THE SENSITIVITY AND RESPONSE
OF WEAKLY ELECTRIC FISH
TO STATIC AND PULSED MAGNETIC FIELDS

June 1, 1970

I. INTRODUCTION.

The study of bioelectrogenesis, particularly in the various species of electric fish, has been of increasing scientific concern in recent years. This interest stems primarily from the potential usefulness of research in this area in contributing to our understanding of a number of fundamental and significant problems. By defining the electric fish's unique sensitivity to electric and magnetic fields, and how it codes and utilizes such sensory information in its detection and navigation behavior, current evidence is providing a more complete concept of such basic questions as migration and territoriality, and is leading toward the development of various bionic devices in the form of underwater sensors and power sources. In addition, knowledge of the effects of magnetic and electric fields on physiological and behavioral processes has assumed great importance in view of man's exposure to drastic changes in such stimuli during space travel.

Living things produce a changing electric field at and near the surface of their bodies; all fish, being sheathed in a conductive substance and living in a conductive medium, produce an electric field that may be detected at relatively great distances. However, there are certain fish which produce electric fields exceeding the norm by hundreds or thousands of degrees of magnitude. The electric eels of the Amazon can produce bursts in excess of 600 volts. Other electric fish, i.e., weakly electric fish, produce continuous fields measured only in millivolts, but by means of interpreting distortions in these fields are able to sense and navigate through their environment to a degree comparable to that of other species in which vision is used for these purposes. The weakly electric fish, having very poorly developed visual abilities, must depend on information acquired through their electric fields in order to survive.

The magnetic field is a form of energy to which all plants and animals are exposed. Its influence on living systems, however, is subtle and not well understood. One approach to studying the effects of magnetic fields upon behavior is through the use of an organism which produces an electric field and uses it as a detection and navigation mechanism. The electric fish is just such an organism, and this report will review a one-year study of two of these species (Sternarchus albifrons and S. leptorhynchus; see Figure 1) which has just been completed

In these fish, impulses are discharged from the tail and received by the head, which becomes positive in regard to the tail. This potential difference creates an electric field about the fish's body, permitting it to detect objects through distortions in the field. Several studies have shown that these fish can perceive a static (constant strength) magnetic field, but only when either the organism or the field is in motion, thus generating a current in the fish. It was thought that the fish was responding to the current generated in itself by the magnet. However, in these experiments the magnetic field was presented as a static field, and the sensitivity of the fish to a pulsed field presented at various frequencies, particularly the frequency at which the fish discharges its own electric field (500-1500 cps), was not investigated. Other investigators have shown dramatic increase in sensitivity to applied A.C. approximating the frequency of the fish's discharge. In addition, the strength of the field was not systematically varied in terms of the gauss level in the fish's proximity. Therefore, there are considerable gaps in our knowledge of the degree of sensitivity of the fish to magnetic fields at various frequencies and strengths. The present study was undertaken to clarify some of these problems regarding the perception of and response to a magnetic field which is systematically varied along several continua.

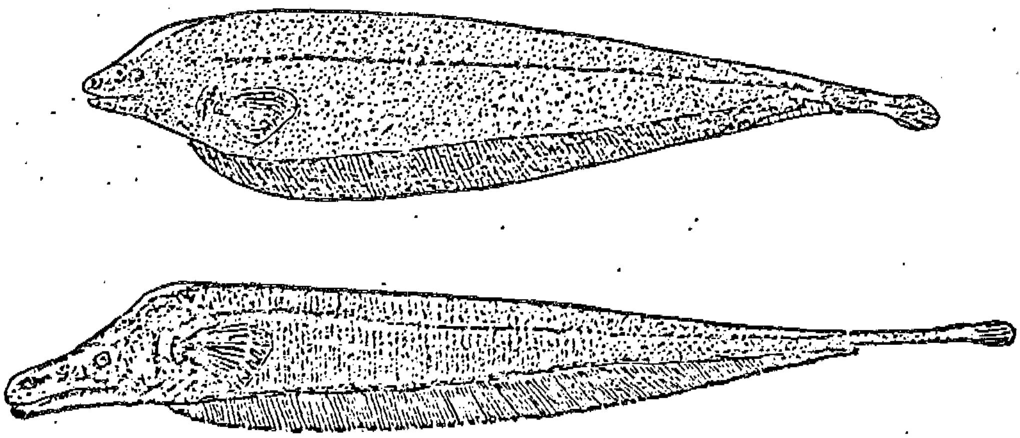

Figure 1. Sternarchus albifrons (top) and Sternarchus leptorhynchus (bottom)

II. BACKGROUND.

Comparatively little work has been done on the sensitivity of weakly electric fish to various types of electrical and magnetic fields, although the evidence that is available indicates that these fish have an extremely low threshold for such stimuli. Lissmann(1958) and Lissmann and Machin (1958), for example, have shown that Gymnarchus niloticus will perceive the movement of a magnet or an electrified insulator when either is moved outside its tank or aquarium.* A small bar magnet was held against the

*Szabo et al. (1969) write that the electroreptors respond to both the presence and movement of an object or field.

wall of the aquarium and moved in a vertical direction, with the result that a "single downward sweep produced a response in the fish if the movement was sufficiently rapid and the distance between the fish and the magnet sufficiently small. With the particular magnet used a response could be elicited at a velocity of about 3 m/sec when the fish was about 50 cm from the magnet" (Lissmann and Machin, p.451). When an electrostatic charge* was moved horizontally in front of the tank, the fish was seen to respond to a voltage of 60 kV when the distance from the fish was 50 cm and the charge was moved at 3 m/sec. The authors conclude that Gymnarchus is able to detect potential gradients of about 0.30 μV/cm in the surrounding water. Table 1 shows the remarkable sensitivity of this species as compared to other fish. It is apparent that the perceptive ability of Gymnarchus is of a different order

Table 1. The sensitivity of six species of fish to direct current. (After Lissmann and Machin, 1958.)

Species	Current density (μA./cm.^{2})
Phoxinus phoxinus (minnow)	10
Cyprinus carpio (carp)	60
C. auratus (goldfish)	16
Parasilurus asotus (catfish)	8
Gasterosteus aculeatus (stickleback)	110
Gymnarchus niloticus	2×10^{-5}

of magnitude than other fish. Since it can detect a direct current of about .15 microvolt per centimeter, an individual sense organ in Gymnarchus should be sensitive to a current change as small as .003 micromicroampere.

Lissmann (1958) has observed that Gymnotus carapo can be conditioned to feed in response to a stationary permanent magnet mounted outside its tank and to inhibit feeding responses when the magnet is absent. He notes that although there is no specifically relevant data, it would seem that this fish should be able to perceive a field of about 10 oersted when moving at a rate of 10 cm/sec.

In a subsequent paper by Machin and Lissmann (1960), it was shown that the receptors responding to small direct currents were also used in the fish's object detection and location. That is, "the sensitivity of the fish to externally applied currents gives information about the electric receptors for object location " (Machin and Lissmann, p.802).

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*A small aluminum cylinder on an insulated handle and charged from a Wimshurst machine was used.

A. Magnetic field effects.

The effects of various types of magnetic fields on living organisms has been a subject of increasing interest in recent years for both theoretical and practical reasons. "Basically, the magnetic field, being a form of energy, just as are light, heat and sound, impinges upon all living organisms whether plant or animal. The question as to its effect on living matter is what we are seeking to learn. Is it an active or passive process? How will an organism react to an environment that is devoid of a magnetic field? Further, what will happen if the field is altered or distorted?" (Caldwell and Russo, 1968, p.233).

Caldwell and Russo studied the effects of an A.C. magnetic field upon the behavior of the Italian honeybee (Apis mellifica), and found that the bee would respond to the magnetic energy field with a stereotyped nodal reaction, i.e., three of the four subjects would situate themselves and become rigidly fixated over one of the magnetic nodes when the magnet was on. Gottlieb and Caldwell (1967) investigated the magnetic field effects on the compass mechanism and activity level of the snail Helisoma duryi endiscus. Using a bar magnet with a weak field (1.5 gauss), they obtained significant effects on the activity level of the subjects.

Since astronauts have and will continue to be exposed to magnetic fields which are much less intense than the Earth's magnetic field while exploring the surfaces of neighboring celestial bodies, "the question arises as to whether the human body has during its evolution become dependent on the presence of the Earth's magnetic field for the maintenance of its normal functional integrity. Accordingly, it has become most important to ascertain whether a low-intensity magnetic field exposure could possibly lead to an impairment of health or performance of an individual" (Busby, 1967, p.7). However, there is also the possibility that astronauts could be exposed to intermittently high-intensity magnetic fields up to 1,000 gauss for varying periods during space travel. Beischer (1963, 1969) and Beischer et al. (1967) have studied the effects of both low- and high-intensity fields on man and animals. Their results show that man does not seem to be affected by a two-week exposure to 50-gamma fields; mice survive a one-hour exposure to 120,000 gauss; and in a low-intensity magnetic field, there is a significant gradual decrease of the scotopic flicker fusion threshold in man.

Agalides has recently completed a series of studies on weakly electric fish, including some work on their sensitivity to moving magnetic fields. Using Gymnarchus and Sternarchus as subjects, he observed that they responded to a permanent bar magnet of 930 gauss. The magnet was moved at 3 m/sec and was perceived by the fish at a distance of 120 cm. This was very close to the fish's sensitivity to static electric fields, and corresponds to a gradient of 3 emu, or $0.03\,\mu V/cm$.

B. Electrosensitivity

Granath et al. (1967) worked with Sternarchus albifrons in their effort to determine its sensitivity to imposed electric fields. To study the frequency response continuum, the authors used a conditioning problem in which both uniform and nonuniform alternating current (A.C.) fields were employed as signals for the subjects to leave a porous cylinder and swim to a vertical plastic tube for a food reward. After the conditioned response was established with high stimulus values, the signal was reduced to determine the threshold of the fish. The results indicated that Sternarchus is most sensitive at its own discharge frequency at room temperature, i.e., in the area of 1,000 cps, with a maximum sensitivity of 0.2 microvolts per cm. However, a secondary maximum was observed at the second harmonic of the discharge frequency.

Watanabe and Takeda (1963) employed the South American gymnotid, Eigenmania, in their study of the effects of externally applied electric current. Like Granath et al., they found that the effective stimulus was an alternating current presented at a frequency very close to that of the fish's own discharge. In this case, Eigenmania has a discharge rate of about 300 cps at 25°C. Their results showed that "when a sinusoidal (or a square pulse) electric signal with a frequency similar to that of the fish's own discharge is applied to the fish, the latter's discharge frequency changes as if to escape from the applied signal frequency. The effectiveness of the stimulus depends on the difference beween the two frequencies (ΔS); when ΔS is more than 10 cps the response is barely recognizable. The smaller ΔS, the more effective the stimulus, except when ΔS is very small, where the response again fails to occur" (Watanabe and Takeda, p.65)

Dewsbury (1966b) believes that stimuli* differ and interact in the kind and/or amount of change they induce in the discharge frequency of weakly electric fish. He observed several different species, but not Sternarchus albifrons, which does not appear to behave in this way. Dewsbury attempts to relate his data to a concept of arousal, wherein discharge frequency changes with arousal level. In another study (1966a), he confirmed the hypothesis that electric organ discharge frequency in gymnotids is higher in darkness than in light. This would normally be expected, although we have not found such evidence in S. albifrons.

The effect of temperature on discharge frequency is a particularly important problem in that the exact nature of this relationship must be known in order to establish baseline data for further study on the fish's discharge behavior. Gallon et al. (1967) and Enger and Szabo (1968) have found that the rate of discharge varies with temperature in mormyrids and

*For example, light-darkness, shock, aeration, metallic objects, and a buzzer (Dewsbury, 1966c).

gymnotids. Their results are summarized in Figures 2 and 3.

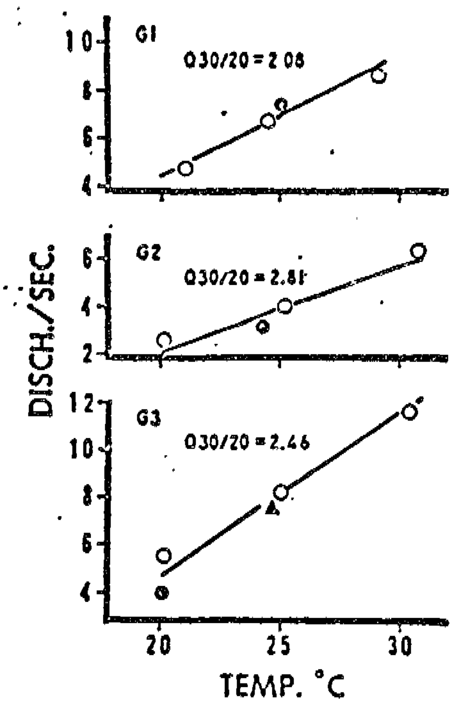


Figure 2. Discharge rate as a function of temperature. Open circles, ascending series; filled circles, return to lower temperature; triangle, second ascending measurement. (After Gallon et al., 1967.)

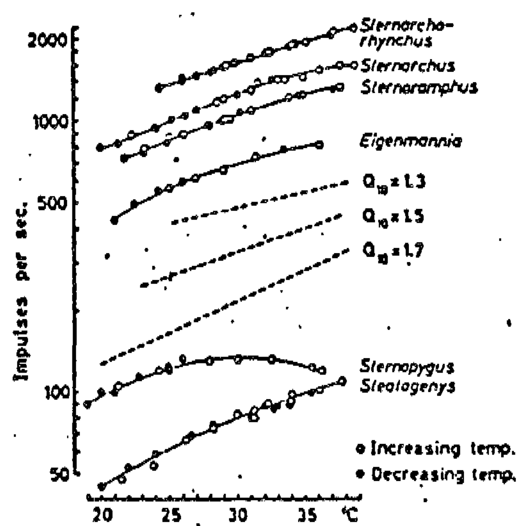


Figure 3. Relation between water temperature and discharge rate. Open circles, increasing temperatures; closed circles, decreasing temperatures; broken lines, Q_{10}- values for comparison. (After Enger and Szabo. 1968.)

Attempts have also been made to condition the discharge rate of mormyrids with both classical and operant methods. Mandriota et al. (1965) report that three species of *Mormyridae* would briefly increase their discharge frequency (conditioned response) in response to light (conditioned stimulus) following training trials in which light was paired with shock (unconditioned stimulus). Mandriota et al. (1968) later discovered that operant (avoidance) conditioning was also effective in these fish and, in fact, was more efficient than classical conditioning in that fewer shocks were required to establish the response.

III. CURRENT STUDY: THE SENSITIVITY AND RESPONSE OF *STERNARCHUS ALBIFRONS* TO STATIC AND PULSED MAGNETIC FIELDS.

A. Problems and hypotheses.

The primary hypotheses of this study were concerned with the problem of determining whether weakly electric fish are sensitive to magnetic fields and, if so, how this sensitivity might vary as the field is changed from a static to an alternating and to a pulsed one, as the frequency of the field is increased or decreased in relation to the normal discharge frequency of the subject, and as the strength of the field is varied. A secondary problem concerned with effects of various drugs on the electrical activity of the fish was also investigated. However, before the data could be collected, it was necessary to find a source from which weakly electric fish could be obtained, develop life-support systems for the subjects, and design and construct the required equipment and apparatus.

1. Subjects.

A total of 18 fish were purchased, consisting of 9 *Sternarchus albifrons*, 6 *S. leptorhynchus*, and 3 weakly electric fish of an unknown species. Most of the specimens were bought from the Cappet Corporation in Alexandria, Virginia, and a few from local pet shops. Four of the fish, all *S. albifrons*, remained healthy during the period of the study, and were the only ones used in the final experiments. Their size is shown in Table 2. With few exceptions, the others died within one week of purchase.

Table 2. Size of the four experimental *S. albifrons*.

Subject	Length
Fish #1	18 cm
Fish #2	21 cm
Fish #3	14 cm
Fish #4	11 cm

The subjects were kept in individual tanks of either 14 or 20 liter capacity. The water was aerated with conventional air pumps working through charcoal and glass wool filters. The temperature was maintained at about 26.8°C and the pH at 6.7 to 6.9. Food consisted of either live or dehydrated brine shrimp. The fish were fed 2 - 3 times a day, and once a week an antibacterial agent was added to the water to suppress the growth of bacteria.

2. Equipment and apparatus.

A plastic Y maze (Figure 4) was constructed for tests with the the static or steady magnetic field. Its three arms were joined at angles of 120°, and the maze itself made of 0.040" sheet styrene fastened with styrene solvent. The water in the maze was drawn from a continuously aerated and filtered source with a pH of 6.8 and a temperature of 26.8°C. It was exchanged every ½ hour, within which time the temperature drop was approximately 0.2°C. However, because of its inadequate size, this maze proved unsatisfactory, i.e., the larger subjects could not be used in it. In addition, with a magnetic field of 8-10 gauss and the magnet centers at the distal end of one test arm, a minimum field of 2 gauss was present at the farthest point in the starting chamber. The field was 4 gauss in the area of the fish's head when the subject was released from the starting chamber. These problems with the Y maze may have contributed to the failure to find any response by the fish to the magnetic field in the initial experiments.

A larger T maze (Figure 5) was then designed and constructed in an attempt to demonstrate a more positive response to one arm at the choice point with the magnetic field as a cue. In the Y maze, the subject appeared to swim into the arm on the side of the starting chamber that the fish was closest to when the door to the starting area was opened. The length and depth of the T-maze arms were much greater than those of the Y maze, permitting the use of the largest specimens. This maze was also provided with continuous filtration and heating. It had a 10-liter capacity, with an auxiliary 16-liter and 50-watt heater. An air lift and siphon were arranged so that heated, filtered water was slowly and continuously fed into the leg of the T from the tank. A return siphon ran from the distal end of each arm to the auxiliary tank. Temperature in the maze was held at 26.8°C by maintaining the temperature in the external tank at 32.5°C. The tank and siphons were wrapped with paper lagging and jacketed with aluminum foil to achieve and hold the desired temperature. The maze itself was made of ¼" sheet clear acrylic plastic, joined with an appropriate solvent. The material proved to be light and strong, and permitted good observation of the fish.

The magnets were made by winding 5 pounds of #12 copper magnet wire on each of 2 aluminum tins of 23 cm diameter. When in use, the

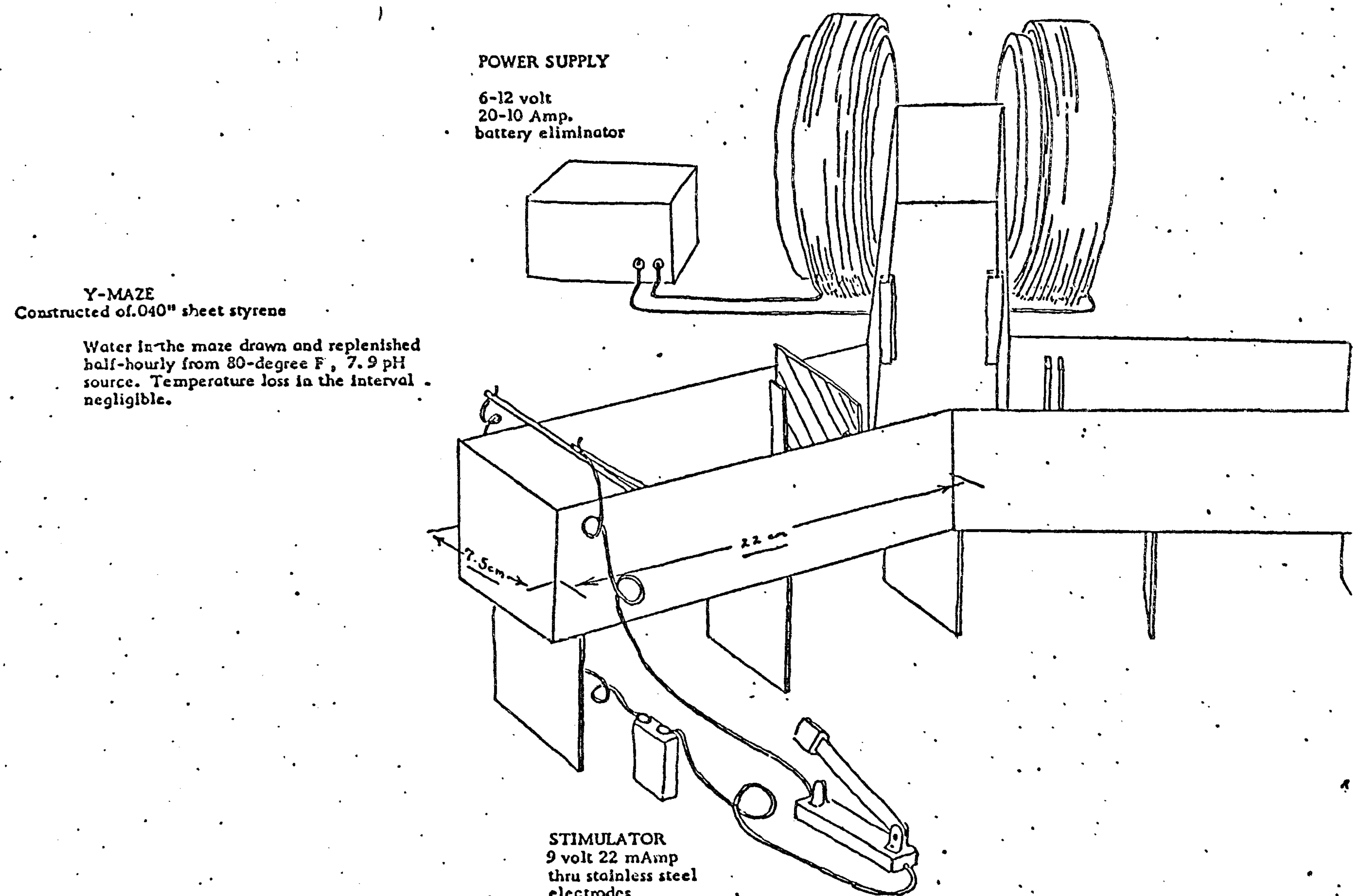


Figure 4. The plastic Y maze shown with the equipment (magnets, power supply and stimulator) used in tests of the static magnetic field.

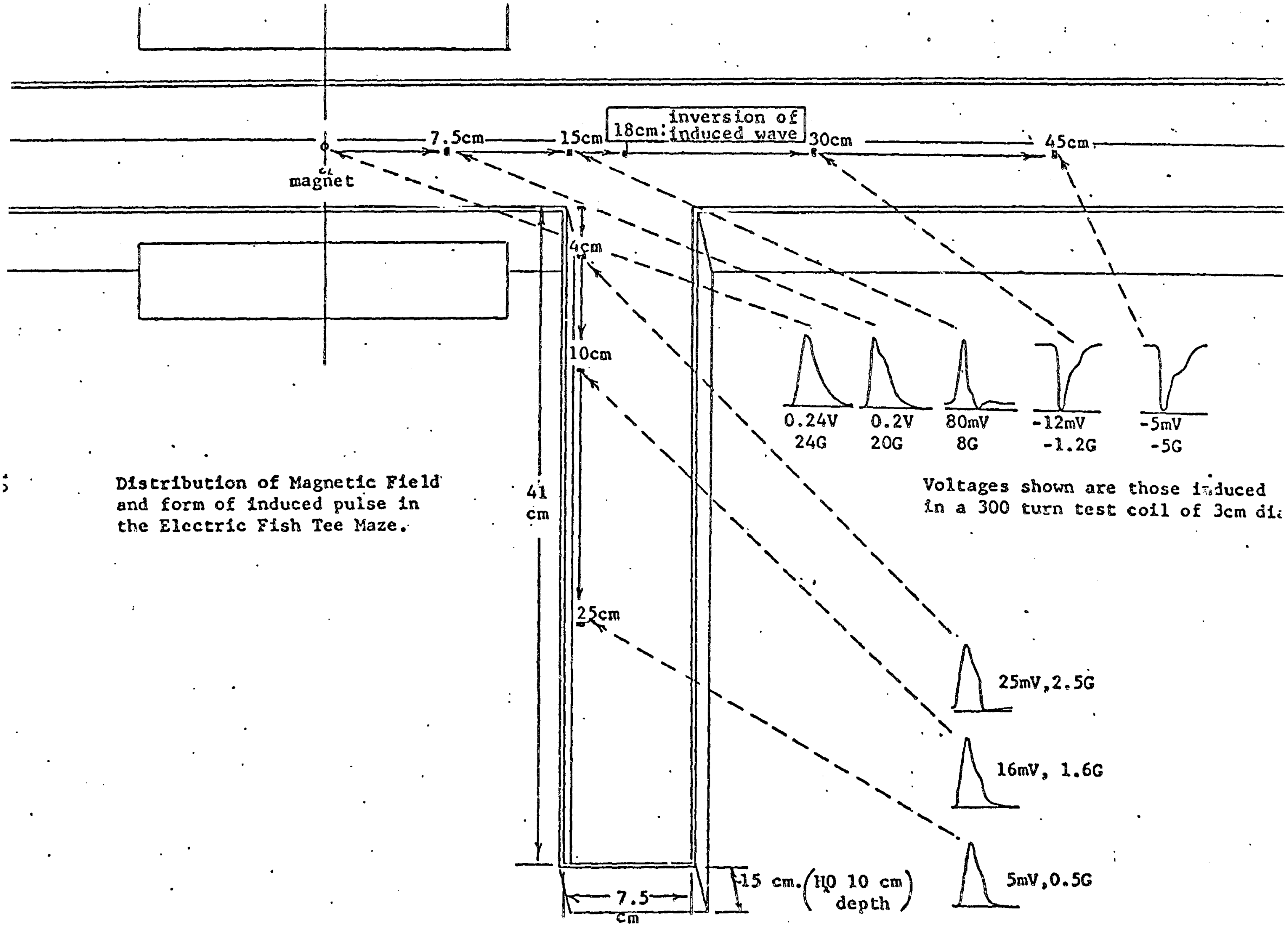


Figure 5. The T maze and the distribution of the magnetic field in it.

2 coils were wired in series and placed on either side of the maze arm, 13 cm apart.

The discharge patterns of the fish were recorded by means of probes of pure carbon rod. Above the water level, these probes were shielded in thickwall aluminum tubing. Shielded cable was used to connect the probes with the oscilloscope input. The oscilloscope was a TEKTRONIX 502 A, and the built-in preamp was found to be sufficient to record these fish at distances over 50 cm, which exceeded our needs for these experiments. In recording, the probe shields, the cable shields, and the scope ground were all connected to a double wrap of heavy aluminum foil around the chamber containing the fish. With this arrangement the "noise" level on the system was held to 0.3 mV, which was acceptable.

The electrical equipment which surrounded the experimental apparatus was a source of an electrical noise electromotive force (EMF) which drove current through the input resistor, R_{input}, of the measuring device (in this case an oscilloscope). The noise power dissipated in such an input resistor is a constant, P_n, so the noise voltage developed at the input of the scope is

$$V_n = \sqrt{P_n R_{input}} \qquad (1)$$

and therefore by reducing the input impedance, R_{input}, noise voltage is reduced. The network shown in Figure 6 reduced the input impedance of the oscilloscope from its usual value of 1 Megohm to 20 kilo-ohm and allowed the input impedances for the two separate beams to be balanced in order to eliminate any assymmetries in the external network. The noise improvement achieved by this method is a factor of 7; the measurements were not affected since the impedance of the source electrodes and tank was about 500 ohms. As long as the source impedance is low with respect to the input impedance of the measuring device the source is not affected by the measurements.

The operation of the device is straightforward. After all of the shields have been connected, the 40K potentiometer is adjusted until the noise on both beams of the oscilloscope is minimized. This is the best operating point.

The distribution and strength of the magnetic field were determined with a test coil of 300 turns, 15 mm in diameter. The induced electromotive force (EMF) was converted into a field strength measurement in gauss by application of Faraday's law

$$EMF = \frac{d\Phi}{dt} \qquad (2)$$

where Φ is the magnetic flux through the circuit. Equation (2) says that the EMF induced in a circuit is equal to the rate of change of the magnetic flux through the circuit. The magnetic flux is

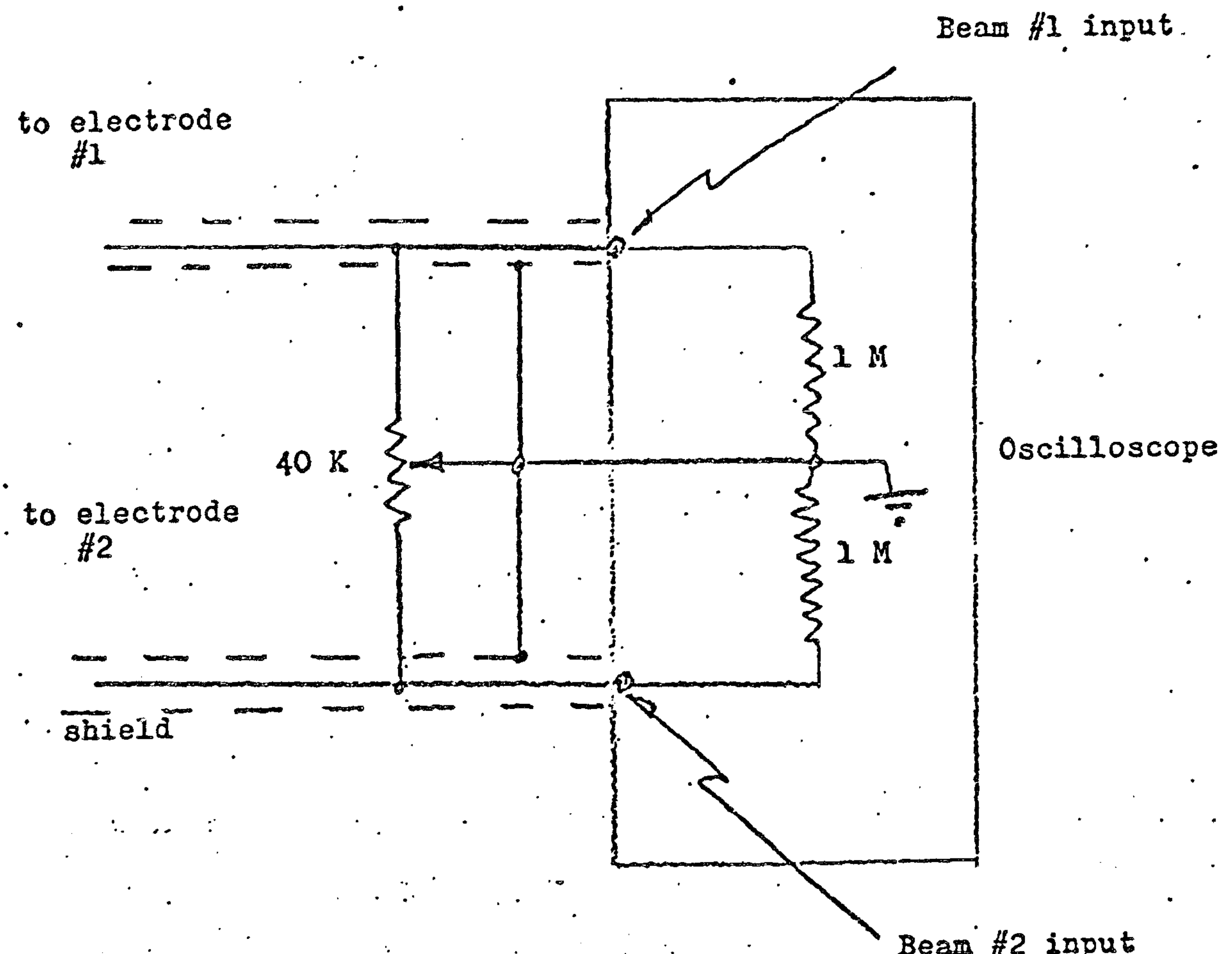


Figure 6. Input impedence reduction network.

been added. By varying the voltage output of the power supply, the voltage output at the signal generator, and by careful adjustment of a variable bias-resistor at the signal input to the transistor "switch", a pulsed field of the desired characteristics was achieved.

The circuit schematic is shown in Figure 7. The circuit consists of four npn transistors, three of which (#2N3055) switch all of the current through the magnet, and one (#2N3054) receives the signal from the signal generator (Lafayette #99-5014) and drives the three power transistors. The resistors in the circuit are bias resistors and the capacitors tend to round off the switching pulses and prevent oscillations.

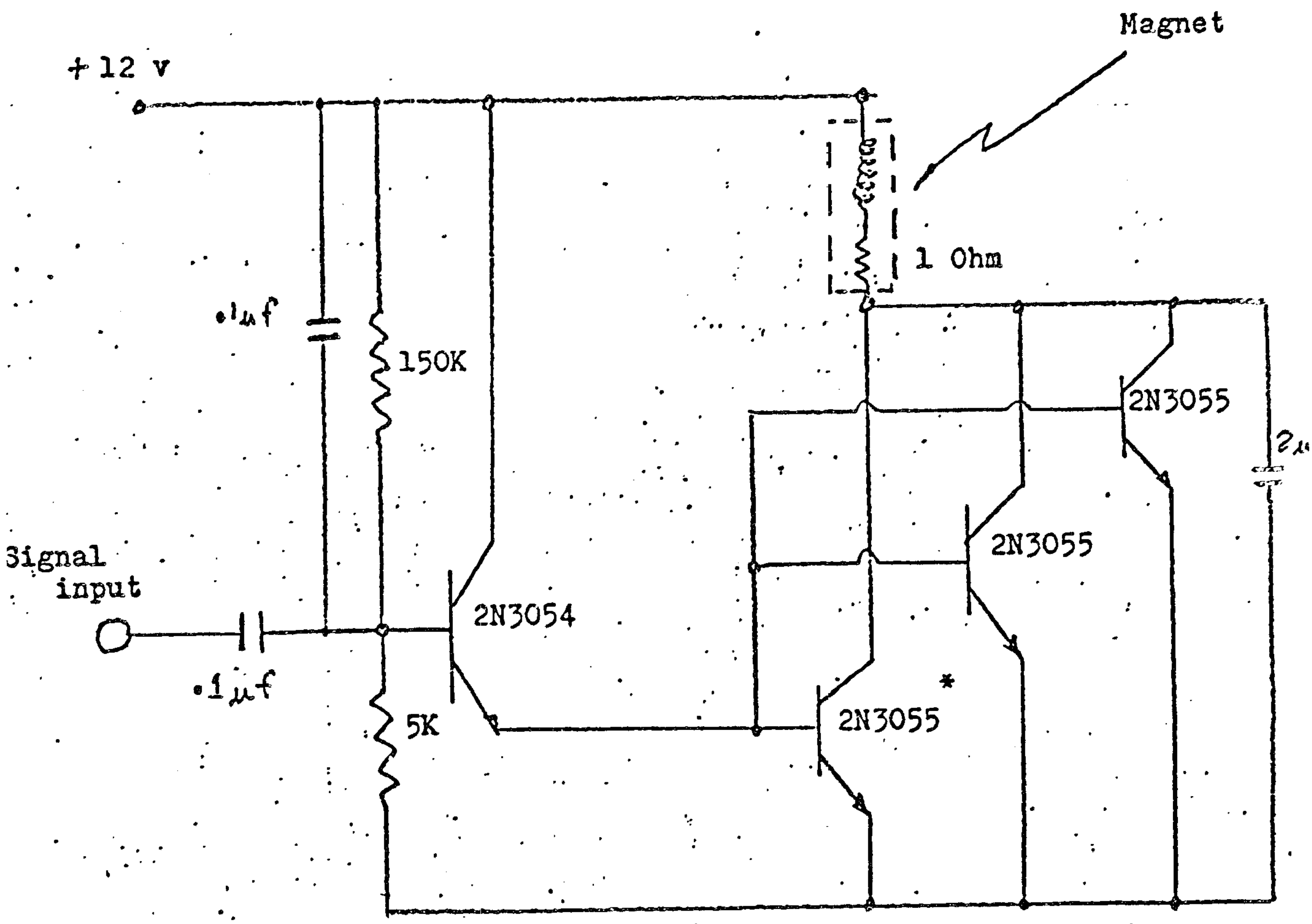
When the sinusoidal signal from the signal generator goes positive the transistor switch turns on and the current flows from the 12V power supply through the magnet. When the signal reaches the negative portion of its cycle, the switch turns off and current is prevented from flowing. By putting in a 1000 Hz signal we therefore put 1000 pulses per second through the magnet with a maximum of 12 amps peak current. The actual current through the magnet is considerably less since the inductance increases the impedance.

The transistors dissipate a great deal of power and must be placed on heat sinks in order to operate properly and to prevent thermal failure.

B. Experiment 1: Temperature-frequency baseline data.

We had observed that the discharge frequency of each fish at a given temperature was different from that of the other fish. Agalides reports that temperature-related frequency changes in S. albifrons are complex, but are on the order of $\Delta 50$ cps/ΔC^{o}, which our work confirmed. Since the current experiments required an accurate prediction of discharge frequency, a study was made of the temperature-frequency relationship in the fish in order to provide baseline data.

Each fish was monitored for frequency at 10-12 points in the 21 to 31°C range and over a period of 6 weeks. The test chamber was a plastic box 25 x 45 x 20 cm, double wrapped on the exterior with heavy aluminum foil. Three liters of water were drawn from the test fish's home tank and placed in the box. Temperature variations were achieved with a heat exchanger made from a plastic pitcher and a length of plastic tubing. The tubing was coiled in the pitcher, which was filled with either hot or cold water. Water from the test apparatus was forced through the tubing at such a rate as to change its temperature 1°C/15 min. When the desired change was achieved, as determined by an electric thermometer, 2 minutes were allowed to elapse, and then the frequency of the test fish was recorded. Before recording, the sensing thermistor of the thermometer was removed from the apparatus because it introduced extraneous signals into the water and, thus, into the oscilloscope used for frequency determinations. Fifteen-minute observation periods indicated that frequency always stabilized in less than 2 minutes.



*Note: The 2N3055's may be replaced by the more costly SK3027

Figure 7. Schematic of magnet switching circuit.

A series of observations with the fish maintained in close fitting rigid styrene tubes showed no variations in either the amplitude or the phase relationships of the discharge accompanying the change in frequency. These results are not in keeping with those of Agalides, who reports amplitude changes.

Within the limits of accuracy of our test situation, we found these fish to have straight-line plots of temperature-frequency response with a range of ±15 to ±50 cps at any given point, depending on the fish. Whether this variation resulted from individual differences or variability in the method is not known, but the experimenters lean toward the latter interpretation. Our laboratory was by no means temperature controlled, and the fish may have been responding to changes in temperature over the entire apparatus, which was not apparent in the small area actually sampled for temperature. The results of this experiment are shown in Figure 8.

C. Experiment 2: Response to unpulsed magnetic fields in the Y maze.

1. Environmental preference using a static magnetic field.

The equilateral Y maze was initially used in an attempt to demonstrate a sensitivity to a relatively strong static magnetic field in the small specimens of S: albifrons and S. leptorhynchus. It was thought that these fish, with electric fields having a maximum potential as observed in our lab of only 6.2 m volt, and an ability to detect one another by means of these fields at distances exceeding 1 meter, would respond (a) to changes in this field induced by a large magnet, or (b) to currents induced in their bodies by such a magnet. However, no gross responses from the fish were observed in either swimming behavior or in electrical discharge pattern when the magnetic coils were arranged so that a magnetic field calculated at 9- 10 gauss was centered in a 40 x 20 x 30 cm aquarium in which a fish had been previously placed. Consequently the Y maze was used for further experimentation.

The dimensions of this maze allowed relatively low levels of the magnetic field in the first 5 cm of the experimental arm with intensity increasing to a maximum of 9 - 10 gauss at 11.5 cm. The overall dimensions of the apparatus allowed minimal swimming room for the four smallest fish: two albifrons and two leptorhynchus 15 - 15.5 cm in length.

The current induced over a short distance in the environment by a standard 9-volt transistor radio battery proved to be a noxious stimulus, and electrodes were installed at the starting point in the event that subjects did not move rapidly to the choice point.

The subject was placed in the starting arm and a short period allowed to elapse. Both experimental species were passive fish and

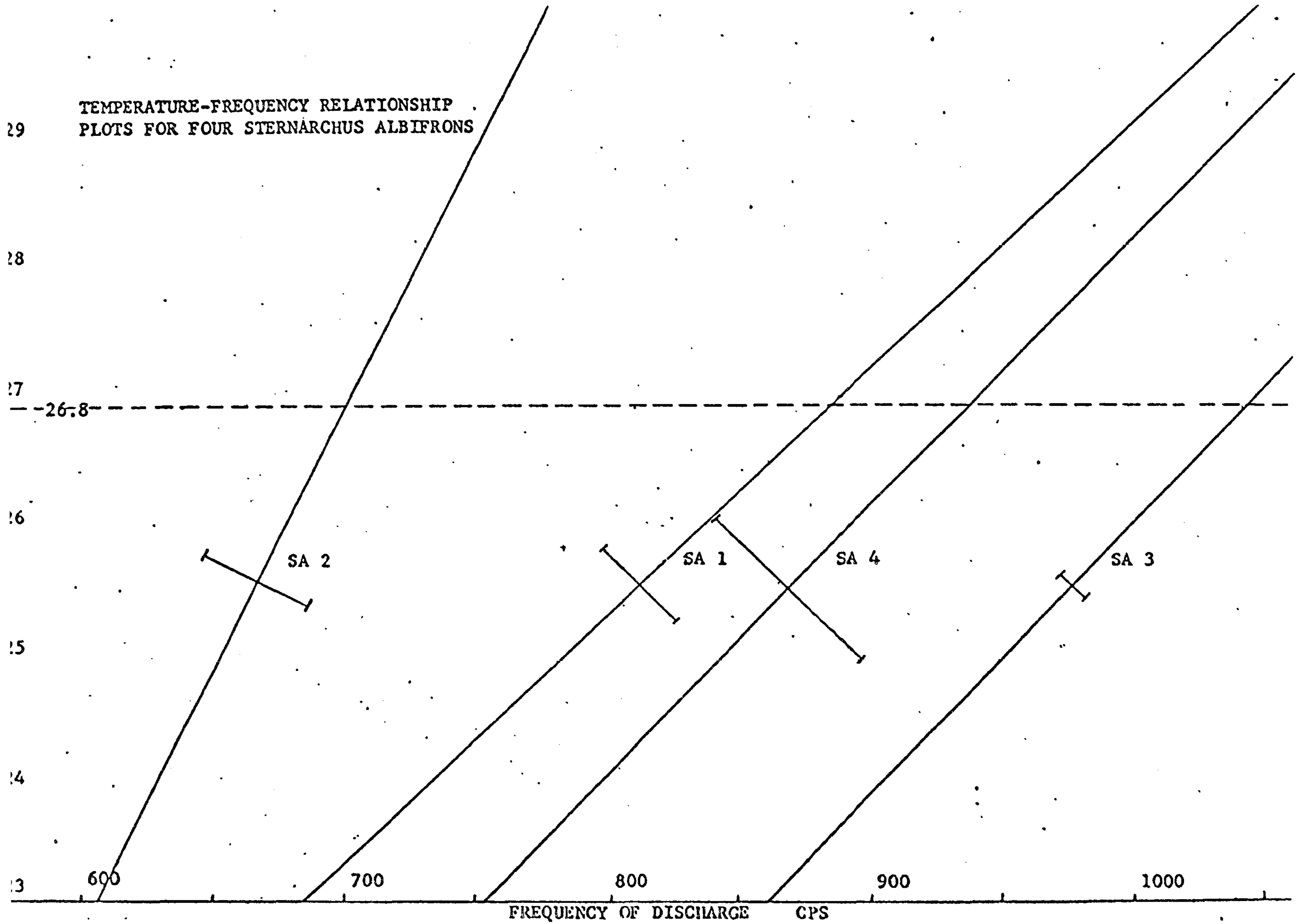


Figure 8. The discharge frequency-temperature relationship.

short accomodation periods of about one minute were sufficient before the door to the choice point was opened. The subject was allowed 2 seconds to move to the choice point. If this had not occurred at 2 seconds, the experimentor made contact in the stimulator circuit. Out of 120 trials, this was necessary only about 10% of the time, largely with one particular fish. Stimulation once initiated was maintained through the trial. The fish is not greatly affected, if at all, except in the area directly between the electrodes, but in order to control the possible effects of other variables, this technique was used.

The magnet was kept at the left arm, and was left on for 10 trials, off for 10 trials, and then on for a final 10. After a trial the fish was allowed to return to the starting chamber by the process of blocking the unoccupied choice arm, waiting till the fish had moved from the other arm, blocking it, and then blocking the starting chamber as the fish returned to it during normal exploratory behavior. These fish are nocturnal and exhibit continuous searching during the dark hours. The hours preceding and during experimental sessions were dark with only low level red illumination. The interval between trials was thus variable, but the fish was kept in an unexcited state. Elapsed time for 30 trials was about 30 minutes.

The results of this series of trials (Table 3) indicated no significant preference or aversion for the static magnetic field, although the subjects did tend to turn left in the maze. The mean percentage of left turns with the magnet off was 52%, and with the magnet on 54.3%.

Table 3. Preference trials in the Y maze with the static magnetic field.

Choices to the left
(Magnet on the left arm)

Fish	Magnet on 10 trials	Magnet off 10 trials	Magnet on 10 trials
S.A.3[1]	30%	50%	60%
S.A.4	40%	50%	40% (magnet off)
S.L.2	50%	60%	70%
S.L.3[2]	70%	60%	60%

[1]This fish required stimulation on the 1st trial.
[2]This fish required stimulation 10 times (3,4,3 distribution)

2. Conditioned response to the static magnetic field.

In a further attempt to obtain some indication that S. albifrons is sensitive to a non-pulsed magnetic field, a conditioning technique was used in which the presence of the field (conditioned stimulus) was paired with electric shock (unconditioned stimulus).

The S was selected on the basis of size, i.e., the most suitably sized fish for the experimental chamber, which consisted of one arm of the plastic water-filled Y maze. Electric shock was administered from a 9-volt battery through electrodes fastened to the walls of the chamber. The two magnets were placed on either side of the arm and activated by an 8-volt, 9-amp power source.

When the fish was placed in the chamber, the magnetic field (9 - 10 gauss) was turned on, and ½ second later, the electric shock was administered for a period of one second, at which point both stimuli were turned off. The S responded in a characteristic manner to the shock with a "startle" reaction (unconditioned response). It was hoped that after a sufficient number of trials the S would respond (conditioned response) in this way to the magnetic field alone, or, when both stimuli were used, would anticipate the presentation of shock by responding to the field in the initial ½-second interval. However, after four series of 25 trials each, giving a total of 100 trials, the S failed to show any response to the magnetic field. Consequently, there was no indication that the fish was able to perceive the non-pulsed magnetic field.

3. Conditioning with the magnets at reduced intensities.

S. albifrons #3 was confined to one arm of the Y maze. Two electrodes were fixed to the sides of this arm, and the magnets placed on either side. In contrast to the first experiment in this series, the magnets received only 4 volts and 4.8 amps from the power supply, producing a magnetic field of considerably less intensity (3½ gauss) than that used previously. In the first experiment, the fish failed to respond to the magnetic field, i.e., it gave no evidence of sensing the field at full strength, and it was decided to attempt another test with the field at half strength on the possibility that the original was too strong, thereby interfering with the fish's afferent processes. With the fish confined to one arm of the maze, the magnetic field was turned on for a period of two seconds, and after the first second, electric shock (9 volts, $200 \mu A/cm^2$) was administered to the subject for one second. At the end of two seconds, both the field and shock were turned off. As expected, the fish responded to the shock (unconditioned stimulus) with a "startle" movement (unconditioned response), but after 50 trials, when the field (conditioned stimulus) was used by itself, there was no anticipatory conditioned response. It appears that the fish did not sense the magnetic field as presented.

A second series of 50 trials were then run with S. albifrons #4 with the magnetic field power source at 2 volts and 1.8 amps. The results, however, continued to be negative. But over the course of the trials, both fish showed some habituation to the electric shock, which had been reduced with a recalibration of the variable resistor to $100 \mu A/cm^2$ at 9v for the second set of trials.

D. Experiment 3: Drug study.

In contrast to various reports in the literature on other gymnotid fish, no stimuli to which Sternarchus would normally be exposed were found to affect their discharge frequency. Such things as noise, physical manipulation, light, dark, feeding, starvation and illness failed to change the frequency of the fish in the current study. As we have seen, frequency changes with temperature in a highly predictable manner, and Watanabe and Takeda (1963) demonstrated a response to applied AC current. They found that AC at the fish's own frequency caused the fish to alter his own frequency in response. The greatest relative changes occurred when the applied current was closest to the fish's own frequency.

In an effort to determine the degree of stability and control the fish is able to maintain over its discharge frequency, a study of the effects of various drugs on their discharge patterns was undertaken. Two depressants, Nembutal (sodium pentobarbital) and Pontocaine (tetracaine hydrochloride), and L-dopa (levodopa) were tested.

Nembutal at 750 mg/liter anesthetized the fish with no effect on the amplitude or frequency of their discharge. The L-dopa effects are discussed separately; they did not show a direct effect on frequency. Pontocaine, however, modified the fish's discharge frequency. At a concentration of 3 mg in 500 ml water, the discharge rate dropped 140 cps. Twenty minutes after a final total dose of 1.12 gms/500 ml, the discharge was 375 cps below the expected level. The fish rested on its side and was unresponsive to stimuli. At this time, the amplitude and phase relationships of the discharge were unaltered. The results are summarized in Table 4.

Table 4. The effects of Pontocaine on discharge frequency.

Time	Dose	Temp.	Drugged Frequency	Normal Frequency	Remarks
09:25	0.375gm	27.5		980 ± 30	
09:30		27.5	839		
09:37	0.375gm				
09:43		27.35	787	965 ± 30	
09:45	0.375gm				
09:51					
09:56		27.2	649	955 ± 30	
10:02					200 ml water replaced with fresh, fish lethargic
10:08		27.1	575	950 ± 30	
10:11					fish lying still

In view of the considerable interest in the neurotropic drug levodopa (L-dopa), and because the experimental techniques developed in the current study are capable of providing direct telemetric evidence of nervous system functions, it was decided to test L-dopa on selected fish in order to determine its effects on their electrical discharge patterns and behavior.

The first subject was S.A.#4, who received the drug for 27 days. Long exposure to relatively large doses is necessary to produce behavioral effects in other species. A technique of repeated injections as one way of achieving this was ruled out as impractical; therefore, a method for dissolving L-dopa into the aquarium water was worked out. Data provided by the manufacturer of the drug (Hoffmann-LaRoche) indicated that L-dopa is not very soluble in water; approximately 0.4% at 80°F. An air-lift was arranged to bubble aquarium water from the 20 liter home tank at a very slow rate through a chamber containing the drug and lined with filter paper. The charcoal was removed from the tank's filter. Every day, weekends excluded, 100 mg of the drug on fresh filter paper was placed in the dispenser. We found that L-dopa, under these conditions, rapidly combined with other substances present to form a heavy, dark, flocculent precipitate, which clogged the tank filter and the filter paper in the dispenser. The principal change was a conversion of the dopamine to melanin, which was later prevented by the addition of 50 mg of ascorbic acid every time L-dopa was added. S.A.#3 also received the ascorbic as a control.

No unusual behavior or alteration in the form or amplitude of the electrical discharge of S.A.#4 were noted for 14 days. Then an increasing disorientation, reduced ability to find food, and abnormal discharge frequencies were noted. On the 21st day of drug experimentation a thorough series of temperature-frequency studies was performed in the previously described manner. These revealed that the slope of the temperature-frequency plot was unchanged, but whereas a variability of $\pm$ 50 cps had been previously noted, variability was now found to be $\pm$ 150 cps as tested over a period of 3 consecutive days. The drug was stopped at the end of this time, the water in the tank changed, and charcoal filtration resumed. Four days after this, the temperature response was still quite erratic. The next close evaluation came 50 days after cessation of the drug. Temperature-frequency response at this time had returned to the pre-drug parameters.

The control, receiving ascorbic acid alone, showed no such effects.

S.A.#2 was given L-dopa and ascorbic acid over 47 days. The dispenser in this case was a plastic funnel suspended with the narrow end of the cone submerged; discs of filter paper, folded in half twice and opened to form a cone lined the funnel. Fifty mg each of dopa and ascorbic acid were placed into the cone and were dispersed by simple diffusion over a period of 2 days. This was a more reliable, less troublesome method of dispensing the drug than that used earlier. In this case, the tank filtration was left intact, but the air flow to the bubbler was reduced, lessening the water flow through the charcoal. We assumed that with an undissolved supply of the drug at hand, an equilibrium would be achieved, and the amount of drug in the water would be constant despite uptake by the fish and/or the charcoal.

Several tests were tried, removing the fish through 2 changes of distilled water which had been aereated and brought to the proper condition with reagent grade chemicals, to test for metabolized dopamine with ferric chloride. However, there were no differences demonstrated in the color or quantity of precipitate between experimental and control fish.

S.A.#2, during and after 47 days on the drug, showed no altered behavior and no change in his electric field.

The drug studies were terminated at this point. The exact cause of S.A.#4's reactions are not definitely known. Because of his small size, the drug may have had more effect on him than on S.A.#2. He may have suffered an illness, or been affected by a toxic buildup of some substance or substances due to a lack of filtration in his tank for 27 days. Another possibility is that the operating filter in S.A.#2's tank may have reduced the concentration of L-dopa below an effective level.

E. Experiment 4: Response to AC and pulsed magnetic fields in the T maze.

1. Conditioning of the sixty-cycle field.

The acrylic plastic T maze was prepared and the apparatus suitably modified to initially produce an alternating magnetic field and later a pulsed, but unidirectional field. A new line of investigation was then undertaken. We were now able to change the intensity of the magnetic field over a considerable range from 0 to over 50 gauss with a simple adjustment of a variable AC ("Variac") transformer, or 0 - 20 gauss with the DC power source. The AC field was pulsed at the 60-cycle commercial frequency; the previously described circuit allowed the DC field to be pulsed from 0 - 1500 cps with no directional change in the field. The changes in frequency and intensity could be made concurrently, although the complete range of intensities could not be achieved at every frequency.

The first trials were run with a 60 cps AC magnetic field at 6 intensity levels (see Table 5). S.A.#3 was placed in the T maze, with the two magnets encircling one arm. The intensity of the magnetic field in that arm was varied by adjusting the voltage on the Variac. Frequency was maintained at a constant 60 cps. At 41 gauss (50 volts), the fish was given 250 trials (on alternate trials, the field was turned on and off). When the field was on, each time the subject entered the experimental arm of the maze it was shocked briefly. With the field off, the S could enter and swim in the arm freely. It was hoped that in this way, i.e., by conditioning the S to avoid the field as an aversive stimulus by pairing it with shock, evidence could be obtained as to whether the fish was sensitive to the field. If conditioning was achieved, then it would be definite that the S could perceive magnetic stimuli, and its threshold for such stimuli determined by lowering the intensity of the field. The first tests (250 trials) were made at 41 gauss. After 100 trials at this level, the fish never entered the arm with the field on, but swam into it when the field was off. Twenty trials were then attempted at 34, 36, 18, 9 and 1 gauss, with similar positive results at the three higher settings. However, at 9 and 1 gauss, behavior became inconsistent, with the S responding correctly about half the time.

Table 5. Sixty-cps trials at intensities from 1 to 41 gauss.

Intensity	No. of trials	Results
41 gauss	250	Positive response
34 gauss	20	Positive response
26 gauss	20	Positive response
18 gauss	20	Positive response
9 gauss	20	Partially positive response
1 gauss	20	Partially positive response

2. Conditioning of variable-frequency fields.

In each series of these trials, the intensity of the magnetic field was held constant while frequency was varied by changes of 100 cps from 500 cps below the fish's (S.A.#3) own frequency to 500 cps above it (Table 6). A total of 1100 trials were run, 100 at each frequency. The method used was similar to that of the previous experiment. That is, the field was turned on and off on alternate trials during each series of 100, and each time the fish went into the arm of the maze with the field on it was shocked. When the field was off, no shock was used. The results in each case were negative; the fish did not learn to respond to the field as a noxious stimulus as we had expected on the basis of previous results, but tended to enter and stay in the field regardless of the shock. Thus, the field seemed to have some positive reinforcement value to the fish. This surprising outcome was checked in another series of 300 trials with S.A.#3, 100 at his own frequency (1040 cps) and 100 each at 540 and 1540 cps. In these tests, however, the intensity of the field was increased to 15 gauss. The results were the same; the S would not avoid the field when paired with shock, but tended to approach under all conditions. This interesting development led to the final and most important experiment in the present study, wherein the preference of the S's for the magnetic field was more fully explored.

Table 6. Conditioning with frequencies from 540 - 1540 cps at 5 gauss.

Frequency (cps)	No. of trials	Results
1540	100	negative
1440	100	negative
1340	100	negative
1240	100	negative
1140	100	negative
1040 (S's own frequency)	100	negative
940	100	negative
840	100	negative
740	100	negative
640	100	negative
540	100	negative

3. Approach response to pulsed fields with frequency and intensity varied.

Up until this point, the evidence was somewhat contradictory and it was not sufficiently clear that the subjects were sensitive and responsive to magnetic fields. Therefore, on the basis of the positive evidence in the last experiment, it was decided to conduct a more comprehensive study of the fish's preference for or approach tendency to the magnetic field.

The T maze was used as before, with the magnets positioned on either side of one arm (Figure 5). Two series of trials were run, one at 10 gauss and the other at 20 gauss. Each of the four specimens of <u>Sternarchus albifrons</u> was put in the maze, and the frequency was adjusted to the subject's own discharge rate, which, in these fish, was 700, 885, 935, and 1,040 cps respectively. In subsequent trials the frequency was raised and lowered 100 and 200 cps above and below each subject's normal discharge rate at 26.8°C. Thus, the experimental design involved changes along two continua, frequency and intensity (Table 7). Under each condition, the fish was placed into the maze, and the number of times it entered the experimental area in the arm between the magnetic coils during a period of 15 minutes with the field off and 15 minutes with the field on was recorded on a counter. Each fish was tested for its tendency to approach the field at five frequency levels ranging from 200 cps below to 200 cps above its own frequency and at two intensity levels. A summary of the results are presented in Tables 8 and 9 and illustrated in Figure 9.

Table 7. Experimental conditions for the approach-response experiment with a pulsed magnetic field.

		10 gauss	20 gauss
+200 cps	S.A.1:1085 S.A.2:900 S.A.3:1240 S.A.4:1135	15 min on, 15 min off	15 min on, 15 min off
+100 cps	S.A.1:985 S.A.2:800 S.A.3:1140 S.A.4:1035		
normal rate	S.A.1:885 S.A.2:700 S.A.3:1040 S.A.4:935		
-100 cps	S.A.1:785 S.A.2:600 S.A.3:940 S.A.4:835		
-200 cps	S.A.1:685 S.A.2:500 S.A.3:840 S.A.4:735		

Table 8. Summary of results for the approach experiment, showing the number of times the subjects entered the experimental area with the field on and off.

		S.A.1		S.A.2		S.A.3		S.A.4		
		10 gauss	20 gauss	10 gauss	20 gauss	10 gauss	20 gauss	10 gauss	20 gauss	total
+200cps	on	36	41	69	56	92	87	27	81	489
	off	44	44	35	49	50	54	6	45	327
+100cps	on	34	44	49	36	59	74	53	78	427
	off	21	17	33	29	42	42	53	52	289
norm. freq.	on	38	38	34	43	27	14	19	23	236
	off	36	28	26	21	29	17	11	16	184
-100cps	on	38	46	44	61	52	50	60	59	410
	off	25	34	28	32	46	27	39	39	270
-200cps	on	33	57	52	72	45	49	54	57	419
	off	44	44	41	41	54	36	40	39	339

As we can see in the total column, there was a very definite tendency for the Ss to enter the area between the magnets significantly more times with the field on than with the field off. For all fish and under all conditions, the experimental area was entered 1,981 times with the field on, and 1,409 times with the field off. Means were calculated for the average number of times the fish entered the area with the field on and off under all frequencies and at the 10 and 20 gauss levels. The results are shown in Table 9. To test the significance of the difference between the combined means, a test was done with the following results:

$\bar{X}$=49.53 (field on mean)
$\bar{Y}$=35.23 (field off mean)
$\bar{D}$=14.30 (difference)
ED_i=562
ED_i^2=14,956
N=40
$\bar{D}_i$=14.30
Sd=10.35

$$\begin{cases} S^2 = \frac{E(x-\bar{x})^2}{N} = \frac{4288}{40} = 107.20 \\ S = \sqrt{107.20} = 10.35 \end{cases}$$

$$\tilde{\sigma}_{\bar{D}} = \frac{Sd}{\sqrt{N-1}} = \frac{10.35}{6.25} = 1.66.$$

$$t = \frac{\bar{D}}{\tilde{\sigma}_{\bar{D}}} = \frac{14.30}{1.66} = 8.61$$

We can thus reject the null hypothesis that the results occurred by chance at the .01 level, i.e., we can be 99% confident that the observed difference was not due to chance.

Table 9. Mean number of times the Ss entered the experimental area with the field on and off at 10 and 20 gauss and overall for all frequencies combined.

	10 gauss	20 gauss	combined
Field on	45.75	53.30	49.53
Field off	35.15	35.30	35.23

In Figure 9, average difference scores were determined by finding the difference between the number of times the Ss entered the experimental area with the field on and with it off, and dividing this number by 4 (the number of Ss). This was then plotted against the various frequencies tested. It can be seen that there are two definite peaks in the approach tendency of the Ss to the field, at -100cps and in the region between +100 to +200 cps. Surprisingly, there was a sharp drop at the subjects' own frequency, which is contrary to what we had expected. Previous reports had indicated that these fish are most sensitive at their own discharge frequency.

After this analysis of the data, it was apparent that the fish were not responding to a pulsed magnetic field in the expected manner, i.e., responses at the frequency of the fish at maze temperature were not the maximal responses observed, nor were the frequencies at which maximal responses were seen related in a periodic manner to the base (26.8°C) frequency of the fish.

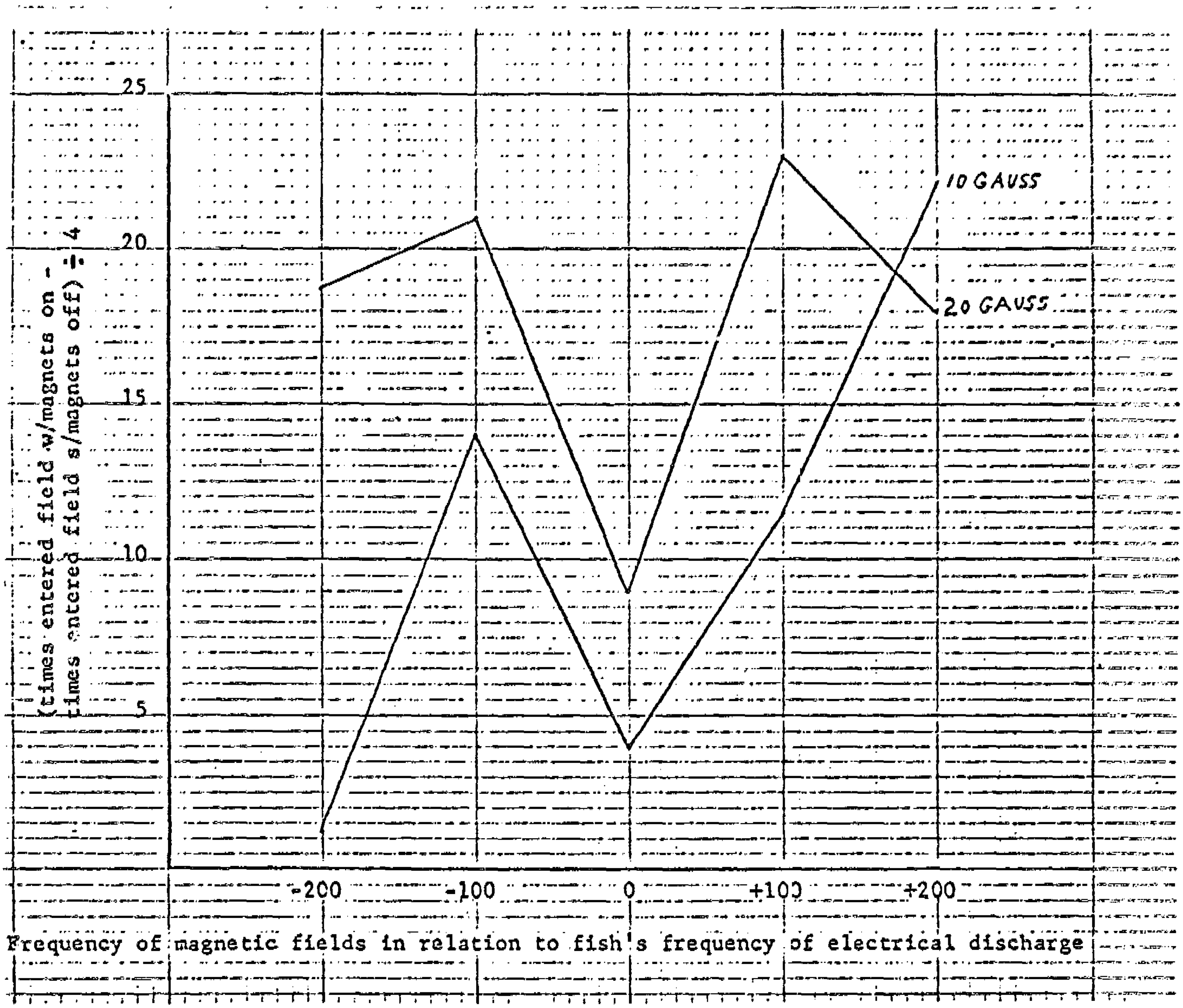


Figure 9. Changes in average difference scores with magnetic field frequency.

Therefore, an additional series of trials were run extending the frequency range of the magnets. A field strength of 20 gauss was used throughout to maximize responses.

The procedure was the same as before. The experimental fish was placed in the maze, the lights were extinguished, and two minutes allowed to elapse before counting began. The number of times in a 15-minute period that the fish entered between the magnetic coils with the magnets off was then recorded. With the electrical input to the magnet and to the switch adjusted to produce 20 gauss and the desired frequency with the standardized pulse as shown in Figure 5 for the magnet longitudinal axis, the entries into the area between the magnets

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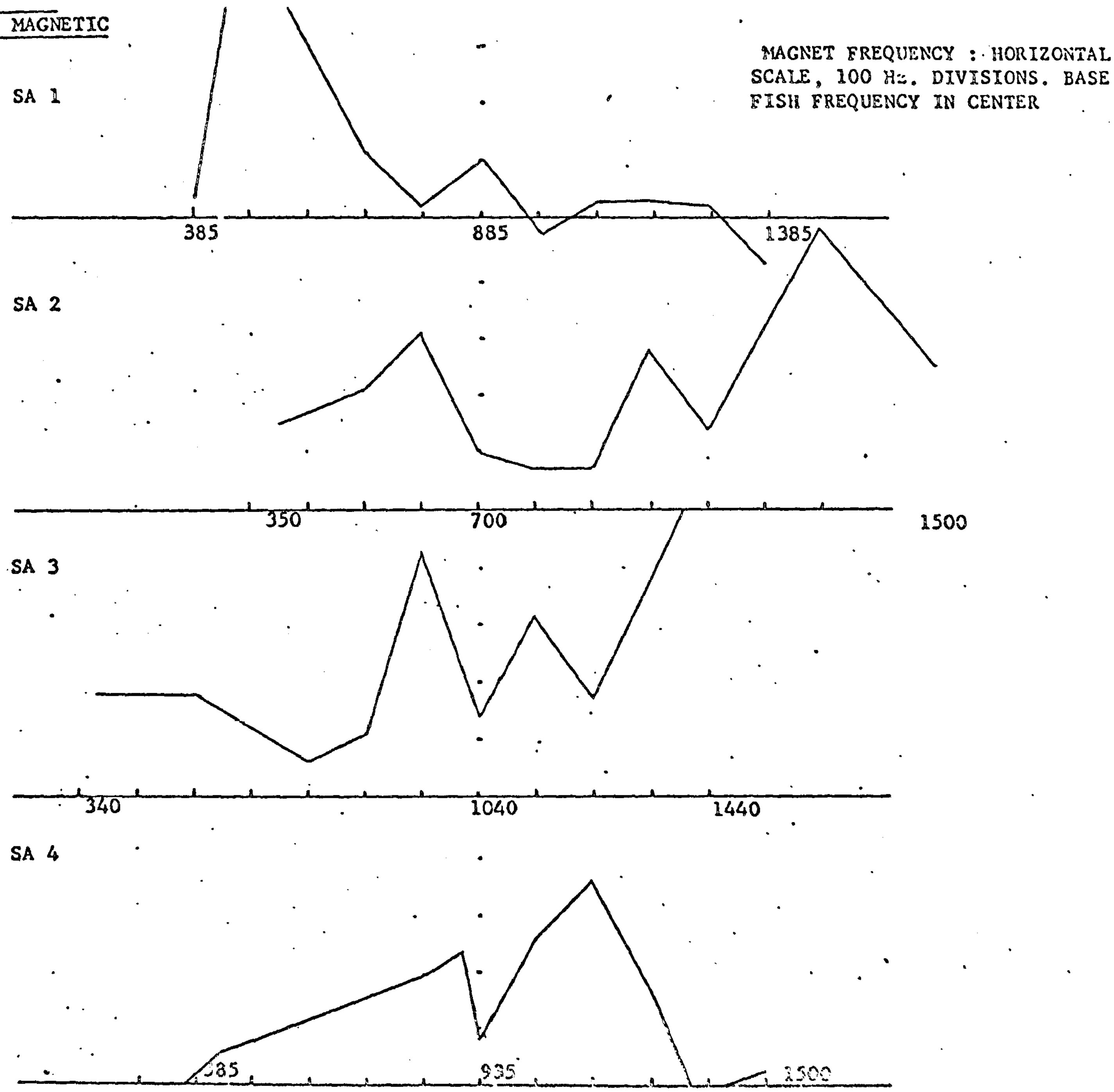

in 15 minutes with the magnets on and off were counted. After each series of half hour trials, the fish was returned to his home tank, the magnets readjusted if necessary to accommodate the frequency of the next subject, and the process started again. In any given day, one fish would have a maximum of two half-hour trials, separated by at least one hour.

The results are shown in Figure 10. These performance curves were drawn by subtracting the number of entries during each control run from the number of entries during the companion experimental run at each magnet frequency level. In actual numbers, the entries under control conditions ranged from 16 to 90 and under experimental conditions ranged from 14 to 87 in a 15-minute period.

Limitations in the equipment prevented the testing of performance at frequency levels of half and double that of the base frequency of each fish. However, the range tested was adequate to show that sensitivity to a magnetic field in Sternarchus albifrons is vastly different from that to an electric current.

All of the data in previous reports with regard to response to magnets have been discussed in terms of the current generated in the fish by the magnetic field. This may be true, but these performance curves clearly indicate that the sensitivity to magnetism is more complex. The literature is in agreement that maximum sensitivity to applied current occurs at the fish's own frequency (Granath, 1967, Figure 11). The results reported here indicate that maximum sensitivity to a magnetic field occurs at a point or points one to three hundred Hertz above and/or below the base frequency. What is most certainly indicated is that maximum sensitivity does not occur at the fish's own frequency with the magnetic field.

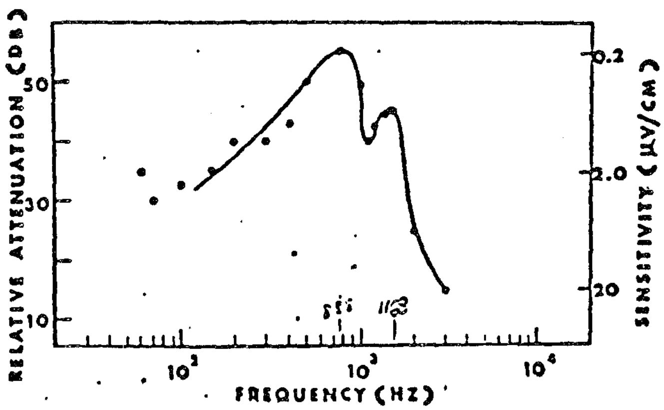

Figure 11. Response spectrum to a uniform AC field. (After Granath, 1967).

If, as our data indicate, the fish respond to more than induced current in a pulsing magnetic field, there is still the problem of defining more clearly the stimuli to which they are responding. A crude model of a fish was achieved by moving an induction coil through the maze. Results are reproduced in part in Figure 5. These wave forms were induced with the axis of the test coil parallel to the axis of the magnetic coils. With the axis of the induction coil perpendicular to the axis of the magnetic coils, results were similar from the distal end of the test arm to the point 15 cm from the magnet center, but induced currents were weaker, 2 - 50 mV as opposed to the 5 - 80 mV shown on the diagram. However, from 15 cm, on toward the magnet center, the induced pulses became more rounded and diminished in strength to about 1 gauss at the center of the magnetic coil. A behavior pattern observed in the fish indicated that the first model, though extremely crude, was better than the second. The fish, in moving from the distal end of the test arm would hesitate at about this 15 - 18 cm area, and then frequently continue to the magnet center in a rush, working their jaws and moving in an excited manner. Interestingly, the induced current pulse in the test coil assumes a wave form that is very like the fish's own discharge at this 15 - 18 cm point in our test apparatus.

One other aspect of observed behavior toward the magnetic field is unexplained. When the fish chose the leg of the T at a point 0 to 10 cm from the intersection, they were observed to sometimes execute a forward roll, frequently two or three in succession with some degree of force. As can be seen from the diagram, there appears to be no individuality in this area of the field. This response was seen to some degree at all frequencies and at 10 and 20 gauss, but seemed to be most common at those frequencies of maximum response to the magnet. A crude three-dimensional plot of the field shows it is cigar shaped. The fish were restricted to an area ± 5 cm above and below the edge of the cigar-shaped field (23 cm in diameter). At this 10 cm point, the lines of equal force would be essentially parallel to the long axis of the arm in the vertical plane, and curving toward the magnet center line in the horizontal plane. Perhaps it is this gradient to which the fish respond in this manner.

F. Summary of results.

(a) The rate of discharge in the electric field of Sternarchus albifrons is a positive function of temperature. In three subjects (S.A.1, 3, and 4) the change was ± 50 cps for 1 degree C. The other specimen, (S.A.2) varied ± 15 cps per 1 degree C.

(b) The fish showed no significant approach or avoidance behavior toward a static (non-pulsed) magnetic field of 9 - 10 gauss in a Y maze.

(c) A conditioning procedure in which electric shock was paired with a static magnetic field of 9 - 10 gauss and 3½ gauss in a Y maze in order to establish an avoidance response was not successful.

(d) In a study of the effects of drugs, Nembutal and levodopa (L-dopa) failed to alter the discharge patterns of the subjects' field, although L-dopa produced a more variable temperature-frequency relationship and some abnormal behavior. Pontocaine, however, modified the discharge frequency by depressing the rate severely.

(e) Conditioning trials were attempted with a 60-cycle AC magnetic field of 1 - 42 gauss paired with electric shock in a T maze. The fish learned to avoid the field at intensities of 34, 26, and 18 gauss, but the results were inconsistent at 9 and 1 gauss.

(f) Additional conditioning trials were run in the T maze with a pulsed, unidirectional field at frequencies ranging from 540 to 1540 cps at 5 and 15 gauss in which the field was paired with shock, but the subject failed to learn to avoid the field. Instead, the fish showed a tendency to stay in the field regardless of the shock it received.

(g) Each subject was tested for an approach tendency to the field in a preference study. The pulsed field was varied in intensity from 10 to 20 gauss, and in frequency from 200 cps above the fish's own frequency to 200 cps below it by decrements of 100 cps. The subjects showed a significant preference at the .01 level for the area between the magnetic coils with the field on as compared with trials with the field off, indicating clearly that they are sensitive to the magnetic stimuli. The preference study showed maximal responses at frequency rates other than those of the fish, in a pattern totally dissimilar to imposed current stimuli.

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V. WHERE - LABORATORY INDEX.

The following is a list of laboratories,uuniversities, and institutes where work is in progress.

University of California
Graduate School
San Diego-LaJolla, California 92038
(Prinipal investigator: Th. Bullock)

The City College of New York
The City College Research Foundation
New York, New York 10031
(Principal investigator: Frank J. Mandriota)

Columbia University
College of Physicians and Surgeons
New York, New York 10027
(Principal investigators: Arthur Karlin; David Nachmansohn)

University of Connecticut
Biological Sciences Group
Storrs, Connecticut 06368
(Principal investigator: Tobias L. Schwartz)

University of Connecticut
Graduate School
Storrs, Connecticut 06268
(Principal investigator: A.W. Wachtel)

University of Maryland
School of Medicine
Baltimore, Maryland
(Principal investigator: L. Holdman)

Pennsylvania Hospital
Philadelphia, Pennsylvania
(Principal investigator: Sumner I. Zacks)