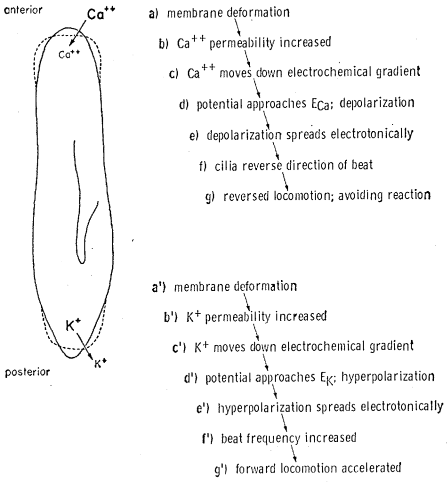

Fig. 3. Summary of steps linking mechanical stimuli with motor reactions of *Paramecium*. The anterior and posterior ends of the organism are shown at the top and bottom, respectively. Major steps leading to either the avoiding reaction or accelerated forward locomotion are outlined near the end of the cell which when stimulated initiates the sequence. The molecular mechanisms involved in steps a, a′, f, and f′ are not known.

to both anterior and posterior stimulation were plotted as functions of the calcium concentration ([Ca^{++}]). This was repeated at constant [Ca^{++}] in a series of potassium concentrations (Fig. 2B).

The peak of the anterior receptor potential (closed circles) showed a slope of 22 mv for a tenfold change in [Ca^{++}]; the peak of the posterior receptor potential (open circles) showed a slope of 50 mv for a tenfold change in [K^+]. These values approach the theoretical slopes of 29 and 58 mv respectively for Ca^{++} and K^+ diffusion potentials at room temperature. Finally, the peak value of the posterior receptor potential (closed circles) is independent of [Ca^{++}], whereas the peak of the anterior receptor potential (open circles) is independent of [K^+] (Fig. 2).

These results lead to the conclusion that a mechanical stimulus to the anterior end induces a transiently increased membrane conductance to Ca^{++}, whereas a similar stimulus to the membrane of the posterior end causes a transiently increased membrane conductance to K^+. As a result, stimulation of the anterior end causes a transient approach of the membrane potential toward the equilibrium level for Ca^{++}, and stimulation of the posterior end a transient potential shift toward the equilibrium potential for potassium.

The external concentrations of calcium and potassium determine their transmembrane electrochemical gradients and hence influence the magnitude and direction of the receptor potentials (Fig. 2) as well as the value of the resting potential (*9*). We chose the concentrations in the standard mediums (Fig. 1) arbitrarily, but they are in the range typical of natural habitats of *Paramecium*.

Parallels between electrical behavior and locomotor behavior are consistent and complete (Fig. 3). For example, the avoiding reaction is increased as the intensity of the stimulus is increased (*1*). This parallels both the increased intensity of ciliary reversal with increased depolarization (*8, 12*) and the increased depolarization as submaximal mechanical stimulation is increased (Fig. 1). Jennings (*5*) also noted that the avoiding reaction occurs only to mechanical stimulation of the anterior end. Hyperpolarization in both *Paramecium* and *Opalina* is accompanied by an increased rate of ciliary beat in the forward-swimming direction (*7, 8, 12*). This parallels the transient increase in swimming rate which occurs in response to a general mechanical stimulus such as a sharp tap applied to the culture vessel (*3*). The dominance of the posterior receptor potential in the case of a generally applied stimulus may result from the greater mechanical sensitivity of the posterior end noted in our experiments.

These findings appear to be unique in demonstrating a direct relation between the coordinated locomotor behavior of an organism and ionic mechanisms of membrane excitability.

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Microvolt Electric Signals from Fishes and the Environment

Abstract. *Pulses in the 0.01 to 40 microvolt range, probably generated by white fiber muscle action potentials, were remotely received through dipole antennae from five fishes and one amphibian in aquarium tests. In natural environments, however, no biologically generated signals have been detected. Received instead were a multitude of similar signals originating from unknown sources. The dominant types of these "atmospheric" signals and their reception rates change diurnally and can easily be confused with the fish-generated signals.*

Intriguing stories about strange signals produced by fishes, based on the work of W. L. Minto, Jr., and his associates, have recently appeared in popular magazines and trade journals (*1*); and Minto and Hudson (*2*) list 130 fishes that emit species-specific signals receivable with dipole antennae in aquarium tanks and, in some cases, the fishes' natural environment. Because the signals are said to be propagated through several hundred meters of water, these workers state that the signals are a novel energy form which they call "hydronic radiations."

Others (*3*) have studied the physics of the question. Here we confirm that by the use of equipment similar to Minto's, signals are receivable from fishes in laboratory tanks. These, however, are extremely weak electric pulses (10^{-14} watt into 500 ohms) most likely resulting from action potentials of white muscle fibers. Further, our field observations indicate that while such fish-generated signals may be receivable at close ranges in their natural environments, the majority of similar signals picked up in large bodies of water are electrically coupled components of ground currents and atmospheric noise originating from physical causes and are not generated by fishes.

Using the equipment shown in Fig. 1, we monitored and recorded numerous signals in freshwater tanks containing fishes and an amphibian at the National Fish Hatchery Public Aquarium, Welaka, Florida. No signals were picked up in tanks holding reptiles or brine shrimp.

Separate tanks containing six albino channel catfish (*Ictalurus punctatus*) approximately 15 to 20 cm in length; three black crappie (*Pomoxis nigromaculatus*) about 13 cm in length; a 25-cm red-breast sunfish (*Lepomis auritus*); a 35-cm amphibian, *Siren lacertina*; and a 50-cm southern stingray (*Dasyatis americana*) produced signal bursts that were correlated with the animals' rapid swimming movements or fright tremors caused by irritating them with a wooden stick. Examples of these signals are shown in Fig. 1. A tank holding a mid-water school of 16 *Tilapia mossambica* (13 to 18 cm in length), however, spontaneously produced sharp, pop-like signals of two to three spikes (Fig. 1D). This observation was repeated five times at random intervals, and the number of these signals increased each time until there was a steady chorus of "pops." Analysis of the taped recordings indicated that the signal rate was 67 pops per minute at the time of the first observation (1830 EDT), increased slightly at dusk (2100 hours) to 200 per minute, and then rose sharply to about 2000 per minute by midnight when the tests ended. The fishes' overt activity did not appear to change during this period.

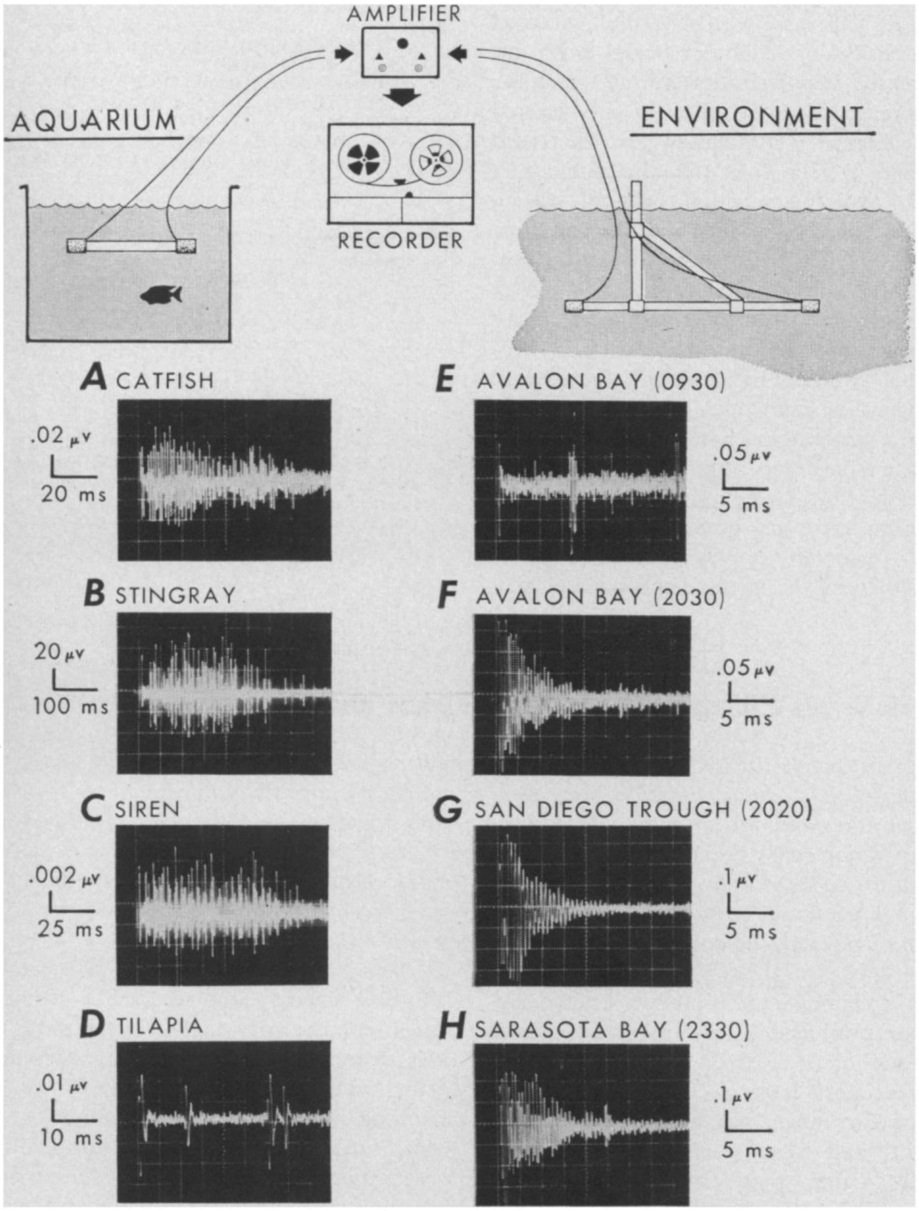

Fig. 1. Equipment used to record electric signals from fishes in the Welaka, Florida, aquarium tests and in various environments. The electrode plates (20-gauge Monel, $6.4\ cm^2$) are rolled to slip over the ends of plastic pipe and are separated by 61 cm in the aquarium antenna and 3 m in the environmental antenna. Coaxial cables (RG-58), with their shields insulated at the electrode terminations, run to a battery-powered Princeton Applied Research amplifier (model CR-4A) where their shields connect with the amplifier guard pin. Output from the amplifier goes to the microphone jack of a UHER battery-operated tape recorder (model 4000 Report). Signals are monitored over a wide frequency band (10 cycle/sec to 300 kc/sec), but recorded in a narrower band (usually 300 cycle/sec to 30 kc/sec) at 19 cm/sec tape speed to reduce the noise level. The taped signals are then further filtered to the 400 cycle/sec to 4 kc/sec band and photographed at various tape recorder speeds.

Experiments were then run using the setup shown in Fig. 2. Two 76-liter plastic tanks, used alternately, one for individual experimental specimens and the other as a control, were enclosed in a darkened double-walled aluminum "Helicop-Hut" to shield against spurious noise. Dipole antennae, constructed of copper-plate electrodes rolled to slip over the ends of 50-cm sections of micarta tubing, were placed on the bottom of the tanks and their coaxial leads run to amplifiers and a tape recorder in a nearby wooden hut.

An albino channel catfish and several individual *Tilapia* (*4*) produced signals strikingly similar to those recorded from tanks containing the same species in the Welaka experiments (Fig. 2, A and B). Figure 2C shows one of the weaker signal bursts recorded from an 8-cm electric catfish (*Malapterurus electricus*). The pickup distance through the dipole antenna modified the pulses to a derivative, diphasic form, but otherwise the signal train pictured is identical in duration and frequency to published data on electric signals for this species recorded with electrodes in direct contact with the fish (*5*). Thus, while repeatable distinctive signals can be recorded from the albino channel catfish and *Tilapia*, they probably are extremely weak electric emissions that lack the coherence of strong electric pulses.

Some signals were elicited by irritating the fishes with a plastic meter stick while others were apparently produced spontaneously, but the fishes were never more than 40-cm from the antenna electrodes. The simultaneously recorded control channel was relatively quiet, with only low-level 60-cycle noise. Occasional radio music and transient signals were received on both channels.

We next attempted to record signals from *Tilapia* held captive in a natural environment. Fortuitously, 450 specimens had been introduced into Lake Jennings, a reservoir covering about 60,000 m^2 near Lakeside, California.

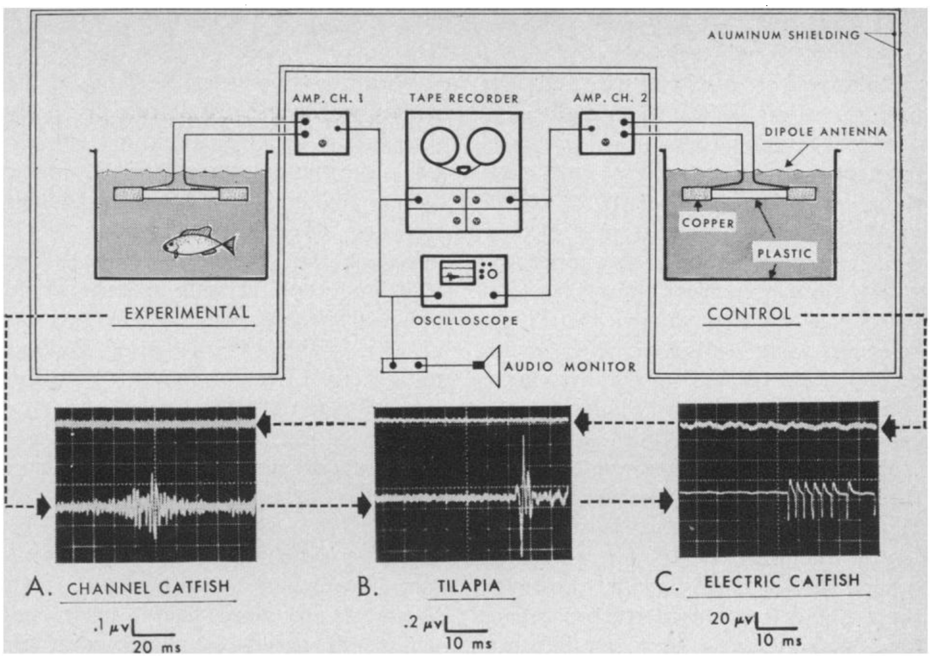

Fig. 2. Equipment used in the controlled experiments, and representative signals received from fishes. Signals are filtered (100 cycle/sec to 10 kc/sec), amplified, monitored, recorded on separate channels of a Precision Instrument Company (model PI-6100) tape recorder at 9.5 cm/sec speed, and photographed at that speed without further filtering. Equipment is run on line voltage. The control channel in (C) was recorded at a 10^4 higher gain than the experimental channel.

Fifty more *Tilapia* were being maintained under observation in a wooden-framed, copper-screened live well (enclosing about 9 m^3 of water) suspended from a raft anchored 135 m from shore. We used the same instrumentation as in the controlled experiments, placing one antenna (experimental) in the live well with the 50 *Tilapia,* and suspending the other antenna (control) at an equal 1-m depth from a wooden float anchored about 20 m from the live well.

From 1603 (PDT) 6 July 1967 to 0700 the next morning 5-minute recordings were made, at hourly or more frequent intervals, with the experimental antenna first in the live well and then suspended in the lake between the well and the raft. The copper screening efficiently shielded against spurious signals, and low background levels were recorded with the experimental antenna in the live well. Relatively high background levels, caused by occasional radio signals and 60-cycle noise, were picked up when the experimental antenna was placed in the lake outside the live well, and were received constantly by the control antenna. Superimposed on this background, during daylight hours, was a steady battery of sharp, individual spikes picked up at the control antenna (similar to Fig. 1E). At dusk, the nature of the dominant signals suddenly changed to a signal burst of descending intensity and of varying duration (similar to Fig. 1, F–H). The audio frequencies of these signals sound respectively like "clicks" and "ricochets." Although click-type signals were still discernible between 2030 and 2045 hours, the ricochet-type signals built up to a crescendo, maintained this level until 2100, dropped rapidly at 2200, and then decreased evenly to a low at 0600, when the click-types were again dominant. When both antennae were in the lake, these signals were received simultaneously. Despite replay and careful monitoring, we can not recognize *Tilapia*-like signals on either channel.

In another daytime test of fishes held captive in a natural environment, no signals were recorded from a tight, slow-milling school of about 200 northern anchovy (*Engraulis mordax*) surrounding a 1-m antenna in a wooden live-bait well open to San Diego Bay waters. The only obvious signals received against a high 60-cycle background were frequent click-types. Their nature or incidence did not change markedly when the antenna was in the bait-well, alongside it, or at various distances to 1.5 km. In both cases, signals were monitored over a wide frequency band (30 cycle/sec to 300 kc/sec). Thus, our failure to record fish-generated signals is probably not due to instrumentation.

We have recorded click- and ricochet-type signals, and the marked increase of the ricochet-types after sundown, in all aquatic environments (including a backyard swimming pool) so far investigated. Equipment is essentially the same as that in the Welaka Aquarium experiments, with the exception of a 3-m spread of electrodes on a polyvinyl chloride pipe frame. Figure 1 shows the system and typical signals recorded in some of these environments; localities and dates of all observations are listed in (*6*).

On the basis of these experiments we believe that the click- and ricochet-type signals are not biologically generated, but are electric signals naturally coupled into bodies of water from earth currents, atmosphere, stratosphere, and outer space. Components of these signals are generally received on long-wire and loop antennae in the atmosphere. They are known to change markedly their nature and activity at different times of day depending on latitude, the inclination of the sun and its activity, and other factors (*7*). Receiving them in water with a dipole antenna apparently changes their characteristics, so that one familiar with atmospheric signals may not recognize their source; because they are similar in form and intensity to fish-generated signals, the two kinds could easily be confused.

It would be wrong, however, to conclude that fish-produced weak electric signals cannot be received in natural environments. In his work with known electric fishes, Lissmann (*8*) used carbon electrodes and amplification of received audio frequencies to locate these fishes in a confined South American stream. Even though his fishes constantly produced electric signals several thousand times stronger than the signals under consideration here, there is no reason why "nonelectric" fishes could not be detected at short ranges under optimum conditions. Further, captive fishes do not always behave normally, and our studies of *Tilapia* and anchovies confined in barren live wells may not be valid.

The controlled experiments, in conjunction with the Welaka Aquarium tests, convincingly demonstrate that some nonelectric fishes, and at least one amphibian, produce receivable electric signals. Consideration of these results in the context of existing information is in order.

Members of nine fish families are known to generate electric pulses: representatives of five of these families produce strong pulses (4 to 550 volts) used for stunning prey and defense; members of four families emit constant, but relatively weak (0.03 to 0.7 volt) signals; and one strongly electric fish, the electric eel, also produces weak electric pulses (*9*). Lissmann (*10*) has clearly shown that these constant weak emissions function in conjunction with a sensory system to detect small impedance changes in the fish's environment. Some work also indicates such fishes communicate with these signals (*11*). The electrogenic tissue of the weakly electric sternarchids is modified nerve fibers. In all other species investigated, however, these highly specialized electric organs have been derived from modification of voluntary muscle tissue (*12*). We should now consider a lower order of electric signal production by fishes.

In 1956 Kleerekoper and Sibakin reported that weak (200 to 300 μv) electric potentials are produced from the anterior region of the sea lamprey, a primitive nonelectric fish, and later associated the generation of these signals with the opening of the respiratory pores (*13*). Dijkgraaf (*14*) mentions monitoring respiratory electric potentials by electrodes in close proximity to the head of a flatfish, but gives no information on method or intensity. Lissmann briefly noted evoking electric signals (no data are given on intensity) from the nonelectric common eel (*15*) and the African catfish (*10*) by causing them to jerk. Recently, Minto and Hudson (*2*) listed 130 fishes belonging to 58 families that produce "hydronic" signals. If we can substitute "electric" for "hydronic," our study supports this aspect of their work. The amplitudes we have recorded (0.01 to 40 μv) are much weaker than any electric emissions from fishes so far reported, and measurements with electrodes in contact with the fish will be necessary to establish maximum voltages. But it would seem that many fishes are electric to some degree. All nerve firings and most muscle contractions produce measurable action potentials. Because the animals are thin-skinned, sheathed in low-resistance mucus, and are living in a conductive medium, these electric emissions are propagated and can be remotely received at various ranges dependent on amplitude of the pulses, salinity of water, and sensitivity of the receiving equipment.

With the exception of *Tilapia*, the signals we have evoked from fishes by stimulating them into rapid movements, jerks, or tremors are strikingly similar to the batteries of action potentials recorded directly from white muscle fibers of the dogfish by Bone (*16*). It is important to note that he could only elicit these potentials by provoking his pithed sharks into vigorous movement. Lissmann's (*10, 15*) recordings of electric signals from the nonelectric catfish and eel were also obtained under duress and probably have a similar origin. In the context of Bone's (*16*) results, the signals received in synchronization with respiratory movements of fishes (*13, 14*), however, are more likely action potentials of nerves associated with the red muscle fibers of the branchial region. Thus, such emissions may be simply a by-product of the animals' normal functions.

What role, if any, these signals play in the lives of fishes remains unanswered, although one would suspect that evolutionary intermediates between "nonelectric fishes" and the highly specialized electric forms do exist, and that they have put such an electric sense to good use. Regardless, reception of these signals would seem to offer a valuable and as yet little-used tool in experiments on fish behavior. In electromagnetically noisy natural environments, however, there appears to be small hope for productive practical applications (*17, 18*).

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6. Strikingly similar ricochet-type signals were recorded at night from: the "Marina Mar" docks, Sarasota Bay, Fla., 15 May 1967; Bradenton Beach Pier, Sarasota Bay, Fla., 16 May 1967; and Naval Undersea Warfare Center docks, San Diego Bay, Calif., 22 May 1967. The change from dominating click-type signals to ricochet-types was recorded in a five-station series spaced at 7-km intervals from the kelp beds off Point Loma, San Diego, Calif., to the middle of the San Diego Trough over 1000 m of water, 25–26 May 1967; in a swimming pool, Point Loma, Calif., 16 June 1967; in Lake Jennings, San Diego County, Calif., 6–7 July 1967; and off Avalon Bay, Catalina Island, Calif., 15–16 May 1968. Fewer signals were received in the small (6.1 by 12.2 m) swimming pool against a high 60-cycle background.
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17. Since editorial review of this paper, the work of B. Lewis, J. Clark, and C. Gordon has been brought to our attention. In a preprint of their paper "Underwater communications via ground currents," given at the Fourth Space Congress, Cocoa Beach, Florida, 3–6 April 1967, they present data and conclusions which are generally in agreement with ours. In the course of their studies off Port Canaveral, Florida, they recorded peculiar electric noises with equipment which is essentially like ours. One type of noise, identified by them as "sferics," looks like our atmospheric "click." Another type was thought to emanate from marine life, and a similar signal was evoked from a small nurse shark isolated in a plastic tank when it was irritated by handling. Allowing for differences in sweep speed of oscilloscopes, this signal looks strikingly like those we have recorded from the channel catfish, stingray, and the siren, but not *Tilapia*. (No data on amplitudes are given.) They concluded that some nonelectric fishes can generate electric signals at will.
18. Additional information on instrumentation and methods was given in paper F8 at the 5th U.S. Navy Symposium on Military Oceanography, Panama City, Fla., 1–3 May 1968. The paper is in press in the proceedings of that meeting.

19. We thank W. Minto and J. Faber for consultation and help, and others who have aided the work. J. Anderson and G. Earhart made facilities available; E. Nakamura air-shipped *Tilapia* specimens from Hawaii; J. Snodgrass loaned tape recordings and consulted; K. Sager, I. Davies, and J. Wilton assisted field operations; S. Kreml gave editorial assistance; and G. Pickwell read the paper. The work was done under SR 104 03 01, Task No. 0588 of the U.S. Naval Ship Systems Command.

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