

Birds, bees and magnetism

A new look at the old problem of magnetoreception

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For the past century or so, the study of magnetic effects on animals has been far from the mainstream of biological research. Many active scientists have scornfully treated this field as a pseudoscience at best, often with good reason. During the last 20 years, however, a variety of discoveries have slowly but radically changed this status. The geomagnetic field is now known to influence reproducibly the behavior and orientation of a variety of organisms ranging from bacteria through vertebrates^{2,3,10,14,15,18,20}; in turn these results imply the existence of some sort of sensory receptors for transducing the geomagnetic field to the nervous system.

Historically, the largest unsolved mystery in biomagnetic studies has been the apparent lack of a satisfactory physical mechanism energetic enough to couple weak geomagnetic stimuli to the nervous system, particularly in terrestrial animals. In the last 3 years, however, the discovery of biochemically precipitated magnetite (Fe_3O_4) in magnetically-sensitive honey bees⁵, homing pigeons¹⁹, and bacteria², as well as in an expanding list of other animals suggests a new hypothesis for explaining magnetoreception: animals may have simple compass receptors. In this short review, I will outline the behavioral studies which have established the existence of magnetoreception, consider possible transduction strategies, and explore the more recent experimental and theoretical work on magnetite-based magnetoreception.

Behavioral evidence for magnetoreception

Isolated reports of animals responding to magnetic cues surfaced repeatedly during the first half of this century, but for the most part the effects were suspiciously weak or unreproducible. (See the discussions by Griffin^{6,7}.) This situation changed dramatically during the late 1960s and 1970s when geomagnetic sensitivity was clearly established in a variety of organisms. Of these, the easiest to reproduce and simplest magnetotactic response is that of Blakemore's bacteria². These anaerobic or micro-aerophilic organisms swim to the north in the Northern Hemisphere, southwards in the Southern Hemisphere, and in both directions at the geomagnetic equator². Magnetotactic green algae of the genus *Chlamydomonas* with a similar geomagnetic response have recently been discovered in Brazil¹⁵.

In higher organisms, the newly-found magnetic responses generally fall into one of two separate categories. The first is the

use of the field direction for compass orientation, and the second is the extraction of time or map information from minute fluctuations in background geomagnetic intensity. The evidence suggests that two separate sensory systems are present.

The late W. Keeton¹⁰ and C. Walcott²⁰ were the first to demonstrate reliably that homing pigeons possess a magnetic compass sense, although this had been claimed much earlier by Yeagley (see Ref. 7). When released at an unfamiliar site on a sunny day, trained birds are normally able to orientate themselves quickly and depart in the homeward direction (see Fig. 1, top row). On cloudy days, however, small

magnets attached to their backs or paired coils wrapped around their heads predictably disorient the bird's departure bearings (see Fig. 1, bottom row). Apparently, the magnetic compass is only used when the primary sun compass is not available. Other experiments on migratory birds as well as pigeons imply that these animals sense the dip angle of the field (e.g. the maximum angle of the field relative to horizontal) and were not able to distinguish magnetic north from south.

Two German scientists, M. Lindauer and H. Martin¹⁴, discovered a variety of similar magnetic compass effects in honey bees. The clearest of these is found in their horizontal waggle dance: if a beehive is tilted on its side so that the normally vertical sheets of honey comb are placed horizontally, the bees can be deprived of their usual gravity reference cue. After this is done, and in the absence of other orientation cues such as polarized light, dances are initially disoriented. 2 or 3 weeks later, however, bees' dance is orientated preferentially to eight points of the magnetic compass (Fig. 2). Stronger background magnetic fields enhance this selectivity for particular orientations, while weak fields reduce it. Other compass responses have since been found in salmon, sharks, rays, cave salamanders, eels and wood mice.

Two common features of the compass sense should be emphasized here because they may have important implications con-

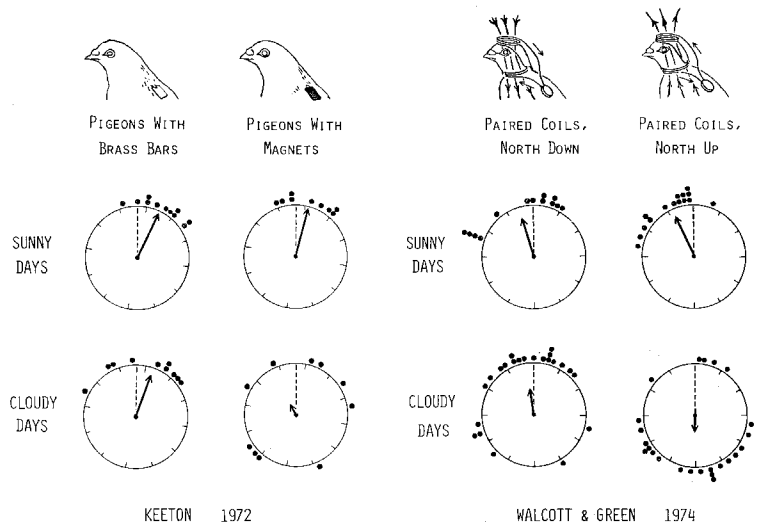


Fig. 1. The influence of magnetic fields on the vanishing bearings of trained homing pigeons. On sunny days (top row of circular diagrams), most birds are able to depart in the general direction of home (dashed lines) with reasonable accuracy (indicated by the length of the mean departure arrows). Magnets, brass bars and coils have no appreciable effect. However, on cloudy days when the sun is not visible (bottom row of diagrams), a small magnet attached to their backs disorients many of the birds, whereas a brass bar of similar size and weight has no effect. Also on cloudy days, paired coils which reverse the dip direction of the field around the bird's head (North up) causes them to fly in the wrong direction, whereas identical coils producing a downward field (like that in the Northern Hemisphere) have little effect. (Data are from Keeton¹⁰ and Walcott and Green²⁰.)

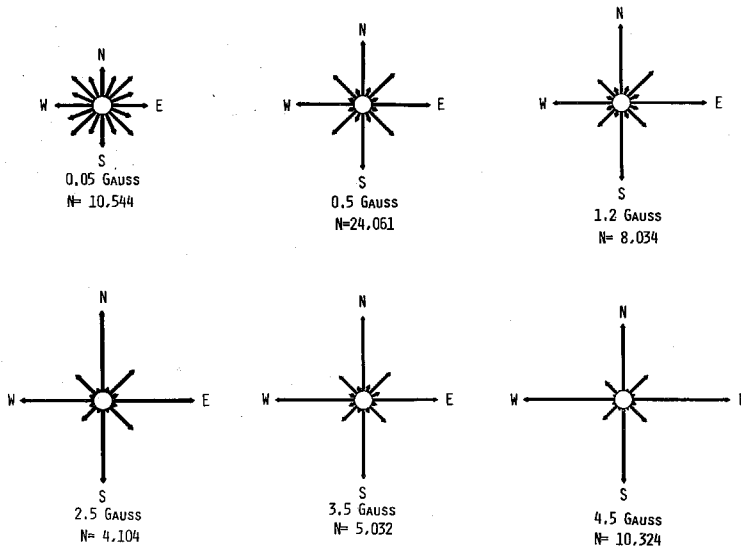


Fig. 2. Horizontal magnetic dance of the honey bee. (Data from Martin and Lindauer¹⁴.) The four cardinal directions (N, S, E and W) shown on the rose diagram for each dance are measured with respect to the local magnetic field in the hive under the conditions described in the text. The N= value tells the number of individual dances measured for each diagram. In weak background fields the orientation is poor, whereas it reaches an apparent maximum in fields stronger than about 2 Gauss. (N.B.: the geomagnetic field is about 0.5 Gauss, or 50 micro Tesla in SI units.) These data can be used to estimate the size of the ferromagnetic particles involved in the honey bee compass response as shown on Figs 6, 7 and 8. Although this horizontal dance is an easily reproduced laboratory response, it is difficult to understand how it could be of any use to bees in the wild. The waggle-dance normally conveys information about a food source from one worker to another, but no such information can be transmitted in this case. Similar eight-fold orientation patterns are sometimes seen in other insects if given a directional cue such as polarized light while standing on a horizontal surface⁵. Honey bee workers probably have a strong urge to dance, and when robbed of all other cues they fall back on a geomagnetic compass and use their instinctive, eight-fold pattern.

cerning the nature of the receptors involved. Firstly, neither birds nor bees seem to detect (or at least use) the polarity of the field. Reversing the vector magnetic direction yields the same behavioral response, implying some form of axial symmetry in the detecting system. As will be discussed later, this type of symmetry is easily produced with a ferromagnetic magnetoreceptor. Secondly, the observed compass behavior often involves finding the maximum dip angle, as demonstrated by the birds, or appears to depend in some way on the horizontal component of the field, as in salmon fry; both of these imply the presence of a gravitational (e.g. a 'horizontal' or 'vertical') component in the behavior. It is, however, difficult to conceive of a magnetoreceptor which would also be sensitive to gravity, as these two forces act independently. Typically, in magnetite crystals of biological origin, geomagnetic forces overpower gravitational effects by factors of between 10^3 and 10^4 . These magnetite particles are simply too small to be significantly bothered by gravity. For this reason, a geomagnetic behavioral response which is influenced by gravity probably depends upon the neurological processing of separate gravity and magnetoreceptive systems.

Magnetointensity reception is the second major type of geomagnetic sensitivity observed in animals, and again the most reliable information comes from the study of honey bees and homing pigeons. If a beehive is placed in a room with constant illumination, temperature and humidity, bees will be deprived of the cues which they normally use to set their circadian rhythm. Under these conditions, Lindauer¹⁴ and Gould³ found that the bees were still able to keep accurate track of time (Fig. 3, top). This ability disappeared on magnetically stormy days or could be artificially abolished by manipulating the external field with Helmholtz coils (Fig. 3, bottom). These experiments imply that the bees were detecting the weak (about 50 nano-Tesla, nT) diurnal variations in the geomagnetic field against the roughly 50,000 nT background. (N.B. 1 nT is sometimes called a gamma.)

Similar levels of geomagnetic sensitivity have been inferred to exist in homing pigeons and migratory birds. W. Keeton and others^{3,18} found that the small (50–1000 nT) geomagnetic fluctuations produced by magnetic storms seriously affected the homeward departure bearings both of pigeons and young ring-billed gulls

released at an unfamiliar site; they found typical deviations which averaged between $0.13^\circ/\text{nT}$ for the pigeons and $2.5^\circ/\text{nT}$ for the gulls. The most striking evidence for magnetointensity reception, however, comes from releasing trained homing pigeons at magnetic anomalies. Walcott¹⁸ found that these magnetically 'bumpy' terrains seriously disrupt the birds' ability to find their way home (Fig. 4 A and B).

Although these results imply that some terrestrial animals are sensitive to weak geomagnetic fluctuations, experiments have not yet been done to determine which components of the field are actually being used by them. I argue that one or more functions of the total intensity are most likely to be involved because the alternative would be for the animal to monitor impossibly small changes in direction. A system designed to monitor the magnitude of the geomagnetic field (a scalar) would be independent of motion or orientation. In the case of the honey bee, for example, the magnetic direction change produced by diurnal variation is at most 0.06° during the course of a day. Before a bee could use this small shift as a time cue, however, it would need to monitor independently its own orientation relative to the world with better precision. However, bees are in constant motion and the accuracy of their physical orientation is subject to cumulative error which should make it difficult for them to detect such a tiny magnetic shift. A similar argument suggests that small fluctuations in either the horizontal or vertical geomagnetic component alone would not be involved due to a cumulative error in the gravity reference system. These predictions can and ought to be checked with suitable behavioral experiments. Note that it is critically important for the various transduction strategies discussed below to be able to account for this sensitivity to weak-field fluctuations.

One other objection which critics have often raised concerns the failure of many attempts to condition animals to magnetic stimuli. In many animals it seems that magnetoreception is a backup sensory system, and without the proper set of releasers (cloudy skies, flying, etc.) the response is difficult to observe. Only two positive reports have been made on homing pigeons, but both effects were weak and neither have been reproduced. However, Walker *et al.*²¹ have found that tuna fish are easily conditioned to weak magnetic stimuli. Tuna are pelagic, migratory fishes which do not possess any obvious means for orientation or long-distance navigation. They are not known to have a sensitive electroreceptive system. The water surface disrupts visibility of the sun and stars, their

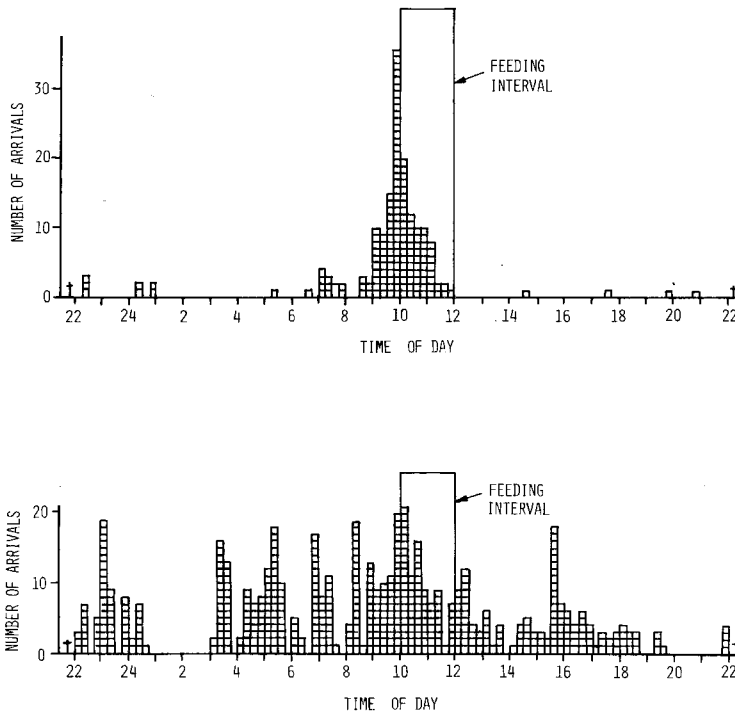
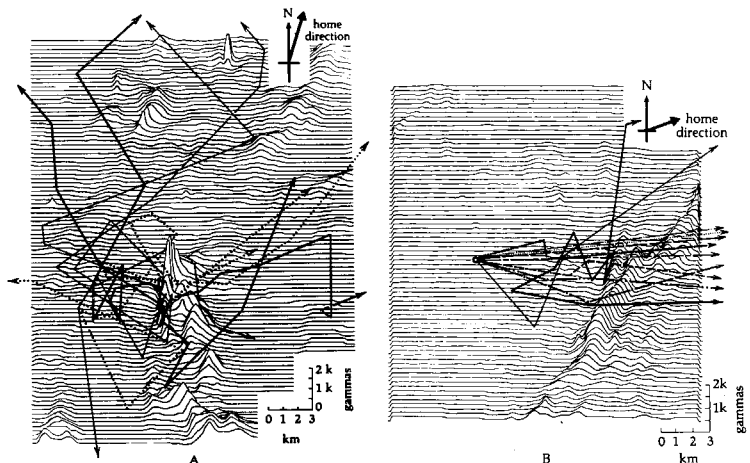


Fig. 3. Circadian rhythm pattern of honey bees and the geomagnetic field (from Lindauer¹⁴). The hive is maintained in an internal flight room with constant illumination, humidity, and temperature, etc. so as to deprive them of their more obvious timing cues. Under these conditions, bees are still able to keep good track of time as indicated by their arrival pattern at the feeder (top histogram, sugar water was offered from 10 a.m. until noon as shown). Bees lost track of time on magnetically stormy days or when an artificial, aperiodic field was superimposed with a set of Helmholtz coils (lower arrival histogram). These experiments and those of Gould⁸ suggest that bees somehow use the geomagnetic field as a time cue (Zeitzgeber) when nothing else is available.

The geomagnetic field does have a small but steady component of diurnal variation which could be used as a clock. From sunrise to sunset solar radiation warms the earth's ionosphere on the day side and generates a predictable pattern of current flow. On the surface, these currents sinusoidally increase the total magnetic field strength during the early morning by about 10–50 nT; it rapidly drops by an equal amount (20–100 nT total) around noon, and returns to the average quiet state around sunset. Little variation is observed at night, and the total change during the day rarely exceeds more than a few tenths of a percent.

Fig. 4. Effect of regional magnetic anomalies on the flight paths of trained homing pigeons released on sunny days at unfamiliar sites (data from Walcott¹⁶, replotted on the USGS aeromagnetic background maps by Gould⁸). Birds released on a magnetically 'bumpy' terrain (A) appear to be totally confused and are unable to home properly from an otherwise normal release site. When released from a magnetically 'flat' area, however, most birds are able to orient themselves quickly and depart in the general homeward direction (B). Note that the central anomaly in (A) is only about 6% of the total field, which is too small to seriously disrupt a magnetic compass sense, and that their primary (sun) compass was shining nicely in the sky. The best interpretation for these experiments is that some function of the geomagnetic intensity (like the total field or regional gradient, etc.) is involved in the bird's ability to determine where it is geographically relative to home. An animal needs some type of 'map' information as well as 'compass' orientation in order to navigate or pilot.



sight is limited to a few hundred meters at most, and they apparently do not have an echo location system as do Cetaceans. All of this and the successful conditioning experiments on them suggest that magnetism plays a primary role in their behavior, and that magnetoreception may be important to other pelagic, migratory animals, such as marine turtles, as well.

Transduction hypotheses

As noted earlier, the physical mechanism through which organisms might detect the weak geomagnetic field has been the most evasive factor in, and the major problem with, magnetoreception theory. Any proposed hypothesis must answer the question of how the action of the geomagnetic field could produce the controlled depolarization of a sensory nerve membrane. To do this, a magnetic signal of some sort must be generated which has a neural coupling energy comparable to or greater than the background thermal energy, kT , where k is the Boltzmann constant and T the absolute temperature. Numerous clever, original, and elegant hypotheses have been proposed for accomplishing this transduction to the ~50 microTesla (0.5 Gauss) geomagnetic field; these include, for example, various forms of electrical induction⁹, optical pumping, cation displacement, interactions between solitons⁸, liquid-crystal effects, and even biological superconductivity. Adey and Bawin¹, and Ossenkomp and Barbeito¹⁷, among several others, have recently reviewed many of these hypotheses. It seems that some of these interactions, if they exist, might be energetic enough to provide the basis for geomagnetic compass reception. However, it is also important for them to provide an

* A package of stable and condensed electromagnetic waves travelling together.

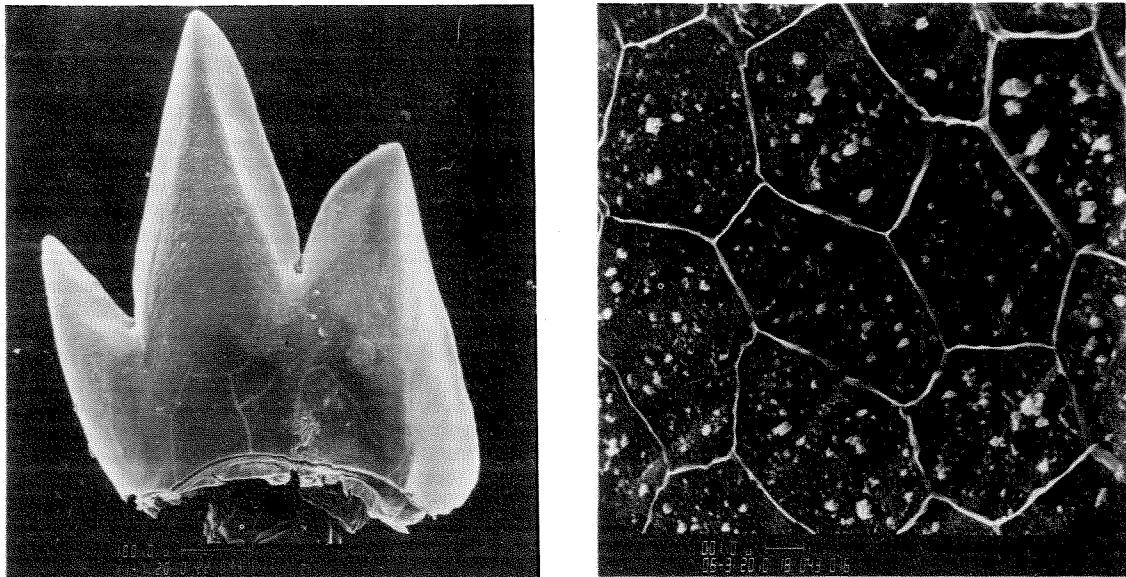


Fig. 5. Magnetite bearing teeth of typical marine chitons (class Polyplacophora). (A) Mature tooth of *Cryptochiton stelleri*. (B) Surface of *Chiton tuberculatus*, showing the organic matrix layers surrounding individual magnetite particles. (SCM micrographs courtesy of Heinz A. Lowenstam.)

explanation for the approximately 10 nT level of sensitivity displayed by honey bees and birds, which few workers have yet done. Although it is not my intent to dismiss prematurely this body of theoretical work, the older, more ignored, and perhaps simpler hypothesis of ferromagnetic interaction which is discussed next seems to satisfy these numerous physical requirements and has at least a comparable degree of experimental support.

The ferromagnetic hypothesis

Prior to 1978, the possibility that animals might make little permanent magnets and use them to construct magnetoreceptors was not taken very seriously. In simplicity, however, this idea must surely be equal to, or better than, anything else which has been proposed. In the geomagnetic field, for example, a single 50 nm cube of magnetite (or almost any other ferromagnetic material) has a coupling energy roughly equal to kT . By itself, the strength of this interaction lends plausibility to the idea that a ferromagnetic material might be responsible for many magnetobiologic effects in animals.

The physical basis for the strength of the ferromagnetic interaction with an earth-strength magnetic field is well known and worth briefly reviewing here. Most of the magnetic properties of ordinary matter arise from the movement of electrons; in particular, the spin and orbital motions of a single electron generate a very small magnetic moment, the magnitude of which is called a Bohr magneton (μ_B). Any magnetic

moment of this sort (μ) will interact with an external magnetic field (B) according to the energy relationship $E = -\mu B \cos(\theta)$, where θ is the angle between the directions of the μ and B vectors. For a single isolated or unpaired electron at room temperature, its energy product in the geomagnetic field ($\mu_B \cdot B_{\text{earth}}$) is only about 10^{-7} kT, far too weak to produce significant biomagnetic effects. Thermal agitation quickly makes the orientation of these vectors random so that their sum is close to zero. Materials with these unpaired electron spins are called paramagnetic; they display a weak magnetization in an external field due to a small preferential alignment of their independently wandering magnetic moments. Extremely high external magnetic fields, much greater than 1 Tesla, are required before paramagnetic interactions become significant at the molecular level.

In ferromagnetic crystals, these unpaired electron spins have been forced into parallel alignments such that their magnetic moments do not cancel, but add together linearly. This alignment force results from a quantum-mechanical exchange acting between adjacent paramagnetic atoms in a properly spaced crystal lattice. The total magnetic moment for a uniformly magnetized ferromagnetic particle is then simply $N\mu_B$, where N is the number of aligned Bohr magnetons present in the whole crystal. A ferromagnetic particle only a few tens of nanometers in size may have millions of these magnetic vectors (several from each paramagnetic atom), and as a group they can produce interaction energies

comparable to kT in the geomagnetic field.

Magnetite, however, has a slightly different flavor of ferromagnetism, called ferrimagnetism. The presence of regularly-spaced oxygen atoms in the lattice makes the magnetons in alternate crystallographic layers antiparallel to each other. The net effect is that moments from the Fe^{3+} ions cancel, and a parallel array of magnetic vectors from Fe^{2+} ions give rise to the ferromagnetic properties. Although magnetite is slightly less magnetic than native iron, for example, crystals larger than about 50 nm in size have energy products with the geomagnetic field which are comparable to kT .

The ferromagnetic transduction hypothesis is not a recent idea. Gustaf Ising⁸ was apparently the first to consider this possibility both experimentally and theoretically. In a 1945 paper, he reports having used a torsion-fiber magnetometer to look for magnetic material in the head of a migratory swallow. Although he was unable to measure any remanence in the bird's head, he realized that his instrument was not sensitive enough to rule out the presence of biologically significant amounts of ferromagnetic material. At about the same time in a review paper on bird navigation, D. R. Griffin⁹ noted that living tissues were 'not known to contain any of the very few ferromagnetic substances . . . which alone are capable of exerting appreciable mechanical forces in the earth's magnetic field'.

In 1962, Heinz Lowenstam¹⁰ at the California Institute of Technology discovered that magnetite was indeed a bio-

chemical precipitate in the radular teeth of chitons (class *Polyplacophora*, Fig. 5). He suggested that this material could be used for magnetoreception, but at the time no reproducible geomagnetic behavioral responses had been observed in animals.

Two independent developments in the 1970s were largely responsible for reviving the ferromagnetic hypothesis. Blackmore's² discovery of magnetotactic bacteria and the subsequent recognition of biochemically precipitated magnetite in them provided a clear example of ferromagnetic orientation in biology. Finally, the development and commercial production of ultra-sensitive superconducting (SQUID) magnetometers used for geophysical research provided the instrumentation that Gustaf Ising needed 40 years ago. Once these instruments were available, it was only a matter of time before someone used

them to search for magnetic material in the birds and bees, as we eventually did^{6,19}.

Subsequent thermomagnetic, X-ray, Mössbauer, or electron diffraction analyses have identified magnetite as the source of the remanence in all cases where it has been extracted, purified, or otherwise examined^{2,5,16,19,21}. Under favorable conditions, the SQUID magnetometers can detect the presence of as little as 0.1 ng of magnetite in samples of up to about 100 ml in volume. For typical vertebrate cells $\sim 50 \mu\text{m}$ in size, this corresponds to about one 0.1 μm crystal for every 30,000 cells. Even with this resolution many tissues are not measurably ferromagnetic. On the other hand, some tissues which could not conceivably be the site of a magnetoreceptor (mouse tumours, for example¹³) are highly magnetic. For vertebrates, the homing pigeon experiments of Walcott and Green²⁰

(Fig. 1) suggest that the receptor is somewhere in or near the head. Based on comparative magnetometry in two species of tuna, marlin, dolphins and pigeons, the only areas consistently rich in magnetite seem to be in the region of the ethmoid bones. Whether or not this is indeed the site of the vertebrate magnetic sense organ awaits the completion of numerous behavioral, neurophysical, and neuro-anatomical studies.

In parallel with this experimental work, recent developments of the physical theory for the ferromagnetic hypothesis have largely been conducted independently by Ellen Yorke²² and myself^{11,12}. Although our approaches differ somewhat, we reach very similar conclusions. We agree that only a few hundred magnetite-based organelles would be sufficient to produce the magnetic compass sense. These organelles are probably tiny ($\sim 0.1 \mu\text{m}$) and the whole system could fit in a very small volume ($\sim 100 \mu\text{m}^3$). An important consequence of this is that the total amount of magnetite required for a compass receptor is not yet detectable with the superconducting magnetometers. An animal with no measurable magnetic remanence could still have an extremely good compass sense. Yorke and I now also agree that an assemblage of magnetite-based organelles in theory could produce the high resolution required for magnetointensity reception^{12,22}. Other sensory systems such as hearing, vision and even electroreception (in elasmobranch fishes) achieve their high sensitivity by integrating over the response from a large number of discrete sensory receptors. In this fashion, the signal-to-noise ratio can be enhanced as \sqrt{N} , where N is the number of independent receptors involved in the array or the number of times each sensor is 'read', or both (a consequence of the central limit theorem). We might similarly expect that the neural circuitry for a magnetointensity sense could extract and integrate a small magnetic intensity-dependent signal from a large number of magnetite-based organelles.

One such intensity-dependent signal is certainly present in the thermally driven 'Brownian' motion of a small magnetite crystal. In an infinitely strong field, a freely rotating crystal will be aligned exactly along the magnetic direction. Thermal bombardment of these particles in a weaker field will disrupt this orientation, and the magnetic vector of the crystal will wander around the true magnetic direction. A crystal will show no net alignment in a null field. Therefore, the variance of motion in a magnetic particle is independent of direction and only a function of the strength of the magnetic field and the background

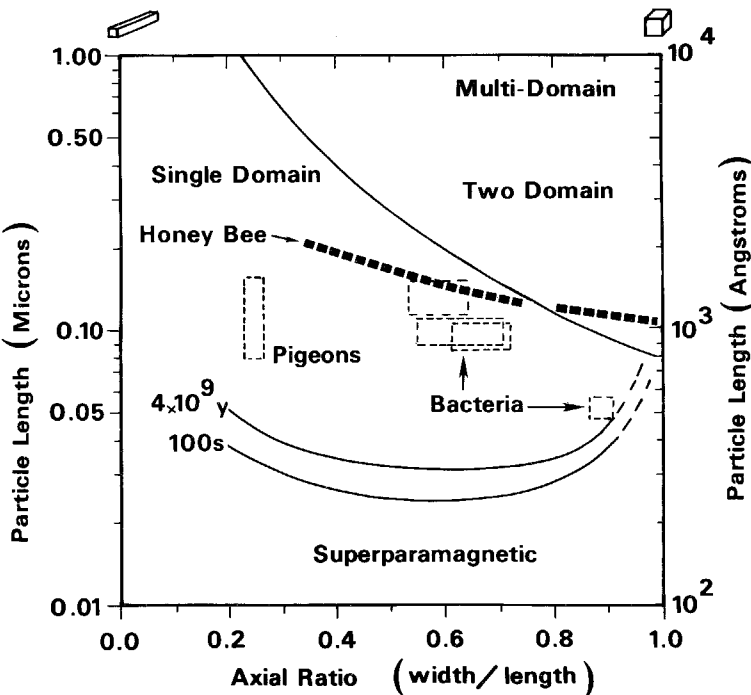


Fig. 6. Size-shape relationships and magnetic properties of magnetite crystals (from Kirschvink and Gould¹²). Each point on this diagram represents a rectangular magnetite crystal of specified size and shape. Points which plot in the upper right area labeled multi-domain or two domain represent crystals with two or more differently magnetized sub-regions within them; their net external magnetism is consequently reduced. Crystals which plot in the single-domain field (central part of the diagram) are those in which a single electron spin direction exists across their entire volume, they are magnetized fully to magnetite's saturation value of 48 mT. The particle shape constrains the magnetic remanence to lie permanently along its length unless forced to move by a strong magnetic pulse. In small single-domain crystals, thermal activation can sometimes cause the direction of the magnetic moment to change relative to the crystal axes. The tendency for this to happen is given by an exponential time constant which depends in a complex manner on the volume and shape of each crystal. For simplicity, two lines have been drawn on the bottom of this figure showing all particles with time constants of 4×10^9 years, and those with 100 s, respectively. A grain size difference of only 1 nm can therefore change this time constant by a factor of 10^{14} . Very small particles in which the magnetic moment moves quickly are termed superparamagnetic because they act like very strong paramagnets. Numerous bacterial and pigeon magnetite crystals which have been measured by electron microscopy are plotted in the single-domain field as shown. The dashed line corresponds to those crystals which have the volume of magnetite estimated by least-squares for the honey bee compass receptor (Figs 7 and 8).

temperature (kT). A signal of this sort could be the basis of the magnetic intensity sense if it were integrated over a large number of organelles as outlined above. Although the use of some component of the variance of motion like this is an obvious possibility; it is not the only one. In any case, a superconducting magnetometer should be able to detect the large numbers of particles (10^6 - 10^7) required for this system. Both honey bees and homing pigeons have been found to have more than enough magnetic particles for this purpose^{5,19}, as have tuna fish, turtles, bats, monarch butterflies, monkeys, humans and an expanding list of other organisms.

The magnetic stability properties of each ferromagnetic particle are additional factors which must be considered in this theoretical analysis. Fortunately, geophysicists have intensively studied these properties for magnetite during the last 20 years because of its importance to the magnetization of rocks (paleomagnetism). If a crystal is too small the magnetic energy (μB) will be much less than the thermal energy (kT); thermal disruption can then make the net remanence wander freely in any direction relative to the crystal. A particle of this sort, termed superparamagnetic, is of little use as a compass because it will not physically align itself in the geomagnetic field (although the moment of the crystal will). Similarly, in a crystal which is too large, the parallel alignment of electron spins will collapse into two or more smaller regions (multi-domains), often with opposite orientations, which reduce the net effective magnetic moment of the particle. As shown in Fig. 6, the best sizes for biological magnets lie somewhere between these extremes in the area labeled 'single-domain', which means the particle is both uniformly and stably magnetized. Note that all crystals from magnetotactic bacteria plot within this area, as do those from the homing pigeon. Natural selection would favor organisms that make single-domain particles if these magnetic properties were important to them.

From a theoretical perspective, it seems necessary to ask next whether or not the ferromagnetic hypothesis is compatible in detail with the existing literature on magnetic behavioral responses in terrestrial animals, and if so, what further predictions concerning the size or configuration of these as yet hypothetical organelles are possible. A start on this approach has already been made with the horizontal magnetic dance data of the honey bee shown in Fig. 2. It seems clear from looking at these dance patterns that the bees' alignment is poor in weak fields, whereas it approaches a maximum in strong fields.

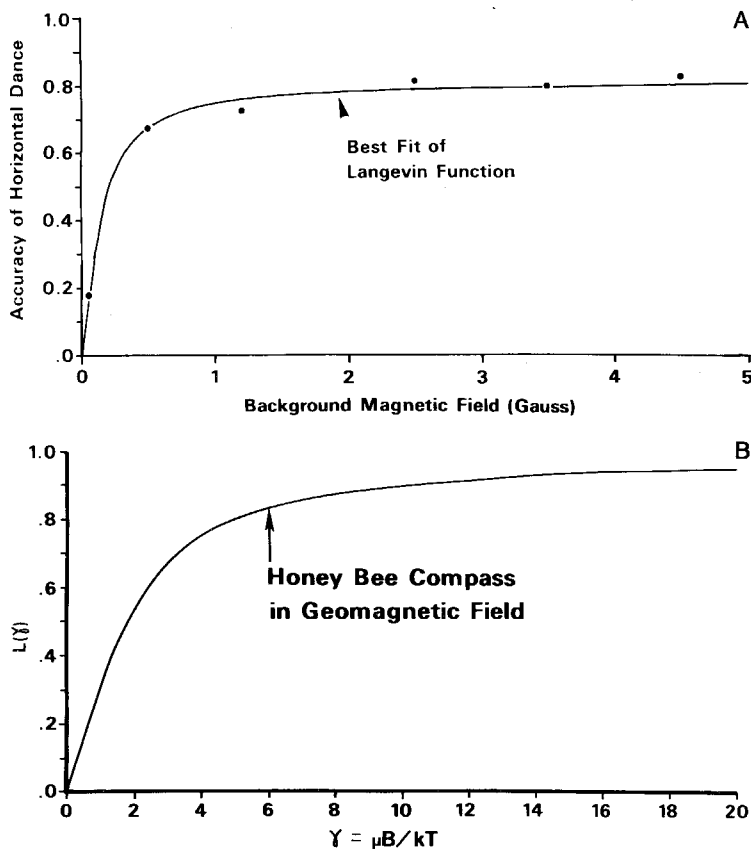


Fig. 7A. A test of the ferromagnetic hypothesis in honey bees using the horizontal dance data of Fig. 2. As a result of thermal agitation, each hypothetical magnetite particle involved in the compass receptor will be slightly mis-aligned from the true direction of the local magnetic field. Over time, however, the average direction of the crystal will coincide with that of the background field, but particles with large magnetic moments or those in stronger magnetic fields will be better aligned than smaller ones or those in weak fields. The accuracy of this alignment is defined as the average cosine of the angle between the field direction and the moment of the particle, which has a range from 0 to 1. This in turn is given by the Langevin function, $L(\gamma) = \coth(\gamma) - 1/\gamma$, where γ is the ratio of the magnetic, μB , to thermal, kT , energies. (The solid line on Fig. 7B shows this function.) In a similar fashion, the data shown in Fig. 2 indicate an increase in the accuracy of the horizontal dance with increasing field strength. A simple, linear measure for the accuracy of this dance response is given by $(D_s - D_r)/D_t$, where D_s is the total number of dances within $\pm 11.4^\circ$ of the N, NE, E, ... directions, D_r is the remaining number of dances which were in the other directions, and D_t is the total. Using the data shown in Fig. 2, this average dance accuracy has been calculated for each of the six background field strengths used by Martin and Lindauer¹⁴, and are shown as the black dots on Fig. 7A. If ferromagnetic organelles are responsible for this behavior, a curve of the form $x \cdot L(\gamma)$ ought to match the data, where x is a linear scaling factor. The best least-squares fit of this function is shown as the solid curve in Fig. 7A and is a reasonable match to the experimental data. A further error analysis cannot be made without the original bee dance angles (G. S. Watson, personal communication), but these are apparently no longer available (H. Martin, personal communication). If all such organelles are independent of one another, the shape of the dance response curve will be scaled by a linear factor of \sqrt{N} , where N is their number. For this reason, the number of these hypothetical organelles is a component of the response scaling factor, x , and as of yet cannot be uniquely distinguished¹¹. As noted in the text, only a few hundred would be necessary in theory to produce the observed response.

Fig. 7B. In the geomagnetic field, the ratio of magnetic to thermal energies ($\mu B/kT$) for this best-fit honey bee compass is about six. As shown by the arrow on this figure, these grains will be reasonably well aligned during normal use. The inferred sizes of these crystals seem well suited for this function - larger grains would not increase the accuracy greatly, whereas smaller ones would reduce it markedly. This size is probably the result of natural selection.

Such a change in alignment is remarkably similar to the change expected for small ferromagnetic compasses subjected to thermal bombardment, as noted earlier. Fig. 7a shows the best-fit comparison between this

bee dance data from Fig. 2 with the theoretical alignment response of a ferromagnetic compass. The magnetic energy, μB , determines the shape of this curve because bees hold their hive temperature (and the

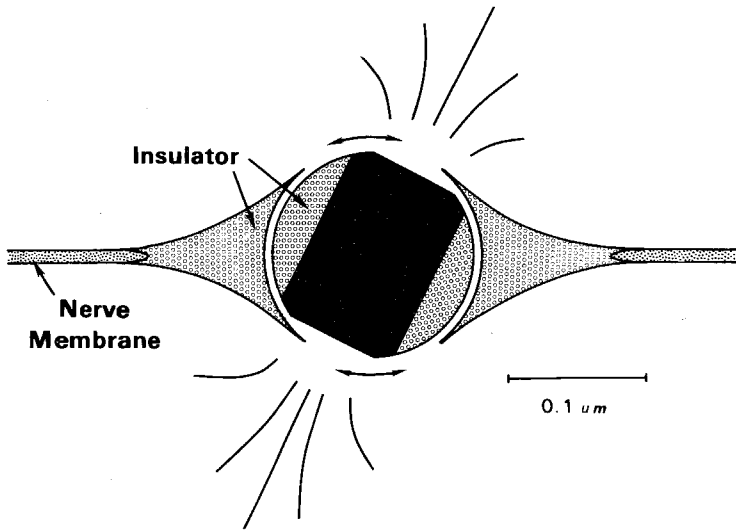


Fig. 8. Cross-section of a hypothetical honey bee compass magnetoreceptor. The magnetite crystal which is free to rotate into alignment in the geomagnetic field has been drawn with a length/width ratio of 0.7 so that it falls in the single-domain field of Fig. 6, with a total volume equal to that estimated from the least-squares fit. Organic insulation in this model surrounds the electrically conductive magnetite crystal, allowing the trans-membrane resistance to vary as a function of the angle between the crystal and the plane of the nerve membrane. The gap between the magnet and the holder is meant to show free rotation of the crystal while still serving as an insulator. If the author were going to design an animal, this is how he would give it a magnetic sense. Nature probably took a different path¹².

thermal energy kT) at a constant 310°K (37°C). B , the background field strength, was controlled by Helmholtz coils during the dance experiments, so the only undetermined variable is the size of the individual magnetic compasses, μ ; it was found by a least-squares fit on the data from Fig. 2 to have a magnetic moment of about 5×10^{-16} J/Tesla⁻¹, which corresponds to a 0.1 μ m cube of magnetite. This volume corresponds to the dashed line on Fig. 6 which intersects the single-domain area as shown. Therefore, these data imply that the dance experiments are compatible with the ferromagnetic hypothesis and also predict the average size of the compass organelles involved. However, this analysis does not tell us the number of crystals.

Magnetite compass receptors of this size will be aligned well in the geomagnetic field as shown by the arrow in Fig. 7b. If

bees made their crystals much smaller, the average alignment accuracy would fall off greatly, whereas larger volumes would only slightly enhance it. The honey bee seems to have struck a balance between the inaccuracy of having too small a compass and the waste of making it too big.

At this stage, a variety of transduction models for these as yet hypothetical magnetoreceptors are possible within the experimental and theoretical constraints outlined above¹². In one particularly simple version, drawn schematically in Fig. 8, a slightly elongate single-domain magnetite crystal would be free to rotate within a specially thickened membrane-support structure. As noted in Table I, magnetite has the lowest electrical resistivity of any known biological material and could depolarize a sensory nerve membrane by shorting across it. With the configuration shown, the angle

of the crystal relative to the plane of the membrane would govern the surface area of the magnetite electrically exposed to the medium, and hence control the size of the local depolarization produced. The frequency at which this hypothetical organelle fires would provide information about the planar angle of the crystal, and three such isolated organelles with different membrane alignments would provide an estimate of the axial direction of the magnetic field. It is important to note that this structure could not be used to determine north from south, nor could it be affected by suddenly remagnetizing it with a sharp magnetic pulse. Either reversing the ambient field direction or changing the magnetic polarity of the crystal could cause it to flip by 180° and produce an identical response. A directional symmetry of this sort has been observed in the magnetic compass behavior of many animals, including the pigeon and bee experiments of Figs 1 and 2.

In summary, the ferromagnetic hypothesis of magnetoreception is theoretically and experimentally compatible with all of the known geomagnetic behavior responses in terrestrial animals. The next major step, of course, is to characterize in detail the microanatomy and ultrastructure of these magnetite crystals as they are situated in their host tissues, and determine whether or not they indeed function as magnetoreceptors. At present we have only a vague knowledge of the function and distribution of these biochemically precipitated magnetite particles, and a great deal of work remains to be done before magnetite's role, if any, in magnetoreception is resolved. The very real possibility of exploring a new sensory system, however, will hopefully attract serious workers into this once-shunned field.

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TABLE I. Unique biochemical and physical properties of magnetite

Physical parameter	Related value	Comment
Ferrimagnetism	48 mT	Only known ferromagnetic material of biochemical origin.
Electrical resistivity	$5 \times 10^{-5} \Omega - m$	Lowest electrical resistivity of any known biological substance (~6000 times less than cytoplasm).
Density	5.1 g cm ⁻³ (5.1×10^3 kg m ⁻³)	Most dense biogenic material.
Hardness	~6 on Moh's scale	Hardest known biological mineral; chitons use it in their teeth ¹⁶ .
Color	Dark, dark blue	Photons absorbed by electrons hopping between Fe ²⁺ and Fe ³⁺ ions.

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