

BIOGENIC MAGNETITE AS A BASIS FOR MAGNETIC FIELD DETECTION IN ANIMALS

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Bacteria, sharks, honey bees, and homing pigeons as well as other organisms seem to detect the direction of the earth's magnetic field. Indirect but reproducible evidence suggests that the bees and birds can also respond to very minute changes in its intensity. The mechanisms behind this sensitivity are not known. Naturally magnetic, biologically precipitated magnetite (Fe_3O_4) has been found in chitons, magnetotactic bacteria, honey bees, homing pigeons, and dolphins. Its mineralization in localized areas may be associated with the ability of these animals to respond to the direction and intensity of the earth's magnetic field. The presence of large numbers ($\sim 10^8$) of superparamagnetic magnetite crystals in honey bees and similar numbers of single-domain magnetite grains in pigeons suggests that there may be at least two basic types of ferrimagnetic magnetoreceptive organelles. Theoretical calculations show that ferrimagnetic organs using either type of grain when integrated by the nervous system are capable of accounting for even the most extreme magnetic field sensitivities reported. Indirect evidence suggests that organic magnetite may be a common biological component, and may account for the results of numerous high field and electromagnetic experiments on animals.

1. Introduction

The behavior and, in particular the orientation of a variety of aquatic and terrestrial animals is apparently affected by the direction and/or intensity of the Earth's magnetic field. Animals in which such effects have been reported span the phyletic spectrum from bacteria (Blakemore, 1975) through vertebrates (Keeton, 1971a,b; Kalmijn, 1974, 1978; see also the reviews by Gould, 1980 and Dubrov, 1978). These behavioral phenomena are particularly dramatic, accessible, and reproducible in magnetic bacteria (Blakemore, 1975), sharks (Kalmijn, 1978), honey bees (Lindauer and Martin, 1968), and homing pigeons (Keeton, 1971a,b; Walcott and Green, 1974). Further, behavioral experiments suggest that these last

two organisms can detect and respond to changes in the Earth's field strength on the order of one to ten parts in 10^5 .

Four magnetic effects have been reported in the honey bee literature as follows: (1) Small but consistent errors in the "waggle dance" language disappear when the magnetic field is cancelled or artificially made too strong (Lindauer and Martin, 1968). These errors apparently depend on the direction, intensity, and rate of change of the field and imply resolutions of 1–10 gamma (10^{-5} G), or 0.1–1 gamma/min (Lindauer and Martin, 1972; Lindauer, 1976; Martin and Lindauer, 1977). (2) When forced to dance on horizontal comb, workers eventually orient themselves preferentially to the eight points of the magnetic compass (e.g., N, NE, E,... Lindauer and Martin, 1972; Martin and Lindauer, 1977; Brines, 1978). (3) In an otherwise featureless hive, worker bees will build sheets of new comb in the same magnetic orientation as in their parent hive. Strong

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magnetic fields are said to disrupt comb orientation (Lindauer and Martin, 1972; Martin and Lindauer, 1973). Finally, (4) in the absence of other cues bees set their circadian rhythms to the weak (50–100 gamma) diurnal variations in geomagnetic field strength (Lindauer, 1976). We have been able to confirm in our laboratory the basic results of experiments (1), (2), and (4) in a preliminary way, and are therefore inclined to believe these remarkable effects.

Homing pigeons show several more obviously adaptive responses to the geomagnetic field than do honey bees. On cloudy days, the static field of a bar magnet (Keeton, 1971) or paired coils (Walcott and Green, 1974) attached to the head disrupts orientation dramatically. This and other work implies that pigeons use a magnetic compass when the sun is not visible. Keeton et al. (1974) observed a systematic, graded release-bearing bias in pigeons which was correlated with natural field variations of 40 gamma or less. On sunny days, Walcott (1978) released pigeons from magnetic anomalies and discovered clear behavioral effects for changes of only 40 gamma/km in the homeward direction. At levels of 3000 gamma/km (6% of the Earth's field strength), pigeons appear totally confused in spite of their clear view of the sun. This suggests that the "map" sense of the homing pigeon may depend on magnetic field information.

Numerous authors have proposed mechanisms through which the geomagnetic field might be detected by an organism. If magnetoreception is a "real" sense analogous to hearing or vision, there should be specialized sensory organelles (magnetoreceptors) directly connected to the nervous system for this purpose. Any mechanism, of course, needs to explain how this physical stimulus could be transduced into the local, graded depolarization of a sensory nerve membrane. Whatever the cause, these graded responses would then be translated into a frequency-coded stream of action

potentials for processing elsewhere. Without such a conversion, an organism simply would not be able to detect the geomagnetic field. The most important constraint on these models is that they should allow for the detection of extremely weak field variations as done by the bees and pigeons.

Prior to the last few years, speculation and theoretical analysis concerning the transduction mechanism has centered mainly on various forms of electrical induction and paramagnetism. In its most elementary form, an induction mechanism supposes that an organism detects the weak electric fields generated by its motion across a magnetic field (Faraday's law). Kalmijn (1974, 1978) has extensively considered this mechanism from both theoretical and experimental approaches, and shows that electroreception can account for the magnetic field detection of the elasmobranch fish (sharks and rays). Their electric organs (the ampullae of Lorenzini) are capable of detecting electric fields as low as $0.01 \mu\text{V/cm}$ (Kalmijn, 1966), well within the necessary range. Similar electric receptors, however, have not been found in terrestrial animals, and the ability of almost stationary birds, and bees to sense the field argues against it. Terrestrial animals also lack the low resistance return path — salt water — which is essential to the elasmobranch system. Further, the detection of extremely weak fluctuations in the field strength suggested from the data on birds and bees would require averaging over many thousands of these rather large electric organs. Cope (1973) has offered a solution to this problem by suggesting the presence of a superconductive Josephson junction, which would have sensitivities on the order of 10^{-11} G (10^{-6} gamma). Although this is an interesting hypothesis, there is as yet no evidence for the required room-temperature superconductivity.

The other often-cited mechanism, paramagnetism, supposes that the temporary alignment of electron spins in some way can be amplified into an observable response. This is a formidable problem, however,

because a single electron on a typical organic molecule interacts only weakly with the Earth's field. Compared to the background thermal energy, kT (k is Boltzmann's constant and T is the absolute temperature), the effect is a small 1 part in 10^6 (see also Neurath, 1964). Nevertheless, many authors feel that these effects might detectably alter rates of chemical reactions (e.g., Haberditzl, 1967) or be amplified through other systems such as optical pumping (Leask, 1977). Unfortunately, these methods do not naturally lead to the high sensitivities displayed by the birds and bees without incorporating large volumes (~several hundred ml) of paramagnetic material into the array.

A more plausible, yet largely ignored, mechanism for magnetic field detection was originally suggested by Lowenstam (1962). He discovered that the radular teeth of a primitive sea mollusc, the chiton (class Polyplacophora), were capped with magnetite (Fe_3O_4). Unlike any other biogenic material, magnetite is both ferromagnetic and an electrical conductor (a ferrite). Our discovery of similar biogenic magnetite in honey bees (Gould et al., 1978) and pigeons (Walcott et al., 1979) as well as its recognition in magnetotactic bacteria (Frankel et al., 1979) and dolphins (Zoeger et al., 1980) suggests that it may play a central role in their magnetoreception. Kirschvink and Lowenstam (1979a) also detected similarly ferromagnetic material (probably magnetite) distributed along the lateral line and in the heads of shark embryos, suggesting that they could have this type of receptor as well. In contrast to paramagnetism, magnetite of the proper size and shape couples strongly with magnetic fields, producing interaction energies on the order of kT . With such a construction material available to organisms, a wide variety of magnetoreceptors are theoretically possible. In the past, however, this type of mechanism has not been considered sensitive enough to account for the detection of extremely weak fluctuations in the geomagnetic field (Yorke, 1979). A goal of

this paper is to show that the large numbers of organic magnetite crystals in honey bees and pigeons *could in theory* account for the detection of these extremely weak pulsations. The simple detection of a magnetic compass direction would require only a few hundreds to perhaps a thousand crystals of magnetite; by averaging over hundreds of millions of grains, however, we find that the detection of very weak fields is realistic.

As a starting point, our theoretical analysis must begin with a summary of the relevant chemical and physical properties of biogenic magnetite. This is necessary because the biological implications of this material have been completely overlooked by most authors in the field (e.g., Pethig, 1979; Dubrov, 1978). Next, we consider several simple transduction geometries which would lead to the necessary depolarization of a sensory nerve membrane. Although we do not necessarily expect these models as shown to conform precisely to nature, they serve at least two worthwhile functions: (1) they permit us to estimate the sensitivity of a detector array, and (2) they should serve to guide future experiments. Finally, the widespread occurrence of biogenic magnetite in higher organisms provides a realistic, unifying theory for many of the unsolved riddles in animal migration and high-field biomagnetic effects.

2. Physical and chemical properties of organic magnetite

2.1. Biosynthesis of magnetite

Although magnetite is synthesized by a variety of organisms, relatively little is known about the metabolic pathway(s) by which it is formed. The mineralization sequence in Chitons (Polyplacophora) is best known because it is displayed continuously in the teeth along the radula and may be similar to that in other organisms (see Towe and Lowenstam, 1967; Kirschvink and Lowen-

stam, 1979b). In chitons ferric iron is first concentrated near the area to be mineralized with the iron storage protein, ferritin. Ferric iron is held in the core of the ferritin macromolecule by an approximately 60 Å subunit of the mineral ferrihydrite ($5\text{Fe}_2\text{O}_3 \cdot 9\text{H}_2\text{O}$, Harrison et al., 1976; Towe and Bradley, 1967). During this buildup, an organic network forms in those areas of the tooth which later will be mineralized. The fibrous organic material makes honeycomb-like compartments of roughly the same size as later mineralized grains ($\sim 0.1 \mu\text{m}$ in diameter). Through an unknown mechanism, external Fe^{3+} is dissolved and reprecipitated again as crystalline ferrihydrite within the organic compartments. Once this organic matrix has been filled, the ferrihydrite is rapidly converted to magnetite — this transition may be seen as a sharp break between red and black in the sequential teeth along the chiton's radula. Because ferrihydrite has a crystal form similar to hematite, this change means that 1/3 of the iron atoms are reduced to Fe^{2+} , the material is dehydrated, and the oxygens are repacked into distorted cubic symmetry. Although the agents responsible have neither been identified nor isolated, enzymes probably control the process. Magnetite in chitons is always formed from ferrihydrite and has never been found as a direct precipitate (Kirschvink and Lowenstam, 1979b). Some evidence suggests that ferritin may be present in magnetotactic bacteria (Frankel et al., 1979), is certainly present in *Azotobacter* (Stiefel and Watt, 1979), and may also be associated with magnetite mineralization in pigeons (Walcott et al., 1979).

2.2. Magnetite crystal structure

At temperatures above 120 K (the Verway transition), magnetite belongs to the cubic system and possesses an inverse spinel structure. Although somewhat distorted, the oxygen atoms are in cubic close packing with an average interatomic spacing just under 3 Å. Both tetrahedral and octahedral

coordination sites exist in the lattice, with tetrahedral outnumbering octahedral by 8 to 1. One-eighth of the tetrahedral sites are filled with Fe^{3+} , the others being empty; half of the octahedral sites are occupied with the remaining Fe^{2+} and Fe^{3+} ions in equal numbers. The resulting density is about 5.1 g/cm^3 , making magnetite the most dense biogenic material known (Lowenstam, 1974).

2.3. Electrical properties of magnetite

As a metallic iron oxide, magnetite has by far the highest electrical conductivity of any known biogenic solid ($\sigma = 2 \times 10^4$ mhos/m, Shuey, 1975). Magnetite conducts electricity roughly 6000 times better than the axoplasm in squid nerves (Kuffler and Nicholls, 1976, p. 134). The high conductivity is due to electrons hopping between Fe^{2+} and Fe^{3+} ions occupying adjacent octahedral sites within the crystal lattice. Each octahedral (Fe^{2+} , Fe^{3+}) ion pair has one conducting electron with only a 0.04 eV activation energy for interatomic hops. Shuey (1975) has reviewed this topic further.

2.4. Origin of magnetism

The inverse-spinel structure of magnetite implies that the tetrahedral and octahedrally-coordinated sites are arranged in alternate coplanar layers perpendicular to the [111] direction. For each tetrahedral Fe^{3+} , there is a corresponding pair (Fe^{3+} , Fe^{2+}) in the adjacent octahedral layer. Within a given layer the individual atomic magnetic moments are generally aligned; between layers, however, a super-exchange quantum-mechanical coupling acts to make their moments antiparallel. The atomic moment of each tetrahedral Fe^{3+} ion is then exactly cancelled by the antiparallel moment of an octahedral Fe^{3+} ion in the next layer. This leaves an ordered array of *parallel* octahedral Fe^{2+} atomic moments throughout the crystal

lattice and gives rise to a type of ferromagnetic behavior known as *ferrimagnetism*. An average saturation magnetization (J_s) of 480 G results from the vector summation of all the parallel Fe^{2+} atomic moments. A uniformly magnetized particle of Volume $V(\text{cm}^3)$ will then generate a magnetic moment, $\vec{\mu}$, with a magnitude given by VJ_s . Kittel (1976) presents a comprehensive review of this subject.

2.5. Stability of magnetization

Magnetic properties of a ferrimagnetic material vary directly as a function of its crystal size and shape, and are illustrated for isolated parallelepipeds of magnetite on the stability diagram of Fig. 1 (after Butler and Banerjee, 1975). The horizontal axis is the ratio of width to length for a given grain, while the vertical is the length. Grains which plot in the single-domain (SD) and superparamagnetic (SPM) areas are those

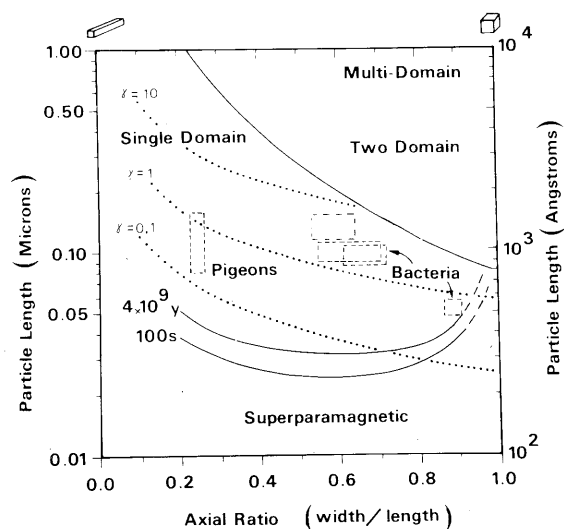


Fig. 1. Magnetic stability diagram for isolated rectangular parallelepipeds of magnetite (after Butler and Banerjee 1975). Bacterial magnetite dimensions are those measured by Blakemore (1975), Frankel et al. (1979), Kirschvink (1980), Moench and Konetzka (1979), and Towe and Moench (in press), and those for the homing pigeons are given in Walcott et al. (1979).

in which a uniform parallel magnetic spin structure exists across the entire volume of the particle. These grains are always magnetized fully to magnetite's saturation value of 480 G. Single-domain grains are those in which the magnetic direction is extremely stable; despite thermal agitation their magnetic direction can remain unchanged relative to the crystal at room temperature through all of geologic time ($>4.5 \times 10^9$ years). In grains smaller than the bottom two lines on Fig. 1, however, thermal activation alters the direction of the remanence, and moments from each grain tend to be randomized or preferentially aligned with local magnetic fields in proportion to their strength. For this superparamagnetic (SPM) behavior, the magnetic direction can change without moving the grain. Banerjee (1976) calculates similar boundaries using elliptical instead of tabular crystals.

Néel (1949) has shown that the characteristic relaxation time required for the magnetic direction of an isolated domain to change spontaneously is:

$$\tau \propto \exp(VJ_s H_c / 2kT) \quad (1)$$

where τ is the relaxation time, V is the grain volume, J_s is the saturation magnetization, H_c is the microscopic coercivity, k and T are the Boltzmann's constant and the absolute temperature, respectively. Thus, the boundary between the single domain and superparamagnetic stability fields on Fig. 1 is temperature as well as size and shape dependent. Above a critical volume, the one-domain state is no longer stable and the atomic moments will not align themselves uniformly through the particle. Two or more domain configurations will form and yield a lower external magnetic field (multi-domain behavior). Most organic magnetites which have been reported are either SD or SPM (Gould et al., 1978; Frankel et al., 1979; Walcott et al., 1979; Kirschvink and Lowenstam, 1979b).

2.6. Shape anisotropy and alternating field (Af) demagnetization

A magnetite crystal of single-domain size will spontaneously magnetize itself fully to saturation (480 G). The direction in which this remanence lies is profoundly affected by the external field at the moment of magnetization and the particle's shape. Less energy is required to magnetize a grain along its length than transversely; this magnetostatic energy or energy of self-demagnetization for an ellipsoid of volume V is given by

$$E = \frac{1}{2}NVJ_s^2, \quad (2)$$

where N is a dimensionless demagnetization factor along the direction of magnetization. Across a long thin rod, for example, $N \simeq 2\pi$ while along its length $N = 0$. Thus, the axis along which N is least is also the minimum energy direction, and the magnetic moment, $\vec{\mu}$, of the particle will tend to lie along it in one of two antiparallel directions.

A strong, externally-applied magnetic field (\vec{B}) has an interaction energy with the grain given by $E = -\vec{\mu} \cdot \vec{B}$ (in vector notation). If this interaction energy is greater than the minimum magnetostatic energy for a fixed grain, the moment $\vec{\mu}$ can be deflected towards the direction of B . The strength of the external field for which $\vec{\mu} \cdot \vec{B}$ exceeds the maximum magnetostatic energy of the grain is termed the blocking or unblocking field, and is the minimum intensity required to flip the direction of magnetic remanence (exclusive of nucleating a new domain). For a long, thin needle of magnetite, $N_{\max} \sim 2\pi$, so it follows that the maximum unblocking field should be near πJ_s , or 1500 G. In actual practice, however, the observed unblocking fields tend to be somewhat lower than this prediction due to nucleation and rapid growth of oppositely-magnetized domains in high magnetic fields (Stacey and Banerjee, 1974).

Based on these properties, paleomagnetists

have devised a means of incrementally randomizing the moments of small magnetic grains dispersed in a rock (or tissue) sample. In this process, the samples are placed in a non-magnetic environment and subjected to a slowly-decreasing sinusoidally-alternating magnetic field. If the peak magnetic field intensity initially exceeds that required to unblock the remanence of a given single-domain grain, its direction of magnetization will oscillate back and forth. When the peak strength of the alternating field decays below this critical level, the remanence of the grain may be left in either direction. An assemblage of such demagnetized elongate grains should have no net remanence, although half of them should still be magnetized in their original direction. The effect of this procedure will be discussed for each of the magnetoreceptor models discussed later.

2.7. Distinctive assays for the biologic identification of magnetite

With the exception of chiton teeth, biogenic magnetite in higher organisms usually occurs in minute quantities, sometimes finely scattered throughout the volume of a tissue. There are several definitive methods for locating, purifying, and identifying it. If enough material is present (e.g., several milligrams), X-ray powder diffraction and/or Mössbauer absorption will suffice (Lowenstam, 1962; Frankel et al., 1979). Because magnetite has the highest density of any biogenic product ($\rho \simeq 5.1$), smaller quantities can be recovered and purified after destruction of other organic material with a 5% sodium hypochlorite solution by simple heavy-liquid centrifugation. Beyond this stage, identification is easy. Atomic absorption or microprobe analysis can give the elemental composition of very small quantities. Magnetite is the only iron oxide which is optically black (dark, dark blue) as a fine powder. Thermal agitation destroys the ferrimagnetic properties near 580°C; this point (the Curie

temperature) can be measured on a sensitive magnetic balance and is usually considered distinctive. The most sensitive technique providing unique identification, however, is electron diffraction on a high-voltage transmission electron microscope (Towe and Lowenstam, 1967; Towe and Moench, in press). At the present time, magnetite is the only known biogenic ferromagnetic material; therefore if the possibility of sample contamination can be eliminated, the mere existence of a liquid nitrogen temperature saturation remanence suggests its presence.

3. Strategies for magnetic field detection

To function as a magnetoreceptor, the ferrimagnetic grains must be connected in some fashion to the nervous system. Given the properties of organic magnetite outlined above, there are a few extremely simple ways in which an organism might construct organelles. We consider here several basic strategies: (1) an isolated receptor; (2) a torque detector; (3) interactions between superparamagnetic grains; and (4) ferrimagnetic-paramagnetic hybrids.

3.1. Isolated magnetoreceptors

The simplest strategy for connecting magnetite to the nervous system would be to place one suitably-sized grain per receptor cell, and have the nervous system integrate the response from many of them. An example of this class of detector is diagrammed in Fig. 2. In this particular model, a small organelle equipped with an isolated grain of organic magnetite is held by hydrophobic protein groups across the membrane of a sensory nerve ending. To be effective, the magnetite crystal should first be of suitable size and shape to plot within the single-domain stability field shown on Fig. 1, thereby allowing it to be permanently magnetized. An elongate form, similar to the pigeon crystals, will generate a considerable magnetic shape anisotropy and

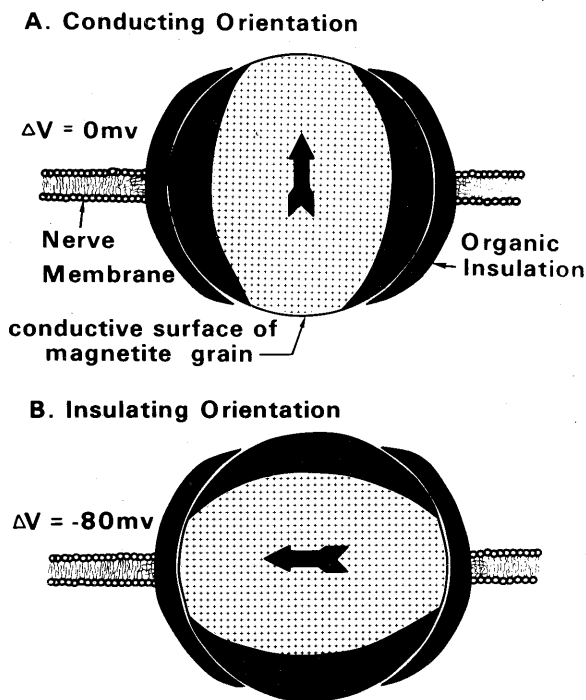


Fig. 2. Membrane-short model. A single-domain magnetite crystal is held in a membrane where it is free to rotate into alignment with the earth's magnetic field. If the grain is partially insulated, only certain magnetic field orientations will result in exposing the uninsulated portions to the external and internal mediums. Since magnetite is an excellent conductor by biological standards, such an alignment will depolarize the membrane, generating a potentially useful signal.

constrain the remanence to lie parallel to its length. Next, the interaction energy between an isolated grain and the external magnetic field ($\vec{\mu} \cdot \vec{B}$) should be somewhat larger than kT , the one-dimensional thermal energy acting to randomize its orientation. Because $|\vec{\mu}| = VJ_s$, the volume of the grain in the earth's ~ 0.5 G field largely determines this interaction energy; consequently, curves of equal energy (corresponding to equal grain volumes) can be drawn on the magnetic stability diagram of Fig. 1. For room temperature (300 K), the curves corresponding to 0.1, 1 and $10kT$ are shown as dotted lines. Most of the biogenic magnetite crystals formed by bacteria and pigeons

clearly have interaction energies within this range.

In some fashion, an isolated crystal must now be able to alter the electric potential which is normally maintained across the membrane of a sense organelle. Excitable nerve membranes which join the sense region usually maintain a potential difference of about -70 mV to -80 mV between their interior and exterior. Electrical depolarization to less than -60 mV to -40 mV drives the membrane potential in the positive direction, leading to an action potential. Motion of the magnetite grain could change the membrane potential in at least two ways: (1) by electrically shorting across it; and (2) by opening or closing ion channels. Because of its simplicity, we will first consider the electrical model.

3.2. The membrane short model

Magnetite has the highest electrical conductivity of any biogenic product or other oxide mineral — its resistivity is only 5×10^{-3} ohm-cm (Shuey, 1975). In Fig. 2, a magnetite grain ($0.2 \times 0.1 \times 0.1 \mu\text{m}$) is diagrammed with an equatorially-wrapped organic insulator such as myelin. A similar insulating body holds it in the membrane while allowing it to rotate (like a ball-in-socket) into alignment with the magnetic field. With this configuration, the surface area of magnetite exposed for electrical conduction is directly controlled by the angle between the external magnetic field and the plane of the membrane. Initially, the electric field acting across the crystal in this situation is quite high — 70 mV over $0.2 \mu\text{m}$ is 3500 V/cm. The instantaneous current density which can flow in response to this is equally large, nearly 7×10^5 A/cm². If current were to flow smoothly for $1 \mu\text{s}$, the fully exposed ($0.1 \mu\text{m}$)² grain could completely depolarize the charge on 10^7 times its own area. Therefore, if *any* magnetite electrically connects with the surrounding medium on both sides of the membrane, the local electric field

immediately drops to zero. Away from this point, the potential will return exponentially back to its resting value in response to the passive membrane cable properties and form a circular region of electrical depolarization. The radius of this circle is determined by the surface area of magnetite exposed, and hence is a function of the angle between the plane of the membrane and the direction of the magnetic field. This electrical depolarization, like any other generator potential arising at a sensory ending, can convert the magnitude of the short into a frequency-modulated stream of action potentials for integration elsewhere.

With three of these organelles in a more-or-less orthogonal arrangement, it is clear that the average frequency of action potentials from each would convey the information necessary to make an estimate of the magnetic field direction. However, the firing frequency also contains information about the magnetic intensity. This information could be coded in either of two ways. For a one-grain/one-cell model, magnetic field intensity is proportional to the variance in firing frequency. To see this, note that each magnetite grain roughly approximates a thermally-driven harmonic oscillator. On the average, the magnetic moment $\vec{\mu}$ of a grain will be distributed around the external field direction, \vec{B} , with an R.M.S. angular deviation given by $(2kT/\mu B)^{1/2}$, not $(kT/\mu B)^{1/2}$ as used by Yorke (1979). If \vec{B} is large, $\mu B \ll kT$ and the grain's moment $\vec{\mu}$ will closely follow the applied field. The organelle will fire regularly with little deviation in frequency. On the other hand, if \vec{B} is small the angular scatter of the grain — its thermally generated "wandering" over time about the external field direction — becomes large and the organelle fires erratically with large deviations in frequency. With proper design, each magnetite crystal could act as an independent estimator of the magnetic intensity, whereas three orthogonal grains would be required to estimate direction.

The other strategy would require two or more magnetite crystals per cell. In a weak field these grains would, again, wander independently about the external field direction. If the cell is arranged so that it requires two or more grains depolarizing it simultaneously to fire, then the firing rate would depend upon the external field direction with respect to the "best" axis of the cell and the net field strength. The field strength dependence is a consequence of the greater probability that two or more grains will be aligned simultaneously in a higher field. In this case, direction would again be specified by the ratio of the three classes of mutually orthogonal cells, but field intensity would now be indicated by the mean firing rate of the cells as a group.

This class of models is subject to an important ambiguity. Since the two sides of a grain must both be exposed to short-circuit the membrane, such a detector (without the specific modifications outlined below) cannot distinguish polarity. If a particular field alignment shorts the cell, the opposite polarity must rotate the grain 180° and again connect the outside and inside electrically. Similarly, AF demagnetization will only flip a grain's magnetic direction, and therefore cannot alter the organelle's response. Of course, this directional ambiguity is familiar: bees, pigeons, and European robins seem to confuse magnetic polarity.

Earlier, we noted that bees and pigeons were apparently able to detect minute variations in geomagnetic intensity on the order of 1 part in 10^5 . This level of sensitivity seems almost impossibly high. However, an animal's nervous system can increase the resolution of any sense by either integrating the response from a large number of organelles, or averaging the output over some amount of time, or both. In each case, the resolution theoretically improves by factors of $N^{1/2}$ and $[I/\tau]^{1/2}$ respectively, where N is the number of independent

organelles, I is the interval over which the integration occurs, and τ is the characteristic rotational response time for the grain (Yorke, 1979). For intensity, the quantity which is being evaluated in this model is essentially the R.M.S. angular dispersion, $(2kT/\mu B)^{1/2}$. It follows therefore, that the theoretical sensitivity $\Delta B/B$ is given by $[2kT/N\mu B(I/\tau)]^{1/2}$. $N\mu$ is the saturation moment for the entire assemblage and is equal to twice the saturation remanence ($2R$) for a dispersion of single-domain grains. The relative sensitivity is then $[2kT/2RB(I/\tau)]^{1/2}$. For a pigeon's magnetic organ, R was found to be about 10^{-5} emu (Walcott et al., 1979). By integrating over one time constant ($I = \tau$) in the earth's field at body temperature (314 K), the bird should be able to sense a change of 1 part in about 2.1×10^4 , or about 4 gamma. The time constant, τ , is physiologically reasonable. Using the derivation of Yorke (1979) for τ and applying it to an average grain of pigeon magnetite (Fig. 1) with a rotational viscosity ten times water, τ would be on the order of 35 ms. Of course, pigeons can take rather longer than 35 ms to make behavioral judgements. By integrating all the signals over, say, 3.5 s (100τ), the pigeon could then, in theory at least, resolve 0.4 gamma changes.

Clearly there is little theoretical difficulty in accounting for the observed and inferred sensitivities of pigeons on the basis of such a magnetite-based receptor. However, a variety of practical difficulties exist with this particular illustration of the membrane-short model. The minimum size of a single-domain grain may be seen from Fig. 1 as about 400 Å, whereas the membrane supporting it could be only about 100 Å thick. The grain simply does not fit very comfortably. Some specialized thickening would probably be necessary. Further, we must consider the electrical junction at the magnetite/fluid interface: for current to flow, an oxidation reaction must occur at one end while something else is reduced at the

other. A suitable mechanism might be to couple the magnetite surface to the cytochrome electron-transport system. Cytochromes pass electrons from one molecule to another via ferrous to ferric transitions, just as octahedral iron atoms in magnetite pass them between lattice sites. It is even possible that magnetite grains could be made to conduct in only one direction by placing part of the electron transport system on one end and the rest on the other. This arrangement would permit the absolute polarity of the field to be detected.

3.3. Sympathetic satellites

As noted earlier, the electrical potential in the generating region of a sensory neuron could also be varied by opening or closing ion channels within the nerve membrane, perhaps by some connection between a single-domain magnetite crystal and a molecular gate or pore located within the lipid bilayer. Because single-domain grains do not fit well within a membrane, they must either be put adjacent to it or be replaced with smaller, superparamagnetic grains which in turn would influence ionic conductivity. One way of making this connection would be to put the channels on smaller, membrane-sized molecules with an elongate magnetite core. If placed near a larger magnetic crystal, these small molecules would align themselves in sympathy with the dominating field of the big grain. The minimum energy configuration is when the small molecules are as close as possible to the larger grain — if their interaction energy is comparable to kT they will cluster around to produce a self-assembling structure with the magnetite-bearing molecules held like satellites around the larger one.

Two thermodynamic constraints must be met for this system to work. First, the length and volume of the small magnetite rods must be such that the magnetostatic energy produced by their shape anisotropy exceeds kT . This will cause the satellite molecules

to rotate into preferential alignment with the magnetic field of the larger grain. The minimum volume of magnetite necessary to balance kT is found from eqn. 2 above as $2kT/NJ_s^2$, where $N = 2\pi$ is the demagnetizing factor transverse to a long rod. Using this we find that the volume of magnetite necessary to equal kT is $6 \times 10^{-20} \text{ cm}^3$. This is equivalent to a ball 48 Å in diameter. Note that ferritin, the iron storage protein involved in magnetite synthesis, has roughly a 70 Å hole in its center typically filled with the mineral ferrihydrite, the direct precursor of magnetite in chiton teeth Fischback and Anderegg (1965) have measured the shape of the iron core of horse spleen ferritin through X-ray scattering, and conclude that under some conditions it forms elongate rods. If the ferrihydrite core of the ferritin molecule were converted into a similar magnetite rod, it would produce the required satellite molecule having an anisotropy energy of $3kT$.

The second thermodynamic constraint on the system is that the magnetostatic energy of interaction between the satellite molecules and the larger crystal should also be greater than kT . If this is true, the detector would be self-assembling and the satellite molecules would be forced into rotational alignment with the local field direction of the larger grain. In vector notation, the interaction energy between two dipole moments $\vec{\mu}_1$ and $\vec{\mu}_2$ separated by a center-to-center displacement vector \vec{x} is given by:

$$E = \frac{\vec{\mu}_1 \cdot \vec{\mu}_2 - 3(\vec{\mu}_1 \cdot \vec{\eta})(\vec{\mu}_2 \cdot \vec{\eta})}{|\vec{x}|^3} \quad (3)$$

where $\vec{\eta}$ is a unit vector parallel to \vec{x} . By taking $\vec{\mu}_1$ as the moment of the magnetite core of the modified ferritin molecule discussed above and assuming the two particles are touching, we find that the minimum moment of the large grain should be $9.4 \times 10^{-15} \text{ emu}$ for a $1kT$ interaction, or the moment of a magnetite grain 335 Å in dia-

meter. This assembly is depicted on Fig. 3. As seen on Fig. 1, a magnetite crystal this size is just outside the single-domain stability field and should exhibit superparamagnetic behavior. Its magnetic moment can therefore rotate in response to the direction of the external field without physical motion of the grain itself. Satellite molecules floating in the adjacent membrane, however, should move in sympathy with the larger grain's moment, opening and closing their attached ionic channels. Note that this structure again would not allow the polarity of the field to be determined, nor would alternating-field demagnetization have an effect. A large grain could equally well be placed

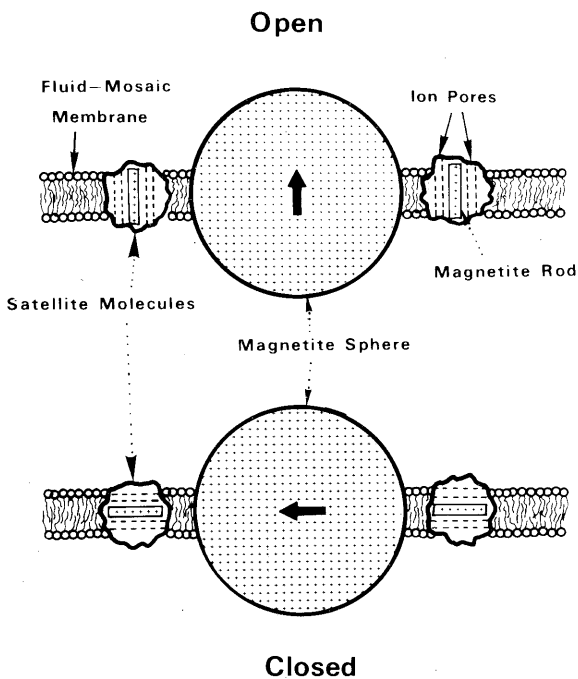


Fig. 3. Sympathetic satellites. The magnetite spheres are superparamagnetic and will statistically align their moments parallel to an external field. Satellite molecules in the surrounding membrane have a magnetite rod in their core, and will align themselves parallel to the local field lines generated by the larger sphere. Top diagram: the external field is perpendicular to the membrane, and ion pores are exposed to the external medium generating a porous membrane. Bottom diagram: the external field is in the plane of the membrane, blocking the pores.

next to the membrane adjacent to the satellite molecules, instead of across it as shown. Single-domain grains, if free to rotate, would serve just as well.

In terms of sensitivity, the theoretical analysis for this detector is similar to that discussed above for the membrane-short model. The net alignment of a moment $\vec{\mu}$ for spherical superparamagnetic grains in an external field B is given by the Langevin function, and has a R.M.S. deviation approaching $(2kT/\mu B)^{1/2}$ (Stacey and Banerjee, 1974) similar to that discussed above for the rotation of single-domain grains. A more exact analysis is given elsewhere (Kirschvink, in review). Although strongly influenced by size and shape, the time-constant τ for motion of the moment $\vec{\mu}$ relative to the grain is given by Neel's relation above, and may range from a few microseconds to several minutes. Each organelle would be relatively imprecise in its response to the external field, but again by averaging over N of them for a time interval I the relative sensitivity becomes $[2kT/N\mu B(I/\tau)]^{1/2}$, as was found before. We have located superparamagnetic magnetite grains close to this size in honey bees as shown and described in Fig. 4. Although the bees also have single-domain grains (Fig. 4 and Gould et al., 1978), the superparamagnetic fraction alone could yield a sensitivity of about 10 gammas if the response were integrated over 1τ ($I = \tau$), and 1 gamma over 100τ .

Clearly, innumerable variants on the above two models for magnetoreception are possible. In all such cases, however, the thermal energy kT must be balanced in some manner against the interaction energy μB ; hence sensitivity derivations similar to those given above should apply. We therefore conclude that the highest degree of magnetic field resolution an animal might achieve is fixed by the amount of magnetite present.

3.4. Torque detectors

Another simple strategy for building

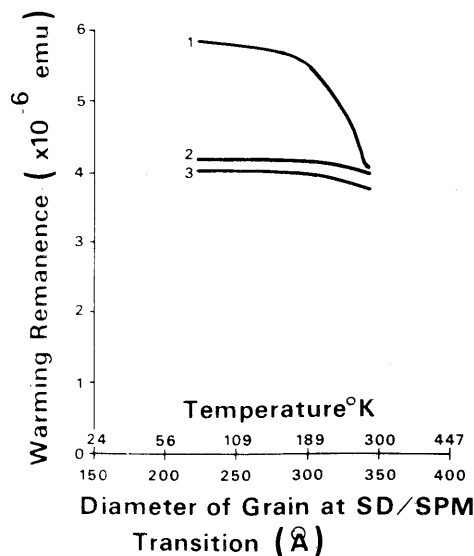


Fig. 4. Superparamagnetic grains in a worker bee. Neel's relationship (eqn. 1) indicates that the relaxation time, τ , for a magnetic domain will increase exponentially as the temperature is lowered. Thus, some grains which are superparamagnetic at room temperature (~ 300 K) will behave as single domains capable of holding remanence at liquid nitrogen temperature (~ 77 K). Conversely, any net remanence held by these domains at low temperature will disappear as they warm in field-free space across their SPM/SD transition (their blocking temperature). The temperature at which the remanence is lost indicates the grain size responsible. If the material is magnetite, a nearly spherical grain 350 \AA in diameter is close to the SPM/SD transition on Fig. 1; eqn. 1 may then be used with this to calibrate the grain diameter vs. temperature along the horizontal axis. To check for superparamagnetic grains, the bee was first cooled to 77 K in the presence of a strong magnetic field (~ 3000 G), forcing all the moments from SD grains into alignment. Curve 1 shows the remanence of the bee as it warmed up inside the field-free region of a cryogenic magnetometer. Most of the remanence is lost as the SD/SPM transition goes from 300 \AA to 350 \AA . A magnetite sphere 325 \AA in diameter has a moment of about 8.6×10^{-15} emu, so about 2×10^8 of them are necessary to account for the lost remanence. Curves 2 and 3 show subsequent warming cycles without exposure to the strong magnet.

a magnetoreceptor is to use a large number of single domain magnets aligned such that their torques add along a common axis. The strategy here is to make the grains

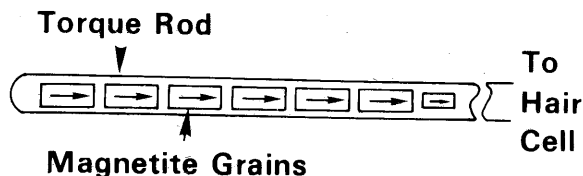


Fig. 5. Torque rod permanent magnet detector. Elongate magnetite crystals are arranged in a row with their moments pointed head-to-tail, and connected to a hair cell or some other mechanoreceptor. A new grain growing at one end will gain a permanent magnetization parallel to the chain as it grows in size through the SPM/SD transition (the blocking volume). Pigeon magnetites are of the proper shape and size for this detector (Fig. 1).

somewhat elongate and place them together in a chain. Demagnetizing fields generated by the shape anisotropy of the long chain will constrain the spontaneous remanence to lie along the long axis. Each domain of magnetic moment $\vec{\mu}$ will feel a torque in the earth's magnetic field of $\vec{\mu} \cdot \vec{B}$. If every domain is magnetized parallel to its neighbors and held, say, in a long rod as sketched in Fig. 5, the rod as a whole will feel a torque approximately equivalent to $(\sum \vec{\mu}) \times \vec{B}$. (For example, $\sim 7 \times 10^{-13}$ dyne-cm in a magnetotactic bacterium). Each of these crystals should plot in the SD stability field of Fig. 1 so as to yield the maximum moment for a given amount of magnetite. At this stage the rod could be connected to a mechanoreceptor such as a sensitive hair cell in a fluid-filled labyrinth or a pressure receptor (Pacinian corpuscle). Virtually any sensitivity could be obtained with this structure by the simple addition of more single domain magnets, and the equations derived above need only to be modified to take into account the mechano-physical properties of the organelle which determines τ . New domains, if formed at one end of the structure, would feel the effect of their nearest SD neighbor if within about 1000 \AA . As the new grains grew in size across the sharp SPM-SD transition of Fig. 1, they would gain a permanent magnetization parallel to the rest of the chain and the

process could be repeated. The final direction of magnetic remanence is thus that of the first crystal to form; this direction, however, should parallel that of the local geomagnetic field at the time it first grew in size across the transition. In some honey bees, the stable natural magnetic remanence probably reflects the orientation of the pupae in the comb before it emerges (Gould et al., 1978), suggesting this type of process. Magnetite forms linear chains in magnetotactic bacteria which both passively torque the organism into alignment and control the polarity of each new crystal as it forms (Blakemore, 1975; Frankel et al., 1979). Pigeons have elongate single-domain magnetite which may also be involved in this type of detector (Walcott et al., 1979; see also Fig. 1). Note that the grains in this model are not held symmetrically — if the magnetic direction of the entire chain is flipped by AF demagnetization, the response of the organelle is different: the chain ought to move in the opposite direction. This type of detector has the potential to distinguish north from south, whereas birds and bees seem unable (or unwilling) to make the distinction. On the other hand, many hair cells seem to measure displacement along a particular preferred axis, and ignore the two directions along that axis in which they are actually being bent (Tautz, 1977).

3.5. Ordered arrays of superparamagnetic grains

Linear arrays. The magnetic interaction between two neighboring superparamagnetic grains is capable of generating either attractive or repulsive forces, depending upon the orientation of their dipole moments. Because the direction of magnetization for a superparamagnetic grain is easily changed in response to an external field, the direction and intensities of the interaction forces could be made to vary as well and produce a response detectable with known mechanoreceptors. Figure 6A shows the basic attrac-

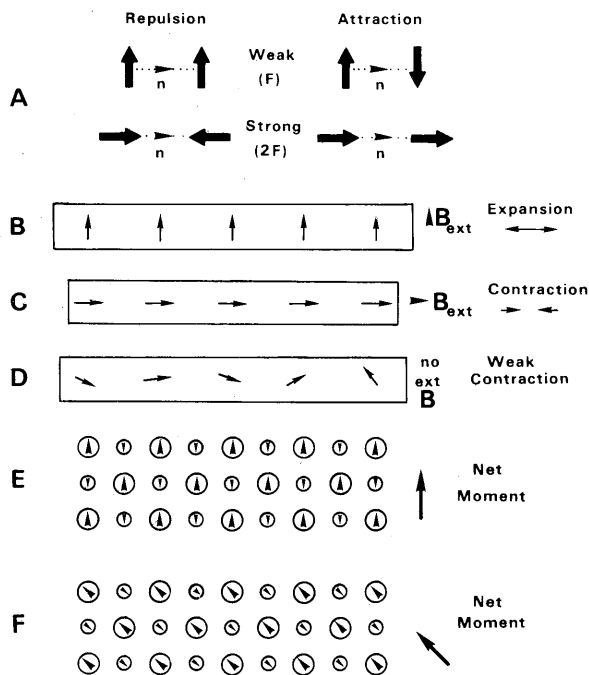


Fig. 6. Superparamagnetic ordered arrays. A. Weak and strong repulsion geometries for two magnetic moments. B–D. Elastic rod transducer. In B, the external field aligns all superparamagnetic moments transverse to the rod; they repel and its length increases. Alignment of the moments parallel to the rod as in C makes the grains attract, causing the rod to shrink. In the absence of an external field (D), the moments either randomize or align so as to reduce any external field; possibly a weak contraction results. Two configurations for a ferromagnetic analogue transducer discussed in the text are shown in E and F. Moments in E parallel the cubic “lattice” and thus lie along the magnetically hard direction, while those in F are along the easy direction. The rotational motion of an animal (and hence the organelle) relative to the geomagnetic field will alter the internal forces and produce a detectable change.

tion and repulsion geometries for two adjacent magnetic moments, $\vec{\mu}_1$ and $\vec{\mu}_2$. A simple linear geometry for this type of detector is an elastic rod with regularly-spaced grains as shown in Figs 6B–D. Adjacent grains are separated far enough such that the dipole field of one acting on its neighbors is less than that of the earth; each moment will then align preferentially

with the external field. If they are too close, the dipole-dipole interaction will dominate and no response will be seen. The configuration of 6B, with the rod perpendicular to the external field, yields grain-to-grain repulsion causing the rod to expand. An external field parallel to the rod (6C) will cause it to contract twice the distance, while zero field will permit the moments to cancel or randomize, yielding perhaps a weak contraction.

Assuming uniform size and roughly spherical grains, two constraints on this system are shown in Fig. 7: (1) the particle size must be below the SPM/SD transition; and (2) the field of one grain upon its neighbors must be less than 0.5 G (the earth's field). From Fig. 1, it can be seen that the SPM/SD transition in equant magnetite grains occurs at about the 400 Å size; thus, the first constraint is met by particles below 200 Å in radius as shown by the horizontal line on Fig. 7. For the second constraint, the grains must be far enough apart such that $2\vec{\mu}/x^3 < 0.5$ G — this radius vs. distance relation plots as the straight line on Fig. 7 labelled 0.5 G. Also shown by dashed lines on this diagram are contours of equal intergrain force, computed from the relation $F = \partial E / \partial x$. The optimum grain size and spacing for this detector is that which yields the maximum

force, shown on Fig. 7 by the shaded triangle; roughly 10^{-10} dyne can be generated in this fashion between adjacent grains. With 10^8 grains such as in a honey bee (Fig. 4), the maximum total force which could be generated is on the order of 10^{-2} dyne. If this were focussed on an area $100 \mu\text{m}^2$, the pressure would be 10^2 dyne/cm², well within the sensitivity range of known mechanoreceptors. The ear, for example, has a threshold of 2×10^{-4} dyne/cm² at the ear drum (Stephens and Davis, 1938).

Lattice arrays. An alternate strategy for constructing a superparamagnetic array detector would be to model it after a ferrimagnetic material (see Stacey and Banerjee, 1974). If a regular array of much more closely spaced grains were enclosed in an elastic matrix, the minimum energy of the external field would be obtained with alternate moments antiparallel as shown on Fig. 6E. A slight reduction of the size of every other grain would correspondingly reduce one set of parallel magnetic vectors, causing the entire structure to have a net magnetic moment. Each grain is then analogous to the individual super-exchange coupled atomic moments within the crystal lattice of a ferrimagnetic material. After a fashion, this entire organelle should have "superparamagnetic" behavior — the minimum

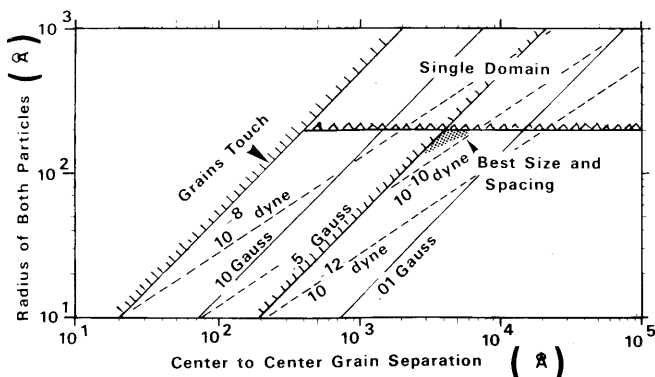


Fig. 7. Interaction force and magnetic field relationships for two SPM magnetite spheres. Both grains are of equal radius (vertical axis). Solid lines indicate grain size vs. separation combinations which yield constant field strength; the dashed lines show constant interaction force. The best separation and grain size to use in the detector of Fig. 8B–D is just below the SD/SPM transition ($r \approx 200$ Å) and far enough apart so that the Earth's field dominates (~ 4000 Å apart).

energy for the structure would be that with the residual moment parallel to an external field. Spacing of 1000 Å between the 325 Å diameter SPM grains observed in bees would generate intergrain forces greater than 10^{-8} dyne; these forces would yield a mechanical deformation analogous to the magnetostriction generated in ferrimagnetic materials. The pressure generated, however, is anisotropic. Along the axis of the external field, net attractive and repulsive forces are nearly balanced; the slight difference in alternating magnetic moments results in only a residual compression. Transverse to the field direction, however, the major interaction between grains is antiparallel attraction ($\uparrow\downarrow$); the organelle should therefore contract along this plane. Note that if a cubic packing arrangement is used, it will be easier to make the net magnetic moment of the organelle lie along one set of orthogonal axes, similar to the existence of a weak, magneto-crystalline anisotropy along the (1,1,1) axes of the magnetite lattice.

Because of the anisotropy, equatorial pressures generated by this cubic organelle as it rotates in a magnetic field should show a fluctuation with a 90° periodicity, perhaps accounting for the cardinal point orientation of honey bees in their horizontal waggle dance (Gould et al., 1980). Further, Martin and Lindauer (1972, 1977) have shown that many magnetic effects are altered in fields greater than 5 G (~ 10 times the earth's field). If the intergrain spacing for this model were 1500 Å with roughly 325 Å SPM particles, the field of one grain upon its neighbor would be roughly 5 G, with intergrain forces near 10^{-8} dyne. Martin and Lindauer's breakdown would then correspond to all magnetic moments lining up to the applied field, saturating and deactivating the detector. This cubic array of magnetic grains might be arranged within the connective tissue surrounding a typical pressure receptor. Note that neither of these superparamagnetic detectors would be influenced by AF demagnetization nor could they detect the polarity of the magnetic field.

3.6. Hybrid detectors

One detector strategy is made possible by combining the different magnetic hybrids in ferrimagnetism and paramagnetism. Since the *local* environment around a magnetite sphere is characterized by high fields and steep magnetic gradients (fields < 4025 G, and gradients of ~ 6 G/Å or 6×10^8 G/cm), the potential for interactions exists. Neurath (1964), Valentinuzzi (1964), and Gross (1964) discuss the experimental effects of such conditions on various organisms and review the theory behind the paramagnetic effects which may be responsible, including molecular redistribution, rotational alignment of paramagnetic ellipsoids, and distortion of bond angles. Of these, rotational alignment requires fields far greater than those produced by magnetite grains, and the effects of bond angle distortion are not immediately expressed. Neither of these could account for magnetic field sensitivity in animals. Translational redistribution, on the other hand, depends upon both the field strength and the field gradient, $B \partial B / \partial x$. Next to a magnetite sphere, this product may be as high as 10^{12} G²/cm. However, our calculations indicate that this strategy cannot explain the behavioral data. The energy difference for the 60 Å ferrihydrite core of a ferritin molecule near a 200 Å diameter superparamagnetic magnetite grain ($r = 200$ Å) is about 1.2×10^{-16} erg.—about 400 times less than kT . Therefore ferritin molecules will *not* cluster around a magnetite sphere. Larger spheres will experience a correspondingly greater force, but the total depth of the local energy well will never exceed about $0.03 kT$ at room temperature. In general, we conclude that paramagnetic interactions with ferrimagnetic materials are not likely to form the basis of a magneto-receptor.

4. Discussion

Clearly, magnetite is a realistic material

to use as a transducer between the geomagnetic field and the nervous system. Either single-domain or superparamagnetic crystals could be used and both are found naturally in large numbers in at least some magnetically sensitive animals. Although many variations are possible, we have discussed only a few models whose magnetic components are known to form biologically, and which could be connected to sensory organs. For example, linear chains of single-domain magnetite crystals are present inside magnetotactic bacteria (Blakemore, 1975; Frankel et al., 1979); single-domain magnetite grains are found in pigeons (Walcott et al., 1979) and in chiton teeth (Kirschvink and Lowenstam, 1979b); and the presence of superparamagnetic grains in bees is inferred through their magnetic warming remanence (Fig. 4). Other suggestions stem directly from the physical and chemical properties of the materials involved, such as using the electrical conductivity of magnetite to alter nerve membrane resistance or forming satellites by reducing the ferrihydrite core of a ferritin molecule to magnetite. In each case, the theoretical sensitivities possible at room temperature by averaging over all the domains through behaviorally realistic intervals exceed by one to three orders of magnitude even the most extreme sensitivities inferred from the literature. In most cases, the models predict the 180° ambiguity about magnetic polarity observed in many animals.

Looking at these models, it is clear that additional work will be required to determine the manner in which the organelles are used, if they indeed exist. There are some simple experiments, however, which may serve to sort the various mechanisms out. In the absence of other cues, honey bees, for example, appear to set their circadian rhythm to the diurnal variations in the geomagnetic field. We do not know what parameter(s) in the field they are recognizing; they could be sensing small angular shifts in field direction, small intensity fluctuations,

or both. An induction mechanism would imply that any change in B could be detected, including those in which the magnitude remains constant. On the other hand, models discussed in this paper suggest that only the total intensity of B is monitored with high accuracy. Thus, a set of experiments are needed in which the bees are exposed first to a constant direction magnetic field with a diurnally-fluctuating intensity and then to one with a constant strength but with the small, diurnal direction changes. A magnetosensory system that monitors total intensity would be of far more use to an animal that constantly changes its orientation in the world than one that depends upon direction as well, hence we expect that bees ought not to recognize the small directional shift (about 0.1°) which gradually occurs during the day. Likewise, migratory or long-distance homing animals would be better served by a "map" sense based on some function of total intensity rather than one based on a directional system.

As of now, however, we can only assume that the concentrations of magnetite in honey bees and homing pigeons are probably related to the ability of these animals to use magnetic field information. Most of the plausible models for magnetite-based magneto sensors discussed above, however, are discouragingly insensitive to external manipulations (such as A_f demagnetization) which could distinguish the permanent-magnet from the paramagnetic and superparamagnetic hypotheses. Of course, the site of magnetite concentration ought also to be the point at which an applied static magnetic field should have the greatest effect. Hence, gluing small permanent magnets to magnetically sensitive animals and correlating their locations with their effects would be suggestive. Also, the direct surgical removal of the magnetic material ought to abolish the magnetic behavior.

In an effort to devise a more useful test for whether or not the magnetite is being used, we have calculated the physical effects

of high magnetic fields and field gradients on magnetite versus other cellular components. The most probable size range for organic magnetite is 100 Å (superparamagnetic) to 1000 Å (single-domain) — from the thickness of a membrane to the size of the pigeon grains. Although the interaction energy for a 100 Å magnetite particle in the earth's field ($\mu \cdot B$) is only $0.003kT$, the external field can be made one to ten thousand times stronger to generate energies far larger than kT — 10^3 — 10^4kT for single-domain grains. This in itself is not too interesting, since the grains (or, in the case of isolated superparamagnetic crystals, the electron spins) would simply be realigned. If, on the other hand, this strong applied field were designed to have a high magnetic gradient, each particle would feel a translational force of dE/dx , or $\mu \cdot dB/dx$. In a gradient of 10^4 G/cm — easily obtained with conventional equipment — and in a fluid with a viscosity of 0.1 P (10 times that of water), a 100 Å magnetite sphere would be moved 2300 microns/day; while a 1000 Å grain would move 23 cm/day. Unfortunately, as yet we do not know how these crystals are held in place and cannot, therefore, predict what damage motion of this sort would produce. Exposure to *high* magnetic field gradients could in principle disrupt or destroy magnetite-based detectors. On the other hand, the paramagnetic nature of organic compounds is too weak to generate interaction energies anywhere near kT , and so these molecules would not be expected to be appreciably displaced in such gradients.

There is, however, one potential worry about the high-gradient test. In thinking about the evolution of magnetite-based magnetic sensitivity in animals, it seems most plausible to suppose that magnetite, that most dense and conductive of biological materials, was already present in organisms serving some other function. From the incidental effect of the earth's magnetic field on these bits of magnetite, this line of reasoning would postulate that evolution

built the specialized and extraordinarily sensitive organs apparently possessed by bees and pigeons. If this is the case, then we must worry what the high gradients might do to this other, hypothetical system.

In looking over the literature, in fact, we find evidence consistent with the notion of a non-sensory use of magnetite. In the well-controlled study of Neurath (1969), for example, the development of frog embryos in a 10^4 G field with a gradient of 8×10^3 G/cm was compared with that of embryos in the earth's field. Even though the eggs were raised at the same temperature and light levels, shared a common nutrient fluid, and came from the same female, the hatching rate of the magnetically treated eggs was reduced by 40% (yielding a probability of the results being due to chance well below 0.001).

Magnetic fields could interact with embryos in any of the three ways mentioned in the discussion of detector strategies: induction, paramagnetism, or ferromagnetism. For induction to have any effect in a static magnetic field (with or without a gradient), a strong current must be flowing in the embryo. Currents with a flux density of 10 – $100 \mu\text{A}/\text{cm}^2$ have been measured (Jaffe and Stern, 1979) flowing in loops of about 1 mm. Except for transient effects which would accompany any rapid onset of current flow or strong magnetic field, the net result in the most extreme case would be the build up of a small static charge on the membrane. This charge would balance the effect of the field on the current loop such that the flow would follow the same path as before the application of the field. This change would alter the local membrane potential by about 1 mV. Whether such a change is of any biological significance in development commensurate with such dramatic increases in embryonic mortality is not known.

As our calculations above indicate, the interaction energies of high fields and gradients with organic, paramagnetic molecules are orders of magnitude below kT . Indeed,

as Neurath suggests, the effects are probably due to the physical displacement of magnetically susceptible substances. Neurath calculated that large *aggregations* of ferritin molecules were the only reasonable candidate, but was unable to locate any of these hypothetical particles. As calculated above, magnetite crystals, with their far stronger magnetic properties, could account for his results and still be much too small to be detected by his optical techniques.

Similar calculations indicate that small, ordered groups of even superparamagnetic domains would be rotated by strong homogeneous fields, thereby disrupting any function they might serve. To illustrate this, suppose that a small group of 100 Å superparamagnetic grains of magnetite were being used to hold two membranes together. The minimum interaction energy of two such particles would be roughly $3kT$ when their moments are aligned head-to-toe, and $1.5kT$ when antiparallel. A group of such grains could be clustered into a two-dimensional, close-packed array (superficially resembling the arrays in gap junctions, for example). Although isolated 100 Å grains are superparamagnetic, the intergrain interaction would force the two hypothetical membranes into a stable, coplanar alignment with an energy of about 0.06 erg/cm^2 . The earth's field would not affect such an array, but a strong static field would realign the moments, thereby disrupting the regular structure (which was, of course, a partial consequence of the stable set of neutral antiparallel alignments of magnetic moments which are overcome in a strong field). In many field orientations, the two membranes would even repel each other strongly. Biological effects of such high static fields (2700 G) are known on certain tissues (e.g., the *zona fasciculata* in mouse adrenal glands (Barnothy and Sümagi, 1969)).

The often dramatic nature of these apparently real effects suggests that any attempt to destroy magnetic organs by exposure to high magnetic field gradients

might have secondary consequences which ought to be explored through suitable control experiments. Still, large effects on magnetic orientation behavior from such treatments combined with little or no effect on other sorts of orientation would be very suggestive; and a differential effect of magnetic gradients over static fields of the same strength would be the strongest evidence of all to indicate that ferromagnetic material, of which magnetite is the only known biological candidate, is the key element in the magnetic field detection system of terrestrial animals.

The models developed and discussed above are intended to stimulate thinking about detector strategies and to serve as testable working hypotheses to guide further research both in behavior and physiological studies. They permit calculations which predict the breakdown of sensitivity at non-biological field strengths on the order of 5 G, the insensitivity in many cases to demagnetization and the physical destruction of certain detectors in large static fields (on the order of 2000 G for 100 Å grains, for example). Note that the total amount of magnetite required in theory for simple direction detection is quite small; a few hundred to thousand grains of magnetite could be used to make an extremely sensitive directional detector without giving the organism a measurable magnetic remanence. Commercially available SQUID magnetometers (Goree and Fuller, 1976) can measure moments greater than about 10^{-8} emu (10^{-10} g of magnetite). Using the sensitivity relation for isolated magnetoreceptors derived above, this barely measurable remanence could provide a sensitivity of nearly 150 gamma. Perhaps this may explain why we found no natural or inducible stable or superparamagnetic remanence in reportedly magnetosensitive cave salamanders and newts (Kirschvink and Gould, unpublished data). Although biogenic magnetite has not been reported in mammals, it should be noted that many of the magnetic effects claimed

by human dowsers (Harvalik, 1979; Rocard, 1964) would be accounted for by analogous detectors based on biogenic magnetite.

5. Conclusions

(1) Behavioral evidence argues against an induction mechanism for magnetically sensitive terrestrial animals.

(2) Conventional paramagnetic interactions, even those due to the locally high magnetic fields and gradients near magnetite grains, are *not* likely to produce observable biomagnetic effects.

(3) If coupled to their nervous systems, ferrimagnetic transducers would enable even stationary or slow-moving terrestrial organisms to detect weak directional or intensity changes in the local magnetic field at least as small as those which have been observed or inferred through behavioral studies of bees and homing pigeons.

(4) Both the single-domain and superparamagnetic grains of magnetite discovered in magnetically sensitive animals could be used in magnetic field detection. Most of the magnetite grain-grain interaction and orientation energies exceed kT , and thus can serve in a variety of ways as transducers between the magnetic field and the nervous system.

(5) Magnetic detection arrays are possible which could monitor the total strength of the geomagnetic field, without regard to the vector direction. Such a system may serve as part of the "map" sense of homing pigeons and migratory animals, providing them with absolute location information to within a few kilometers.

(6) The hypothesis that organic magnetite may play other roles in biological systems in addition to magnetoreception would account for many of the detrimental effects of strong magnetic fields reported in the literature.

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Appendix

Magnetic units and relationships

Throughout this paper, we have used Gaussian cgs units due to the simplicity of the system. To avoid confusion, fundamental relations for converting to other units are given here.

Magnetic moment

1 emu (electromagnetic unit) = 10^{-3} Am²; for a grain of volume V (cm³) and saturation magnetization J_s (emu/cm³), the moment $\vec{\mu} = VJ_s$. 1 emu = 1 erg/G = 10^{-3} J/T.

Magnetic intensity, magnetization

1 G = 1 emu/cm³ = 10^3 A/m = 10^{-4} T = 10^{-4} W/m².

1 emu/g = 1 Am²/Kg.

1 gamma = 10^{-5} G = 10^{-9} T.

1 G = 1 Oersted in a vacuum.

Energy relations

1 erg = 1 emu · 1 G ($E = -\vec{\mu} \cdot \vec{B}$).

(1 emu)² = 1 erg · cm³

$kT = 4.1 \times 10^{-14}$ erg, where k is Boltzman's constant and $T = 300$ K.

To convert the Gaussian cgs equations used here to the rational MKS system, note that the constant $\mu_0/4\pi = 10^{-7}$ Wb/Am = 10^{-3} G m/A = 1, which is why the Gaussian cgs system is simpler.

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