Savage-Rumbaugh *et al*. (*1*). First, taking into account the fact that the brain of the pigeon is smaller than that of the chimpanzee, and not wishing to tax the relatively limited information-processing capacity of our subjects, we used 3 rather than 11 stimulus objects. Second, we did not attempt to reverse the informer and observer roles. (We believe that this can be done but is not essential to the demonstration of interanimal communication.) Third, we used colors rather than foods as the stimulus objects to avoid the possibility that our subjects would fail to "distinguish between the use of a food name as its name and the use of that name as a request for food" (*1*). Fourth, events in all interanimal test sessions in our experiment were controlled by electromechanical equipment, eliminating possible experimenter cuing effects and the need for "experimenter-blind" conditions. Fifth, our observer could not simply duplicate the symbol provided by the informer but instead had to decode the symbol into its referent. Sixth, we did not vary the position of our symbols. (Position was no doubt significant to our subjects, just as the position of letters and figures in mathematical notation is significant to mathematicians.) Seventh, every conversation in our experiment was initiated by the observer's spontaneous request for information. Finally, the observer sustained the informer's cooperation by thanking her with a food reward for supplying information.

We have thus demonstrated that pigeons can learn to engage in a sustained and natural conversation without human intervention, and that one pigeon can transmit information to another entirely through the use of symbols.

It has not escaped our notice that an alternative account of this exchange may be given in terms of the prevailing contingencies of reinforcement. Jack "initiated the conversation" by pecking the WHAT COLOR? key because a peck at that key had illuminated it and because this illumination had been reliably followed by the illumination of one of the symbol keys. This was, in turn, the occasion upon which a peck at the THANK YOU key, followed by a peck at a corresponding color key, had produced reinforcement. Jill responded to Jack's "request for information" because the illumination of the WHAT COLOR? key was the occasion upon which looking at the hidden color and then pecking a corresponding symbol key had been reinforced. The performances were established through standard fading, shaping, chaining, and discrimination procedures (*6–9*). A simi-

lar account may be given of the Rumbaugh procedure (*10*), as well as of comparable human language (*11*).

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4. If the birds had responded at random to the symbol and color keys, they would have been correct on only about 11 percent of the trials. They responded correctly on more than 50 percent of the trials of the first interanimal test.
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Sun Compensation by Bees

Abstract. *In both their navigation and dance communication, bees are able to compensate for the sun's movement. When foragers are prevented from seeing the sun for 2 hours, they compensate by extrapolation, using the sun's rate of movement when last observed. These and other data suggest a time-averaging processing strategy in honey bee orientation.*

When a forager bee returns to the hive from a good source of food, she performs a dance which specifies the location of the food. On the usual vertical comb in a dark hive, she converts the direction of
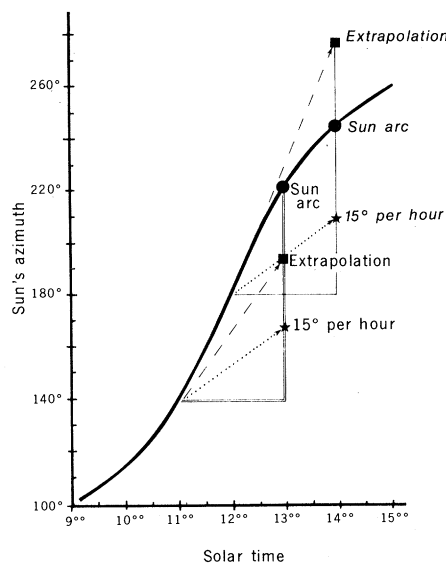

Fig. 1. The sun's azimuth movement at 40°N near the summer solstice is plotted along with the predictions of three compensation hypotheses for both a morning experiment (11 a.m. closing and 1 p.m. opening) and a noon experiment (noon closing and 2 p.m. opening). The sun's rate of azimuth movement changes quickly at this time of year. For example, at dawn the rate is 7.5° per hour, while near noon it is 44° per hour.

the food source with respect to the sun's azimuth into a dance angle with respect to vertical (*1*). Recruits decode the dance and use the direction information to find the food (*1*, *2*; *3*, p. 149). As such, the sun is the primary reference cue for honey bees. The sun, however, moves, and so is a problematical landmark for the many species that use it for navigation. The sun's exact rate of movement in azimuth depends in a complicated way on the date, time of day, and latitude. For example, at the summer solstice the rate increases by a factor of 6 from dawn to midday, changing most rapidly just before and after noon (Fig. 1). For the dance communication system to work, and even for foragers to find their way back home, animals must compensate for the sun's movement. Honey bees appear to accomplish this task by means of a time-averaged extrapolation.

The first direct evidence for compensation came from bees that danced for extended periods in the hive without leaving. Frisch noticed that the dance angle slowly shifted counterclockwise (*3*, p. 347), reflecting the clockwise movement of the sun (and hence, the counterclockwise relative motion of the stationary food source with respect to the sun). Later Meder (*4*) convincingly demonstrated compensation during foraging. We now know this ability to be

widespread, particularly among invertebrates with homes to get back to (3, p. 449; 5).

There are at least three general explanations of how animals could compensate for the movement of the sun.

1) They come programmed to perform spherical geometry. Since the sun moves at a constant rate of 15° per hour along its arc in the sky, its future azimuth could be calculated by simply moving the sun the appropriate distance along the arc, and then dropping another arc perpendicular to the horizon from this point. The intersection with the horizon would specify the azimuth. Such a system would allow precise compensation. (Alternatively, the bees could with similar accuracy memorize the pattern of azimuth movement one day and use it on the next.)

2) Bees might extrapolate the sun's azimuth by using the most recently observed rate of movement. Such a system would yield a good approximation, at least over moderate intervals, and would require less complicated processing.

3) Bees might extrapolate the sun's azimuth by using its average rate of movement (15° per hour). Even this crude estimate would be of much use over short periods, and present data do not exclude this simplest of possibilities (3, p. 362).

These three hypotheses may be distinguished by taking advantage of the extreme variation in the sun's movement near the solstice. If bees could be prevented from seeing the sun for a time, and so would not be able to update their information, their behavior would indicate which of the three predictions (if any) is correct. For example, if the hive were closed an hour before solar noon (at which time the sun is moving 25° per hour), and opened 2 hours later, the three predictions would differ greatly (Fig. 1). Specifically, the actual movement of the sun would be 85°, the extrapolation 50°, while the 15° per hour estimate would be 30°. Similarly, if the hive were closed at noon (with the sun moving 44° per hour) and opened 2 hours later, the sun would have moved in azimuth only 66° while the extrapolation would now be 88°. The 15° per hour estimate would again be 30°.

A hive was established and a group of 20 to 30 individually numbered foragers were trained to a station 100 m NNW or 150 m SSW. When the time came to close the hive, a system of one-way doors trapped the bees inside upon their return. The hive was then moved to a new location several miles away to guard against the possibility that the foragers

might navigate by means of landmarks (3, p. 334). An array of stations which were identical to the one used for training and which offered the same food was set out. The hive was reopened 2 hours after it was first closed and the initial arrival location in the array of numbered foragers was recorded.

Both the morning-closing and noon-closing experiment were run three times (Fig. 2). In all six experiments, forager bees behaved as if they had extrapolated the rate the sun was moving before the hive was closed. The very different geometrical relationships of the morning- and noon-closing predictions exclude any bias toward any particular direction
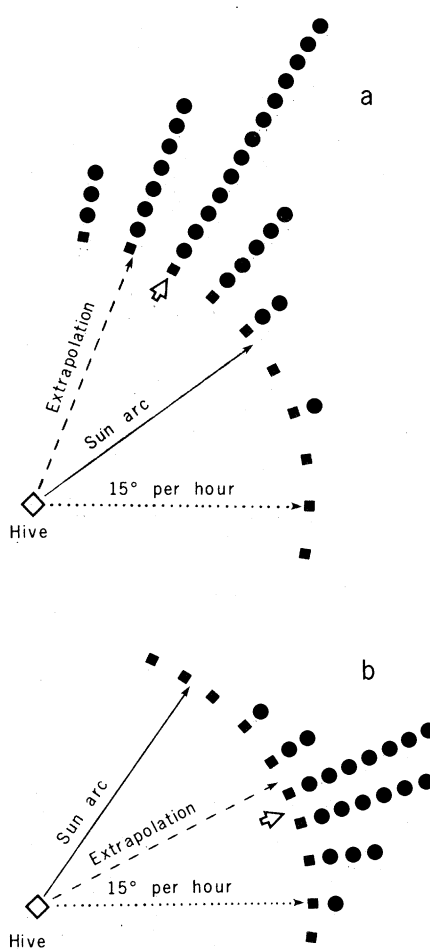

Fig. 2. Results of sun compensation experiments. Each dot represents the initial arrival location of a trained, individually numbered forager in the array after the hive was reopened. The data are pooled from three repetitions in each case. (a) Results of experiments on the noon closing and 2 p.m. opening indicate that the bees overestimated the sun's movement. Open arrows indicate the mean direction. In each case, foragers behaved as if they judge direction by extrapolating the sun's rate of movement 20 minutes prior to closing the hive. (b) Results from the morning closing (11 a.m.) and opening (1 p.m.) experiments indicate that the foragers underestimated the sun's movement while shut in the hive.

or part of the array, or the possibility of any sort of intermediate or compromise strategy.

Closer inspection of the results shows that the bees appear in all six experiments to have used an extrapolation rate which was about 20 minutes out of date. This observation is reminiscent of Lindauer's unexplained report (6) that the indication of direction by foragers when the food source itself is moved continuously in azimuth lags behind by about 20 minutes even though the dancing bees had just flown to the new location, and had observed the sun while doing so.

Taken together, these various experiments with 20-minute orientation lags suggest that bees may have a time delay built into their orientation programs which averages new information with old (averaging serves, for example, to overcome the limits posed by the bees' poor visual acuity) and substitutes extrapolation when new data are not available. The width of this temporal window for navigation would appear to be about 40 minutes judging from two other experiments. In one, Lindauer moved a feeding station abruptly every half hour by 10° to 20°. The foragers quickly found the new location, but their dances continued to reflect the old location and only slowly shifted toward the new direction (6). After 30 minutes—about five to ten round trips to the feeder—only about 75 percent of the necessary correction in dance direction had taken place. From the data, it seems clear that full correction would have been accomplished by 40 minutes. Similarly, the errors in dance direction induced by the earth's magnetic field (missweisung) also disappear slowly over a period of 40 minutes after the earth's field is canceled (7). In the past, this has been interpreted as evidence for a paramagnetic mechanism of magnetic field detection, although the sensor properties necessary to explain this "adaptation time" paramagnetically are virtually impossible (8). Although it could be a consequence of a particular permanent magnetic detector system (9), it seems at least as likely that each of these curious results are simply manifestations of a general, time-averaging processing strategy for orientation information, and that the extrapolation rate measured here represents a similar 40-minute average which is, of necessity, 20 minutes slow.

The above results raise the question of when, how, and with regard to what system of reference bees measure the sun's azimuth movement. At first glance, it seems unlikely that bees could measure the motion directly, but at least one spe-

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,
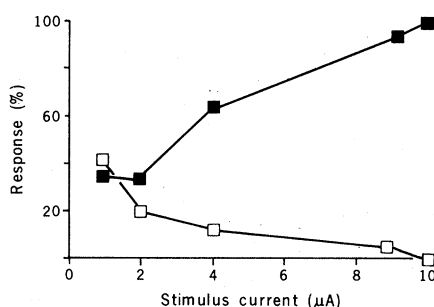

Fig. 1. Frequency of conditioned responses to a weak electric field as a function of stimulus strength. A stimulus of 1 μA produced a field of 0.2 μV/cm at 4 cm from the electrodes. The decreasing proportion of escape responses (■) and the increasing proportion of incomplete responses (□) at the lower 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.

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.

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-