end orientation data revealed a significant effect of conductivity on EOD cessation distance in all three cases ($p < .001$ for combined and parallel data; $p < .05$ for end-to-end data.)

The appropriateness of a power function in describing the data indicates several things:

1) At very low water conductivities, EOD cessation distance should be large. As conductivity is raised, EOD cessation distance will decrease, eventually approaching an asymptote. The slope represents the rate at which the function decreases, and the y-intercept is the log of the theoretical EOD cessation distance at a water conductivity of absolute zero.

2) The fact that behavioral responses can be predicted so accurately at middle range values suggests that the behavioral response is closely tied to a physical threshold value. A fish does not cease discharging when it "wants to," but rather when the electrical field of the other fish reaches a certain intensity.

Interestingly, cessation distances obtained from similar-sized (11 cm) Gnathonemus petersii concur with the power functions described herein (Moller and Szabo, in preparation). Thus, the equation may be useful in predicting EOD cessation distances in other species and situations, as well.

Effect of fish size. The relative sizes of the fish had a significant effect on which fish ceased discharging in response to the approach of a conspecific. If, in a given experiment, one member of a pair showed EOD cessation on at least 75% of trials, that fish was scored as the "stopper" in the pair. In 11 out of the 14 pairs (79%) in which there was a consistent "stopper," it was the smaller fish which stopped. A Z-test for significance of a proportion showed that the smaller fish in a pair was significantly more likely to stop discharging than was the larger ($p < .05$).

Reverse tube movement. In this section I will present data collected as the moving tube was returned to its original position during the second half of each trial. These data, therefore, were obtained as the distance between the tubes was increasing.

The EOD rebound burst. A response observed in the experiments which has not been reported previously is an EOD rebound burst. In some pairs, the fish that had ceased discharging in response to proximity of a conspecific remained silent throughout the one minute of stationary recording, and resumed discharging only when the tubes were moved apart at the end of the trial (Figure 3). As the intertube distance increased, the electrically "silent" fish resumed discharging with a high frequency burst of EODs which lasted several seconds. Compared with the fish's mean EOD repetition rate before cessation, the initial mean rebound rate almost doubled. The rebound burst was observed in 11 pairs of fish on 29 of the 168 experimental trials, at three of the five water conductivities. The intertube distance at which the rebound burst occurred was also affected by water conductivity, with larger distances recorded under low conductivity conditions (Table 1).

Effect of rebound burst on EOD activity of the other fish. On 62% of the trials where a rebound occurred, the rebound burst of one fish produced a change in the EOD pattern of the other member of the pair, indicating that the fish can interact electrically at distances exceeding those associated with the initial cessation response monitored during the forward tube movement. On 9 trials (31%), the rebound burst was followed by a 2 to 3 second elevation of the other fish's discharge rate, on 5 trials (17%) by 2 to 3 second decrease, and on 4 trials (14%) by an EOD cessation lasting several seconds (Figure 3). Changes in discharge rate were detected by visual inspection of the EOD record. On the remaining 11 trials (38%) there was no detectable change in the fish's discharge rate.

Individual EOD and electric field gradient (EFG) measurements.

To estimate the electric field conditions to which a recipient fish in its shelter tube was exposed, we measured the amplitudes of the four most prominent phases of an individual EOD under different conductivity conditions and at different interfish distances.

TABLE 1

EOD REBOUNDS AS A FUNCTION OF CONDUCTIVITY

Conductivity	Mean Rebound* Distance	Number of Rebounds	% of Trials on Which Rebounds Occurred
52 μS/cm	156.5 cm	13	37%
314 μS/cm	123.8 cm	8	21%
678 μS/cm	63.1 cm	8	21%

*Parallel and end-to-end orientation data combined.

EOD amplitude changes at different conductivities. Peak-to-peak EOD amplitudes of each of three fish were measured at 8 water conductivities. This was done by confining a fish to one of the shelter tubes and recording its EODs through the electrodes at either end of the tube. Individual EODs were displayed on a Tektronix 502A oscilloscope, then photographed and measured.

The EOD of *B. niger* consists of four characteristic phases: a small head-negative phase (a), a large head-positive phase (b), followed by a slightly larger head-negative phase (c), and a small head-positive fourth phase (d). Figure 5 illustrates the effect of different water conductivities on the individual EOD. The amplitudes of all four phases decreased with increasing conductivity. The peak-to-peak amplitude of the two largest phases (b, c) shrank to 50% of the 10 µS/cm size under 120 µS/cm conditions, and to 30% of the 10 µS/cm size under 300 µS/cm conditions. This relationship can be expressed by the logarithmic function: $\log y = -0.68\ x + 3.68$, with y expressing the EFG in mV/cm, and x the water conductivity in µS/cm (correlation coefficient = 0.95).

Electric field gradient (EFG) measurements: Changes in EOD amplitude at different distances from fish. For both end-to-end and parallel tube orientations I determined the EFG (from a fish resting in one of the shelter tubes) between the recording electrodes of the second, empty tube for various intertube distances (Figures 6a and b). The size of the EFG fell off as a power function with increasing distance between the recording electrodes and the EOD-generating fish. The correlation coefficients for the logarithmically plotted data

Figure 5

Electric organ discharge (EOD) waveforms from Brienmomyrus niger at different water conductivities. Peak-to-peak amplitude decreased as conductivity increased; a, b, c, and d refer to four phases of EOD waveform.

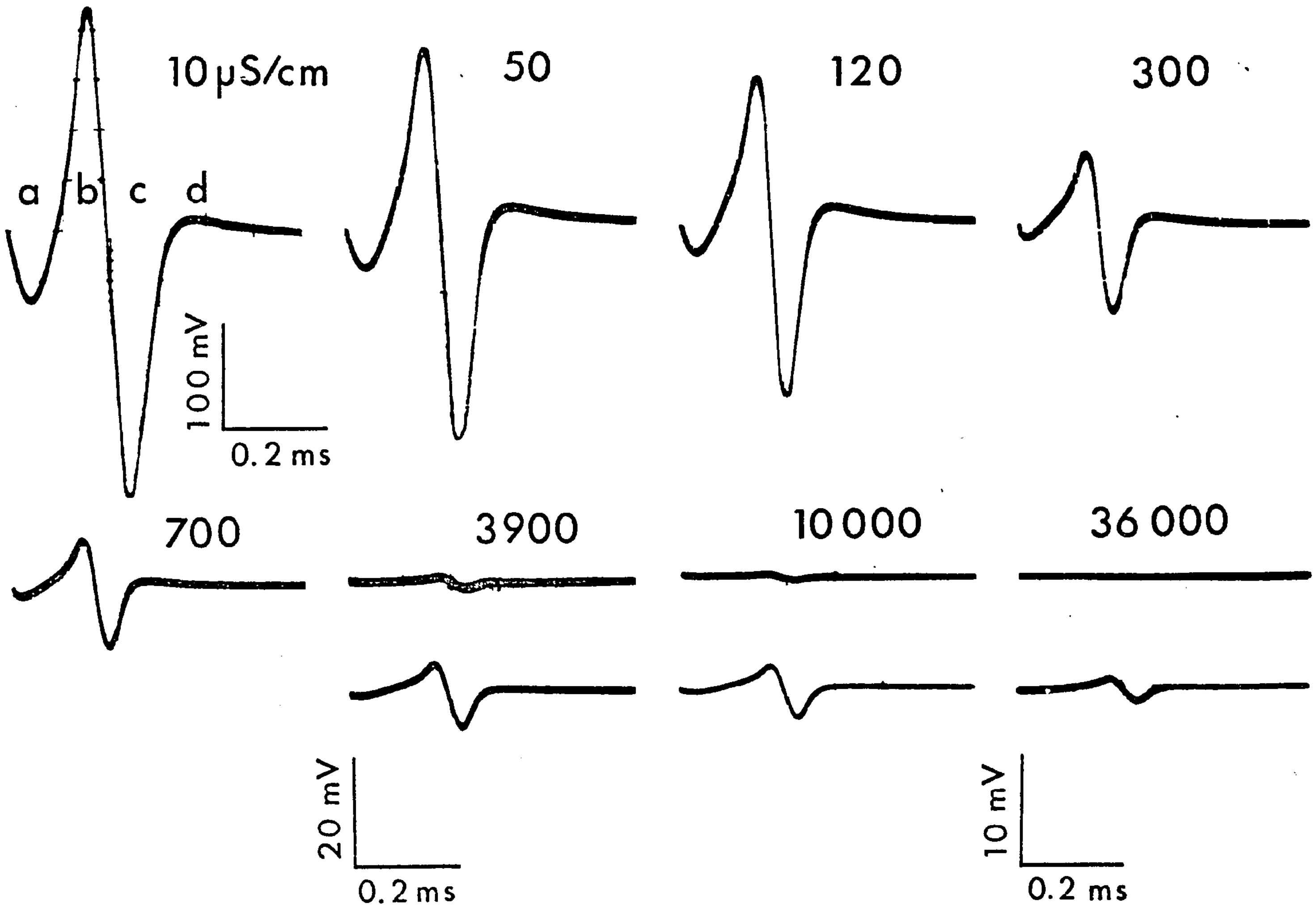
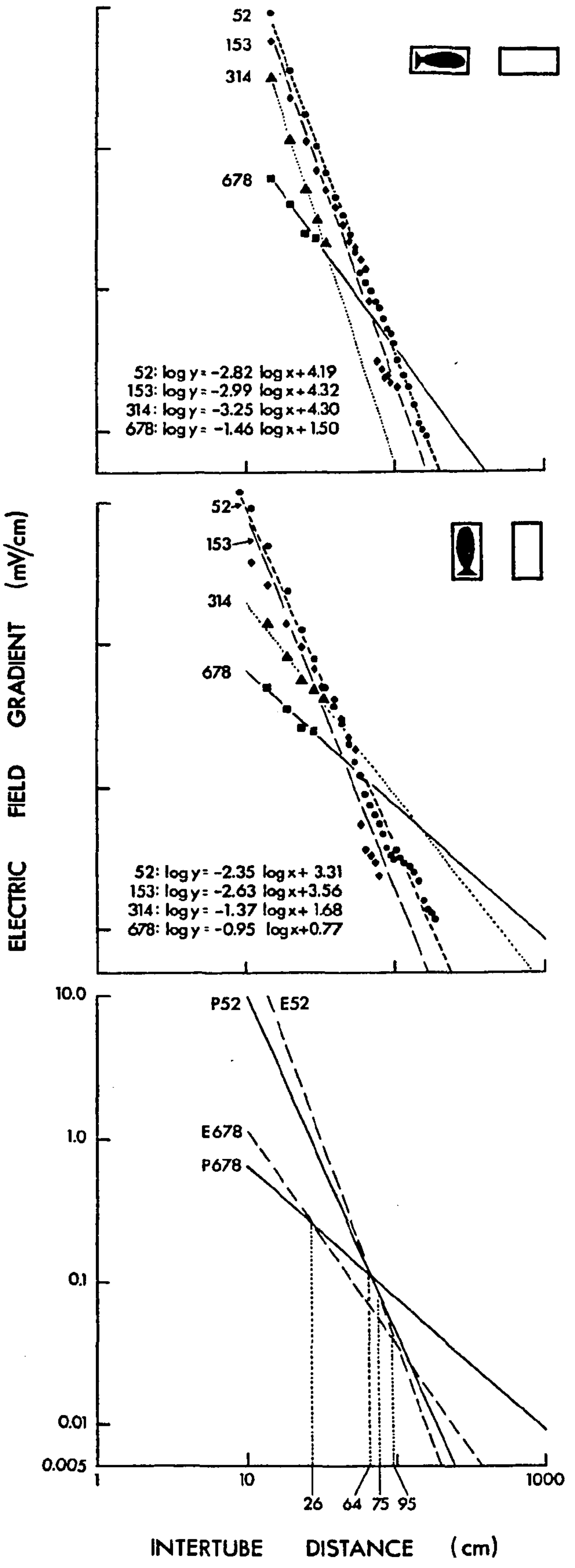

10 μS/cm
a
b
c
d
100 mV
0.2 ms
50
120
300
700
3900
10 000
36 000
20 mV
0.2 ms
10 mV
0.2 ms

Figure 6

Electric field gradient (EFG) as a function of intertube distance. EFG was monitored from empty tube as it was moved toward and away from stationary tube containing live fish. (a) end-to-end tube orientation, (b) parallel tube orientation. EFG decreased exponentially with increasing distance from fish. In both orientations, the most rapid decline of the EFG occurred at low conductivities. (c) Comparison of end-to-end and parallel tube orientations under lowest and highest conductivity conditions. At 26 cm (conductivity: 678 µS/cm) and 75 cm (52 µS/cm) the EFGs were equal for end-to-end (E) and parallel (P) tube orientations. At 64 cm (P) and 95 cm (E) respectively, the EFGs were equal for the lowest and highest conductivity condition.


52
153
314
678
52: log y = -2.82 log x + 4.19
153: log y = -2.99 log x + 4.32
314: log y = -3.25 log x + 4.30
678: log y = -1.46 log x + 1.50
52
153
314
678
52: log y = -2.35 log x + 3.31
153: log y = -2.63 log x + 3.56
314: log y = -1.37 log x + 1.68
678: log y = -0.95 log x + 0.77
ELECTRIC FIELD GRADIENT (mV/cm)
10.0
1.0
0.1
0.01
0.005
P52
E52
E678
P678
1
10
1000
26
64
75
95
INTERTUBE DISTANCE (cm)

ranged from r = 0.962 to r = 0.999. The respective equations (as determined by least-squares linear regression where y represents EFG and x represents distance from fish) are indicated in Figure 6. In both the end-to-end and parallel tube orientations, the most rapid rate of decline of the EFG occurred at the lowest conductivities (52 and 153 µS/cm).

Two important results of the EFG measurements are illustrated in Figure 6c, which compares the end-to-end and parallel EFG functions at the lowest (52 µS/cm) and highest (678 µS/cm) conductivities:

1) A comparison of the two conductivities showed that at points near to the fish, the strength of the EFG was greater at low conductivities. Up to an interfish distance of 64 cm for the parallel orientation (intercept of lines P678 and P52 in Figure 6c) and 95 cm for the end-to-end orientation (intercept of E678 and E52 in Figure 6c), the strength of the EFG was markedly greater at the lower conductivity.

2) A comparison of the two tube orientations showed that at all conductivity levels, the initial EFG was higher and the rate of decline more rapid in the end-to-end than in the parallel orientation (compare lines E52 and E678 to P52 and P678 in Figure 6c). At points close to the fish (within 26 cm at 678 µS/cm and within 75 cm at 52 µS/cm) the EFG was higher in the end-to-end than in the parallel orientation. However, the end-to-end EFG declined more rapidly, so at distances greater than 26 and 75 cm (for 678 and 52 µS/cm, respectively), the EFG in the parallel orientation exceeded that in the end-to-end orientation.

Comparison: EOD cessation distances and associated EFGs. Table II illustrates the relation between the fish's behavioral response (EOD cessation at a particular distance) and the associated EFG which was calculated from the appropriate equations in Figures 6a and b. As was mentioned previously, with increasing conductivity, the EOD cessation distance decreased (Table II, columns 1 and 4). Correspondingly, with increasing conductivity, the size of the EFG at EOD cessation distance increased (Table II, columns 2 and 5).

It is likely that the attenuation of the emitted electric signal at high conductivities (cf. Figures 5 and 6) is a principal cause of the associated decrease in EOD cessation distance. However, a smaller EOD cessation distance could also result from a rise in electroreceptor threshold at high conductivities.

The rise in EFG values at EOD cessation distances as conductivity was increased supports this suggestion. In the end-to-end orientation, for example, the fish ceased discharging at 52 μS/cm when the field gradient produced by the other fish's discharge reached 0.046 mV/cm. At 153 μS/cm, however, discharge cessation did not occur until the field gradient was over four times stronger. This suggests that the sensitivity of the fish's electroreceptors may decrease as conductivity is raised. Columns 3 and 6 in Table II show the ratios of the EFGs at 153, 314, and 678 μS/cm to the EFG at 52 μS/cm. Using this ratio as a behavioral index of receptor sensitivity, I found that the threshold at 153 μS/cm was approximately 4 times higher, and at 314 μS/cm approximately 8 to 10 times higher than at 52 μS/cm for both end-to-end and parallel tube orientations. The relationship between

TABLE II

ELECTRIC FIELD GRADIENTS AT ELECTRIC ORGAN DISCHARGE CESSATION DISTANCES AS COMPUTED FROM EQUATIONS IN FIGURE 6

	End-to-End			Parallel		
Conductivity	(1) D_E (cm)	(2) EFG_E (mV/cm)	(3) Ratio	(4) D_P	(5) EFG_P	(6) Ratio
52	90.9	0.046	1.0	134.6	0.020	1.0
153	47.7	0.198	4.3	60.5	0.075	3.8
314	28.5	0.372	8.1	54.9	0.199	10.0
678	21.5	0.359	7.8	23.4	0.299	15.0

EOD cessation distance and cessation distance EFG (for all conductivities and tube orientations) can be expressed by the logarithmic function: $\log y = -1.55 \log x + 1.73$, where y represents EFG and x represents EOD cessation distance (Figure 7).

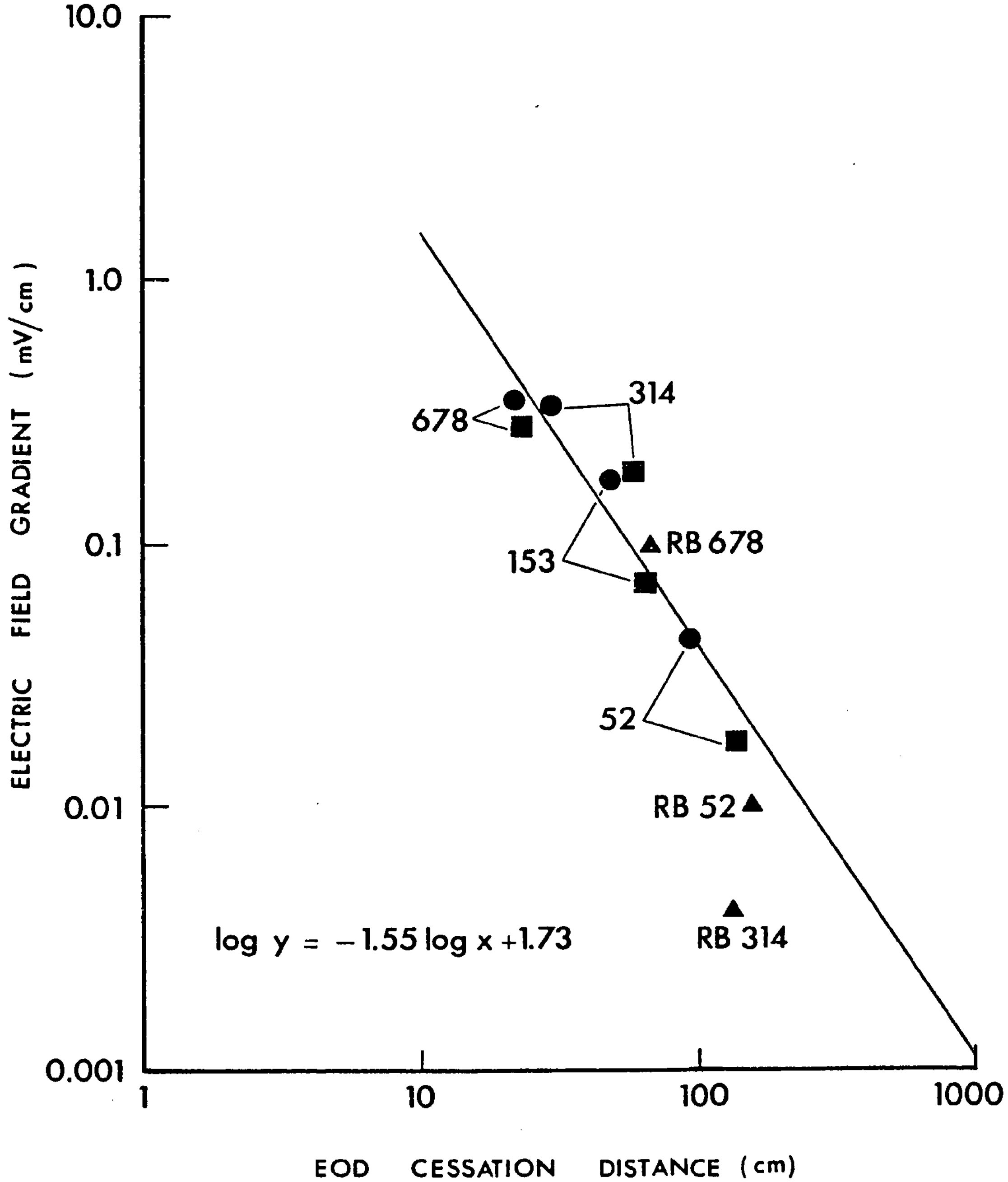
The EOD cessation distances obtained for parallel tube orientation were consistently larger than those for end-to-end orientation at all water conductivities, and the EFGs calculated for each cessation distance were therefore consistently smaller for the parallel orientation (Table II). The most pronounced difference in EOD cessation distance was at the lowest conductivity (52 µS/cm): 90.9 cm for end-to-end orientation vs. 134.5 cm for parallel orientation. This result is in accordance with our finding that for interfish distances exceeding 75 cm (cf. Figure 6c) the EFG was larger for parallel than for end-to-end orientation.

Discussion

In the following pages, I will discuss EOD cessation by one fish as a response to the presence of a conspecific. As was mentioned in the Methods section, a fish's "presence" refers to both its body and its EODs. Since each fish was present both physically and electrically, I could not be absolutely certain whether EOD cessation was a response to a conspecific's physical presence or to its EODs. The method used by a fish to detect the physical presence of a conspecific differs from that used to detect its electrical presence. In the present experiment, EOD cessation could have been a response to the conspecific's body, as detected through active electrolocation, or to its EODs, as detected through electrocommunication. (The mechanics of

Figure 7

Threshold curve showing the relationship between electric organ discharge (EOD) cessation distance and the electric field gradient calculated for this distance (insert: equation for linear regression line). Circles: end-to-end; squares: parallel data. Numbers indicate conductivity conditions in µS/cm. RB and triangles: EOD rebound data.


10.0
1.0
0.1
0.01
0.001
1
10
100
1000
ELECTRIC FIELD GRADIENT (mV/cm)
EOD CESSATION DISTANCE (cm)
314
678
153
RB 678
52
RB 52
RB 314
log y = −1.55 log x +1.73

both electrolocation and electrocommunication have been discussed previously.)

There are, however, several lines of evidence which suggest that EOD cessation represented a response to the other fish's EODs--electrocommunication--rather than to its physical presence:

1) Fish show EOD cessation in response to EOD-like electrical stimuli when no other fish is physically present. Moller (1970) found that *Gnathonemus petersii* ceased discharging when presented with low frequency, low intensity electrical stimuli which simulated the resting EOD activity of another fish.

2) When two fish are present, they react to each other's EODs. Using a paradigm similar to the one in this experiment, Moller and Bauer (1973) found that at a "threshold interfish distance" (about 30 cm) there was a significant negative correlation in the EOD repetition rates of two *G. petersii*. An EOD frequency increase by one fish caused a temporary EOD cessation in the other fish.

3) The range of electrolocation is much smaller than the range of electrocommunication. Using a conditioning procedure, Belbenoit (1970) showed the spatial range of the electrolocating system in mormyrids to be about 4 cm. Push and Moller (1979) found average electrolocation distances for *G. petersii* to be 5.4 cm for highly conductive objects (aluminum cubes) and 7.0 cm for non-conductive objects (plastic cubes). Both of these distances are much smaller than the 30 cm electrocommunication distance reported by Moller and Bauer.

4) In the present experiment, the EOD cessation distance at every conductivity exceeded the range within which the fish is able

to electrolocate. On the basis of these findings, it can be concluded that EOD cessation is a social display related to electrocommunication, and that this response is mediated by the fish's large electroreceptors, the knollenorgans, which respond to the EODs of another fish. In the following discussion, therefore, "presence" will refer to the presence of EODs plus body (except as otherwise noted), but with the understanding that the EODs are probably the more important factor determining the other fish's response.

The EOD Cessation Response

When two fish were confined to shelter tubes at opposite ends of a large tank and when the distance separating them was decreased, there was a point at which one fish reacted to the presence of the other by halting its electric organ discharge activity. It was shown that this EOD cessation was a response to the presence of a conspecific and not a response to movement of the shelter tube or to some other disturbance. As such, this response was used as a behavioral criterion to assess the range of electrocommunication.

Several investigators have suggested that EOD cessation represents a "hiding" response, by means of which one fish attempts to render itself electrically undetectable to another (Bennett and Steinbach 1969; Cleworth 1969). Westby and Box (1970) reported a significant negative correlation between instances of aggressive behavior and time spent in electrical silence in Gymnotus carapo. This finding suggests that the fish which shows EOD cessation is the more submissive fish. Westby and Box also noted that electrically silent fish were attacked less frequently. Kramer (1976) noted that *Gnathonemus petersii* which had been attacked and bitten by conspecifics often ceased discharging altogether. He suggested that discharge cessation was effective in avoiding attack by a conspecific.

In the natural habitat of mormyrid fish, where the water is often quite turbid and visibility is limited, EOD cessation is probably an especially effective hiding strategy. The present experimental conditions simulated the natural habitat in that there was no possibility of visual contact between the fish. In addition, cues arising from a fish's movement were eliminated, and chemical and auditory signals were greatly attenuated by the shelter tubes, leaving the EOD as the single most important indicator of a fish's presence. Thus in the present experiment, even more than in the natural habitat, discharge cessation would help to conceal a fish from a conspecific.

Further support for the hiding response interpretation of EOD cessation comes from the finding that the smaller member of a pair of fish showed the response significantly more frequently than did the larger. Bell, Myers, and Russell (1974) found that after a dominance hierarchy had been established in a pair of fish, EOD rate increases by the dominant fish often evoked EOD cessations in the submissive fish. They also noted that the larger member of the pair was more likely to achieve dominant status.

Thus, the present results support the suggestion that EOD cessation represents an attempt by one fish (usually the smaller, submissive fish) to hide from another (usually larger, dominant) fish by making itself electrically undetectable.

Effect of water conductivity. Water conductivity had a profound effect on the interfish distance at which EOD cessation occurred. The EOD cessation distance remained fairly constant at low conductivities (2 and 52 μS/cm) and then dropped off rapidly under higher conductivity conditions. This finding is in agreement with results reported by Bell, Bradbury, and Russell (1976), who measured peak-to-peak voltage of the EOD at points in the water near a discharging *G. petersii*. They reported that peak-to-peak voltage rose as water conductivity decreased, levelled off at about 50 μS/cm, and remained constant as conductivity was further decreased. In the natural habitat of mormyrid fish, water conductivity is normally quite low (Gosse 1963; Hopkins 1972; Moller, Serrier, and Belbenoit 1976; Moller et al. 1979). Bell et al. suggest that the relative insensitivity of peak-to-peak EOD voltage to changes in conductivity below 50 μS/cm could simplify the analysis process in electrolocation, because a conductivity fluctuation would not have such a great effect on the strength and shape of the fish's EOD-produced electric field.

It is also possible that the electrocommunication process may be facilitated at low water conductivities. Knudsen (1974) reported a positive correlation between the length of a fish and the size of that fish's electric field. This field characteristic could provide information on size or age of a fish, and thus play a role in intraspecific recognition. Knudsen (1974) stated:

> The steepness of the slope of the dipole moment [an absolute measure of the magnitude of an electric fish's field] versus fish length plot is a significant point in this regard. . . . [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 <u>under standard conditions</u> (emphasis added).

As has been shown, at high conductivities, a small change in conductivity can produce a large change in amplitude of the EOD (and, therefore, in strength of the electric field). By contrast, variations in conductivity below 50 µS/cm have a negligible effect on EOD amplitude. The low conductivities normally encountered by the electric fish in its natural habitat may provide the "standard conditions" which enable the fish to estimate accurately the size of other fish on the basis of their electric field strengths.

The decrease in interaction distance at high conductivities is correlated with a rapid attenuation in amplitude of the fish's EOD and possibly with a rise in electroreceptor threshold. Several investigators have modeled an electric fish as a <u>Thevenin</u> equivalent (Harder et al. 1964; Knudsen 1975; Heiligenberg 1977) with the electric organ as its voltage source in series with an inner resistance, R_i, and an outer resistance, R_o, represented by the surrounding water and any objects near the fish.

The actual source voltage, V (measured between the fish's head and tail), under external load can be expressed by $V = \frac{Vmax}{1 + \frac{R_i}{R_o}}$, with Vmax representing the source voltage of the electric organ in the absence of external load. With R_i remaining constant, it follows that a decrease in water resistivity (which is equivalent to an increase in conductivity) will result in attenuation of the peak-to-peak source voltage as shown in Figure 5.

I assume that a sender fish's electric organ discharge signal affects the recipient's electrosensory system and, subsequently, the recipient's own electric organ discharge behavior. The decrease in EOD cessation distance under higher conductivity conditions could be due to the following: regardless of external resistivity, the fish's electroreceptors may have a set threshold at which the animal begins to respond to electroreceptive input from a conspecific's electric organ discharges. Perception of attenuated conspecific signals would necessitate shorter interfish distances (cf. Figure 4).

However, the fish's electroreceptors also "see" the external load (Bennett 1971; Knudsen 1974). Thus the possibility exists that the behavioral criterion, EOD cessation distance, is determined not only by signal intensity, but also by conductivity-dependent receptor sensitivity.

To investigate this further, I used the linear regression estimate for the relation between electric field gradient and EOD cessation distance (see Figure 6a and b) to calculate the electric field gradients associated with each EOD cessation distance (Table II). The results of these calculations showed that the EFG at EOD cessation distance did not remain constant but increased with conductivity. Using the estimated threshold value at 52 µS/cm as a standard, I also calculated for all other conductivity levels the interfish distance at which the electroreceptor would "see" the standard. In all instances, the calculated distances exceeded the empirical ones.

To assess the relative decrease in receptor sensitivity at higher conductivity levels, I used the EFG at 52 µS/cm as the standard and determined the ratio between the threshold gradient at each higher conductivity level and the standard (Table I). For both tube orientations, the relative receptor threshold increased about four- and eight-fold for 153 and 314 µS/cm, respectively. (Ratios for the higher conductivity differ, and may reflect empirical difficulties in establishing the least-square regression estimate.)

Thus, water conductivity affects both signal intensity and receptor sensitivity, and both together help determine the distance at which a fish begins to respond behaviorally to another's electric organ discharges.

Many mormyrid species spawn during the rainy season when the streams and lakes are inundated and conductivity is low (Blache 1960; Okedi 1969; Kirschbaum 1975; Blake 1977). A large electrocommunication range under these conditions could facilitate mate attraction and parent-young interactions (Westby and Kirschbaum 1977). During the non-breeding, dry season, when water conductivity is high, a smaller communication range might allow a greater number of fish to inhabit the same area without interfering with each other electrically.

It is clear that fluctuations in water conductivity will affect electrolocation performance as well. Moller et al. (1979) studied the diurnal activity patterns of mormyrids in the Swashi River, a tributary of Lake Kainji, Nigeria, and found that locomotor activity peaked during the nighttime hours. Thus these fish, like the ones in the present study, could not rely on visual cues for navigation. This fact, combined with the finding of a higher EOD frequency at night, suggests that the fish may depend to a great extent on active electrolocation for navigation. Since water conductivity affects the ranges of both electrolocation and electrocommunication, it is clear that this variable will affect locomotor behavior in the natural habitat.

During the daytime, the Swashi River mormyrids were inactive, hiding under rocks or submerged tree trunks. Moller et al. estimated the interfish distances during the daytime to be 5 to 10 meters. As has been discussed previously, water conductivity directly affects the strength of a fish's EOD-produced electric field and, therefore, the degree of overlap of the fields of neighboring fish. In order to be free of the disruptive effects of another fish's field, each fish must maintain a certain distance from its neighbors. At different conductivities, the optimal distance among fish inhabiting the same area may vary.

Effect of Tube Orientation. It was predicted that since parallel orientation of two fish results in maximum potential across the skin of the receiver, the fish should respond to each others' EODs at larger distances in the parallel than in the end-to-end orientation, particularly at low conductivities. The EOD cessation distances obtained for parallel tube orientation were indeed larger than those for end-to-end orientation at all water conductivities (Table II), and the most pronounced difference in cessation distance was at the lowest conductivity (52 μS/cm): 90.0 cm for end-to-end orientation vs. 134.5 cm for parallel orientation. These cessation distances are large compared with the length of the fish, and the electric field under these conditions approaches that of a dipole field (Knudsen 1975).

The EOD Rebound Burst.

The characteristic EOD cessation response of mormyrid fish to low intensity, conspecific electric signals (Moller 1970; Moller and Bauer 1973) has served as a behavioral criterion to assess the range of electrocommunication. It has been suggested that the EFG associated with the EOD cessation distance reflects a threshold value for the fish's electrocommunication range (Moller 1970). However, a threshold EFG of about 0.05 mV/cm translates into a receptor stimulus of about 0.5 mV (in a 20 cm fish), which is above threshold for most large receptors (Bennett 1971b). Thus, EFGs determined for EOD cessation distances must reflect a motivational rather than a sensory threshold--that is, when the presence of a conspecific becomes sufficiently disturbing or threatening, the subordinate fish displays temporary electrical "silence." Both fish may in fact have detected each other's EODs long before one fish stopped discharging.

The discovery of the EOD rebound burst provides evidence that the range of electrocommunication among mormyrid fish exceeds that reported previously. When the fish were moved apart while one was still electrically "silent," I found that this fish (in 17% of overall trials) resumed EOD activity with a high frequency rebound burst, which in turn influenced the EOD activity of the other fish in 62% of the cases (11% of overall trials). These interactions occurred at inter-fish distances considerably greater than EOD cessation distances (cf. Table 1).

The average EFGs at rebound distances were 0.01 mV/cm at 52 µS/cm, 0.04 mV/cm at 314 µS/cm, and 0.1 mV/cm at 678 µS/cm. A comparison of the EFGs at rebound distances with those at cessation distances showed that (with the exception of those at 314 μS/cm) the rebound data fitted the logarithmic threshold curve (Figure 7). Thus, the empirically derived equation relates two of the fish's behavioral thresholds (EOD cessation and rebound) with ambient conductivity conditions.

It is still unclear what the EOD rebound burst represents. The distance at which the EOD rebound occurs could mark the boundary of the fish's communication field. Perhaps, during reverse tube movement, the electrically "silent" fish resumes discharging when it can no longer detect the other fish's EODs.

Two considerations make this an unlikely possibility:

1) If the rebound burst were a response to a physical threshold, one would expect it to occur more reliably than it did. Why should some fish demonstrate a response to a threshold intensity and others not?

2) If the rebound burst by Fish B occurs when the EODs of Fish A are no longer detectable, it is hard to understand how B's rebound burst could influence the EOD rate of A. At the rebound distance, both animals should be too far apart to detect each other's EODs. Fish A should not detect B's rebound burst, and therefore should not respond to it.

This finding pushes the boundaries of the communication field out even farther. It is possible that the fish can detect each other's EODs at very great distances, greater than those at which either EOD cessation or rebound occur.

Nevertheless, the EOD cessation and rebound responses do occur. If they do not represent simple detection threshold responses, what do they represent?

An interesting hypothesis is that information may be transmitted by means of these responses. To see this, one must step back from the context of the experiment and look at the stimuli and responses that are involved in these behavioral interactions.

In the first behavioral interaction, the EOD cessation response, the stimulus situation consists of one fish discharging at a "normal" rate (not exceeding 10 Hz), coupled with decreasing distance between the fish. The response shown by another fish to this stimulus is a cessation of discharging which may last from several seconds to more than one minute. This behavioral interaction has been observed at distances up to one meter.

In the second behavioral interaction, the EOD rebound burst, the stimulus consists of one fish resuming electric discharging following a period of electrical "silence." The discharge rate during this EOD rebound is considerably higher than normal (greater than 10 Hz). This EOD pattern is coupled with increasing distance between the fish. The response shown by another fish to this stimulus is a brief (2-3 second) change in EOD rate. This change may take the form of an EOD cessation, or a brief increase or decrease in EOD rate. This behavioral interaction has been observed at distances up to 1.5 meters.

What this comparison demonstrates is that two different discharge patterns evoke two different behaviors in response. This raises the possibility that information is transmitted in these behavioral interactions. Further research must be directed at discovering whether information is, indeed, transmitted in these behavioral interactions, and what type of information is contained in various discharge patterns. It is now possible only to speculate on the information that may be transmitted in the EOD cessation and rebound behaviors.

The point at which one electric fish stops emitting EODs (the EOD cessation distance) may be the point at which the fish is "too close" (in terms of an aggressive interaction) to a discharging conspecific. In the present study, the fish could not flee when brought in range of one another. A response a fish could make when the other fish's EODs became sufficiently "disturbing" or "threatening" was to cease emitting EODs. Several researchers have suggested that EOD cessation represents a "hiding" response, by which a submissive fish makes itself electrically undetectable to a dominant conspecific. The finding that the smaller fish in a pair was more likely to cease discharging lends support to this interpretation.

Along the same lines, it is possible that the EOD rebound burst represents a release from an inhibitory effect of one fish's discharges on the other fish. If enforced proximity to a conspecific forces a fish into electrical "hiding", the EOD rebound burst may represent "coming out of hiding" as the fish are moved apart.

The possibility must also be considered that the fish resume discharging after a certain amount of time has elapsed, regardless of interfish distance. Since, under present conditions, the tubes were always moved apart at the end of one minute after EOD cessation, it was not possible to determine whether the fish relied on time or distance.

One bit of evidence to support the "release from inhibition" explanation is the nature of the rebound burst itself. As was mentioned previously, when discharging resumes, the rate is elevated for a short period before returning to normal (hence the term "burst"). This is a characteristic of behavioral inhibition, as discussed by Hinde (1966):

> Consideration of cases in which the inhibitory effect is produced by an external stimulus shows how either positive or negative after-effects of one activity on another can come about . . . [T]he undulatory movement of the dorsal fin of a sea horse can be inhibited by peripheral stimulation: when the latter ceases, the movements of the dorsal fin are resumed, and for a while have increased amplitude (von Holst 1936).

While the "release from inhibition" explanation of the EOD rebound seems plausible, the possibility must also be considered that the rebound burst is a non-social response. The rebound burst may, for example, represent active electrolocation.

It must be recalled that while a fish is hiding by remaining electrically silent, it is also not engaging in active electrolocation. As a result, it is electrically blind to objects in its near environment except as sensed through passive electrolocation. Szabo and Fessard (1965) have shown that a fish may not notice objects introduced into its environment when it is electrically silent. Only after the next discharge does the fish show by increasing its EOD frequency that it has detected the object. Hagiwara and Morita (1963) suggested that an EOD frequency increase represents a more frequent scanning of the environment through active electrolocation. It may be that the rebound burst is an attempt to explore the environment following a period of electrical silence.

Further experiments are needed to determine whether the EOD rebound burst is social in nature (i.e., involving an interaction between the two fish) or whether it is a non-social behavior such as active electrolocation. The discovery of those instances in which the rebound burst of one fish influenced the EOD pattern of the second fish tends to support an interpretation of the response as socially based (cf. S. A. Altmann's definition of social communication as "a process by which the behavior of an individual affects the behavior of others"). Further research is required to ascertain why the rebound burst, and the other fish's response to it, only occur irregularly, and to specify those factors which govern the expression of these behaviors.

INTRODUCTION TO PART II

EFFECTS OF WATER CONDUCTIVITY ON SPACING IN FREE-SWIMMING MORMYRID FISH

The results reported in Part I demonstrated that an environmental factor, water conductivity, significantly affected the range of interaction in pairs of weakly electric fish. The next question was whether conductivity would affect interaction in a more natural situation, that is, in a free-swimming situation.

It has been demonstrated that weakly electric fish use both electric and non-electric cues in spacing. Moller (1976) showed that electric organ discharges are part of a mechanism to maintain group cohesion in the mormyrid *Marcusenius cyprinoides*. Abolition of EODs resulted in the disappearance of such group behaviors as parallel line-up and single file swimming. Moller suggested that in the natural habitat of these fish, EODs might serve as social signals to keep a group together during nighttime migrations or in turbid water.

In a series of experiments on the role of sensory systems in social spacing in another mormyrid species, *G. petersii*, Moller et al. (1979, and in preparation) showed that both vision and electric organ discharges contribute to group cohesion.

Thus, the available evidence suggests that, along with other sensory systems, the electrosensory system is involved in the maintenance of social spacing. I showed in Part I that water conductivity changes affect the electrosensory system. The task in Part II was to assess the effect of changes in water conductivity on group cohesion among free-swimming fish.

It is important to emphasize a difference in the experimental conditions in Parts I and II. In Part I, the fish were confined within shelter tubes which blocked or greatly attenuated any mechanical, chemical, visual, or auditory interactions between the two fish. Therefore, the fish predominantly depended on their EODs to detect one another. In a free-swimming situation, however, a fish is exposed not only to electrical stimuli from conspecifics, but also to a host of non-electric cues such as those mentioned above. The more the fish use non-electric cues in determining optimal interfish distances, the smaller should be the effect of water conductivity manipulation.

To increase the possibility of detecting a conductivity-produced effect while still preserving a free-swimming situation, I took the following steps:

1) To eliminate the role of visual stimuli, I conducted experiments under very bright illumination. It has been shown that mormyrids can perform visually guided responses only under dim light conditions (less than 64 lux: DeFazio 1979; Teyssedre and Moller in prep.). The median illumination during the experiments in Part II was approximately 4000 lux. rendering the fish in all probability functionally blind.

2) To enhance the likelihood of detecting potential conductivity effects, experiments were performed under an extremely wide range of conductivities: from 10 µS/cm, which is close to distilled water, to 4000 µS/cm, a value higher than that usually encountered by mormyrids in the laboratory or in their natural habitat.

Experiment 1:

Effect of group size on spacing and activity

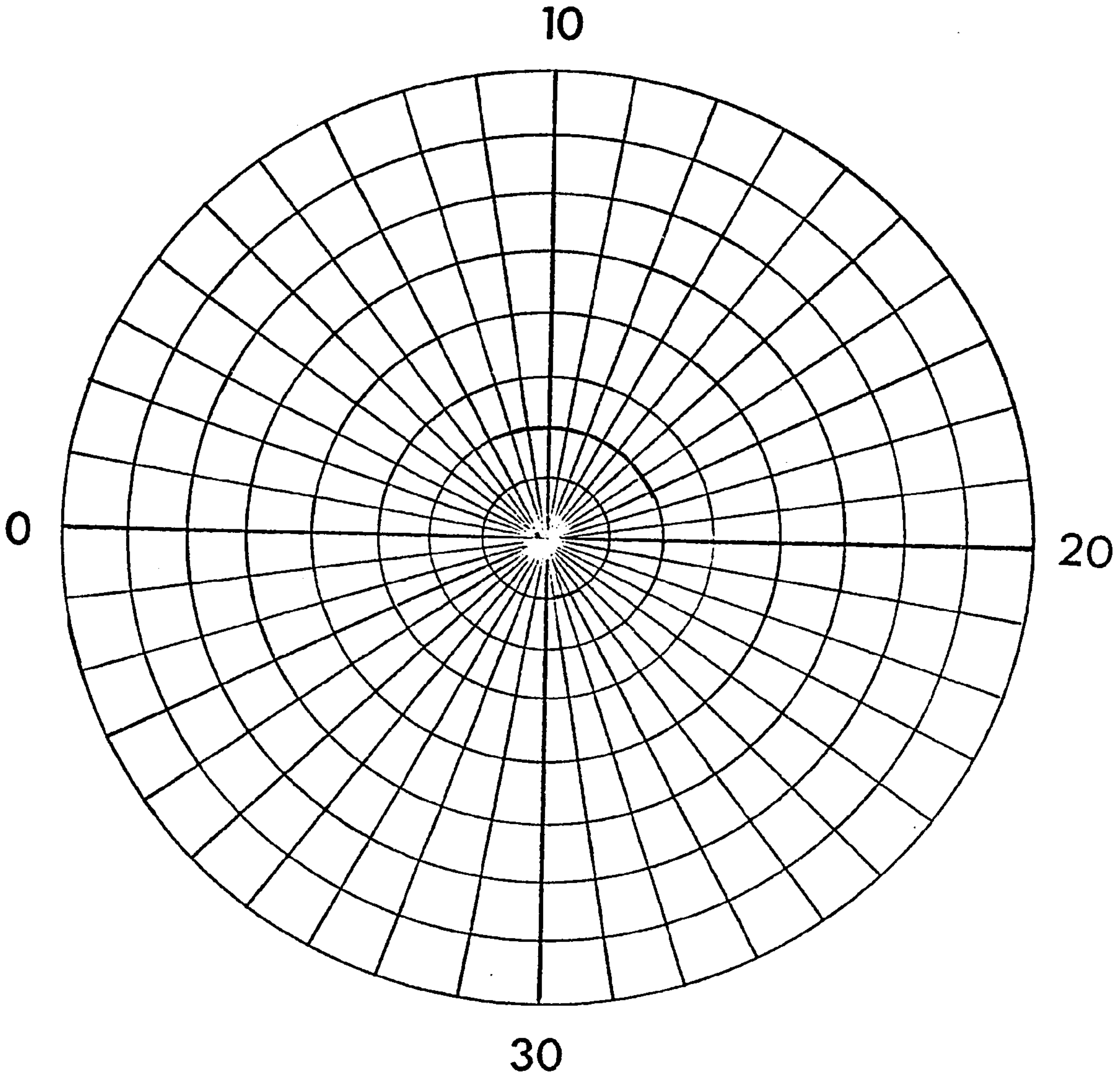
In Part I, I examined the efect of water conductivity on interaction distance in pairs of confined fish. It was desirable to use more than two fish in the free-swimming experiments in Part II to increase the likelihood of interaction among fish, and to obtain more nearest neighbor distance measurements from each experiment. But before I increased the number of fish, it was necessary to determine whether there were qualitative differences in the behaviors shown by groups of two fish and larger groups, since such differences might obscure the effects of water conductivity on spacing. Accordingly, in Experiment 1, I held environmental conditions constant while varying the number of fish in the experimental tank from 2 to 9 individuals.

Methods

Fish were housed and maintained as described in Part I. Experiments were carried out in a circular tank 150 cm in diameter and 50 cm deep, with water level kept at 40 cm. The bottom of the tank was demarcated into 40 pie-shaped wedges of 9 degrees each (Figure 8). Concentric rings 10 cm apart marked increasing distances from the center of the tank. Thus it was possible to express the two-dimensional position of any fish in terms of its polar coordinates: angular deviation and distance from tank center. Results of pilot studies indicated that the fish always remained at the bottom of the tank, so it was possible to make accurate calculations of distances among fish on the basis of their two-dimensional polar coordinates.

Figure 8

Overhead view of tank used in Part II


10
0
20
30

A camera was mounted two meters above the tank, allowing overhead photographs to be taken at predetermined intervals over a period of time. Water temperature was kept at 23°C ± 1.3°C. Ambient illumination level, which was monitored during many of the experiments, ranged from 493 to 17,936 lux (median value: 3,931 lux).

Experiments were conducted as follows: a group of fish, whose members had been housed individually for at least three days prior to testing, was placed into a bottomless cylindrical plastic mesh cage approximately 25 cm in diameter in the center of the observation tank. The experiment began when the cage was removed. For the next 25 minutes, a photograph was taken every 5 minutes, for a total of 5 photographs per experiment. In addition, the locomotor activity of the fish was timed twice, during the first and last 5 minutes of the experiment. Locomotor activity was recorded whenever at least one fish was in motion, and the activity measurements consisted of the number of seconds of activity during the 5 minute period. At the end of the experiment the fish were returned to a communal holding tank, which housed up to 20 fish.

In Experiment 1, this procedure was repeated with groups of fish ranging in size from 2 to 9 individuals, with conductivity held constant at 78.7 ± 4.1 µS/cm. Between 1 and 6 different groups of fish were tested at each "fish density" condition.

Data Analysis

Each experiment yielded 5 overhead photographs of the experimental tank. From each photograph, the polar coordinates (angular deviation and distance from tank center) were determined for each of the fish at the point where a line through the pectoral fins intersected a line through the longitudinal axis of the fish. A computer program was written to calculate from these polar coordinates the distance from each fish to its nearest neighbor. The use of nearest neighbor distance as a measure of spatial distribution in groups of animals has been discussed by Clark and Evans (1954) and Campbell and Clarke (1971). Each photograph yielded an individual nearest neighbor distance (NND) for each fish, as well as the mean NND for that photograph. The means from the 5 photographs comprising an experiment were then used to compute a mean NND for the experiment as a whole. Mean NNDs and activity scores were compared across "fish density" conditions by means of two-tailed one-way and two-way ANOVAs, trend analyses, and t-tests. Least-squares linear regressions were used to test for any correlation between light intensity and NND, or activity.

Results

Effect of group size on nearest neighbor distance (NND)

Results of the NND measurements indicate that the number of fish in a group had a significant effect on the distances maintained among members of the group. The histograms in Figure 9 show the mean NND as a function of group size. Fish maintained larger NNDs when the number of fish in the tank were fewer than four than when more than four fish were present. That is, up to a group size of 4, the spacing pattern did not change. When the low density (2-4 fish) condition was compared with the high density (5-9 fish) condition, a statistically significant difference emerged (Figure 10). A t-test showed significantly larger NNDs in the low density condition ($p < .02$).

Figure 9

Mean nearest neighbor distance (shaded histograms) and mean activity (unshaded histograms) as a function of group size. The number of fish in a group ranged from 2 to 9.

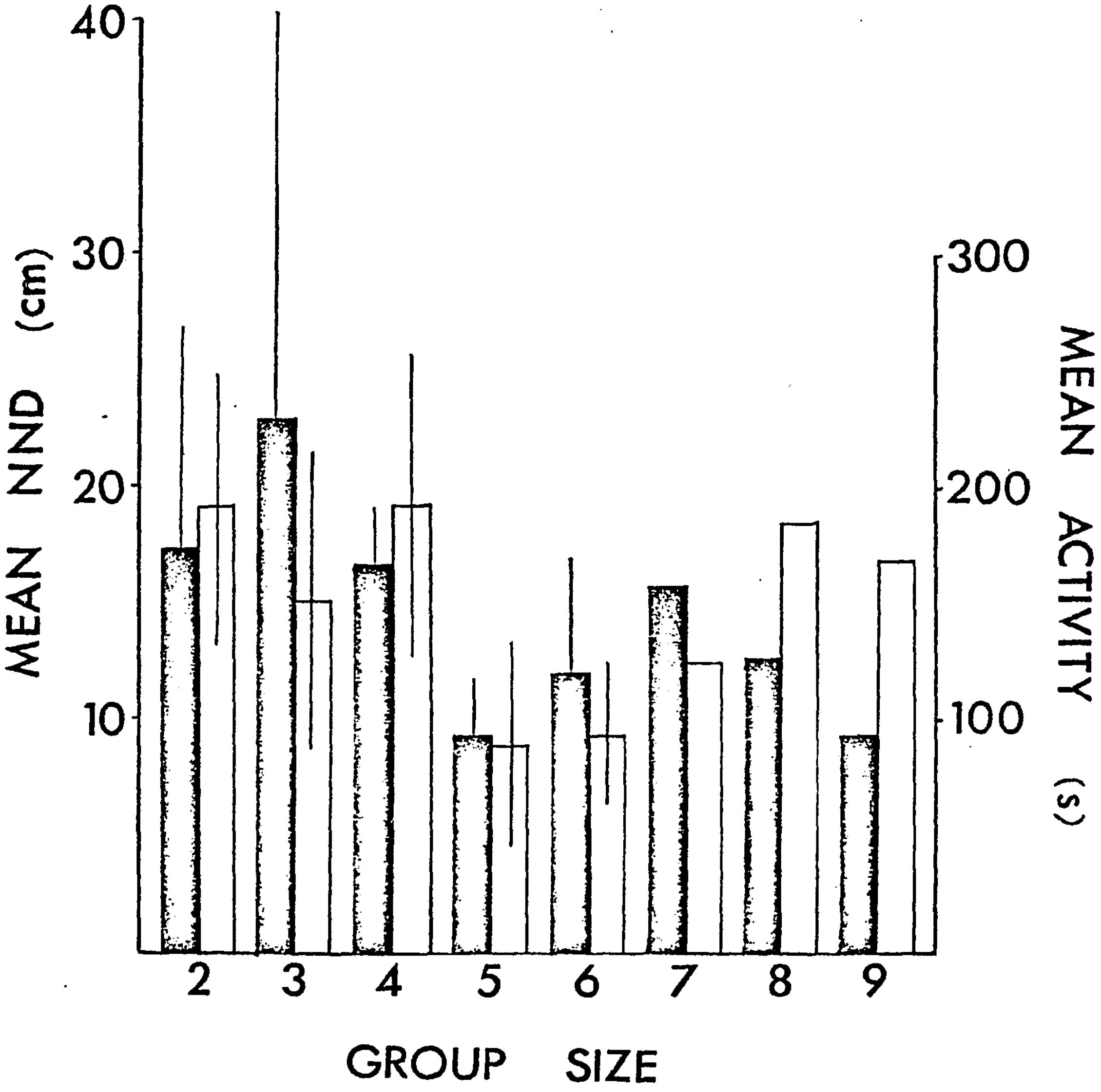
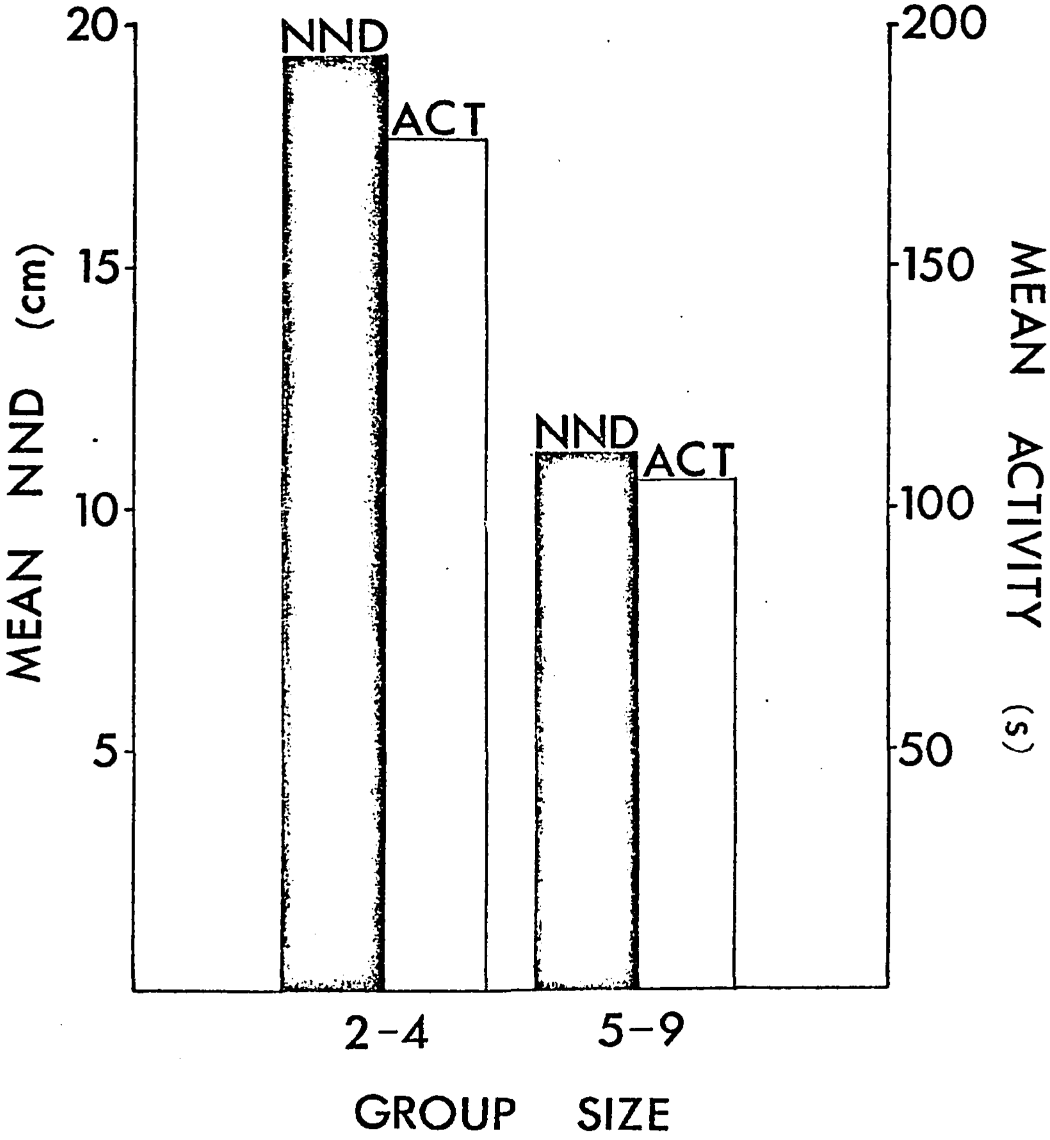

40
30
20
10
MEAN NND (cm)
300
200
100
MEAN ACTIVITY (s)
2
3
4
5
6
7
8
9
GROUP SIZE

Figure 10

Mean nearest neighbor distance and mean activity as a function of group size. "Low density": groups ranging in size from 2 to 4 fish. "High density": groups ranging in size from 5 to 9 fish.


NND
ACT
NND
ACT
20
15
10
5
200
150
100
50
MEAN NND (cm)
MEAN ACTIVITY (s)
2-4
5-9
GROUP SIZE

One-way ANOVAs showed no significant differences among NNDs within either low or high density conditions ($p > .20$ in both cases). A trend analysis revealed no significant trend in NNDs as a function of group size ($p > .20$).

Effect of group size on activity

The number of fish in the observation tank had a marked effect on activity, with the fish showing more activity when fish density was low than when it was high (Figures 9 and 10). This occurred despite the fact that with the present method of measuring activity (see Methods), the likelihood of activity is increased as group size is increased. Again the break between low and high density conditions occurred between 4 and 5 fish. Results of a two-factor mixed ANOVA indicated that group size significantly affected activity scores ($p < .05$). Further tests showed, however, that the difference was between low and high density conditions. A t-test revealed a highly significant difference ($p < .001$) in activity between low and high density groups, while one-way ANOVAs performed on each group showed no significant differences in activity within either low or high density conditions (low density, $p > .20$; high density, $p > .10$). A trend analysis showed no significant trend in activity as a function of group size ($p > .20$).

Discussion of Experiment 1

Although Experiment 1 was undertaken primarily to determine the number of fish that should be used in the second experiment, the results indicated that group size had a significant effect on spacing behavior. Both nearest neighbor distances and amount of activity were greater when only a few fish were present in the experimental tank. Interestingly, NND and activity did not decrease in a stepwise manner with each additional fish, as demonstrated by results of the trend analyses. Rather, the significant differences occurred between small groups (2-4 fish) and large groups (5-9 fish), with no significant differences in NND or activity occurring within each group.

Several investigators have reported behavioral differences between small and large groups of fish. Kavaliers (1980) studied the effect of group size on circadian activity of the killifish, _Fundulus heteroclitus_. He found that in groups of five, the fish dispersed throughout the tank and behaved as isolated individuals, whereas a group of 25 fish functioned as a "cohesive, . . . interacting social unit." In addition, the circadian activity of the 5-fish group was much more variable than that of the 25-fish group.

Partridge (1980) examined the effect of group size on the structure and behavior of minnow schools and found, as I did in the present study, qualitative differences between small and large groups. He reported that schools of 4-6 fish were better integrated than schools of 2-3, as evidenced by lower response latencies in group movement and degree of cohesion among members of the groups. He also found that NNDs decreased as the number of fish increased. He reported that mean NND expressed in terms of body length (mean NND/mean fish length) was 2.0 body lengths (BL) for 2-fish schools and less than 0.9 BL for 4-fish schools. In the present experiment small groups (2-4 fish) had a mean NND of 1.8 BL, while large groups (5-9 fish) had a mean NND of 1.0 BL.

While reporting a "considerable" difference in NNDs between 2-fish schools and 4-6 fish schools, Partridge noted that NNDs for 4, 5, and 6-fish schools were not significantly different from one another. This is analogous to the finding herein of significant differences between small and large groups, but minimal variability within each group.

The studies just cited demonstrated that the number of fish in a group significantly affects such aspects of the group's behavior as circadian activity and distance and direction of a fish from its nearest neighbor. The basic difference seems to be that fish in large groups tend to behave as members of the group, while fish in small groups tend to behave as individuals.

An additional difference between large and small groups in this study was in activity. Large groups showed significantly lower activity levels than did small groups. This finding, taken together with the differences in NNDs, suggests that when many fish are present, they tend to band together in a fairly stationary group. When only a few fish are present, they stay farther apart, swim around more, and generally behave more as isolated individuals than as group members.

It appears, therefore, that mormyrids, like non-electric fish, form different types of groups depending upon the number of fish in the group, with large groups maintaining NNDs about half the size of those in small groups. In both mormyrids and non-electric fish the transition from small to large is abrupt--between 4 and 5 individuals for *B. niger* and between 2 and 3 for minnows. A difference which was not reported for non-electric fish is that members of large groups were less active than members of small groups.

Experiment 2

Effect of water conductivity on spacing and activity

In this experiment, the spacing and activity of different groups of 4 fish were observed at different water conductivities.

Manipulation of environmental variables as a tool in the study of mormyrid social spacing behavior

Water conductivity. In varying water conductivity, one changes the sensory environment of the fish. The functioning of the electric organ and the electrosensory system are affected by conductivity changes. The system works most efficiently at relatively low conductivities, as was demonstrated in Part I.

At high conductivities the output voltage of the electric organ is so low that the fish is almost rendered electrically silent (cf. Figure 5). Thus, conductivity manipulation provides a way of reversibly inhibiting the fish's electric organ discharges, so that the fish can neither signal to distant conspecifics nor make use of its active electrolocation system. Other methods of inhibiting EODs are either irreversible (surgical section of the neural innervation to the electic organ) or potentially disruptive to the normal behavior of the fish (coating the electric organ with non-toxic material). Another disadvantage of the above methods is that they also result in inhibition of cutaneous receptors in the area of the electric organ. By contrast, it is possible through conductivity changes to suppress to varying degrees only the electrosensory system, leaving all other sensory systems intact. Thus, by raising water conductivity to a high level, it is possible to study spacing behavior in reversibly silenced fish.

Light intensity:

As has been mentioned, mormyrids have been found to use vision under very dim light conditions. Thus reversible "blindness" may be produced by conducting experiments under high illumination.

Methods

The methods used in Experiment 2 were identical to those described for Experiment 1, with the following exception: in Experiment 2, the group size was held constant at 4 fish. Six different groups of fish were tested at each of 4 water conductivities: 10, 92, 1000, and 4000 µS/cm. Mean NNDs and activity scores were compared across conductivity conditions by means of one-way and two-way ANOVAs, trend analyses, and t-tests.

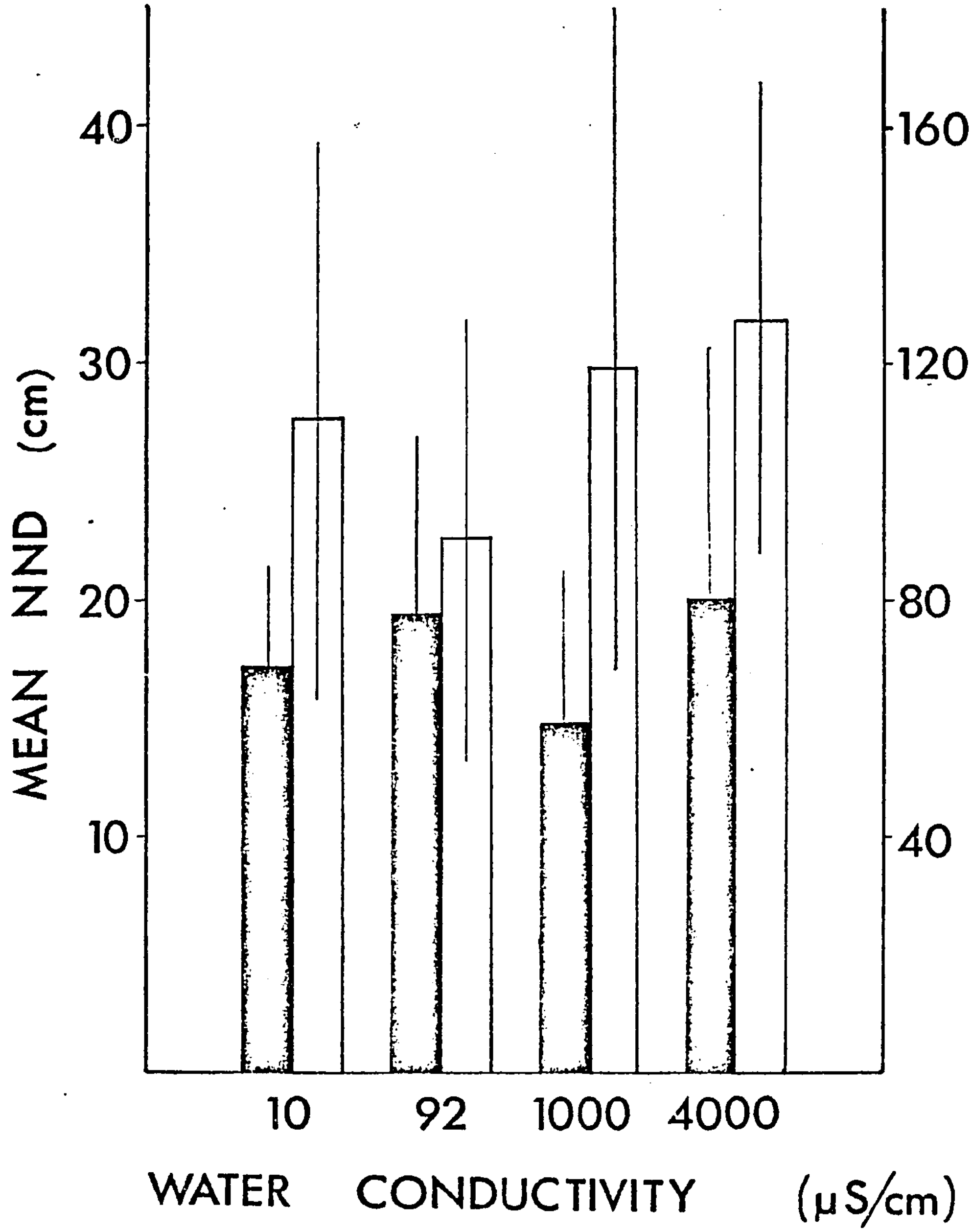
Results

Effect of water conductivity on NND

In contrast to its large role in determining EOD cessation distance in Part I, water conductivity had a negligible effect on NNDs in the free-swimming situation. The histograms in Figure 11 represent mean NND at each of the four conductivities. Results of a two-factor mixed ANOVA to test for effects of conductivity on NND and within-experiment changes in NND showed that conductivity did not significantly affect NND ($p > .20$). Neither were there any significant trends as NND as a function of water conductivity ($p > .20$).

Figure 11

Mean nearest neighbor distance (shaded histograms) and mean activity (unshaded histograms) as a function of water conductivity.


MEAN NND (cm)
MEAN ACTIVITY (s)
10
20
30
40
40
80
120
160
10
92
1000
4000
WATER CONDUCTIVITY (μS/cm)

Effect of water conductivity on activity

Water conductivity did not markedly influence the fishes' activity scores. There was a slight tendency toward greater activity at high conductivities, but the trend was not significant ($p > .20$). Results of a two-factor mixed ANOVA revealed no significant differences among activity times at different conductivities ($p > .20$). The histograms in Figure 11 show mean activity at each conductivity.

Within-experiment changes in NND and activity

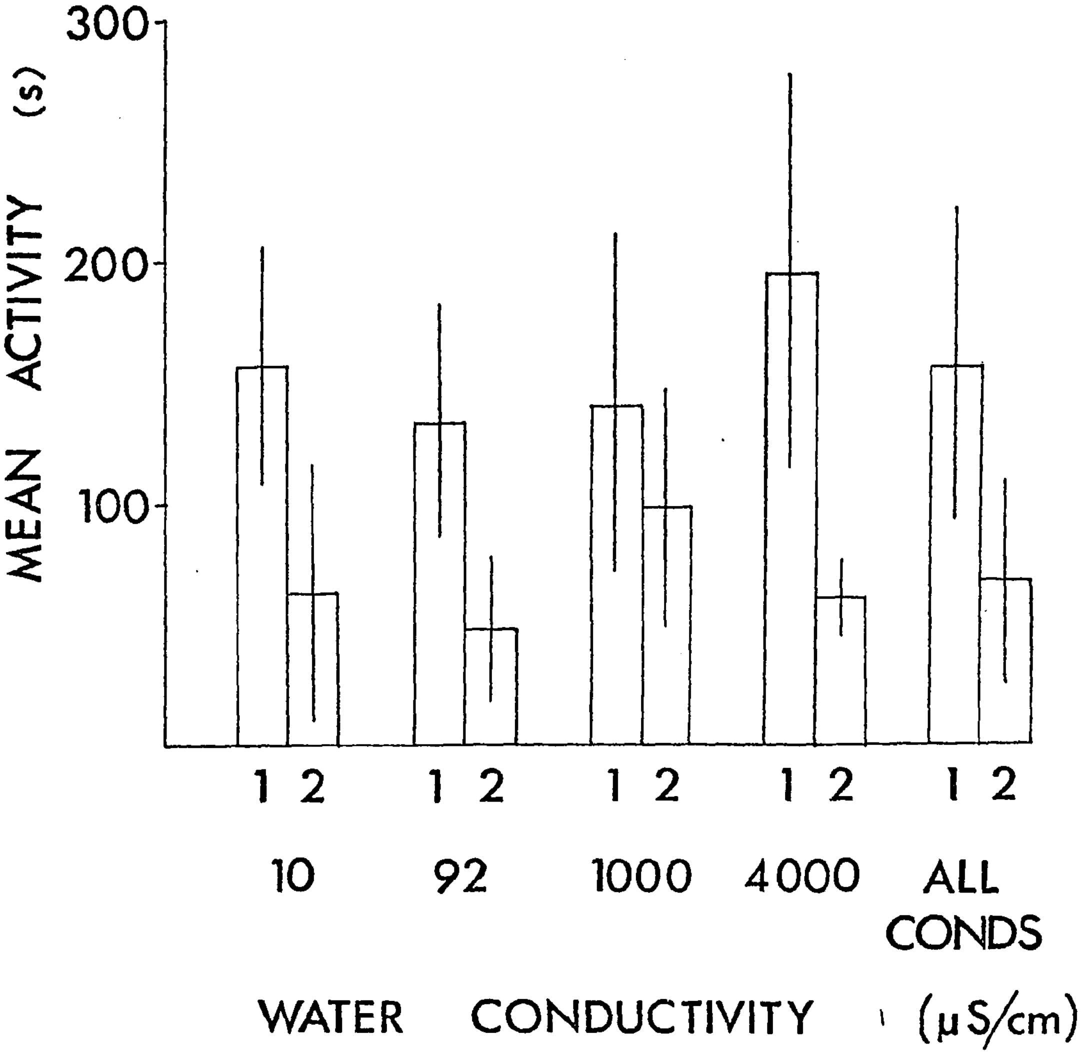
Serrier and Moller (in press) reported that over the course of a series of 10 minute experiments, members of a group of *Gnathonemus petersii* showed a decrease in activity. To determine if there were changes in either NND or activity within the 25 minute experimental periods used in this study, I examined both as a function of time during the experiment.

Both NND and activity changed over the course of the 25 minutes. Fish had a slight tendency to stay farther from each other, which was reflected in an increase in mean NND over the 5 photographs that comprised an experiment. This increase was not significant, however (two-factor mixed ANOVA, $p > .10$).

Activity was monitored during the first and last 5 minutes of each experiment. Figure 12, which shows the mean activity during the first and last 5 minutes of the experiments at each conductivity, reveals that at every conductivity there was a decrease in activity over the course of the 25 minutes. The results of a two-factor mixed ANOVA showed this decrease to be highly significant ($p < .001$).

Figure 12

Mean activity during the first (Activity 1) and last (Activity 2) 5 minutes of the 25-minute experiments. At all conductivities activity decreased over the course of the experiment.


300
200
100
MEAN ACTIVITY (s)
1 2
1 2
1 2
1 2
1 2
10
92
1000
4000
ALL CONDS
WATER CONDUCTIVITY (µS/cm)

Effect of light intensity on NND and activity.

As has been mentioned, mormyrids have been shown to use vision only under dim light conditions (DeFazio 1979). Teyssedre and Moller (in prep.) reported that G. petersii could suggessfully perform an optomotor task at illumination levels up to 64 lux, while at higher levels they failed to do so. All illumination levels measured in this experiment were substantially higher than 64 lux, so the likelihood is that the fish were functionally blind. Not surprisingly, there were no significant correlations between light intensity and NND or activity in either Experiment 1 or 2 (t-test for significance of correlation, $p > .10$ in all cases).

Discussion of Experiment 2 and General Discussion

In Experiment 2, the social spacing of free-swimming mormyrids was examined as a function of changes in water conductivity.

In this experiment it was desirable to eliminate visual cues in order to enhance potential conductivity effects and also to keep the experimental conditions as similar as possible to those in Part I. Accordingly, all experiments were performed under bright illumination.

Conductivity was varied so that at 10 and 92 μS/cm electrosensory input was enhanced. At 1000 μS/cm, the amount of electrosensory input was considerably reduced, and at 4000 μS/cm it was almost completely eliminated. The fish tested at low conductivity were deprived only of visual cues, and can therefore be considered "blind," while the fish tested at 4000 μS/cm, deprived of both visual and electrosensory cues, can be considered "silent" as well as "blind." The animals tested at 1000 µS/cm represent "blind" fish with partial electrosensory deprivation.

It has been shown that, although conductivity did not significantly affect activity or NNDs, there were slight, though insignificant, trends toward greater activity and larger NNDs at the highest conductivity (cf. Figure 11). "Silent and blind" fish were slightly more active and stayed farther apart than did "blind only" fish.

It is instructive to compare these results with those from an experiment which was conducted using a related mormyrid species, Gnathonemus petersii (Moller et al. 1979). Fish in this experiment had been surgically rendered blind, or electrically "silent," or both blind and "silent." As in the present experiment, groups of 4 fish were allowed to swim freely in a circular area, and were photographed from above. NNDs were determined as described herein, and activity was monitored throughout the experiments. The amount of time the fish spent together as a group was also monitored. The fish were considered to be grouped when in an aggregation of at least 3 animals the NNDs among individuals did not exceed one body length.

NND comparisons

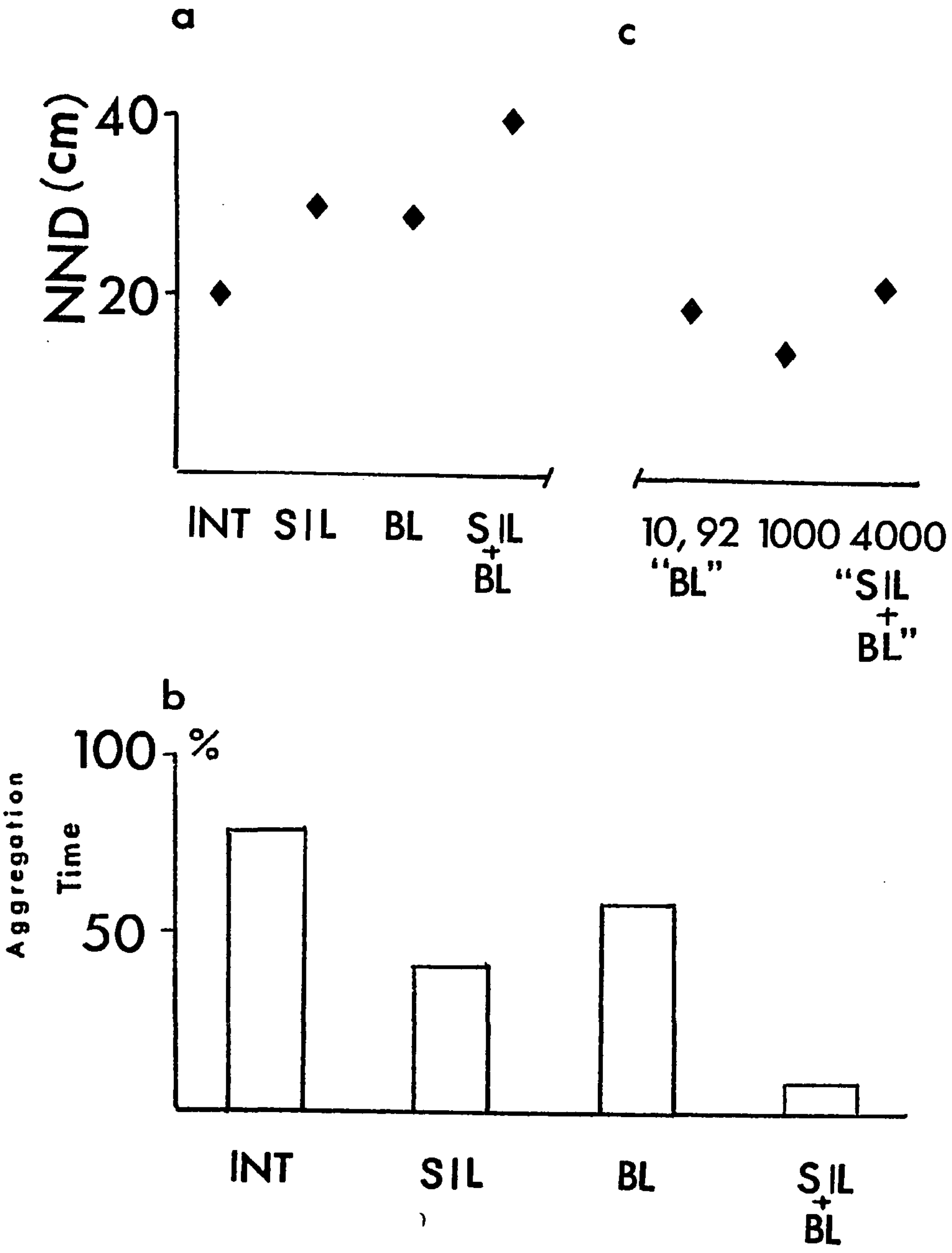
Figure 13a shows the mean NNDs in groups of G. petersii which had been surgically deprived of none (intact), one (silent or blind), or two (silent and blind) sensory systems. Mean NND increased as the amount of sensory information available to the fish was reduced. In particular, a comparison of intact with silent fish and of blind with silent and blind fish reveals that the elimination of electrosensory input reduced the cohesiveness of a group of fish. This is borne out

Figure 13

a) Nearest neighbor distances in groups of fish surgically deprived of none, one, or two sensory systems (after Moller et al.).

b) Percentage of time spent as a group by fish deprived of none, one, or two sensory systems (after Moller et al.).

c) Nearest neighbor distance as a function of water conductivity in the present experiment.


a
c
NND (cm)
40
20
INT
SIL
BL
SIL + BL
10, 92 "BL"
1000
4000 "SIL + BL"
b
100
%
Aggregation Time
50
INT
SIL
BL
SIL + BL

by the other measure of cohesiveness, time spent as a group. Figure 13b shows that fish deprived of electrosensory input (silent, silent and blind) spent less time as a group than did fish which could use this system (intact, blind).

A similar trend is evident in the results of the present study. Figure 13c shows mean NNDs measured in groups of Brienomyrus niger which were deprived to varying degrees of electrosensory input. Fish which could use electric cues tended to stay somewhat closer together than fish which could not, although it is unclear why the smallest NNDs were measured in the fish which were partially deprived of electrosensory input.

Activity comparisons

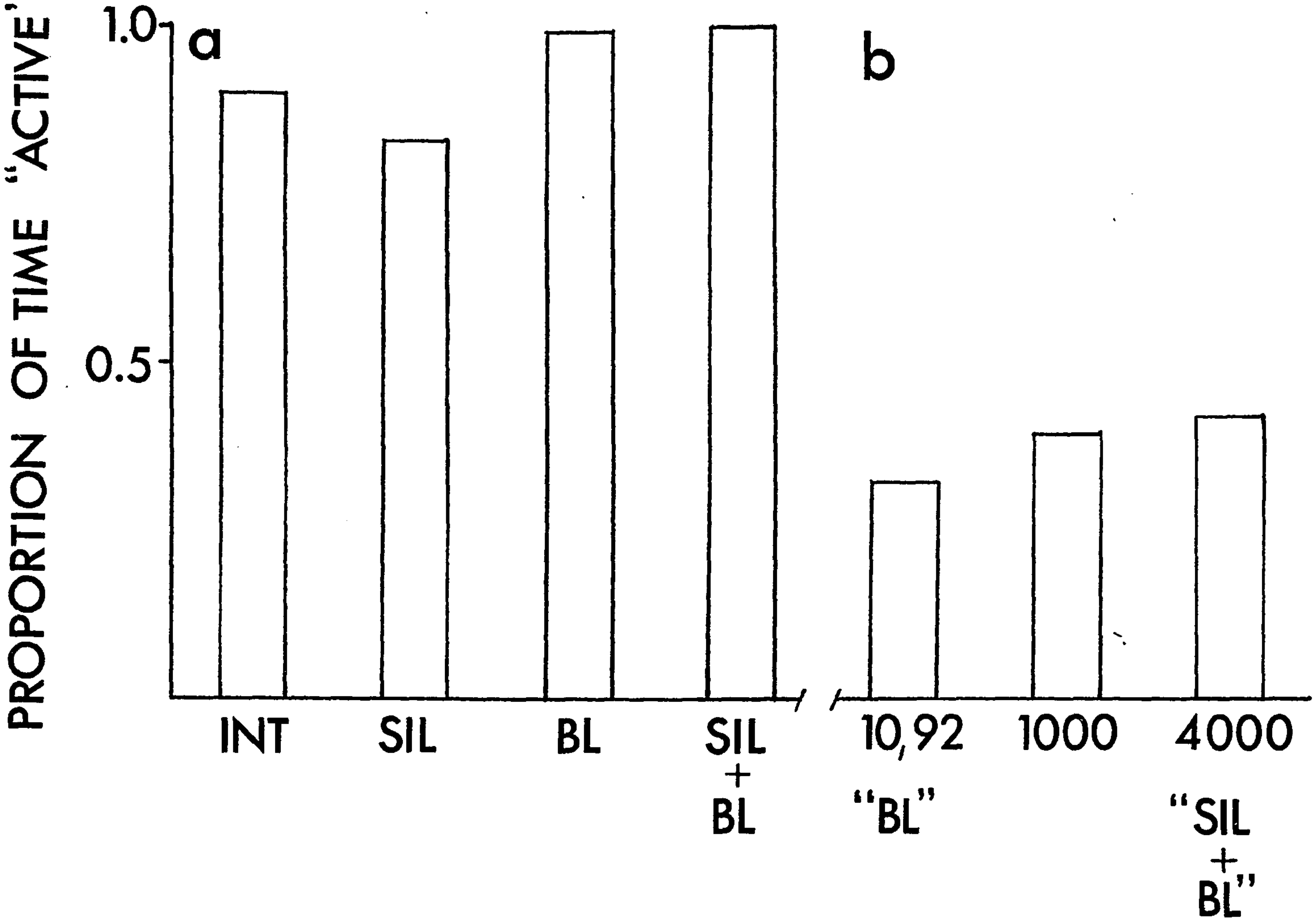
Figure 14a shows the percentage of time spend in activity by Gnathonemus petersii with varying degrees of sensory deprivation. There was a slight trend toward increasing activity as the amount of sensory input to the fish was reduced. The same trend is evident in the results of the present experiment (Figure 14b). Brienomyrus niger which were completely deprived of electrosensory input were more active than those with partial electrosensory deprivation, and these fish in turn were more active than those which could use electric cues. Differences in overall amount of activity between G. petersii and B. niger reflect species differences.

Results of NND and activity measurements suggest that the presence of electrosensory input contributed to the maintenance of a social group in both G. petersii and B. niger. The effect of

Figure 14

a) Percentage of time spent in activity by groups of fish surgically deprived of none, one, or two sensory systems (after Moller et al.).

b) Percentage of time spent in activity as a function of water conductivity by groups of fish in the present experiment.


PROPORTION OF TIME "ACTIVE"
1.0
0.5
a
b
INT
SIL
BL
SIL + BL
10,92 "BL"
1000
4000 "SIL + BL"

electrosensory deprivation on spacing was much smaller in the present experiment, however.

Over a range of conductivities from 10 to 4000 µS/cm, nearest neighbor distance varied only slightly (cf. Figure 11). Activity measurements showed more variability, but still did not change significantly as a function of conductivity.

In Part I, conductivity changes affected the fish's electric organ output voltage and its electrosensory system, and therefore affected social behaviors mediated through the electrosensory system. In Part II, conductivity changes also affected the fish's electrosensory system, but did not affect social spacing behaviors. A question raised by these results is: why did conductivity have such a significant effect on spacing-related behavior in Part I, and no effect at all in Part II?

The following possibilities may be considered:

1) The behavioral difference may stem from a difference in the amounts of sensory information available to the fish in the two types of experiment. In Part I, the fish were confined to shelter tubes which prevented them from receiving mechanical, chemical, auditory, or visual cues to each other's presence. Each fish had to depend on electric signals to detect the other fish. It is therefore not surprising that water conductivity, which influences the strength of the electric signal, had a pronounced effect on interaction distance.

In Part II, the fish were allowed to interact freely. Thus they were able to utilize mechanical, chemical, and possibly auditory cues in addition to EODs to detect one another.

By relying on other cues more, the fish may have relied on electric cues less--hence the negligible effect of changes in conductivity on spacing. This interpretation does not imply that the fish do not use electrosensory informmation in spacing. It merely states that electric cues are but one source of sensory information available to the free-swimming fish.

Other investigators have made similar discoveries regarding the sensory cues to which animals attend. In a study of an illness-induced taste aversion, Wilcoxon et al. (1971) found that when quail were given a compound (visual + gustatory) conditioned stimulus, followed by an illness-inducing drug, they later associated the illness with the visual cue, but not with the gustatory one. When only a gustatory CS was used in training, however, the quail were able to attend to this cue and learn the association between taste and illness.

This finding is analogous to the one herein. When only one sensory cue was available (gustatory), the quail were forced to rely on it, but when several cues were available (visual + gustatory) the gustatory cue was ignored in favor of cues that were more salient to the animal. Similarly, when the fish had to depend on electrical cues because no others were available, they did so, but when a variety of cues was present, the fish may have attended less to electric cues.

2) Fish may maintain a group structure regardless of variations in sensory input.

It is possible that variations in conductivity might not produce corresponding changes in spacing patterns if other forces existed to keep the fish grouped. That is, if, for some reason, maintenance of a group structure is the most important consideration, the fish may compensate for even extreme changes in EOD amplitude of conspecifics.

Maintenance of a group structure may be traceable to specific differences between the experimental tank and the fish's natural habitat. Williams (1964) has argued that fish form schools or groups primarily as a means of seeking cover. He further noted that species of fish most likely to school are those whose natural habitats are lacking in cover. In the natural habitat of mormyrid fish there is ample cover in the form of submerged rocks and tree trunks under which individuals may hide. In their study of the distribution of mormyrids in an inlet of the Swashi River in Nigeria, Moller et al. (1979) reported detecting individual large mormyrids hiding under such protective shelters.

By contrast, the tank used in the present experiment was conspicuously free of hiding places. The fish, therefore, may have stayed close to one another mainly for shelter, while ignoring environmental stimuli (EODs) which might normally affect the spacing patterns of a group of fish.

Preliminary support for this interpretation has been reported by Senchyna (personal communication). He observed the spacing behavior of six specimens of the weakly electric mormyrid <u>Petrocephalus</u> <u>stuhlmanni</u>, first in an aquarium containing no protective shelters, and then in one containing individual shelter tubes spaced approximately 13 cm apart. Senchyna's observations, like the ones described herein, were conducted under natural daylight.

In the "no shelter" condition, the fish formed a close group, with a maximum interfish distance of less than one body length. In the second condition, however, the group disbanded and each fish occupied a separate shelter. These findings support the suggestion that cover-seeking may be a primary reason for the maintenance of a group structure by fish in a shelter-free environment.

To test the effects of water conductivity in a free-swimming environment, therefore, it would be necessary to provide a large number of closely spaced shelters in the experimental tank, and then to vary water conductivity. If members of the group of fish chose shelters that were farther apart at low conductivities, this would indicate that conductivity can affect spacing in a "natural" environment.

3) The finding that nearest neighbor distance remained between 15 and 20 cm regardless of changes in water conductivity is interesting in light of the fact that this distance has been found to be the boundary of the fish's electrolocation field. It is therefore possible that the fish's spacing behavior is primarily controlled by the electric reafferences from the sender's self-generated EODs and not so much by foreign, conspecific signals. Further experiments will have to consider the effect of water conductivity on electrolocation under conditions of social interaction among mormyrid fish.

The present results have shown that water conductivity is an environmental factor that can profoundly affect the behavior of electric fish. Therefore, conductivity can no longer be ignored in the design of studies on electrocommunication and electrolocation.

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