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City University of New York, 1992

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Short-Range Navigation in the Weakly Electric Fish *Gnathonemus petersii* L. (Mormyridae, Teleostei)

by

Peter Cain

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1992

This manuscript has been read and accepted by the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

SHORT-RANGE NAVIGATION IN THE WEAKLY ELECTRIC FISH, GNATHONEMUS PETERSII L. (MORMYRIDAE, TELEOSTEI)

by

Peter Cain

Advisor: Professor Peter Moller

This two-part investigation examined the role of electrolocation and vision in short-range navigation and orientation in Gnathonemus petersii, a weakly discharging electric fish. Each fish was placed in one compartment of an aquarium divided in half with a clear plastic wall. An aperture connecting the compartments appeared in one of three positions determined by randomized block design. The experimental chamber provided a novel environment the fish began exploring. The length of time (T) it took the fish to find an aperture in the wall, the height (H) they contacted the wall and the electric organ discharge (EOD) rate were recorded. In part I, 70 fish were divided into two groups: experiment 1, five groups of ten fish each; experiment 2, one group of 20 fish. The goal was to determine the effect of selective sensory deprivation on the fish's ability to locate the aperture. Fish with a functioning electric organ located the aperture faster, increased the height they contacted the wall, and changed their EOD rate.

In the second experiment, the aperture position remained fixed, and 20 fish learned to find and use the aperture. After four trials, the electric organ of ten fish was surgically rendered inoperative (silenced). The next day, all 20 fish were tested. There were no differences between intact and electrically-silent groups in time and height measures.

In Part 2, one hundred fish were divided into two groups of 50 fish each. The goal was to determine if fish with various degrees of sensory deprivation could learn the location of a fixed aperture. In experiment 1 the position of the aperture was raised by 10 cm after four trials. Over four trials, intact, blind, silent, and sham-operated fish learned the position of the aperture. When the aperture was raised immediately following trial 4, fish with a functioning electric organ decreased the time to find the aperture, and increased the height they touched the wall. In experiment 2, following four trials to familiarize the fish with the environment, the water level was raised by 10 cm (leaving the aperture in place). When the water level was raised, all fish increased the height they contacted the wall.

This increase, in response to a rapid change in water depth, suggested that all fish used hydrostatic pressure cues to maintain depth orientation.

The data show that G. petersii develop a central expectation or internal representation of their environment involving electrosensory and hydrostatic cues. As the environment becomes more familiar, the fish cease to attend to electrosensory information, and navigate according to the central expectation.

PREFACE/ACKNOWLEDGEMENTS

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GENERAL INTRODUCTION

Spatial orientation and navigation in animals involves many senses, including vision, hearing, chemoreception, tactile senses, and the vestibular sense. Weakly electric fish possess an additional electric sense that assists in social communication (Hopkins, 1980, 1986; Moller et al., 1989; Kramer, 1990) and electrolocation or object location (Heiligenberg, 1977; Bastian, 1990; von der Emde, 1990). Electrolocation has also been implied as a means by which these animals navigate. Weakly electric fish, the African mormyriforms and South American gymnotiforms, use their electric organ discharge in concert with specialized receptors to distinguish objects differing in resistivity, capacitance and voltage-generating properties (Bastian 1986) from the surrounding water.

Lissmann and Machin (1958) found that *Gymnarchus niloticus* could discern a 2 mm glass rod at 2.5 cm. Belbenoit (1970) found that blinded *Gnathonemus petersii* could distinguish between plastic and metal rods, 2 cm in diameter from a distance of 4 cm, and that they could learn to choose one type of electrical conductor over another. When Belbenoit silenced a fish's electric organ, it was still able to discriminate between metal and plastic rods, but not as successfully as the intact fish. This discrimination was probably due to ampullary receptor stimulation. Bastian (1976) examined the range of electrolocation by moving metal and plastic objects near gymnotids and measuring the responses of single electroreceptors and cerebellar neurons. He determined that electroreceptor activity increased with metal objects and decreased with plastic. Electroreceptor response to the object decreased as a negative power function of its distance from the fish. Meyer et al. (1976) and Feng (1977) showed that weakly electric fish orient themselves relative to the substrate using electrolocation.

The ability to move to a location that is beyond the reach of the animal's senses may involve both orientation and navigation. Orientation refers to an organism's ability to determine a direction relative to external cues. Navigation is the organism's ability to compensate for changes in position relative to a goal or end point (not detectable to the senses) through the use of one or more sensory modalities. Once the goal is detected, orientation describes all subsequent behavior (Baker 1978).

Orientation and navigation in fish have attracted scientific interest in part because of the economic importance of fish, but also because of widespread interest by zoologists and others in the phenomenon of animal migration. Bluefin tuna, for example, make multiple transatlantic crossings (Mather et al. 1967), and salmon migrate from their natal streams and rivers to the oceans. Salmon subsequently return to these streams to spawn, navigating over great distances with remarkable accuracy (Hasler & Schwassmann 1960). Quinn and Bannon (1982) have shown that sockeye salmon smolts may use both celestial and magnetic cues. According to Mann et al. (1988) and Walker et al. (1984), both sockeye salmon and yellowfin tuna may navigate over long distances by detecting changes in the earth's magnetic field. Identification of natal streams and rivers, however, appears to be based on olfactory memory and imprinting (Wisby & Hasler 1954).

Weakly electric mormyrid fish also exhibit migratory behavior. Mormyrids are primarily river dwellers, but also inhabit lakes and tributary streams, often in highly turbid waters (Petr 1967, 1968; Blake 1977b; Moller et al. 1979; Hopkins 1986). Mormyrid fish are nocturnal and seek shelter during the day (Lissmann 1958; Moller et al. 1979, Hopkins 1981). Moller et al. (1979) found that several species moved out of stream habitats to the river at night and returned by morning. Hopkins (1986) suggested that a preferred stream location may be occupied daily by the same fish. Many species also migrate seasonally, ascending rivers and their tributaries, to spawn in the swamps flooded during the rainy season (Corbet 1960, Okedi 1969). In the course of their daily and seasonal migration, the fish may leave familiar habitats and swim into unfamiliar, novel environments.

Möhres and zu Oettingen-Spielberg (1949) showed that bats behave differently in novel and familiar environments. It appears that in familiar environments bats reduce the input of sensory information available via echolocation (Griffin 1958). In this study, I examined the navigation and orientation behavior of the weakly electric mormyrid fish, _G_. _petersii_, in novel and familiar environments. The sensory information attended to during navigation in novel environments may be different from that used in familiar surroundings. By selectively interfering with the fish's sensory input and comparing their performances in novel and familiar environments, I attempted to determine which sensory channels were necessary for navigation and orientation. In every case, the fish's task was to locate a circular opening in a partitioned aquarium.

The first experiment (Part I) focused on the fish's performance in a novel environment. Over the course of fifteen trials, intact fish and fish deprived of vision and/or their electric organ discharge were presented with one of three aperture heights, randomly determined. The fish were presented with each aperture height five times, but the order of appearance was not predictable. In contrast, the second experiment (Part I) established a familiar environment. Intact fish were presented with a fixed aperture position for four trials. After the fourth trial, ten of the twenty fish had their electric organ discharge silenced surgically. The next day, I tested whether the fish without electrosensory feedback could find the aperture or had now lost this ability.

In Part II, experiments 1 and 2, the fish were presented with a fixed aperture on four consecutive days. In experiment 1, I examined the effects of selective sensory deprivation (as in experiment 1, Part I) on fish's ability to learn the aperture location over four days. On the fifth trial, which followed immediately after the fourth, the fish had to find the aperture after it was raised ten centimeters. Experiment 2 (Part II) followed the protocol of the experiment 1. However, instead of raising the aperture height immediately after the fourth trial, the water level was quickly raised ten centimeters, and consequently, the fish had to find the aperture in deeper water.

These manipulations allow me to examine the contributions of the electrosensory system, vision, and hydrostatic pressure to navigation behavior of fish in changing or stable environments. I discuss the physiological basis of electrolocation, appearance of a search strategy, and the development of a central expectation (Bell 1986). In this study I propose a role for each in short-range navigation behavior of the weakly discharging electric fish, *G. petersii*.

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PART I: SHORT-RANGE NAVIGATION IN NOVEL AND FAMILIAR ENVIRONMENTS IN THE WEAKLY ELECTRIC FISH, GNATHONEMUS PETERSII L. (MORMYRIDAE, TELEOSTEI)

The present manuscript was formatted for publication in Ethology (Paul Parey Verlag, Hamburg). Portions of this work were published in the Abstracts of the Animal Behavior Society (Annual Meetings, Binghamton, N.Y. 1990).

Abstract

We investigated electrolocation in _G. petersii_ and its involvement in navigation in novel and familiar environments. We hypothesized that the sensory information attended to during navigation in novel environments was different from that used in familiar surroundings. By selectively interfering with the fish's sensory input and comparing their performances in novel and familiar environments, we attempted to determine the sensory channels necessary for navigation and orientation. Experiments were conducted in a 200 l aquarium divided into two compartments. The fish had to find a circular aperture in the divider wall. Exp. 1: The position of the aperture was shifted randomly to one of three positions. We assigned 50 naïve fish to five treatment groups (10 fish each): intact, blind, electrically 'silent', blind & 'silent', and sham-operated animals. Fish were tested for 15 trials over 30 days. Exp. 2: To examine the fish's dependence on electrosensory feedback, we familiarized an additional 20 fish to a fixed aperture position. Subsequently, the electric organ was rendered surgically inoperative in 10 fish. The dependent variables were: (1) the height the fish contacted the divider, (2) the time to locate the aperture, and (3) the fish's electric organ discharge

rate. *G. petersii* depend on active electrolocation in a novel environment. There were significant differences between the amount of time it took fish with a functioning electric organ to find the aperture and fish without a functioning electric organ ($F_{13,600} = 3.01$, $P < 0.0005$). The fish distinguish and use local contrasts of conductivity for navigation. Over time, the fish optimized their ability to find the aperture. When the aperture was fixed, the fish learned its position and no longer depended on active electrolocation. We interpret and discuss this behavior as evidence for a 'central expectation'.

Introduction

African mormyrid fish generate electric organ discharges (EODs) that serve in social communication (HOPKINS 1980, 1981; KRAMER 1990) and in electrolocation (LISSMANN & MACHIN 1958; HEILIGENBERG 1977; BASTIAN 1990). Defined as the ability to distinguish objects in the surrounding water based on their resistivity, capacitance, or voltage-generating properties (BASTIAN 1986), behavioral evidence for active electrolocation is well documented (LISSMANN & MACHIN 1958; BELBENOIT 1970; HEILIGENBERG 1977; MEYER 1982; TOERRING & MOLLER 1984; BASTIAN 1986, 1990; VON DER EMDE 1990).

Mormyrids are primarily river dwellers, but also inhabit lakes and tributary streams, often in highly turbid waters (PETR 1967, 1968; BLAKE 1977b; MOLLER et al. 1979; HOPKINS 1980). MOLLER et al. (1979) found that several species moved out of stream habitats, occupied during the day, to the river at night and returned by morning. Many species migrate, ascending rivers and their tributaries, to spawn in the swamps flooded during the rainy season (CORBET 1960, OKEDI 1969). In the course of their daily and seasonal migration, the fish may leave familiar habitats and swim into unfamiliar, novel environments. Electrolocation has been inferred as the mechanism by which these animals navigate.

In this study we examined the short-range navigation of the weakly electric fish Gnathonemus petersii in novel and familiar environments. By selectively interfering with the fishs sensory input and comparing their performance in these two types of environments, we identified the necessary sensory channels for successful navigation. Since animals seem to reduce their reliance on sensory input once familiar with a given habitat (GRIFFIN 1958), we were particularly interested in the importance of vision and electrosensory feedback to the fish in novel and familiar situations.

The fish's task was to locate a circular opening in a partitioned aquarium. In the first experiment (novel environment), intact fish and fish deprived of selected sensory input were tested with the aperture presented in random order in one of three positions. In the second experiment (familiar environment), intact fish were presented with a fixed aperture position. After the electric organ was surgically rendered inoperative ('silenced'), we tested whether the fish could find the opening, or deprived of electrosensory feedback, had lost this ability.

Mormyrids are nocturnal and often found in turbid water. We have investigated electrolocation in this context. According to TEYKE (1989), blind cave fish (Anoptichthys jordani) developed 'cognitive maps' of their environment based on lateral line input. In light of this research, and our findings, we address the existence of a central expectation (BELL 1986) in G. petersii and its role in electronavigation.

General Materials and Methods

Subjects

Seventy weakly electric elephantnose fish, Gnathonemus petersii, of both sexes, ranging from 141 to 210 mm standard length (SL), were obtained from a local importer (African Fish Imports, Hackensack, NJ) and housed individually in 22 l aquaria. Fish were fed tubifex worms and maintained on a phase-shifted light/dark cycle (L:D = 12:12, lights on at 1500h). All experiments were conducted during the fish's subjective night. Water conductivity and temperature were maintained between 135 and 165 μS/cm and 20 to 23 °C, respectively.

Fish were transported to and from the experimental tank in a one gallon plastic aquarium lined with a plastic bag. Both the aquarium and the bag were black to prevent light from reaching the fish. Fish were transferred between aquaria using a standard aquarium fish net. Fish were placed in the experimental tank at the water surface by the wall opposite the aperture. Scoring began once the fish had righted itself and began swimming. The experimental tank provided a novel environment that the fish began exploring.

Apparatus

Experiments were conducted in a dark and acoustically insulated room. A 200 l aquarium (92.0 x 46.5 x 45.5 cm) was divided into two equal compartments with clear Plexiglass (Fig. 1). The divider was split in the middle and slotted to receive four Plexiglass squares 10.2 cm on a side. The only means of access from one compartment to the other was a circular aperture (diameter: 64 mm) in one of the squares. The position of this square could be shifted to change the height of the aperture. In position 1, the center of the aperture was 7.6 cm from the bottom, in position 2, it was 17.7 cm, and in position 3 it was 27.8 cm. Based on

HEILIGENBERG's (1977) computations, we estimated the electrolocation distance for a disk 64 mm in diameter to be 12 to 15 cm. The absolute boundary may vary from fish to fish depending on a fish's size, however, there was no evidence that fish could detect the aperture at 15 cm. We marked the divider wall location and the maximum (15 cm) electrolocation boundary on either side on the front of the aquarium. Water depth was 30.5 cm and marked in 5 cm increments at the electrolocation boundaries and the divider wall. Over the course of the experiments, water conductivity and temperature ranged from 135 to 165 μS/cm and 19 to 24 °C, respectively.

In order to observe and record the fish's behavior, three red General Electric 7C5 lamps illuminated each compartment of the aquarium: one placed overhead at the end wall, and the other two, 25 cm apart, 20 cm from the bottom, behind translucent white acrylic covering the back wall. Only the compartment containing the fish was illuminated. The illuminance was 0.23 foot-candles in the lighted compartment, and 0.14 foot-candles in the dark one. G. petersii can detect long wave length light (575 to 725nm), although the fish are most sensitive to 525nm light (CIALI 1989).

The fish's movements were recorded with a video cassette recorder (Panasonic NV-2800) using a low-light video camera (GBC Model CCD 500) and a wide-angle lens (Panasonic KF 85A auto-iris, f1.5, 8.5 mm) placed 1.45 m from the aquarium. EODs were monitored with a pair of Ag/AgCl electrodes extending from Plexiglass tubes attached to the opposite ends of the tank. EODs were recorded via a custom-made differential amplifier on one track of a cassette recorder (Marantz CD-330) and also on one track of the video cassette recorder. A wooden box lined with a grounded aluminum wire mesh screen covered three sides and the top of the aquarium to prevent light and electrical interference.

Surgical Procedures

Blinding was done through bilateral enucleation. Fish were anesthetized with MS-222 (3-aminobenzoic acid ethyl ester, methanesulfonate salt, Sigma Chemical Co.) buffered with sodium bicarbonate (1:20,000). The mucous membrane and skin covering the eye were removed. The eye was lifted, the optic nerve severed proximal to the eye, and the eye removed from its socket. To render fish electrically 'silent', subjects were lightly anesthetized with MS-222, and the motor neurons innervating the electric organ were severed. Locomotor behavior was not affected as the tail is controlled by tendons connected to muscles anterior to the caudal peduncle. We returned the fish to their home tank after the anesthesia wore off. Sham-operation involved anesthesia, removing three or four scales from the caudal peduncle, and puncturing the skin with a fine scalpel. Blinding was simulated by removing the mucous membrane covering the eyes of anesthetized fish. Fish were given one week to recover from surgery. All procedures were examined and approved by the Hunter College Institutional Animal Care and Use Committee (Protocol #: PM/PC 6/13/90).

Analysis

We analyzed four dependent variables: (1) the height fish first made physical contact with the center divider (H), (2) the time elapsed between crossing the electrolocation boundary and locating the aperture (T), (3) the fish's mean EOD rate per trial (using Apple-Scope software from R.C. Electronics), and 4) the number of times the fish crossed through the aperture per trial (where applicable). We measured the height fish contacted the wall in order to examine whether these bottom-dwelling fish would modify their behavior in order to locate or approach the aperture. The time measure (T) was derived by subtracting the amount of time from the fishs entry into the tank to crossing the electrolocation boundary from the time from entry to locating or crossing through the aperture. Statistical analyses were performed using SPSS/PC+ Vol.2 software. Analysis of variance was used to determine the effect of surgical treatment, experience as measured by trial, and aperture position. Post hoc comparisons between treatment groups and trials were made with protected t-tests and paired sample t-tests. The comparisons were protected from Type I error with Fisher's Significance Difference and the Bonferroni inequality (EDWARDS 1985). Where necessary, the degrees of freedom were corrected for sphericity (Mauchly test) with Huynh-Feldt Epsilon (SPSS/PC+ Vol.2).

Learning the position of the aperture was defined as significant sudden or gradual decrease in the time measure (T) and a significant increase in divider crossings (C) where applicable. These changes may be accompanied by a significant increase in the height measure (H).

Experiment 1: Variable Aperture Position

The fish in its natural habitat may seek an opening around plants, rocks or in an earthen bank. As a discharging mormyrid fish swims, its electroreceptors (mormyromasts) code the conductance of the objects in the environment. A fish would be in the best position to locate an opening if the highest concentration of mormyromasts (located on the head and face) were positioned to detect conductances above, below, or directly in front of the fish.

Materials and Methods

Subjects and Experimental Procedure

We randomly assigned 50 naïve fish to five treatment groups of 10 fish each: intact, blind, electrically 'silent', blind & 'silent', and sham-operated animals. We allocated treatment groups randomly to test days before beginning the experiments. The five treatment groups were divided into two larger units; one unit of three and one unit of two. Each unit was tested on alternate days. While the change in aquarium size and handling initially may have been stressful, all fish were treated equally throughout the experiment. Adaptation to handling and the experimental apparatus occurred to all the fish over the 30 day experimental period. On each trial, we rotated the order of presentation of the treatment groups to the test environment. Over the course of 15 trials, fish were presented with one of three aperture heights on each trial. Each aperture position appeared five times, one position per trial, as determined by randomized group design. Each trial lasted a maximum of 300 s. A fish was scored to have found the aperture, if (1) it swam through the aperture up to the caudal margin of the operculum, or (2) it swam to the non-illuminated side, within the 300 s period. In either case, we turned off the lights for 60 s before returning the fish to its home aquarium. If it did not find the aperture within 300 s, T was scored as 301 s, and we returned the fish to its home aquarium after 60 s in darkness.

Results

Time

There was a significant interaction between treatment and experience ($F_{53,599} = 1.79$, $P = 0.001$). Over 15 trials, the treatment group affected the time (T) to find the aperture ($F_{4,45} = 70.43$, $P < 0.0005$). Subjects with a functioning electric organ (intact, blind, sham-operated) located the aperture significantly faster than the electrically silent subjects (silent, blind & silent) ($F_{1,48}$ = 264.68, $P < 0.0005$). In all discharging fish (Fig. 2 a-c), T decreased over the first three trials, whereas in silent fish (Fig. 2 d, e) T remained at a high level throughout all trials. There were no significant differences between discharging groups. In intact fish, T remained under 60 s for the remainder of the trials.

The amount of experience the fish gained over trials (Fig. 2) had a significant effect on T ($F_{13,599}$ = 4.58; $P < 0.0005$). When we separated trials into two groups, trials 1-3 versus trials 4-15, and compared discharging versus non-discharging fish, treatment group had a significant effect on T ($F_{1,48}$ = 155.77, $P < 0.0005$). The interaction resulted from the difference between trials 1-3 versus 4-15 on the discharging fish ($F_{1,29}$ = 28.67, $P < 0.0005$).

Compared with the three discharging groups (intact, blind, sham-operated), silent fish (silent and blind & silent) were not successful finding their way out of the illuminated compartment. Figures 2 d, e show that these fish took significantly longer to find the aperture than the intact ($t = 15.08$, df = 18, $P < 0.0005$) or the blind fish ($t = 11.92$, df = 18, $P < 0.0005$). There was no evidence that these fish improved their performance over trials as did discharging fish. Fish limited by the loss of active electrolocation and vision would occasionally discover the aperture by contact with their chin appendage. There was no difference between blind & silent fish (T = 268.3 s) and silent fish (T = 267.5 s) over 15 trials.

The position of the aperture affected the time measure ($F_{2,90}$) = 3.16, $P < 0.05$). It took the fish significantly longer ($t = 2.47$, df = 49, $P < 0.02$) to find their way through the highest aperture, position 3, (162.7 s, SE = 15.3) than through position 2 (140.4 s, SE = 15.0). There was no difference between positions 1 and 2, and positions 1 and 3. There was no interaction between treatment group and aperture position.

Height

The treatment group did not affect the height (H) fish made contact with the divider wall. The position of the aperture had no effect on H; there was no significant interaction between aperture position and treatment group.

The amount of experience the fish gained over trials (Fig. 3) had a significant effect on H ($F_{14,623} = 3.94$; $P < 0.0005$), and there was a significant interaction between surgical treatment and experience ($F_{55,623} = 1.45$; $P < 0.05$).

The height at which fish with active electrolocation contacted the divider wall differed (intact, blind, sham-operated) from silent fish (silent, blind & silent). This difference was due to experience ($F_{13,633} = 3.06$, $P < 0.0005$). The effect of experience on height for groups with active electrolocation was linear ($t = 3.86$, $df = 14$, $P < 0.002$). Experience significantly affected the height fish with active electrolocation contacted the divider wall ($F_{14,378} = 4.21$; $P < 0.0005$). There were no such differences between the two silent groups. When we divided the trials into two groups (1-3, 4-15) and compared the discharging with the non-discharging fish, there were significant differences in H due to experience ($F_{1,48} = 27.64$, $P < 0.0005$) and interaction between experience and treatment ($F_{1,48} = 5.68$, $P < 0.05$). For both the electrolocating and non-electrolocating fish, the interaction effect was due to experience, i.e. the difference between the first three trials and the last 12 trials.

Electric Organ Discharges

The treatment group did not affect the mean EOD rate ($F_{2,27} = 3.22$, $P = 0.06$). Over the course of 15 trials, the mean EOD rate increased, reached a maximum between trials 5 and 10, and returned to the initial rate (Fig. 4). These changes were significant ($F_{7,193} = 2.85$, $P < 0.02$).

To evaluate the fish's navigation strategies, we examined the relationships between the three dependent variables in the intact, and blind & silent groups. In the intact group, time was inversely related to EOD rate ($r = - 0.57$, $P < 0.05$). There was no correlation between the height at which the fish contacted the divider and the EOD rate. The fish spent the least amount of time in the illuminated compartment when their EOD rates were highest. Peak EOD rates were correlated with optimal performance which underscored the importance of the fish's electrosensory system for navigation in a novel environment. Under the present conditions other sources of sensory input, vision in particular, did not compensate for the loss of active electrolocation.

In intact fish the correlation between time to find the opening and the height measure was $r = - 0.53$ ($P < 0.05$); in blind & silent fish it was $r = - 0.095$.

Thus, the higher intact fish contacted the divider, the less time they spent in the illuminated compartment. In the absence of visual and electrosensory input there was no relationship between time and height measures.

Experiment 2: Fixed Aperture Position

In this experiment, intact fish were presented with a fixed aperture position for four trials. In contrast to the novel environment presented to fish in experiment 1, this experiment established a familiar environment (the fixed aperture). We hypothesized that the fish would learn the aperture location in four trials. We tested whether electrolocation was necessary to locate the aperture after four trials.

Materials and Methods

Subject and Experimental Procedure

A group of 20 G. petersii was housed and maintained as described in experiment 1. The testing apparatus was the same as in experiment 1. Each of the 20 fish was placed in the experimental tank for a minimum of 300 s, and a maximum of 20 min. Scoring started after a fish was placed in the experimental tank. The fish was allowed 300 s to swim from one compartment to the other. When the fish swam through the aperture, lights were turned off. After 15 s the compartment containing the fish was illuminated. This procedure was followed for a maximum of 20 min per day for four consecutive days. If the fish did not swim to the other compartment within 300 s, it was returned to its home tank. The total score for each trial was the mean of the combined individual mean scores. The water level remained constant at 30.5 cm. The aperture remained in the same position, 17.7 cm from the bottom, for four consecutive days. After this period the fish were divided into two groups. One group of ten fish remained intact, the other ten were rendered silent (procedures as described in experiment 1). All fish were tested no later than 24 h following surgery. All trials (1-5) were conducted on consecutive days.

In addition to the dependent variables defined in experiment 1 (T, H, EOD), we recorded the frequency (crossings/trial) the fish crossed through the aperture (C) after the lights were turned on.

Analysis

Data collection and analysis were the same as in experiment 1. Each data point for trials 1-4 in Fig. 5 represents the mean obtained from 20 intact fish. Trial 5 consisted of the first attempt of each fish to find the aperture, thus the number of crossings (C) is always 1. We were not interested in the amount of time it took fish to learn the new location. The two data points on trial 5 represent the means of ten intact and ten silent fish, respectively. For details concerning the statistical analysis, see experiment 1, Analysis.

Results

With the aperture height held constant at 17.7 cm, the fish reduced the time (T) to find the aperture, and increased the height (H) they contacted the wall over 4 days. Thus, fish learned the location of the aperture, increased the number of times they swam from one compartment to the other, and became less dependent on active electrolocation.

Time

There was a significant decrease in T ($F_{3,48} = 3.34$; $P < 0.05$) as the fish became familiar with the environment (Fig. 5 a). T decreased significantly between trials 1 and 3 ($t = 2.12$, $df = 19$, $P = 0.047$) and 1 and 4 ($t = 3.21$, $df = 19$, $P = 0.005$). Although the newly silenced fish (97.3 s, SE = 44.9) took longer than the intact fish (45.3 s, SE = 17.1) to find the aperture on trial 5, this difference was not significant.

Height

As the fish learned the position of the aperture, H increased significantly in the direction of the aperture ($F_{3,54} = 6.24$; $P = 0.001$) (Fig. 5 b). H increased significantly between trials 1 and 3 ($t = 2.73$, $df = 19$, $P = 0.013$) and 1 and 4 ($t = 3.85$, $df = 19$, $P = 0.001$). On trial 5, the mean H values for intact and silent groups did not differ significantly (intact: 7.9 cm, SE = 2.52; silent: 8.7 cm, SE = 2.37). The absolute values dropped on trial 5, but this is within normal variation (see exp. 1, Fig. 3).

Divider Crossings

As the fish gained experience, the mean frequency of crossings (C) increased significantly (Fig. 5c) from 10.75 (SE = 2.95) on trial 1 to 25.25 (SE = 3.67) on trial 4 ($F_{3,54} = 7.46$, $P < 0.0005$). The number of crossings also increased significantly from trial 1 to trial 2 ($t = 3.03$, df = 19, $P = 0.007$).

Comparison of Experiments 1 and 2

To evaluate the navigation strategies of intact fish in novel and familiar environments, we compared time and height data from trial 4, the critical trial in experiment 1 (Fig. 2), with its counterpart in experiment 2 (Fig. 5). There was no significant difference in the time measure in intact fish (experiment 1: T = 85.5 s, SE = 23.2; experiment 2: T = 81.5, SE = 25.9). There was a significant difference, however, between H on trial 4 in experiments 1 and 2 ($t = 2.04$, df = 38, $P < 0.05$).

The time data indicated that intact and sham-op fish in experiment 1 learned to expect an aperture in the divider wall. However, the corresponding height data suggested that they did not modify the height they contacted the wall as rapidly as the fish in experiment 2, where they learned a fixed aperture position.

Discussion

Active electrolocation is the primary source of information for navigation in a novel environment by weakly electric fish. G. petersii deprived of this sensory modality cannot navigate in a novel environment. Other senses do not compensate for the loss of electrolocation. Fish deprived of vision, but with their electric organ intact, were able to locate the aperture. Sighted fish lacking a functioning electric organ were unable to locate the aperture. When the aperture remained in the same position, the fish became familiar with its location and found the aperture even after the electric organ was silenced.

MÖHRES AND ZU OETTINGEN-SPIELBERG (1949) found that bats (Rhinolophus ferrum-equinum, Myotis myotis) could find the entrance to a cage easily after being trained to feed inside. When the experimenters rotated the cage, so that the door was now 90° from its original position, the bats were less successful locating the entrance; in fact, they made fewer attempts. While MÖHRES AND ZU OETTINGEN-SPIELBERG did not interfere with the sensory capabilities of the bats, they showed that there was a distinct difference between Erstorientierung (novel environment orientation) (GRIFFIN & GALAMBOS 1941, 1942; DIJKGRAAF, 1946; as cited in MÖHRES AND ZU OETTINGEN-SPIELBERG, 1949) and Wiederorientierung (familiar environment orientation).

GRIFFIN (1958) found that bats (Eptesicus fuscus) learned a path around obstacles to a feeding place. After a bat learned the path, GRIFFIN changed the location of the obstacles. When the animal attempted to retrace the path it had learned, it collided with the repositioned obstacles. The bat tried the original route a second time before locating the new opening.

While the bat was negotiating its environment, GRIFFIN (1958) recorded the ultrasonic vocalizations which were labeled 'pulses' or 'clicks'. The bats emitted these pulses at different rates depending on their activity. Bats at rest might emit a few pulses per second. Those actively crawling around or preparing to take off raised their emission rate to 20 Hz. Bats preparing to land or flying around small obstacles could increase the rate to 50 Hz. The emission rate of a bat attempting to retrace its path was a "normal rate of roughly 20 Hz" (GRIFFIN 1958). It appears that in a familiar environment the bat reduces the amount of sensory input from echolocation, and therefore collides with the obstacles. CHASE (1983) discovered that while bats relied on echolocation when flying at night and attended to olfactory and acoustic cues when feeding, they showed a distinct preference for visual cues during escape. Thus, the level of attendance to a sensory modality can change according to behavioral or environmental context.

These findings provided the foundation for our investigation of the navigation behavior in G. petersii. During the 15 trials in experiment 1, fish with a functioning electric organ required less and less time to find the aperture despite the random change of its position. The aperture constituted an object (disk) of higher conductivity relative to the low conductivity of the plastic dividing wall. This condition was the reverse of standard electrolocation paradigms in which objects of higher or lower conductivity than the surrounding water were placed at varying distances from the animal (HEILIGENBERG 1973, PUSH & MOLLER 1979). For example, LISSMANN & MACHIN (1958) determined that electric fish were sensitive to potential differences induced by externally applied electric or magnetic fields, and could discriminate objects with a conductivity different from the surrounding water.

TOERRING & BELBENOIT (1979) and TOERRING & MOLLER (1984) related locomotor behavior (probing motor acts) with patterns of EOD activity in fish that approached novel objects. BELBENOIT (1970) showed that blinded _G. petersii_ discriminated between plastic and metal rods from a distance.

In our experiments the aperture had the same conductivity as the water and differed only relative to the surrounding plastic wall. As the discharging fish approaches the divider, the plastic wall causes a decrease in the transepidermal voltage in the body region closest to the wall (HEILIGENBERG 1977) and therefore, a decrease in electroreceptor (mormyromast) afference (BASTIAN 1976). Since the aperture conducts the electric current equally well as the surrounding water, the response of mormyromasts aligned with the aperture will be similar to that of electroreceptors not impinged upon by the plastic wall. We suggest that the fish assesses relative contrasts in conductivity (HOPKINS 1983), and are not restricted to discriminating objects differing in conductivity from the surrounding water (MEYER 1982). In the fish's natural habitat, this is similar to searching for an opening in a wall of rocks or earthen bank.

When a fish swims toward the middle aperture position in the divider wall, this places the highest concentration of electroreceptors in the optimal position to detect contrasts in the electric field above, below, or directly in front of the fish. Thus, the fish would be in the best position to detect the aperture. As the fish gained experience, there was evidence for such a search strategy as indicated by an increase in the height of contact with the divider wall. Except for the blind & silent fish, all fish touched the wall closer to the middle position (17.7 cm) as the experiment progressed.

The decrease in time necessary to find the aperture coincided with an increase in the fish's EOD rate. The decrease in time indicated that the fish were able to predict the existence of the aperture. The time decrease was followed by a decrease in EOD rate (cf. Figs. 2 a and 4 a).

The change in the behavior observed may be described as a collection of associative learning events. The fish may learn an association between the aperture and (1) a wall with specific electrical characteristics, (2) the external electric field generated by the lamps, and (3) for sighted fish, an illumination gradient. Swimming through the aperture may have provided an association between the aperture and (1) the electroreceptor response across the fish's body, (2) the presence and absence of an external electric field, and (3) again for sighted fish, lights on and lights off. Thus, both classical and operant conditioning processes may be involved in the acquisition of information necessary for navigation and orientation.

We propose that fish having established an internal representation of the aperture location no longer require increased electrosensory input to find the aperture. This acquired representation is consistent with a hypothesis by BELL (1989), who suggested an electric organ corollary discharge (EOCD)-driven central expectation generator. He proposed this generator as a mechanism for detection of novelty and change in the fish's environment.

As the discharging fish swims through its environment, mormyromasts code the conductance of objects in the fish's environment. The fish receives patterns of afferent responses from mormyromast receptive fields (BASTIAN 1975); thus, objects are assumed to be represented in the CNS as patterns of stimulation of these receptive fields (BELL 1986).

TEYKE (1989) found that blind cave fish (Anoptichthys jordani) developed an internal representation ('cognitive map') of their environment based on information from lateral line input. Blind cave fish released in a new or modified environment increased their swimming speed and optimized lateral line organ stimulation. This increased activity was apparently triggered by a mismatch between the internal representation and the actual environment. After 2-4 h in the new environment, swimming speed was reduced, and the fish avoided obstacles, and maintained swimming performance. After 6 h the fish had acquired a new internal representation of their environment. An analogous activity occurs in G. petersii, although the information appears to be acquired faster. The addition of novel objects, alteration of a familiar environment, or a completely new environment produce a mismatch between the pattern in the central expectation generator evoked by previous EODs (BELL 1986) and the pattern evoked in response to the new stimuli. This mismatch elicits a novelty response characterized by an acceleration in EOD rate (LISSMANN 1958, SZABO & FESSARD 1965, HEILIGENBERG 1976, GRAU & BASTIAN 1986) and probing motor acts (TOERRING & BELBENOIT 1979, TOERRING & MOLLER 1984).

From the findings of experiment 1, we predicted that if the aperture position remained fixed, the fish would learn its location. Our predictions were confirmed in experiment 2. The fish found the aperture more rapidly and contacted the wall increasingly closer to its actual height as the trials progressed. The rapid increase of H suggested that the fish could 'predict' where in the wall the aperture was located.

In experiment 1, fish were unable to locate the aperture without active electrolocation. Fish with a functioning electric organ raised the EOD rate as they explored the environment and reduced the rate as they gained experience. They enhanced their performance once they had located the aperture. In experiment 2, the fish learned the location of the fixed aperture and also improved their performance with experience. In experiment 2, however, the fish were able to find the aperture even after they had been silenced. Thus, having established an internal representation of the aperture position using electrosensory feedback, they depended less on active electrolocation. If the lateral line provided sufficient information to locate the aperture, blind and silent fish would have found it. Fish deprived of vision and electrolocation, yet having intact olfactory and gustatory systems, did not find the aperture.

Our study allowed the fish to swim freely in order to solve a problem they may face in their natural environment. Our data show that weakly electric fish rely on active electrolocation in unfamiliar or novel environments and navigate guided by a central expectation in familiar areas. Thus, fish moving from their nocturnal feeding grounds to their familiar diurnal resting place (HOPKINS 1981) might depend less on active electrolocation as compared with fish that migrate from the deep water of the river regions inhabited during the dry season to the flooded swamps and breeding areas of the rainy season.

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Fig. 1: Schematic representation, not to scale, of the experimental tank (92.0 x 46.5 x 45.5 cm) and recording apparatus. The wooden cover, lined with aluminum screen to reduce electrical interference, was cut away to show the location of the recording electrodes (E), the three possible aperture positions, 64 mm in diameter,(dotted circles) and the lamp placement (L). Marked lines on either side of divider wall denote electrolocation boundary.

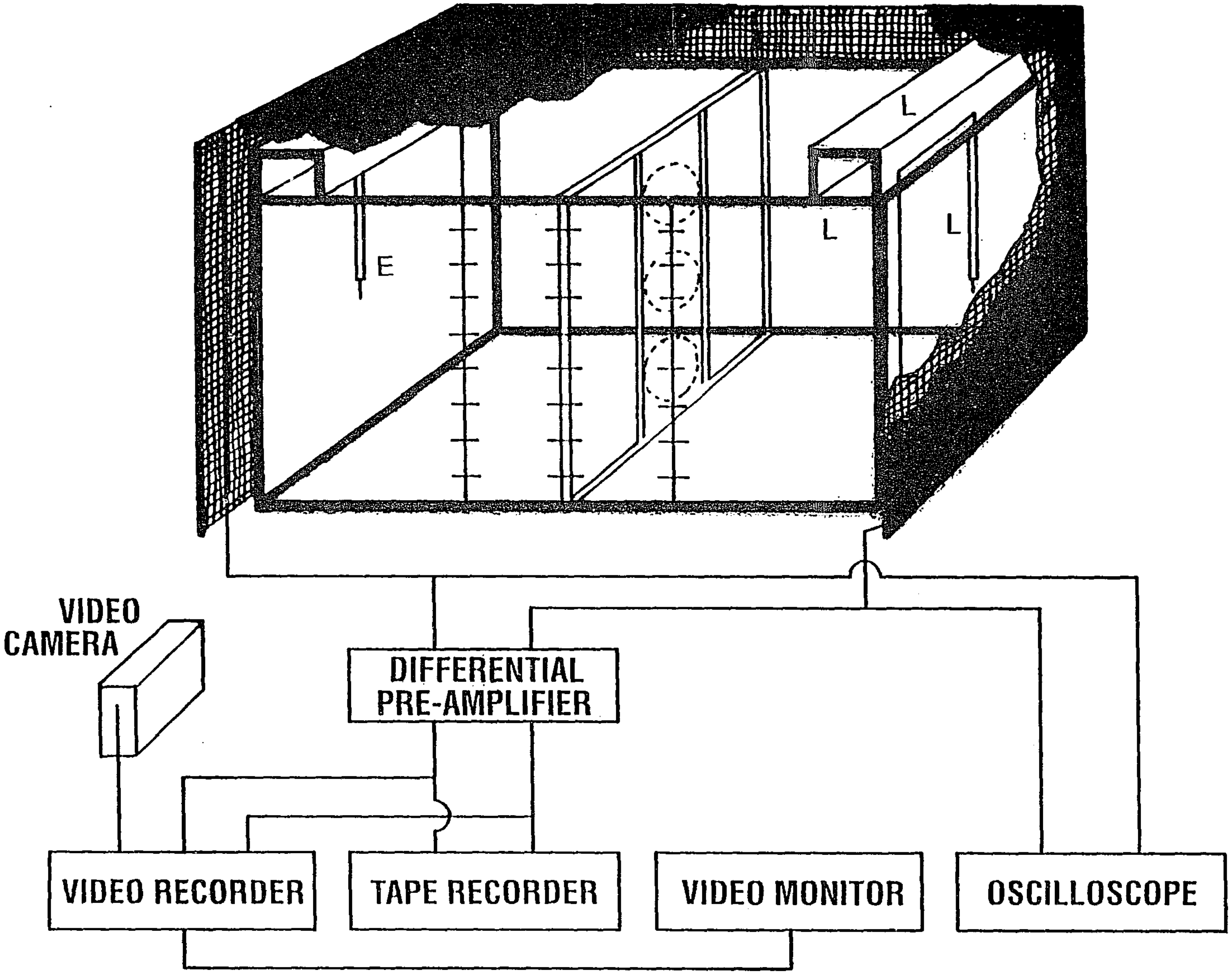
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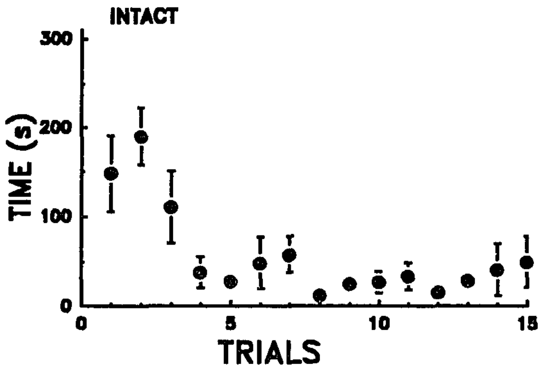
Fig. 2: Amount of time to find the aperture. Each graph (a-e) identifies the treatment group and the mean (± SE) time per trial it took the fish of that group to find the aperture after crossing the electrolocation boundary. Over 15 trials, fish with an electric organ discharge (a-c: intact, blind, and sham-operated) reduced the time while fish without a discharge (d,e: silent, blind & silent) did not.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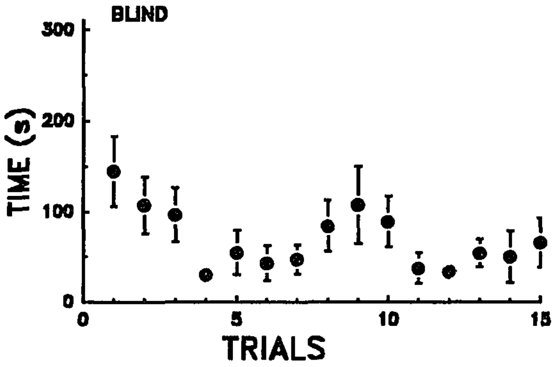
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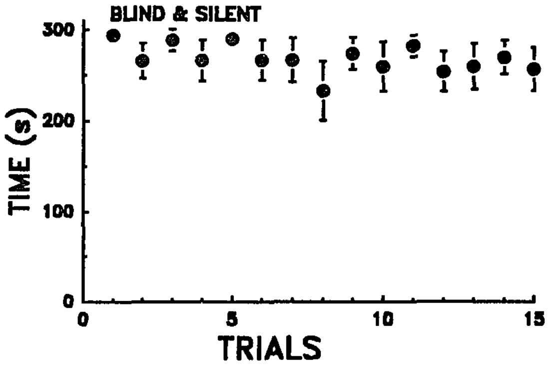
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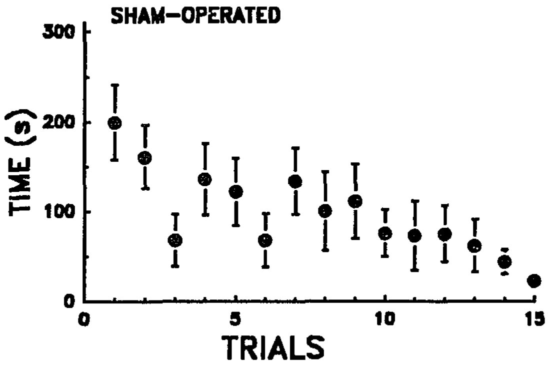
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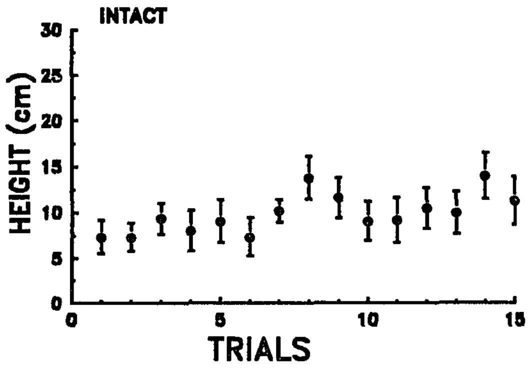
Fig. 3: Height of contact with the divider wall. Mean (± SE) height per trial fish of each treatment group first touched the divider wall. Fish with an electric organ discharge (a-c: intact, blind, and sham-operated) increased the height over 15 trials, while fish without a discharge (d,e: silent, blind & silent) did not.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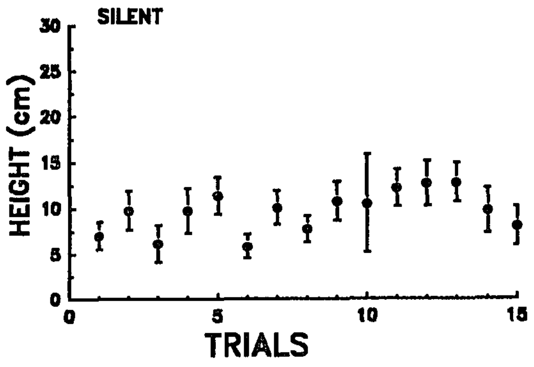
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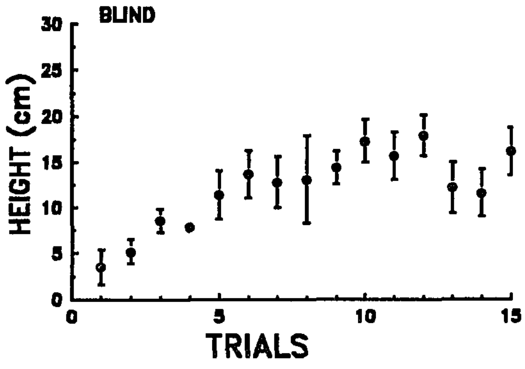
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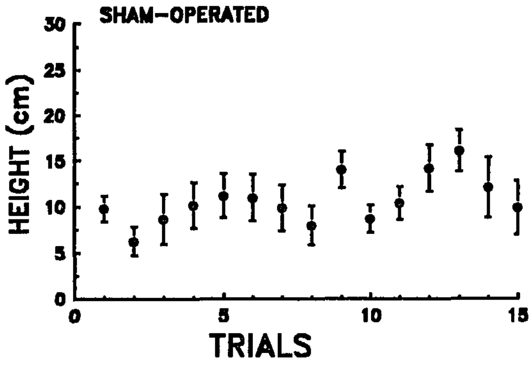
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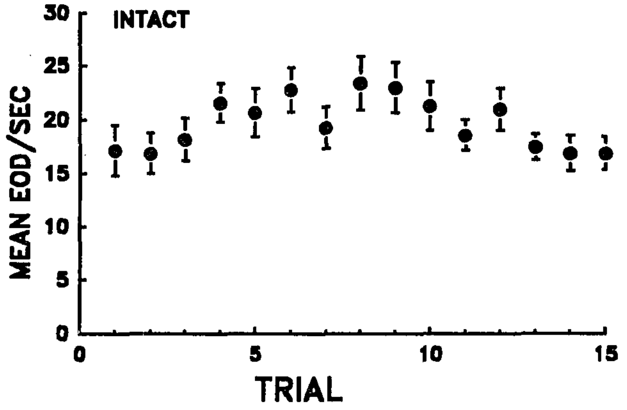
Fig. 4: Electric organ discharge (EOD) rate while searching for the aperture. Mean (± SE) EOD rate per trial of each treatment group. The rate per trial is the mean of the combined average EOD rates per trial of each fish in that treatment group. Intact and sham-operated fish (a, c) increased EOD rate for 8 trials, then decreased it over the next 7 trials. Blind fish (b) increased EOD rate for 5 trials, then decreased.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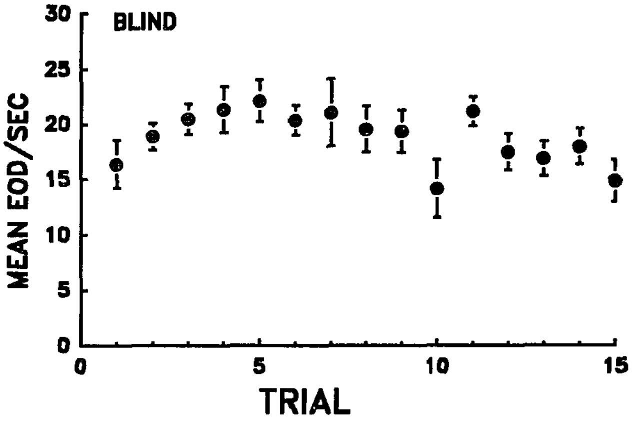
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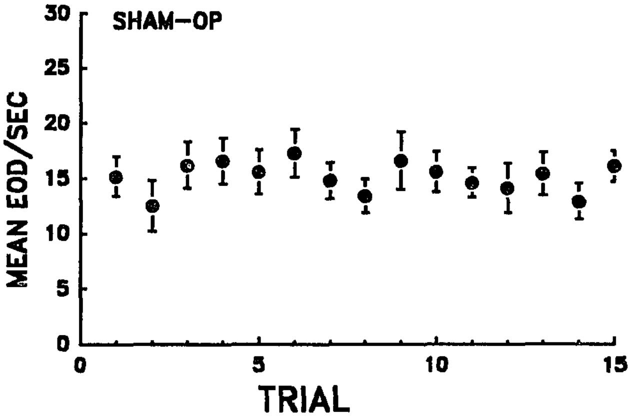
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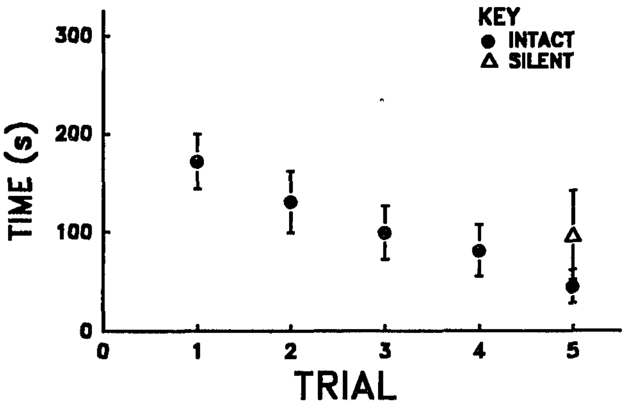
Fig. 5: Performance of fish in a familiar environment. Aperture position held constant (17.7 cm from aquarium floor). After 4 trials, 10 of 20 fish had their electric organ 'silenced' surgically. Trial 5: mean scores from the first attempt of intact and 'silenced' fish to find the aperture. (a) Trials 1-4, mean (± SE) time per trial to find the aperture of 20 intact fish; trial 5, mean (± SE) time of the intact and silenced fish. (b) Trials 1-4, mean (± SE) height per trial fish touched the divider wall; trial 5, mean (± SE) heights of intact and silent fish. (c) Trials 1-4, mean (± SE) number intact fish crossed from one compartment to the other. Over 4 trials, intact fish decreased the time to find the aperture, increased the height they contacted the wall closer to the aperture height, and increased the number of times they crossed from one compartment to another. Fish with their electric organ 'silenced' after trial 4 did not differ from intact fish on both time and height measures: silent fish found the aperture equally well as intact fish.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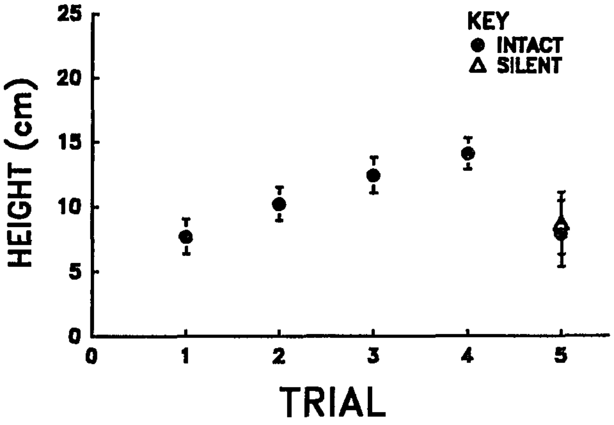
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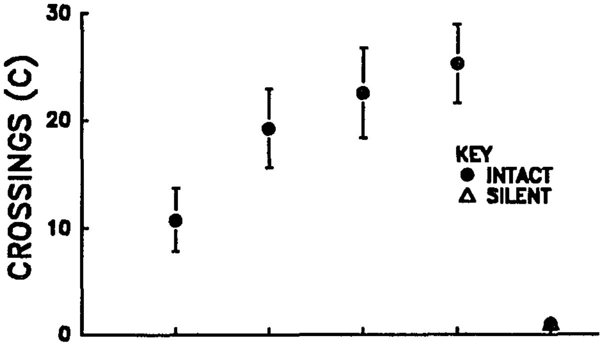
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PART II: SENSORY CUES AND NAVIGATION IN A FAMILIAR ENVIRONMENT IN THE WEAKLY ELECTRIC FISH, GNATHONEMUS PETERSII L. (MORMYRIDAE, TELEOSTEI)

The present manuscript was formatted for publication in Animal Behaviour (Academic Press, London, New York). Portions of this work were published in the Abstracts of the Animal Behavior Society (Annual Meetings, Binghamton, N.Y. 1990).

Abstract. Gnathonemus petersii use electrolocation to navigate. The goal of this study was to determine if intact fish and fish with various degrees of sensory deprivation could learn the location of an aperture. By selectively manipulating environmental cues (aperture height and water depth) the contributions of the electrosensory system, vision, and hydrostatic pressure were examined. Experiments were conducted in a 200 l aquarium divided into two compartments. The fish's task was to find a circular aperture in the divider wall. Exp. 1: The position of the aperture was raised by 10 cm after the fish had become familiar with its original location. Exp. 2: The water level was raised by 10 cm (leaving the aperture in place). I assigned 50 naïve fish to five treatment groups of ten fish each: intact, blind, electrically 'silent', blind & 'silent', and sham-operated animals. I analyzed four dependent variables: (1) the height the fish contacted the divider, (2) the time to locate the aperture, (3) number of crossings, and (4) electric organ discharge rate. Intact, blind, silent, and sham-operated fish learned the position of the aperture. When the aperture was raised intact fish found the new aperture with no difficulty, whereas blind, silent, and sham-operated fish were slow finding the new position. When the water level was raised all fish

increased the height they contacted the wall. This increase, in response to a rapid change in water depth, suggested that all fish used hydrostatic pressure cues to maintain depth orientation, and that those fish that had learned the aperture height used these cues to locate its position. I suggest that _G_. _petersii_ develop an internal representation (or central expectation) of their environment involving electrosensory and hydrostatic cues. As the environment becomes more familiar, the fish cease to attend to electrosensory information, and navigate according to the central expectation. At each depth fish develop an electrosensory 'image' of their immediate environment, and associate a specific image with a specific depth.

Weakly electric fish use their electric organ discharges in social communication (Hopkins 1980, 1981, 1986; Kramer 1990) and in object location (Heiligenberg 1977, Bastian 1990, von der Emde 1990). Cain (Thesis, Part 1) found that an African weakly electric fish, *Gnathonemus petersii*, can locate an aperture with increasing efficiency, even when the aperture position randomly changes from trial to trial. Based on these results, Cain (Thesis, Part 1) proposed that *G. petersii* establish an internal representation or central expectation (Bell 1986) of the environment.

The goal of this study was twofold: (1) to determine if intact fish and fish with various degrees of sensory deprivation could learn the exact location of an aperture, and (2) if they did learn, and environmental cues were changed, would the fish adjust to the change or search for the aperture in the old location. These questions were examined from two perspectives: (1) the aperture was moved, and (2) the water level was changed. These manipulations allowed me to examine the contributions of the electrosensory system, vision, and hydrostatic pressure.

GENERAL METHODS

Subjects

One hundred naïve weakly electric elephantnose fish, Gnathonemus petersii, ranging from 150 to 220 mm standard length (SL), were obtained from a local importer (African Fish Imports, Hackensack, NJ) and housed individually in 22 l aquaria. Fish were fed tubifex worms and maintained on a phase-shifted light/dark cycle (L:D = 12:12, lights on at 1500 h).

Apparatus

Experiments were conducted in a dark and acoustically insulated room. A 200 l aquarium (92.0 x 46.5 x 45.5 cm) was divided into two equal compartments with clear Plexiglass (Fig. 1). The divider was split in the middle and slotted to receive four Plexiglass squares 10.2 cm on a side. The only means of access from one compartment to the other was a circular aperture (diameter: 64 mm) in one of the squares. The position of this square could be shifted to change the height of the aperture. In position 1, the center of the aperture was 7.6 cm from the bottom, in position 2, it was 17.7 cm, in position 3, it was 27.8 cm. Three red General Electric 7C5 lamps illuminated each compartment of the aquarium:

one placed overhead at the end wall, and the other two, 25 cm apart, 20 cm from the bottom, behind translucent white acrylic covering the back wall. The illuminance was 0.23 foot-candles in the lighted compartment, and 0.14 foot-candles in the dark one. The experiments were conducted during the fish's subjective night.

Based on Heiligenberg's (1977) computations, I estimated the electrolocation distance for a disk 64 mm in diameter to be 12 to 15 cm. The absolute boundary may vary from fish to fish depending on the fish's size, but there was no evidence that fish could detect the aperture at 15 cm. I marked the divider wall location and the maximum (15 cm) electrolocation boundary on either side on the front of the aquarium. The water depth was 30.5 cm and marked in 5 cm increments at the electrolocation boundaries and the divider wall. Over the course of the experiments the water conductivity and temperature ranged from 135 to 170 μS/cm and 19 to 24 °C, respectively.

The fish's movements were recorded with a video cassette recorder (Panasonic NV-2800) using a low-light video camera (GBC Model CCD 500) and a wide-angle lens (Panasonic KF 85A auto-iris, f1.5, 8.5 mm) placed 1.45 m from the aquarium. Electric organ discharges were monitored with a pair of Ag/AgCl electrodes extending from Plexiglass tubes attached to the opposite ends of the tank. Discharges were recorded via a custom-made differential amplifier on one track of a cassette recorder (Marantz CD-330) and also on one track of the video cassette recorder.

Surgical Procedures

Blinding was done through bilateral enucleation. To render fish electrically 'silent', subjects were lightly anaesthetised with MS-222, and the motor neurons innervating the electric organ were severed. Sham-operation involved anaesthesia, removing three or four scales from the caudal peduncle, and puncturing the skin with a fine scalpel. Blinding was simulated by removing the mucous membrane covering the eyes of anaesthetised fish. For additional detail on surgical procedures, see Cain (Thesis, Part 1).

Analysis

I analyzed four dependent variables: (1) the height the fish contacted the center divider (H), (2) the time elapsed between crossing the electrolocation boundary and locating the aperture (T), (3) the frequency the fish crossed through the aperture after the lights were turned on (C), and (4) the fish's mean EOD rate per trial (using Apple-Scope software from R.C.Electronics). We measured the height fish contacted the wall in order to examine whether these bottom-dwelling fish would modify their behavior in order to locate or approach the aperture. The time measure (T) was derived by subtracting the amount of time from the fishs entry into the tank to crossing the electrolocation boundary from the time from entry to locating or crossing through the aperture. Statistical analyses were performed using SPSS/PC+ Vol.2 software. Analysis of variance was used to determine the effect of surgical treatment, experience as measured by trial, and aperture position. Post hoc comparisons between treatment groups and trials were made with protected t-tests and paired sample t-tests. The comparisons were protected from Type I error with Fisher's Significant Difference and the Bonferroni inequality (Edwards 1985). Where necessary, the degrees of freedom were corrected for sphericity (Mauchly test) with Huynh-Feldt Epsilon (SPSS/PC+ Vol.2).

Learning the position of the aperture was defined as significant sudden or gradual decrease in the time measure (T) and a significant increase in divider crossings (C) where applicable. These changes may be accompanied by a significant increase in the height measure (H).

EXPERIMENT 1: EFFECT OF APERTURE POSITION

Methods

I assigned 50 naïve fish to five treatment groups of 10 fish each: intact, blind, electrically 'silent', blind & 'silent', and sham-operated animals. Scoring started after a fish was placed in the experimental tank. The fish was allowed 300 s to swim from one compartment to the other. When the fish swam through the aperture, the lights were turned off. After 15 s the compartment containing the fish was illuminated. This procedure was followed for a maximum of 20 min per day for four consecutive days. If the fish did not swim to the other compartment within 300 s, it was returned to its home tank.

On day 4, following the last observation of trial 4, each fish was confined to a net at the surface of the water with the lights and recording equipment off. The aperture was raised by 10.1 cm to 27.8 cm (position 3). Trial 5 started when the compartment was illuminated, the recording equipment was started, and the fish released from the net. The data collected for trial 5 were restricted to the first observation of the subject to locate the aperture.

Results

Time

The time (T) elapsed between crossing the electrolocation boundary and locating the aperture was affected by treatment group ($F_{4,45} = 13.17$, $P < 0.0005$), and trial ($F_{3,135} = 6.52$ $P < 0.0005$) for trials 1-4 (Fig. 2). There was a significant decrease in T between trials 1 and 3 ($t = 3.25$, $df = 49$, $P < 0.05$). There was no interaction between treatment group and trial.

Discharging fish (intact, blind and sham-operated) found the aperture significantly faster than non-discharging fish ($F_{1,48} = 26.14$, $P < 0.0005$). Experience, as measured by trial, had a significant effect ($F_{3,137} = 5.08$, $P < 0.05$) on the time measure for discharging fish; T decreased over trials. There were no significant differences in T between the intact, blind and sham-operated fish (Fig. 2 a-c). There was a difference ($t = 5.19$, $df = 18$, $P < 0.01$) between the two non-discharging groups (Figs. 2 d, e) with silent fish finding the aperture faster than blind & silent fish.

Blind fish spent less time in the illuminated compartment than silent ($t = 3.71$, $df = 18$, $P < 0.05$), and blind & silent fish ($t = 10.21$, $df = 11.04$, $P < 0.01$). The fact that there was a significant difference between the two silent groups (silent and blind & silent) (Fig. 2 d, e), and no difference among the sighted fish (intact, sham-operated, and silent fish) (Fig. 2 a, c, d), suggested that silent fish used vision to locate the aperture.

When the aperture was raised for trial 5, fish with a functioning electric organ performed better than fish without an electric organ discharge ($F_{1,49} = 11.22$, $P < 0.01$). There were no differences among groups with a functioning electric organ. Silent fish spent less time in the illuminated compartment on trial 5 than the blind & silent fish ($t = 5.16$, $df = 18$, $P < 0.01$). There were no significant differences in T between the intact ($\bar{X} \pm SE = 118.4 \pm 42.2$ s), blind ($\bar{X} \pm SE = 122.7, \pm 38.67$), or the sham-operated ($\bar{X} \pm SE = 137.2 \pm 38.8$ s), and the silent fish ($\bar{X} \pm SE = 175.9 \pm 37.6$ s).

When I compared with the last observation in trial 4 with trial 5 (Fig. 2), blind fish ($t = 2.44$, $df = 9$, $P = 0.04$) and sham-operated fish ($t = 2.86$, $df = 9$, $P = 0.02$) took significantly longer to find the new location.

Height

The height the fish contacted the divider wall (H) was affected by treatment group ($F_{4,45} = 14.5$, $P < 0.0005$), the amount of experience as measured by trial ($F_{3,135} = 13.51$, $P < 0.0005$), and by the interaction between treatment group and trial ($F_{12,135} = 3.51$, $P < 0.0005$) (Fig. 3). The first significant increase in H, when all treatment groups were combined, appeared between trials 2 and 3 ($t = 3.14$, $df = 49$, $P < 0.05$). Discharging fish contacted the wall significantly higher than non-discharging fish ($F_{1,48} = 31.65$, $P < 0.0005$). There were no significant differences between fish with a functioning electric organ (Fig. 3 a-c). Once again, as with the time measure, the difference between the two non-discharging groups (Figs. 3 d, e) was significant ($t = 3.23$, $df = 18$, $P < 0.05$).

Blind fish made contact with the divider wall higher than silent fish ($t = 4.20$, $df = 18$, $P < 0.01$), and blind & silent fish ($t = 8.11$, $df = 17$, $P < 0.01$). The height intact ($\bar{X} \pm SE = 12.1 \pm 1.1$ cm) and sham-operated fish ($\bar{X} \pm SE = 11.6 \pm 3.6$ cm) touched the wall was not significantly different from that in silent fish. Sighted fish may display negative phototaxis. Blind & silent fish touched the wall consistently lower than any other group.

When the aperture was raised for trial 5, treatment group had a significant effect on H ($F_{1,49} = 7.08$, $P < 0.01$). There were no significant differences in H between fish with a functioning electric organ. Blind fish touched the wall higher than silent ($t = 4.20$, $df = 18$, $P < 0.01$), and blind & silent fish ($t = 8.11$, $df = 18$, $P < 0.01$). The change in aperture position did not effect significant differences between the last observation of trial 4 and the fish's first and only attempt of trial 5.

Divider Crossings

The most obvious indicator that the fish had located and used the aperture was the number of times they crossed (C) from one compartment to another (Fig. 4). There were differences in the number of crossings between treatment groups ($F_{4,45} = 10.42$, $P < 0.0005$). There was also an effect due to experience ($F_{3,127} = 7.11$, $P < 0.0005$), but no significant interaction effect between treatment group and experience.

Discharging fish crossed more often than non-discharging fish ($F_{1,48} = 32.98$, $P < 0.0005$). There were no significant differences among groups with a functioning electric organ (Fig. 4 a-c). There was no difference among the sighted groups, i.e. intact, sham-operated, and silent fish. However, silent fish crossed more often than blind & silent fish (Fig. 4 d, e) ($t = 3.93$, $df = 18$, $P < 0.05$).

Intact fish crossed more often than blind & silent fish ($t = 4.18$, $df = 18$, $P = 0.01$). Blind fish crossed more often than silent fish ($t = 4.83$, $df = 18$, $P < 0.01$) and blind & silent fish ($t = 7.49$, $df = 18$, $P < 0.01$). Sham-operated fish also crossed more often than blind & silent fish ($t = 4.49$, $df = 18$, $P < 0.01$).

These results were predicted by the time and height data. Fish with a functioning electric organ found the aperture faster, and thus crossed the divider more frequently. Surprisingly, the number of crossings by the silent fish increased as the fish gained experience and the differences between silent and blind & silent fish were significant, while the differences between silent and intact and sham-operated fish were not. Silent fish apparently attended to visual cues.

Electric Organ Discharge

The electric organ discharge rate was not affected by treatment level. The effect of experience (trials) was significant ($F_{3,81} = 2.83$, $P = 0.04$). There was also an interaction between treatment level and trial ($F_{6,81} = 16.52$, $P < 0.0005$) (Fig. 5). Intact fish increased their discharge rate linearly from trials 1-4 ($t = 4.97$, $P < 0.001$). Blind fish decreased their discharge rates linearly ($t = 3.89$, $P = 0.004$) as did sham-operated fish (t = -7.85, P = 0.0005) (Fig. 5). I will discuss these differences further below. When the aperture height was raised for trial 5, the discharge rate did not change significantly from trial 4 in all three groups.

EXPERIMENT 2: EFFECT OF WATER LEVEL

Methods

A batch of 50 naïve G. petersii was divided into five groups of ten fish each as described in experiment 1. The experimental apparatus and procedures were the same as in experiment 1. Fish were trained as in experiment 1. After the last training session on day 4, I raised the water level 10 cm within 5 min, from 30.5 to 40.5 cm, while the aperture height remained unchanged. The added water was of the same temperature and conductivity as the aquarium water.

RESULTS

Time

The amount of time (T) the fish spent in the illuminated compartment after crossing the electrolocation boundary differed according to treatment group ($F_{4,45} = 14.75$, $P < 0.0005$), trial ($F_{3,135} = 19.1$, $P < 0.0005$) and as a result of the interaction between treatment group and trials ($F_{12,135} = 5.89$, $P < 0.0005$) (Fig. 6). There was a significant difference in T between trials 1 and 2 ($t = 3.54$, df = 49, $P < 0.05$), indicating that it took the fish two trials to learn the aperture location. The difference in T between the discharging and non-discharging groups was significant ($F_{1,48} = 51.69$, $P < 0.0005$). There were no significant differences among fish with a functioning electric organ (Fig. 6 a-c) or between the two non-discharging groups (Figs. 6 d, e).

Intact fish found the aperture faster than the silent fish ($t = 3.99$, df = 18, $P = 0.01$), and blind & silent fish ($t = 6.49$, df = 18, $P < 0.01$). Blind fish found the aperture faster than silent fish ($t = 3.48$, df = 18, $P = 0.05$) and blind & silent fish ($t = 7.95$, df = 18, $P < 0.01$). Sham-operated fish found the aperture faster than both silent fish ($t = 3.30$, df = 18, $P = 0.05$) and blind & silent fish ($t = 6.99$, df = 18, $P < 0.01$).

When the water level was raised for trial 5, fish with a functioning electric organ spent significantly less time in the illuminated compartment than silenced fish ($F_{1,49} = 36.23$, $P < 0.00005$). In all groups there were no significant differences in T between the last observation on trial 4 and trial 5.

Height

The height the fish contacted the divider (H) differed according to treatment group ($F_{4,45} = 14.38$, $P < 0.0005$), trial ($F_{3,135} = 19.1$, $P < 0.0005$), and also as a result of the interaction between treatment level and trial (experience) ($F_{12,135} = 2.42$, $P = 0.007$) (Fig. 7). The height the fish touched the divider was significantly higher on trial 2 than on trial 1 ($t = 4.69$, df = 49, $P < 0.01$). There was a significant difference between the discharging and non-discharging groups ($F_{1,48} = 44.94$, $P < 0.0005$). There were no significant differences among fish with a functioning electric organ (Fig. 7 a-c) or among non-discharging fish (Figs. 7 d, e).

Intact fish made contact with the divider wall higher than silent fish ($t = 3.94$, df = 18, $P < 0.01$) and blind & silent fish ($t = 8.29$, df = 18, $P < 0.01$). Blind fish made contact with the divider higher than blind & silent fish ($t = 6.05$, df = 18, $P < 0.01$). Sham-operated fish also made contact with the divider wall higher than blind & silent fish ($t = 6.44$, df = 18, $P < 0.01$).

When the water level was raised for trial 5 , the fish with a functioning electric organ contacted the wall significantly higher than silenced fish ($F_{1,49} = 13.79$, $P < 0.0005$). The blind fish contacted the divider wall significantly higher on trial 5 than they did on the last observation of trial 4 ($t = 3.11$, $df = 9$, $P = 0.01$).

Divider Crossings

The number of times the fish swam through the aperture was affected by treatment group ($F_{4,45} = 8.67$, $P < 0.0005$) and trial ($F_{3,135} = 17.13$, $P < 0.0005$). The number of crossings on trial 1 was significantly less than on trial 2 ($t = 3.24$, $df = 49$, $P < 0.05$). There was a significant difference between discharging and non-discharging groups ($F_{1,48} = 25.93$, $P < 0.0005$). There were no significant differences among fish with a functioning electric organ (Fig. 8 a-c) or between the two non-discharging groups (Figs. 8 d, e).

Electric Organ Discharge

There was no difference in the discharge rate due to treatment group. Experience (number of trials) had a significant effect on the discharge rate ($F_{2,56} = 4.03$, $P < 0.01$) as did the interaction between treatment and trial ($F_{4,56} = 13.18$, $P < 0.0005$) (Fig. 9).

The change in electric organ discharge rate in intact fish (t = 4.82, P = 0.001) is described by a quadratic function with highest rates on trials 1 and 4, and a minimum on trials 2 and 3 (Fig. 9 a). Blind and sham-operated fish did not exhibit a change in electric organ discharge rate over the first four trials (Fig. 9 b, c). When the water level changed on trial 5, intact and sham-operated fish increased their discharge rates.

DISCUSSION

The goal of this study was twofold: (1) to determine if intact fish and fish under various degrees of sensory deprivation could learn the exact location of an aperture, and (2) if they did learn and the cues were changed, would the fish adjust to the change or search for the aperture in the old location. These questions were examined from two perspectives: (1) the aperture was moved, and (2) the water level was changed. The analyses allowed me to examine the cues the fish attended to before and after learning.

In this study, fish with a functioning electric organ that were presented with a fixed aperture learned its location: the amount of time it took the fish to find and swim through the aperture decreased, the height at which the fish contacted the divider wall increased, and the number of aperture crossings increased. Cain (Thesis, Part 1) proposed that G. petersii establish an internal representation or central expectation (Bell 1986) of the environment through the electrosensory system. Once familiar with the environment the fish no longer depended on electrolocation.

In a study of the navigation behaviour of G. petersii, Cain (Thesis, Part 1) showed that fish with a functioning electric organ can locate an aperture with increasing efficiency, even when the aperture position randomly changes from trial to trial. Locating the aperture is based on the fish's ability to discriminate contrasts in electrical conductance (Bastian 1986, Cain et al., Part 1).

Electrosensory system

At the start of the first experiment, intact fish emitted low discharge rates, and were therefore limited in the acquisition of environmental information. As the experiment progressed intact fish increased their discharge rate and found the aperture more rapidly. The fish maintained a high rate when the position was changed, and had no difficulty locating the aperture.

Blind and sham-operated fish started the experiment with high discharge rates that decreased with experience. These fish did not raise the discharge rate when the aperture height was changed, searched for the aperture in its former location and had difficulty finding the new location. The silent fish also had difficulty finding the new aperture location.

I suggest that the formation of a central expectation is facilitated by high discharge rates. In intact fish the formation of central expectation was delayed initially because of the limited electrosensory input due to a low discharge rate. Blind fish formed a central expectation more rapidly because of their higher initial discharge rate. Consequently, intact fish, not having established a central expectation yet, found the new aperture position. Blind fish, having established a central expectation, searched at the old position.

Vision

Mormyrids have poor visual acuity; their vision is optimally adapted to low-light conditions (McEwan 1938, Teyssèdre & Moller 1982, Ciali 1989). Visual cues can act in concert with electrosensory feedback to facilitate group cohesion, conditions permitting (Moller et al. 1982). Under the present low light conditions, silent fish apparently learned the aperture location visually, but were not able to find its new location as quickly as under familiar conditions. Evidence for a role of vision in navigation was provided by Cain (Thesis, Part 1) who found that electrically silent fish increased the height they contacted the divider wall whereas blind & silent fish did not. It appears that in the first experiment silent fish formed an internal expectation without electrosensory input that resulted in these fish searching for the aperture at the old location. There was no evidence for this in the second experiment.

Hydrostatic pressure

When I raised the water level, all fish increased the height they contacted the divider wall. The change in water level did not affect the time it took discharging fish to find the aperture. Silent fish found the aperture faster than blind & silent fish when the water level increased.

The increase in water depth changed two possible references: (1) the hydrostatic pressure relative to the aperture position, and (2) the distance between the aperture and the water surface. The change in water depth did not change the distance between the aperture height and the aquarium floor.

Weakly electric fish orient to the substrate using electrolocation (Meyer et al. 1976, Feng 1977). If discharging G. petersii learned the aperture height using electrosensory information to determine the distance from the aquarium floor, none of the fish should have increased the height they contacted the divider wall. If G. petersii determined swimming depth based on electrosensory information from the air-water interface (Knudsen 1975), silent and blind & silent fish should not have increased the height at which they contacted the divider wall. Contrary to these predictions, all fish increased the height they contacted the wall. This increase, in response to the rapid 10 cm change in water depth, strongly suggested that the fish learn the aperture height using hydrostatic pressure cues. Considering the reported sensitivity of teleost fish to water pressure (0.5-20 cm H_2O: Blaxter & Tytler 1972, Blaxter 1980), such mechanism seems highly plausible. The data also provide evidence that weakly electric fish attend to hydrostatic pressure cues to maintain depth orientation. Blind & silent fish, unable to respond to electrosensory and visual information, decreased their swimming depth (as measured by the height they contacted the divider wall) in the same direction as the water level change. The pressure receptors may be located at the swim bladder and the pro-otic bulla (Blaxter 1980).

Lateral-line

Teyke (1989) demonstrated that blind cavefish (Anoptichthys jordani) were able to establish an internal representation (cognitive map) of their environment over a 6-hr period using lateral-line information. While lateral-line involvement may play a role in object location in mormyrid fish (Toerring & Moller 1984), my data show that G. petersii did not use such information to locate the aperture. While blind fish decreased the time to locate the aperture, blind & silent fish were unable to find it: both groups possessed a functioning lateral line, but only fish with a functioning electric organ were successful. Lateral line cues were not attended to (Bastian, 1990). It is possible that the acquisition of lateral-line based cues may take longer than the 5 min available in these experiments.

Other sensory modalities

Mormyrids can hear (Stipetic 1939) and vocalize (Rigley & Marshall 1973, Crawford et al. 1987, Bratton & Kramer 1989). The fish were occasionally monitored; no acoustic signals were detected. There was no evidence for chemical cues involved with locating the aperture. Fish deprived of vision and electrolocation yet having intact olfactory and gustatory systems did not find the aperture. Within the 5 min allotted, blind & silent fish were occasionally able to locate the aperture using tactile cues through their chin appendage.

Mormyrid fish possess a number of sensory modalities that provide information about their environment. Which modality (vision, hydrostatic, electrosensory) provides the primary information depends on the environmental and/or behavioral context. In this investigation, by comparing the affects of selected sensory deprivation, I established that G. petersii develop an internal representation (or central expectation) of their environment involving electrosensory and hydrostatic cues. As the environment becomes more familiar, the fish cease to attend to electrosensory information and navigate according to the central expectation. At each depth fish develop an electrosensory 'image' of their immediate environment. Thus, the fish associate a specific image with a specific depth. With the acquisition of a central expectation, the fish can reduce the energy expended on electric discharge activity necessary to orient and navigate. When the actual afference (electrosensory, hydrostatic, or visual input) differs from the image stored in the central representation, as would be the case in a novel environment (Szabo & Fessard, 1965; Ciali, 1988), the fish increase their electric activity to increase sensory information and thus modify the central expectation.

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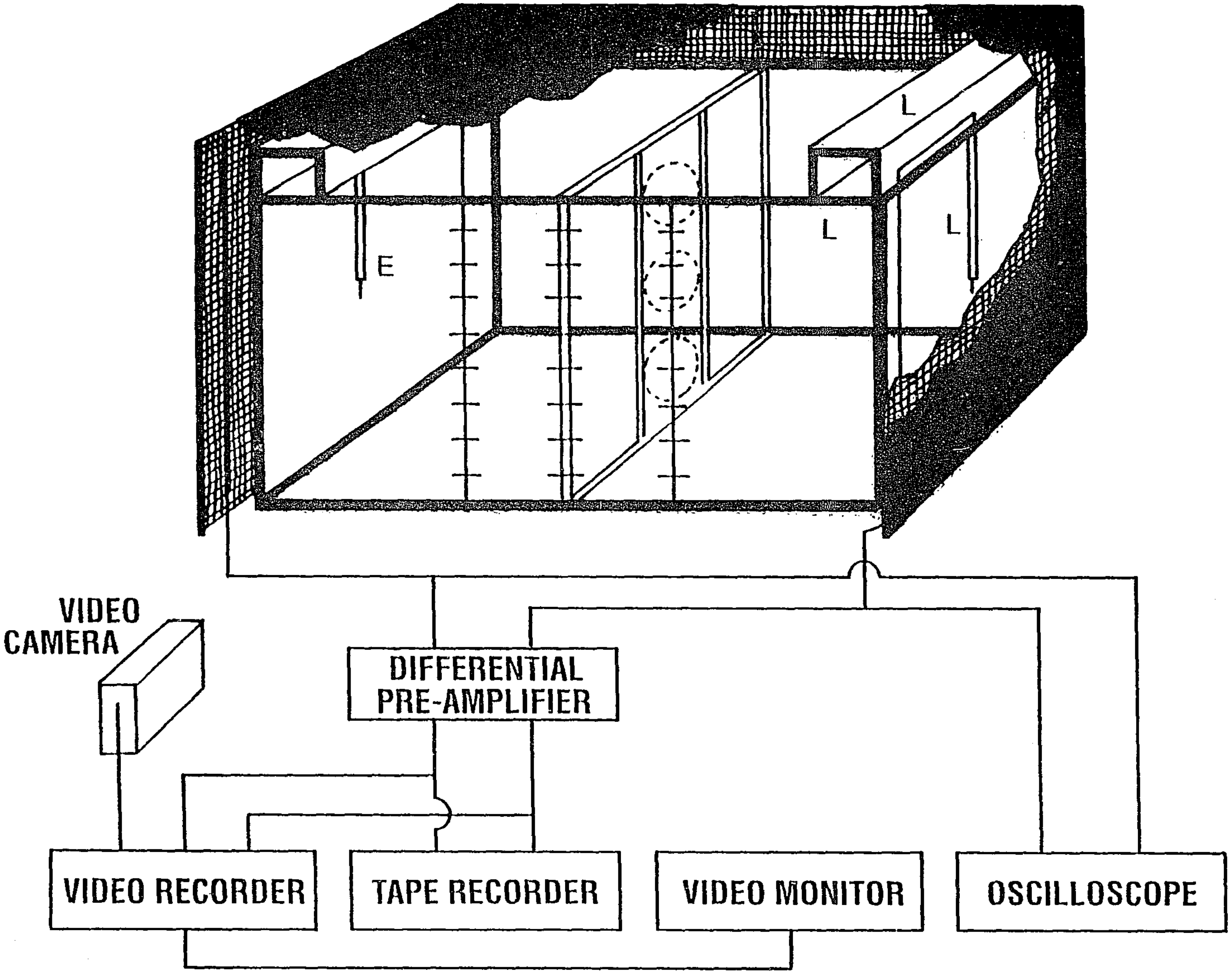
Figure 1. Schematic representation (not to scale) of the experimental tank (92.0 x 46.5 x 45.5 cm) and recording apparatus. The wooden cover, lined with aluminum screen to reduce electrical interference, has been cut away to show the location of the recording electrodes (E), the three possible aperture positions (dotted circles) and the lamp placement (L). Marked lines on either side of divider wall denote electrolocation boundary.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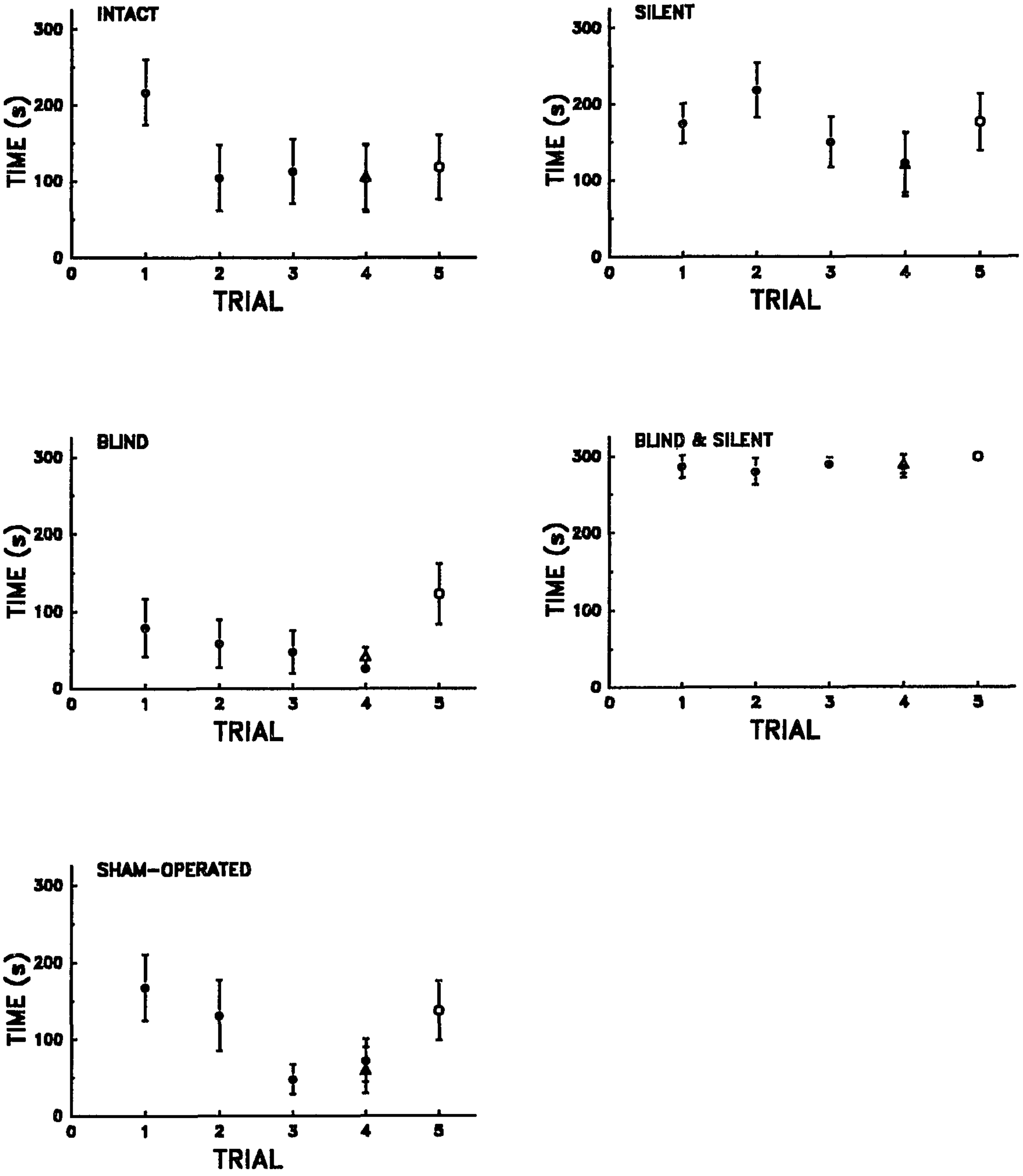
E
VIDEO CAMERA
DIFFERENTIAL PRE-AMPLIFIER
VIDEO RECORDER
TAPE RECORDER
VIDEO MONITOR
OSCILLOSCOPE

Figure 2. Amount of time to find the aperture for each treatment group. Trials 1-4: aperture position held constant (17.7 cm from aquarium floor). Symbols represent the mean time in sec. (± SE). Trial 5, immediately following trial 4, the aperture height was raised 10 cm; symbols represent mean scores (± SE) from the first attempt of fish to find the aperture. Over 4 trials, fish with an electric organ discharge and the silent fish decreased the amount of time to find the aperture. Blind & silent fish did not decrease the time. There was no difference in time between trials 4 and 5 for the intact, sham-operated and silent fish. Blind fish took longer to find the aperture on trial 5 than on trial 4.


INTACT
SILENT
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BLIND & SILENT
SHAM-OPERATED
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Figure 3. Height of contact with the divider wall by treatment group. Trials 1-4, aperture height was held constant (17.7 cm from aquarium floor). Symbols represent mean height in cm (± SE). Trial 5, immediately following trial 4, the aperture height was raised 10 cm; symbols represent mean (± SE) height of first attempt to find the aperture. Fish with an electric organ discharge and silent fish increased the height they contacted the divider wall over 4 trials. Blind & silent fish did not. There was no difference between trial 4 and trial 5 for any treatment group.

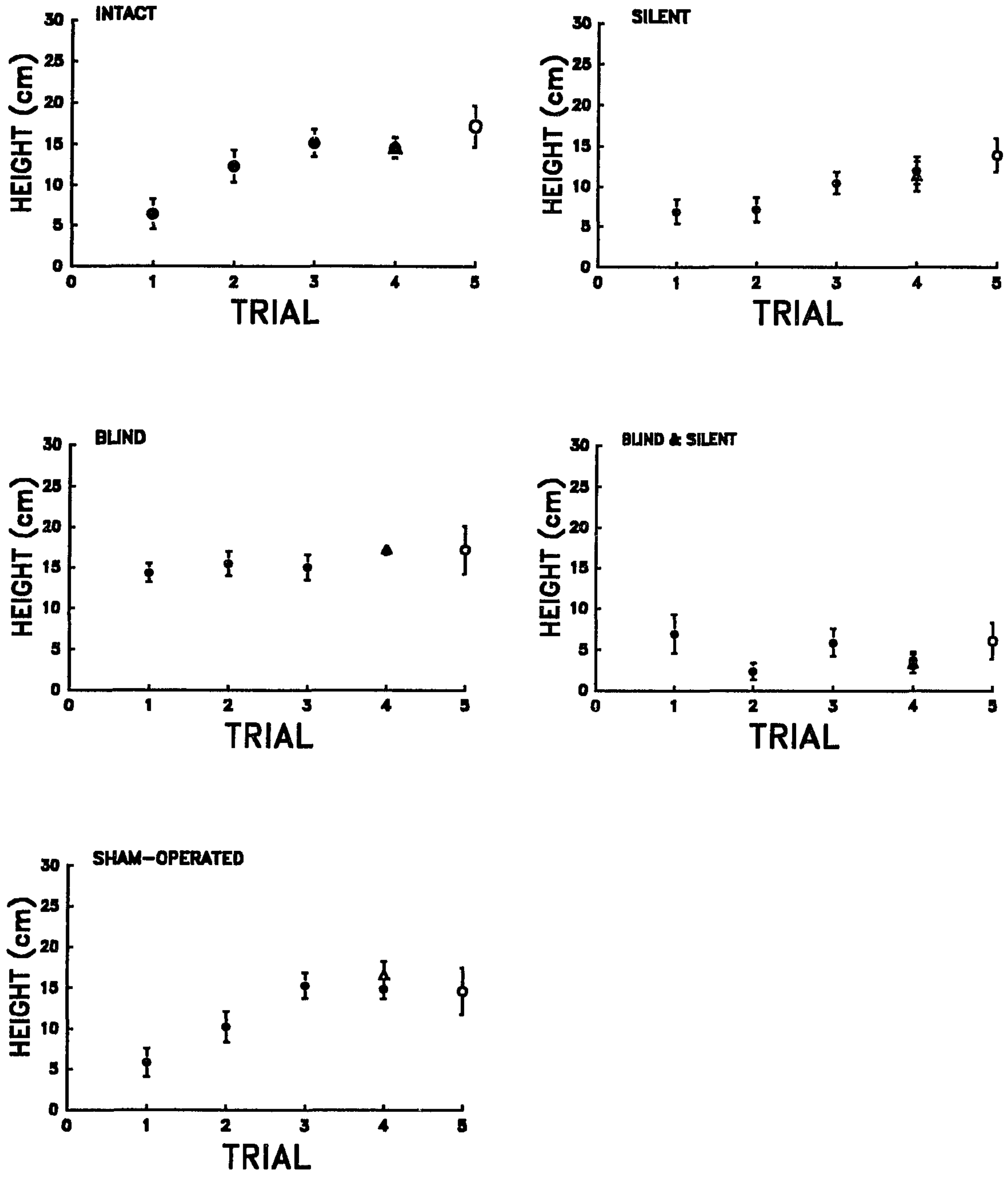
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Figure 4. Number of crossings from one compartment to the other. Aperture height was held constant (17.7 cm from aquarium floor). Mean (± SE) number of times per trial fish crossed from one compartment to the other, by treatment group. Fish with an electric organ discharge and silent fish increased the number of crossings; blind & silent fish did not. Trial 5 scored only the first attempt to find the aperture, so the number of crossings is always one.


INTACT
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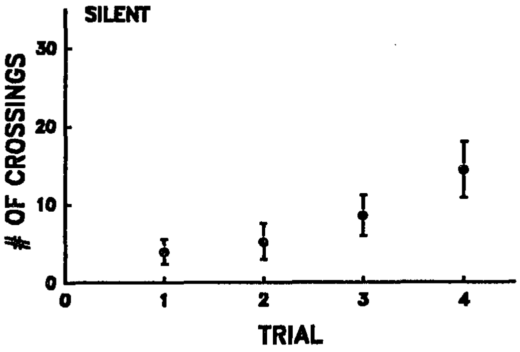
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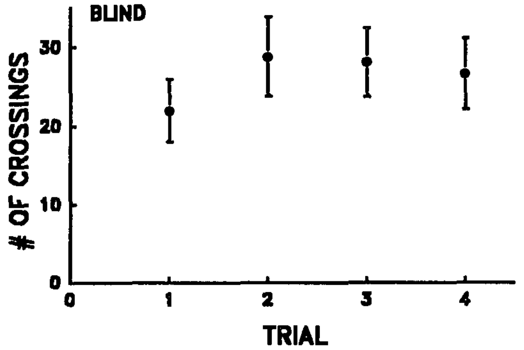
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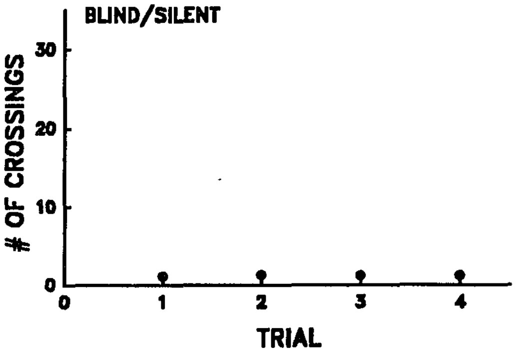
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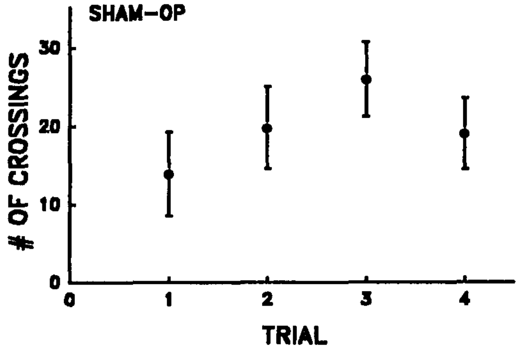
SHAM-OP
OF CROSSINGS
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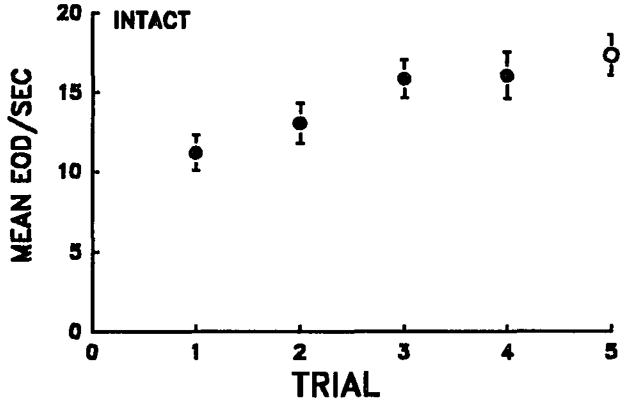
Figure 5. Electric organ discharge rate of each group while learning aperture position. Trials 1-4, the mean (± SE) EOD rate per trial of each treatment group. The rate per trial is the mean of the combined average EOD rates per trial of each fish in that treatment group. Trial 5, immediately following trial 4, the aperture height was raised 10 cm; symbols represent mean (± SE) electric organ discharge rate during first attempt to find the aperture. Intact fish increased their discharge rate over 5 trials, while the blind and sham-operated fish decreased their rates over 4 trials, and showed no difference between trials 4 and 5.


INTACT
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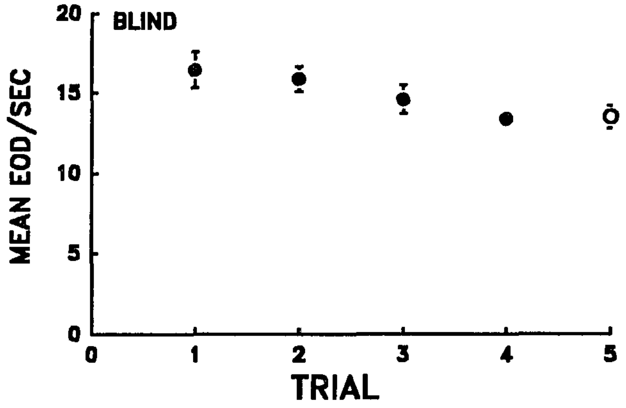
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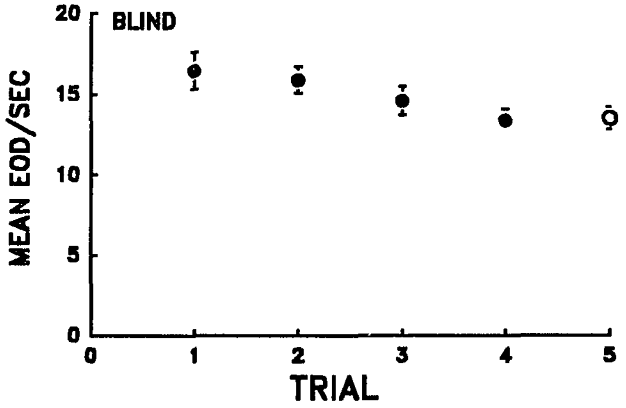
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Figure 6. Amount of time to find the aperture for each treatment group. Trials 1-4: water level was held constant at 30.5 cm. Open triangle on trial 4 represents mean of last attempt to find aperture. Symbols represent the mean time in sec. (± SE). Trial 5, immediately following trial 4, water depth increased 10 cm; symbols represent mean scores (± SE) from the first attempt of fish to find the aperture. Over 4 trials, fish with an electric organ discharge decreased the amount of time to find the aperture. Silent and blind & silent fish did not. There was no difference in time between trials 4 and 5, or between the last attempt on trial 4 and trial 5 for intact, blind and sham-operated fish. There were no differences between trials 4 and 5, and the last attempt of 4 and trial 5 for the non-discharging fish.

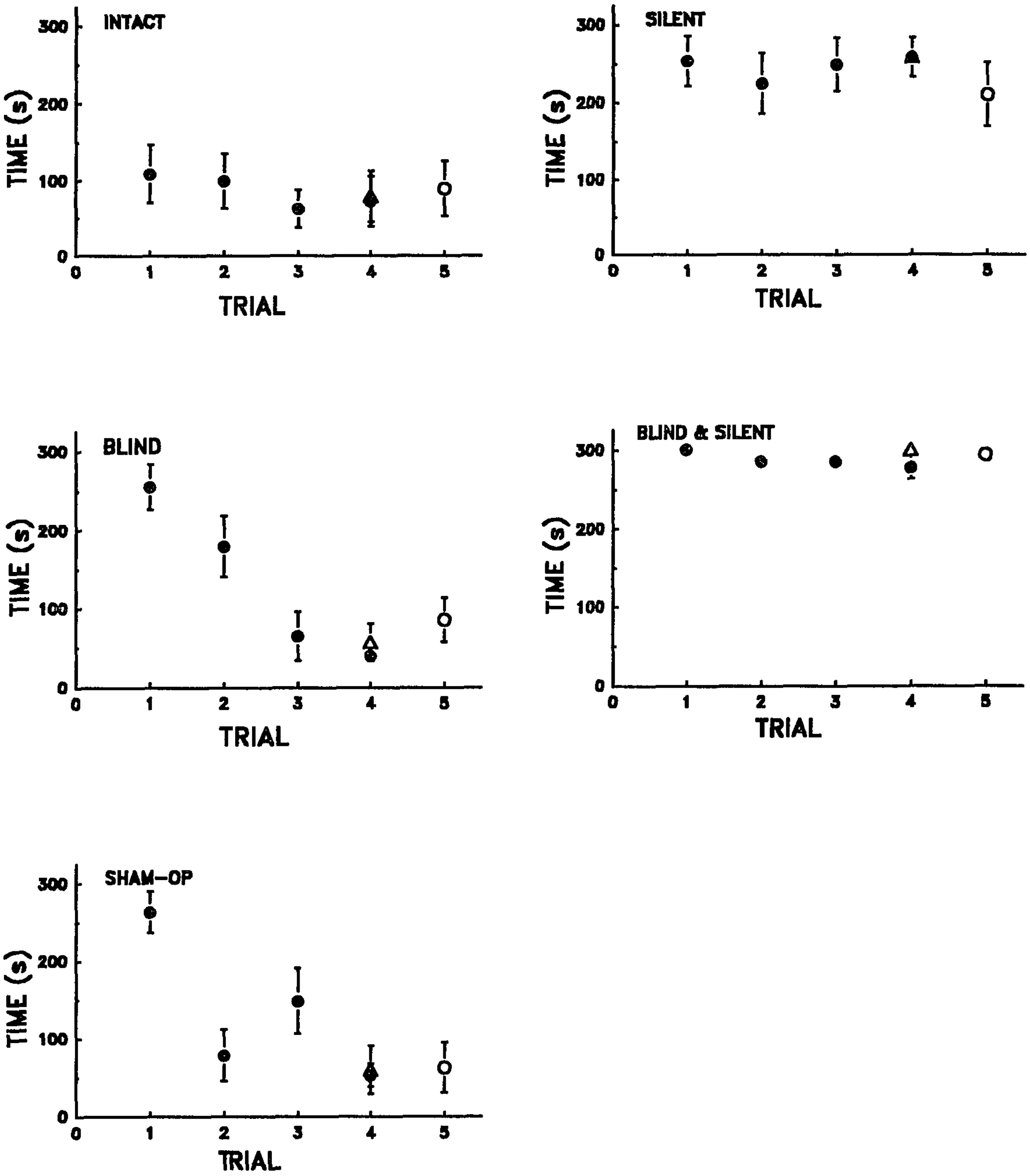
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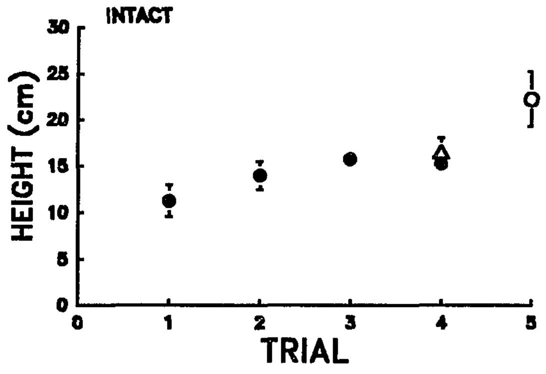
Figure 7. Height of contact with the divider wall by treatment group. Trials 1-4, water depth was held constant at 30.5 cm. Symbols represent mean height in cm (± SE). Trial 5, immediately following trial 4, the water depth raised 10 cm; symbols represent mean (± SE) height of first attempt to find the aperture. Fish with an electric organ discharge and silent fish increased the height they contacted the divider wall over 4 trials. Blind & silent fish did not. All fish increased the height they contacted the divider wall on trial five. Fish with a functioning electric organ contacted the wall higher than silenced fish. The blind fish contacted the divider wall higher on trial 5 than they did on the last attempt of trial 4.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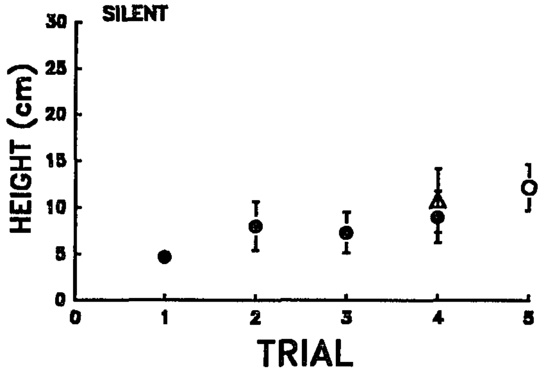
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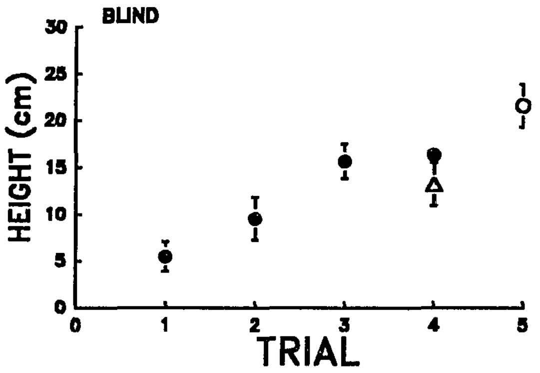
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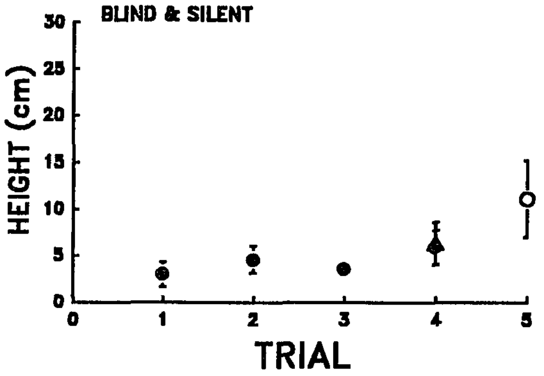
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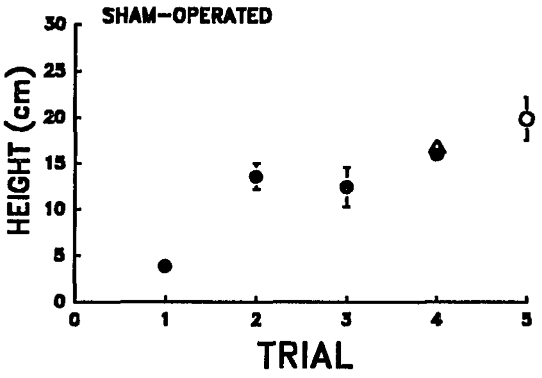
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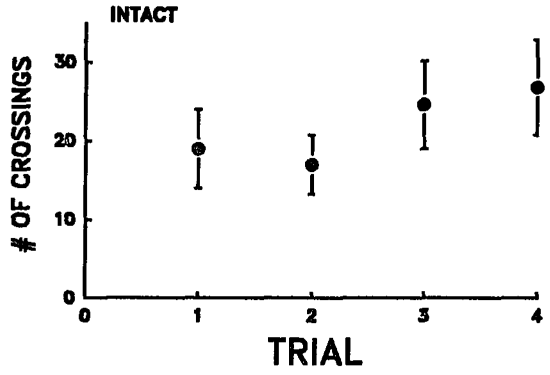
Figure 8. Number of crossings from one compartment to the other. Over 4 trials, discharging fish increased the number of times they crossed from one compartment to another. The non-discharging fish did not.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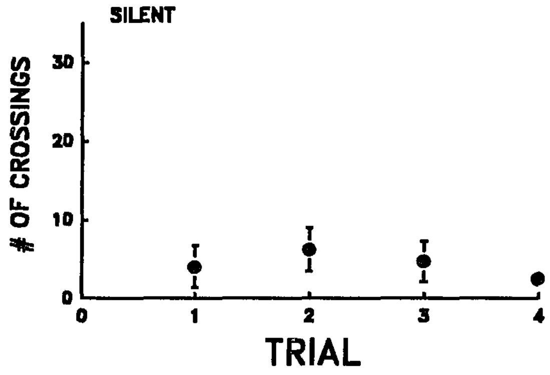
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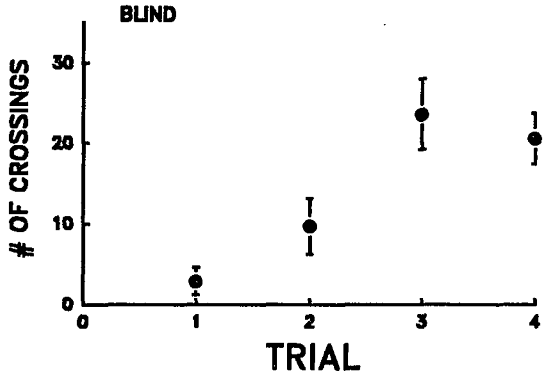
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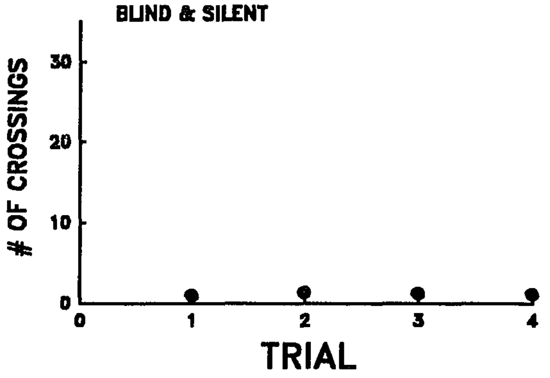
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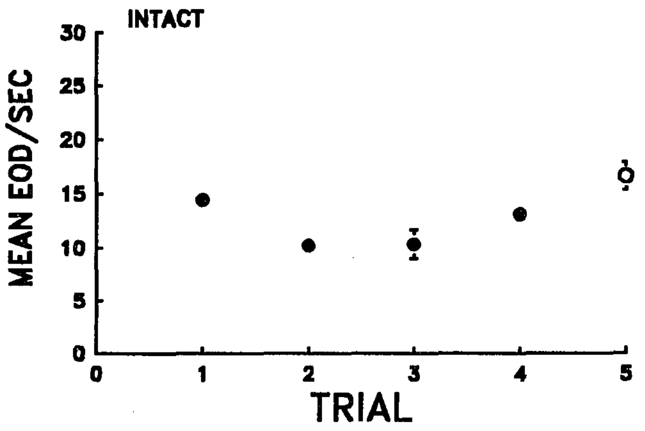
Figure 9. Mean (± SE) electric organ discharge (EOD) rate per trial of each treatment group while learning the aperture position. The rate per trial is the mean of the combined average EOD rates per trial of each fish in that treatment group. There was no difference in the discharge rate between treatment groups. Intact and sham-operated fish increased their discharge rate on trial 5.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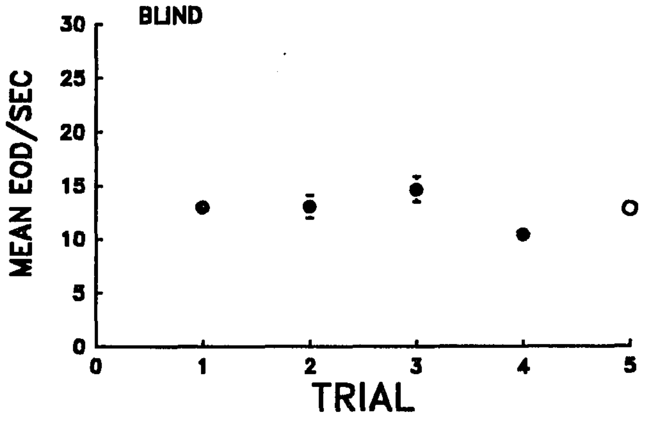
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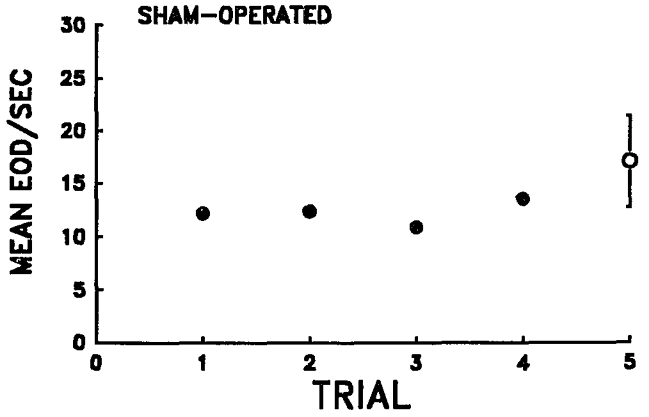
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