cies of arthropod can (10). Any alternative requires the bees to use a fixed reference system—landmarks or magnetic north, for example. The nature of this reference, which may explain the ability of experienced foragers to navigate and dance on totally overcast days (3, p. 336; 11), is unknown. In any case, the extrapolation strategy seems a surprisingly simple system for what is, in other respects, such a complicated animal, and may represent one of a set of optimal compromises between navigational accuracy and the complexity of information processing necessary to achieve that accuracy.

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Electroreception in the Ratfish (*Hydrolagus colliei*)

Abstract. *Behavioral and neurophysiological experiments and anatomical work indicate that the ampullar structures on the head of fish of the subclass Holocephali are sense organs responsive to weak electric fields and are functionally and structurally homologous to the ampullae of Lorenzini in elasmobranchs. It is concluded that, as in elasmobranchs, these organs are used to detect bioelectric and other natural electric phenomena in the environment.*

Chimaeras or ratfish (subclass Holocephali) are a primitive group of relatively rare benthic marine fish whose ancestors were the dominant durophagous fish in the Paleozoic seas (1, 2). Like elasmobranchs, which they resemble in some morphological aspects, ratfish possess numerous pores, covering much of the rostrum, that are apertures of jelly-filled tubes that run subcutaneously for some distance and terminate in innervated ampullae. Although several functions have been ascribed to the ampullae of Lorenzini in elasmobranchs, they are now known to be electrosensory organs used to detect naturally occurring electric fields (3–7). To the best of our knowledge, there has been no experimental work on the ampullar organs in ratfish, primarily because of the obscurity and inaccessibility of most species that inhabit the archibenthos. The ampullar organs have been theorized to function in mechanoreception (8–10), temperature reception (11), mucus secretion (12, 13), and (based on homology with the organs of sharks) electroreception (14, 15). This study is apparently the first investigation of the behavior and neurophysiology of electroreception in ratfish. In addition to adding a new subclass to the list of known electrosensitive fish, our experiments provide information that may be useful to phylogenists and those concerned with the evolution of electrosensory organs.

One species, *Hydrolagus colliei*, is relatively accessible on the Pacific Coast of the United States, where it is occasionally found in shallow water (16). Living specimens for behavioral experiments were obtained by hook and line (with squid used for bait) in Monterey Bay, California, in about 75 m of water. Specimens for electrophysiological experiments were obtained at 85 to 360 m by hook and line, longline, or trawl.

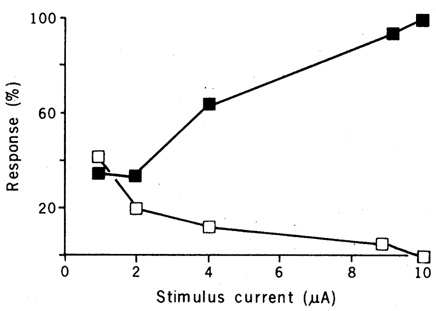

Fig. 1. Frequency of conditioned responses to a weak electric field as a function of stimulus strength. A stimulus of 1 μA produced a field of 0.2 μV/cm at 4 cm from the electrodes. The decreasing proportion of escape responses (■) and the increasing proportion of incomplete responses (□) at the lower stimulus currents indicate that the stimulus is approaching threshold, which must lie below 1 μA. Escape or incomplete responses never occurred without the conditioning stimulus in trained fish, and an unconditioned control never exhibited either response. There were 6, 13, 27, 20, and 14 trials at 10, 9, 4, 2, and 1 μA, respectively.

The sensitive electroperceptive capability of *H. colliei* was demonstrated by conditioning the fish to respond to the presence of a current generated by a bipolar electrode. The experiments were conducted in a toroidal aquarium (2 m outside diameter by 1 m inside diameter by 0.5 m deep) constructed of nonmetallic materials (fiber glass, wood, and Plexiglas) to prevent the introduction of interfering galvanic fields. The aquarium was housed in an enclosure roofed with white, translucent polystyrene, which reduced the intensity of the light inside the tank to levels comparable to those in the fish's natural environment. A dim light on a 12-hour light-dark cycle provided the minimum illumination necessary for observation at night, when the fish was most active and responsive. An observer sitting at the center of the toroid studied the behavior of the specimen as it swam continually against the circling flow of seawater.

A d-c or 5-Hz square-wave stimulus (50 percent duty cycle) from a current source of 1 to 10 μA was passed between two 3*M* KCl-agar electrodes 5 cm apart on the floor of the aquarium (17). By prodding with a glass rod, the animal was conditioned to avoid the electric current by reversing the direction of its swimming. No behavioral change in the presence of the electric field was observed prior to conditioning. One ratfish, left unconditioned as a control, never exhibited a response to the stimulus.

In the conditioned escape response, the animal reacted instantaneously when the current was turned on by sharply jerking its body and abruptly erecting its dorsal spine. It rose off the bottom by rapidly undulating its pectoral fins and turned completely around. This escape behavior was observed in response to stimuli of 1 to 10 μA and occurred in 100 percent of the trials in which the 10-μA stimulus was used.

A number of incomplete responses, characterized by a turn of less than 180° but accompanied by the startle reaction, were observed with increasing frequency as the stimulus intensity was reduced. As Fig. 1 shows, an increasing proportion of failures and incomplete responses occurred at the lower current levels. We interpret this as an indication that the stimulus level was approaching the absolute threshold sensitivity of *H. colliei*.

The field was mapped and found to resemble a typical dipole field, with the portion that would normally occur sym-

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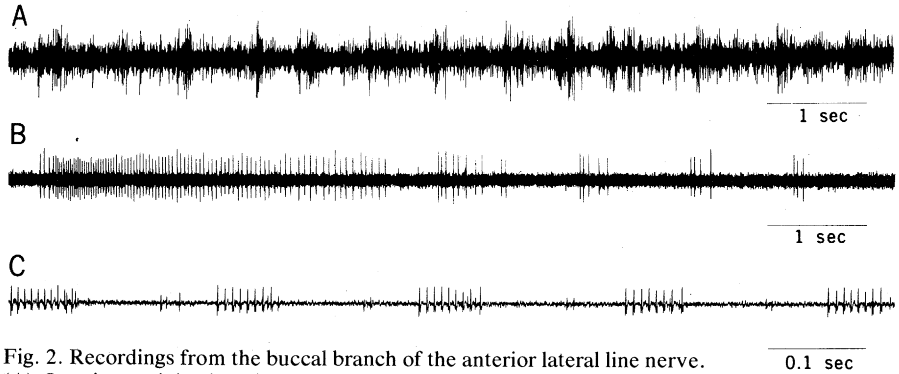

Fig. 2. Recordings from the buccal branch of the anterior lateral line nerve. (A) Ongoing activity in a bundle of axons. Note bursts due to opercular movements. (B) Response to a step of current to 10 μA. Note adaptation. (C) Response to a 50 percent duty-cycle square wave at 5 Hz.

metrically below the floor of the aquarium reflected back by the floor (*18*). The intensity of the field produced by a 1-μA stimulus decreased rapidly to 0.2 μV/cm at 4 cm from the electrodes. Since the animal frequently responded to the stimulus at a distance greater than 4 cm from the electrode, we estimate the absolute threshold sensitivity of *H. colliei* to be less than 0.2 μV/cm. This sensitivity is comparable to that of other electrosensitive fish and 1,000 to 10,000 times greater than that of an ordinary fish (*19*).

Neurophysiological monitoring of the response of the nerve fibers from the ampullar receptors, which were stimulated by an electric field, indicated that these organs are the electroreceptors.

The electrophysiological activity of the nerves from the buccal group of ampullae was recorded in situ in the inner buccal ramus of the anterior lateral line nerve (*20*). First, the fish was anesthetized with tricaine (MS 222; 50 mg/liter). The buccal nerve was reached in the orbit by removing the eye, or reached by dissection at a point, rostral to the eye, where the nerve passes superficially between the tubes of the ampullae and the integument. Bundles of the nerve fibers were dissected free and suspended in air on two silver hook electrodes, amplified differentially, and monitored on an oscilloscope and a speaker. Electrical stimulation was provided by a carbon electrode (*21*) in seawater near the head or in air on the buccal ampullar openings. A second carbon electrode was immersed in the seawater bath. Once recording began, no anesthetic was used.

Generally, in bundles in which we could demonstrate sensitivity to electrical stimuli, we also found considerable ongoing activity. In some cases this activity had a surging quality that was phase-related to the gill-cover (opercular) motion (Fig. 2A). The ongoing activity could be increased or decreased (depending on polarity) by applying current from electrodes in the water. We do not know whether the ongoing activity was truly spontaneous or was in response to standing fields in our setup; it may even have been in response to temperature or pressure gradients. In bundles in which there was no demonstrable electroreceptive activity, there was no spontaneous activity either. In these bundles, lateral line neuron activity was often present in response to mechanical stimuli.

Figure 2, A and B, shows the responses of a single first-order neuron from the buccal branch of the anterior lateral line nerve. Figure 2B shows the response to a step of current to 10 μA when the electrode on the ampullar pore became negative with respect to the seawater bath. These responses are in accordance with those seen in elasmobranchs: the firing rate at the peak of the response is about 100 per second and there is clear adaptation to the stimulus. A time constant for adaptation is estimated to be about 1 second. It was not possible to estimate the current density and, therefore, the amount of current flowing through the receptor (*22*).

As mentioned above, we encountered many lateral line units and recorded several. Their identity was determined by the presence of mechanical sensitivity (touch), which was always maximal at one of the lateral line branches. These units were often exquisitely sensitive to water motion but were never electrically excitable.

These results correspond to those obtained for the ampullae in elasmobranchs. In view of the past controversy regarding the phylogenetic and taxonomic relationship of the Holocephali and the Elasmobranchii (*2, 13, 23*), this similarity would seem to favor closeness rather than distance between the two. It seems reasonable that ratfish utilize their electrosensory ability to detect naturally occurring electrical phenomena in the environment, as do sharks and rays. Kalmijn (*5, 24*) has shown that elasmobranchs can use this ability to locate hidden prey, and may navigate by sensing the potentials arising in the ampullae through electromagnetic induction as ocean currents or the fish themselves move through the earth's magnetic field.

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18. Potentials between two Ag/AgCl electrodes mounted 1 cm apart on a manipulator were amplified with a high-impedance amplifier and displayed on an oscilloscope. Potentials for vectors at right angles in the *x-y* plane were measured and added vectorially.
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