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Magnetic compass orientation in C57BL/6J mice

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We report evidence for a robust magnetic compass response in C57BL/6J mice. Mice were trained to build their nests in one of four magnetic directions by creating a light gradient along the long axis of a rectangular cage and positioning a nest box at the opposite (dark) end. The mice were then tested overnight in a circular, visually symmetrical arena in one of four magnetic field alignments. The positions of the nests built in the test arena showed strong unimodal orientation in the magnetic direction coinciding with the dark end of the training cage.

Magnetic compass orientation has been demonstrated in all vertebrate classes, including fish, amphibians, reptiles, birds, and mammals, as well as in a variety of invertebrates (for reviews, see R. Wiltschko & W. Wiltschko, 1995; W. Wiltschko & R. Wiltschko, 2005). In mammals, early attempts to demonstrate magnetic compass orientation produced mixed results or had serious methodological flaws (August, Ayvazian, & Anderson, 1989; Madden & Phillips, 1987; Mather & Baker, 1981; Sauvé, 1988). More recent studies, however, have yielded convincing evidence for the use of magnetic field information in two families of mole rats and the Siberian hamster, *Phodopus sungorus*. Zambian Ansell's mole rats, *Cryptomys anselli*, and blind mole rats, *Spalax ehrenbergi*, show a innate preference to build their nests in magnetic easterly to southeasterly directions; rotation of the horizontal component of the magnetic field produces corresponding rotation of the nest positions (Burda et al., 1991; Burda, Marhold, Westenberger, Wiltschko, & Wiltschko, 1990; Kimchi & Terkel, 2001; Marhold, Beiles, Burda, & Nevo, 2000; Marhold, Wiltschko, & Burda, 1997). In *S. ehrenbergi*, the magnetic compass also appears to be involved in housekeeping behaviors (e.g., location of food storage and defecation areas), labyrinth maze learning, and path integration (Kimchi, Etienne, & Terkel, 2004; Kimchi & Terkel, 2001). Siberian hamsters also use magnetic compass cues to position nests and can learn to position nests along an arbitrary axis with respect to the magnetic field (Deutschlander et al., 2003). In contrast to mole rats, however, the hamsters' responses are relatively weak and bimodally distributed.

In the present article, we report the development of an assay that elicits robust unimodal magnetic compass orientation in inbred C57BL/6J mice. Specifically, we show that these mice can be trained to position their nests with a high degree of accuracy in a learned direction relative to the magnetic field. Previous studies have shown that C57BL/6J mice also perform well in spatial tasks—for example, modified Morris water maze tasks (e.g., Stavnezer, Hyde, Bimonte, Armstrong, & Denenberg, 2002; Wahlsten, Cooper, & Crabbe, 2005)—making them an excellent model organism for future studies of the relative importance of local spatial cues (familiar landmarks) versus global directional cues (the geomagnetic field). Genetic knockouts of genes that have been implicated in magnetoreception (e.g., cryptochromes; Ritz, Adem, & Schulten, 2000) are also available in C57BL/6J mice (Sancar, 2004). Consequently, this strain of mice can be used to investigate the molecular mechanisms underlying the magnetic compass sense and, if knockout studies are successful, to compare the performance of mice with and without a functional magnetic compass sense in a variety of spatial and directional tasks.

METHOD

Study Animals, Breeding, and Care

For this study, C57BL/6J stocks obtained from the Jackson Laboratory (JAX) were bred in the laboratory. After weaning, the mice were held in same-sex sibling groups in clear polycarbonate cages lined with wood shavings under a 15:9-h light:dark photoperiod

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(light 0500–2000 h, EST). Food (rodent pellets 2018, Harlan Teklad) and water were provided ad lib. The experiments took place between June 10 and October 31, 2005. All the experimental procedures were approved by the Virginia Tech Animal Care Committee.

Training

For training, male mice were taken from the breeding colony and transported to the Behavioral Testing Facility (BTF) of the Department of Biological Sciences at Virginia Tech, located approximately 6 km from the main campus. The BTF consists of a central "hub" building supplying electricity, filtered to minimize radio frequency interference, and forced air for heating and cooling, via underground ducts to four satellite buildings. The satellite buildings are double walled to minimize sound transmission and are constructed of nonmagnetic materials. The mice were trained and tested in two separate satellite buildings, located approximately 50 m apart.

The procedures for both training and testing were derived from earlier experiments in our laboratory with Siberian hamsters (Deutschlander et al., 2003). The mice were trained individually in separate cages (48 × 25.5 × 16 cm) with a layer of pine shavings as bedding and were provided with three nestlets (pulped, sterilized, cotton fiber pressed into flat, 5 × 5 cm pieces; Ancare) for nest building and with food and water ad lib. A black plastic nest box was placed against one end, with the entrance facing toward the center of the cage. Four shelving units, each holding three mouse cages on separate shelves, were centered in the middle of the training room (3.5 × 3.5 m), so that the shelving units faced in magnetic directions that differed by 90º (i.e., 70º, 160º, 250º, and 340º; see Figure 1). The cages were placed on the shelves with the nest box at the back, in the shadow of the overlying shelves (*dark end*). The entrance of the nest box faced outward toward the open end of the shelf. Food and a water bottle were provided at the open end of the cage (*light end*). Mice typically built nests in the nest box at the dark end of the cage. Any nests that were built outside of the nest box were placed into the nest box as soon as discovered, usually the day after the mouse was first put into training. Overall, this occurred in approximately half of all the mice that were subsequently tested (i.e., 58% of the 31 mice that built nests in the testing arena meeting our a priori criteria [see below] and 35% of the mice [$n = 7$] that did not build nests meeting these criteria).

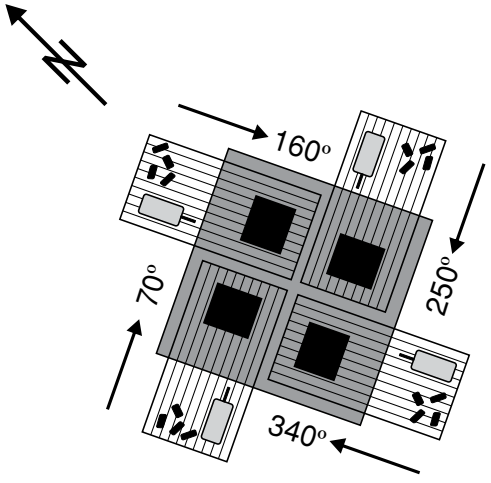

Figure 1. Schematic drawing of the setup used to train C57BL/6J mice to place their nests in a given magnetic direction. Four vertical shelves, each holding three mouse cages stacked on top of each other, were centered in the middle of the training room (large square), so that each shelf faced in one of four magnetic directions (i.e., 70º, 160º, 250º, and 340º). The cages were placed on the shelves so that the nest box was at the sheltered (*dark*) end with the entrance facing out. Food and water were provided at the outer (*light*) end. The light gradient encouraged the mouse to build its nest in the nest box at the dark end of the cage.

Individual mice were randomly assigned to one of the four training directions and were trained for a minimum of 5 days (average, 11 days; range, 5–24 days; discrepancy between length of training was mainly due to testing outage caused by bad weather and the availability of personnel for testing) before being tested for magnetic compass orientation. During both training and testing, the mice were held on a 15:9-h light:dark photoperiod (light, 0500–2000 h, EST), maintaining the same light cycle as the main breeding colony. Training and testing buildings were kept at an average temperature of 21.0ºC (range, 15.6º–24.3ºC) and an average relative humidity of 38% (range, 32%–50%).

Testing

Testing arena. The mice were tested individually in a large (88-cm diameter), radially symmetric, circular arena made of black polyethylene and surrounded with black curtains to block any visual cues. A 75-W, 12-VDC tungsten/halogen light source (ECY; EiKO Ltd.) projected through a 1.2 × 1.2 m white Plexiglas sheet centered above the arena provided diffuse illumination during the light phase of the photoperiod.

Testing fields. The mice were tested in four different alignments of the magnetic field: the ambient magnetic field (magnetic north [mN = 360º]) and three shifted fields with magnetic north at geographic east (mN = 90º), south (mN = 180º), or west (mN = 270º). The three shifted fields were produced by adding horizontal artificial field(s) aligned 135º clockwise (east field), 135º counterclockwise (west field), or both (south field) to the ambient magnetic field (Figures 2 and 3). The shifted fields closely resembled the ambient geomagnetic field in inclination (±1.5º) and total intensity (±2%), measured with a Fluxgate magnetometer (Applied Physics Systems, model 520A). Magnetic fields were produced by a pair of horizontal, perpendicularly aligned, cube-surface coils wrapped on a wooden frame with a linear dimension of ~1.2 m surrounding the testing arena (see Phillips, 1986a). The coils were powered by a custom, current-regulated power supply (Design Solutions Inc.) located in the hub building and connected to the coils by means of shielded wire run through an underground conduit. The outputs of the power supply were equipped with EMI filters (Dearborn 1JX2459) to minimize low-level radio frequency fields, which have been shown to disrupt magnetic compass orientation in a migratory bird (Ritz, Thalau, Phillips, Wiltschko, & Wiltschko, 2004). Each coil was double wrapped in a four-element configuration (Merritt, Purcell, & Stroink, 1983) and was controlled by reversing the direction of current flow in one of the two strands of wire (Kirschvink, 1992; Phillips, 1986b). When the current flow through the two wraps of one of the cube-surface coils was antiparallel, the fields produced by the two wraps of the coil canceled out. When the flow was parallel, the fields produced by the two wraps added together and produced the artificial field. The output of the power supply was the same in all four magnetic field treatments (Figure 3), regardless of whether current was flowing in a parallel or an antiparallel direction through the two wraps of each coil (in the ambient magnetic field [mN = 360º], the current flow was antiparallel in both coils), so any associated artifacts (heat, vibrations, etc.) were the same. Training cages (Figure 1) were also enclosed in a double coil system, identical to that used in testing. However, the current to these coils was set to zero.

Testing procedure. The mice, on average 74 days old (range, 60–85 days), were tested individually, one per night. Tests began in the late afternoon, 2–3 h before the beginning of the dark phase of their light cycle, and ended the next morning. Each mouse was tested in one of the four magnetic field alignments (see Figure 3 and above; individual mice were tested only once). Before a mouse was placed into the arena, the arena floor was covered with a thin layer of pine shavings. Four pieces of food, four nestlets, and four small cups with water were placed symmetrically around the center of the arena.

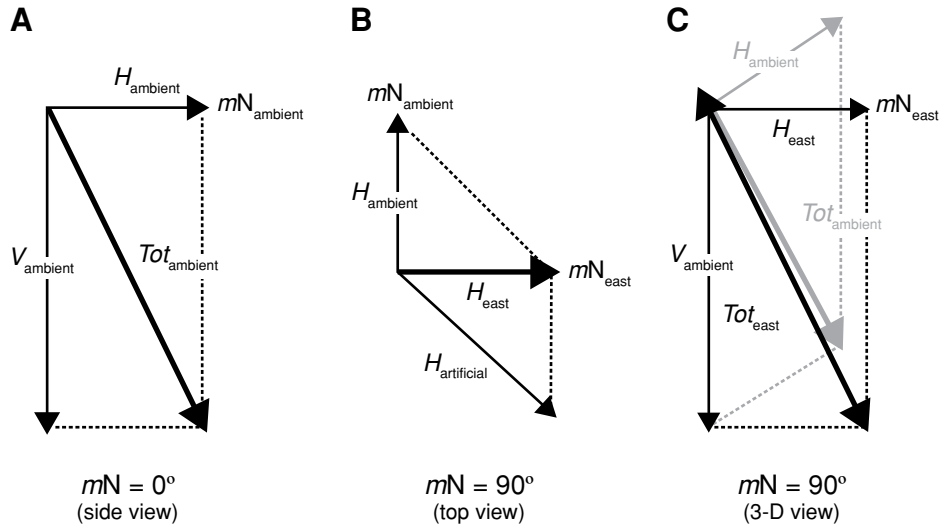

Figure 2. Production of artificial magnetic field. (A) Ambient magnetic field (*m*N = 0º; side view) showing horizontal component ($H_{ambient}$), vertical component ($V_{ambient}$), total field ($Tot_{ambient}$), and horizontal azimuth—that is, the direction indicated by a dipole compass ($mN_{ambient}$). (B) East field (*m*N = 90º; top view) showing addition of artificial field ($H_{artificial}$) produced by horizontal coil aligned 135º clockwise of $mN_{ambient}$, resulting in a horizontal component (H_{east}) equal in intensity to $H_{ambient}$ but rotated 90º clockwise (mN_{east}). (C) East field (*m*N = 90º; 3-D view) showing summation of H_{east} (vector sum of $H_{ambient}$ and $H_{artificial}$; see Figure 1B) with $V_{ambient}$ to produce a resultant field with a total intensity (Tot_{east}) and inclination (i.e., vertical angle) equal to that of the ambient field. Not shown is the west field (*m*N = 270º), which is produced by summation of an artificial horizontal field of the same intensity as that used to produce H_{east} but aligned at 135º counterclockwise of $mN_{ambient}$. This results in a horizontal component (H_{west}) equal in intensity to $H_{ambient}$ but rotated 90º counterclockwise. Also not shown is the south field (*m*N = 180º), which is produced by summation of the artificial fields from *both* horizontal coils with the ambient field. This produces a horizontal component (H_{south}) equal in intensity to $H_{ambient}$ but rotated by 180º. Use of the stationary double coil system, therefore, made it possible to produce four testing fields with horizontal components that were more or less equal (i.e., $H_{ambient} = H_{east} = H_{west} = H_{south}$). Because the vertical component ($V_{ambient}$) is unaffected by the horizontal coils, the three rotated fields (*m*N = 90º, 180º, and 270º) also closely resembled the ambient field (*m*N = 0º) in inclination and total intensity (Figure 1B). See Phillips (1986a) for details.

Once the arena was prepared, the observer walked to the training building, where a mouse was removed from its cage and placed in a light-tight container for transport to the testing building. During transport, the container was rotated slowly to prevent the mouse from gathering directional information about the direction of displacement. Once inside the testing building, the mouse was removed from the transport container and placed in an elevated release chamber in the center of the arena. The observer then left the room, waited for 60 sec, and then lowered the bottom of the release chamber, using a hydraulic mechanism, releasing the mouse into the arena.

Between trials, the wood shavings, nestlets, and food pieces were removed from the arena and discarded, and the arena was thoroughly cleaned with BioKleen (BioSentry Inc.) and 70% ethanol.

Data Recording and Testing Criteria

The following morning, the experimenter recorded the position and quality of the nest. The directional choice of the mouse was determined by recording the bearing of the nest from the center of the arena to the nearest 5º. The topographic bearing (location within the arena), magnetic bearing (bearing relative to magnetic north of the testing field), and trained bearing (bearing relative to the trained magnetic direction) were recorded for each nest.

On the basis of our earlier experiments with hamsters (Deutschlander et al., 2003) and preliminary experiments with mice (Edgar, 2004), we established the following testing criteria. (1) We did not test on nights when thunderstorms were in the area and excluded tests carried out during nights when a thunderstorm unexpectedly occurred ($n = 2$). (2) A nest had to incorporate at least 50% of the nesting material, be cup shaped, and be positioned in the outer two thirds of the arena (nests were excluded if they were in contact with the base of the release device, which consisted of a 34-cm-diameter, 10-mm-thick Plexiglas disk in the center of the arena floor). As in the earlier experiments with hamsters and preliminary experiments with mice, nests not meeting these criteria were not significantly oriented with respect to the trained magnetic direction ($\alpha = 102.8º$–$282.8º$, $r = .14$, $p = .76$, $n = 14$).

Statistical Analysis

Since directional responses form continuous distributions (e.g., 360º and 1º are adjacent values), they were analyzed using standard circular statistics (Batschelet, 1981). The data were pooled in three different ways: (1) absolute, or *topographic*, bearings, (2) *magnetic* bearings (angular deviation from magnetic north = 0º), and (3) *trained* bearings (angular deviation from the trained magnetic direction; see Figure 4). The resultant vector was calculated for each distribution of pooled bearings by vector addition, treating each individual bearing as a unit vector. The mean vector length (r) was obtained by dividing the length of the resultant vector calculated for each distribution by the sample size; r provides a measure of the clustering in the distribution of bearings, ranging in value from 0.0 for a uniform distribution to 1.0 for a distribution in which all the bearings are in a single direction. The Rayleigh test was used to

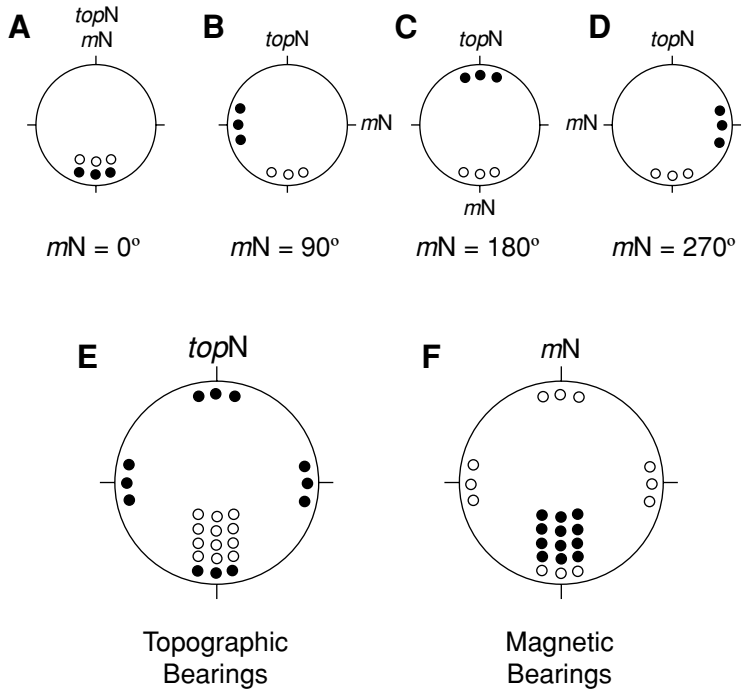

Figure 3. Use of four symmetrical testing fields to distinguish magnetic and nonmagnetic orientation. (A–D) Hypothetical responses of individual mice, with an equal number tested in each of four symmetrical testing fields (each mouse tested only once). (E) Pooled distribution of absolute, or *topographic*, bearings. Topographic bearings of mice orienting to nonmagnetic cue are clustered, whereas topographic bearings of mice showing a consistent magnetic compass response are uniformly distributed. (F) Pooled distribution of magnetic bearings. Magnetic bearings of mice orienting, relative to a nonmagnetic cue, are uniformly distributed, whereas those of mice orienting with respect to the magnetic field are clustered. To distinguish a "fixed," or innate, magnetic compass response from a learned magnetic compass response, magnetic bearings are rotated so the expected magnetic direction for each training group is at 0° (see Table 1). Each data point represents the hypothetical position of a nest built by an individual mouse. Solid symbols, mice orienting relative to the magnetic field; open symbols, mice orienting relative to a nonmagnetic directional cue present in the testing arena; *m*N, magnetic north; *top*N, topographic north.

determine whether the clustering of bearings was greater than would be expected by chance; critical values for r as a function of sample size were obtained from Table H in Batschelet. Given the bimodal magnetic compass orientation observed in hamsters (Deutschlander et al., 2003), we used the method of doubling the angles to test for bimodality ($r_{\text{bimodal}} > r_{\text{unimodal}}$); the Rayleigh test was used on the distribution of doubled bearings to test for bimodal orientation (Batschelet, 1981). A 95% confidence interval around the mean bearing was used to test whether the clustering in the distribution of bearings plotted relative to the trained magnetic direction was consistent with orientation in the trained direction. The Watson U^2 test was used for comparisons between groups, and circular–linear correlation for analyzing effects of number of days in training on deviation from the trained direction (Batschelet, 1981).

RESULTS

The topographic distribution of nest bearings in the arena was indistinguishable from random ($\alpha = 145°$, $r = .23$, $p = .195$, $n = 31$; see Figure 4A and Table 1), indicating that there was not a significant source of nonmagnetic bias in the testing arena. The distribution of the nests relative to the magnetic field (ignoring the direction of training) showed a relatively weak, bimodal distribution ($\alpha = 164°–344°$, $r = .36$, $p = .018$, $n = 31$; see Figure 4B and Table 1). In contrast, when the magnetic bearings were plotted with respect to the trained magnetic direction (i.e., the direction corresponding to the dark end of the training cage), the bearings were strongly, unimodally oriented ($\alpha = 352°$, $r = .69$, $p < .0001$, $n = 31$), and the 95% confidence interval for the mean bearing included the trained direction (see Figure 4C and Table 1). There was a weak effect of the length of time that the mice were trained prior to testing. Deviations from the trained magnetic direction decreased slightly as days in training increased (circular–linear correlation, $r = .35$, $p = .03$, $n = 31$).

Figure 5 shows the distribution of magnetic bearings obtained from the mice trained in each of the four magnetic directions (cf. Table 2). The scatter in the distribution of bearings was greater for the mice trained along the

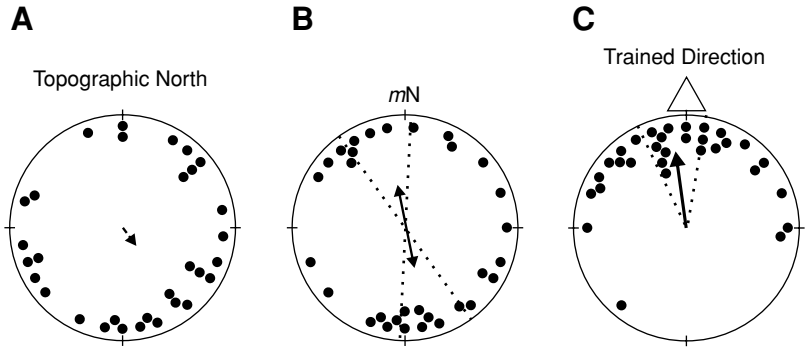

Figure 4. Orientation of C57BL/6J mice trained to build their nest in a learned magnetic direction and tested in a visually symmetrical circular arena. Each data point represents the position of a nest built by an individual mouse. (A) Absolute topographic bearings in arena. (B) Bearings relative to magnetic north (*m*N) in the arena = 0º. (C) Bearings relative to the trained magnetic direction = 0º (the training direction is indicated by the large triangle outside the circle). Arrows give the mean vector for the distribution of the nests (broken arrows for mean bearings that did not differ significantly from a random distribution according to the Rayleigh test), and the dotted lines are the 95% confidence intervals for the mean bearing of nonrandom distributions. Double-headed arrows indicate bimodal distributions ($r_{bimodal} > r_{unimodal}$; see the Method section). The lengths of the arrows are proportional to the mean vector length *r* (scaled so the radius of the circles corresponds to *r* = 1), which provides a measure of the degree of clustering in the distribution of the bearings. See the text and Table 1 for detailed information.

E–W axis (70º and 250º) than for the mice trained along the N–S axis (340º and 160º; Watson U^2 test, $U^2 = 0.24$, $p < .02$, $df_1 = 14$, $df_2 = 17$; see Table 2), a pattern also observed in the magnetic compass orientation of adult *Drosophila melanogaster* (data from Phillips & Sayeed, 1993). The significance of the difference in orientation along the N–S and E–W axes will be discussed in detail elsewhere (Dommer, Tran, & Phillips, 2006).

DISCUSSION

Our findings indicate that C57BL/6J mice are capable of goal-directed magnetic compass orientation. The mice readily learned the direction of the nest box in their training cages and positioned their nests in the testing arena in this learned direction, relative to the magnetic field. The response of mice differs from that of mole rats from two different families, which exhibit a "fixed," or innate, directional tendency relative to the magnetic field (Burda et al., 1991; Burda et al., 1990; Kimchi & Terkel, 2001; Marhold et al., 2000; Marhold, Wiltschko, & Burda, 1997). The nonrandom distribution of magnetic bearings in our study (Figure 4B) suggests that there may be a weak directional preference in laboratory mice, similar to the fixed easterly or southeasterly preference in mole rats, although in our mice this preference is bimodal. However, the strong unimodal clustering evident when the magnetic bearings are plotted relative to the trained magnetic direction (Figure 4C), indicates that the primary component of orientation by the mice is a true magnetic compass (menotactic) response.

The findings in mice are consistent with the earlier evidence for a learned magnetic compass response in Siberian hamsters, although the hamsters' response was bimodal and exhibited greater scatter (Deutschlander et al., 2003). The precision with which the mice in the present study positioned their nests (especially the mice trained along the N–S axis) indicates that the magnetic compass provides an accurate source of directional information that is likely to be useful in a variety of behavioral contexts. Future studies are needed to determine whether mice use magnetic compass cues in other forms of directional orientation (e.g., maze learning and path integration, as suggested by a recent study of mole rats; Kimchi, Reshef, & Terkel, 2005).

At present, nothing is known about the mechanism of magnetoreception in mice. Interestingly, the magnetic compass of mole rats differs from that found in other terrestrial vertebrates. In mole rats, the magnetic compass appears to be mediated by a mechanism involving permanently magnetic material, presumed to be particles of biogenic magnetite (Kimchi & Terkel, 2001; Marhold, Burda, Kreilos, & Wiltschko, 1997; Marhold, Wiltschko, & Burda, 1997). In contrast, the magnetic compass of songbirds and amphibians is light dependent (Deutschlander, Borland, & Phillips, 1999; Freake & Phillips, 2005; Phillips & Borland, 1992; W. Wiltschko & R. Wiltschko, 2005) and sensitive to low-level radio frequency fields (Phillips & Freake, 2006; Ritz et al., 2004), consistent with a magnetoreception mechanism involving a light-sensitive biochemical reaction (Ritz et al., 2000). On phylogenetic grounds, therefore, mice and hamsters would be expected to also have a *magnetite-based* magnetic compass like that in mole rats. Unlike the subterranean mole rats, however, most rodents have well-developed vision and are active above ground at light levels similar to those experienced

Table 1
Orientation of C57BL/6J Mice Trained to Build Their Nests Into a Learned Magnetic Direction and Tested in a Circular Arena

Mouse ID	Trained Magnetic Direction (º)	Direction of Testing Field (º)	Topographic Nest Bearing (º)	Magnetic Nest Bearing (º)	Direction Relative to Trained Magnetic Bearing (º)
AB-2-A	340	270	240	330	350
AB-2-E	160	180	0	180	20
AB-3-A	70	90	140	50	340
AB-3-B	250	360	110	110	220
AC-1-A-3	160	360	145	145	345
AD-2-C	160	270	30	120	320
AE-2-B	340	90	50	320	340
AE-2-D	340	90	80	350	10
AF-2-A	160	90	285	195	35
AF-2-C	70	180	340	160	90
AG-2-B	160	360	180	180	20
AH-2-A	250	180	50	230	340
AH-4-A	70	180	205	25	315
AH-4-C	340	90	40	310	330
AK-1-C	70	360	120	120	50
AM-1-A	160	90	260	170	10
AM-2-B	160	270	0	90	290
AM-2-C	340	180	145	325	345
AN-1-A	70	90	120	30	320
AS-2-A	160	360	170	170	10
KK-6-A	340	180	185	5	25
KK-6-B	250	90	290	200	310
TT-3-D	340	270	230	320	340
UU-2-A-2	340	360	250	250	270
UU-2-C	250	180	120	300	50
UU-3-B	250	360	190	190	300
XX-3-A	340	270	250	340	360
YY-2-D	250	270	95	185	295
YY-2-E	70	270	50	140	70
ZZ-3-E	70	90	160	70	360
ZZ-3-F	70	360	165	165	95

by nocturnally migrating birds and amphibians. On the basis of their visual ecology, therefore, mice and hamsters would be expected to have a light-dependent, inclination-sensitive compass like that of birds and newts. Characterization of the mechanism(s) of magnetoreception in different groups of rodents will help to determine whether phylogenetic constraints or sensory ecology has played a primary role in the evolution of this sensory mechanism.

Table 2
Summary of Orientation of C57BL/6J Mice Relative to the Trained Magnetic Direction

Trained Magnetic Direction	α	r	p	n
Mean Orientation Relative to Magnetic North = 0º				
70º	95.0º	.60	.054	8
160º	158.0º	.84	.001	8
250º	200.8º	.61	.107	6
340º	325.1º	.87	.0002	9
Mean Orientation Relative to Trained Direction = 0º				
70º + 250º	353.6º	.48	.036	14
160º + 340º	351.1º	.85	<.0001	17

Note—Summary of the orientation of groups of mice trained to build a nest in one of four magnetic directions (70º, 160º, 250º, or 340º) and the same data grouped by trained axis (70º + 250º, or 160º + 340º). α = mean orientation; r = mean vector length. See Figure 3.

Development of a robust magnetic compass assay in a model organism such as C57BL/6J mice opens up a wide range of possibilities for investigating the mechanism(s) underlying sensitivity to the geomagnetic field, including investigations of (1) neural mechanisms (e.g., using inducible transcription factors to map neural pathways involved in processing magnetic information (Nemec, Altmann, Marhold, Burda, & Oelschläger, 2001); (2) molecular mechanisms (e.g., using knockout strains lacking functional copies of genes that have been implicated in magnetoreception [e.g., cryptochromes; Ritz et al., 2000]); and (3) biophysical mechanisms (e.g., observing effects of low-level radio frequency fields that have been shown to disrupt magnetic compass orientation in organisms with light-dependent [photoreceptor-based?] magnetoreception mechanisms [Ritz et al., 2004] and/or pulse remagnetization that has been shown to affect magnetic responses in organisms with non–light-dependent [magnetite-based?] magnetoreception mechanisms [Beason, Wiltschko, & Wiltschko, 1997; Fleissner et al., 2003; Marhold et al., 1997; Munro, Munro, & Phillips, 1997; W. Wiltschko, Munro, Beason, Ford, & Wiltschko, 1994]).

C57BL/6J mice have also proven to be excellent experimental subjects for laboratory studies of spatial behavior (e.g., Stavnezer et al., 2002; Wahlsten et al., 2005). The evidence for a well-developed magnetic compass sense in

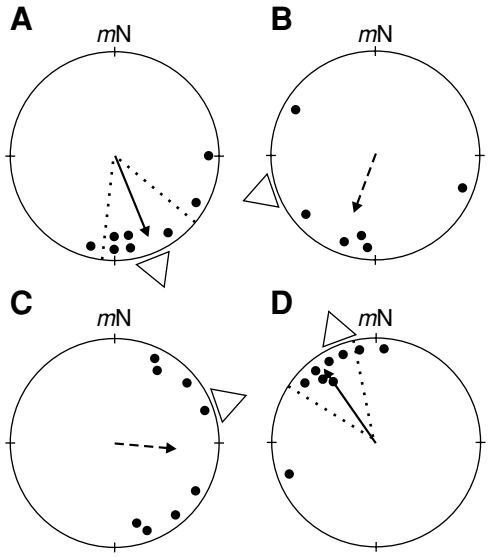

Figure 5. Magnetic orientation of C57BL/6J mice relative to the trained magnetic direction: (A) 160º, (B) 250º, (C) 70º, and (D) 340º. Each data point indicates the magnetic bearing of a nest built by an individual mouse (magnetic north, *m*N = 0º). The training direction of each group is indicated by the large triangle outside the circles. Each distribution includes magnetic bearings from all four testing fields (see Figure 3). Arrows give the mean vector for the distribution of the nests (broken arrows for mean bearings that did not differ significantly from a random distribution according to the Rayleigh test), and the dotted lines are the 95% confidence intervals for the mean bearing of nonrandom distributions. The lengths of the arrows are proportional to the mean vector length *r* (scaled so the radius of the circles corresponds to *r* = 1), which provides a measure of the degree of clustering in the distribution of the bearings. See Table 2 for statistical details.

mice raises the question of why previous studies of spatial behavior in rodents have failed to provide evidence for the involvement of magnetic cues (e.g., August et al., 1989; Madden & Phillips, 1987; Sauvé, 1988; Schleich & Antinuchi, 2004). One possibility is that these studies have failed to provide the necessary conditions for the magnetic compass to operate; it has taken our lab more than 20 years to identify conditions that elicit a robust magnetic compass responses in epigeic rodents (see Deutschlander et al., 2003; Madden & Phillips, 1987; present study).

Another possibility is that the use of magnetic compass information may be highly task specific. Consistent with the latter possibility, we have recently developed an assay that elicits robust auditory compass orientation to a single-directional sound source in C57BL/6J mice (Edgar, Sloan, Muheim, & Phillips, 2006);[1] we know of no evidence that rodents can use a single sound source to solve a place navigation task (e.g., Rossier, Haeberli, & Schenk, 2000). Identifying the physical conditions and behavioral contexts in which mice use different sources of directional information will be an interesting avenue for future research.

Evidence for magnetic sensitivity in four distinct families of rodents (Figures 4 and 5 and earlier references) indicates that this sensory ability is widespread in rodents. As we learn more about the taxonomic distribution of the magnetic sense(s) in rodents (as well as in fish, amphibians, reptiles, and birds; for a review, see R. Wiltschko & W. Wiltschko, 1995; W. Wiltschko & R. Wiltschko, 2005), the presence of a magnetic sense in at least some other groups of mammals seems increasingly likely. This invariably leads to the question of whether there is a magnetic sense in humans. To date, there is no compelling evidence for magnetic sensitivity in humans (Baker, 1980; Fildes, O'Loughlin, Bradshaw, & Ewens, 1984; Gould & Able, 1981). However, as we gain a better understanding of the physical conditions necessary for rodents and, possibly, other mammals to detect the geomagnetic field, as well as the behavioral contexts in which they use this source of directional information, there will be increasing pressure to address this question again in humans. Do humans have an unconscious magnetic sense that plays a role in spatial positioning (e.g., one similar to the vestibular system's role in ideothetic path integration; Etienne, Maurer, Boulens, Levy, & Rowe, 2004; see also Kimchi et al., 2004)? Are there effects of electromagnetic fields on human physiology due to biophysical processes left over from a magnetically sensitive ancestor? Or, conversely, is there a taxonomically widespread process involving radical pair intermediates (e.g., a cryptochrome-based photoreception system; Ritz et al., 2000) or magnetite particles (Kobayashi & Kirschvink, 1995) subserving some other function but exhibiting an intrinsic sensitivity to electromagnetic fields that was the antecedent of the magnetic sense(s) in other organisms? With the development of an assay for studying magnetic field sensitivity in a model organism such as C57BL/6J mice, it seems likely that the next 5–10 years will see many new developments in our understanding of this as yet poorly understood sensory ability.

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NOTE

1. The auditory compass assay was developed as a control for the magnetic compass assay, to make it possible to distinguish effects of gene knockouts (e.g., knockouts of the cryptochrome genes) that are specific to the magnetic compass.

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