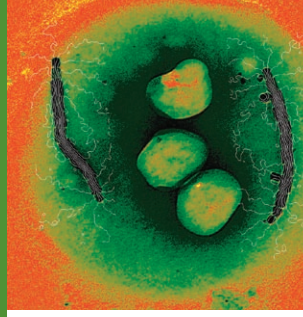
Magnetic Nanocrystals in Organisms



False-color TEM image and superposed magnetic induction map of a bacterial cell containing two single chains of magnetite magnetosomes. The contour spacing is 0.5 rad.

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Ferrimagnetic nanocrystals are present in virtually every organism. They are used by bacteria, algae, mollusks, insects, and vertebrates either for navigating in the geomagnetic field or for hardening their tissues. Advanced transmission electron microscopy techniques, including electron holography, reveal the complex interplay between the physical and magnetic properties and biological functions of ferrimagnetic nanocrystals in bacteria. Although some information is now available about magnetic sensory systems in more complex organisms, much further research is required to understand fully the origin and function of biomagnetism.

KEYWORDS: biomagnetism, nanocrystals, electron holography, magnetotaxis, magnetoreception

FUNCTIONS OF MAGNETIC MINERALS IN ORGANISMS

Magnetic crystals in a living organism were first reported almost fifty years ago by Heinz Lowenstam, who described a coating of magnetite on the radula of the chiton, a rock-clinging marine mollusk (Lowenstam 1962). In the preceding years, Salvatore Bellini, working at the University of Pavia, had observed that the movement of certain bacteria was guided by an external magnetic field. However, his observations were not published in an international journal, and magnetotactic bacteria were first described in a landmark paper by Blakemore (1975), who observed intracellular iron-rich inclusions that were later identified as magnetite (Frankel et al. 1979). Although many organisms are known to contain ferrimagnetic nanoparticles or to navigate using the geomagnetic field (TABLE 1), in many cases the relationship between the presence of the magnetic particles and navigation is still uncertain. Indeed, one way in which magnetic particles in organisms are classified is according to whether they are thought to harden or protect their living host, to serve as navigational aids, or to have unknown functions.

Magnetotaxis is the simplest approach used by an organism to achieve magnetic orientation and is employed by prokaryotes such as bacteria and algae. The presence of ferrimagnetic nanocrystals in such cells (FIG. 1) results in the passive alignment of the cells with the geomagnetic field. The cells then move actively using flagella. Most magnetotactic bacteria live in chemically stratified aquatic environments, either in the sediment or in the water. Magnetite-bearing bacteria live at the interface between oxic and anoxic layers, but greigite-producing cells are found below this interface, under anaerobic conditions. Since the geomagnetic field has a vertical component (except at the magnetic equator), **magnetotaxis** is thought to be beneficial to the cells by guiding them to swim "up" or "down" to their preferred habitat (Bazylinski and Frankel 2004) (FIG. 2A).

A more sophisticated navigational system is used by insects and vertebrates, which are too large for the weak geomagnetic field to align them passively. Instead, these organisms perform true navigation by identifying or following the direction and/or intensity of the local geomagnetic field (Lohmann et al. 1999) (FIG. 2B). Birds, honeybees, turtles, and other animals use their magnetic sense to find migration routes or to navigate to feeding or nesting grounds.

As noted by Suzuki et al. (2006), only two macroscopic animals can be attracted by a hand magnet: the chiton and the scaly-foot snail (FIG. 3). The chiton forms nanocrystalline magnetite as a hardening material on the surface of its radular teeth, which are used to grind algae and other food from rocks. The scaly-foot snail is found in a deep-sea

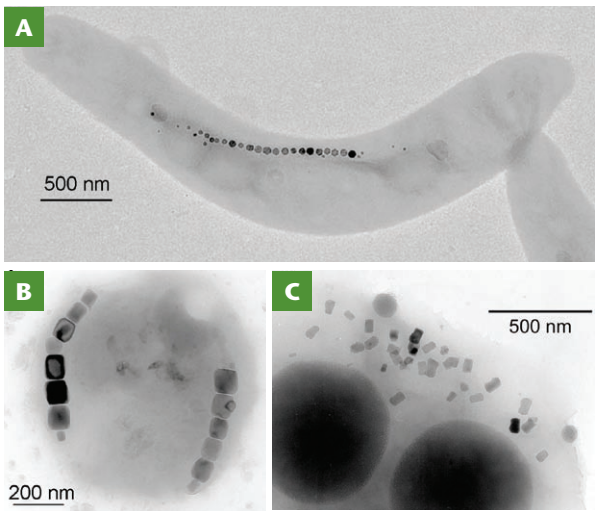

FIGURE 1 Bright-field TEM images of magnetite-bearing magnetotactic bacteria. (**A**) *Magnetospirillum gryphyswaldense* cell containing a single chain of cuboctahedral magnetite magnetosomes (some are darker than others because they are aligned with a major zone-axis close to the direction of the electron beam and thus produce strong diffraction contrast). (**B**) Spherical cell (coccus) containing two single chains of slightly elongated magnetite particles. (**C**) Scattered, elongated, irregularly shaped magnetite magnetosomes in a coccus. The two large dark regions are polyphosphate granules.

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hydrothermal field in the Indian Ocean. It shares its habitat with other predator mollusks and is thought to be protected from them by the scales on its foot. These scales contain several iron sulfide species, including ferrimagnetic greigite. Magnetite or maghemite crystals are found in the human brain, but their functions are still unknown (Kirschvink et al. 1992).

MAGNETIC PROPERTIES OF BIOMAGNETS

To date, only three magnetic minerals, magnetite (Fe_3O_4), maghemite (Fe_2O_3), and greigite (Fe_3S_4), have been confirmed to occur inside organisms. These minerals are present in minute amounts and are often identified on the basis of incomplete or inconclusive evidence. Magnetite appears to be the most widespread biogenic magnetic mineral. Greigite is the only magnetic sulfide mineral that has been confirmed in organisms. All three minerals have spinel structures; magnetite and greigite are isostructural and maghemite is an oxidized derivative of magnetite. For the magnetic properties of these minerals, see Table 1 in Harrison and Feinberg (2009 this issue).

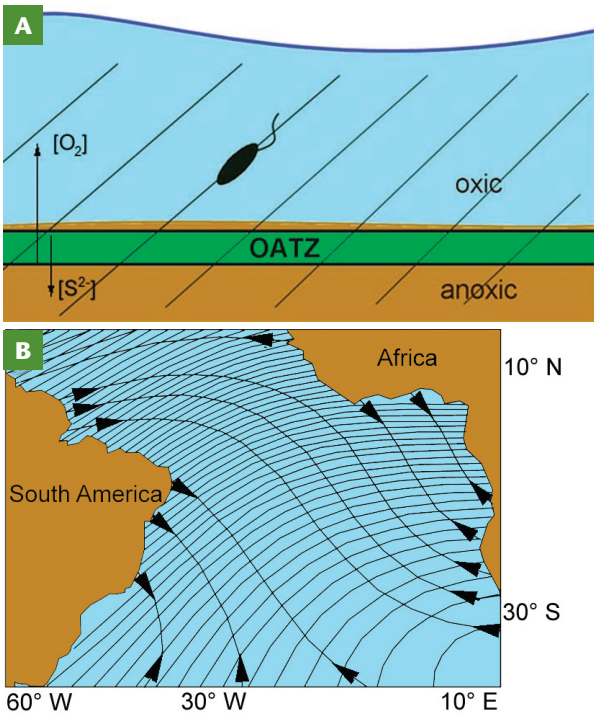

Figure 2 (**A**) Magnetotactic bacteria are aligned passively by the geomagnetic field and swim actively along the field vector (diagonal lines). This behavior enables cells to find "up" and "down" directions and thus to reach their optimal positions in the oxic–anoxic transition zone (OATZ) efficiently. (**B**) Lines of equal intensity and inclination of the Earth's primary magnetic field in the South Atlantic. Isodynamic lines (arrowed) are aligned approximately NW–SE and are shown with a spacing of 1 μT. Isoclines are aligned roughly NE–SW and are shown with a separation of 2°. Since magnetic intensity and inclination define a geographic location uniquely in this region, animals can potentially use such magnetic parameters to identify their position. (B) is adapted from Walker et al. (2002)

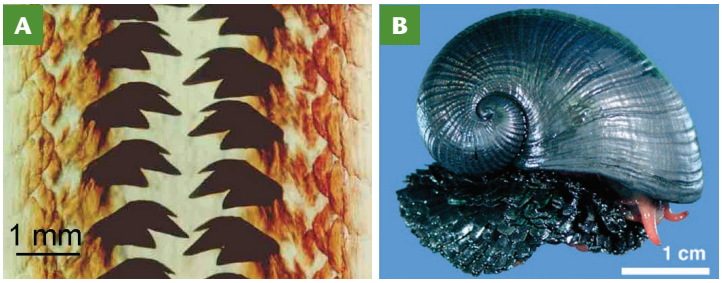

Figure 3 (**A**) Image of magnetite-coated "teeth" on the radula of a chiton, from the late Heinz A. Lowenstam. Reproduced with permission from the website of the Geobiology Group at Caltech (www.gps.caltech.edu/options/geobiology/image6.html) (**B**) Greigite-bearing sclerites on the foot of a scaly-foot snail. Reproduced from Suzuki et al. (2006)

The physical and chemical properties and the arrangements of the magnetic crystals in an organism determine their magnetic behavior. If the ferrimagnetic particles are used by the organism for hardening or for iron storage, then the physical properties of the mineral grains are unlikely to be constrained tightly. If the minerals are used for magnetic orientation, then their size, shape, orientation, and arrangement all need to be controlled strictly.

The magnetic grains that grow inside organisms typically have sizes ranging from a few to a few hundred nanometers (nm). In magnetite, equidimensional (i.e. not elongated) grains with sizes between ~30 and 120 nm are magnetic single domains (SD). Bacteria, fish, and many other animals are known to contain magnetite particles in this size range (Table 1). Isolated magnetite crystals below ~30 nm in size are superparamagnetic (SPM) at room temperature, which means that thermal energy continuously changes their directions of magnetization, and as a result the grains do not have a stable magnetic remanence. Magnetite grains of this size occur, for example, in pigeons and humans. Isolated equidimensional magnetite grains larger than ~120 nm usually contain two or more magnetic domains separated by domain walls; they are termed "multidomain" (MD). In such grains, the magnetization direction is approximately uniform in each domain but differs between adjacent domains.

An elongated grain is typically magnetized parallel to its long axis, since the demagnetizing energy is then minimized (see Harrison and Feinberg 2009). The crystalline anisotropy is minimized if the magnetization is parallel to an "easy axis," which is [111] in magnetite and [100] in greigite at room temperature. The magnitude and direction of the magnetization in an individual grain therefore depend on the competing effects of grain size, shape, and crystallographic alignment. Isolated magnetic grains rarely occur in organisms, which usually contain assemblages of crystals. Depending on their spatial arrangements, interactions between individual particles can then influence the magnetic states within them.

A magnetotactic bacterial cell can be regarded as a magnetic dipole (a rigid compass needle) with a magnetic moment, $\mathbf{M}$, on which the geomagnetic field, $\mathbf{B}$, exerts a torque. So long as the magnetic energy $\mathbf{M}\cdot\mathbf{B}$ is significantly (at least ~10 times) larger than the thermal energy, kT, the cell will be aligned predominantly with the external magnetic field (Fig. 4a) (Bazylinski and Frankel 2004). In order to have a stable and large-enough magnetic moment, the optimal solution for the cell is to make chains of well-aligned SD particles that have a permanent magnetic moment and cannot be remagnetized by the weak geomagnetic field.

In complex organisms, such as fish and birds, magnetoreception systems based on ferrimagnetic particles must be sensitive enough to detect slight changes in the direction and intensity of the geomagnetic field. Several hypothetical systems that may satisfy this requirement have been proposed, two of which are illustrated in Figures 4b and 4c. One possible magnetic sensor contains elements that are similar to the chains of SD magnets in bacteria (Kirschvink and Gould 1981). Kirschvink (1992) and Walker et al. (2002) proposed that, when the chains are tilted by an external magnetic field, ion channels open and send a signal to the brain (Fig. 4b). A second hypothetical system involves the presence of vesicles containing magnetite particles between

2 and 5 nm in size. Since the crystals are in the SPM size range, they do not have a permanent magnetic moment. However, in the presence of an external field the vesicles change their shape and, if they are closely spaced, attract or repel one another (Fig. 4c) (Davila et al. 2003), therefore deforming the membrane to which they are attached and opening ion channels. Animals may use a variety of magnetoreception systems, some of which may contain elements similar to those shown in Figure 4. Such systems can only be identified and understood if the physical properties of their ferrimagnetic components are characterized thoroughly.

MAGNETOSOMES IN MAGNETOTACTIC BACTERIA

Off-axis electron holography (EH) is a transmission electron microscopy (TEM) technique that provides quantitative information about the magnetic properties of individual ferrimagnetic nanocrystals. EH has been used to study the magnetic properties of magnetosomes, which are intracellular, membrane-enclosed ferrimagnetic nanocrystals in magnetotactic bacteria (Faivre and Schüler 2008). Characteristically, the sizes, morphologies, and arrangements of the crystals vary from strain to strain (Fig. 1). Thus, magnetotactic bacteria provide a natural laboratory in which the magnetic properties of nanocrystal assemblages can be studied.

Figure 5 shows EH results obtained from a double chain of magnetite crystals in an air-dried bacterial cell. The [111] axes of the crystals (marked by the line of white arrows in Figure 5a) are approximately parallel to the chain axis, as measured using high-resolution TEM (Fig. 5b) and electron diffraction (Fig. 5c) (Simpson et al. 2005). In contrast, the crystallographic directions perpendicular to the chain axis are randomly distributed. Assuming that air drying has not affected the relative orientations of the crystals, the chain is therefore analogous to beads on a string, in which biological control appears to be stricter in setting the [111] magnetocrystalline easy axis of each crystal to be parallel to the chain axis than in constraining its orientation about this direction. Since the crystals are elongated along [111], i.e. parallel to their magnetic easy axes, shape and magnetocrystalline anisotropies combine to produce the largest possible magnetic moment for each crystal. As a result, the crystals contain single magnetic domains that are oriented parallel to each other and to the chain axis, and exhibit little magnetic flux leakage (Fig. 5e). In similar magnetosome chains, the magnetization directions of crystals that are small enough to be superparamagnetic at room temperature (if they were isolated) can be constrained to lie along the chain axis as a result of magnetostatic interactions with neighboring crystals.

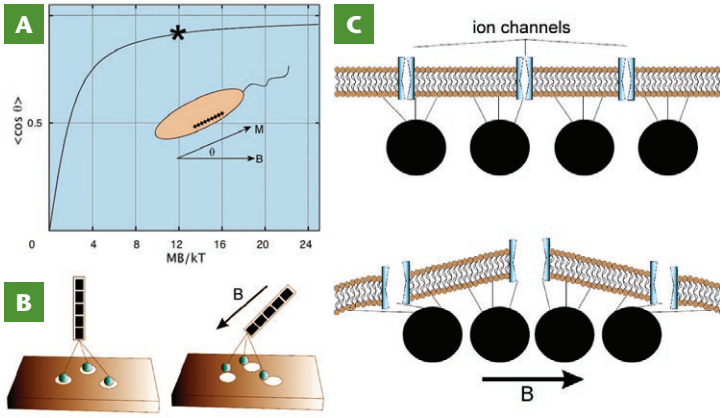

Figure 4 (**A**) For a single magnetotactic bacterial cell, which contains a permanent magnetic dipole, **M**, that is inclined to the geomagnetic field, **B**, at an angle of θ, the ratio between the magnetic energy, **M**·**B**, and the thermal energy, kT, determines the average angle between the cell and the geomagnetic field. Most wild-type magnetotactic bacteria have a sufficient number of magnetosomes to be aligned parallel to the geomagnetic field at least 90% of the time, as indicated by the asterisk. (**B**) Hypothetical magnetic sensor in vertebrates, based on single-domain magnetite particles. A chain of SD crystals is attached by actin-like strands to mechanically gated ion channels in a membrane. The ion channels are activated by the movement of the chain in response to an external magnetic field (indicated by the arrow). (**C**) Hypothetical magnetic sensor in vertebrates, based on superparamagnetic magnetite particles. The black circles represent vesicles that are filled with SPM particles and attached to a membrane. In response to an external field, **B**, the vesicles move towards each other and deform the membrane, thereby opening the ion channels and triggering a nervous signal. (B) is adapted from Walker et al. (2002), based on Kirschvink (1992), and (C) from Davila et al. (2003).

Table 1 EXAMPLES OF MAGNETIC MINERALS AND THEIR FUNCTIONS IN VARIOUS ORGANISMS

Organism	Mineral	Domain state	Biological function	Key references
Bacteria	magnetite and/or greigite	SD, SPM	orientation	Blakemore (1975) Science 190: 377; Frankel et al. (1979) Science 203: 1355; Bazylinski and Frankel (2004) Nat. Rev. Microbiol. 2: 217; Faivre and Schüler (2008) Chem. Rev. 108: 4875
Algae, protists	magnetite	SD	orientation	Lins de Barros et al. (1981) Annal. Acad. Brasil. Cienc. 54: 258
Worm	magnetite	SPM	?	Cranfield et al. (2004) Proc. Roy. Soc. B271: S436
Chiton	magnetite	SD	hardening	Lowenstam (1962) Bull. Geol. Soc. Amer. 73: 435
Armored snail	greigite	SD	protection	Suzuki et al. (2006) Earth Planet. Sci. Lett. 242: 39
Honeybee, butterfly, ant	magnetite	SD	navigation?	Gould et al. (1978) Science 201: 1026; Acosta-Avalos et al. (1999) J. Exp. Biol. 202: 2687
Termite	magnetite	SPM, SD	navigation?	Maher (1998) Proc. Roy. Soc. B265: 733
Lobster	magnetite?	SD	navigation?	Lohmann (1984) J. Exp. Biol. 113: 29
Newt	magnetite	SD	navigation?	Brassart et al. (1999) J. Exp. Biol. 202: 3155
Bony fish	magnetite	SD	navigation	Walker et al. (1984) Science 224: 751; Diebel et al. (2000) Nature 406: 299
Sea turtle	magnetite?	?	navigation?	Irwin and Lohmann (2005) J. Comp. Physiol. A191: 475
Homing pigeon (and other birds)	magnetite, maghemite	SPM	navigation	Walcott et al. (1979) Science 205: 1027; Hanzlik et al. (2000) BioMetals 13: 325
Bat	magnetite?	SD	navigation?	Holland et al. (2008) PLoS ONE 3: e1676
Dolphin, whale	magnetite	SPM, SD, MD	navigation?	Zoeger et al. (1981) Science 213: 892
Human	magnetite/ maghemite, hematite	SD, SPM	?	Kirschvink et al. (1992) Proc. Nat. Acad. Sci. 89: 7683; Quintana et al. (2004) J. Struct. Biol. 147: 166; Collingwood et al. (2008) J. Alzheimer's Dis. 14: 235

Significantly, in any cell containing more than one linear chain of magnetosomes, the magnetization directions of the individual chains are observed to be parallel to each other. Intuitively, one might expect that the magnetization directions of two closely spaced neighboring chains, such as those shown in Figure 5a, would be antiparallel to achieve optimal flux closure. However, the double chain acts almost like a single bar magnet. The stability of the parallel magnetization state of the double chains may be assisted by a shift of half a magnetosome length along the axis between the two chains (as in Figure 5a), as suggested by magnetostatic calculations (Hanzlik et al. 2002).

Some cells contain partial chains or scattered crystals. In Figure 6, a disordered arrangement of magnetite crystals results in a range of colors in a magnetic induction map recorded using EH; these colors correspond to the different directions of magnetization inside different particles. The magnetic flux lines are concentrated within the crystals and lie parallel to the elongation direction of each particle. Since the elongation direction also coincides with the [111] crystalline easy axis, shape and magnetocrystalline anisotropies reinforce each other. In contrast to well-ordered chains such as those shown in Figure 5, a disordered arrangement of magnetosomes is not optimal for magnetotaxis. Nevertheless, the dominating blue and green colors suggest that the net magnetic moment of the cell is still sufficient for effective navigation in the Earth's magnetic field, and measurements confirm that this is indeed the case.

In contrast to magnetite crystals, the shapes and sizes of iron sulfide crystals vary significantly within a cell, as do their crystallographic orientations. The cover image of this issue of *Elements* shows an example of a rod-shaped, dividing cell that contains multiple chains of greigite magnetosomes with random shapes and orientations (Kasama et al. 2006). Although many of the crystals appear to be only weakly magnetic in an induction map recorded using EH, they are confirmed to be greigite on the basis of electron diffraction patterns. Their apparently weak or absent magnetization may result from their magnetic induction directions being almost parallel to that of the electron beam, and so not measured using electron holography. The disordered three-dimensional arrangement of the crystals results in the magnetic field following a meandering path between adjacent crystals.

By studying the fine details of magnetic induction maps, it can be concluded that, in general, shape anisotropy is the most important factor in controlling the magnetic microstructures of ferrimagnetic crystals in bacteria, followed by interparticle interactions, and, least important, magnetocrystalline anisotropy. As illustrated by these examples, some magnetotactic bacteria biomineralize well-ordered chains of magnetite that have highly regulated magnetic properties, whereas other cells exert less control over the properties of their magnetosomes. In these latter cases, the organism compensates for this reduced efficiency by synthesizing a correspondingly larger number of magnetosomes.

The magnetic moments of individual cells can be measured quantitatively using EH (Table 2). Even though the measured magnetosome chains differ in the number, size, shape, and arrangement of magnetosomes, both their magnetic moments and their magnetic moments per unit length are closely similar. In all of the cells that have been studied using EH, the magnetosomes were observed to result collectively in a permanent magnetic dipole moment that is sufficient for magnetotaxis.

MAGNETIC PARTICLES IN ANIMALS

Magnetoreception in animals is an exciting field of research, most of which is still unknown territory (Lohmann et al. 2007). A large number of behavioral studies have been carried out since the 1970s and have established that various birds, fish, reptiles, amphibians, and insects use magnetic cues for navigation (see Wiltschko and Wiltschko 1995 and Table 1). However, the mechanisms of magnetoreception are still mostly unknown, and putative magnetosensor systems have been proposed only for some species. As there is no conclusive evidence that humans have a conscious magnetic sense, analogies based on our own experience cannot be used when studying magnetic sensing in animals. In addition, since magnetic field lines penetrate tissue, there is no need for external sensory organs, and magnetic sensory systems can be located anywhere in the

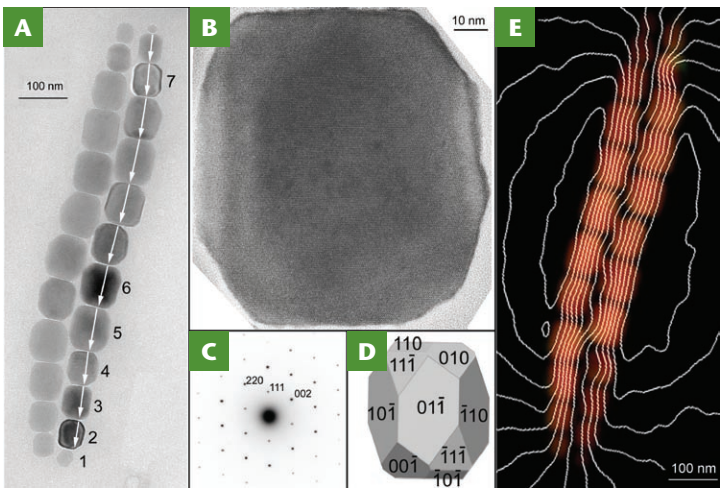

Figure 5 (**A**) Bright-field image of a double chain of magnetite magnetosomes from a single bacterial cell. The orientations of the crystals marked 1 to 7 were determined using electron diffraction. The white arrows are approximately parallel to [111] in each crystal. (**B**) High-resolution TEM image, (**C**) selected-area electron diffraction pattern and (**D**) morphological model of crystal 4 in (A). (**E**) Magnetic induction map recorded using off-axis electron holography from the double chain of magnetite magnetosomes in (A). The magnetic phase contours show that each particle is a single magnetic domain, uniformly magnetized parallel to the chain. The contour spacing is 0.3 rad. Figure adapted from Simpson et al. (2005)

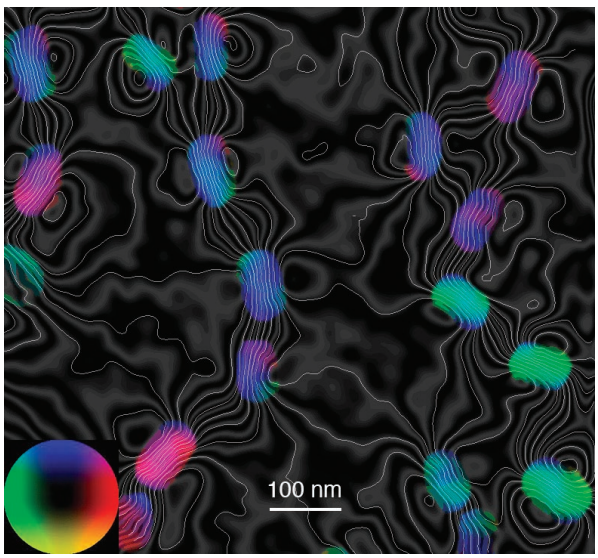

Figure 6 Magnetic induction map of partial chains and scattered magnetite crystals in a cell of a freshwater magnetotactic bacterium. The colors indicate the direction of the projected magnetic field, according to the color wheel shown. Image obtained by Ed Simpson

body. This makes it a highly challenging task to find magnetoreceptors in macroscopic organisms, particularly if they rely on the presence of a small number of magnetic nanocrystals (Kirschvink et al. 2001).

Magnetoreception has been studied most thoroughly in homing pigeons, in which iron-bearing neurons have been found at three pairs of distinct locations in the upper beak (Fig. 7). Since the dendritic cells are oriented in three mutually perpen dicular directions in the pairs of areas that are marked with white dots in Figure 7b, the response of the entire system may enable the bird to obtain information about magnetic field intensity and direction. The neurons in these regions contain several "beads" of ~1 µm vesicles filled with ~5 nm particles (Fig. 7c). The morphologies and sizes of the magnetic particles were measured from TEM micrographs of histological sections, and were identified as magnetite/maghemite using electron diffraction and magnetometry (Hanzlik et al. 2000). Magnetic interactions between the beads could result in their movement. This could open gated ion channels and provide the necessary impulse for a neuronal signal. In addition to the beads, rows of ~1 × 1 × 0.1 µm iron-bearing platelets occur in the neurons (Fig. 7c). Electron diffraction patterns indicated that the platelets were amorphous (Fleissner et al. 2003), and thus their role in magnetoreception remains obscure. Further experi mental work, involving microstructural and EH measure ments, is needed to understand the interactions between the various magnetic elements in this complex system.

Very little information is available about magnetic sensory systems in other vertebrates. SD magnetite particles that resemble those from magnetotactic bacteria have been extracted from the nasal cavity of salmon (Mann et al. 1988). In trout, iron-rich particles in the olfactory epithelium were imaged using confocal laser-scanning microscopy and magnetic force microscopy and were interpreted as chains of SD magnetite (Diebel et al. 2000). However, these features were only partially characterized, and the ultrastructure of the magnetic sensory system remains largely unknown. Even less information is available about magnetic sensing in other animals (Table 1), in which the identity and grain size of magnetic crystals are typically identified only using bulk magnetic methods.

Whereas magnetite and greigite nanocrystals in bacteria are optimized for navigation, magnetic crystals used for hardening are not. Greigite crystals in the scaly-foot snail (Fig. 3b) are highly elongated (~120 nm long and ~15 nm wide), such that most of them would be expected to support single magnetic domains. However, superparamagnetic particles are also present and the orientations of the greigite laths are random, suggesting that the magnetic material has not been optimized by evolution for magnetic orientation of the organism. Instead, the mechanical properties of the sclerite material are perfect for protection, since the iron sulfide layer is harder and stiffer than human enamel and stiffer than molluscan shell nacre (Suzuki et al. 2006).

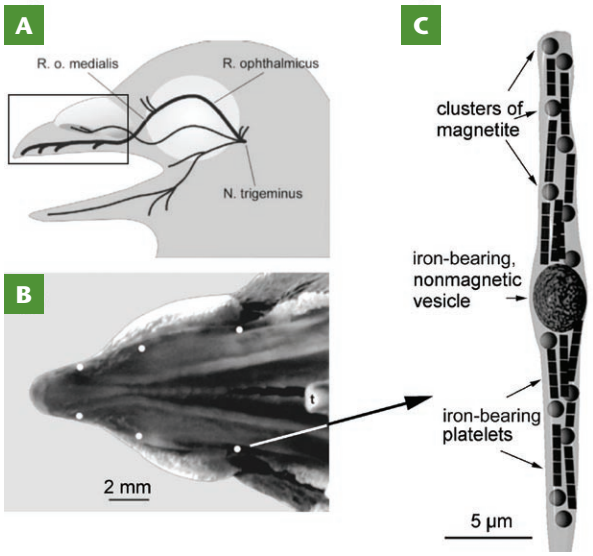

Figure 7 Magnetoreception system in the homing pigeon. (**A**) Pigeon head showing nerves in the upper-beak region that are thought to be involved in magnetoreception. (**B**) View of the upper beak from below. Ferrimagnetic particles occur in dendritic cells located in six distinct areas, marked by white spots. (**C**) Schematic diagram of a single neuron containing a nonmagnetic vesicle in the center, several 1-micrometer-sized "beads" filled with superparamagnetic ~5 nm magnetite crystals, and strings of iron-bearing, amorphous platelets. (A) and (B) are adapted from Fleissner et al. (2003); (C) is adapted from Fleissner et al. (2007)

Magnetic particles have been found in the human brain in both magnetic SD (Kirschvink et al. 1992) and SPM (Quintana et al. 2004) size ranges. The presence of SPM magnetite particles in amyloid plaques is thought to be associated with neurodegenerative diseases such as Alzheimer's. EH has been used to study plaques that contain 2 to 7 nm magnetite particles and to confirm the absence of magnetic induction in these particles (Collingwood et al. 2008). The size distribution of the nanoparticles indicates that they may have formed from a ferritin precursor.

MAGNETOFOSSILS

Magnetite nanocrystals interpreted to be produced by magnetotactic bacteria have been described in sediments and rocks of various ages (Kopp and Kirschvink 2008). The magnetofossil record extends to the Cretaceous and perhaps

Table 2 MAGNETIC MOMENTS OF INDIVIDUAL BACTERIAL CELLS MEASURED USING ELECTRON HOLOGRAPHY

Bacterial strain	Magnetosome mineral	Average length of each magnetosome (nm)	Number of magneto-somes in chain	Magnetic moment ($A \cdot m^2$)	Length of chain (µm)	Magnetic moment per unit length ($A \cdot m^2/\mu m$)	Reference
Magnetospirillum magnetotacticum MS-1	Magnetite (single chain)	~45	22	5×10^{-16}	1.2	4.2×10^{-16}	Dunin-Borkowski et al. (1998)
MV-1	Magnetite (single chain)	~60	15	7×10^{-16}	1.6	4.4×10^{-16}	Dunin-Borkowski et al. (1998)
Uncultured coccus	Magnetite (double chain)	~80	25	1.7×10^{-15}	0.95	1.8×10^{-15}	Simpson et al. (2005)
Uncultured, rod-shaped cell	Greigite and possibly magnetite (double chain)	~60	57	9.0×10^{-16}	2.19	4.1×10^{-16}	Kasama et al. (2006)
Uncultured, dividing, rod-shaped cell	Greigite and magnetite (multiple chain)	~60 (greigite) ~80 (magnetite)	~155	1.8×10^{-15}	2.94	6.1×10^{-16}	Kasama et al. (2006)

as far back as the late Archean. The identification of magnetofossils is based on criteria that include the narrow size and shape distributions, distinctive morphologies, chemical purity, and chain arrangement of intracellular magnetite. Based on such criteria, Kopp and Kirschvink (2008) developed a scheme for assessing the robustness of magnetofossil identification. Since inorganic processes and extracellular biomineralization can also produce nanocrystalline magnetite, the identification of magnetofossils in both terrestrial and extraterrestrial rocks is highly ambiguous without the stringent use of such schemes.

In principle, magnetofossils could originate from organisms other than bacteria. Given the probably minute amounts of magnetic nanocrystals in animals, and the fact that animals are less abundant than bacteria, it is not surprising that no magnetofossils have been described as originating from fish, birds, or other animals. However, magnetite particles with unusual shapes have been found in sediments deposited at the Paleocene–Eocene Thermal Maximum and have been identified as magnetofossils on the basis of their physical and chemical properties (Schumann et al. 2008); these particles include spearhead- and spindle-shaped, 4 µm long particles that are different from any known biogenic or abiogenic magnetite populations. Schumann et al. (2008) speculated that environmental conditions resulted in a high availability of iron, thus favoring the diversification of unknown magnetite-forming eukaryotes.

OUTLOOK

Biogenic magnets have fascinating combinations of physical and magnetic properties and biological functions. However, except for magnetic particles in magnetotactic bacteria, relatively little is known about them. Further work is needed to understand magnetic sensing in animals and the roles of magnetite particles in humans. A key challenge is the localization and preparation of tissues that contain ferrimagnetic particles. Once such samples are available, advanced analytical techniques, including electron holography, can be used to provide detailed characterization of the structures, compositions, arrangements, and magnetic properties of biogenic nanomagnets.

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