Invited Paper

Magnetite Biomineralization and Geomagnetic Sensitivity in Higher Animals: An Update and Recommendations for Future Study

Joseph L. Kirschvink

Division of Geological and Planetary Sciences, The California Institute of Technology, Pasadena

Magnetite, the only known biogenic material with ferromagnetic properties, has been identified as a biochemical precipitate in three of the five kingdoms of living organisms, with a fossil record that now extends back nearly 2 billion years. In the magnetotactic bacteria, protoctists, and fish, single-domain crystals of magnetite are arranged in membrane-bound linear structures called magnetosomes, which function as biological bar magnets. Magnetosomes in all three of these groups bear an overall structural similarity to each other, which includes alignment of the individual crystallographic [111] directions parallel to the long axis. Although the magnetosomes represent only a small volume fraction in higher organisms, enough of these highly energetic structures are present to provide sensitivity to extremely small fluctuations and gradients in the background geomagnetic field. Previous experiments with elasmobranch fish are reexamined to test the hypothesis that gradients played a role in their successful geomagnetic conditioning, and a variety of four-turn coil designs are considered that could be used to test the various hypotheses proposed for them.

INTRODUCTION

Geomagnetic Sensitivity in Animals

Once considered highly unlikely, behavioral evidence now suggests that a variety of living organisms respond to the geomagnetic field. Although many such claims have been made during the past 100 years few were ever successfully defended. During the past 20 years, however, plausible experiments have been described, which, in several cases, have been replicated by independent groups. This list now includes the magnetotactic bacteria [Blakemore, 1975; Frankel and Blakemore, this issue] and eukaryotic algae [Torres de Araujo et al., 1986], honeybees [Martin and Lindauer, 1977; Walker and Bitterman, 1985, and this issue], sharks and rays [Kalmijn, 1978a,b, 1984], sockeye salmon [Quinn, 1980; Quinn et al., 1981, Quinn and Brannon, 1982], tuna [Walker, 1984], eels [Tesch 1974; Karlsson, 1985], homing pigeons [Keeton, 1972; Walcott and Green, 1974], migratory birds [Southern, 1978; Wiltschko, 1972], salamanders and newts [Phillips, 1977; Phillips and Adler, 1978; Phillips, 1986], wood mice [Mather and Baker, 1981], and cetaceans [Klinowska, 1985, 1986; Kirschvink et al., 1986]. The methods used to demonstrate these responses include laboratory orientation and conditioning experiments and correlational and experimental studies in the field.

Although it is tempting to presume from the above studies that a magnetic sense is a common property among living organisms, it is important to note a number of problems in the behavioral study of magnetic sensitivity in animals. First, most of the orientation studies depend on large numbers of observations and elaborate statistical analysis of the data, which exhibit a high degree of variability [e.g., Moore 1988]. In addition, small changes in apparatus can lead to loss of previously demonstrated responses to magnetic field stimuli [Emlen, 1975]. Second, a large proportion of conditioning studies have yielded negative results, and attempts to replicate at least some of the studies reporting positive results have ended in failure [Kreithen and Keeton, 1974; Carman et al., 1987]. Third, field correlation studies such as those on migratory birds and cetaceans lack the control over alternate stimuli that is possible in laboratory experiments. In addition, the results of recent sensory impairment experiments in which time-varying fields produced by coils mounted on the heads of homing pigeons have been inconsistent and difficult to interpret [Lednor and Walcott, 1983; Papi et al., 1983; Teyssedre, 1986]. However, in areas where we have evidence obtained from different approaches within species (for example, with honeybees in laboratory orientation and conditioning experiments [Walker and Bitterman, this issue]), this supports strongly the hypothesis that at least some animals are sensitive to the geomagnetic field.

Geomagnetic Navigation?

The work cited above also illustrates the problem that laboratory studies can demonstrate the existence of response to a given stimulus but tell little about its use in nature, whereas field studies do not permit the experimental control necessary to establish and analyze responses to the stimuli that actually are used in navigation. With pelagic marine animals, these problems are compounded by the difficulty and expense not only of maintaining and carrying out experimental studies on animals in the laboratory but also of working in an opaque medium at sea. An important step toward overcoming these problems was taken by Klinowska [1985], who reasoned

that otherwise healthy whales that strand themselves alive must have made a serious navigational mistake of some sort and that analyzing the circumstances surrounding such strandings might identify the sensory modality responsible for the mistake. She found an association between live stranding positions and areas where negative magnetic anomalies intersect the British coast, leading her to suggest that cetaceans may possess a magnetic navigation system of some sort.

Although most biologists were (and still are) skeptical of Klinowska's results, in some respects they resemble the response of homing pigeons released at geomagnetic anomalies [Walcott, 1978], and as such it was certainly worthwhile testing her hypothesis elsewhere. Sufficient data, in terms of both dense coverage of the magnetic field and adequate records of strandings, are available for the eastern U.S. coastline and have permitted a test of Klinowska's observations here [Kirschvink et al., 1986]. Despite the initial skepticism, results from this study are very similar to hers. Nine of the 14 species in the U.S. data display significant to very highly significant associations with the most conservative measures that could be devised, as does the entire data set when pooled. In her most recent paper, Klinowska [1986] reported that this basic association has since been observed in Canada and New Zealand, implying that cetacean live stranding sites are associated with local magnetic anomalies in four widely separate and geologically diverse locations (England, eastern Canada, the United States, and New Zealand).

The fundamental question posed by these studies is how the association of strandings with magnetic anomalies arises: Is it fact or artifact? First, and most often suggested, is that it is simply a spurious result of some sort. There is obviously danger inherent in any correlative analysis, yet if used properly, they sometimes reveal important relationships. In the case of the cetacean strandings, it is possible that the animals were guided by some stimulus other than the geomagnetic field. This would be far more interesting than the hypothesized magnetic sense, however, because the other stimulus would have to be correlated in its own right with whatever causes the magnetic anomalies. On the U.S. Atlantic continental margin, most of the source rocks that produce the magnetic anomalies are buried by a blanket of up to 14 km of nonmagnetic sediment. One might still suggest that cetaceans can detect differences in the basement geology through some sort of echo location system (which would require sensitivity on the order of that achieved only recently in seismology), yet the magnetic stranding associations are apparent even in the mysticete whales, which are not known to have echo location abilities.

The other main hypothesis that could account for the cetacean stranding results is that these animals are indeed sensitive to small anomalies in the geomagnetic field and that under some conditions these features play an as yet unknown role in the whales' orientation and navigation. Several developments during the past 10 years make this hypothesis less absurd than it might otherwise seem. First, as discussed below, there is now a plausible sensory mechanism that could permit an organism to detect such small variations in the background geomagnetic field. Second, several other organisms also seem to respond to weak anomalies or fluctuations in the geomagnetic field, including the disorientation of birds at magnetic anomalies and by geomagnetic storms [Keeton et al., 1974; Walcott, 1978]. In two cases, spatial gradients in the field also appear to be associated with the ability of animals to condition to magnetic stimuli in the laboratory (e.g., the honey bees of Walker and Bitterman [1985, and this issue] and the tuna of Walker [1984]). Unlike many other

claims of magnetic sensitivity, these particular results are *not* weak effects; they do not require extensive statistical treatment of the data; and many of the results have been replicated by independent groups (e.g., the author's group at Caltech has replicated the Walker and Bitterman magnetic anomaly conditioning experiments on honeybees). This convergence of so many separate organisms with the same general type of sensory response may indicate that sensitivity to magnetic gradients is a parameter of importance for the animals (discussed further in the final section of this paper). Finally, and as a result of discoveries in marine geophysics over the past 30 years, we now know that the magnetic anomalies over the oceans are far more regular and less complex than those over land [Vine, 1966]. In view of these arguments, we believe that this hypothesis of a geomagnetic navigation system in cetaceans is a more viable explanation for the stranding results than the alternative explanation outlined above.

THE HYPOTHESIS OF MAGNETITE-BASED MAGNETORECEPTION

Behavioral results such as those cited above and reviewed extensively by numerous authors [e.g., Able, 1980; Gould, 1980; Ossenkopp and Barbeito, 1978; and chapters in Kirschvink et al., 1985a] pose at least two fundamental questions for biology. First, what is the mechanism through which the weak geomagnetic field is perceived by organisms; second, what parameters of the field do organisms use for navigation, homing, and orientation? The areas of research defined by these questions overlap extensively because the sensory system must be able to provide the nervous system with the information necessary to yield the observed behavior. Evidence from the behavioral studies suggests that organisms detect at least two parameters of the field. They seem to possess a simple compass, or system to determine magnetic field direction, and a higher-resolution sense able to resolve fluctuations of less than 1% in the intensity of the background geomagnetic field [Kirschvink and Walker, 1985].

Although a large variety of possible reception schemes have been proposed for magnetic field detection in animals, the most plausible include dependence of certain chemical reactions on external magnetic fields [Leask, 1977; Schulten and Windemeuth, 1986], some form of induction-based electroreception [Kalmijn, 1974, 1978a,b, 1984; Jungerman and Rosenblum, 1980; Rosenblum et al., 1985] and the use of organelles based on small permanent magnets made of magnetite [Kirschvink and Gould, 1981]. It seems clear from the work of Jungerman and Rosenblum [1980] that electroreception is not a viable hypothesis for extremely small organisms, such as honeybees, because the small conducting loops needed to induce measurable electric currents are difficult to fit within them (obvious anatomical structures should have been discovered by now). Rosenblum et al. [1985] have shown that the most sensitive electroreceptors known (those in elasmobranch fishes) do not have sensitivity sufficient to account for the behavioral responses to the weak (nanotesla level) fluctuations in the background field displayed by the birds [Walcott, 1978; Keeton et al., 1974; Southern, 1972, 1978], honeybees [Lindauer, 1977; Gould, 1980], and cetaceans [Klinowska, 1985; Kirschvink et al., 1986]. Similar arguments may well apply to the optical and chemical pumping hypotheses proposed by Leask [1977] and Schulten and Windemeuth [1986], although the necessary theoretical analyses of the constraints placed on sensitivity by these mechanisms have yet to be carried out.

The other plausible sensory mechanism, which is based on ferromagnetism, is

energetic enough to account for both the magnetic compass sensitivity and the apparent magnetic navigational abilities of animals. Organisms that are able to precipitate crystals of a ferromagnetic mineral such as magnetite (Fe_3O_4) could use the motion of the crystals in a variety of ways to transduce the geomagnetic field into signals that can be processed by the nervous system [Ising, 1945; Gould et al., 1978; Yorke, 1979, 1981; Kirschvink and Gould, 1981]. This ferromagnetic hypothesis lends itself to several testable predictions, some of which are capable of distinguishing it from any of the other hypotheses. These predictions are the following. First, magnetically sensitive animals must be capable of *biochemically* precipitating a ferromagnetic material; it is not enough to incorporate external contaminants. Second, this material, when formed, must have a variety of magnetophysical properties conducive to use as a geomagnetic transducer. (For example, the particles must be uniformly magnetized and large enough to align themselves with the geomagnetic field despite the randomizing influence of Brownian motion.) Third, there must be a mechanical coupling between each compass particle and a mechanoreceptor, or at least a functionally equivalent mechanism allowing the position of the particle to be monitored by a sensory organelle. In conjunction with this, the link between the sensors (whatever and wherever they are) and their processing centers in the brain should be located. Finally, the behavior of these organisms can be tested to distinguish ferromagnetic from electrical or paramagnetic effects.

Clearly, the case for a ferromagnetic sensory system in higher animals is far from made. The following sections of this paper describe the progress that has been made during the past 10 years and make recommendations for further tests of the hypothesis.

MAGNETITE BIOMINERALIZATION
The Search for Magnetic Sensory Organelles

Because magnetite is the only known biogenic mineral that is ferromagnetic at room temperature [Lowenstam, 1981; Lowenstam and Kirschvink, 1985], it is important to review briefly the history of its discovery in animals and what is known of its phyletic distribution and biological function. More extensive discussions of this subject are provided by Kirschvink [1983] and in the volume edited by Kirschvink et al. [1985a].

Lowenstam [1962] first discovered biochemically precipitated magnetite as a capping material in the radula (tongue plate) teeth of chitons (marine mollusks of the class Polyplacophora). He and his students were able to demonstrate the biological origin of this material through a variety of radioisotope tracing studies and by detailed examination of the tooth ultrastructure [Towe and Lowenstam, 1967; Nesson, 1969; Kirschvink and Lowenstam, 1979; Nesson and Lowenstam, 1985]. The presence of a layer of biogenic magnetite on a chiton tooth is illustrated in the scanning electron micrograph shown in Figure 1. Prior to this discovery, magnetite was thought to form only in igneous or metamorphic rocks under high temperatures and pressures. In the chitons, the magnetite serves to harden the tooth caps, enabling chitons to extract and eat endolithic algae from within the outer few millimeters of rock substrates. Nesson and Lowenstam [1985] report the results of detailed histological and ultrastructural examinations of magnetite formation within the radula and note that the process begins with an initial transport of metabolic iron to the posterior end of the radula sac.
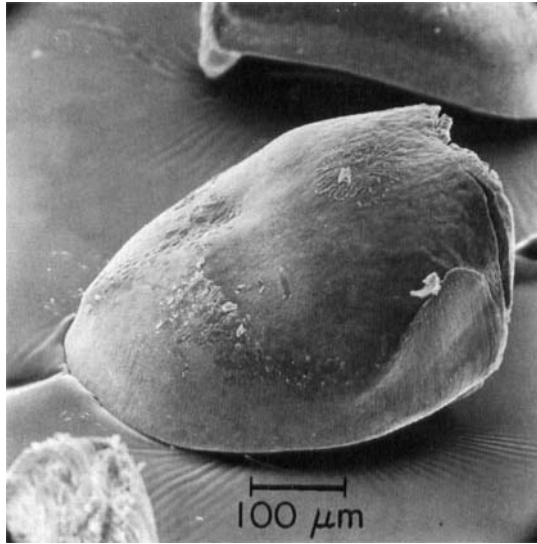
Fig. 1. Scanning electron micrograph of a typical chiton tooth from *Chiton tuberculatus* (from Barbados). A 20-μm-thick layer of fine-grained biogenic magnetite covers the concave surface of the tooth. Magnetite is one of the hardest biogenic minerals, and the denticle mineralization allows the animal to scrape endolithic algae from rocks in the intertidal zone.

This iron is deposited as the mineral ferrihydrite within a preformed organic mesh of proteinaceous material [Towe and Lowenstam, 1967], forming one or two distinct rows of reddish teeth. Through an unknown process, this ferrihydrite is converted rapidly to magnetite, through a nontopotactic reaction, coupled with iron reduction and recrystallization [Kirschvink and Lowenstam, 1979].

Magnetotactic bacteria were the second organisms found to contain biogenic magnetite [Blakemore, 1975; Frankel et al., 1979; Towe and Moench, 1981]. These bacteria precipitate one or more chains of submicrometer magnetite crystals bound together by an organic matrix material, termed *magnetosomes* [Balkwill et al., 1980; See Frankel and Blakemore, this issue]. These structures are mineralized in situ after the organic structure of the magnetosome is in place and are the only subcellular organelles in bacteria known to be surrounded by a proper lipid bilayer membrane [Gorby et al., 1988]. The bacteria control all aspects of the biomineralization process, including the crystal habit, particle shape, composition, and crystallographic orientation of the particles [Towe and Moench, 1979; Kirschvink, 1983; Mann, 1985]. All bacterial magnetite crystals examined to date are single magnetic domains, which means that they are uniformly and stably magnetized and have the maximum magnetic moment per unit volume possible for magnetite. The magnetosomes act as simple compass needles, which passively torque the bacterial cells into alignment with the earth's magnetic field and allow them to seek the microaerophilic zone at the mud–water interface of most natural aqueous environments. These bacteria swim to the magnetic north in the northern hemisphere [Blakemore, 1975], to the magnetic south in the southern hemisphere [Kirschvink, 1980; Blakemore et al., 1980], and both ways on the geomagnetic equator [Frankel et al., 1981; Chang and Kirschvink, 1989]. Magnetite-bearing magnetosomes have also been found recently in a eukary-

otic magnetotactic algae, with each cell containing several thousand crystals (Torres de Araujo et al. [1986]; see also discussion of the large "bacterium," which is probably a protozoan, in Vali et al. [1987]). The ability suddenly to "remagnetize" the cells and change their swimming direction by 180° with a strong magnetic pulse is unequivocal proof that the magnetotactic behavior of these microorganisms is due to single-domain ferromagnets [Kalmijn and Blakemore, 1978].

In higher organisms other than the chitons, the presence of ferromagnetic particles was first discovered using ultrasensitive magnetometers based on Rf-biased Superconducting Quantum Interference Devices (SQUIDs), particularly the type originally developed for use in rock magnetism [Goree and Fuller, 1976; Fuller et al., 1985]. Unlike similar devices commonly used to measure external magnetic fields of biological origin, these instruments are designed to measure the total magnetic *moment* of room temperature samples placed within a Helmholtz-coil pickup loop. Samples are isolated from the liquid-helium temperature components by a superinsulated vacuum, and the entire measurement chamber is enclosed within a superconducting bottle that excludes all external magnetic fields. Under these conditions, the SQUID moment magnetometers detect only the total magnetic moment arising from within the sample. This moment is the vector sum of all particles that are permanently magnetized (e.g., ferromagnetic) and have their moments aligned; all the other cellular iron is "invisible" by this technique. Because the samples are held inside the superconducting detection coils, the instruments operate very near the theoretical limits of their sensitivity. In most laboratories, however, airborne contaminants severely limit the effective resolution that can be achieved.

The author and his collaborators first examined honeybees and homing pigeons with these magnetometers [Gould et al., 1978; Walcott et al., 1979]. Moderate precautions were taken to avoid contaminating the samples, and effective sensitivities in the 10^{-10} Amp · meter^2 noise range were achieved. The bees had been raised in an environmentally controlled flight room at Princeton and had never been allowed to forage outside, whereas the first pigeons were from a loft that had been heavily selected for cloudy day homing for many generations. Both the bees and the heads of the homing pigeons acquired induced remanent magnetic moments that were significantly above the background noise levels. Fine-grained magnetite was identified by its Curie temperature as a likely source of the remanence in both organisms. Furthermore, eggs, larvae, and young pupae of the bees had no measurable magnetic material, whereas the older pupae developed magnetic remanence within 2 days of the time they emerged as adults. The magnetite therefore must be of biologic origin; nothing enters or leaves the pupae during this time. Jones and MacFadden [1982] and MacFadden and Jones [1985] have reported a similar series of events for the monarch butterfly. Magnetic material apparently is absent from eggs and caterpillars but forms slowly in the "inert" chrysalids during metamorphosis.

Despite these interesting results, however, subsequent attempts to locate the magnetite particles in situ and to characterize their cellular ultrastructure in the bees and in the homing pigeons were not successful (e.g., Kuterbach et al. [1982]; Walcott and Walcott [1982]; the material identified by Beason and Nichols [1984] as magnetite cannot be so; this would imply a magnetic moment for the head several thousand times stronger than reported). A straightforward calculation based on the total measured magnetic moment shows that the single-domain magnetite is initially present in most of these organisms in concentrations of at best a few parts per 10^9.

Compared to any other histological study, the histological location of the magnetite in situ is clearly a needle in the haystack. There is no other case known in biology where the ultrastructure of a biological structure, present in such minute concentrations, has been resolved.

Several other problems have plagued these studies, largely as a result of this dilute concentration of the magnetic particles and the extraordinary sensitivity of the magnetometer systems. First, the dissections were conducted in "dirty" environments, and often the tissue samples became progressively more magnetic each time they were handled. Many of the more useful magnetic techniques, such as determining the coercivity spectrum or the acquisition of anhysteretic remanence, require up to 100 repetitive measurements per sample; these experiments could not be carried out without prohibitive levels of contamination building up. Second, both the honeybees and homing pigeons normally live in dirty environments, and the skin, feathers, and other surface material (including eyes) invariably contain magnetic contaminants. Third, there are as yet no published techniques for specifically staining histological sections for the presence of magnetite. Finally, during the course of these studies, it became clear that ferromagnetic material is sometimes present in tissues that are highly unlikely to have a sensory function (murine tumors, for example; Kirschvink et al. [1982]). In some organisms, such as the whales, the background levels of magnetic material were such that very few nonmagnetic tissues could be located [Zoeger et al., 1981; Bauer et al., 1985]. (Implications of this material are discussed in the next section.)

During the past 5 years, the laboratory techniques required to identify, extract, and characterize ferromagnetic particles in animal tissue have been improved greatly. The most important step in this regard was the construction of a magnetically shielded, dust- and particle-free, clean laboratory at Caltech. When operated in an uncontrolled (dirty) environment, the SQUID moment magnetometers generally have noise levels in the 10^{-10} Amp $\cdot$ meter^2 range, which would be produced by the remanent magnetic moment of about two nanograms of single-domain magnetite. When operated in a clean laboratory environment, however, the background resolution of these instruments can be as low as 5×10^{-12} Amp $\cdot$ meter^2, or roughly 20 times better. This clean laboratory environment further permits detailed dissections and repetitive measurements of magnetic properties to be made without the contamination problems mentioned above.

Automated procedures for collecting data on the magnetic properties of biological samples, including their coercivity spectra, remanence acquisition characteristics, and anhysteretic properties, have also reduced the contamination problem. Largely as a result of extensive calibration studies conducted over the past 30 years by geophysicists studying rock and mineral magnetism [e.g., Cisowski, 1981; O'Reilly, 1984], these data now can be used to place constraints on the size, number, and composition of the ferromagnetic particles present as well as to provide information concerning how closely the particles are packed together. In parallel with these developments, there are now good wet laboratory techniques for extracting the ferromagnetic particles from the bulk tissue, viewing them with a transmission electron microscope, and identifying the minerals present with electron and X-ray diffraction [Walker et al., 1985, 1988; Mann et al., 1988].

Much of the search for magnetic sensory organelles has focused on juvenile migratory fishes because they are easy to dissect, are free from most terrestrial
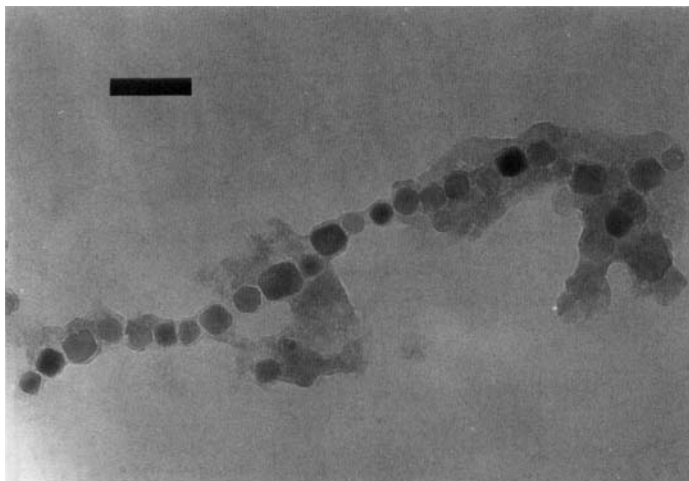
Fig. 2. Typical chain of single-domain magnetite (magnetosome) extracted from sockeye salmon *Oncorhynchus nerka* [Walker et al., 1988; Mann et al., 1988]. Bar = 100 nm. (Micrograph courtesy of S. Mann, University of Bath, Bath, England.)

sources of contamination, and have lower background levels of magnetic material in their tissues than do the adults or terrestrial animals. Many of them also have been shown to respond to magnetic field stimuli [e.g., salmon: Quinn, 1980; tuna: Walker, 1984; and eels: Tesch, 1974; Karlsson, 1985]. In all three species investigated so far (the yellowfin tuna *Thunnus albacares* [Walker et al., 1984], the chinook salmon *Oncorhynchus tshawytscha* [Kirschvink et al., 1985b], and the sockeye salmon *O. nerka* [Mann et al., 1988; Walker et al., 1988]), the tissue from within the dermethmoid region of the skull is the only consistently magnetic structure. The results imply the presence in the dermethmoid tissue of up to 100,000,000 interacting single domains of magnetite organized into arrays or chains like those in the magnetosomes of the magnetotactic bacteria [Balkwill et al., 1980; Stolz et al., 1986]. Extraction and analysis of diffraction spectra for the magnetic material uniquely identified the particles as single-domain magnetite [Walker et al., 1984, 1985; Kirschvink et al., 1985b]. Magnetite crystals are produced throughout life in numbers more than sufficient to mediate their orientation responses to the magnetic field.

More recent work with high-resolution transmission electron microscopy on extracts from the sockeye salmon has shown that the magnetite crystals are organized into linear, organically bound chains a few micrometers in length, with up to 80 crystals per chain (Fig. 2). Furthermore, individual crystals have their [111] axes (the "easy" direction of magnetization) aligned along the length of the chain [Mann et al., 1988], as do those from the magnetosomes of the magnetotactic bacteria. This is an exciting discovery for both cellular biology and geobiology: the same (or at least morphologically similar) subcellular organelle in two groups that diverged over 1.5×10^9 years ago, prior to the evolution of the eukaryotic cell. As the fossil record of the magnetotactic bacteria now extends back in time nearly 2×10^9 years, the magnetosomes in higher organisms could have been inherited through the process of serial endosymbiosis during the formation of the eukaryotic cell, about 1.6×10^9 years ago [Chang and Kirschvink, 1989].
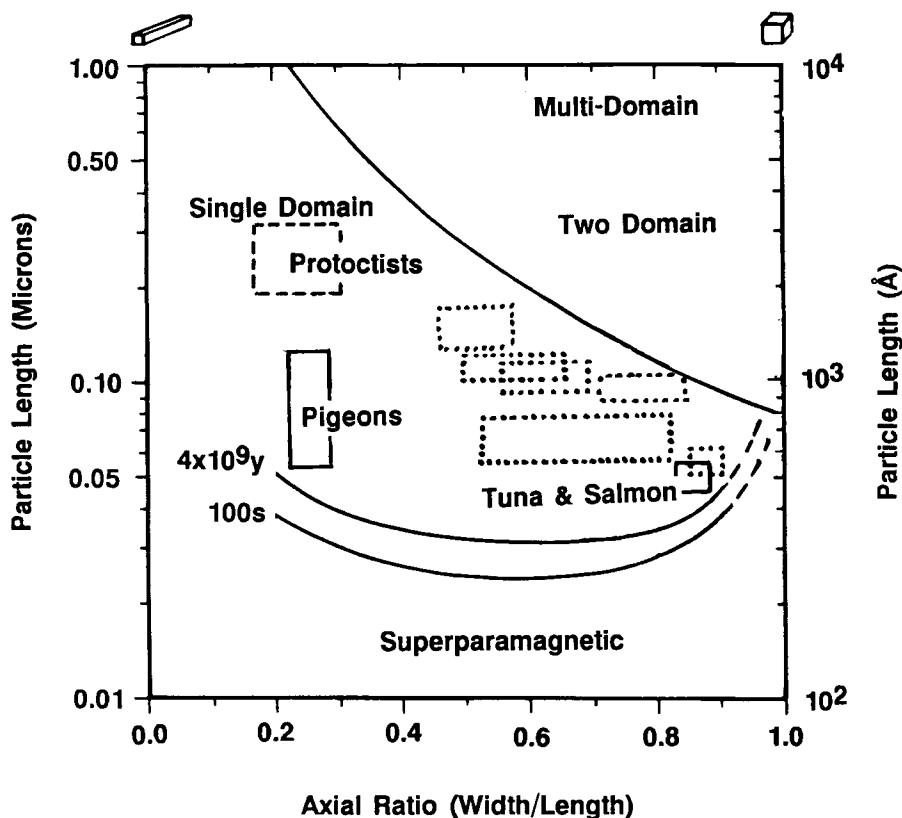
Fig. 3.   Size and shape distribution of magnetite particles formed by magnetotactic bacteria, protoctists, pigeons, and pelagic fish plotted to the domain stability field diagram for magnetite as calculated by Butler and Banerjee [1975]. Dotted outlines show the shapes and sizes for various types of magnetic bacteria as compiled by McNeill et al. [1988]. All these measurements indicate that the crystals are single magnetic domains, as would be expected from the process of natural selection for use as biological bar magnets [Kirschvink and Gould, 1981].

In summary, only the first two predictions of the ferromagnetic hypothesis outlined above have been verified experimentally in higher organisms, in contrast to the microorganisms. Magnetite of clear biogenic origin has been identified in a variety of magnetically sensitive animals and it is composed of the single-domain crystals best suited for magnetoreception. The single-domain stability field for magnetite shown here in Figure 3 illustrates this for a variety of biogenic magnetites extracted from bacteria, pigeons, and fish. Beyond this, none of the behavioral or neuroanatomical experiments yet performed on metazoans either has found the receptors involved or has identified the physical basis of the sense (electro-, chemo-, para-, or ferromagnetic). This statement holds true even for the elasmobranch fish; although Kalmijn [1978a,b, 1981, 1982, 1984] has demonstrated both a magnetic compass sensitivity and an astounding electrical sense, there is as yet no firm experimental link between them (e.g., sharks might have both mechanisms). The closest approach yet to localizing the receptor, however, is reported by Walker and Bitterman [this issue], who found that small magnets mounted on the front of the

honeybee abdomen [the known locus of magnetite biomineralization; Gould et al., 1978] interfered with their ability to condition to magnetic anomalies. Thus the magnetite in bees is in the vicinity of the magnetoreceptors, an observation that is consistent with, but does not strictly confirm, the ferromagnetic magnetoreception hypothesis.

As a result of these studies it has been possible to refine the magnetite-based magnetoreception hypothesis to make two specific predictions about the organization of magnetoreceptor organelles and the constraints these will place on the magneto-sensory behavior of animals possessing them. First, Kirschvink et al. [1985b] noted that the magnetite-based magnetoreception hypothesis can be tested definitively in species that respond to magnetic field polarity. Alignment of the magnetite particles by a DC-biasing field of a few microtesla, followed by a strong magnetizing pulse of opposite polarity to the bias field, will remagnetize the particles and cause reversal of the response to magnetic field polarity compared with the response of control animals (this is simply a variation on the now classic pulse-remagnetization experiment of magnetotactic bacteria by Kalmijn and Blakemore [1978]). Initial results on honey bees escaping from two-exit mazes are positive [Kirschvink and Kobayashi-Kirschvink, 1989]. Second, using the thermally driven variance model of Kirschvink and Gould [1981], Kirschvink and Walker [1985] showed that magnetite-based magnetoreceptors will directly influence the value of the Weber fraction (dI/I), the threshold sensitivity to magnetic field intensity as a function of background field intensity. Rather than remaining constant over a wide range of stimulus intensities, as it does for a variety of other sensory modalities, the Weber fraction for a magnetite-based magnetoreceptor system should behave as the inverse of the sensitivity. Sensitivity should be a maximum (with a low Weber fraction) in earth-strength fields, and it should drop off rapidly in either stronger or weaker background fields. In contrast, a Weber fraction that declines with increasing background field intensity is predicted for an induction-based system, because electroreceptors, in elasmobranch fishes at least, are tuned to maintain a constant threshold sensitivity to electrical field change independent of background field intensity [Clusin and Bennett, 1979].

Unfortunately, the robust behavioral responses to the relevant geomagnetic field parameters necessary to test these two predictions have yet to be obtained in vertebrates. For example, relatively few claims of responses to the directional polarity of the magnetic field have been made, the only exceptions being for salamanders [Phillips, 1986], salmon fry [Quinn, 1980], and bobolinks [Beason and Nichols, 1984]. Our one attempt at pulse remagnetization of Quinn's salmon fry was not successful because of his failure to elicit the previously observed orientation response (Quinn changed the apparatus slightly prior to our participation in the experiment). The bird orientation data is again based on extensive averaging, and it is not clear how conclusive pulse remagnetization would be. At this point, the salamanders may be the best organism with which to try pulse remagnetization. Other vertebrates whose response to magnetic field direction has been analyzed in detail appear to respond to magnetic field inclination, ignoring north–south polarity [see, e.g., Wiltschko, 1972; Emlen, 1975; Walcott and Green, 1974; Quinn and Brannon, 1982]. Impulse remagnetization experiments therefore will be inconclusive with these species; the remagnetization of a magnetite-based compass would yield the same behavioral response [Kirschvink and Gould, 1981]. There is evidence that tuna and honeybees respond to spatial variations in magnetic field intensity in conditioning experiments

[Walker, 1984; Walker and Bitterman, 1985, and this issue]. However, the procedures used in these studies are not suitable for psychophysical analysis of the response by either the tuna or the bees to magnetic field intensity. Future progress will clearly depend on the development of robust behavioral responses to magnetic field stimuli that will permit these tests of the ferromagnetic magnetoreception hypothesis.

Other Ferromagnetic Material

Because most of these studies have focused on the search for a new type of magnetic sensory organelle, very little attention has been given to ferromagnetic material in tissues for which a sensory function is improbable. Many tissues from larger vertebrates that have been examined using the superconducting moment magnetometers contain up to a few parts per million (ppm) of ferromagnetic material, particularly in older individuals. These include fish [Walker et al., 1985; Kirschvink et al., 1985b], turtles [Perry et al., 1985], birds [Presti, 1985], bats [Buchler and Wasilewski, 1985], whales [Zoger et al., 1981; Bauer et al., 1985], rodents [Mather, 1985], and primates [Kirschvink, 1980, 1981a,b; Baker, 1985]. Perry et al. [1985] extracted some of the magnetic material from their turtle samples and were able to identify the material as magnetite with X-ray and electron diffraction. Although they found a large fraction of particles under 0.5 μm in size, there were numerous spherical (framboidal) grains with diameters in excess of 50 μm. The surface texture of these spherical particles is truly unique, with surface features unlike those of magnetic particles formed through cosmic or industrial processes. Their abundance, distinctive textures, and presence well within the tissues argue that they are true biochemical precipitates rather than contaminants. In terms of the distribution of magnetic material within the tissues, the Bauer et al. [1985] study is by far the most definitive; they were able to sample material from several species and, in some cases, multiple individuals. They found relatively high levels of magnetic material in the cerebellum, midbrain, corpus callosum, and dura, whereas the cerebrum was found to contain far less magnetic material. (This pattern is similar to that found by Kirschvink [1981a] in a rhesus monkey.)

Despite these discoveries of biogenic magnetite in other vertebrates, similar work has not yet been conducted properly on humans. Magnetic material of an as yet unidentified composition was detected in human adrenal tissue [Kirschvink, 1981b], but the material has not been characterized further using these new techniques. Other work on humans has focused on the presence of exogenous particles in lung tissue [Moatamed and Johnson, 1986] or has not distinguished the magnetic material from laboratory-induced contaminants. However, the presence of truly biogenic magnetite in humans would have profound implications in several biomedical areas. In recent years, several medical groups have discovered that magnetic resonance images (MRI) weighted by the T1 and T2 spin echoes correlate with the observed distribution of stainable ferric iron in human brain tissue [Gomori et al., 1985; Drayer et al., 1986a,b]. These spin echoes are produced in the presence of heterogeneous magnetic susceptibilities and have been interpreted as arising from irregular distributions of paramagnetic iron (deoxyhemoglobin, ferritin, and hemosiderin). Minute concentrations of magnetite, however, are capable of yielding the same results and, if formed by metabolic reduction of existing ferric iron, would have a similar distribution within the tissue. It is amusing that Gomori et al. [1985] exclude this possibility by simply stating that "there is no physiologic ferromagnetic material." (This statement is

actually based on the work of Brittenham et al. [1982], who studied the magnetic susceptibility of human iron stores. Unfortunately, their techniques were not capable of detecting small levels of ferromagnetic material against a larger paramagnetic or diamagnetic background. The superconducting moment magnetometers, which operate with the tissue samples in a zero magnetic field, are sensitive *only* to ferromagnetic material.) Of course, both paramagnetic and ferromagnetic effects may be mixed together in these medical studies, and only a direct search for ferromagnetic particles can answer this question.

The presence of ferromagnetic material in human tissue would also have a direct bearing on attempts to perform risk assessment for exposure to strong magnetic fields. MRI imaging systems are becoming common diagnostic tools, and often patients are exposed to fields and gradients well in excess of 1.5 tesla. To date, all assessments of the potential hazards of such exposure have focused on the side effects of electrical induction or on possible diamagnetic and paramagnetic interactions [Tenforde and Budinger, 1986]. Ferromagnetic interactions, however, are typically 1,000,000 to 10,000,000 times more energetic and, because of the lack of information concerning the presence and distribution of ferromagnetic material in human tissues, have not been included in past analyses. The importance of this omission is substantial; recent developments in the technology of superconducting materials virtually guarantee that large-scale human exposure to intense magnetic fields will continue. In their report of a liquid nitrogen-temperature superconductor, Wu et al. [1987] note that their material remains superconducting in fields in excess of 80 tesla, unlike more conventional superconductors, which usually return to normal (nonsuperconducting) in fields of a few tesla at most. Therefore, these high-temperature superconductors not only will decrease the operating expense of MRI systems but they could permit the use of much stronger fields. High-temperature superconductors may also make other technologies feasible, including superconducting power lines and magnetically levitated trains, both of which would result in increased human exposure to strong magnetic fields.

GEOMAGNETIC FIELD GRADIENTS IN CONDITIONING EXPERIMENTS
The Kalmijn Experiment

As was discussed above, work on several groups of organisms suggests that homing and migratory animals may be sensitive to fluctuations in the field strength of less than 4%, with a threshold of perhaps 0.1% [e.g., Keeton et al., 1974; Walcott, 1978; Lindauer, 1977; Klinowska, 1985; Kirschvink et al., 1986]. The diversity of species across which these effects appear to be present leads to the hypothesis that weak anomalies in the field are a parameter of importance to the animals; it is certainly clear from a geophysical perspective that geomagnetic anomalies, and the marine magnetic lineations in particular, contain information that would be of great use for a migrating or homing animal [see, e.g., Skiles, 1985]. If these weak cues are indeed of importance, then it should be possible to design laboratory-based conditioning experiments that elicit similar responses.

Although numerous attempts have been made to condition laboratory animals to respond to magnetic stimuli, only a few have yielded positive results. Of these, the work on rays [Kalmijn, 1978a,b, 1984], tuna [Walker, 1984], and honeybees [Walker and Bitterman, 1985, and this issue] are most easily compared because they measure

discrete responses to altered conditions rather than directional preferences in orientation arenas [e.g., Phillips, 1977, 1986; Quinn, 1978]. In comparing these studies, however, it is clear that Kalmijn's interpretation of the sensory cues to which the rays were responding is at variance with experimental results obtained in studies on honeybees and tuna. Spatial variations in the applied magnetic fields seem to be the important stimuli for these latter animals, whereas Kalmijn infers that the rays responded to an altered direction in an otherwise uniform magnetic field. It therefore seems worthwhile to reexamine carefully from a theoretical perspective the experimental design used by Kalmijn at Woods Hole, Massachusetts, to set constraints on the actual range of magnetic gradients that should have been present, and in particular to see whether his conditioning success could have been dependent in part on the presence of gradients. Several alternative coil configurations for producing more uniform fields will also be considered as possible future alternatives to test this reinterpretation.

At Woods Hole, Kalmijn [1978a,b, 1981, 1982, 1984] used an impressive pair of Helmholtz coils 5 m in diameter to alter the horizontal component of the geomagnetic field. Two circular saltwater aquaria 1.8 m in diameter were housed in a wooden shed within the coils, and all conditioning experiments were performed in the upper tank, which was about 0.5 m above the center of the Helmholtz system. The coils were used to reverse the direction of the horizontal field component, thereby changing the direction of magnetic north to the (geographic) south. The actual strength of the field in both cases, however, was adjusted to match that of La Jolla, California (26 microtesla), where the particular species of ray was obtained. The animals were trained to swim to the magnetic east and enter a small enclosure to avoid punishment, and the direction of the field was altered in a quasirandom fashion between trials. The interest in this experimental design centers on the actual homogeneity of the altered field. The Helmholtz configuration is the traditional method for producing a small volume of space with uniform characteristics around the center of the coil system, and it is easy to construct. At the center point, both the first and second derivatives of the applied field are zero, which makes the one-radius coil separation useful for many applications. Unfortunately, the field uniformity decays rapidly with distance from the central area, so it is important to calculate the pattern of the altered magnetic fields at arbitrary points around the 1.8-m-diameter saltwater tanks in which the rays were swimming during the conditioning experiments. This can be accomplished by treating each coil of the Helmholtz pair as a separate current loop, and then summing the north, east, and down components produced by each coil with the corresponding geomagnetic components. These field components produced by circular coils are readily calculated numerically using elliptical integrals of the first and second kinds [Stratton, 1941].

Figure 4A shows the contours of total field intensity (in nanotesla) for a 2 × 2 m horizontal plane resting 0.5 m above the center of the Woods Hole Helmholtz system. The pattern shown is what should be produced when the horizontal component is inverted and strengthened to 26 microtesla as was used in the Kalmijn experiment. The magnetic components produced by the coils are summed vectorially with the ambient field at Woods Hole (horizontal 18.9, vertical 52.5 microtesla). As is apparent in Figure 4, the heterogeneities are comparable in magnitude to those implicated in many of the bird and honeybee experiments mentioned above.

This analysis makes plausible the hypothesis that the elasmobranchs in

A. Helmholtz Coil Pair

B. Rubens' Cube-Centered Coils

C. Modified Lee-Whiting 4-Coil Design

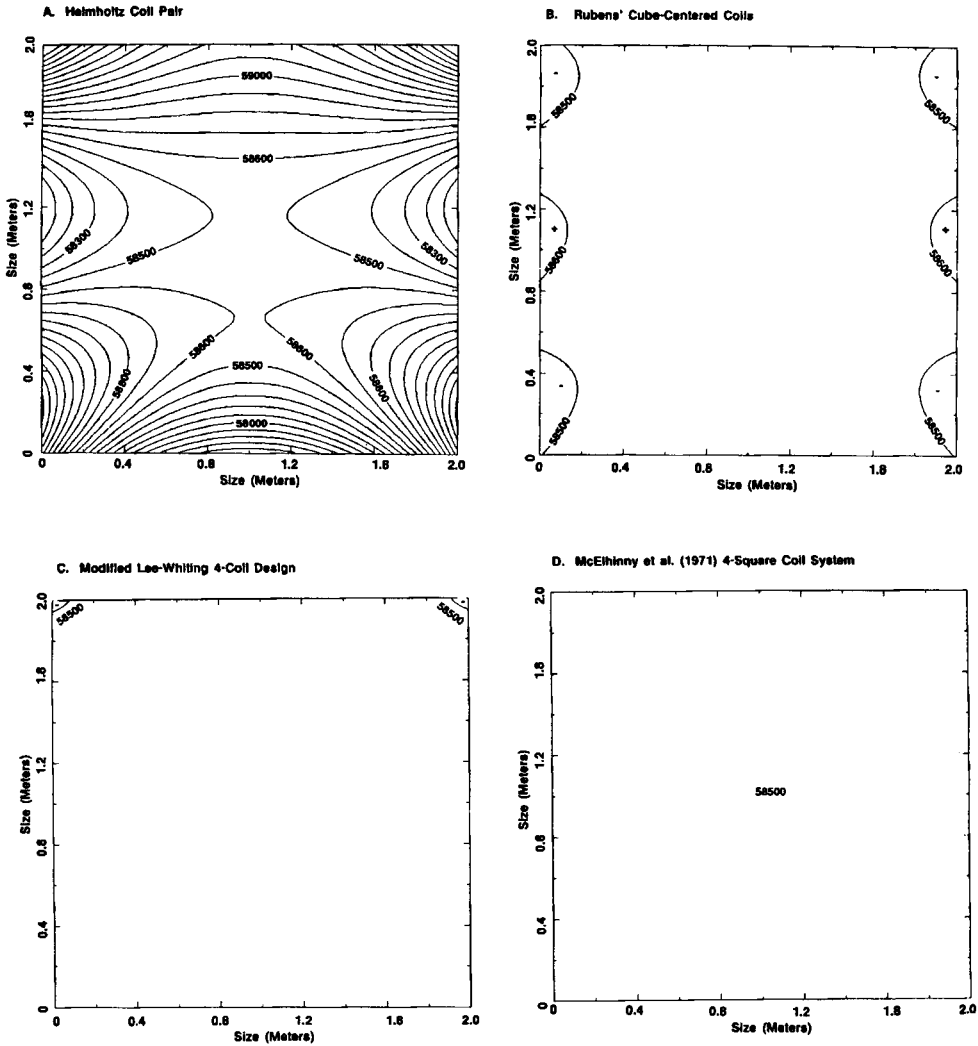D. McElhinny et al. (1971) 4-Square Coil System

Fig. 4.   Comparison of magnetic field uniformity produced by four different coil designs using both circular and square coil systems. All calculations are based on a 5 m diameter (or square side) for the largest coil in the system, arranged to reverse the horizontal component of the geomagnetic field at the center of the system and to increase it to 26 microtesla as used by Kalmijn [1978a]. Contours on each diagram are for the total strength of the field, with numbers in nanotesla (gamma). The figures are calculated for a 2 m square horizontal plane located 0.5 m above the center of the coil system. Design A is a standard Helmholtz design of two circular coils separated by their radius, with equal current flow. Design B is from Rubens [1945]; it uses five square coils of equal dimension spaced one-fourth of their size apart, with a current ratio of 19:4:10:4:19. Design C is a modification of a special case of Lee-Whiting [1955], which uses four coils of equal radius spaced along the axis of a cylinder (in units of the radius) at −0.941:−0.243:+0.243:+0.941, with a current ratio of 9:4:4:9 (the ideal current ratio should be 2.26, rather than the 9/4 or 2.25 used in this calculation). Design D is described by McElhinny et al. [1971] and uses two pairs of square coils with radius ratios of 0.956:1.00:1.00:0.956, spaced along the central axis (again, in units of the radius) at distances of −1.05,−0.288,+0.288,+1.05, with current ratios of 21:11:11:21. As described in the text, the gradients present in the Helmholtz configuration may be enough for the rays studied by Kalmijn to detect but would be eliminated by using one of these other configurations or by using the analysis of Lee-Whiting [1957] to design an additional pair of coils for his existing Helmholtz configuration.

Kalmijn's experimental apparatus were responding to the gradients in the applied fields. If so, this would imply that the rays could distinguish the eastern from the western target by some nonmagnetic method such as vision of the sandy bottom, touch, or smell, and they learned to go to the eastern target when the field in the tank was uniform and to the western one when the irregularities were present. Although they were clearly detecting the magnetic field, it is not clear which of its components was responsible for the successful discrimination. With the available data, there is no sure way of distinguishing between this hypothesis and that of a magnetic compass cue originally suggested by Kalmijn [1978a,b].

Coil Designs

It is possible to design and build coil systems with much higher uniformity than that provided by the Helmholtz arrangement. The four-coil systems in particular yield large uniform volumes relative to their size, and many have eighth-order uniformity [Lee-Whiting, 1955]. Several designs ranging from spherical [Everett and Ose-meikhian, 1966] to square [Alldred and Scollar, 1967; McElhinny et al., 1971] have also been studied extensively. Figure 4B–D shows results of calculations made using conditions similar to those for the Woods Hole Helmholtz design but using some of these other configurations. The Rubens [1945] system of five cube-centered square coils will reduce these variations by a factor of about 100 (Fig. 4B) but unfortunately has periodic wiggles of about 40 nanotesla across the central area. A system of four equal-radius circular coils, slightly modified from one of Lee-Whiting's [1955] special cases, reduces the variability by a factor of about 400 (Fig. 4C). Finally, the system of four square coils described by McElhinny et al. [1971] yields a factor of improvement of nearly 500 (Fig. 4D), which is why it is commonly used in rock magnetism laboratories to produce uniform fields. It is even possible to use Lee-Whiting's designs to retrofit an existing pair of Helmholtz coils with wing coils that will produce field uniformity comparable to that in Figure 4C or D. It would be exceedingly interesting to know whether Kalmijn's rays would condition to magnetic stimuli in altered fields with this degree of uniformity.

ACKNOWLEDGMENTS

REFERENCES

Able KP (1980): Mechanisms of orientation, navigation and homing. In Gauthreaux SA Jr (ed): "Animal Migration, Orientation, and Navigation." New York: Academic Press, pp 283–373.
Alldred JC, Scollar I (1967): Square cross-section coils for the production of uniform magnetic fields. J Sci Instrum 44:755–760.
Baker RR (1985): Magnetoreception by man and other primates. In Kirschvink JL, Jones DS, MacFadden

BJ (eds): ''Magnetite Biomineralization and Magnetoreception in Animals: A New Biomagnetism.'' New York: Plenum Press, pp 537–562.

Balkwill DL, Maratea D, Blakemore RP (1980): Ultrastructure of a magnetotactic spirillum. J Bacteriol 141:1399–1408.

Bauer GB, Fuller M, Perry A, Dunn JR, Zoeger J (1985): Magnetoreception and biomineralization of magnetite in cetaceans. In Kirschvink JL, Jones DS, MacFadden BJ (eds): ''Magnetite Biomineralization and Magnetoreception in Animals: A New Biomagnetism.'' New York: Plenum Press, pp 489–507.

Beason RC, Nichols JE (1984): Magnetic orientation and magnetically sensitive material in a transequatorial migratory bird. Nature 309:151–153.

Blakemore RP (1975): Magnetotactic bacteria. Science 190:377–379.

Blakemore RP, Frankel RB, Kalmijn AJ (1980): South-seeking magnetotactic bacteria in the southern hemisphere. Nature 286:384–385.

Brittenham GM, Farrell DE, Harris JW, Feldman ES, Danish EH, Muir WA, Tripp JH, Bellon EM (1982): Magnetic susceptibility measurements of human iron stores. N Engl J Med 307: 1671–1675.

Buchler ER, Wasilewski PJ (1985): Magnetic remanence in bats. In Kirschvink JL, Jones DS, MacFadden BJ (eds): ''Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism.'' New York: Plenum Press, pp 483–488.

Butler RF, Banerjee SK (1975): Theoritical single-domain size range in magnetite and titanomagnetite. J Geophys Res 80:4049–4058.

Carman GJ, Walker MM, Lee AK (1987): Attempts to demonstrate magnetic discrimination by homing pigeons in flight. Animal Learning Behav 15:124–129.

Chang S-BR, Kirschvink JL (1989): Magnetofossils, the magnetization of sediments, and the evolution of magnetite biomineralization. Annu Rev Earth Planetary Sci 17:169–195.

Cisowski S (1981): Interacting vs. non-interacting single-doman behavior in natural and synthetic samples. Phys Earth Planet Int 26:56–62.

Clusin WI, Bennett MVL (1979): The ionic basis of oscillatory responses of skate electroreceptors. J Gen Physiol 73:703–723.

Drayer BP, Burger P, Darwon R, Riederer S, Herfkens R, Johnson GA (1986a): Magnetic resonance imaging of brain iron. Am J Neuroradiol 7:373–380.

Drayer BP, Olanow W, Burger P, Johnson GA, Herfkens R, Riederer S (1986b): Parkinson plus syndrome: Diagnosis using high field MR imaging of brain iron. Radiology 159:493–498.

Emlen ST (1975): Migration: Orientation and navigation. In: ''Avian Biology, Vol. 5'' Farner DS, King JR (eds), Academic Press, N.Y. PP. 129–219.

Everett JE, Osemeikhian JE (1966): Spherical coils for uniform magnetic fields. J Sci Instrum 43:470–474.

Frankel RB, Blakemore RP, Wolfe RS (1979): Magnetite in freshwater magnetotactic bacteria. Science 203:1355–1356.

Frankel RB, Blakemore RP, Torres de Araujo FF, Esquivel EMS, Danon J (1981): Magnetotactic bacteria at the geomagnetic equator. Science 212:1269–1270.

Fuller M, Goree WS, Goodman WL (1985): An introduction to the use of SQUID magnetometers in Biomagnetism. In Kirschvink JL, Jones DS, MacFadden BJ (eds): ''Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism.'' New York: Plenum Press, pp 103–151.

Gomori JM, Grossman RI, Goldberg HI, Zimmerman RA, Bilaniuk LT (1985): Intracranial hematomas: Imaging by high-field MR. Radiology 157:87–93.

Gorby YA, Beveridge TJ, Blakemore RP (1988): Characterization of the bacterial magnetosome membrane. J Bacteriol 170:834–841.

Goree WS, Fuller M (1976): Magnetometers using Rf-driven SQUIDS and their applications in rock magnetism and paleomagnetism. Rev Geophys Space Phys 14:591–608.

Gould JL (1980): The case for magnetic sensitivity in birds and bees (such as it is). Am Sci 68:256–267.

Gould JL, Kirschvink JL, Deffeys KS (1978): Bees have magnetic remanence. Science 202:1026–1028.

Ising G (1945): Die physikalische Moglichkeit eines Tierischen Orientierungsinnes auf Basis der Erdrotation. Ark Mat Astron Fys 32A:1–23.

Jones DS, MacFadden BJ (1982): Induced magnetization in the monarch butterfly, *Danaus plexippus* (Insecta, Lepidoptera). J Exp Biol 96:1–9.

Jungerman RL, Rosenblum B (1980): Magnetic induction for the sensing of magnetic fields by animals—an analysis. J Theor Biol, 87:25–32.

Kalmijn AJ (1971): The electric sense of sharks and rays. J Exp Biol 55:371–383.

Kalmijn AJ (1974): The detection of electric fields from inanimate and animate sources other than electric organs. Handbook Sensory Physiol 9:147–200.

Kalmijn AJ (1978a): Experimental evidence of geomagnetic orientation in elasmobranch fishes. In Schmidt-Koenig K, Keeton WT (eds): "Animal Migration, Navigation, and Homing." Berlin: Springer-Verlag, pp 347–353.

Kalmijn AJ (1978b): Electric and magnetic sensory world of sharks, skates, and rays. In Hodgson ES, Mathewson RR (eds): "Sensory Biology of Sharks, Skates, and Rays." Washington DC: U.S. Government Printing Office, pp 507–528.

Kalmijn AJ (1981): Biophysics of geomagnetic field detection. IEEE Trans Magnet 17:1113–11124.

Kalmijn AJ (1982): Electric and magnetic field detection in elasmobranch fishes. Science 218:916–918.

Kalmijn AJ (1984): Theory of electromagnetic orientation: a further analysis. In Bolis L, Keynes RD, Maddrell SHP (eds): "Comparative Physiology of Sensory Systems." Cambridge: Cambridge University Press, pp 525–560.

Kalmijn AJ, Blakemore RP (1978): The magnetic behavior of mud bacteria. In Schmidt-Koenig K, Keeton WT (eds): "Animal Migration, Navigation, and Homing." Berlin: Springer-Verlag, pp 354–355.

Karlsson L (1985): Behavioral responses of european silver eels (*Anguilla anguilla*) to the geomagnetic field. Helgolander meersuntdersuchungen 39:71–81.

Keeton WT (1972): Effects of magnets on pigeon homing. In Galler SE (ed): "Animal Orientation and Navigation." NASA SP-262, pp 579–594.

Keeton WT, Larkin TS, Windsor DM (1974): Normal fluctuations in the earth's magnetic field influence pigeon orientation. J Comp Physiol 95:95–103.

Kirschvink JL (1980): South-seeking magnetic bacteria. J Exp Biol 86:345–347.

Kirschvink JL (1981a): Ferromagnetic crystals (magnetite?) in human tissue. J Exp Biol 92:333–335.

Kirschvink JL (1981b): Biogenic magnetite (Fe_3O_4): A ferrimagnetic mineral in bacteria, animals, and man. In Watanabe H, Iida S, Sugimoto M (eds): "Ferrites: Proceedings of the ICF3." Pp 135–138.

Kirschvink JL (1983): Biogenic ferrimagnetism: A new biomagnetism. In Williamson S, Romani G-L, Kaufman L, Modena I (eds): "Biomagnetism: An Interdisciplinary Approach." New York: Plenum Press, pp 501–531.

Kirschvink JL, Dizon AE, Westphal JA (1986): Evidence from strandings for geomagnetic sensitivity in cetaceans. J Exp Biol 120:1–24.

Kirschvink JL, Gould JL (1981): Biogenic magnetite as a basis for magnetic field sensitivity in animals. Biosystems 13:181–201.

Kirschvink JL, Jones DS, MacFadden BJ (eds) (1985a): "Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism." New York: Plenum Press.

Kirschvink JL, Kobayashi-Kirschvink A (1989): Is geomagnetic sensitivity real? Replication of the Walker-Bitterman conditioning experiment in honey bees. Am Zool (in press).

Kirschvink JL, Lowenstam HA (1979): Mineralization and magnetization of chiton teeth: Paleomagnetic, sedimentologic, and biologic implications of biogenic magnetite. Earth Planetary Sci Lett 44:193–204.

Kirschvink JL, Tabrah F, Batkin S (1982): Ferromagnetism in two mouse tumors. J Exp Biol 101:321–326.

Kirschvink JL, Walker MM (1985): Particle-size considerations for magnetite-based magnetoreceptors. In Kirschvink JL, Jones DS, MacFadden BJ (eds): "Magnetite Biomineralization and Magnetoreception in Animals: A New Biomagnetism." New York: Plenum Press, pp 243–254.

Kirschvink JL, Walker MM, Chang S-BR, Dizon AE, Peterson KA (1985b): Chains of single-domain magnetite particles in chinook salmon, *Oncorhynchus tshawytscha*. J Comp Physiol A 157: 375–381.

Klinowska M (1985): Cetacean live stranding sites relate to geomagnetic topography. Aquatic Mammals 11(1):27–32.

Klinowska M (1986): Cetacean live stranding dates relate to geomagnetic disturbances. Aquatic Mammals 11(3):109–119.

Kreithen ML, Keeton WT (1974): Attempts to condition homing pigeons to magnetic stimuli. J Comp Physiol 91:355–362.

Kuterbach D, Walcott B, Reeder RJ, Frankel RB (1982): Iron-containing cells in the honey bee *(Apis mellifera)*. Science 218:695–697.

Leask MJM (1977): A physiochemical mechanism for magnetic field detection by migratory birds and homing pigeons. Nature 267:144–145.

Lednor AJ, Walcott C (1983): Homing pigeon navigation: the effects of in-flight exposure to a varying magnetic field. Comp Biochem Physiol 76A:665–671.

Lee-Whiting GE (1957): "Uniform Magnetic Fields." Ottawa: Atomic Energy of Canada, Ltd., Chalk River Project Research and Development, Report CRT-673. 28 p.

Lindauer M (1977): Recent advances in the orientation and learning of honeybees. Proc XV Int Cong Entomol. Washington DC, pp 450–460.

Lowenstam HA (1962): Magnetite in denticle capping in recent chitons (polyplacophora). Geol Soc Am Bull 73:435–438.

Lowenstam HA (1981): Minerals made by organisms. Science 211:1126–1131.

Lowenstam HA, Kirschvink JL (1985): Iron biomineralization—A geobiological perspective. In Kirschvink JL, Jones DS, MacFadden BJ (eds): "Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism." New York: Plenum Press, pp 3–15.

MacFadden BJ, Jones DS (1985): Magnetic butterflies: A case study of the monarch (Lepidoptera, Danaidae). In Kirschvink JL, Jones DS, MacFadden BJ (eds): "Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism." New York: Plenum Press, pp 407–415.

Mann S (1985): Structure, Morphology and crystal growth of Bacterial magnetite. In Kirschvink JL, Jones DS, MacFadden BJ (eds): "Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism." New York: Plenum Press, pp 311–332.

Mann S, Sparks NHC, Walker MM, Kirschvink JL (1988): Ultrastructure, morphology and organization of biogenic magnetite from sockeye salmon, *Oncorhynchus nerka*: Implications for magnetoreception. J Exp Biol 140:35–49.

Martin H, Lindauer M (1977): Der Einfluss der Erdmagnetfelds und die Schwerorientierung der Honigbiene. J Comp Physiol 122:145–187.

Mather JG (1985): Magnetoreception and the search for magnetic material in rodents. In Kirschvink JL, Jones DS, MacFadden BJ (eds): "Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism." New York: Plenum Press, pp 509–536.

McElhinny MW, Luck GR, Edwards D (1971): A large volume magnetic field free space for thermal demagnetization and other experiments in paleomagnetism. Pure Appl Geophys 90:126–130.

McNeill DF, Ginsburg RN, Chang S-BR, Kirschvink JL (1988a): "Magnetostratigraphic dating of shallow-water carbonates from San Salvador, the Bahamas." Geology 16:8–12.

Moatamed F, Johnson FB (1986): Identification and significance of magnetite in Human tissues. Arch Pathol Lab Med 110:618–621.

Moore BR (1988): Magnetic fields and orientation in homing pigeons: Experiments of the late W.T. Keeton. Proc Natl Acad Sci USA 85:4907–4909.

Nesson MH (1969): "Magnetite Biomineralization in Chiton Teeth." PhD thesis, California Institute of Technology.

Nesson MH, Lowenstam HA (1985): Biomineralization Processes of the Radula Teeth of chitons. In Kirschvink JL, Jones DS, MacFadden BJ (eds): "Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism." New York: Plenum Press, pp 333–363.

O'Reilly W (1984): "Rock and Mineral Magnetism." London: Blackie Publishing Co.

Ossenkopp KP, Barbeito R (1978): Bird orientation and the geomagnetic field: A review. Neurosci Biobehav Rev 2:255–270.

Papi F, Meschini E, Baldaccini NE (1983): Homing behavior of pigeons released after having been placed in an alternating magnetic field. Comp Biochem Physiol 76A:673–682.

Perry A, Bauer GB, Dizon AE (1985): Magnetoreception and biomineralization of magnetite in amphibians and reptiles. In Kirschvink JL, Jones DS, MacFadden BJ (eds): "Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism." New York: Plenum Press, pp 439–454.

Phillips JB (1977): Use of the earth's magnetic field by orienting cave salamanders *(Eurycea lucifuga)*. J Comp Physiol A121:273–288.

Phillips JB (1986): Two magnetoreception pathways in a migratory salamander. Science 233:765–767.

Phillips JB, Adler K (1978): Directional and discriminatory responses of salamanders to weak magnetic fields. In Schmidt-Koenig K, Keeton WT (eds): "Animal Migration, Navigation, and Homing." Berlin: Springer-Verlag, pp 325–333.

Presti DE (1985): Avian Navigation, Geomagnetic Field Sensitivity, and Biogenic Magnetite. In Kirschvink JL, Jones DS, MacFadden BJ (eds): "Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism." New York: Plenum Press, pp 455–482.

Quinn TP (1980): Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. J Comp Physiol A137:243–248.

Quinn TP, Brannon EL (1982): The use of celestial and magnetic cues by orienting sockeye salmon smolts. J Comp Physiol A147:547–552.

Quinn TP, Merrill RT, Brannon EL (1981): Magnetic field detection in sockeye salmon. J Exp Zool 217:137–142.

Rosenblum B, Jungerman RL, Longfellow L (1985): Limits to induction-based magnetoreception. In Kirschvink JL, Jones DS, MacFadden BJ (eds): "Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism." New York: Plenum Press, pp 223–232.

Rubens SM (1945): Cube surface coils for producing uniform magnetic fields. Rev Sci Instrument 16:243–245.

Schulten K, Windemeuth A (1986): Models for a physiological magnetic compass. In Maret G, Boccara N, Kiepenheuer J (eds): "Biophysical Effects of Steady Magnetic Fields." New York: Springer-Verlag, pp 99–106.

Skiles DD (1985): The geomagnetic field: Its nature, history, and biological relevance. In Kirschvink JL, Jones DS, MacFadden BJ (eds): "Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism." New York: Plenum Press, pp 43–102.

Southern WE (1972a): Influence of disturbances in the earth's magnetic field on ring-billed gull orientation. Condor 74:102–105.

Southern WE (1972b): Magnets disrupt the orientation of juvenile ring-billed gulls. Bioscience 22:476–479.

Southern WE (1978): Orientational responses of ring-billed gull chicks: A re-evaluation. In Schmidt-Koenig K, Keeton WT (eds): "Animal Migration, Navigation, and Homing." Berlin: Springer-Verlag, pp 311–317.

Stratton JA (1941): "Electromagnetic Theory." International Monograph Series on Physics. New York: McGraw-Hill Book Co. 615 pp.

Stolz JF, Chang S-BR, Kirschvink JL (1986): Magnetotactic bacteria and single-domain magnetite in hemipelagic sediments. Nature 321:849–951.

Tenforde TS, Budinger TF (1986): Biological effects and physical safety aspects of NMR imaging and in vivo spectroscopy. In Thomas SR, Dixon RL (eds): "NMR in Medicine: Instrumentation and Clinical Applications." New York: American Association of Physicists in Medicine, pp 493–548.

Tesch F-W (1974): Influence of geomagnetism and salinity on the direction choice of eels. Helgol Wiss Meeresunters 26:382–395.

Teyssedre A (1986): Radio tracking of pigeons previously exposed to random oscillating magnetic fields. Behavior 96:265–276.

Torres de Araujo FF, Pires MA, Frankel RB, Bicudo CEM (1985): Magnetite and magnetotaxis in algae. Biophys J 50:375–378.

Towe KM, Lowenstam HA (1967): Ultrastructure and development of iron mineralization in the radular teeth of *Cryptochiton stelleri* (Mollusca). J Ultrastructural Res 17:1–13.

Towe KM, Moench TT (1981): Electron-optical characterization of bacterial magnetite. Earth Planetary Sci Lett 52:213–220.

Vali H, Forster O, Amarantidis G, Petersen N (1987): Magnetotactic bacteria and their magnetofossils in sediments. Earth Planetary Sci Lett 86:389–400.

Vine FJ (1966): Spreading of the ocean floor: New evidence. Science 154:1405–1415.

Walcott B, Walcott C (1982): A search for magnetic field receptors in animals. In Papi F, Wallraff HG (eds): "Avian Navigation." Berlin: Springer-Verlag.

Walcott C (1978): Anomalies in the earth's magnetic field increase the scatter of pigeon's vanishing bearings. In Schmidt-Koenig K, Keeton WT (eds): "Animal Migration, Navigation, and Homing." Berlin: Springer-Verlag, pp 143–151.

Walcott C, Gould JL, Kirschvink JL (1979): Pigeons have magnets. Science 184:180–182.

Walcott C, Green RP (1974): Orientation of homing pigeons altered by a change in the direction of an applied magnetic field. Science 184:180.

Walker MM (1984): Learned magnetic field discrimination in yellowfin tuna, *Thunnus albacares*. J Comp Physiol A155:673–679.

Walker MM, Bitterman ME (1985): Conditioned responding to magnetic fields by honeybees. J Comp Physiol A157:67–73.

Walker MM, Kirschvink JL, Chang SBR, Dizon AE (1984): A candidate magnetic sense organ in the yellowfin tuna, *Thunnus albacares*. Science 224:751–753.

Walker MM, Kirschvink JL, Dizon AE (1985): Magnetoreception and biomineralization of magnetite: fish. In Kirschvink JL, Jones DS, MacFadden BJ (eds): "Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism." New York: Plenum Press, pp 417–438.

Walker MM, Kirschvink JL, Perry AS, Dizon AE (1985): Methods and techniques for the detection, extraction, and characterization of biogenic magnetite. In Kirschvink JL, Jones DS, MacFadden BJ (eds): "Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism." New York: Plenum Press, pp 154–166.

Walker MM, Quinn TP, Kirschvink JL, Groot T (1988): Production of single-domain magnetite throughout life by sockeye salmon, *Oncorhynchus nerka*. J Exp Biol 140:51–63.

Wiltschko W (1972): The influence of magnetic total intensity and inclination on directions preferred by migrating European robins *(Erithacus rubeccula)*. In Galler SR, Schmidt-Koenig K, Jacobs GJ, Belleville RE (eds): "Animal Orientation and Navigation." NASA SP-262. Washington DC: U.S. Government Printing Office, pp 569–578.

Wu MK, Ashburn JR, Torng CJ, Hor PH, Meng RL, Gao L, Huang ZL, Wang YQ, Chu CW (1987): Superconductivity at 93°K in a new mixed-phase Y-Ba-Cu-O compound system at ambient pressure. Phys Rev Letts 58:908–910.

Yorke ED (1979): A possible magnetic transducer in birds. J Theor Biol 77:101–105.

Yorke ED (1981): Sensitivity of pigeons to small magnetic field variations. J Theor Biol 89:533–537.

Zoeger J, Dunn JR, Fuller M (1981): Magnetic material in the head of a common Pacific dolphin. Science 213:892–894.