

MAGNETIC ORIENTATION IN A SMALL MAMMAL,
PEROMYSCUS LEUCOPUS

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ABSTRACT.—We displaced white-footed mice (*Peromyscus leucopus*) 40 m away from their home areas and released them in a circular arena. Mice concentrated their exploratory and escape activity in the portion of the arena corresponding to home direction. In another group of mice, we reversed the horizontal component of the geomagnetic field surrounding them during displacement. These individuals concentrated their activity in areas of the circular arena opposite home direction. Mice were not likely using visual, chemical, or kinesthetic cues to establish home direction. Tissues of *P. leucopus* exhibit strong isothermal remanent magnetization and may contain biogenic ferrimagnetic material. Our results suggest that white-footed mice have a magnetic sense and use the geomagnetic field as a compass cue.

Many kinds of animals use the geomagnetic field as a compass-orientation cue (Kirschvink et al., 1985a). Magnetotactic organisms include bacteria (*Aquaspirillum magnetotacticum*; Frankel et al., 1979, 1981), bees (*Apis mellifera*; Gould, 1980; Gould et al., 1978, 1980; Lindauer and Martin, 1968), elasmobranchs (*Urolophus halleri*, *Triakis semifasciata*; Kalmijn, 1982), teleosts (*Thunnus albacares*, *Oncorhynchus tshawytscha*; Walker et al., 1984), amphibians (*Eurycea lucifuga*, *Notophthalmus viridescens*; Phillips and Adler, 1978), and birds (*Erithacus rubecula*, *Sylvia borin*, *Columba livia*, *Passerina cyanea*, *Dolichonyx oryzivorus*; Beason and Nichols, 1984; Lednor, 1982; Ossenkopp and Barbeito, 1978; Wiltschko, 1983). Little research has been done on magnetic-field perception in mammals. Whether human beings are capable of deriving directional information from the geomagnetic field remains controversial (Baker, 1980, 1981; Gould and Able, 1981; Kirschvink et al., 1985a). Mather and Baker (1981) reported that European woodmice (*Apodemus sylvaticus*) use the Earth's magnetic field as a compass-orientation cue.

With exception of magnetotactic mud-dwelling bacteria (Frankel et al., 1979, 1985; Lins de Barros and Esquivel, 1985), the sensory basis for magnetic-field perception is unknown. There is considerable interest in the role played, if any, by biogenic magnetite (Fe_3O_4) in magnetoreceptor organs. Kirschvink (1982) and colleagues (Kirschvink and Gould, 1981; Kirschvink and Walker, 1985) reviewed possible designs of a magnetite-based magnetoreceptor. Histological and magnetometric analysis of tissues from bees (*Apis mellifera*; Gould et al., 1978; Kuterbach et al., 1982; Walcott, 1985; Walcott and Walcott, 1982), tuna (*Thunnus albacares*; Walker et al., 1984, 1985a), birds (*Columba livia*, *Dolichonyx oryzivorus*; Beason and Nichols, 1984; Walcott et al., 1979; Walcott and Walcott, 1982) and dolphins (*Delphinus delphis*; Zoeger et al., 1981) frequently show close association between iron-rich cells and nerve tissue. The ethmoid region of a range of vertebrates is especially rich in magnetic material (e.g., chinook salmon [*Oncorhynchus tshawytscha*; Kirschvink et al., 1985a, 1985b], tuna [*Thunnus albacares*; Walker et al.,

1984], pigeons [*Columba livia*; Walcott and Walcott, 1982], humans [Baker et al., 1982; 1983], and mice [*Apodemus sylvaticus*; Mather, 1985; Mather et al., 1982]).

We used a modification of the Mather and Baker (1980, 1981) experimental design to test if white-footed mice (*Peromyscus leucopus*) are capable of using magnetic cues in compass orientation. Following standard methods in cryogenic-superconducting-quantum-interference-device magnetometer analysis of biological samples, we examined tissues from *P. leucopus* for remanent magnetization.

METHODS

We conducted field experiments in southern Rhode Island and at the National Zoological Park's Conservation and Research Center in Front Royal, Virginia. Field sites consisted of deciduous forest bordering open field. All forest-field edges were in an east-west direction. Sherman live traps were set for a few meters into the woods in late afternoon. Traps were examined the following morning at approximately 0600 h. Captured animals were placed individually in a transportation device and carried 40 m north or south into the open field. Each animal then was released into a circular arena marked into eight 45° sectors. Two arenas were used during the study; one made of galvanized steel was 35 cm in diameter with sides 22 cm high, the other was of opaque plastic 32 cm in diameter with 15.5-cm-high sides. From the floor of the observation arena, mice were unable to see forest canopy below 20–25 m. Canopy heights at the experimental sites usually were <20 m. Immediately after releasing an animal into the arena, we covered the enclosure with a plate of semitransparent smoked plastic and recorded the compass bearing of the sector in which the animal was located at 10-s intervals for 4 min. The observer stood on either the east or west side of the arena (determined by coin toss) and the orientation of the arena relative to north was changed haphazardly between trials. After the 24 instantaneous samples (Altmann, 1974) were completed, we removed the mouse from the arena, clipped away a small patch of hair from its head (to distinguish new captures from recaptures in subsequent trapping), and released it. Only adults or individuals that had completed their post-juvenile molt were used in the experiments and no mouse was used twice. Fecal pellets or urine deposits left by experimental mice (this occurred infrequently) were removed from the arena immediately. The arena was wiped clean between experimental days. The experiments were conducted from March to September in 1983 and 1984.

The protocol followed by Mather and Baker (1980, 1981) was similar to ours but they used a cross-shaped arena whereas our was circular. A cross-shaped arena permitted a mouse to move in four directions (each arm of the cross). Our circular arena was less restrictive and we were able to record the position of a mouse relative to eight possible directions (each 45° sector). Mather and Baker (1981) found that *Apodemus sylvaticus* concentrated their activity in that part of the test arena corresponding to home direction. If *Peromyscus* behave similarly, mice displaced to the north should concentrate their activity in the southern sectors of the arena and mice displaced to the south should show an orientation response to the north. The purpose of these displacements was to determine if white-footed mice demonstrate an orientation response by concentrating their activity in a particular portion of the circular arena, and to serve as the control for reversed-magnetic-field displacements.

The transportation device consisted of a 17.5-cm-diameter plastic tube (27.5 cm long) wrapped with copper wire. Attached to the tube was a container holding a 12-V wet-cell battery. When current was allowed to pass through the coil, a $3.4 \cdot 10^{-5}$ tesla (0.34 Gauss) magnetic field was established. When the device was held so that the coil-induced magnetic field was opposite the horizontal component of the geomagnetic field, the resultant magnetic field was of the same strength as the Earth's field but of opposite direction. Mice were placed (with their heads pointing toward true magnetic north) in a 3-cm-diameter plastic tube inserted in the center of the larger plastic enclosure. Foam rubber surrounded the tube containing the mouse and the tube itself was sealed at both ends with foam rubber plugs. In this way, mice were unable to assess visual, chemical, or tactile cues during displacement. In the control replicates, the battery was disconnected and the mouse inside the device experienced the natural geomagnetic field.

A second group of mice was tested in the same manner as the controls except that during displacement current from the battery was allowed to pass through the coil surrounding the area in which the mouse was located and the direction of the horizontal component of the geomagnetic field was reversed 180°. The electrical circuit to the coil was broken just before removing the mouse from the transportation device. If *Peromyscus* uses the polarity of the geomagnetic field as an orientation cue, then mice displaced in the reversed field should show an orientation response 180° away from home direction.

From the 24 instantaneous samples for each mouse, we calculated the mean compass bearing of an

individual's activity. The first-order estimate of the mean of the instantaneous samples gave us a measure of the portion of the arena in which mice spent the most time (Altmann, 1974). We used the vector length r of the mean angle as an estimate of the variation in the 24 observations. An individual mouse was considered to have selected a direction if r was >0.35 (that vector length where $P < 0.05$ that the 24 instantaneous sample angles are uniformly distributed). We used second-order calculations (Childs and Buchler, 1982) to derive estimates of the mean angle and vector length of the orientation response of all mice in the control or experimental replicates. The fundamental units of analysis (responses among mice) are statistically independent. Each of the 24 behavioral observations for an individual mouse probably was not statistically independent from preceding or subsequent samples. However, group comparisons were not done using the instantaneous sample angles for individuals. Moore's R^* statistic (Moore, 1980; = D^* in Batschelet, 1981) was used to test if the orientation response of control or experimental mice was uniformly distributed or clustered in a particular direction. The Mardia-Watson-Wheeler test (B) was used to determine if two samples of angular data were drawn from the same population. All calculations of circular statistics were done using algorithms provided by Batschelet (1981).

We followed standard methods in our analyses of rodent tissues for magnetic material (Kirschvink, 1983; Walker et al., 1985b). The following tissues were dissected with non-metallic cutting tools: head, rostrum (all tissue anterior to the plane formed by the leading edge of the zygoma), cranium (tissue posterior to the plane of the zygoma), thorax (tissue between the diaphragm and cervical vertebrae), lumbar (all tissue posterior to the diaphragm), skin, and gut (intestines, stomach, and esophagus). Tissues were tied to cotton thread and lowered into the sensing region of a cryogenic-superconducting-quantum-interference device. The thread was magnetically clean (maximum natural remanent magnetization of $2 \cdot 10^{-12}$ tesla [$2 \cdot 10^{-8}$ emu]). Each sample was measured two or three times and replicates averaged. Saturation isothermal-remanent magnetization was measured immediately after tissues were exposed to a 0.5 tesla (5,000 Gauss) magnetic field for approximately 10 s. The thread used to lower samples into the device was not magnetized for these measurements.

RESULTS

The mean orientation angle (relative to home = 0°) for all controls was 359° ($r = 0.23$, $R^* = 1.28$, $P < 0.01$, $n = 43$; Fig. 1a). Data obtained from the Virginia study site were especially variable. The mean angle for the Rhode Island controls was 1° ($r = 0.29$, $R^* = 1.39$, $P < 0.01$, $n = 34$; Fig. 1b). Results of control displacements show that orientation responses were not uniformly distributed but clustered in the home direction.

If *P. leucopus* uses the geomagnetic field as a compass, then mice subjected to the reversed magnetic field during displacement should show an orientation response 180° from home direction. The mean angle of orientation for all mice displaced in the reversed magnetic field was 163° relative to home direction ($r = 0.17$, $R^* = 0.89$, $P = 0.10$, $n = 41$; Fig. 1c). Again, trials conducted in Virginia were variable. The mean angle of the direction taken by the mice displaced in Rhode Island was 153° ($r = 0.24$, $R^* = 1.14$, $P < 0.025$, $n = 31$; Fig. 1d).

Orientation of all mice (the total data set) displaced in a reversed magnetic field was markedly different from that of all mice displaced in the normal geomagnetic field ($B = 176$, $P < 0.001$, $n = 84$). It might be argued that the data are biased by including those responses not significantly concentrated in a particular direction (i.e., where the vector length r of a mouse's response is <0.35). Excluding nonsignificant responses from the data had little effect in comparison of control and experimental mice; they still were significantly different ($B = 117$, $P < 0.001$, $n = 68$).

Orientation responses of mice used in the preceding analyses were adjusted relative to home direction (i.e., home = 0°). When the data were not so adjusted, control and experimental mice did not select a particular compass direction (control $\bar{\phi} = 231^\circ$, $r = 0.03$, $R^* = 0.17$, $P > 0.9$, $n = 43$; experimental $\bar{\phi} = 59^\circ$, $r = 0.08$, $R^* = 0.04$, $P > 0.9$, $n = 41$).

We stood on either the east or west side (randomly chosen) of the circular orientation arena while observing mice. To test if mice were responding to the observer rather than home direction, we adjusted the orientation responses of mice so they were relative to the observer's position at the arena during the 4-min period of instantaneous sampling. In this way, an orientation response of 180° would indicate that a mouse concentrated its activity in that portion of the arena opposite

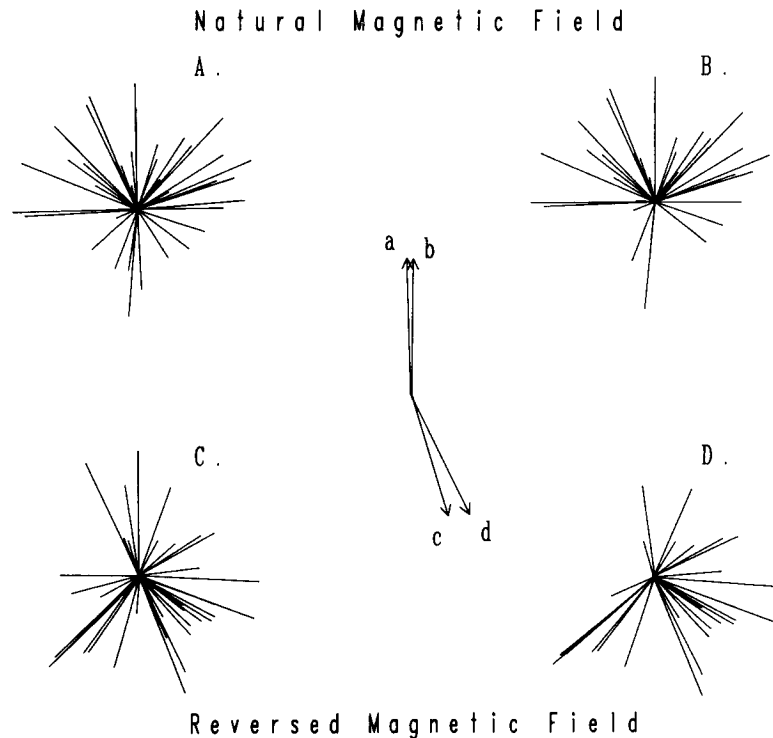


FIG. 1.—Orientation responses of mice displaced in normal and reversed magnetic fields. The direction of each vector is the mean of 24 angles measured on an individual mouse. The length of each vector is proportional to the first-order estimation of r for each individual's orientation response. Home is to the top. (A) Mice displaced in the natural geomagnetic field, Virginia and Rhode Island data combined. (B) Mice displaced in the natural geomagnetic field, Rhode Island data only. (C) Mice displaced in the reversed magnetic field, Virginia and Rhode Island data combined. (D) Mice displaced in the reversed magnetic field, Rhode Island data only. The mean direction of the vectors from each figure is shown in the middle. The lower case letters (a-d) correspond to the source of the data (A-D).

the observer. An orientation response of 0° would indicate that the subject concentrated its activity on the same side of the arena as the observer. Although the mean angle of orientation for both control and experimental mice was opposite the observer, the distribution of angles in each group was uniform (control $\bar{\phi} = 191^\circ$, $r = 0.14$, $R^* = 0.87$, $P > 0.1$, $n = 43$; experimental $\bar{\phi} = 181^\circ$, $r = 0.07$, $R^* = 0.37$, $P > 0.5$, $n = 41$). These results indicate that the different orientation responses of mice displaced in a normal and reversed magnetic field are not a result of observer effect.

Although a compass positioned at mouse level inside the metal arena indicated true northward direction, it is possible that galvanized steel distorted the geomagnetic field within the chamber. To control for this uncertain source of error, we switched to the plastic arena. Results obtained using the plastic and metal arenas for the normal field displacements were not significantly different ($B = 15$, $P > 0.1$, $n = 43$). Similarly, there was no significant difference in results obtained from the two types of arenas for displacements under reversed field conditions ($B = 26$, $P > 0.1$, $n = 41$). Responses of mice displaced in the normal geomagnetic field and observed in the plastic arena were home-directed ($\bar{\phi} = 351^\circ$, $r = 0.30$, $R^* = 1.36$, $P < 0.005$, $n = 26$). Mice displaced in the reversed magnetic field and observed in the plastic arena showed a response 140° different from that of the controls ($\bar{\phi} = 131^\circ$, $r = 0.15$, $R^* = 0.72$, $P > 0.10$, $n = 22$). Distributions of responses measured from mice displaced in normal and reversed magnetic fields and observed in the plastic arena were significantly different ($B = 90$, $P < 0.05$, $n = 48$).

TABLE 1.—Isothermal remanent magnetization of tissues from *Peromyscus leucopus*. Values presented are 10^{-10} tesla (10^{-6} emu)/g tissue.

Tissue	n	\bar{x}	SD
Whole head	6	3.1	1.1
Cranium	5	3.7	4.8
Rostrum	4	0.9	0.8
Skin	6	51.2	17.1
Gut	3	58.7	12.3
Thorax	6	20.8	34.8
Lumbar	6	3.6	3.2

Tissues from *P. leucopus* were magnetic (Table 1). The extremely high values for gut, skin, and possibly thorax may be a result of superficial contamination or ingestion of contaminated particles. The remaining tissues exhibited lower, but consistent isothermal-remanent magnetization. We do not believe that the magnetic remanence measured from *P. leucopus* tissues was solely a result of contamination obtained when preparing specimens for magnetometer analysis. Heads of big brown bats (*Eptesicus fuscus*) are magnetic (Buchler and Wasilewski, 1982, 1985). To test if isothermal-remanent magnetization in bats was caused by superficial contamination by magnetic particles in the laboratory, we washed four *E. fuscus* heads in 10% HCl solution for 9 h in an ultrasonic cleaner. After this treatment, the heads lost approximately 43% of their original mass yet retained 66% of their isothermal-remanent magnetization. If the source of such magnetization in *E. fuscus* was superficial contamination, the acid solution would have dissolved magnetic particles on the surface of the tissue (Kirschvink, 1983) and resulted in a marked drop in isothermal-remanent magnetization. This was not the case. We prepared *P. leucopus* tissues in the same manner and in the same laboratory as the bat heads. We assume if bat heads were not contaminated, rodent tissues were not either.

DISCUSSION

White-footed mice displaced 40 m away from their home area concentrated escape and exploratory activity in a circular arena in a direction that corresponds to home. Mice displaced in the same manner, except in a reversed magnetic field, concentrated their activity in the portion of the circular arena opposite home direction. Responses of control mice differed from those of experimental mice and the direction of the difference was consistent with the hypothesis that *P. leucopus* uses the geomagnetic field to derive compass information. Results obtained at the Virginia site were more variable than those obtained in Rhode Island. We do not know why this is so.

It is unlikely that mice used the position of the sun as an orientation cue because experiments were terminated when shadows appeared in the circular arena. Chemical cues could not have provided information on compass direction because the circular arena was covered with translucent plastic during the test period and the plastic tube holding mice was sealed on both ends with foam rubber during displacement. Visual cues were denied mice during displacement and the walls of the circular arena were sufficiently high to obstruct view of the forest canopy. Kinesthetic information (Mittelstaedt and Mittelstaedt, 1982) was the same for both experimental and control mice, thus cannot be used to explain the different orientation response between the two groups.

Results from the magnetometry analyses indicate that tissues from *P. leucopus* are magnetic. Further analyses need to be conducted to determine if the source of magnetization is biogenic magnetite (Kirschvink, 1983; Walker et al., 1985b). The ethmoid region of *P. leucopus* heads was not especially magnetic. Buchler and Wasilewski (1982, 1985) reported a similar distribution of isothermal-remanent magnetization in tissues from bats (*Eptesicus fuscus*); however, several investigators found especially rich concentrations of magnetic material in the ethmoid region of a variety of vertebrates (Baker et al., 1983; Kirschvink et al., 1985a, 1985b; Walcott and Walcott,

1982; Walker et al., 1984). Further anatomical, physiological, and behavioral studies are needed to determine if biogenic magnetite is associated with the magnetoreceptor organ.

Results of our study are consistent with those obtained by Mather and Baker (1981) for *Apodemus sylvaticus*. These data suggest the presence of a magnetic sense in class Mammalia. However, this conclusion must be considered tentative until further research is done. The utility of the experimental design offered by Mather and Baker (1980) and used in this study (in modified form) requires further examination. Sauve (1985) followed Mather and Baker's (1980) experimental protocol and was unable to obtain evidence of a home-directed response in *Apodemus sylvaticus* when displaced in unaltered magnetic-field conditions.

It is not known if mice are using the horizontal vector of the geomagnetic field as an orientation cue. The device that we used, as did Mather and Baker (1981), reversed the direction of the horizontal component of the Earth's field but also changed the inclination of the resultant magnetic vector. Wiltschko and Wiltschko (1972) argued that some species of birds use the inclination of the geomagnetic field, not the horizontal vector, to derive direction information. Determining the component of the geomagnetic field used as a compass cue will require further experimentation with different coil configurations.

A magnetic sense of direction may be associated with homing behavior in mice. In general, homing success decreases with increasing displacement distance (Joslin, 1977). Whether homing is goal-oriented or involves random search is controversial (Bovet, 1978). Bovet's (1984) "critical-distance" hypothesis incorporates both goal-directed and random-search processes. His data on movements of displaced red squirrels (*Tamiasciurus hudsonicus*) suggest that the initial track taken by a displaced animal is goal-oriented (toward home). If familiar terrain is not reached after some "critical distance" is traveled, the animal returns to the starting place (release site) and searches for home in a different direction. Bovet (1984) proposed that the "critical distance" corresponds to the maximum distance covered previously on spontaneous exploratory forays away from home. How home direction is assessed is unknown; however, our results and those of Mather and Baker (1981) open the possibility of a magnetic compass.

Traditionally, homing experiments consist of capturing an animal, displacing it some distance away from the capture site, and monitoring its movements upon release. The sudden displacement of an animal outside its home area has no regular counterpart in nature. It is unclear how homing behavior manifests itself in an animal's lifetime. One possibility is exploratory behavior. Exploration is thought by some to be an extremely important aspect of an animal's life history (Baker, 1978). Through exploratory forays outside its home area, an animal learns of alternative foraging patches, shelter sites, and potential mates. Exploratory excursions may be prerequisite to successful dispersal (Baker, 1978; Lidicker and Caldwell, 1982). Unfortunately, little field research has been conducted on animal exploration. Bovet (1984), however, presented several maps of exploratory forays taken by red squirrels. His data show that the outward-bound (away from home) component of an excursion outside the home area is not congruous with the often linear inward-bound (return to home) component. Our results and those of Mather and Baker (1981) suggest that a magnetic compass may be used by an animal to determine home direction in unfamiliar terrain. The ecological and evolutionary importance of magnetoperception, homing, exploration, and orientation in small mammals will remain uncertain until additional research is done.

Future investigators of magnetoperception would be well served by reviewing the history of research in other taxonomic groups, especially birds and humans (Keeton, 1974; Kirschvink et al., 1985a; Ossenkopp and Barbeito, 1978; Walcott, 1982; Wiltschko, 1983). Careful design is fundamental to any experiment but especially so in studies of magnetotaxis. Because the sensory modalities experienced by human beings may not include cues critical to animals, and because it is not altogether clear what cues animals may be using, challenges in designing "clean" experiments are significant. Two decades of research on birds has shown that avian orientation and navigation systems usually are based on redundant suites of cues; when one cue becomes unavailable (e.g., obstruction of the sun or stars by clouds), attention shifts to another (e.g., magnetic field, sounds—Walcott, 1982; Wiltschko et al., 1983). Which cues are primary and

secondary is dynamic and can change with age or experience (Wiltschko, 1983; Wiltschko and Wiltschko, 1981; Wiltschko et al., 1983).

Until the suite of orientation cues used by rodents is better understood, signal-to-noise ratios in experimental data may be low. Avian magnetobiologists have been particularly successful in clarifying if, how, when, and why certain species of birds use magnetic cues because of critical data obtained in replicating experiments and careful scrutiny of empirical data. In essence, avian ethologists have filtered the various source components of noise from the data, thus have increased the strength of the resulting signal. Animal magnetoperception has been a controversial field. In the case of avian orientation, this controversy has led to increased refinement of experimental design, data analysis, and in the end, a better understanding of avian orientation and migration. Similarly, research on magnetoperception in humans or the existence of a magnetite-based magnetoreceptor presently is catalyzed by a healthy measure of controversy (Kirschvink et al., 1985a). There is no reason to expect that studies of mammalian magnetoperception will be spared from conflicting or ambiguous results. We hope that, as seen in research on other taxa, controversy will play a central role in stimulating investigators to replicate experiments and design better ones.

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