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SHORT COMMUNICATION

HONEYBEES CAN BE TRAINED TO RESPOND TO VERY SMALL CHANGES IN GEOMAGNETIC FIELD INTENSITY

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It has been demonstrated repeatedly (Kirschvink & Kirschvink, 1989; Walker *et al.* 1989; Walker & Bitterman, 1985, 1989) that free-flying honeybees can be trained to respond to local anomalies in the geomagnetic field, but none of the training methods previously available has been sensitive enough for threshold studies. Here we report some determinations of intensity thresholds with a new and more powerful technique that permits objective measurement of response.

The training apparatus, set into a laboratory window facing east, consisted of a hinged Plexiglas panel in which two Plexiglas tubes, each 2·5 cm long and 2·5 cm in inside diameter, were mounted 14 cm apart, with their axes aligned horizontally. Around each tube were two coplanar, concentric coils that produced a sharply focused magnetic anomaly extending horizontally from the entrance to the tube. Inside each tube, at the intersection of the axis and plane of the coils, was a food well. The tube design and the pattern of the anomaly are shown in Fig. 1. A screen of fine plastic mesh separated the observer from the animal.

The coils around each tube had equal dipole moments (area × current) with antiparallel directions and different diameters. The field from the inner coil dominated and produced the anomaly close to the tube, while the moments of the two coils cancelled each other out further away from the tube. Each coil was doubly wrapped, with the two sets of windings so connected that they could be energized independently to induce parallel or antiparallel fields that summed or cancelled, with the very small amount of heat produced by passage of current the same in both cases. For further details of the coil design, see Kirschvink & Kirschvink (1989).

Individual honeybees were pretrained to fly back and forth between their hives and the training window. A single animal was selected at random from a group at a feeding station providing 10–15 % sucrose solution, carried in a matchbox to the window, and set down at a drop of 50 % sucrose solution near the entrance of the tunnel in one of the tubes (the left for some animals, the right for others). The coils of the tube were activated to produce the local anomaly that would be the positive stimulus (S+) at the outset of the subsequent discriminative training; the

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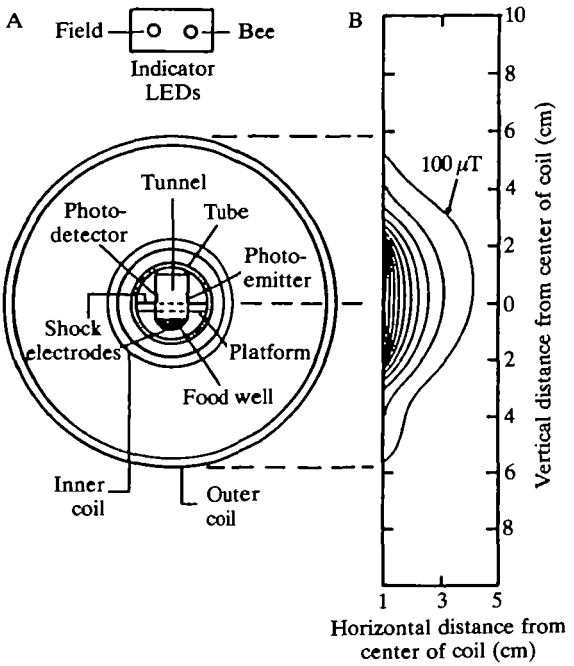


Fig. 1. (A) Diagram of one of the tubes seen from inside the laboratory. The LED labeled Field signals to the experimenter that the coils are innervated to produce an anomaly, and the LED labeled Bee signals the presence of the subject at the food well. Shock delivery is signaled by a tone. (B) Magnetic total intensity contours were calculated in an east–west vertical plane (the laboratory window faces east) by summing the vector components of the local Hawaiian field with those produced by 1 A of current flowing through the coils. Contours at intervals of 100 μT are shown for the region 1–5 cm from the center of the coils.

alternative tube (in the ambient Hawaiian field) was closed. While the animal was feeding, it was marked with a spot of colored lacquer and, after feeding to repletion, was allowed to return to the hive. The bee usually returned to the tube after a few minutes, but, if not, it was recaptured at the feeding station, where it usually could be found, and placed again at the tube. The first time the bee returned of its own accord was counted as the first pretraining visit. The next time the animal returned, the tube in which it had previously fed was closed and the anomaly was shifted to the other, which now was open and baited with sucrose. There followed four further pretraining visits in which the sucrose together with the anomaly were shifted from one tube to the other, the tube in the ambient field always being closed. Between these visits, the sucrose was moved inwards gradually until the animal was taking it from the well.

In the discriminative training, both tubes were open on each visit. The food well in the anomalous field (S+) contained sucrose, and the food well in the ambient field (S−) contained tap water, unacceptable to the animal and distinguishable

only by taste. Contact of the proboscis with the water was punished automatically by a very mild shock (3 V d.c. pulsed at 1000 Hz) on all visits except the first on which such contact occurred. Error was defined as a signal from a photodetector at the food well or – because an animal could occasionally taste the water without breaking the photobeam – a signal from a shock-detecting circuit, whichever occurred first; normally, the two detectors operated almost simultaneously. After making an error, the animal was free to correct its choice, each visit ending with feeding to repletion and return to the hive. The anomalous field was on the left in half the visits and on the right in the rest, in balanced quasi-random order.

On its first day of training, the animal was permitted as many visits as necessary to achieve a criterion performance of six correct choices in succession (chance probability = 0·016) or seven correct choices out of eight (chance probability = 0·03) with an S+ current of 1 A (intensity of the anomaly at the photobeam approximately 30 times earth strength). Then the animal was shut out for the night, or, if enough time remained, training to the same criterion continued at 0·1 A. On subsequent days, the animal was trained to the same criterion at progressively reduced currents (see the points plotted in Fig. 2) until it failed at some level to reach the criterion in 32 visits. At the beginning of a day, the animal was retrained to the same criterion at the lowest current level it had discriminated successfully on the previous day. It was the subjective impression of the experimenters that with the higher currents the bees seemed to be able to make the discrimination before landing, but with lower currents they tended to land and approach the well tentatively before either retreating or advancing to drink, although no systematic data are available on this point.

In Fig. 2, the individual performances of nine animals are plotted in terms of the number of visits required to satisfy the criterion with the criterion visits themselves excluded; that is, a zero is plotted for any current level if the first six choices of the bee were correct or if seven of the first eight choices were correct, and the curve terminates at the lowest intensity discriminated. The training of several other bees was begun, but they stopped coming to the laboratory (usually from one day to the next) before their thresholds could be determined. All but two of the nine bees for which threshold determinations could be made accomplished the initial discrimination well within 32 visits, and all continued to perform accurately for extended periods before finally failing at some current level to meet the criterion within the 32-visit limit. Note that, in the training of the first four animals, the current was reduced abruptly from 0·1 to 0·01 A, but for the rest the change was more gradual, as it was for all animals at levels below 0·01 A. Shown also in Fig. 2 is the proportion of animals meeting the criterion at each current level. The two poorest animals (nos 6 and 9) succeeded at 2×10^{-3} A (intensity of the anomaly at the food well 2600 nT, 6 % of background) and the best animal (no. 7) succeeded at 2×10^{-5} A (intensity 26 nT, 0·06 % of background) but not at lower currents. The threshold current, estimated from the median performance, is 2×10^{-4} A (260 nT, 0·6 % of background).

Although numerous hypotheses about the way in which animals might respond

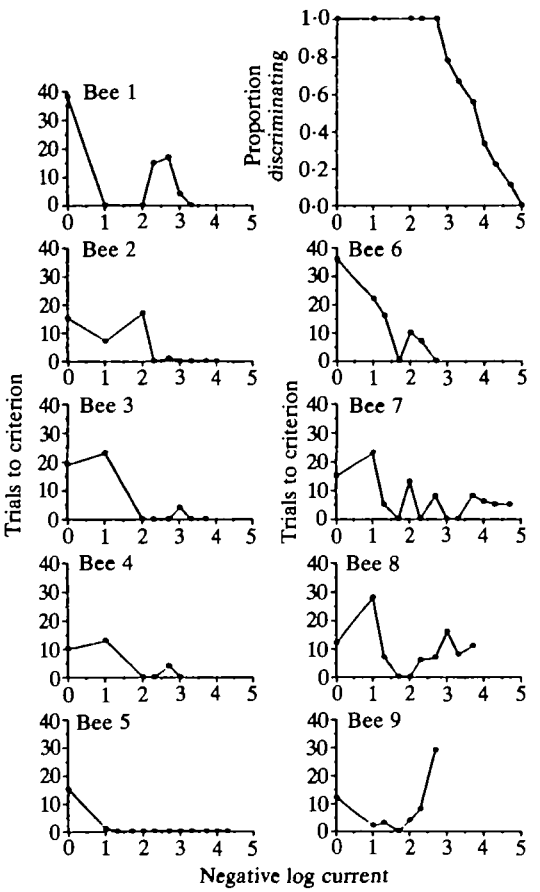


Fig. 2. The performance of each of nine honeybees plotted in terms of the number of trials required to satisfy the criterion for each of a series of anomalies of decreasing intensity indexed by the current (in amps) passed through the coils used to produce the anomalies. With a current of 1 A, the intensity of the anomaly at the point of reinforcement was about 30 times the background intensity, and with a current of 10^{-5} A, at which the best animal failed, the intensity of the anomaly was 0·03% of background. The training of any animal ended if, at any current level beyond the first, it failed to meet the criterion of discrimination in 32 visits, and the plot for each animal terminates at the lowest intensity discriminated. Plotted in the upper right hand corner is the proportion of animals meeting the criterion at each current level. For further details, see text.

to magnetic field direction have been proposed (e.g. Jungerman & Rosenblum, 1980; Korall & Martin, 1987; Leask, 1977) only the ferromagnetic transduction hypothesis (Kirschvink & Gould, 1981) provides a plausible mechanism for the sensitivity of honeybees to localized anomalies that we have found here. The discovery of large numbers of superparamagnetic and single-domain magnetite particles in the anterodorsal abdomen (Gould *et al.* 1978) and the finding that magnetic but not copper wire impairs magnetic discrimination by honeybees,

when mounted close to the magnetite (Walker & Bitterman, 1989), support the ferromagnetic transduction hypothesis.

Preliminary results for bees trained in the situation described here indicate that the effect of magnetic wire is highly localized. (The wires used were of stainless steel, 0·36 mm in diameter and 1–2 mm in length.) One of two bees with magnetic wire attached to the anterodorsal abdomen reached the criterion of discrimination only after 87 visits at 1 A and failed to discriminate at 0·1 A; the other failed in 120 visits at 1 A. In contrast, two control animals carrying copper wire reached the criterion after 7 and 20 visits, respectively, on the first day of training. Two bees with magnetic wire attached to the thorax reached the criterion at 1 A after 42 and 48 visits, respectively. A bee with a magnetic wire attached to the posterodorsal abdomen succeeded after five visits on the first day and went on to discriminate at 2×10^{-4} A (0·6 % of background) on the second day.

Although it is tempting to speculate on the biological significance of our results, we believe that caution is advisable. The sensitivity we have demonstrated is consistent, for example, with the suggestion (Martin & Lindauer, 1977) that the solar quiet daily variation in the geomagnetic field might serve to entrain the circadian rhythm, although the changes in the orientation to gravity of waggle dances which provide the behavioral indices of sensitivity to daily geomagnetic variation (Lindauer & Martin, 1972) are weak and highly variable (Towne & Gould, 1985). Furthermore, the diurnal geomagnetic signals are embedded in considerable noise of similar amplitudes and time scales (Skiles, 1985). Our results are consistent also with the possibility that honeybees use the geomagnetic field for navigation, as has been suggested for homing pigeons (Keeton, 1972). The technique of attaching magnetic wires to individual bees permits impairment experiments such as those that have been made with pigeons (Keeton, 1972); success in returning to the hive after feeding to repletion at a remote site could be measured for marked animals carrying magnetic or nonmagnetic wires.

Our technique makes it possible also to test the prediction from the ferromagnetic transduction hypothesis that sensitivity to change in intensity will be low in weak fields, increase rapidly to a maximum at about earth strength, and decline in fields above earth strength (Kirschvink & Walker, 1985). The results of such measurements should permit estimation of the magnetic moment of candidate magnetite-based receptors and so guide the search for them.

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