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DISCRIMINATION OF ELECTRIC SIGNALS: IMPLICATIONS FOR ELECTROCOMMUNICATION IN THE AFRICAN ELECTRIC CATFISH *MALAPTERURUS ELECTRICUS* (GMELIN 1789) SILUROIDEI, MALAPTERURIDAE

by

JOHN R. VAN WETTERING

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THE CITY UNIVERSITY OF NEW YORK

Abstract

DISCRIMINATION OF ELECTRIC SIGNALS: IMPLICATIONS FOR ELECTROCOMMUNICATION IN THE AFRICAN ELECTRIC CATFISH MALAPTERURUS ELECTRICUS (GMELIN 1789) SILUROIDEI, MALAPTERURIDAE

by

John R. Van Wettering

Adviser: Professor Peter Moller

The strong electric organ discharge (EOD) of the African electric catfish, *Malapterurus electricus*, functions as part of the fish's predatory and defensive behavior. Like other siluriforms, these catfish also possess ampullary electroreceptors (small pit organs) that can detect direct current and low-frequency alternating current. This study examines the responsiveness of *Malapterurus* to artificially generated pulsed stimuli to explore the possibility that these catfish detect and recognize conspecific EODs.

Three experiments were conducted using a model electric catfish to deliver controlled electric stimuli to individual subjects. The first experiment was designed to explore *Malapterurus*' responsiveness to a range of stimulus

pulse durations. Locomotor activity, sheltering, electrode contact, and EOD production were recorded in the presence of volleys of artificial pulses. Durations ranged from 0.375 to 6.0 ms including a condition mimicking the naturally occurring 1.5 ms pulse. Catfish did not respond differentially to these pulses.

A second experiment examined differential responding to patterns consisting of simulated EODs, including patterns mimicking defensive and predatory type volleys. These volleys were of short or long duration, and of either low- or high-frequency. Malapterurus did not discriminate between stimulus volleys based on either frequency or volley duration alone. The fish, however, were able to distinguish between defensive and predatory volleys based on naturally occurring combinations of these two parameters.

In the third experiment, subjects were tested for their response to stimuli of different amplitudes. Because the EOD amplitude of Malapterurus increases as the fish grow, and because Malapterurus does not discharge during conspecific encounters, it was hypothesized that EOD amplitude can provide information to conspecific competitors signalling size. Electric catfish withdrew and maintained their distance from a model generating EOD amplitudes greater than their own and approached a model generating relatively low amplitude stimuli.

Although the discharge of Malapterurus electricus is used as a powerful tool in predation, the present study has provided sufficient evidence for the EOD's role in intraspecific communication.

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INTRODUCTION

For thousands of years mankind has known of the existence of strongly discharging electric fish such as the freshwater African electric catfish, Malapterurus and the marine electric rays, Torpedinidae (review: Moller, 1995). Because evolution had shaped the electric organ discharges (EODs) of these fish into powerful tools for both defense and predation, there was little doubt as to their function. In the middle of the last century, weak electric discharges were discovered in the marine electric ray (Raja). Early evolutionary biologists, including Charles Darwin (Darwin, 1866) were puzzled by the absence of transitional stages leading to stronger and stronger discharges. The function of the weak EOD was also unknown.

By the turn of the century scientists had discovered the electrogenic abilities of African mormyrid and South American gymnotid fish whose EODs measured only a fraction of a volt. Whereas strong EODs were known to be used in predation the utility of weak EODs remained a mystery until Lissmann (1958) found evidence for the electrosensory functions of these discharges. The identification of specialized electroreceptors in mormyriform and gymnotiform fishes, along with behavioral evidence, demonstrated that weak EODs function in both electrolocation and electrocommunication.

Over the last twenty years, several species of marine stargazers and freshwater catfish have been shown to produce electric discharges of weak to intermediate amplitudes. The use of EODs in social interactions by some of these fish has been shown and there is speculation regarding this function in others (Mikhailenko, 1971; Bratton, 1987; Hagedorn, Womble, & Finger, 1990; Baron, Orlav, and Golubtsov, 1994a; Baron, Morshnev, Olshansky, and Orlav, 1994b). These examples, while providing evidence for the evolutionary transition from weak to strong EODs, have at the same time made the distinction between weakly and strongly discharging electric fish less clear. This raises the possibility that the EODs of strongly electric fish, such as Malapterurus, at one time served a purpose other than predation and defense.

Laboratory experiments by various investigators over the past few decades have provided some evidence linking strong EODs to communication. Lissman and Machin (1963) showed that catfish electroreceptors are sensitive to the type of electrical signals that constitute Malapterurus' EOD. Preliminary studies providing evidence of EOD-like signal detection in the electric catfish were conducted by Bauer (1968). Kastoun (1971, 1972) investigated electrocommunication in Malapterurus more directly. He found that electric catfish can discriminate situation-specific, conspecific EODs.

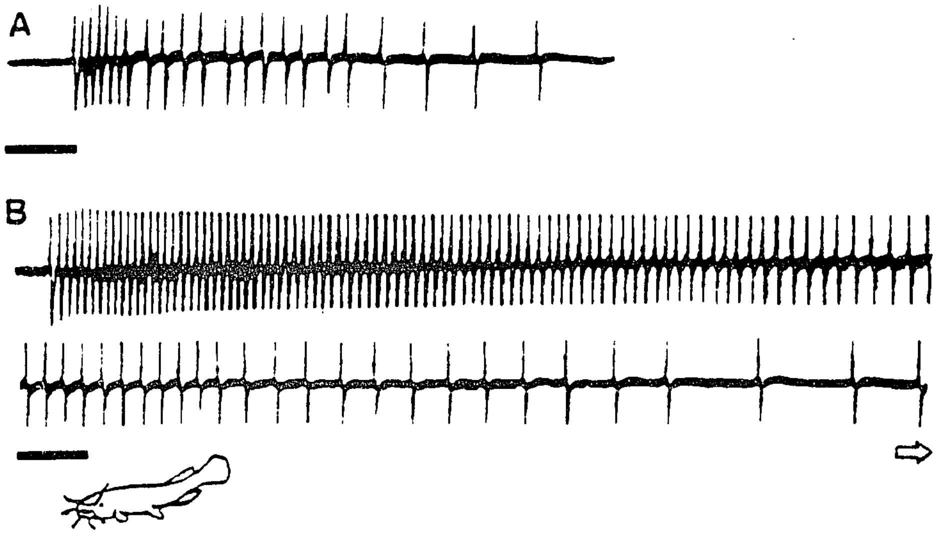
In order for the EOD of the electric catfish to have achieved its present high intensity, there must have at one time existed a selective advantage for a catfish with a weak electrogenic capability. The possibility exists that a strong EOD could evolve to its present state from a weak EOD that served primarily in electrocommunication. It is also possible that original function of the electric organ did not disappear during this transition. The present study reexamines the function of the strong electric discharge in an attempt to provide implications for electrocommunication in Malapterurus.

Electrogenesis in Malapterurus

African electric catfish, family Malapteruridae, are widespread throughout the freshwater systems of tropical Africa. The most common species is Malapterurus electricus, Gmelin 1789 (Siluroidae, Malapteruridae, Lacép. 1803). Two additional species are recognized, M. microstoma, which has a range restricted to the Zaire basin, and M. minjiriya, which was collected in Nigeria and identified by Sagua (1987). The three differ in morphological characteristics including number of gill rakers, vertebrae, and anal fin rays, as well as the shape and size of the mouth, snout and adipose fin. All three species possess an electric organ that has evolved from anterior body musculature (Howes, 1985). This organ is capable of producing high-voltage discharges that serve both a defensive and predatory function. In the field, the electric catfish is known to be primarily a piscivorous (Sagua, 1979), nocturnal predator (Moller, 1975; Belbenoit, Moller, Serrier, & Push, 1979). Electric catfish generally produce relatively short discharge volleys in response to mechanical stimuli, while longer ones accompany prey capture behavior. Defensive volleys consist of 3-67 individual pulses with an average of 16, whereas feeding volleys contain 14-562 pulses with an average of 133 (Bauer, 1968). Electric organ discharge (EOD) frequency has been recorded up to 500 Hz. Defensive volleys, on the average, have a lower discharge frequency than predatory ones (Figure 1) and decrease more quickly after an initial high-frequency phase that usually characterizes both types. Malapterurus can generate an EOD with an amplitude of up to 350 V. The pulse duration is about 1-2 ms (Bennett, 1971). Bauer (1968) recorded a duration of 1.88 ms at 23.7 C° in a 15.5 cm specimen.

The electric organ of Malapterurus is innervated by two large neurons that are located bilaterally (Bennett, Nakajima, & Pappas, 1966). The cell bodies located in the spinal cord each send out a single axon which innervates an entire side of the electric organ. These two electromotor neurons, though not in direct contact, are closely coupled electrotonically. This insures that discharge activity involves both cells through electrotonic propagation of the

Figure 1: Examples of electric organ discharge volleys in Malapterurus. (A) Defensive volley type. (B) Predatory volley type. Adapted from Belbenoit et al. (1979) as modified in Moller (1995). Time bars = 20 ms.

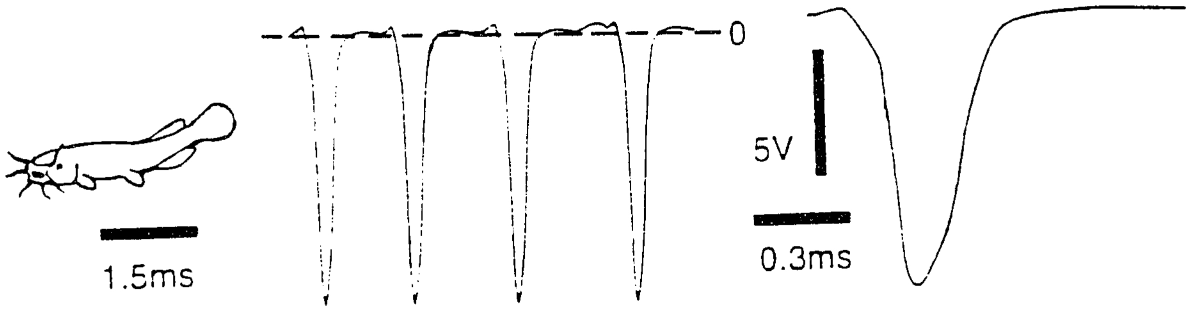

A
B

neural signal. Excitatory transmission to the giant neurons was believed to be totally electrotonic, since there was no evidence of chemical synapses. More recent evidence shows that they are in fact nicotinic cholinergic, but with a very low concentration of nicotinic ACH-receptor sites and acetylcholinesterase (Eldefrawi, Shaker, Mansour, Warnick, & Albuquerque, 1981).

Pacini's Law states that the innervated faces of the electroplates of an electric organ become negative during a discharge, irrespective of the anatomical orientation of the organ. This law was thought to hold true for all electric fish species with the exception of Malapterurus. The reason for this seeming irregularity is that the face of the electroplate which is active during the main portion of the discharge is not that on which the nerve terminates, but is instead the non-innervated face (Keynes, Bennett, & Grundfest, 1961). Thus, EODs consist of volleys of monophasic pulses, each with the head appearing negative to the tail. However, Bennett (1971) showed that the EOD of Malapterurus, like that of other electric fish, does have a small head positivity (Figure 2). The electric catfish makes use of a synchronization mechanism which ensures that electroplates at the two extremities of its electric organ fire at roughly the same moment. A peripheral delay takes place that varies along the length of the fish in order to compensate for the difference in neural conduction time.

Figure 2: The EOD waveform of <u>Malapterurus electricus</u>.

Adapted from Bennett, 1979 as modified in Moller, 1995.


1.5ms
0
5V
0.3ms

Recordings made of the EOD of Malapterurus in its natural habitat (Lake Kainji, Nigeria) showed a range of volley types varying in length between 2 ms and 8 s, and consisting of 2-600 pulses (Belbenoit et al., 1979; review: Moller & Rankin, 1995). Volleys were generated intermittently and always contained an initial high-frequency phase, followed by a gradual decline in frequency. Additionally, several lower frequency EODs would precede a volley on occasion (38% of recordings) and sometimes occurred independently as well. Such phases were termed pre-volley activity, and were an exclusive feature of nocturnal recordings. Other recordings made in the natural habitat of the catfish contained the same short-duration (1-5 pulses) bursts and these were found to be much more common than in captivity (Bauer & Belbenoit, unpublished). Belbenoit et al. (1979) hypothesized that such pre-volleys could act in one of two ways. They may serve in prey capture by producing a startle response in nearby prey fish, thus facilitating their location through lateral line orientation.

The discharge activity of the electric catfish was observed to follow a 24 hr cycle in the field, with constant low levels throughout the day, followed by a peak five times greater during the hour after sunset (Belbenoit et al., 1979). Following this, the discharge frequency level gradually declined, reaching its low point shortly after sunrise. It was believed that Malapterurus was feeding most successfully early in the night, and many volleys recorded at this time were longer than those produced during daytime hours. Laboratory investigations have shown that long volleys (>14 pulses) are often indicative of feeding behavior (Bauer, 1968), and these represented 19% of the total recorded in the field. Shorter volleys may have resulted from contacts with non-conspecific, non-prey fish or violent intraspecific encounters such as those observed in captivity by Rankin and Moller (1986).

The EOD of Malapterurus electricus has been analyzed in regard to temporal patterning during social encounters (Rankin, 1984; Rankin & Moller, 1986, 1992; Moller & Rankin, 1995). The number of pulses per volley varied depending on the species encountered during interspecific interactions which took place in the context of a resident/intruder paradigm. The greatest number of pulses were produced in response to contact with Clarias gariepinus, a bottom dwelling competitor. This was followed in order of volley length by encounters with Polypterus palmas, another bottom dweller. Fewer pulses were directed toward midwater fish (Carassius auratus and Oreochromus melanothereon). Resident catfish, on average, produced EODs containing more pulses than intruders. Volley length was greater during contacts with Polypterus, while discharge frequency was higher for Clarias than for other partner types. For both of these measures there was no significant difference between resident and intruder Malapterurus.

Rankin and Moller (1986) examined conspecific encounters in Malapterurus were examined using a resident/intruder experimental design. They observed that smaller resident fish would flee from a larger intruder if the size discrepancy was greater than 5 cm. Ritualized stereotypic behaviors were recorded between similar sized fish. These included lateral and open mouth displays, as well as direct contact, pushing, and biting. With the exception of contact, none of these behaviors were observed when electric catfish were paired with non-conspecifics. Such interspecific contacts were usually accompanied by EOD behavior, however, this was less likely when Malapterurus were small. Alternatively, EODs were rare during conspecific encounters. Discharges did sometimes accompany biting, and these were about evenly distributed between the fish being bitten and those doing the biting. Rankin and Moller (1986) hypothesized that species discrimination was based on chemical cues and size discrimination on mechanical cues.

An open field study conducted in a large tank examined the spacing patterns and interactions among groups of between one and five Malapterurus electricus (Rankin, 1984). When two fish were together, lateral displays occurred during the first half hour, after which none were observed over a period of three days. The fish which broke off displaying remained submissive during this time. When a third fish was introduced to the experimental tanks the first contact between it and the dominant fish was usually accompanied by lateral displays. The duration of these displays were shorter if the newcomer was small. Larger fish triggered longer lasting displays culminating in the newcomer being bitten by the dominant fish. In these instances bites were accompanied by EODs. No displays were observed between newcomers and non-dominant fish. Dominant fish spent significantly more time in shelters than submissive fish, and would at times exclude them. An overall analysis showed that neither prior residency or size could fully account for the establishment of dominance (Rankin, 1984).

The ability of Malapterurus to use its EOD during social interactions was first investigated by Kastoun (1971, 1972). Experiments were conducted by connecting two tanks containing subjects via electrodes, thus eliminating non-electric sensory cues. During trials in which the stimulus consisted of mechanically tapping the glass wall of the aquarium, the catfish housed therein emitted volleys of 2-5 pulses, which were termed flight or defensive volleys. This in turn caused the fish in the electrically coupled tank to perform an escape response and hide in its shelter. In response to prey fish the catfish produced volleys of 14-562 pulses (predatory discharges). The fish receiving these signals through the electrodes exhibited search responses. When fish were touched with wooden sticks they tried to bite them and produced volleys of 21-113 pulses to which the electrically connected Malapterurus responded by attacking objects (attack volleys). It was not determined how the subjects were able to discriminate between predatory and attack volleys since the number of pulses overlapped. Volleys did however vary in amplitude, and pulse pattern (Kastoun, 1971). At no time did any fish receiving EODs via electrodes respond with discharges of their own. An attempt to replicate Kastoun's findings by Smalls (unpublished) did not yield significant differences between treatment conditions.

Electrogenesis in Other Species

The Malapteruridae have been considered unique among the siluriforms in possessing an electric organ. Bioelectric fields can, however, also be generated by muscle contractions that cause impedance variations in the skin tissue of other teleosts (Howes, 1985). Recently, a group of African synodontid catfish (Mochokidae) were found to produce weak electric signals in both continuous and burst-like fashion (Hagedorn et al., 1990). These fish are able to discharge independent of sound production, therefore their electrogenesis is not considered a byproduct of sonic organ musculature. The electric organ, however, seems to be derived from sonic muscle, the removal of which abolished EODs. Of the three species of synodontids described, two discharged spontaneously (one of these in a continuous pattern) in the 50-100 μV range. The other generated bursts only when disturbed, with the signal much stronger at 10-30 mV/cm in amplitude with the electrodes placed directly over the electric organ. There was speculation as to the adaptive significance of the evolution of this electrogenic ability and the possibility of its involvement in electrolocation or communication (Hagedorn et al., 1990). Preliminary evidence that the EODs produced by synodontids function in a social context was presented by Baron et al. (1994b).

Lissmann and Machin (1963) suspected that another siluriform fish (Clarias sp.) was capable of electrogenesis. Recent evidence that weak EODs are in fact produced by Clarias gariepinus was discovered by Baron et al. (1994a). The head-positive monophasic EOD pulses generated by these catfish were shown to be distinct from myogenic potentials based on their higher amplitude. Pulse duration varied between 5 and 260 ms, and pulses were produced individually as well as in series. Clarias did not emit pulses spontaneously or in response to mechanical stimuli, but seemed to discharge only during aggressive interactions with conspecifics (Baron et al., 1994a). Although no specific electric organs were identified in Clarias, it was hypothesized that these catfish display a primitive stage in the evolution of fresh-water electric organs. Thus, the discovery of weak electric discharges in siluriform fish may hold a key to the phylogeny of electrogenesis in Malapterurus.

The South American electric eel, Electrophorus electricus produces strong electric discharges via the Main and Hunter's organs, which serve in predation and defense, much like in the electric catfish. As seen in Malapterurus, the volley type produced is situation-specific, with defensive bursts containing on the average far fewer pulses than predatory ones (reviewed in Bauer, 1968). Observations of Electrophorus in the field showed that it often congregates during feeding (Cox, 1938). It was hypothesized that the strong EODs produced for predatory purposes may function as a social signal (Bullock, 1969). Electrically mediated parental and reproductive behaviors in the species have also recently been reported (Schwassmann, 1992). It should be noted, however, that unlike the electric catfish, Electrophorus also possesses a weakly electric Sachs' organ and a portion of the Hunter's organ produces weak discharges. Further, the electric eel is a gymnotiform, and as such possesses tuberous and ampullary receptors (Bennett, 1971).

Various species of marine torpedo ray are known to use their strong EOD to stun prey for capture. Recent field experiments involving Torpedo californica have shown that in addition to discharging in the presence of living and dead prey fish, Torpedo initiates long predatory volleys in the presence of simulated bioelectric fields detected via ampullary electroreceptors (Lowe, Bray, & Nelson, 1994). Studies of another strong electric marine torpedo ray, Torpedo marmorata, found EODs accompanying predation and mechanical stimulation, but showed no evidence of intraspecific communication in the species (Belbenoit, 1986).

Several species of stargazers, Astroscopus (Uranoscopidae), the only marine teleosts with an electric organ, have a discharge that lies between weak and strong (Bennett, 1971). Astroscopus has also been shown to discharge in the presence of prey fish and artificial stimuli (Pickens & McFarland, 1964). In this genus, however, the relatively low-amplitude EODs produced (5 V: Bennett, 1971) has led to speculation regarding their utility in predation. Pickens and McFarland (1964) found that the EOD did not harm prey fish and the swiftness of the feeding event seemed to render prey immobilization unnecessary. Social use of the EOD in Astroscopus is unknown.

Electric discharges produced by a close relative of Astroscopus, the Black Sea stargazer, Uranoscopus scaber

(Mikhailenko, 1971), and also by the marine skate, Raja clavata (Mikhailenko, 1971; Bratton, 1987), can be perceived and responded to by conspecifics. EOD amplitude in these fish range from a few hundred millivolts to a few volts. Both emit sexually dimorphic volleys which vary seasonally. In Uranoscopus, short bursts of electric discharges serve to repel competitors and to capture prey galvanotactically, while long EOD volleys function in individual attraction. This second type occurs only in the summer when the fish are spawning (Mikhailenko, 1971). In the skate Raja clavata, the discharge of the female is at maximal amplitude in the spring and summer, and could serve to attract the male. The male EOD is at peak amplitude in the summer and autumn and is suspected to play a role in group cohesion during migration. It was noted that during mating the female always swims in front of the male, whereas during migration a male always swims at the head of the group (Mikhailenko, 1971). Because of the transition in EOD intensity it is apparent that a clear cut distinction can no longer be made between weak and strong electric species.

Sensory Systems and Electroreception in Catfish

Moller and Rankin (1995) have reviewed the non-electric and electric sensory capacities of M. electricus. In many catfish species vision is poorly developed when compared to other senses, and Malapterurus is no exception.

Ebbesson and O'Donnel (1980) found that the visual centers including the optic tectum were small and poorly differentiated, which is believed to be a result of inhabiting a visually deprived environment. Taste, smell, electric and lateral line senses are generally more developed in catfish, which are mostly bottom dwellers. This is not unexpected since most species, including Malapterurus, are active and hunt nocturnally, and/or inhabit turbid water. Lateral line receptors can detect water displacements in the aquatic environment which are most often produced by other living organisms (Flock, 1967). Although it has been claimed that electric catfish may produce sound through the use of muscles attached to either side of the air bladder (Walker, 1969), this is considered unlikely (Moller & Rankin, 1995).

Catfish have a specialized sense of taste mediated to a large degree by barbels, which also aid in tactile sensation (Atema, 1980). Malapterurus electricus has six barbels, two maxillary and four mandibular. Taste buds cover the rest of the body as well, and taste projection areas of the brain are large. This external taste apparatus serves to locate food at a distance, while taste buds located inside of the mouth screen final intake. Amino acid compounds play a major role in gustatory stimulation. The external and internal taste senses have been functionally separated, and the ablation of the olfactory sense does not alter their effectiveness (Atema, 1980).

Olfaction plays an important role in the detection of live prey by catfish. Like taste, the organs of smell are well developed, as are the corresponding brain areas, and sensitivity to amino acids is acute. Olfactory detection and discrimination can be effectively abolished by blocking the nares (Herbert & Atema, 1977). Studies have shown that bullhead catfish (Ictalurus nebulosus) can discriminate between male and female conspecifics, and yellow bullheads (Ictalurus natalis) can recognize individuals via pheromones and even detect changes in status after fighting (Todd, Atema, & Bardach, 1967). These abilities are lost when a fish is deprived of its sense of smell. The chemical stimuli mediating such behavior are primarily contained in the mucus, but urine and fecal excretions also contribute.

Like several other teleosts (Mormyriformes, Gymnotiformes) and all catfish species examined thus far, Malapterurus has electroreceptive capabilities. Electrosensitive fish can detect electric fields emanating from different sources. These include fields of non-living physical and chemical origin, bioelectric fields from electric organs, and those from other living sources. Electroreception can function in various ways, including detection of inanimate objects and of living organisms, in social communication, and in short and long range navigation (Kalmijn, 1974; review: Moller & Rankin, 1995).

Electrosensitivity is well established in siluriform fishes. The electroreceptors of freshwater catfish, including Malapterurus, are the ampullary receptors or so called "small pit organs" (Bennett, 1971) located along the body. These receptors cover most of the external surface of the catfish, with the exception of the barbels.

Ampullary receptors occur in both electric and non-electric fish. They have been demonstrated to operate in detecting DC and low-frequency AC fields of external origin. These receptors may be visible as very small openings in the skin. Their well insulated canals transmit electrical current received by the sensory epithelium of the ampullary receptors. Freshwater siluroids have a high skin resistance and an internal resistivity lower than the surrounding water, so that voltage gradients of DC fields are excluded from the rest of the animals' interior. Catfish have been observed demonstrating compass-orientation to horizontally directed homogeneous DC electric fields (Peters & Wijland, 1974). The threshold current density for this was 8×10^{-12} A/mm^2 in water with a resistivity of 25 Ohm·m. Behavioral responses have been obtained from Malapterurus by introducing an electric field to an experimental tank by magnetic induction (Bauer, 1968; Kastoun, 1972). The fish will pivot on their body axis in order to head orient toward a source of local, DC, and pulsed DC dipole fields.

In a homogeneous DC field Malapterurus shows a galvanotactic response. The threshold for this as well as for barbel and fin movement responses is lowest during anodal orientation of the head. The fish are less sensitive if the long axis of the body is aligned perpendicularly to the field, and the threshold becomes higher still when the fish faces the cathode (Kastoun, 1972). Galvanotaxis is maximal in field densities of 4.1 μA/mm^2 and disappears if the density exceeds 9.2 μA/mm^2. The effect also disappears with repeated stimulation. The galvanotactic response to pulsed DC is less pronounced in electric catfish than in non-electric fish (Kastoun, 1972). Swimming in an imposed electric field, Malapterurus shows a preference for the heterogeneous zones over homogeneous zones and, depending on initial orientation, will swim toward such areas. Kastoun (1972) observed that in an AC field the threshold for locomotion was 0.2 μA lower than in DC fields. An increase in field density above 9.2 μA/mm^2 led to general excitement, locomotion and stereotypic swimming patterns.

In studies of the ampullae of Lorenzini of elasmobranch fishes it was found that the impulse frequency of this electroreceptor underwent a two-phase change in response to single brief pulses of electric current. The first phase is in the same direction as the response to DC, which is an increase from 0 to 70-100 Hz, but lasting only 100-500 ms. The second change occurs in the opposite direction and is up to 10 times as prolonged as the first

(Murray, 1965). A given envelope of repeated pulses are as effective as DC of an equivalent charge per second. This, however, does not hold true when the inter-pulse interval or IPI exceeds 200 ms because this would cause the change in impulse frequency to follow each individual pulse stimulus. Increases in stimulus intensity of up to 1000 times threshold value will cause an increase in response frequency up to the maximum rate. Values above this cause a decrease in frequency, probably due to saturation of the receptors.

When the small pit organs of ictalurid catfish are stimulated with high-frequency volleys of short, monopolar pulses, they respond only to changes in the average DC value. This observation lends support to the assumption that the catfish responds to slow changes in electric fields rather than to rapid ones (Roth, 1972). The ampullary electroreceptor may encounter such slow changes when the fish is moving relative to another fish or when it is in close vicinity of another fish, responding to its respiratory movements (myogenic potentials). Roth (1972) measured the effective range for such detection at 7 cm. Ampullary organs can thus perceive the presence of other fish. In <u>Malapterurus</u>, it has not yet been determined whether the bioelectric fields given off by prey fish can evoke strong electric organ discharges (Bauer, 1968).

The detection and location of a DC field in a living organism has been referred to as low-frequency passive electrolocation (Kalmijn, 1974; Bell, 1979). The receptor cells of the ampullary organs transmit electrosensory information to bipolar ganglion cells of the lateral line nerves, which in turn relay signals to the rhombencephalon (Finger, 1986). Central processing of such signals in catfish occurs in the posterior lateral line lobe which receives input from ampullary afferents. Two cell types occur here, one in which firing is accelerated by outside positive stimuli as are the primary afferents, and another whose firing is slowed by the same stimuli (Finger, 1986). Electrophysiological recordings have determined the frequency response of the ampullary electroreceptors in freely swimming catfish. This range was measured at 0.03-25 Hz with greatest sensitivity between 3 and 7 Hz (Peters & Buwalda, 1972).

It has been demonstrated that ictalurid catfish emit electric fields consisting of a strong stationary DC component over which a fluctuating AC component is superimposed (Peters & Bretschneider, 1972). The steepest voltage gradients occur close to the mouth (cathode) and gill slits (anode). The AC component corresponds to respiratory movements and is only one tenth as strong as the DC component. It has been hypothesized that in addition to detecting inanimate and animate electric field sources, the electroreceptive system of these catfish may serve to detect the fields generated by conspecifics. This could result in a form of electric recognition or intraspecific communication (Moller & Rankin, 1995). It has been further postulated that behaviors such as mouth display, touch, and lateral display, usually described in terms of visual criteria, are likely to involve modulation of the DC field (Finger, 1986). This too may represent an important component of social signalling (Moller & Rankin, 1995).

By measuring the electroreceptive ability of the African catfish Clarias, Lissmann and Machin (1963) had already concluded that the ampullary receptors had a greater sensitivity to wide single pulses than to DC. This indicated that the sensory signal was initiated by both the beginning and end of the pulse. Furthermore, sensitivity to low-frequency volleys (10-20 Hz) was very similar to that for single pulses of corresponding durations. Perception time was consequently short enough to allow the fish to respond to the first pulse. Even at higher frequencies (50-500 Hz) the fish were extremely sensitive, especially at pulse widths greater than 5 ms. Sensitivity ranged from a threshold field gradient of between less than 1 μV/cm and 10 μV/cm (Lissmann & Machin, 1963).

Bauer (1968) attempted to determine whether Malapterurus was able to detect external electric signals. He found that catfish conditioned to get food from a pair of galvanic "tweezers" would subsequently respond to an electric stimulus by searching for food. Signal detection was dependent on the positioning of the subject's body with respect to the dipole. Using a square wave of 1.5 ms duration, Bauer (1968) tested the sensitivity of Malapterurus in a homogeneous electric field. Maximal responding was elicited when fish were in parallel with the stimulus electrodes.

In experiments involving electroreceptor sensitivity in the electric fish Gymnarchus niloticus, Machin and Lissmann (1960) trained a standard response to an electrical stimulus. By pairing a food reward with single pulses and volleys of pulses, subjects were conditioned to increase swimming speed and approach a feeding trough. In order to determine whether Malapterurus was sensitive to the frequency range of pulsed direct current used in the present studies, two subjects were similarly conditioned to give a standard response to simulated EOD volleys (see Appendix B). Catfish initiated locomotion activity to stimuli from 1-625 Hz. This result indicated that the ampullary electroreceptors of Malapterurus electricus are sensitive to low-frequency (including single pulses) as well as relatively high-frequency volleys.

Models and Artificial Stimuli

Traditional ethological techniques such as playback experiments that employ models are often used to separate the feedback between sender and receiver and to control the contents of communicatory signals. Such a model was constructed to generate electrical stimuli in the present experiments. Artificial EODs have been used in playback experiments involving communication in weakly electric fish (review: Moller, 1995). Davis and Hopkins (1988), for example, made use of non-moving electrical models to mimic the EOD of Gymnotus carapo while investigating signal localization in the species. These models used a waveform generator to produce sine waves that elicited not only approach responses, but aggressive attacks as well. Yet, while affording a good deal of control over the signal produced, models such as this may be inferior to the playback of recordings containing naturally produced signals in eliciting behavioral responses. When digital recordings of the EOD of G. carapo were tested against synthetic mimics (sine waves), subjects took a more circuitous route when approaching the latter (Scudamore & McGregor, 1993). In the fish's natural habitat, the existence of sympatric, electrically active predators (Electrophorous) could partially explain caution in responding to novel signals. Such indirect approach behavior in the presence of a model may therefore be related to the degree with which the model effectively reproduces the natural signal.

Some researchers have made use of microprocessor systems that digitally synthesized "natural" signals which were then presented to test fish via dipole carbon electrodes (Hopkins & Bass, 1981; Kramer & Zupanc, 1986; Kramer & Otto, 1988). The tanks in these studies were provided with porous shelters and the dipoles were situated symmetrically to the fish inside of these. This computer operated apparatus provided both pulse-type and wave-type EODs with continuous, on-line frequency and amplitude control. Such a system made it possible to produce species specific, as well as sex-specific EODs in a highly controlled manner. This represented a significant improvement over the use of signals recorded on magnetic tape as triggers for pulse generators, a system that could not always be as easily manipulated. This is especially true since function or pulse generators produce sine, square, and sawtooth waves which do not always resemble the natural EOD waveform of weakly electric species (Kramer & Weymann, 1987).

Square-wave pulses have, however, been employed in studies on weakly electric fish possessing complex electrosensory systems. Pulse duration, which is a key component of the EOD of weakly discharging species, can be easily manipulated using square waves. Investigators (Moller, 1970; Kramer and Kuhn, 1994) have used monopolar square waves to determine the significance of pulse interval sequences for species recognition in two species of mormyrids. In these studies the investigators were interested in separating the effects of waveform from those of inter-pulse interval (IPI). Pulse pattern alone was shown to be sufficient for species recognition in mormyrids. Pulse intervals are often important signal components in mormyrid mating and spawning (Crawford, 1991).

Models such as those mentioned above have distinct advantages for studies investigating electrosensory capabilities of fish. First, they remove confounding sensory information by eliminating visual, olfactory, and tactile cues. They also allow for precise stimulus measurement and control. The amount of control provided by a computer operated system is necessary to mimic natural weakly electric mormyrid and gymnotid signals in which waveform, polarity, number of phases, and inflections in the pulse are critical. Such precise control is not, however, essential to mimic the EODs of Malapterurus. A pulse generator can produce negative polarity monophasic square pulses which closely match those of the electric catfish. The fish's ampullary electroreceptors are not specialized for communication, as are certain tuberous receptors of weakly discharging electric fish, so that an exact waveform match should not be as critical. Pulse duration, inter-pulse interval, volley duration, frequency, and amplitude of the signal, can be mimicked with accuracy using a pulse generator in combination with a waveform generator and a physiological stimulator.

Rationale and Objectives

The main objective of the present study was to determine whether Malapterurus is responsive to changes in EOD volley parameters. Such responsiveness may have implications for electrocommunication in the species. Field observations were conducted initially to collect information about the electric activity of Malapterurus in nature and to obtain information on its ecology, including water conditions, food items, and territory size. This information was incorporated in the experimental designs used in the laboratory.

A series of three laboratory experiments was conducted in order to test the hypothesis that Malapterurus is responsive to changes in EOD parameters. In the first experiment, EOD pulse duration was varied systematically for presentation to subjects. A 1.5 ms condition was included to represent the species-typical pulse duration. Pulse duration has been demonstrated to be an important parameter in communication in other electric fish species (review: Moller, 1995). The objective of this study was to provide evidence on the differential responsiveness of catfish to a range of pulse duration values.

The rationale for the second experiment was based on the work of Kastoun (1971, 1972), who demonstrated behaviorally that Malapterurus could discriminate between situation-specific EOD volleys produced by conspecifics.

These included both predatory and defensive type volleys. It was concluded that electric catfish are capable of detecting the discharges of neighboring fish and of making use of the information contained within the volleys (Kastoun, 1971, 1972). The objective of Experiment 2 was to obtain data on Malapterurus' behavior in the presence of simulated predatory and defensive stimulus. It was hypothesized that these volley types would yield differential responding. By using a model to provide greater control over the stimulus in the present study it was also possible to investigate the relative importance of the frequency and volley duration components in communication.

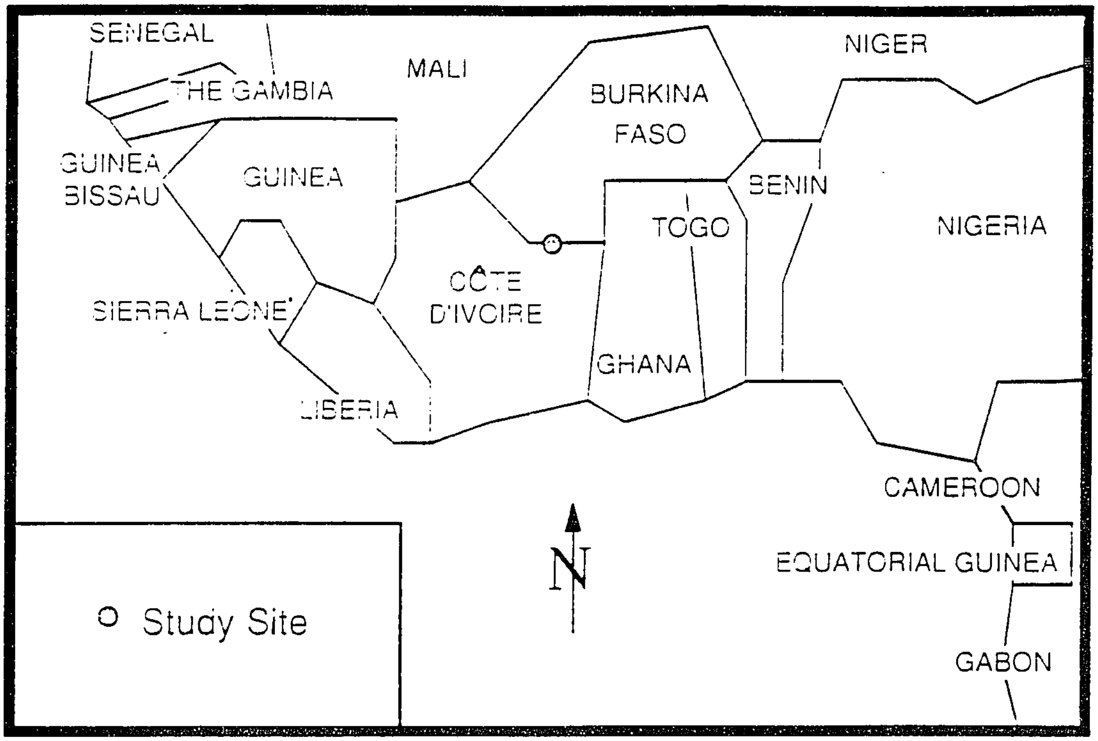
In the third experiment, the influence of conspecific EOD amplitude on behavior was investigated, and the results were evaluated in relation to their adaptive consequences (Maynard Smith & Parker, 1976). The rationale for this investigation is based on the absence of EODs from ritualized displays in Malapterurus (Rankin & Moller, 1986). It is possible that discharging does not usually accompany other display components because the EOD provides information about the fish's physical size. It was hypothesized that subjects would avoid relatively high-amplitude stimuli, while approaching low-amplitude volleys. Thus, the objective for the manipulation of stimulus amplitude was to demonstrate that Malapterurus changes its behavior based upon the relative strength of the EODs received.

FIELD OBSERVATIONS

Field observations were made on a local population of Malapterurus during April of 1990, on the Comoé River adjacent to the Kafolo Research Station in Côte d'Ivoire, West Africa (Figure 3). This survey, together with the work of Belbenoit et al. (1979) made it possible to establish information regarding spacing patterns, ecology and EOD activity of this species in nature. In April, at the end of the dry season, the river was barely flowing. Catfish were not located in the more open waters (although they were netted there by local fishermen), but were discovered in small pools formed along rock outcroppings. These seemed to be fed by the river from below, as they did not dry up, but it appeared that the fish could not escape. It was concluded that some of the spacing patterns found were a direct result of environmental conditions. The shortest distance between two fish was 6 m, and this occurred in a large pool (10x20 m) containing three residents. Smaller pools contained only individual specimens. Small cichlid fish as well as weakly electric mormyrids were also found in these pools.

Daily recordings were made at 8, 10, 12, 14, 16, and 1800 hr, with 5 min samples taken from four sites. Pairs of electrodes were placed in pools near rocky shelters where

Figure 3: Location of the main field study site along the Comoé River in Côte d'Ivoire, West Africa.


SENEGAL
THE GAMBIA
MALI
NIGER
BURKINA FASO
GUINEA BISSAU
GUINEA
BENIN
TOGO
NIGERIA
SIERRA LEONE
CÔTE D'IVOIRE
GHANA
LIBERIA
CAMEROON
EQUATORIAL GUINEA
GABON
N
Study Site

the fish were hiding. Tests of the water conditions measured temperature at a very high 34-35 °C, with a conductivity of 210 μs/cm. Water hardness was 28 ppm total, 12 ppm Ca, and 8 ppm Mg. The pH was recorded at 8.30-8.35. Following a thunderstorm the turbidity of the water remained too high to be read on the Jackson scale, and it was murky in appearance. Ambient light readings varied greatly throughout the day. The noontime range was between 570 and 32,700 lux.

An analysis of the EOD recordings (Apple II+ computer, "Applescope" software from RC Electronics, Santa Barbara, CA) showed that there was no significant variation in amount or type throughout the daytime. Both short, defensive or disturbance type volleys, as well as long feeding type volleys were present, with the former more common. Single pulses occurred at numerous times throughout, but were often indiscernible from background noise. Volleys contained between 1 and 8 separate groups of pulses, or "trains", and up to 130 individual pulses, with a maximum duration of 2860 ms. Average volley length was 629 ms, and the average number of pulses was 36. In support of Belbenoit et al. (1979), long feeding volleys were observed following sunset and seemed to be more frequent, but these were not recorded systematically.

Fish captured by local fishermen from the Comoé, as well as from an area of the Bandama River adjacent to the

Lamto Research Station to the south, were measured and weighed (Table 1). An analysis of stomach contents was performed on a few specimens in order to know what prey types the catfish were feeding on. A fairly complete sampling of the ichthyo-fauna of the river was also conducted for comparative purposes. Most catfish had empty stomachs, but a few contained the partially digested remains of small Tilapia and other organic material. EOD recordings were made from some captured specimens using a digitizing storage oscilloscope with a computer interface (Figure 4). The discharge amplitude of one catfish (T.L. 49 cm) measured 220 V (temperature = 27 °C).

Neighboring catfish established small home areas in large pools and isolated individuals occurred in more confined areas. This indicated that Malapterurus is territorial. Intraspecific competition for resources was particularly high during the dry season. It seemed likely that territorial encounters were important in establishing residency in the field. The electroreceptive ability of Malapterurus could function in the establishment of territory by detecting interlopers, provide clues as to the availability of prey in the area, or even assess the size of potential competitors.

Table 1: Physical measurements made of Malapterurus electricus in the field. Weights were not obtained from Comoé River fish because they were re-released. Sex could only be determined in the larger specimens. S.L. = standard length (tail not included). T.L. = total length.

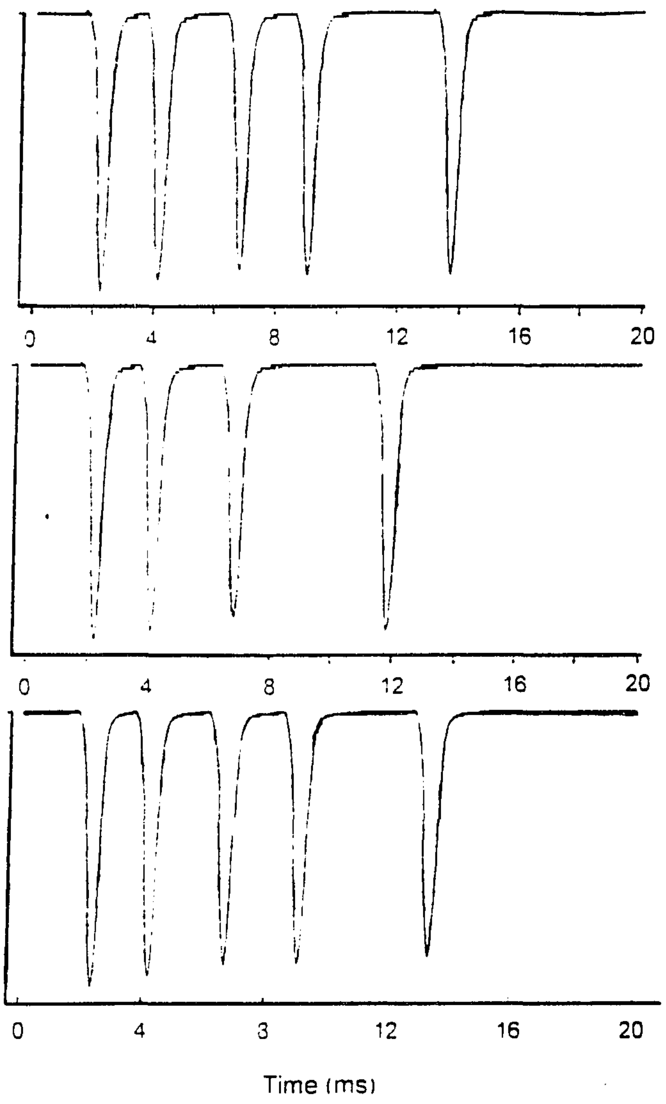
* EOD measured 220 V.

Table 1

Measurements of Malapterurus in the Field

Fish ID	River	S.L.(cm)	T.L.(cm)	Weight(g)	Sex
LTE01	Bandama	30.9	36.2	815	F
LTE02	Bandama	29.0	33.0	713	F
LTE03	Bandama	27.0	31.8	436	-
LTE04	Bandama	25.0	28.0	376	-
LTE05	Bandama	17.8	20.5	128	-
LTE06	Bandama	15.0	17.0	86	-
KFE01	Comoé	18.4	21.5	-	-
KFE02*	Comoé	49.2	56.3	-	M
KFE03	Comoé	30.2	34.6	-	-

Figure 4: Recordings made of the EOD of a relatively large Malapterurus electricus (T.L. 49 cm) captured in the field. Amplitude measured 220 V at the dorsal surface in water (temperature = 27 °C). Figure courtesy of B. Kramer.


0
4
8
12
16
20
0
4
8
12
16
20
0
4
8
12
16
20
Time (ms)

EXPERIMENT 1A: ROLE OF PULSE DURATION I

The first experiment tested the effect of pulse duration on electroreceptor mediated behavior. Although ampullary receptors are known to be maximally responsive to DC and low-frequency AC stimuli, repeated high-frequency AC monopolar pulses have been shown to be as effective as DC of the equivalent charge per second (Murray, 1965; Roth, 1972). Also, according to Lissmann and Machin (1963) the ampullary receptors of Clarias catfish are sensitive to single pulses as well as volleys of from 10 to 500 Hz. In light of these observations, it seemed possible that a range of conspecific discharge frequencies may be detectable by Malapterurus. This includes low-frequency defensive type volleys as well as high-frequency (up to 500 Hz) predatory discharges. Since the effective range for the detection of low-amplitude DC fields emanating from other fish was measured at 7 cm in Ictalurus (Peters & Bretschneider, 1972), stimulation by conspecific EODs will be sufficiently strong within this distance and probably much beyond it.

The length of the individual pulse in Malapterurus is reported at between 1 and 2 ms (Bennett et al., 1966; review: Bauer, 1968) with an average of around 1.5 ms at 20-30 °C, and is temperature dependent. Recordings made of EODs in the Comoé River showed individual pulse durations of

1.5 ms at a very high 34-35 °C. It was hypothesized that pulse widths of between 1 and 2 ms would be the most effective in eliciting a behavioral response. Pulses outside this range, either shorter or longer, should be less effective. This should hold true even if the 1.5 ms value did not evolve through selection for features that optimize communication in the species. It has recently been theorized (Moller, 1995) that selective pressure related to predation may have played a role in shaping the EOD duration (see general discussion). Should this be the case, there is still no reason to assume that the naturally occurring waveform would not be the most effective.

Discrimination of pulse duration is dependent on the way in which electric stimuli are received and processed. It is possible, for example, that some degree of stimulus generalization exists, or that catfish respond only to the onset, or to both the onset and offset of a single pulse or group of pulses (Lissmann & Machin, 1963). A series of pulses might also be responded to in terms of its DC component. In volleys where the signal rises unidirectionally from the zero current base line there is a net DC flow equal to the average current of the stimulus (Offner, 1967). Increasing EOD pulse duration may therefore result in the creation of supernormal stimuli due to resulting increase in the DC component of the signal, and result in greater responding. Changes in the size of the DC component also depend on the interval between successive pulses, the IPI (Bell & Russell, 1978; Finger, 1986). The shorter or longer IPIs that accompany changes in EOD frequency would necessarily change the overall DC value of a given volley and theoretically allow for the discrimination of frequencies. Malapterurus then, may recognize conspecific signals by changes in the DC portion of the volley. Pulse duration would, however, remain important.

Parameters of the electrical stimuli that were held constant for all conditions include the following: (1) The IPI was kept constant throughout all pulse duration conditions. This was considered more important than holding frequency constant for two reasons: (a) Adjusting IPIs to produce equal frequencies would mean that longer pulse durations, which already produce stronger electric fields than shorter pulses (using equal IPIs), would generate even greater ones. (b) The amount of time which separates consecutive pulses (onset time) is important with regard to receptor recovery. (2) Volley duration, which represents the total stimulus duration for a given trial was held constant. In doing so, equal stimulus presentation times were obtained. (3) The amplitude of the stimuli was held constant for all trials at a value close to that produced by the fish.

The most effective electrocommunicatory signal was expected to contain pulses 1.5 ms in duration. By stimulating subjects with pulse durations longer or shorter than, and equal to the fish's own EOD, it was possible to test this hypothesis. Assumptions regarding the behavioral responses of Malapterurus, the dependent variable in this study, were culled from prior research by Bauer (1968), Kastoun (1971, 1972), and Rankin and Moller (1986). It was anticipated that appropriate stimuli would elicit general excitement and exploratory type activity, not necessarily directed at the source of stimulation itself. More direct responses such as an attack on the stimulus producing electrodes, or movement away from the source of stimulation, along with entering the shelter tube, were also considered possible. Additionally, the subjects might produce EODs of their own in response to stimulation, although this was considered unlikely in light of the results obtained by Rankin and Moller (1986). For these reasons, measurements included total time spent inside the shelter during a trial (all trials began with subjects at rest inside shelters), time spent actively swimming, tallies of overt behaviors by type (lateral display, biting, etc.), and the recording of EODs.

Methods

Subjects

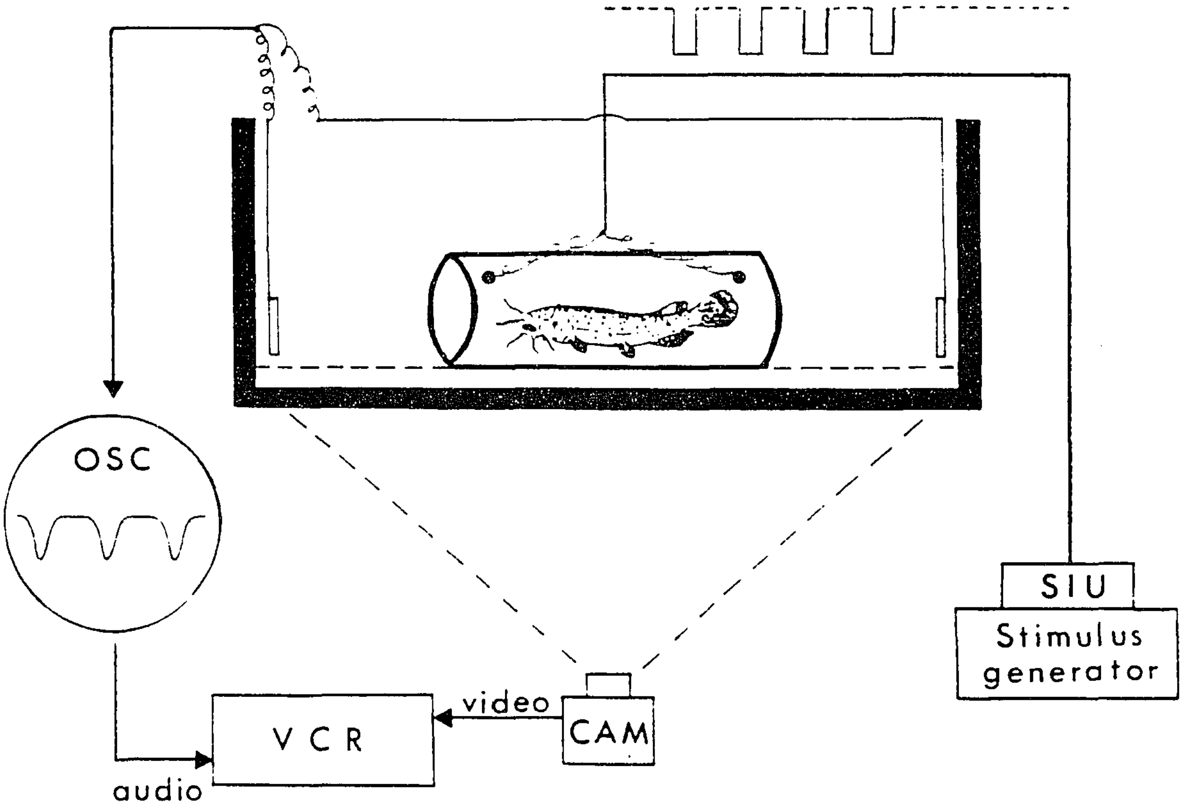
Twenty-four experimentally naive African electric catfish, Malapterurus electricus, total length (T.L.) 15-25 cm, served as subjects. Catfish in this size group are juveniles and sub-adults of undetermined sex (Balon & Coche, 1974). All catfish were obtained through a local fish importer and were wild caught.

Subjects were housed individually in 22.4 l, all glass aquaria (41x26x21 cm). Each home tank was provided with a ceramic shelter tube and a corner filter. Water temperature was maintained at 24±1 °C, with a pH of 7.0 and a conductivity of 100±10 μS/cm. All fish were kept on a 12:12 light/dark cycle, with lights on from 23:00 to 11:00 hrs. Subjects were fed weekly with goldfish (Carassius auratus <5 cm), with the last feeding taking place 3 days prior to testing.

Apparatus

The experimental setup is illustrated in Figure 5. A 200 l all glass aquarium measuring 42x50x91 cm served as a test tank. Water conditions were kept the same as those for home tanks. A 75 W white incandescent bulb illuminated the tank. Light intensity readings at the water surface ranged from 650 lux (right and left sides) to 1550 lux (center). A clear plastic shelter tube 7.6 cm in diameter and 15 cm long was fastened to the floor at the center of the tank parallel to its long sides. The shelter caused an illumination attenuation of approximately 12%. To avoid

Figure 5. Schematic of the experimental setup for Experiments 1 and 2. SIU = stimulus isolation unit. (Figure is not drawn to scale).


OSC
SIU
Stimulus generator
video
CAM
VCR
audio

electrical noise from the aquarium heater, it was removed one hour prior to testing.

EODs were monitored using a pair of Ag/AgCl electrodes affixed to the center of the two side walls. A Tektronix Model 503 Oscilloscope was used to monitor both natural and artificial EODs. All electric discharges were recorded on the audio track of a Sony AV 3200 video recorder. Overt behavior was recorded on videotape using the video recorder and a Sony AV 3200 camera placed 1.5 m in front of the test tank.

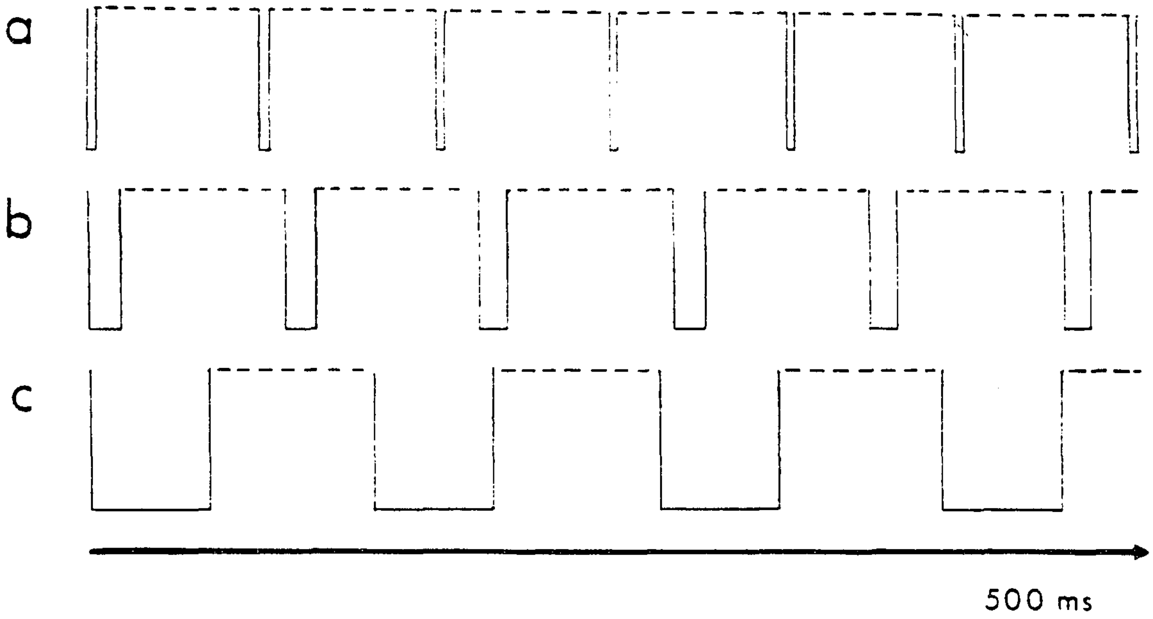
Electrical stimuli were generated using a Grass Model S44 Solid-State Square Pulse Stimulator that produced gating currents for input to a Tektronix Type 162 Waveform Generator. Delays and durations of the stimulus volleys could be adjusted with the S44 Stimulator. The 162 Waveform Generator provided a negative going sawtooth wave that was used to trigger a Tektronix Type 161 Pulse Generator and allowed for the adjustment of the inter-pulse interval (IPI). The Type 161 Pulse Generator supplied calibrated rectangular output pulses of adjustable duration and amplitude, of either polarity. Pulse amplitude could be adjusted between 0 and 50 V, with pulse durations of 10 μs to 100 ms. The pulse generator was connected to a Dion Electronix Type B Isolation Unit in order to separate the stimulus circuit from the current generating circuit.

The stimulus was transmitted via a pair of carbon electrodes, the tips of which extended 0.5 cm from the opposite ends of a rubber tube (15 cm length; 1 cm diameter). This "model" was attached to the tank bottom by suction cups at a distance of 10 cm from the rear wall of the aquarium and 11 cm from the center of the shelter tube, and aligned parallel to it. The polarity of the electric field was positive on the left side of the tank and negative on the right side.

Procedure

The simulated EOD pulse types used in this experiment are shown in Figure 6. Pulse durations of 1.5 ms were used to represent the natural EOD. The other conditions were 0.375, 0.75, 3.0, and 6.0 ms, plus a control group receiving no EODs. The 6.0 ms condition was chosen because it corresponds to those pulse widths that were especially effective, even at high frequencies, in triggering ampullary receptor firing in Clarias (Lissmann & Machin, 1963). The IPI was defined as the period of time between the end of one pulse and the onset of the next. The IPI used in all cases was 8.5 ms, resulting in a frequency of 100 Hz in the 1.5 ms condition, which represents a frequency value well within the fish's natural range (Bauer, 1968; Belbenoit et al., 1979). Frequencies for the other conditions varied according to their pulse duration. The volley duration was set at 500 ms for all groups. Pulse amplitude was

Figure 6: Examples of the simulated EOD pulse types used in Experiment 1. (A) 0.375 ms, (B) 1.5 ms, and (C) 6.0 ms pulse durations.


a
b
c
500 ms

maintained at 25 V, measured at the stimulus electrodes in water. Attenuation of the stimulus amplitude over distance is shown in Appendix A. The resulting electric field gradient (voltage/distance) fell within the range of that produced by subjects recorded in their home tanks and corresponds to measurements made by Rankin and Moller (1986).

All subjects were given a three day (72 hr) adaptation period in the experimental tank prior to testing. Testing took place 90 min prior to lights off, when the fish normally become active. Continuous recordings were made with the video camera and electrodes throughout each session. Sessions began with a single fish inside the plastic shelter tube, oriented so that the head faced the direction of the positive stimulus electrode (anode). Fish were gently moved into the tube 15 min prior to testing using a plastic rod if necessary.

Each trial began with the initiation of a stimulus volley and terminated with the presentation of the next volley two min later, the onset of which constituted the start of the next trial. Subjects were tested for a total of 25 trials during a 50 min period which constituted one experimental session. Control fish were recorded for 50 min with no stimulus presented. Subjects were run in random order using a between groups design. Six groups of four subjects representing the 5 pulse duration conditions

(0.375, 0.75, 1.5, 3.0, and 6.0 ms) plus the control were tested. Following each session the subjects were returned to their home tanks. The test tank, shelter, and model were thoroughly wiped with aquarium sponges between subjects to remove odor cues.

Analysis

The location and behavior of fish were analyzed from the video tape. The "Observer" version 2.0, an event recording software package (Noldus Information Technology, the Netherlands) was used to collect frequency data on the occurrence of behavioral events and mark the onset and offset of duration measures for behavioral states. Both duration and frequency of activity was analyzed across groups using a single classification Model I ANOVA (Sokal & Rohlf, 1981). This was done for total duration of swimming activity, total number of swimming bouts initiated per session, and number of times a change in activity occurred within 2.5 s following stimulus presentation. The latter analysis was to determine the immediate response, if any, to stimulus presentation. In control trials, the 2.5 s period at the onset of each 2 min period was analyzed.

Further, percentage of time spent inside of the shelter tube was analyzed using a Model I ANOVA. Percentage data were arcsine transformed prior to analysis. Additional data on nested behavior classes such as swimming inside shelter, were collected and analyzed as well. Differences between particular groups were obtained using the T-method (Sokal & Rohlf, 1981) for multiple comparisons among pairs of means based on equal sample sizes (unplanned comparisons).

Any other behavior occurring with sufficient frequency, such as the display components classified by Rankin and Moller (1986) including electrode contact, lateral or open mouth displays, and biting, along with any EODs, was subjected to ANOVAs and paired comparisons. EODs were analyzed using an oscilloscope with a computer interface (Apple II+ computer and "Applescope" software developed by RC Electronics, Santa Barbara, CA). Volley duration and frequency were examined.

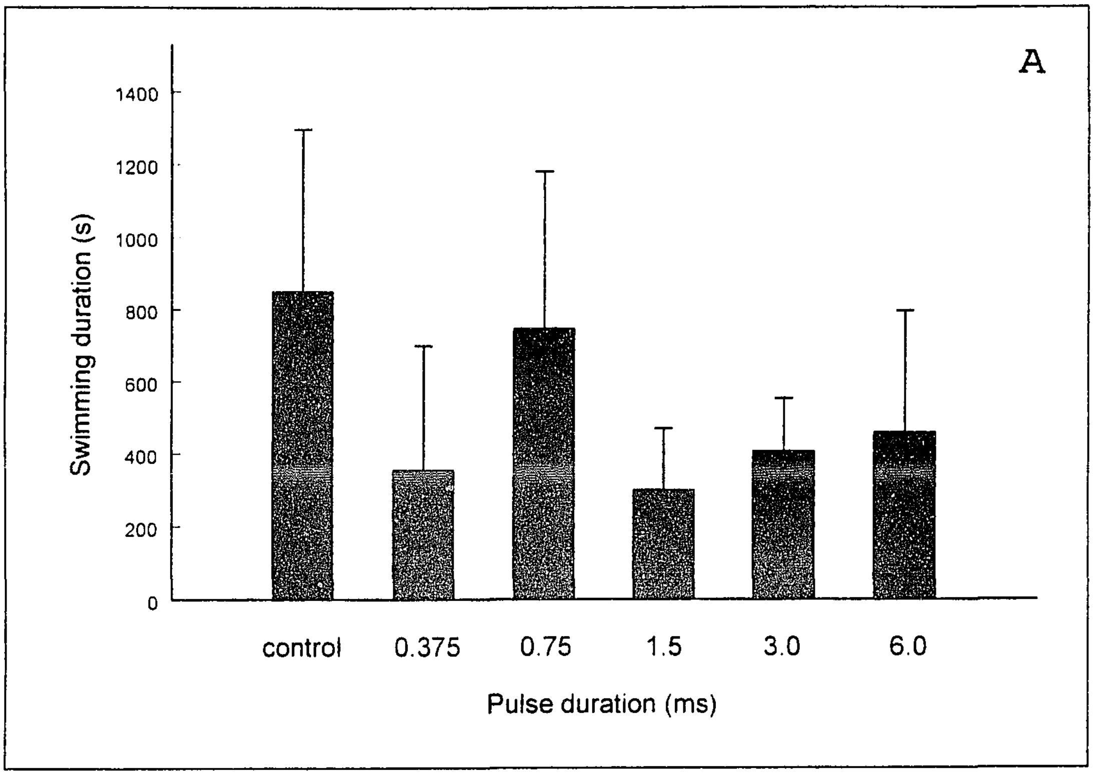
RESULTS

The mean duration of swimming activity was somewhat higher during control sessions and for the 0.75 ms condition. A one-way ANOVA, however, established that there was no significant difference between conditions ($\underline{F}_{5,23}$=0.453, $\underline{P}$>0.05). The 1.5 ms condition, which represents the naturally occurring pulse duration, showed the least amount of swimming activity (Figure 7A). A large between subject variability resulted in a high standard error throughout. An analysis of mean swimming bouts during the test session also failed to establish significant differences across pulse width conditions, including control ($\underline{F}_{5,23}$=0.360, $\underline{P}$>0.05). The four longest pulse durations produced comparable swimming bout averages, with lower mean bouts occurring in the 0.375 ms and control conditions (Figure 7B). Again, the between subject variability was very high.

The mean percentage of time spent inside the shelter tube was greater for stimulus conditions than for the control (Figure 8). However, fish under most pulse conditions spent similar amounts of time in the shelter and there was no significant difference between groups ($\underline{F}_{5,23}$=2.317, $\underline{P}$>0.05, data were arcsine transformed). Subjects having the highest mean swimming duration also had

Figure 7: A. Mean duration of swimming activity as a function of simulated EOD pulse duration.

B. Mean number of swimming bouts initiated as a function of pulse duration.


A
Swimming duration (s)
1400
1200
1000
800
600
400
200
0
control
0.375
0.75
1.5
3.0
6.0
Pulse duration (ms)

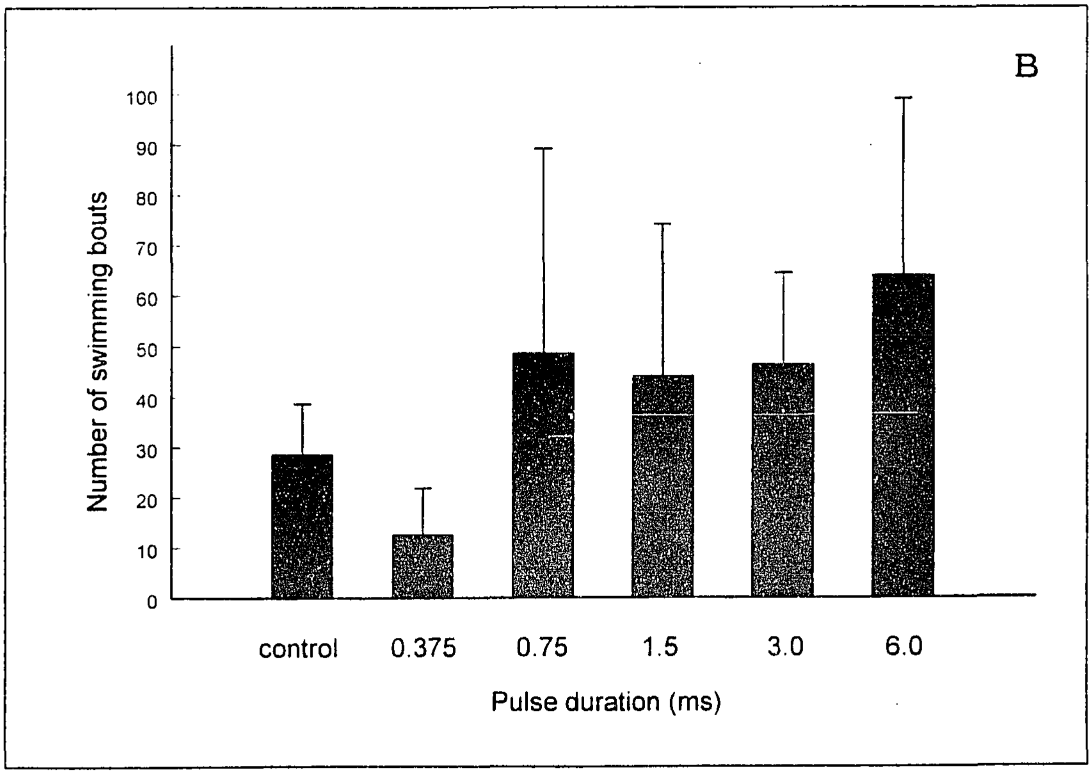
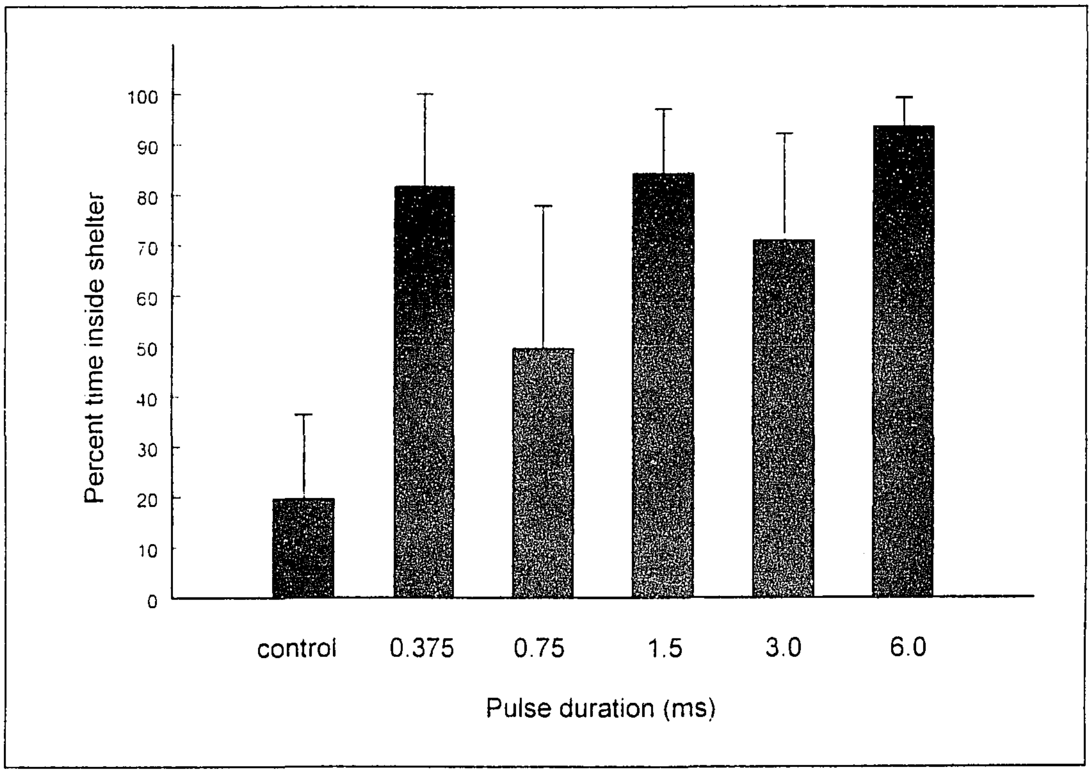

B
Number of swimming bouts
100
90
80
70
60
50
40
30
20
10
0
control
0.375
0.75
1.5
3.0
6.0
Pulse duration (ms)

Figure 8: Effect of pulse duration on the time (in percent) spent inside the shelter tube.


Percent time inside shelter
100
90
80
70
60
50
40
30
20
10
0
control
0.375
0.75
1.5
3.0
6.0
Pulse duration (ms)

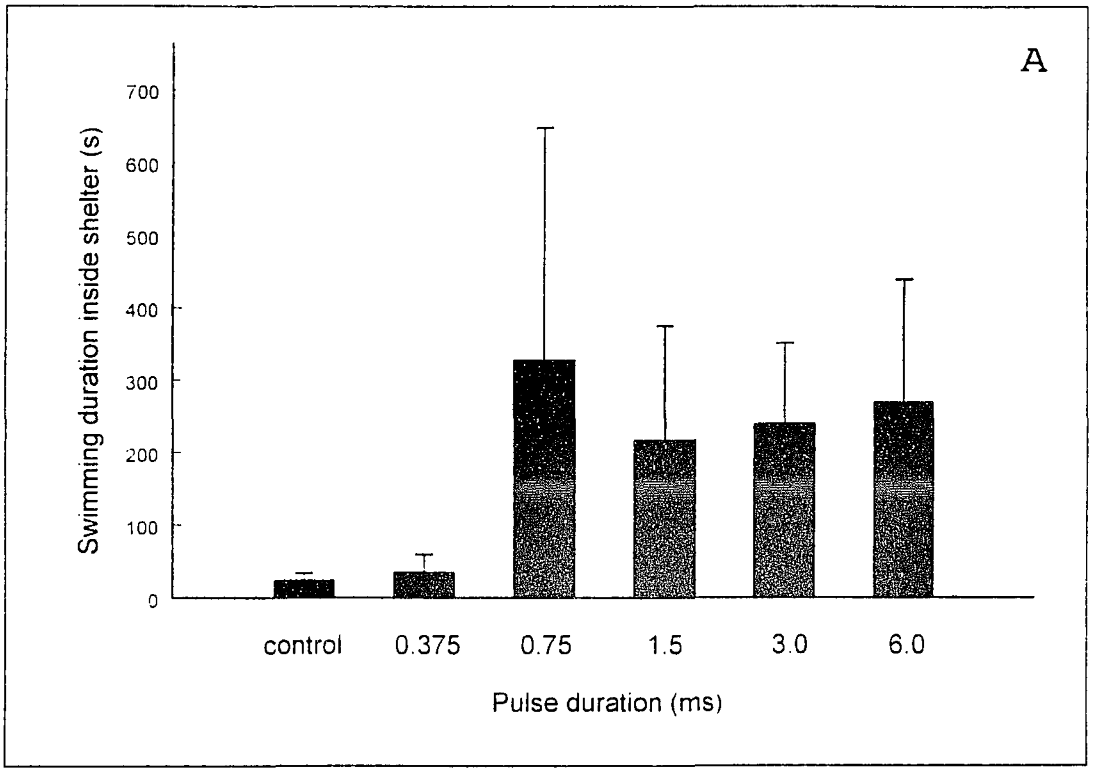
the lowest total time inside the shelter. These fish were found in the 0.75 ms and control groups. It should be noted that since swimming activity could occur inside the shelter tube (see below) these two events were not mutually exclusive.

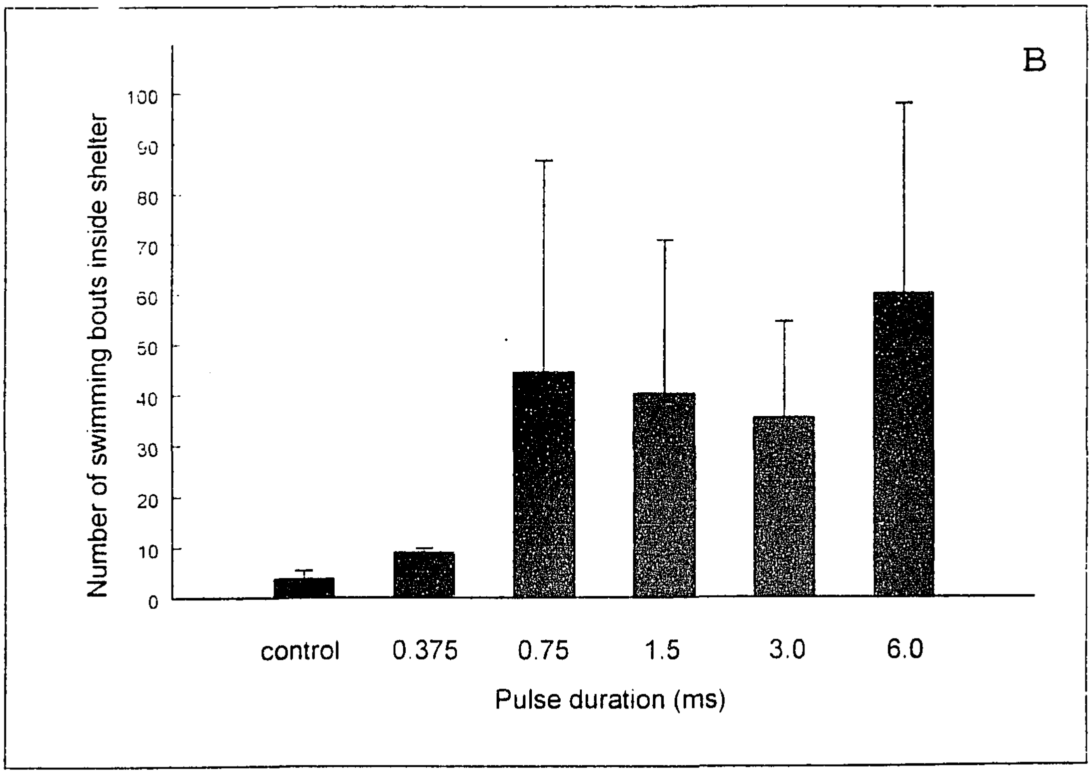
"Nested swimming duration inside the shelter" (amount of time spent swimming inside shelter tube) was examined across treatment conditions (Figure 9A). Subjects in the 0.75 ms condition spent the least amount of time inside the shelter tube of all conditions, except in the control condition, and exhibited the highest mean swimming duration inside the shelter. For the 0.375 ms and control conditions, the values were very low, as were the standard errors, while the three longest pulse widths resulted in similar mean durations and high standard errors. There was no overall significant difference between groups ($\underline{F}_{5,23}=0.563$, $\underline{P}>0.05$).

An analysis of the mean number of swimming bouts inside the shelter showed a pattern comparable to the previous measure (Figure 9B). The 6.0 ms condition did, however, show a slightly higher value than the other pulse conditions. As in the duration measure, there was no significant difference between treatments ($\underline{F}_{5,23}=0.620$, $\underline{P}>0.05$). Between subject variability and standard error was very high. The mean number of swimming bouts inside the shelter approached that for overall mean swimming bouts,

Figure 9: Comparison of "nested swimming activity inside shelter" (amount of time spent swimming inside shelter tube) as a function of pulse duration. A. Duration of swimming activity occurring inside of the shelter.

B. Mean number of swimming bouts initiated inside of the shelter.


A
Swimming duration inside shelter (s)
0
100
200
300
400
500
600
700
control
0.375
0.75
1.5
3.0
6.0
Pulse duration (ms)

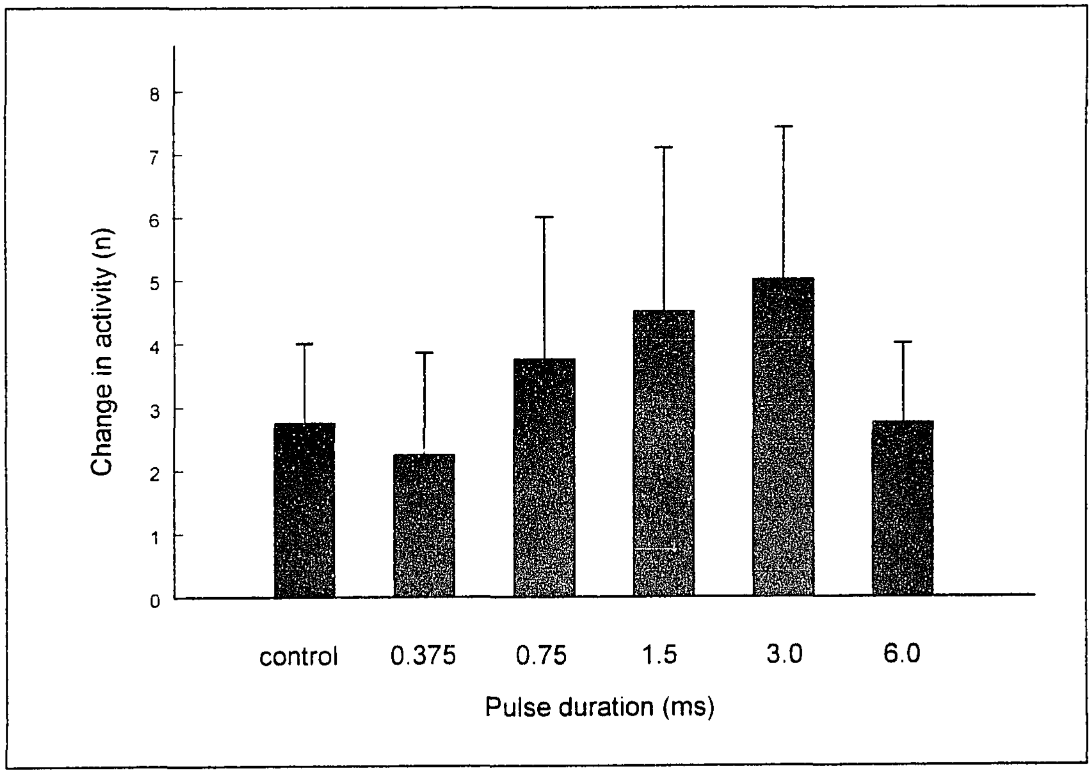

B
Number of swimming bouts inside shelter
0
10
20
30
40
50
60
70
80
90
100
control
0.375
0.75
1.5
3.0
6.0
Pulse duration (ms)

indicating that a large majority of swimming bouts occurred inside the shelter tube, except under control conditions.

Figure 10 shows the number of times a change in activity followed stimulus presentation within 2.5 s. This includes both the initiation of swimming in subjects that were at rest at the time of stimulation, as well as the change to a resting state in those fish that were actively swimming during stimulus presentation. Change in activity occurred most frequently in the 3.0 ms condition, followed by the 1.5 ms group. The smallest amount of change in activity following stimulus presentation occurred in the 0.375 ms condition. For the control group, the 2.5 s period immediately following each 2 min mark was analyzed. Again, there was a high standard error and no significant difference between pulse durations ($\underline{F}_{5,23}$=0.309, $\underline{P}$>0.05).

Catfish did not exhibit EODs with sufficient frequency to permit their analysis. EODs were generated on only two occasions during the entire experiment. Additionally, no subjects made physical contact with the stimulus electrodes during this experiment. Other overt behaviors also occurred too infrequently to lend themselves to quantitative analysis.

Figure 10: Influence of pulse duration on changes in activity following stimulus presentation. Mean number of times subjects switched from swimming to resting or from resting to swimming during the 2.5 s post-stimulation period.


Change in activity (n)
0
1
2
3
4
5
6
7
8
control
0.375
0.75
1.5
3.0
6.0
Pulse duration (ms)

DISCUSSION

The results indicate that Malapterurus does not discriminate between pulse durations over a range of 0.375-6.0 ms. There was no indication that the 1.5 ms condition represented an optimal signal for any of the behavioral measures analyzed. Overall, there was a large amount of variability in behavior between individuals in most groups. Replication using a within-subjects design could potentially eliminate the high standard errors that occurred in this study (see Experiment 1B).

Catfish in the control group had the highest mean swimming duration, while exhibiting a relatively low mean number of swimming bouts. This indicates that active fish may inhibit their locomotor activity as a result of stimulation; swimming during stimulus trials usually only occurred for short periods at a time. Subjects in the control condition also spent less time inside of the shelter when compared with the groups receiving stimulation. Only a very small amount of the swimming activity of control subjects took place within the shelter tube. Subjects in the five stimulus conditions, however, had nested swimming duration and nested swimming bouts that were proportional to the overall occurrence of these activities.

Since the 0.375 ms condition was the least effective pulse duration in eliciting behavioral responses, there exists the possibility that Malapterurus is, to some extent, attending to the DC component of the signals. This assumption is reinforced by the fact that stimulation with 6.0 ms pulses, which have the largest DC component, produced the largest number of swimming bouts. The 6.0 ms pulse duration is optimal in triggering the firing of ampullary receptors in other catfish species (Lissman & Machin, 1963). It is also possible that catfish are simply responding to the onset of the volley, and perceiving it as a single unit. Pulses may also be grouped into larger units as a result of physiological constraints; subjects may not be capable of processing individual pulses due to receptor recovery time, given the relatively high frequencies used. That catfish can respond to frequencies of up to 500 Hz, as Lissman and Machin (1963) found, does not mean that they attend to the individual pulses contained in such high-frequency volleys.

The virtual absence of EOD production was not surprising. As Rankin and Moller (1986) observed, during encounters with conspecifics, EODs were rarely produced, and even then, only during the escalation of hostilities. The present experiment supports this finding, in that subjects did not discharge in response to the artificial stimuli.

EXPERIMENT 1B: ROLE OF PULSE DURATION II

Because the behavioral measures analyzed in Experiment 1A did not yield significant differences between treatment conditions, the effect of the experimental manipulation of pulse durations was tested again using a within-subjects design. It was believed that by doing so the effects of the large inter-individual variability would be eliminated. Subjects would now serve as their own controls.

Two of the previous conditions (0.75 ms and 3.0 ms) were eliminated, leaving the naturally occurring 1.5 ms condition, as well as the 0.375 and 6.0 ms conditions along with the control. By decreasing the number of conditions an adequate number of trails could be presented for each, while keeping the total number of trials per session equal to that in Experiment 1A. Inter-pulse interval, volley length, frequency, and amplitude were held constant at the same values as in 1A.

Methods

Subjects

Twelve experimentally naive African electric catfish, Malapterurus electricus, (T. L. 15-25 cm) served as subjects. The condition and maintenance of the fish prior to testing was the same as in Experiment 1A.

Apparatus

The apparatus used in this experiment was the same as for Experiment 1A.

Procedure

Subjects received the same three day adaptation period to the test tank as in 1A. Again, subjects were tested 90 min prior to lights out. Testing began with the fish inside the shelter tube, with head oriented toward the positive stimulus electrode. Audio and video recordings were made continuously throughout each test session. Both artificial and natural electrical activity was monitored via the oscilloscope.

As in 1A each trial consisted of the presentation of one stimulus volley and the 2 min interval including and following it. Each trial terminated with the onset of the next stimulus volley. Using a within-subjects design, each fish was subjected to the four conditions (control, 0.375, 1.5, and 6.0 ms: Figure 6), grouped into blocks of six trials each, for a total of 24 trials. The order of presentation of the four conditions was counterbalanced. Each test session lasted for a total of 48 min. Following testing, subjects were returned to their home tanks and the experimental apparatus was thoroughly cleaned.

Analysis

Video taped recordings were analyzed using "The Observer" version 2.0 event recording software. Activity, location, and overt behaviors (electrode contact) were scored. Both duration and frequency data was analyzed using a one-way repeated-measures ANOVA (Sokal & Rohlf, 1981). This included swimming duration, number of swimming bouts, percent of time spent in shelter, and activity changes immediately following presentation of the stimulus (within 2.5 s). Differences between conditions were further subjected to unplanned comparisons. Any EODs produced by subjects were analyzed with an oscilloscope/computer interface as in 1A.

RESULTS

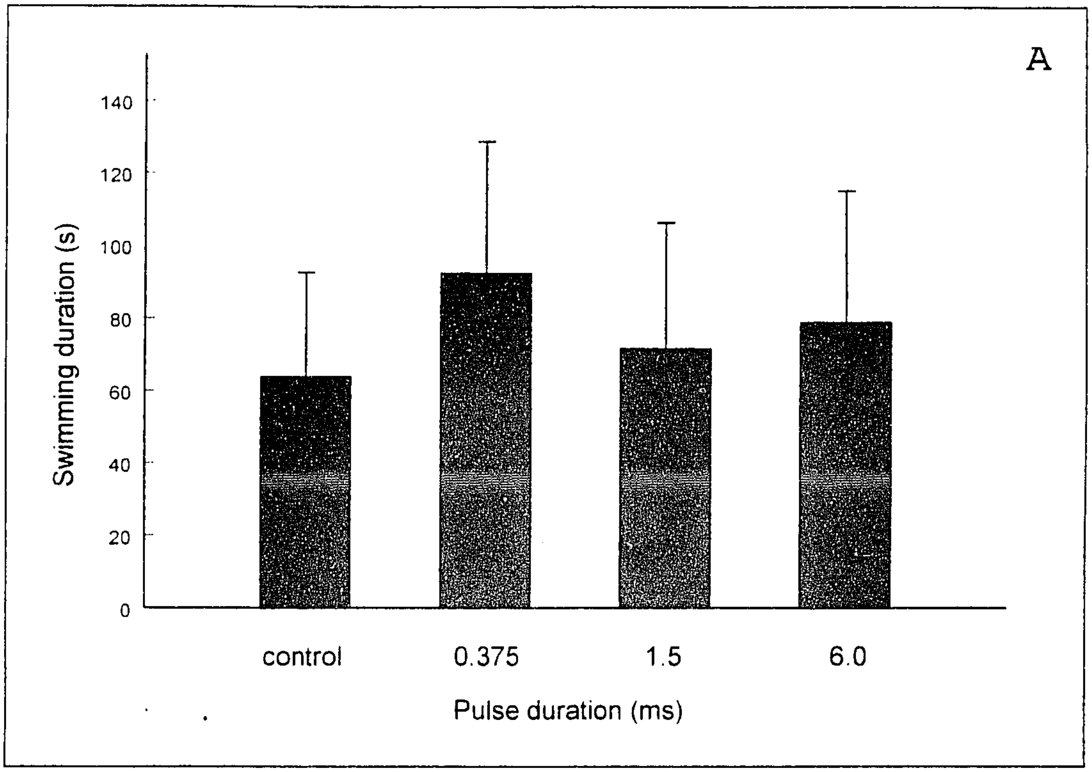
Total swimming duration increased slightly during stimulus conditions as compared with control trials (Figure 11A). The overall difference between treatments, however, was not significant ($F_{3,11}$=0.492, P>0.05). The number of swimming bouts also increased during stimulus trials (Figure 11A), but differences between treatments were, again, not significant ($F_{3,11}$=0.672, P>0.05).

Under stimulus conditions, the catfish spent about the same amount of time inside the shelter tube, regardless of the pulse duration (Figure 12). When the stimulus was present, the fish spent slightly more time inside the shelter than during control trials without simulated EODs, but this effect was not significant ($F_{3,11}$=1.264, P>0.05, arcsine transformation).

The number of times the subjects made physical contact with the stimulus electrodes increased in the presence of stimulation, as compared to control trials when no contacts occurred (Figure 13), although the overall frequency of this behavior was low. The 6.0 ms EOD elicited the most frequent contacts. Because of the high standard error, differences in amount of electrode contact were not significant ($F_{3,11}$=1.340, P>0.05). Other overt behaviors, including EODs, were too infrequent to be considered for

Figure 11: A. Mean duration of swimming activity as a function of simulated EOD pulse duration.

B. Effect of pulse duration on the mean number of swimming bouts initiated.


A
Swimming duration (s)
140
120
100
80
60
40
20
0
control
0.375
1.5
6.0
Pulse duration (ms)

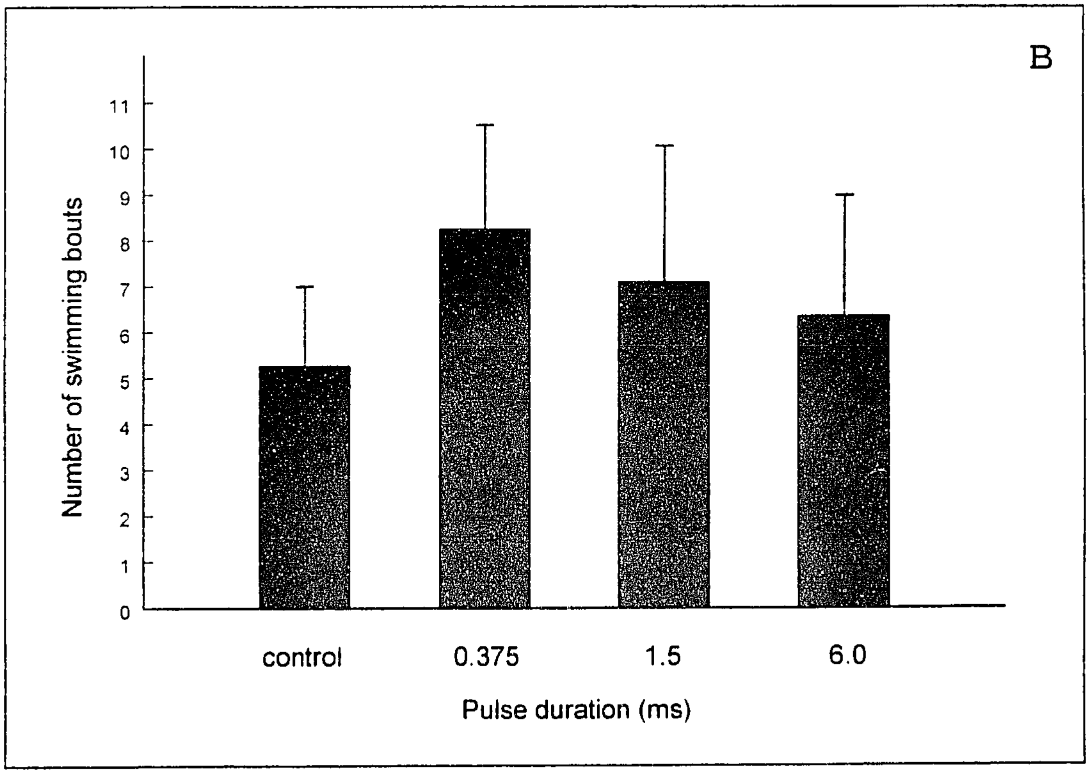

B
Number of swimming bouts
11
10
9
8
7
6
5
4
3
2
1
0
control
0.375
1.5
6.0
Pulse duration (ms)

Figure 12: Mean amount of time (in percent) spent inside shelter as a function of pulse duration.

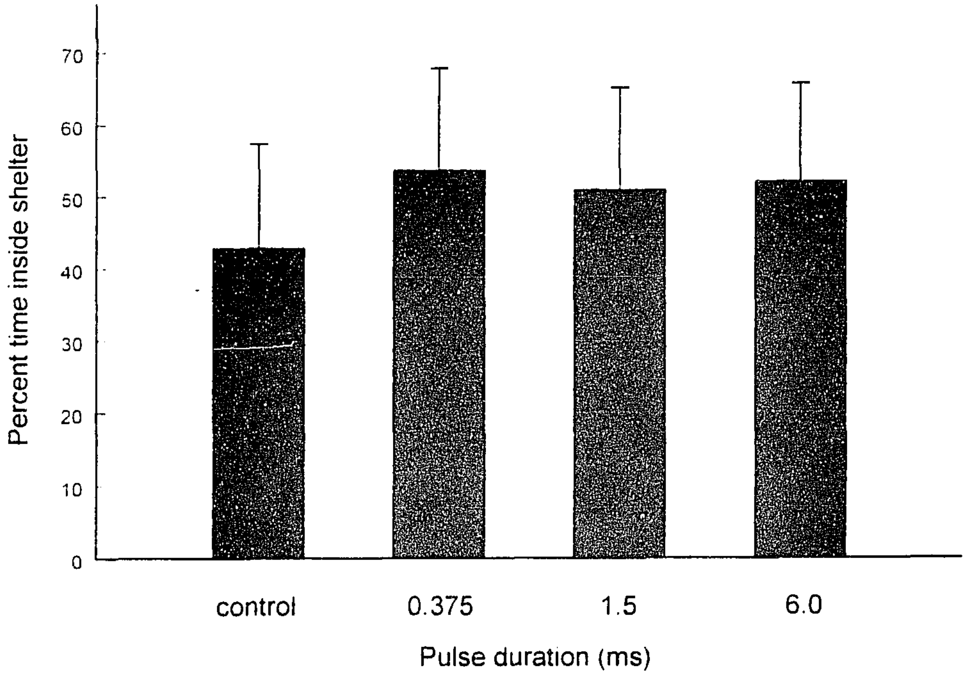
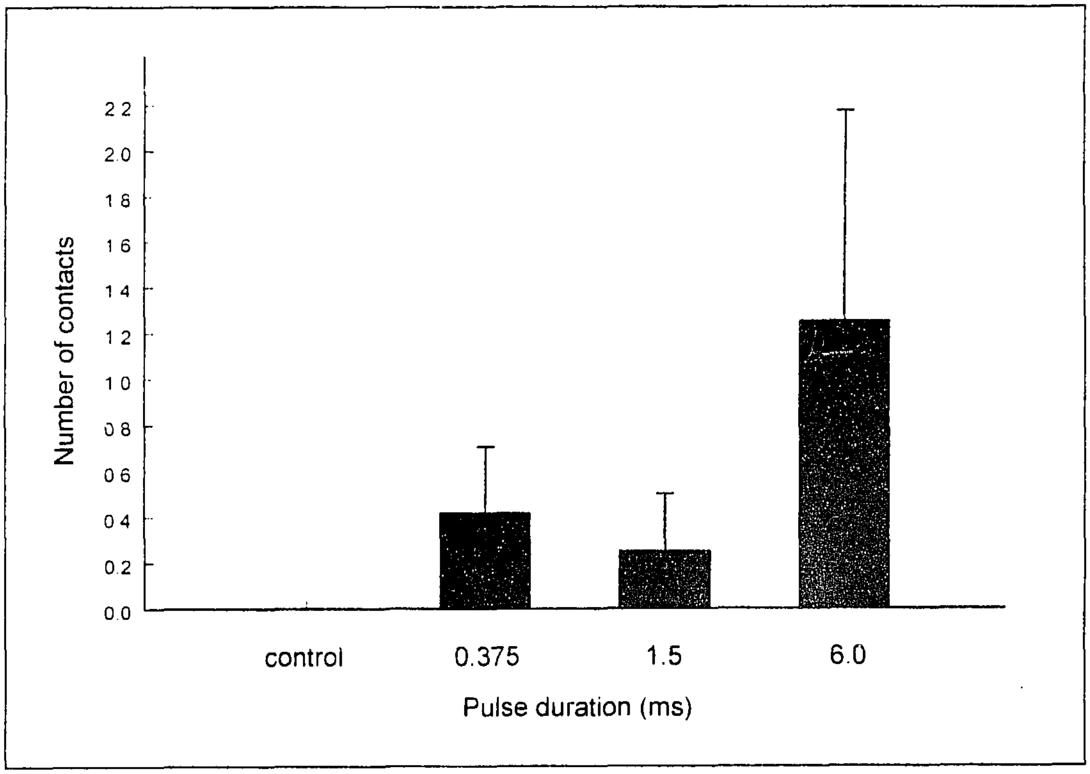

Percent time inside shelter
0
10
20
30
40
50
60
70
control
0.375
1.5
6.0
Pulse duration (ms)

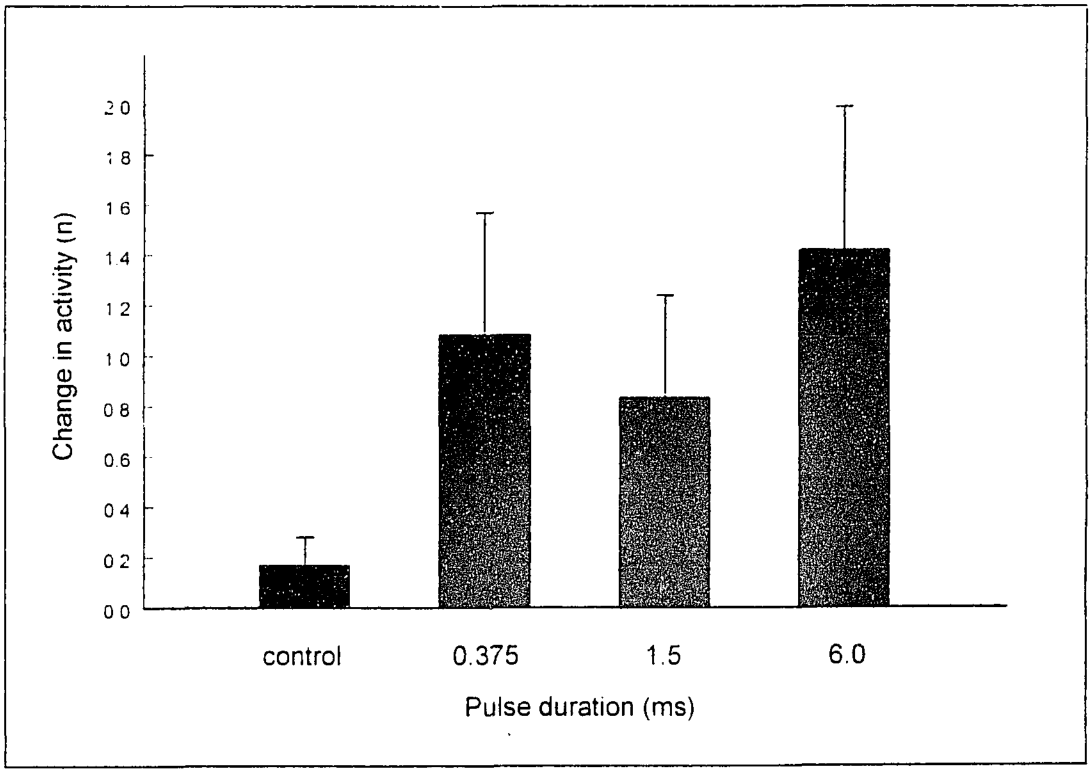
Figure 13. Effect of pulse duration on the mean frequency of contacts made with the stimulus electrodes.


Number of contacts
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
control
0.375
1.5
6.0
Pulse duration (ms)

further analysis.

The activity of the catfish during the 2.5 s immediately following the stimulus presentation was again analyzed (Figure 14). In control trials the fish were observed for 2.5 s following each 2 min mark. The number of times that catfish initiated swimming or resting activity following stimulus presentation was greater under stimulus conditions than during controls. The 6.0 ms EOD was the most effective stimulus. Overall, however, there was no significant difference across treatment conditions ($\underline{F}_{3,11}=2.200$, $\underline{P}>0.05$).

Figure 14: Changes in activity following stimulus presentation. Mean number of times subjects switched from swimming to resting or from resting to swimming during the 2.5 s post-stimulation period as a function of pulse duration.


2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Change in activity (n)
control
0.375
1.5
6.0
Pulse duration (ms)

DISCUSSION

The results indicate that subjects did not significantly alter their swimming activity over the range of treatment conditions. Like the results reported for Experiment 1A, with a between-subject design, stimuli in the 1.5 and 6.0 ms conditions produced a similar number of swimming bouts and total swimming duration. However, rather than resulting in a shorter swimming duration and a lower frequency of swimming bout initiation, as previously found, the 0.375 ms pulse duration elicited more swimming than the other pulse durations. In comparing the results of both experiments, it can be concluded that pulse duration does not have an effect on swimming behavior under the experimental conditions.

The results of this study agree with those of Experiment 1A in regard to the duration of time spent inside the shelter tube. Subjects again spent an almost identical percentage of time in the shelter regardless of pulse condition, although in the present study the control condition produced an nearly equal amount of shelter use as well. Pulse duration alone was not sufficient to produce differences in the shelter use of catfish based on the combined findings of Experiments 1A and 1B.

Unlike Experiment 1A, some catfish made physical contact with the stimulus electrodes. Electrode contact was infrequent, resulting in a very high standard error of the mean. None of the subjects, however, made stimulus electrode contact during the control condition, whereas at least one fish made contact during each of the three pulse conditions. Four subjects in total made contacts during one or more conditions. The 6.0 ms condition elicited the most frequent contacts, again pointing to the possible influence of longer pulse durations. Although there was no significant difference between pulse durations, the results indicate that Malapterurus possesses the ability to locate and approach the source of electrical stimulation.

The association of a change in activity with the presentation of simulated EODs shows a clearer delineation between stimulus and control conditions than during the previous study. Changes in activity, from resting to swimming, and vice versa, were uniformly low in the absence of stimulus presentation. The smaller total numbers attained were due, in part, to the experimental design by which subjects received only six volleys per condition, consequently providing only six opportunities to change activity. As was the case in the analysis of electrode contact, the 6.0 ms condition was the most effective stimulus, which may indicate the effectiveness of a larger DC component for signal reception.

In attempting to control variables such as IPI, volley duration, and amplitude in Experiments 1A and 1B, the artificial signals did not resemble the two types of volleys that commonly characterize the fish's natural EODs (Bauer, 1968; Belbenoit et. al, 1979). By using a mid-range frequency value (100 Hz) and volley length (500 ms), the model catfish was generating neither defensive nor predatory type volleys. EOD type, as defined by characteristic frequency and volley duration may be crucial in triggering specific behavioral responses (Kastoun, 1971, 1972; see Experiments 2A and 2B). The artificial stimuli employed here did not permit this type of discrimination. In addition, EOD amplitude may be an important factor in determining behavioral responding in Malapterurus (see Experiment 3). Because the amplitude of the artificial signal was held constant, but subjects' own EOD amplitudes varied, this may account for some of the inter-subject variability in activity and location, as well as the absence of significant differences between treatment groups.

As in Experiment 1A, subjects did not respond to stimulus presentation with electric organ discharges of their own.

The use of a within- subject design did little to remove the high variability found within treatment groups. It is possible that presenting fish with one pulse duration could have influenced their response to later conditions.

Since it was important to easily view and record all behavioral responses, a transparent shelter tube was utilized during Experiments 1A and 1B. It seemed preferable to switch to opaque shelters for future studies in order to provide some shielding from the light source, the assumption being that such a tube would make a superior hiding place. By making the shelter more "desirable" it will make the analysis of location (inside vs. outside shelter), an important factor in Experiment 2, more meaningful.

Furthermore, since activity in Malapterurus increases following sunset (Belbenoit et al., 1979) testing during the remaining studies will take place during the beginning of the dark cycle under red light illumination. The wavelengths produced by a red light source should fall outside the detection range of Malapterurus (Ebbesson & O'Donnel, 1980). An accurate assessment of location and activity measures was considered a priority for Experiments 2 and 3, and red light was sufficient for the purposes of video taping these behaviors. EOD recording would naturally be unaffected by the new setup.

EXPERIMENT 2A: DEFENSIVE VS. PREDATORY VOLLEYS

Kastoun (1971, 1972) proposed that Malapterurus was not only able to perceive conspecific discharges, but could discriminate between volley types and exhibit appropriate, situation specific responses. His research not only demonstrated the potential for electrocommunication in this species, but also discovered in what capacity it may function. That the electric catfish produces two distinctly different EODs in predatory and defensive situations has been well documented (Bauer, 1968; review: Moller & Rankin, 1995). Predatory volleys are generally long (up to 8 s) and have a higher frequency (up to 500 Hz). Defensive bursts are much shorter, consist of fewer pulses, and are generally of much lower frequency (Bauer, 1968; Belbenoit et al., 1979). Defensive volleys contain an average of 16 pulses whereas predatory volleys have an average of 133, and up to as many as 600. Attack volleys (Kastoun, 1971) and prey chasing volleys (Bauer, 1968) have also been characterized.

By connecting tanks containing electric catfish via electrodes, Kastoun (1971, 1972) was able to eliminate visual, olfactory and lateral line cues during his experiments. However, by employing this method he sacrificed strict control over the electric signals being produced and transmitted. The temporal pattern of the stimuli could not be predicted or manipulated. Thus, important EOD parameters, namely frequency, volley duration, and number of pulses per volley were subject to variation from trial to trial. For this reason Kastoun's experiments needed to be replicated, this time using an artificial stimulus source in order to introduce more control. Another advantage of using a model to mimic EODs is the elimination of feedback from the receiver to the sender by breaking the loop.

It was hypothesized that Malapterurus would be able to process EOD stimuli to the extent that discrimination between predatory and defensive type volleys would take place. Predatory volleys were expected to elicit higher activity levels than defensive ones. A more specific response to predatory volleys could be the type of hunting behavior characterized by an exploratory swimming around the tank as described by Kastoun (1971), sometimes in the form of a stereotypical figure eight. Additionally, attack responses could be directed toward objects in the tank, as were produced in response to EODs elicited by mechanical stimulation of the signalling fish in Kastoun's experiment. This was considered possible due to the fact that the pulse number and frequency that accompanied biting behavior and elicited attack in conspecifics (attack volleys) overlapped with those of a predatory nature. In addition to producing comparatively lower activity levels, presentations of defensive type volleys were expected to result in escape responses and hiding in the shelters provided (Kastoun, 1971).

Methods

Subjects

Twelve experimentally naive Malapterurus electricus (T. L. 15-25 cm) served as subjects. Maintenance and pretreatment was the same as in Experiment 1.

Apparatus

Subjects were tested in the same 22.4 l, all glass aquaria (41x26x21 cm) which served as their home tank. Each tank was provided with an opaque ceramic shelter tube 6 cm in diameter and 14 cm in length. Water temperature was maintained at 24±1 °C, with a pH of 7 and a conductivity of 100±10 μS/cm. All fish were kept on a 12:12 light/dark cycle, with lights on from 23:00 to 11:00 hrs. During testing, a 60 W red light bulb was used to permit recording of the fish's behavior while simulating darkness. At the water's surface under red light, light intensity readings averaged approximately 120 lux at the center of the tank's surface. The aquarium filters and heaters were removed 1 hr prior to testing.

Stimuli were generated by the apparatus described in

Experiment 1. The "model catfish" was attached to the center of the left side of each testing tank by suction cups at a distance of 10 cm from the tank bottom, and parallel to it. The electrode tips were 13 cm from the front and rear tank walls, with the anode nearest the front wall.

Procedure

All subjects received a minimum adaptation period of one week to the test tank prior to testing. Testing took place during the first hour following lights off. A between-subjects design was used, with six fish receiving defensive stimuli and six receiving predatory. Each session consisted 12 min block of one of the two treatment conditions. The total session length was 12 min. The inter-trial interval was 2 min, amounting to a total of 6 trials in each session. Each trial began with the onset of the stimulus volley.

Testing was done by generating artificial EODs for presentation to the subjects. Pulse width was 1.5 ms and amplitude was set at 25 V (see Appendix A). These parameters were held constant for all trials. The defensive volleys (low-frequency/short duration) were produced at a frequency of 57.1 Hz and were 210 ms in duration, for a total of 12 pulses with an IPI of 16 ms. For predatory volleys (high-frequency/long-duration), frequency was held at 250 Hz with a volley duration of 1000 ms. These volleys contained 250 pulses and had an IPI of 2.5 ms. All of these parameters fell within the ranges given for the respective discharge types as reported in the literature (Bauer, 1968; Bennett, 1971; Rankin & Moller, 1986).

Analysis

Activity and location duration data were tallied. Differences in swimming duration and percent of time spent inside shelter were analyzed using t-tests (Sokal & Rohlf, 1981).

RESULTS

A comparison of mean swimming duration is shown in Figure 15. A two-tailed t-test showed that swimming duration was significantly higher in the predatory volley condition ($\underline{t}$=3.757, $\underline{df}$=10, $\underline{P}$<0.01).

Figure 16 shows the percentage of time spent inside the shelter as a function of volley type. Fish receiving defensive type stimuli spent significantly more time inside of the shelter ($\underline{t}$=2.276, $\underline{df}$=10, $\underline{P}$<0.05, two-tailed, arcsine transformation).

At no time during this study were EODs produced by any of the subjects.

Figure 15: Swimming duration as a function of volley type. Subjects receiving predatory stimuli had significantly higher amounts of swimming activity ($\underline{P}<0.01$).

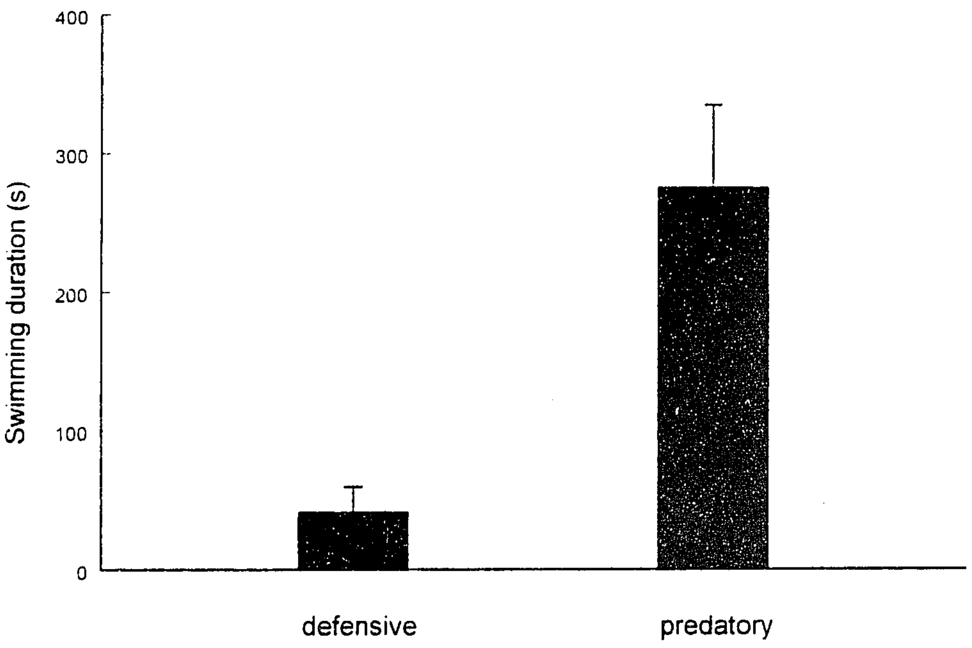
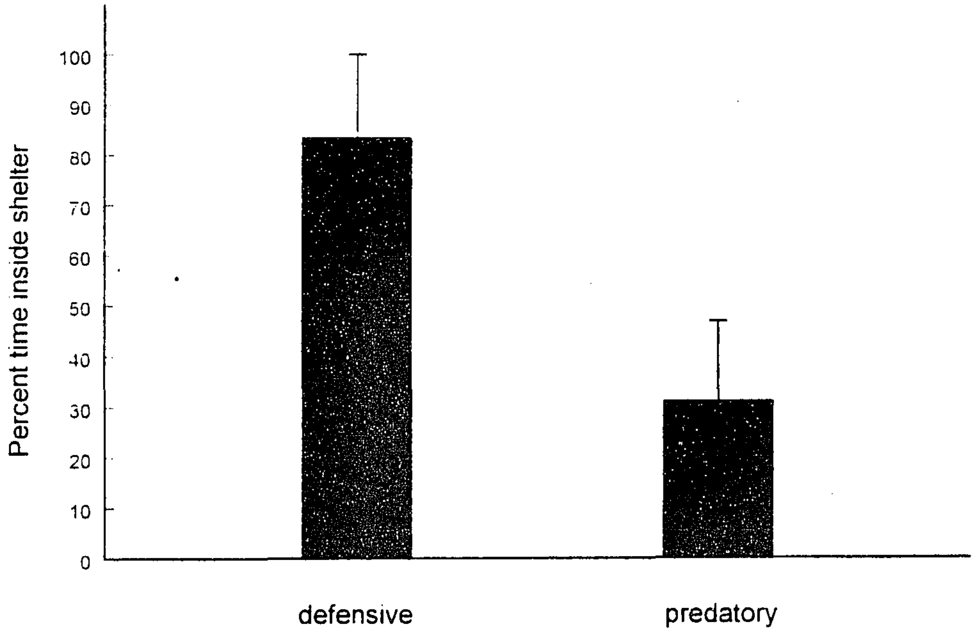

Swimming duration (s)
400
300
200
100
0
defensive
predatory

Figure 16: The effect of volley type on percentage of time spent inside shelter. Fish receiving defensive volleys spent significantly more time inside the shelter ($\underline{P}<0.05$).


Percent time inside shelter
0
10
20
30
40
50
60
70
80
90
100
defensive
predatory

DISCUSSION

Stimulation with predatory volleys produced higher activity levels in Malapterurus. The increase in swimming duration over that obtained during stimulation with defensive volleys is indicative of the prey search behavior described by Bauer (1968) and Kastoun (1971, 1972). This result supports Kastoun's (1971, 1972) findings that catfish receiving predatory volleys engaged in increased activity and "hunting" behavior. By increasing their activity, subjects improved their chances of encountering potential prey in the area. When fish were presented with defensive type volleys, swimming activity was significantly lower and more time was spent inside of the shelter tubes than during the predatory condition. The location of catfish inside the shelters corresponds with the hiding behavior described by Kastoun (1971, 1972). When Malapterurus takes shelter or remains inside of a shelter tube, its protection from potential danger is increased.

The results of this experiment clearly indicate that electric catfish have the ability to discriminate between situation-specific conspecific discharges and respond to them in an adaptive manner. For Malapterurus, both the strategy of decreasing activity in the presence of potential danger and of increasing it around potential prey confers an advantage. Catfish also gain by taking shelter upon electrically sensing the defensive behavior of a neighbor. At the same time, leaving a shelter can increase hunting success when a conspecific's discharge "broadcasts" its own predatory activity. Adventitious communication strategies in this species are therefore maintained because they benefit the receiver. Attending to changes in the electric discharge activity of neighboring fish is an adaptive strategy.

EXPERIMENT 2B: ROLE OF FREQUENCY AND VOLLEY DURATION

In Experiment IIA Malapterurus was shown to discriminate between simulated defensive and predatory type volleys. The stimuli used to test this ability differed in both volley duration and frequency. It was possible that fish were attending to either one of these variables alone or to a combination of the two. In an attempt to separate the effects of volley duration and frequency, two additional conditions were tested. One was low-frequency, long-duration and the other high-frequency, short-duration.

It was hypothesized that, as in Experiment 2A, defensive trials would yield less swimming activity than predatory. Defensive stimuli would also result in greater amounts of time being spent inside the shelter tube. Further, it was postulated that stimulation with either the two new, non-natural frequency/volley duration combinations would yield levels of swimming and sheltering in between those found in response to defensive and predatory stimulus conditions. It was expected that the catfish would not respond differentially to the two new conditions even though discrimination between them may be possible based on receptor physiology. The reason for this is that the signal components of each condition (duration and frequency), would send conflicting messages as to the receiver's appropriate behavioral response.

Methods

Subjects

Twelve experimentally naive Malapterurus electricus (T.L. 15-25 cm) served as subjects. Maintenance and pretreatment was the same as in Experiment 1.

Apparatus

The same testing apparatus was used as in Experiment 1, except for the replacement of the white light bulb with a 60 W red light bulb to permit recording of the fish's behavior during the dark cycle, and the use of a shelter made from a red translucent tube instead of a clear one. Illumination with red light produced light intensity readings at the water's surface of from 30 (right and left sides) to 120 (center) lux. The red shelter tube attenuated the illumination approximately 35%. In addition, the aquarium filter was removed prior to testing.

The stimulus generating apparatus was the same as in Experiment 1.

Procedure

All subjects received a three day adaptation period to the test tank as in the previous experiments. Testing took place during the first hour following lights off. A within-subject design was employed. Each session consisted of a 6 min baseline control period followed by a 12 min block of each of the four treatment conditions, and finally a 6 min post test control period. The total session length was 60 min. The order of presentation of the four stimulus conditions was counterbalanced. The inter-trial interval was 2 min, amounting to a total of 6 trials in each condition. Each trial began with the onset of the stimulus volley.

As in Experiment 2A, testing was done by generating artificial EODs for presentation to the subjects. Again, pulse width was held constant at 1.5 ms and amplitude was set at 25 V (see Appendix A). Defensive (low-frequency/short-duration) and predatory (high-frequency/long-duration) volley parameters remained the same as in Experiment 2A. The low-frequency/long-duration and high-frequency/short-duration volleys were 57.1 Hz and 1000 ms (57.1 pulses, 16 ms IPI) and 250 Hz and 210 ms (52.5 pulses, 2.5 ms IPI) respectively.

Analysis

Video tapes were scored using "The Observer" version 3.0 software package. Differences in swimming duration and percent of time spent inside the shelter (hunting vs. hiding) were analyzed using a two-way repeated-measures

ANOVA (Sokal & Rohlf, 1981). In addition, a descriptive analysis of both the number of swimming bouts and the number of resting bouts occurring 2.5 s of following stimulus presentation. These analyses will show the overall effects of treatment conditions in addition to the separate effects of volley duration and frequency, and any interaction between the two.

RESULTS

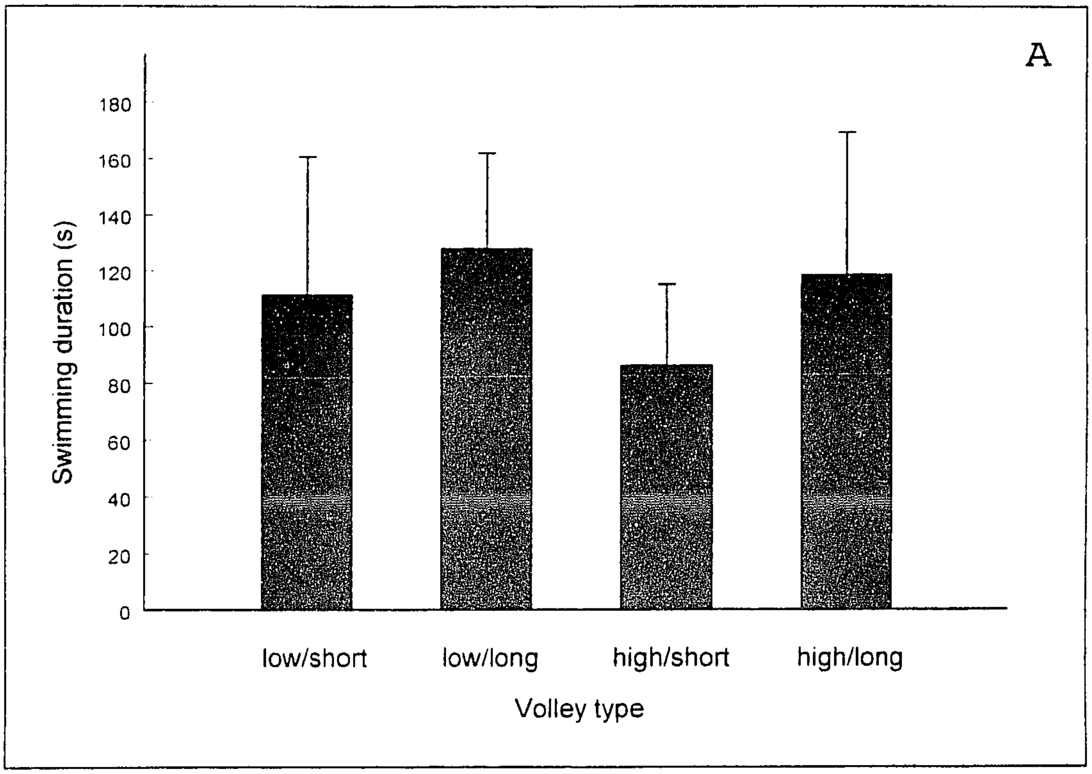
Figure 17A shows the mean swimming duration across treatment conditions. The time spent swimming was slightly longer in the two long-duration conditions. The results of the two-way ANOVA, however, showed no significant difference between frequencies ($F_{1,11}=0.197$, $P>0.05$) or volley durations ($F_{1,11}=1.069$, $P>0.05$). There was also no significant interaction of the effects of frequency and volley duration on swimming duration ($F_{1,11}=0.062$, $P>0.05$). Across all treatments there existed a high within-subject variance.

An analysis of swimming bout frequency failed to show a significant difference between volley types (Figure 17B). A two-way ANOVA indicated that frequency ($F_{1,11}=0.057$, $P>0.05$) and volley duration ($F_{1,11}=2.772$, $P>0.05$) did not effect swimming frequency. Although the low-frequency, short-volley condition had an appreciably lower number of swimming bouts, the interaction ANOVA failed to reach significance ($F_{1,11}=4.158$, $P>0.05$).

The percentage of time spent inside the shelter was similar across all four treatments, with the two low-frequency conditions yielding only slightly higher in-shelter durations (Figure 18). There was no significant difference between frequencies ($F_{1,11}=2.556$, $P>0.05$, arcsine transformation). There was also no significant effect of

Figure 17: A. Mean duration of swimming activity as a function of frequency and volley duration.

B. Effect of volley type on the mean number of swimming bouts initiated.


A
Swimming duration (s)
0
20
40
60
80
100
120
140
160
180
low/short
low/long
high/short
high/long
Volley type

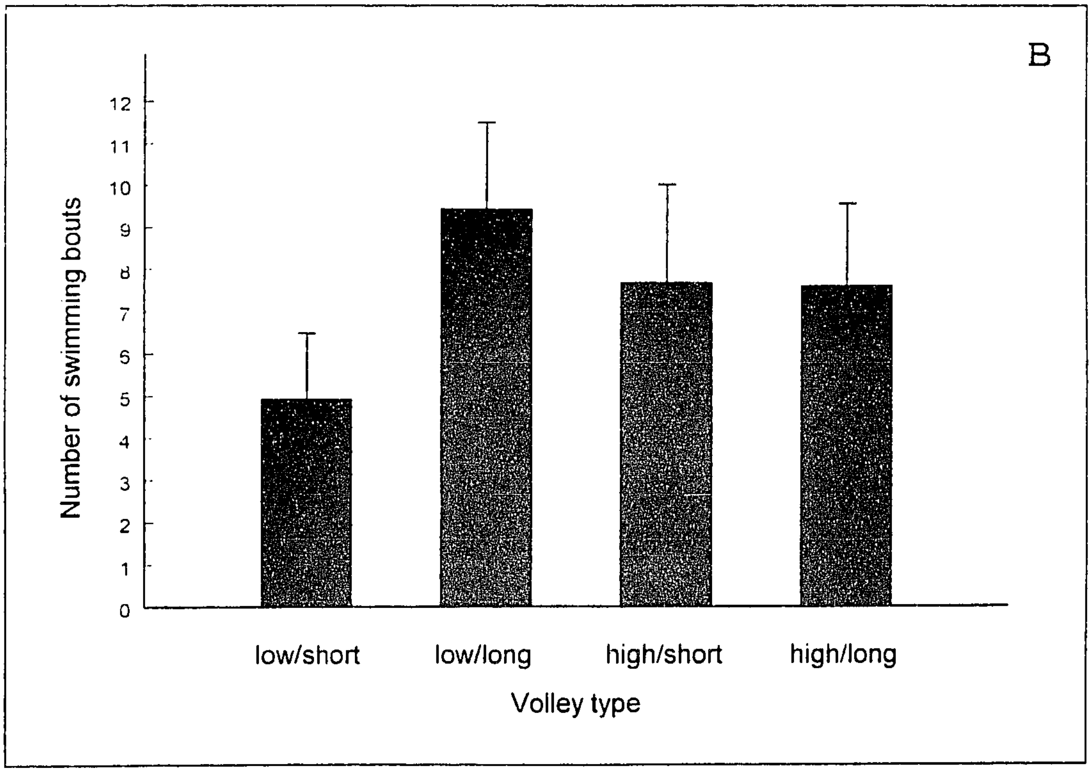
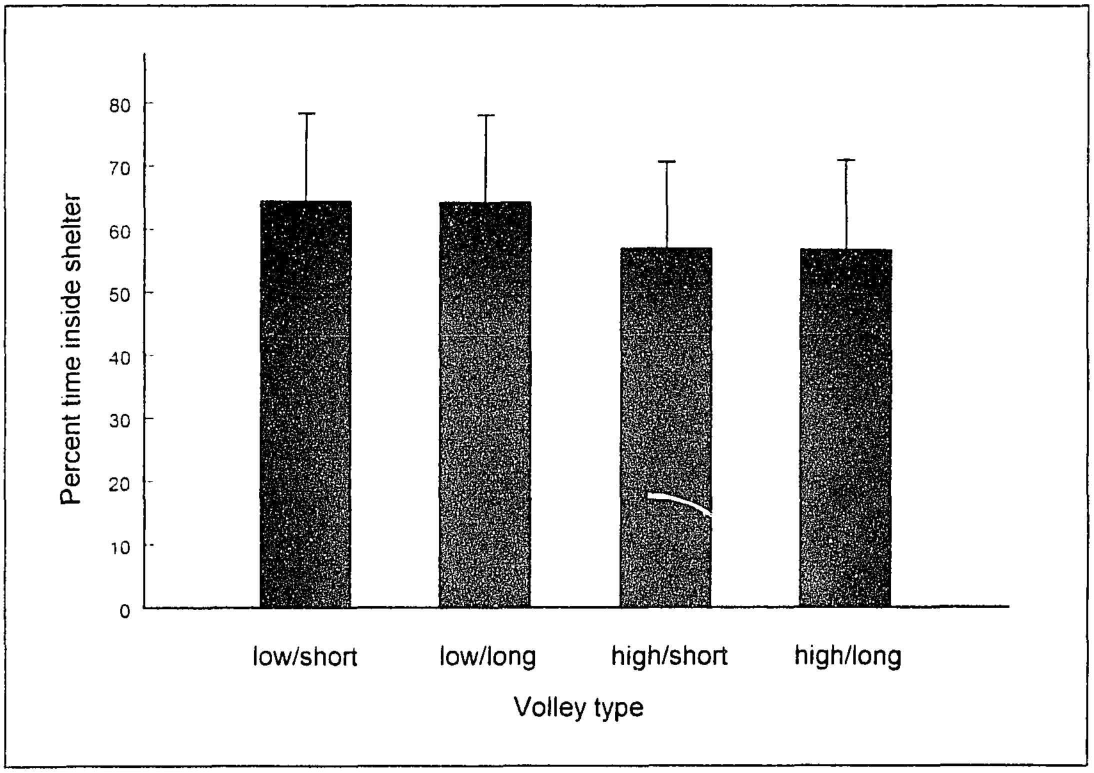

B
Number of swimming bouts
0
1
2
3
4
5
6
7
8
9
10
11
12
low/short
low/long
high/short
high/long
Volley type

Figure 18: Average time (in percent) spent inside shelter as a function of volley frequency and duration.


Percent time inside shelter
80
70
60
50
40
30
20
10
0
low/short
low/long
high/short
high/long
Volley type

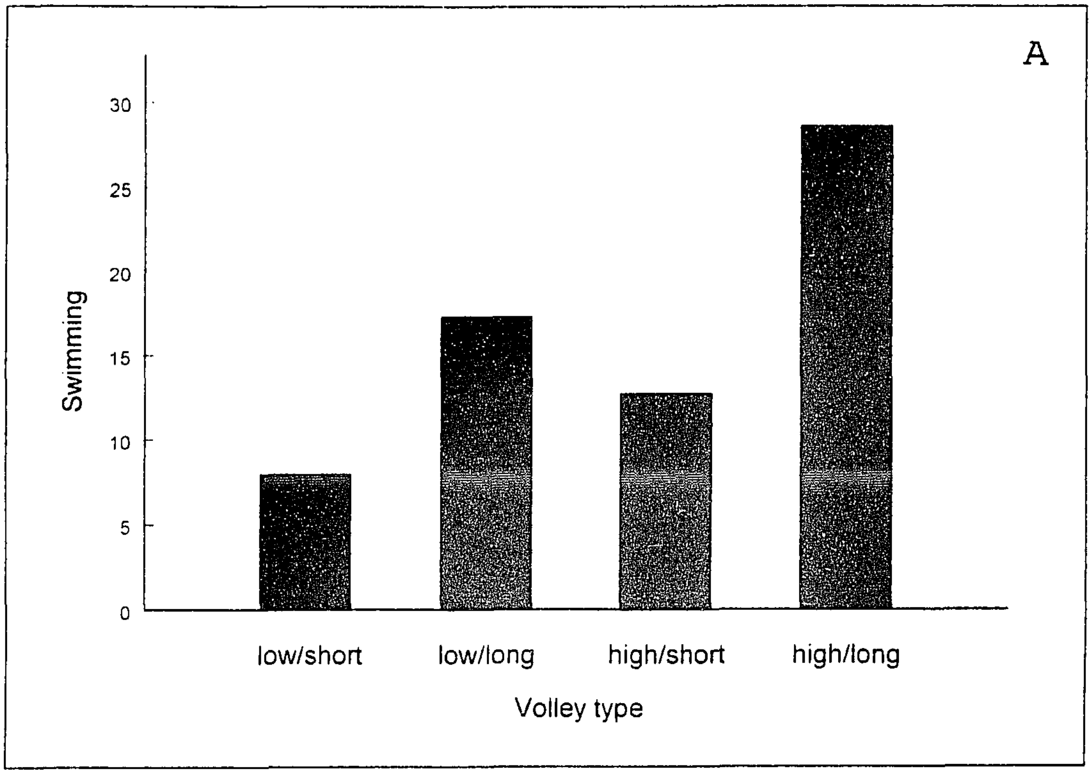
volley duration on in-shelter duration ($\underline{F}_{1,11}$=0.029, $\underline{P}$>0.05, arcsine transformation) or interaction between the two ($\underline{F}_{1,11}$=0.023, $\underline{P}$>0.05, arcsine transformation). Standard error of the mean across conditions was relatively high, indicating a significant amount of inter-individual variability.

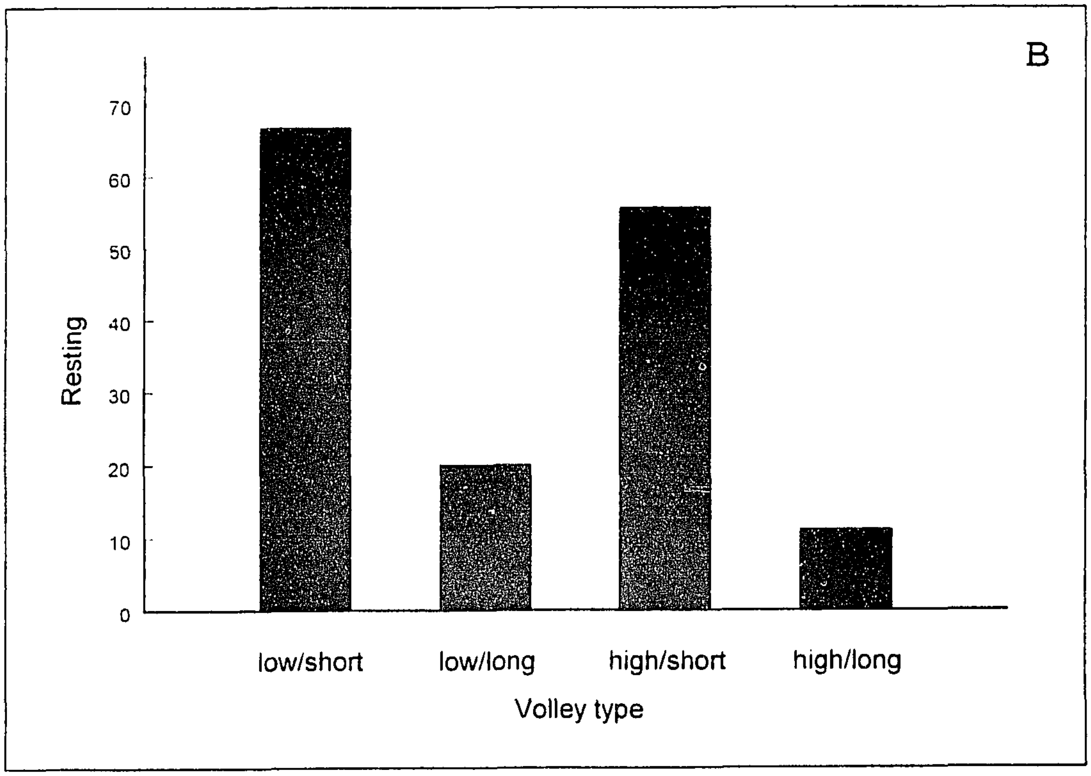
The analysis of change in activity following stimulation was separated into two components: the initiation of post-stimulus swimming and of post-stimulus resting, respectively. Because of differences in the number of fish resting at the time of stimulation, there were unequal opportunities for fish in all conditions to initiate swimming and resting activity. For this reason, the percentage of subjects resting that subsequently began swimming, and subjects swimming that ceased swimming (rested) within the 2.5 s following stimulation is shown in Figure 19.

The percentage of swimming bouts that followed stimulation was lowest during low-frequency/short-duration, defensive type trials. Predatory type, high-frequency/long-duration volleys yielded the highest percentage of swimming bout initiation. The low-frequency/long-duration and high-frequency/short-duration conditions produced mid-range amounts of post-stimulus swimming activity. There was also a noticeable effect of volley duration. The percentage of post-stimuli resting followed almost the opposite pattern as

Figure 19: A. Effect of volley type on the percent of swimming initiation by resting fish during the 2.5 s interval following stimulus presentation. Fish receiving low-frequency/short-duration (defensive type) volleys initiated a lower percentage of swimming bouts than those receiving high-frequency/long-duration (predatory type) volleys.

B. Percentage of resting bout initiation in swimming fish during the 2.5 s interval following stimulus presentation as a function of frequency and volley duration. Fish receiving high-frequency/long-duration (predatory type) volleys showed a lower percentage of resting than those receiving low-frequency/short-duration (defensive type) volleys.


A
Swimming
30
25
20
15
10
5
0
low/short
low/long
high/short
high/long
Volley type


B
Resting
70
60
50
40
30
20
10
0
low/short
low/long
high/short
high/long
Volley type

that for swimming. The presentation of low-frequency/short-duration volleys to subjects that were actively swimming resulted in the highest percentage of resting bout initiation. Alternatively, stimulation with high-frequency/long-duration volleys resulted in the smallest percentage of fish initiating resting. As in the previous analysis, the two "non-natural" conditions produced moderate values which fell between those for defensive and predatory type volleys. Once again, a duration effect was evident.

While two of the twelve subjects produced EODs during testing, at no time did an EOD occur immediately following stimulation.

DISCUSSION

In order to understand Malapterurus' ability to discriminate between defensive and predatory EODs, the experimental design attempted to separate the effects of the frequency and volley duration components. In doing so, two "non-natural" conditions were created (low-frequency/long-duration and high-frequency/short-duration). These, as expected, resulted in response levels that fell in between those elicited by the naturally occurring volley types for most behavioral measures. It can be concluded that the frequency component of these stimuli is responsible for the communication of one type of EOD mediated conspecific behavior, while the volley duration is characteristic of another. High-frequency/short-duration volleys, for example, have a predatory type frequency, and a duration that is characteristic of a defensive EOD. As a result, activity levels recorded for fish in this condition were higher than those recorded during stimulation with defensive type stimuli and lower than those for following predatory volley stimulation. The inherent dual nature of such signals may have lead to conflict in the receiver and resulted in the observed response levels (see Figure 19).

Neither the frequency nor the volley duration components of the test signals resulted in a significant difference in overall activity and location measures. Whereas the amount of time spent inside the shelter appeared to be influenced slightly more by the frequency component of the stimulus, the analysis of swimming duration and number of swimming bouts points more in the direction of the influence of volley duration. In no instance was interaction between the two variables found. Therefore, the effect of frequency did not depend on volley duration, and the effect of volley duration did not depend on frequency. The results of Experiments 2A and 2B suggest that the naturally occurring combinations of the two factors, as manifest in predatory and defensive volleys, are both necessary and sufficient for discrimination.

A descriptive analysis of activity immediately following stimulus presentation did show an effect of volley duration. The combinations of frequency and volley duration representing defensive and predatory discharges (low-frequency/short-duration and high-frequency/long-duration respectively) showed clear differences in terms of initiating a change in behavioral state. During trials in which defensive stimuli were presented, resting subjects rarely began swimming, whereas during the presentation of predatory-type stimuli, initiation of swimming was greatest. The opposite trend was apparent for resting behavior, with defensive-type volleys producing the most resting and predatory volleys the least.

The results demonstrate that changes in frequency or volley duration of the stimulus signal alone are insufficient to produce significant discrimination. Even the defensive and predatory-type volleys failed to elicit significant differences in activity and location measures (seen in Experiment 2A). Only the descriptive analysis of post-stimulation changes in activity showed a difference between these two conditions. It is possible that the experimental design was partly responsible for the disparate results between Experiments 2A and 2B. In attempting to tease apart the effects of frequency and volley duration, two conditions were added in Experiment 2B. Due to their composition, these conditions created conflicts for the subjects since, as expected, they did not clearly signal defensive or predatory information. When incorporated into the within-subject design, the novel stimuli could have influenced responding during subsequent testing with other treatment conditions as well, including defensive and/or predatory blocks.

EXPERIMENT 3: ROLE OF EOD AMPLITUDE

Contests between Malapterurus are highly ritualized and include lateral displays, open mouth displays, and pushing. Very few EODs accompany these overt behaviors (Rankin & Moller, 1986). Such contests could represent attempts at assessing size, which is correlated with resource holding potential or RHP (Maynard Smith & Parker, 1976). Escalation of hostilities would be indicated by the occurrence of biting, as has been demonstrated in other fish species (Bronstein, 1984; Turner & Huntingford, 1986). Selection favors abilities to acquire information as well as the concealment of cues regarding a contestant's own RHP. Although ritualized forms of assessment may evolve, as seen in Malapterurus, contests will not be settled peacefully if a reliable estimate of RHP cannot be made in a short period of time, and at little expense (Parker & Rubenstein, 1981). In such cases, escalation of hostilities will ensue.

The almost complete absence of EOD behavior during intraspecific interactions in Malapterurus electricus may be due to the likelihood that EODs are not harmful to conspecifics. The presence of fatty tissue covering the body surface (Howes, 1985) may create insulation to protect Malapterurus from conspecific electric shocks. Kastoun (1972) showed that electric catfish were never injured by AC stimuli and were tolerant of DC intensities of up to 3500 $\mu A/cm^2$. The display components observed by Rankin and Moller (1986) prior to escalation in Malapterurus (open mouth, lateral) are selected for their ability to settle contests without injury, yet the EOD is not part of these ritualized displays. This may be because the production of EODs does not aid contestants in gathering information or because EOD amplitude cannot be bluffed. The few EODs reported during conspecific encounters accompanied biting, and therefore could be considered part of the escalation of hostilities. This is not always the case, however, since during approximately half of the observations it was the fish being bitten which discharged (Rankin & Moller, 1986). An attacked fish could, however, be using its discharge defensively. It is possible that EODs are harmful to the inside of a fish's mouth or to a wound caused by a bite.

The question as to why EODs are not part of the ritualized display behavior of Malapterurus may actually be related to the electroreceptive ability of the species. The EOD might convey discernable information regarding size. If this is true, then it follows that selection exists in favor of concealing such cues (Parker & Rubenstein, 1981). This section will provide evidence for this, and offer an explanation as to why Malapterurus does not discharge during contests. It is hypothesized that "not discharging" represents the evolutionarily stable strategy.

The component of the EOD which is most likely to provide a competitor with an assessment of size (and RHP) is its amplitude. This is because the strength of the discharge increases as the fish grow (Balon & Coche, 1974; Rankin & Moller, 1986). Thus, by not discharging, contestants are in effect be withholding information on their physical size. The strategy of concealing an RHP cue, while at the same time gathering information on the fitness of a competitor, confers an advantage.

The assessment of relative EOD amplitude would also necessitate that catfish have information regarding the strength of their own EOD (obtained through internal or external feedback) for comparison with that of a conspecific competitor. Amplitude data would also need to be combined with information regarding the location of the source of the signal in order for a receiver to extrapolate the physical size of "the sender". The source of stimulation, such as a conspecific or artificial source, could potentially be determined via the electrosensory system based on electric field geometry. The actual strategy employed by Malapterurus in locating an electric dipole is, however, unknown. Methods of electric dipole location found in the literature necessitate movement on the part of the receiver. Catfish may orient parallel to the vector direction of the electric field and swim forward in this alignment to update information in order to determine the area of maximum intensity, as described for Gymnotus carapo by Davis and Hopkins (1988). Another possibility involves making a more direct approach to the dipole source, as has been observed in sharks, with the fish's body aligned with the electric field, providing continuous feedback on both sides (Kalmijn, 1987). Given either scenario, it is assumed that Malapterurus would move toward a source of low-amplitude stimulation. Such a signal could either represent a small conspecific, close by, or a larger fish at a distance sufficiently far to prevent a complete assessment of maximal intensity. If signal strength is sufficiently large, however, a withdrawal response should result.

The use of an electric catfish model to substitute as a contestant that does discharge makes it possible to determine whether or not amplitude can be differentially responded to by a receiver. It is hypothesized that catfish will avoid or withdraw from artificial EODs of greater amplitude than their own, and that relatively low-amplitude stimulation will result in approach behavior.

Methods

Subjects

Twenty experimentally naive Malapterurus electricus (T.L. 10-15 cm) served as subjects. All maintenance procedures and pre-treatments remain the same as in

Experiments 1 & 2.

Apparatus

As in the previous experiments, a 200 l all glass aquarium measuring 42x50x91 cm served as the test tank. The test tank was illuminated from above by a 75 W incandescent bulb during the light cycle and a 60 W red bulb during the dark cycle. No shelter tube was used in this experiment so as not to interfere with location preference. To measure distance from the electrodes the bottom surface of the tank was marked at the middle of the long axis forming two areas, area L on the left side, and area R on the right. Each area was further subdivided into nine units of 5 cm each, numbered one through nine along the bottom, moving towards the center of the tank from the two sides. These markings facilitated tallying of subjects' location during testing. The aquarium filter and heater were removed prior to testing.

Stainless steel recording electrodes were positioned at the midpoint of both the front and rear walls of the test tank. A pair of carbon stimulus electrodes (the model "artificial electric catfish" described in Experiment 1A) was attached to each of the two side walls of the test tank at a height of 4 cm. Stimuli were delivered via the model catfish on either the left or right side during an experimental session.

In place of the stimulus isolation unit previously described a UTC model CVP-3 60 W isolation transformer was used. This allowed for a larger current needed for this experiment while maintaining signal isolation. Voltages were adjusted between conditions.

Procedure

Ten subjects were tested under the low-amplitude condition and ten under the high-amplitude condition. Five fish from each group received stimulus presentations from the left side electrodes, and five were stimulated from the right side. Subjects were assigned to conditions randomly and were tested in random order.

Each subject was placed in the test tank 30 min prior to lights out. The three day adaptation period to the test tank was eliminated to control for effects of residency. Testing began 30 min into the dark cycle. At the start of each session the subject's position was recorded and the first stimulus volley was delivered. A second volley was presented 90 s later, followed by a third, final volley 3 min later. Each subject's behavior was recorded during stimulation, between stimuli, and for an additional 30 s following the final stimulus presentation. Thus, each session lasted a total of 5 min.

Subjects were presented with volleys containing pulses of either greater or smaller amplitude than their own. The low-amplitude condition was set at 6.25 V and the high-amplitude was 100 V. These values were recorded at the electrode tips in water of 100 µS/cm conductivity. The attenuation of these voltages over distance are shown in Appendix A. EOD amplitudes obtained along the dorsal surface of several subjects averaged around 25 V. Pulse width, IPI, and volley duration were held constant. These were 1.5 ms, 2.5 ms and 1000 ms respectively, for a total of 250 pulses at a frequency of 250 Hz. These parameters fell within the natural ranges reported in the literature (Bauer, 1968; Bennett, 1971).

Each fish's initial swimming path (direction and distance) in relation to the stimulus electrodes was noted. The final location of each subject at the end of the 5 min test session was recorded. Following testing, subjects were returned to their home tank and the test tank was cleaned.

Analysis

Frequency data regarding the location of subjects at the 5 min mark (end of session) were analyzed using a chi-square test of independence. Subjects were scored as being either on the side of the test tank where stimulus presentation occurred (+), or on the side away from the stimulus electrodes (-). In addition, the overall distance from the stimulus electrodes at the end of the test session was analyzed using a t-test for independent samples.

Analysis was also made of data recorded on the subjects' initial choice of direction. A fish could either swim toward (+) or away from (-) the stimulus electrode, or remain in place. A t-test was employed to determine the significance of the difference between the initial and final distance from the electrodes as a function of amplitude. Any EODs produced by subjects were analyzed using an oscilloscope/computer interface as previously described.

RESULTS

Seven out of ten subjects under the low-amplitude condition were located in the half of the test tank containing the stimulus electrodes at the end of the 5 min test session. Alternately, only one of the ten subjects receiving high-amplitude stimulation was located on the side of the tank containing the stimulus electrodes at the completion of the test trials (Table 2). Chi-square analysis of subject location showed a significant difference between the two groups ($\underline{X}^2=8.0$, $\underline{df}=1$, $\underline{P}<0.005$).

The distance from the stimulus electrodes following stimulation (3 volleys) was compared between the two conditions. For fish receiving low-amplitude volleys, the mean (±SE) final distance from the electrodes was 37.50±10.00 cm. The high-amplitude condition resulted in a final distance of 71.50±5.68 cm. A two-tailed t-test showed this distance to be significantly shorter for the low-amplitude condition ($\underline{t}=-2.955$, $\underline{df}=18$, $\underline{P}<0.01$). Fish receiving high-amplitude stimuli were located significantly further from the model electric catfish (Figure 20).

During stimulation with low-amplitude volleys, four fish swam toward the stimulus electrodes, and three others displayed orientation responses toward them. An orientation response is defined as the pivoting of the body axis so that

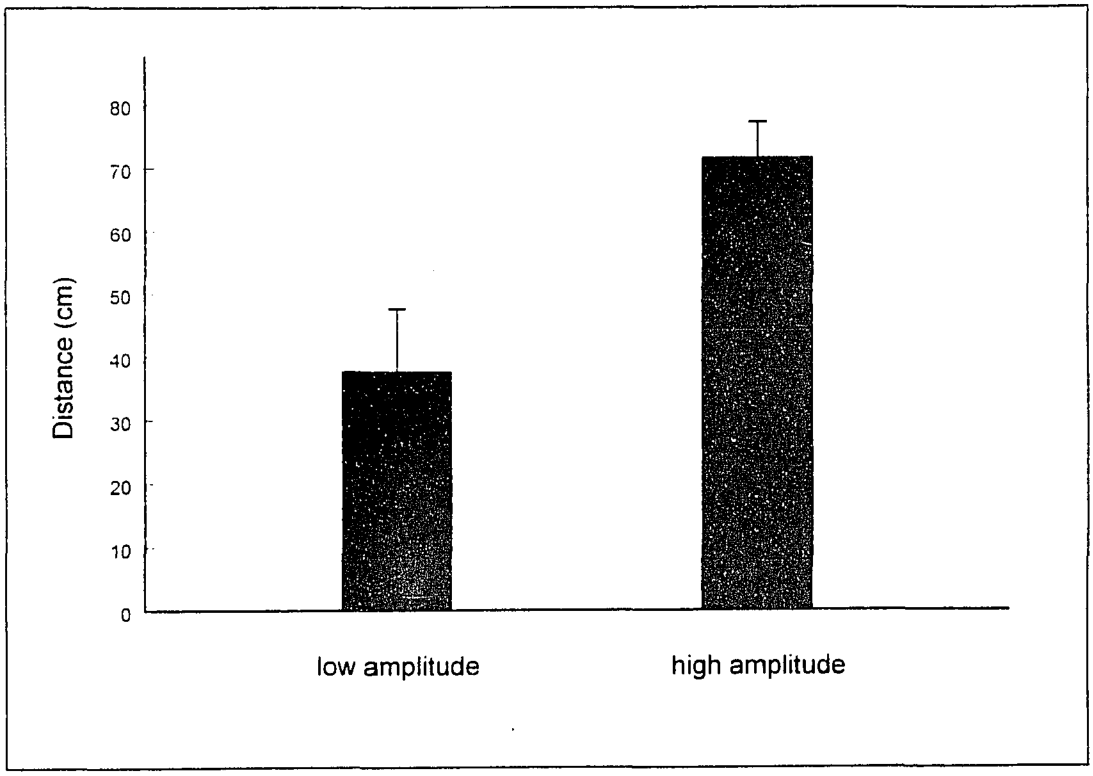
Table 2. Analysis of location measures obtained in Experiment 3. R = right side and L = left side of the test tank. The "change" value reflects the difference between pre-test and post-test locations relative to the stimulus electrodes. Asterisks indicate subjects that finished a session on the side that they were stimulated on.

Table 2

Location of Subjects Before and After Testing

Subject	Amp.	Side of Stimulation	Location of Fish Start	Finish	Change
ME49	Low	Right	R2	R1*	+1
ME57	Low	Right	L4	R8*	+7
ME58	Low	Right	R8	R8*	0
ME62	Low	Right	R4	R4*	0
ME63	Low	Right	L6	R1*	+12
ME51	Low	Left	R1	R1	0
ME53	Low	Left	L4	L4*	0
ME59	Low	Left	R3	R3	0
ME67	Low	Left	L1	L1*	0
ME69	Low	Left	R2	R5	+3
ME52	High	Right	L6	L4	-2
ME56	High	Right	R5	R5*	0
ME60	High	Right	L6	L5	-1
ME61	High	Right	R2	L6	-11
ME68	High	Right	L2	L4	+2
ME50	High	Left	R2	R2	0
ME54	High	Left	R9	R4	-5
ME55	High	Left	R3	R3	0
ME64	High	Left	R1	R1	0
ME65	High	Left	R1	R3	+2

Figure 20: Mean (±SE) distance from stimulus electrodes following the 5 min test session as a function of stimulus amplitude. The distance was significantly higher for the high-amplitude condition ($P<0.01$)

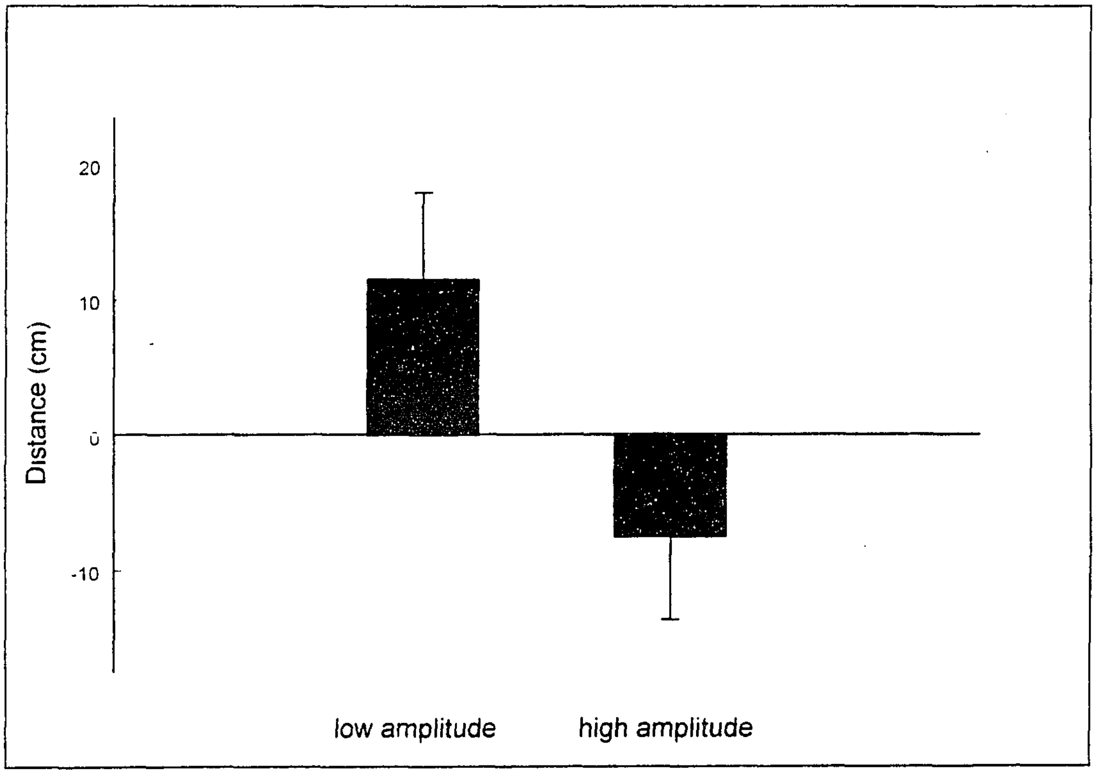

Distance (cm)
80
70
60
50
40
30
20
10
0
low amplitude
high amplitude

the head region faces the source of stimulation (see Kastoun, 1971). None of the subjects under this condition swam away from the stimulus electrodes, and no anodal or cathodal preference was noted. Under the high-amplitude condition, none of the fish swam toward the stimulus source initially, although one fish swam back and forth across the test tank throughout the session. Two subjects did, however, display orientation responses toward the stimulus electrodes. Four of the ten subjects receiving high-amplitude stimulation swam away from the active electrodes. The other subjects in both groups remained inactive at the bottom of the tank. The overall change location from beginning to end of the session is also shown in Table 2.

An analysis of the actual distance travelled in relation to the stimulus electrodes from the catfish's starting position to their location at the end of 5 min showed that fish in the low-amplitude condition traveled an average of 11.5±6.46 cm toward the source of stimulation (Figure 21). Conversely, subjects in the high-amplitude group traveled 7.5±6.16 cm away from the active electrodes. This difference was significant using a two-tailed t-test for independent samples ($\underline{t}=2.129$, $\underline{df}=18$, $\underline{P}<0.05$).

None of the catfish generated EODs during this experiment.

Figure 21: Mean (±SE) distance travelled in relation to the stimulus electrodes as a function of stimulus amplitude. Subjects in the low-amplitude condition swam toward (+) the electrodes, while those in the high-amplitude condition swam away (-). This difference was significant ($\underline{P}<0.05$).


Distance (cm)
20
10
0
-10
low amplitude
high amplitude

DISCUSSION

The assessment of body size, as an indicator of RHP, can play an important role in determining the outcome of contests (Maynard Smith & Parker, 1976; Bronstein, 1984). Large asymmetries in body size are likely to produce either approach or avoidance, depending on the direction of the difference. One implication of the results of Experiment 3 is that Malapterurus can associate EOD amplitude with body size, or in some other way perceives amplitude as a measure of fitness. The fish can discriminate differences in EOD amplitude and respond to them differentially. Based on inference, the fish has information regarding its own EOD strength that can be used for comparison with the extraneous signal. Artificial EODs were intended to transmit "true" information as compared to the ritualized, non-electric displays that occur under natural conditions (Hinde, 1981; Markl, 1985). The electric stimuli thus allow a more rapid assessment by the receiver.

The results suggest that electric catfish will approach conspecifics if they produce EODs with amplitudes smaller than their own. A smaller amplitude accompanies smaller body size, which in turn confers an inferior RHP, and indicates to a competitor the possibility of defending or obtaining territory at minimal cost. Conversely, the identification of a larger conspecific through a comparison of EOD amplitudes results in avoidance due to the potential high cost of engaging in conflict and a low probability of winning.

Although the majority of subjects receiving low-amplitude stimuli either approached or oriented toward the active electrodes, some did not. One reason for this could be that all subjects in this study were essentially intruders and the signalling model catfish could therefore be perceived as a resident. Since a larger intruder could lose in a conflict involving a smaller resident (Henderson and Chiszar, 1977), a cautionary strategy may be advantageous in these situations. To test this possibility further experiments to determine the responses of resident vs. non-resident catfish would be necessary. It should be noted that most of the subjects that did not change position during testing with low-amplitude stimuli were already in relatively close proximity to the electrodes at the onset of stimulation. A second possible explanation for some subjects' failure to respond is that they might have required additional stimulus cues (olfactory, lateral line) in order to complete their assessment, which may also hold true for those giving only an orientation response.

Four subjects receiving the high-amplitude signals swam away from the electrodes, apparently detecting a size discrepancy that did not favor engaging in conflict.

Although the response (fleeing) was the same, the assessment was made on the basis of the EOD (in the absence of any other cues), rather than on the stereotypic ritualized overt behaviors described during conspecific encounters by Rankin and Moller (1986). Again, those subjects which only pivoted their body axis to head-orient toward the stimulus source, as well as those that did not move, may have needed further stimulus cues in order to make an assessment. Also, most of the non-responding fish were initially located away from the stimulus electrodes at the onset of EOD presentation. Therefore, it may be surmised that these subjects were sufficiently far away from the source of the high-amplitude EODs that further locomotor activity was not appropriate. It is also possible that it would be disadvantageous for such fish to move, thereby attracting attention, prior to gathering as much information as possible.

The change in location was significantly different between subjects responding to the two amplitude conditions. The fish decreased their distance from the electrodes under the low-amplitude condition, while this distance increased under the high-amplitude condition. This observation might suggest that Malapterurus was discriminating the asymmetry in EOD amplitude, that is, its own versus the artificially produced one. Fish then responded in a predictable manner (approach or withdrawal) when faced with a situation in which there was no concealment of electric cues and, consequently, no concealment of size information. Also, since subjects did not discharge, they concealed information regarding their own size.

Whether or not Malapterurus can locate the exact source of stimulation requires further testing. Fish swimming toward a low-amplitude signal may have been attempting to determine to what degree the signal strength would increase as they approached. It is possible that a low-amplitude signal could represent either a small conspecific, close by, or a large conspecific at a distance with its signal greatly attenuated. In the latter case the subject would be using its approach to gain further information about the other fish's EOD amplitude, thus locating the source by seeking the area of greatest intensity (Davis & Hopkins, 1988). It may then be concluded that most fish receiving high-amplitude EODs, without actively attempting to locate the source of stimulation, determined that the stimulus intensity was sufficiently large enough to avoid.

GENERAL DISCUSSION

Like other strongly discharging electric fishes, Malapterurus electricus discharges only intermittently. The absence of spontaneous EOD activity, characteristic of wave-type and pulse-type weakly discharging electric fishes, all but excludes the possibility of a communication system based on frequency modulations or periods of "social silence" in the electric catfish (see review: Moller, 1995). However, since relatively little is known about the social behavior of strong electric fishes, particularly during reproduction, the possibility that some form of discharge activity is involved during intraspecific interactions cannot be excluded. Initial positive results in this regard from research on stargazers (Mikhailenko, 1971), electric eels (Schwassmann, 1992) and electric catfish (Kastoun, 1971, 1972) support this conclusion. The present study has provided further evidence for the "adventitious" detection and discrimination of situation-specific conspecific signals in electric catfish. In addition, significant results were obtained in support of the hypothesis that EOD amplitude is discriminable, which may explain why Malapterurus rarely discharges during territorial contests.

Under the present experimental conditions, the pulse duration component of Malapterurus electricus' EOD did not appear to be discriminable. There were no significant differences between Malapterurus' responses to a range of pulsed DC stimuli. These results lead to continued speculation regarding the evolution of a rather stable (though temperature dependent), species typical value of 1.5 ms. Since the strong electric discharge mainly serves in delivering a shock to potential prey fish and/or non-conspecific competitors (Bauer, 1968; Rankin, 1984; Rankin & Moller, 1986, 1992; Moller & Rankin, 1995), the EOD waveform characteristics may in fact serve to optimize this ability. The pulse duration could have evolved to its current state based on adaptations that maximize output strength under given environmental conditions. Characteristics of the aquatic environment that are important when evaluating the EOD include conductivity, salinity, pH, and temperature.

A comparison of the predatory capabilities of strongly discharging electric fish with techniques employed by the electrofishing industry was made by Bauer (1968), and explored in greater depth by Moller (1995). The success of electrofishing methods relies on the fact that fish subjected to DC electric fields are attracted to the electrode's anode through galvanotaxis. Anodal approach is usually followed by galvanonarcosis, a form of paralysis and muscular tetanus (review: Kalmijn, 1974). The main goal of modern electrofishing is to achieve a wide attraction zone, while limiting galvanonarcosis to a smaller area in the proximity of the anode (Bohlin, Harmin, Heggberget, Rasmussen, & Saltveit, 1989). Interestingly, technical specifications for optimizing electrofishing equipment nearly parallel the naturally occurring EOD of strongly electric species (review: Moller, 1995).

One similarity, which is of primary interest in its relevance to the present study, is that the use of pulsed DC was recommended for electrofishing in freshwater streams and lakes (Bohlin et al., 1989). The monophasic discharge of Malapterurus (and also Electrophorus) has a large DC component, and the volley can be considered a pulsed DC event (Moller, 1995). Furthermore, Bohlin et al. (1989) indicated that when using pulsed DC, the pulse length should be adjusted to more than 1 ms, and frequencies above 50 Hz should be used. Attraction range, it was found, could be increased by increasing the pulse length and/or the output frequency. The species typical EOD pulse duration of Malapterurus, in addition to those of Electrophorus and the electric ray Torpedo, seems ideally suited to the task of "electrofishing". The optimal frequencies suggested by Bohlin et al. (1989) also fall within the range of the catfish's predatory volley, although they are somewhat lower.

Just as the high frequencies produced when generating predatory volleys increase hunting success, the 1.5 ms pulse duration may be evolutionarily stable because it maximizes the predatory effectiveness of the EOD. Bauer (1968) noted that pulse duration can vary with changes in water temperature. Durations of up to 2-3 ms at temperatures of 20-25 °C have been reported in the literature (review: Bauer, 1968). Such variation may represent an adaptation that enables Malapterurus to maintain optimal prey stunning ability over a given temperature range.

In the lakes and rivers of Africa, the electric catfish lacks natural predators, with the possible exception of the tigerfish, Hydrocynus brevis and, possibly, man. Malapterurus also has few rivals for resources, although sympatric catfish (Clarias sp.) may at times compete successfully (Moller & Rankin, 1995). Based on the aggressive interactions observed between Malapterurus conspecifics in the lab (Rankin, 1984), and the high population density reported in the field (Brichard, 1978) it may be concluded that intraspecific conflict is not a rare event in these fish. The fact that newly imported catfish often bear scars from bites and missing barbels is further evidence of prior hostile encounters (personal observation). Spacing patterns during the dry season along the Comoé River (personal observation) also attest to the fact that Malapterurus is a highly territorial species. The detection of conspecific electric discharges may play an important role in the establishment and maintenance of a home range.

The poor visual system of Malapterurus (Ebbesson &

O'Donnel, 1980), together with the low visibility often encountered in its native waters, lends support to the view that the EOD functions in guarding territory. Although olfaction is important during social interactions between siluriform fishes (Todd et. al, 1967), the effective range of this sensory system does not approach that of the ampullary electroreceptors (Lissman & Machin, 1963; Roth, 1972; Peters & Wijland, 1974) given the electric field densities produced by Malapterurus' EOD. Therefore, the detection of EODs may provide the first warning that a conspecific has entered the area. By receiving and recognizing these EODs, resident catfish are better able to detect intruders inside the perimeter of their home range. Catfish trying to locate and establish territories can detect the electric discharges of resident fish as well, and choose to avoid conflict, or challenge for ownership.

In addition to its role in the defense of the home range and the recognition of conspecific territories, resident catfish may use their electroreceptive ability to detect the EOD activity of neighbors in adjoining territories. Discharges occurring outside the home range that do not indicate a competitive threat, could still contain useful information. The ability of Malapterurus to discriminate between defensive and predatory volley types was demonstrated by Kastoun (1971, 1972), and is supported by the results of Experiment 2. Such discrimination is useful in determining both the presence of danger and the "advertisement" of near-by food availability. The "overhearing" of a neighboring catfish's electrical activity provides a selective advantage which increases the survival chances of the receiver. This type of adventitious communication has been shown to be adaptive in both inter-specific and intra-specific interactions (Markl, 1985). The discrimination of, and differential responding to conspecific defensive and predatory EOD volleys provide some of the strongest implications for electrocommunication in Malapterurus electricus.

It is known that certain frequency and pulse duration parameters may be used to delineate volleys types in Malapterurus electricus (Bauer, 1968; Kastoun, 1971, 1972; Belbenoit, et. al, 1979). The inclusion of the low-frequency/long-duration and high-frequency/short-duration conditions in Experiment 2B was intended to allow a separation of the frequency and volley duration components in order to determine if either one alone was sufficient to produce discrimination. It was found that changes in either characteristic alone did not elicit significant changes in activity and that it is the combination of the two that is being attended to. When EOD frequency and volley duration combine to meet natural criteria (predatory, defensive), the stimulus can then be interpreted and categorized.

The make-up of a naturally occurring discharge is often even more complex than those produced artificially in Experiment 2. As Bauer (1968) indicated, both defensive and predatory volleys begin with a high-frequency phase, but in defensive EODs the frequency rapidly decreases. In predatory volleys there is a longer lasting decrease and occasional increases throughout. Such increases never reach the initial high-frequency value, however (Bauer, 1968). Add to this the fact that long volleys are sometimes partitioned into two or more "trains" of pulses that follow each other in close succession (Rankin and Moller, 1992). This complexity could account for why frequency or duration alone did not account for the discrimination of volley types. Further, it can be concluded that the responses elicited by the two 'novel' conditions used in Experiment 2 was a result of the subjects' inability to conclusively categorize them as either defensive or predatory.

Several investigators have reported other volley types in the electric catfish (review: Moller & Rankin, 1995). Bauer (1968) mentioned "chase volleys" which accompanied hunting activity and preceded predatory volleys in larger fish. Kastoun (1971) described "attack volleys" that were characterized by a greater number of pulses than defensive volleys, but fewer than predatory ones. And, whereas Bauer (1968) elicited defensive EODs by tapping fish with a wooden rod, Kastoun's (1971) catfish attacked when similarly provoked, producing attack volleys. To obtain defensive discharging, Kastoun (1971) tapped the glass sides of the aquaria. Kastoun (1971) could not determine how subjects receiving attack and predatory type stimuli could discriminate between the two (as evidenced by differences in overt behavior) due to the overlapping volley characteristics. Thus, beyond concluding that the low-frequency/long-duration and high-frequency/short-duration conditions used in Experiment 2 were not readily discriminable, the possibility exists that these volleys more closely resembled a different discharge type altogether. Discrimination of an artificial stimulus as an attack volley, for example, could produce the activity levels obtained under either one or both of these 'novel' conditions. Although overt activity such as attacking objects in the experimental tank as described by Kastoun (1971) was not observed in this study, it may explain the occurrence of aggressive electrode contact in Experiment 1B.

In order to determine whether the discrimination of electric signals found in the present study has implications for electrocommunication in Malapterurus it is necessary to establish a suitable definition of communication. From the many attempts to describe animal communication systems in terms of their function and adaptive significance a few relevant points are presented here. Wilson (1975) defined communication as occurring when the action or cue given by an organism alters the behavior of another in a manner adaptive to either one or both of the participants. Electric catfish are known to engage in stereotypical, ritualized displays (Rankin, 1984; Rankin & Moller, 1986, 1992) which include the withholding of EODs prior to escalation, and can be considered adaptive to both parties. At the same time, there is evidence of adventitious communication in the form of interception of conspecific signals (Kastoun, 1971, 1972) which is adaptive to the receiver only. For the purpose of the present study the inclusiveness of Wilson's (1975) definition makes it acceptable and appropriate, whereas its breadth makes an examination of additional features necessary.

Tavolga (1970) outlines only three criteria that are required for communication to take place. These are an emitter, an energy output or stimulus, and a receiver. An electric catfish can be considered an emitter because it produces an energy change in the immediate environment by means of behavioral and/or physiological events. The energy output exists in the form of the strong electric discharge that serves as a stimulus. Finally, a conspecific will be considered a potential receiver if it can detect this energy change through its electrosensory organs, the ampullary receptors. Reception of stimulus energy must be determined by an observable physiological or behavioral event. Conspecific EOD detection can be demonstrated behaviorally in Malapterurus by changes in the fish's locomotor activity or its location within a test tank (Kastoun, 1971).

Green and Marler (1979), define communication as the transmission of information from one animal to another. A structural or behavioral adaptation for signal production, transmission, reception, or any combination of the three is a prerequisite. As in the previous definitions, intent on the part of the sender is not a criterion (Green & Marler, 1979). Thus, the need for specialization in some form does not preclude adventitious communication in which one organism benefits from receiving another's signals without any benefit to the signaller. This is found mostly in interspecific interactions, but can occur between conspecifics, as in the case of a kleptogamic interloper which is attracted by the signals of a male competitor and makes use of this information to usurp a potential mate (Markl, 1985). Such a strategy is illustrated by the behavior of male field crickets (Gryllus integer) who wait quietly on the edge of territories to intercept females attracted by the resident males' calling (Cade, 1979). Kastoun's (1971) findings regarding volley discrimination in Malapterurus, which were supported by the results of Experiment 2, could appropriately be classified as adventitious communication, since the sender shows no evidence of intent and apparently does not benefit from the subsequent actions of the receiver. In this case, predation and the avoidance of predators, rather than the availability of mates, is communicated.

Burghardt (1970) includes the notion of "intent" on the part of the emitter when defining communication. According to his definition, the signal an emitter sends must also confer a selective advantage to it or its group when responded to. It has further been argued that the sender of a signal is selected to manipulate the behavior of the receiver to its own advantage (Dawkins & Krebs, 1978). In adventitious communication, such as that demonstrated in Malapterurus by Kastoun (1971), the advantage was on the part of the receiver, rather than the sender. EODs were not produced with the "intent" of intraspecific communication, but served other functions, such as prey capture and defense. However, the inclusion of notions such as "intent" and "advantage" to the sender may apply to Malapterurus in the context of the ritualized intraspecific encounters described by Rankin (1984) and Rankin and Moller (1986, 1992), in which contestants were thought to "manipulate" each other's behavior to their own advantage. The minimal production of discharges during such encounters indicates the potential effectiveness of an EOD to transmit information. The results of Experiment 3 support this hypothesis.

According to game theory optimality models, a conflict between animals that have a difference, or asymmetry, in size or age is an example of a contest with unequal RHPs.

Fitness cues, such as physical size, may be used to settle ownership of a territory or a dispute involving access to mates (Maynard Smith & Parker, 1976). An evolutionarily stable strategy (ESS) is a behavior which is adaptive, is predominant in a population, and can be predicted of a given individual. One type of ESS is to permit an asymmetric cue to settle a contest without escalation. Large asymmetries which are easily identified lower the likelihood of escalated contests. For closely matched opponents (symmetrical contests) fights tend to escalate or increase in length (Maynard Smith & Parker, 1976). Contests will be settled peacefully only if reliable estimates of RHP and resource value can be obtained through other, less costly means, such as by display. Receptor capabilities can, on occasion, limit the contestants' assessing abilities. In addition, in a given situation, some degree of selection for bluffing or even concealment of cues may exist. In situations where escalation does occur, animals will use the more overtly aggressive components of the conflict to further increase information (Parker & Rubenstein, 1981). In fact, role assessment may improve as the cost of contests increase.

Most communication is bidirectional with the interactants switching between the roles of sender and receiver. In contests aimed at assessing resource holding potential or RHP (Maynard Smith & Parker, 1976), for example, each opponent plays the role of both sender and receiver at the same time or in turn. The "manipulation" observed in such contests is largely due to the advantage gained by the sender in not forcing the receiver to immediately escalate the conflict. This behavior is also a consequence of the inability to grade threat displays quickly resulting from a lack of sufficient information (Markl, 1985). In order to successfully establish and defend territory in nature, Malapterurus electricus must engage in contests with conspecifics. Ritualized communication in this species involves the manipulation of a competitor through means such as pushing and lateral displays (Rankin & Moller, 1986) designed to gather information while preventing the rapid escalation of hostilities.

The "conflict hypothesis" (Hinde, 1981) shows that displays are ritualized in a manner that makes them more effective in eliciting responses from other individuals, as opposed to transmitting true information about subsequent actions. The latter function, according to Hinde (1981), has often incorrectly been ascribed to the traditional ethological view of communication. In conflict scenarios, display behavior probably does not serve to convey accurate information, as this could be disadvantageous. These situations instead tend to produce displays of stereotypical intensity which permit contestants to assess one another's

RHP. The results of Experiment 3 indicate that Malapterurus can discriminate EOD amplitude, which may explain the omission of electric discharges from the display repertoire of this species. The production of EODs during conspecific encounters would allow catfish to quickly grade the threat posed by a competitor. Providing an opponent with sufficient information on which to base an assessment of fitness would be at cross purposes with the "conflict hypothesis" and would probably not occur in organisms in which displaying is the ESS (Markl, 1985). There is no advantage to the sender in transmitting easily interpretable information regarding RHP (Maynard Smith & Parker, 1976). This explains why, in Experiment 3, when a catfish detected an EOD that was smaller or larger than its own, it often responded rapidly, and in a manner that indicated it had already completed its assessment.

An investigation of the agonistic interactions of Betta splendens confirmed the importance of body size in determining social status in males. Several small sized opponents responded to their larger partners by escaping immediately even before any biting (Bronstein, 1984). Dominance potential was apparently assessed on the basis of visual cues. In addition to size, prior-residency effects resulted in dominance, with the magnitude of agonistic advantage being directly proportional to the duration of residency. In studies involving territorial behavior in bluegill sunfish (Lepomis macrochiris), Henderson and Chiszar (1977) found that large residents exhibited more aggressive responses to both large and small intruders than did small residents. Yet, large intruders were dominated by small residents, indicating that greater size or age did not automatically result in an aggressive advantage.

Social assessment among fish species is not always visually mediated, and may involve olfaction, as seen in siluriforms (Todd et al., 1967; Atema, 1980), or even electrosensory cues as in weakly electric fish species (Kramer, 1979; Squire & Moller, 1982; reviews: Kramer, 1990; Moller, 1995). Although there is no direct evidence that the EOD provides information regarding a fish's fitness, the results of Experiment 3 indicate that electric catfish can discriminate EOD intensity, which is correlated with size, and thus, RHP. Fish approached "electrically smaller" models, while avoiding sources of high-amplitude stimulation. The effects of residency were controlled in the present study; all subjects were presumably non-residents. In light of the results obtained, it might be useful to conduct further studies that include resident conditions for comparison. It is hypothesized that resident catfish would approach high-amplitude stimuli with significantly greater frequency than non-residents. This conclusion is based on the results of studies done on other fish species (Henderson & Chiszar, 1977; Turner, 1994).

The behavioral findings of the present study support the neurophysiological data on the processing of electrical stimuli by the ampullary electroreceptors. Limitations set by the receptor mechanism of the small pit organs restrict Malapterurus' ability to discriminate signals based on pulse duration, frequency, volley duration, and intensity. Recording from the afferent nerve fibers, Roth (1972) found that a change in the impulse frequency occurred at the onset and termination of rectangular current stimuli. With longer pulses, this change in frequency was not as great as with short pulses. The conduction velocity of the afferent nerve fiber was measured at approximately 10 m/sec (Roth, 1972), a relatively slow rate when compared with normal lateral line nerve fibers. Lissman and Machin (1963) reported a receptor recovery time of 20 ms, from results obtained in their work on Clarias. From the results of Experiment 1, it may be concluded that although subjects detected the presence of pulsed stimuli, based on an increase in ampullary firing rate, the ability to discriminate pulse duration was limited by receptor processing time (20 ms).

In Experiment 2, stimuli of the same frequency, but different volley durations yielded differential responding. The ability of Malapterurus to discriminate between volley durations may be based on electrosensory events at the time of stimulus onset and offset as described by Roth (1972). Given that the relatively slow conduction of the ampullary receptors together with the 20 ms time constant (Lissman and Machin, 1963) create a "smoothing" of the individual pulses, the beginning and end of a stimulus volley may trigger the greatest change in firing rate. A volley of sufficiently high frequency could in effect be categorized as a single long pulse. The catfish may therefore discriminate volley duration based on changes in the firing rate of the small pit organs.

Using stimuli consisting of high-frequency volleys of short, monopolar pulses, ampullary receptors were found to respond only to changes in the average DC value (Roth, 1972). In addition, Bell and Russell (1978) found initial acceleration of the afferent discharge rate followed by a deceleration, after stimulation of the ampullary receptors with monophasic pulses. Since biphasic pulses did not produce this effect the DC component of the signal was assumed to be responsible. Repeated pulses have been found to be as effective for ampullary stimulation as DC events of equivalent charge per second, as long as the inter-pulse interval (IPI) did not exceed 200 ms (Murray, 1965). The ability of the ampullary electroreceptors to detect differences in the DC component of an EOD could be responsible for the discrimination of volley types based on frequency. In Experiment 2, the IPI was varied to produce two frequency measures, resulting in a change in the DC component of the signal. Subjects could thus use detectable differences in average DC value to discriminate between high-frequency and low-frequency volleys.

Ampullary receptors are tonically active when stimulation is absent (Zakon, 1986). When the receptors are subjected to pulses of positive polarity the afferent firing rate increases as voltage increases. Negative voltages inhibit firing, resulting in a decrease in spike activity below tonic activity levels. Increasingly larger amplitudes reduce the afferent firing rate until it is totally suppressed (Zakon, 1986). The results of Experiment 3 indicate that Malapterurus can discriminate amplitude differences in pulsed stimuli. Neurophysiological evidence that ampullary receptors respond to changes in pulse voltages illustrate the mechanism by which such discrimination occurs. Orientation and swimming behaviors, such as those displayed by catfish in Experiment 3, may function in gathering amplitude information through an assessment of changes in voltage and polarity.

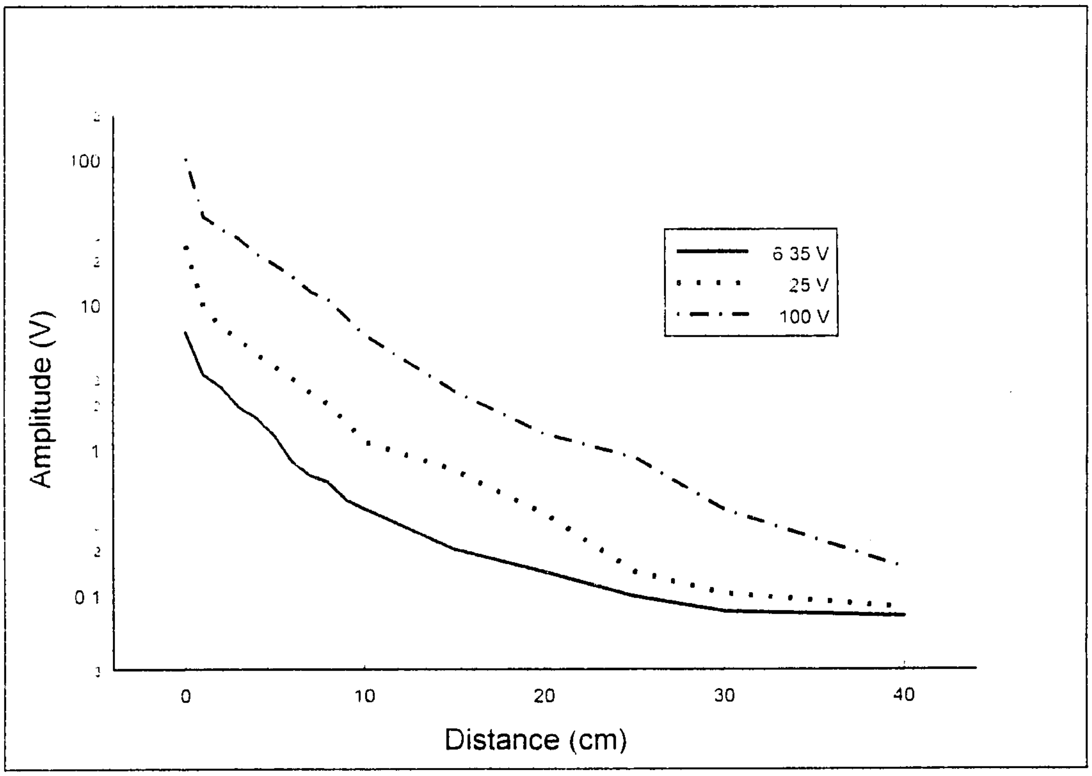
The results of the present study imply that Malapterurus is capable of detecting, discriminating, and responding to the electric organ discharges of conspecifics. Strong EOD volleys that are primarily used during predation and defense, can also assume a communicatory role during social encounters and may play a role in the establishment and maintenance of territory. Although fine discrimination of the waveform does not seem to occur, the fish attend to other components of the signal, including frequency, volley duration, and amplitude. Catfish were able to discriminate signals that correspond to naturally occurring situation-specific volleys types. The present study also supports the hypothesis that contests between electric catfish do not include the EOD as part of the ritualized display because it contains discriminable amplitude information that is relative to body size and resource holding potential.

In reexamining the function of the strong electric discharge the present study has provided support for the hypothesis that the early evolutionary stages of the strong electric organ functioned in electrocommunication. From the evidence provided here for the discrimination of electric signals by Malapterurus it may be concluded that although the EOD now serves predominantly in predation and defense, a rudimentary electrocommunication system is still functional.

APPENDIX A

The attenuation of the voltage values used in the present study are shown in Figure 22. Attenuation was measured over distance using a pair of stainless steel electrodes 15 cm apart. The electrode tips were held parallel to the ends of the stimulus electrodes and moved away in 1 cm increments to a distance of 40 cm. Water conductivity was 100 μS/cm and temperature was 24 °C.

Figure 22: Attenuation measurements of the stimulus voltages over distance. Amplitude values are plotted logarithmically. The values at 0 cm are the voltages in water with the recording electrodes in direct contact with the stimulus electrodes. Water conductivity = 100 μS/cm; temperature = 24 °C. To obtain electric field gradient at a given distance, divide voltage by 15 (inter-electrode distance).


100
10
1
0.1
Amplitude (V)
0
10
20
30
40
Distance (cm)
6.35 V
25 V
100 V

APPENDIX B

Catfish, including Malapterurus, are routinely affected by electric fields in their natural habitat. Electric stimuli detected by the ampullary electroreceptors of silurids have been demonstrated to have biological significance (Kalmijn, 1974), including, but not limited to, the detection of DC fields emitted by prey. These small pit organs were found in Malapterurus electricus by Szamier and Bennett (cited by Bennett, 1971). Kastoun (1972) noted that electric catfish would turn towards local, DC, and pulsed DC dipole fields. This capability is referred to as low-frequency passive electrolocation.

Lissmann and Machin (1963) determined the electrical sensitivity of various siluroid species, including Malapterurus, training animals to give "a standard response" (see Machin and Lissmann, 1960) when an electric field was applied to aquaria using a magnet. Further studies done with Clarias catfish employed unidirectional current pulses or "pulsed DC". It was concluded that the effectiveness of stimuli was determined by pulse rate, amplitude, and pulse duration. Results also showed that a "smoothing" of the electrical stimulus took place with a time constant of 20 ms, indicating that catfish operate in a rather low-frequency range when detecting electric fields. Thus, the catfish responds to slow, rather than rapid changes in electric fields (Roth, 1972).

The range of frequency response of the ampullary receptors of catfish was placed at 0.03-25 Hz by Peters and Buwalda (1972) with greatest sensitivity in the area of 3-7 Hz. Corresponding with the 20 ms time constant, Lissman and Machin (1963) found that sensitivity to low-frequency volleys of 10-20 Hz was similar to that for single pulses. Yet, responding occurred to high-frequency (up to 500 Hz) volleys as well. In such cases it is likely that fish are responding to stimulus onset and then "smoothing" the volley or reacting only to changes in the average DC value of the signal (Roth, 1972).

Since electric catfish seem to make use of their passive electrosensory ability to detect conspecific signals it was considered necessary to investigate the sensitivity of this system to frequencies within the range of those that they produce naturally. A range of pulsed stimuli frequencies to which Malapterurus is sensitive, was determined by conditioning a standard response, the initiation of swimming activity, to simulated EOD volleys, and then testing subjects under a range of frequency conditions. Bauer (1968) successfully conditioned electric catfish to produce a swimming response to electric stimuli by initially placing food at the end of a pair of galvanic tweezers. In the present study, the presentation of prey (goldfish, Carassius auratus) was paired with electrical stimulation.

Methods

Subjects

Two experimentally naive African electric catfish, Malapterurus electricus, (T. L. 15-20 cm) served as subjects. The condition and maintenance of the fish prior to testing was the same as in Experiment 1.

Apparatus

The apparatus used in this experiment was the same as for Experiment 2, including electrode positioning and the use of a red shelter tube. However, in place of the stimulus isolation unit, a UTC model CVP-3 60 W isolation transformer was used, as in Experiment 3, and no video recording equipment was used.

Procedure

Each subject was introduced to the test tank and, following a three day adaptation period, remained there for the duration of the training and testing sessions (25 and 21 days respectively). Sessions were conducted two to four days apart, and took place at approximately the 30 min mark following lights out.

Training followed a Pavlovian conditioning paradigm (Pavlov, 1927). Each training session began with the subject at rest, and consisted of the presentation of a series of three stimulus volleys followed 2 s later by the introduction of two to three goldfish (<u>Carassius auratus</u> <5 cm) to the test tank. The presence of goldfish served as an unconditioned stimulus (US) that triggered an unconditioned response (UR), swimming activity, in <u>Malapterurus</u> (Bauer, 1968). The training volleys (see below) represented the conditioned stimulus (CS) that were paired with the US during training sessions.

During stimulus presentation, subjects' behavior was recorded. Each subject was required to reach a criterion of five consecutive sessions in which artificial EOD stimulation alone resulted in the initiation of swimming activity. Reaching criterion indicated that swimming had become a conditioned response (CR), and testing sessions could begin.

Stimuli consisted of three consecutive volleys with an inter-volley interval of 500 ms. Volley duration was held constant at 1000 ms. All volleys contained pulses 1.5 ms in duration and 25 V in amplitude. Training volleys had a 2.5 ms IPI, resulting in a frequency of 250 Hz and a total of 250 pulses per volley. Testing volleys varied in IPI, frequency, and number of pulses per volley (Table 3).

Testing sessions were conducted in the same manner as training sessions, but using different stimulus parameters. Stimuli frequencies varied systematically across test conditions and were presented in ascending and descending order from the 250 Hz training value (Table 3). Presentation order was counterbalanced between subjects. Goldfish were presented, as during training, and served to prevent extinction of the CR.

When a catfish responded positively, by swimming during stimulus presentation, the following test session would test the next frequency in the series. If a fish did not respond to a given frequency value, it would be presented with the same stimulus during subsequent testing sessions until a response did occur. If responding failed to occur for five consecutive sessions, testing was terminated.

Analysis

The data were analyzed to determine the range of EOD frequencies to which subjects respond. Responses to each frequency value were tallied.

Table 3. Stimulus values used during test trials in Appendix B. Training volleys were 250 Hz with a 2.5 ms inter-pulse interval (IPI).

Table 3
Stimulus Values for Appendix B

Ascending Trials		Descending Trials	
IPI (ms)	Freq. (Hz)	IPI (ms)	Freq. (Hz)
2.0	286	3.2	213
1.6	323	5.0	154
1.3	357	8.0	105
1.0	400	20.0	47
0.8	435	40.0	24
0.5	500	100.0	10
0.2	588	200.0	5
0.1	625	800.0	1

RESULTS

Subjects reached training criteria quickly (seven and five days respectively). Following training both catfish gave the standard response to each stimulus value on its first presentation with only one exception. One subject did not respond to the 357 Hz condition until the second session it was presented. It was noted that this fish had a parasitic infestation at this time for which it was effectively treated. In every other instance, responding occurred during, or immediately (within 1 s) following the three artificial EOD volleys, and prior to the introduction of the goldfish.

These results indicate that Malapterurus electricus is sensitive to sequences of pulsed DC current in a frequency range of 1-625 Hz. This does not preclude the possibility of attaining responses to lower or higher frequency values by changing the volley duration or pulse duration respectively.

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