

II

ELECTROMAGNETIC ENERGY
AND REGULATION OF LIFE
PROCESSES

Bacterial Biomagnetism and Geomagnetic Field Detection by Organisms

**RICHARD P. BLAKEMORE, NANCY A. BLAKEMORE,
RICHARD B. FRANKEL***

Department of Microbiology, University of New Hampshire
Durham, New Hampshire, and *Francis Bitter
National Magnet Laboratory, M.I.T.
Cambridge, Massachusetts

INTRODUCTION

The Earth is a magnet. Its dipole character results from massive currents within the molten portion of its core. These currents, driven presumably by gravitational energy, induce, in the manner of a self-sustaining dynamo, a global dipolar magnetic field with a magnitude of roughly 0.7 gauss at the poles. Although the ancient Chinese were familiar with the polar alignment of magnetized needles, geomagnetism became science with the publication in 1600 of William Gilbert's classic exposition *De Magnete, Magneticisque Corporibus Et De Magno Magnete Tellure: Physiologia Nova, Plurimis & Argumentis & Experimentis Demonstrata*. Gilbert's predecessor, Peter Peregrinus de Maricourt in his *Epistola de Magnete* of 1269, had noted that a magnetized needle (compass) left free to float on water, merely rotates, coming to rest with its axis lying in the north-south plane, and is not pulled in a northward direction. He did not perceive that the source of the magnetism causing the compass deflection was the Earth itself. Other predecessors of William Gilbert had believed such magnetism was extraterrestrial or was due to some remote "magnetic mountains." Gilbert fashioned lodestone spheres which he called *terrellas* or little Earths; a term indicating his suspicion that the Earth itself was a magnet. By studying the interactions between his *terrellas* and small bits of iron wire, he arrived at a novel and experimentally based philosophy of the attractive behavior or "coition" of ferromagnets, and presented in his book the first inductive rationale for the concept of terrestrial magnetism.

The direction of a magnetic field is, by convention, the direction in which the north-seeking end of a compass needle points. Gilbert showed that this is inward (downward) at the Earth's north geographic pole and outward (upward) at the south pole. Thus, the geomagnetic field inclines upward in the southern hemisphere, is totally horizontal at the magnetic equator, and is inclined downward in the northern hemisphere. Earth's magnetic field intensity has been more-or-less constant during the 3.5 billion year history of life on Earth. Evidence preserved in the paleomagnetic record of sediments

indicates that changes of the geomagnetic field direction associated with meanderings and reversals of the magnetic poles have been gradual. Major dipole reversals require thousands of years.

It is not surprising that organisms have adapted to exploit geomagnetism as a directional cue for guidance in migration and homing. However, it was not until the 1970's that good experimental evidence was obtained that animals sense the Earth's magnetic field.

ANIMAL ORIENTATION AND HOMING

Keeton (1, 2) demonstrated that small bar magnets, but not brass control bars, fastened near the heads of homing pigeons disrupted their homing ability under overcast conditions. (On sunny days pigeons use the sun for navigation.) Walcott et al. (3) extended and confirmed these field studies using small energized coils to produce uniform or homogeneous magnetic fields in the pigeon's head region. These scientists learned that pigeons could be disoriented with uniform magnetic fields directed antagonistically to Earth's. On overcast days pigeons flew directly away from the home loft direction if the experimentally contrived magnetic field in their head region was directed upward. Upward, as mentioned previously, is antiparallel to the direction of the normal geomagnetic field in the northern hemisphere in which these studies were conducted. Pigeons released at sites of magnetic anomaly did not home well, either with or without attached magnets or coils, suggesting that birds may also rely upon a magnetic map in addition to a magnetic compass (2, 4). Studies by Lindauer and Martin in the same decade revealed that honeybees incorporate information about the Earth's magnetic field into their tail-wagging dances to communicate direction of nectar sources (5, 6). Their comb-building activities (7) and circadian rhythms are also examples of behavior influenced by the geomagnetic field (8).

In more recent studies, other migratory birds including the European robin (9) and bobolink (10) have been shown by means of conditioned behavior responses to detect the geomagnetic field. The list of organisms either known or highly suspected on the basis of behavior experiments, to be able to sense the geomagnetic field also includes planaria (11), mud snails (12), salamanders (13), elasmobranch fishes (14, 15), yellowfin tuna (16), woodmice (17), and possibly humans (18, 19). In the case of humans however, the results appear equivocal and controversial at the present time.

How do creatures detect the geomagnetic field? One strategy which appears to have evolved among elasmobranch fishes makes use of the Faraday effect. Kalmijn (15) showed that elasmobranchs could be trained to respond to changes in the geomagnetic field. He postulated that when swimming or drifting at right angles to the Earth's magnetic field at 100 cm/sec, these creatures could induce field gradients in their head

region of $0.4 \mu\text{V}/\text{cm}$. Fields of only $0.01 \mu\text{V}/\text{cm}$ were sufficient to elicit electrophysiological responses in these animals. Thus, sharks, skates and rays appear to detect the geomagnetic field by transducing magnetic information to electrical information which they can sense using special electroreceptive organs called ampullae of Lorenzini in their snouts. This electromagnetic inductive mechanism requires that the animal be in a highly conducting medium such as seawater. For aerial animals, the Faraday effect would require a circular electrically-conducting loop of millimeter dimensions within the animal's tissues (20). Hence, it is not a likely candidate for geomagnetic field detection in birds, insects or terrestrial life forms because no structural evidence for such conducting loops exists.

A second way in which creatures might sense geomagnetism is through direct magnetic dipole interactions with the Earth's field. To do so, organisms would need a permanently magnetic substance within their tissues. However, until 1975, the only known instance of strongly magnetic material in a biological system was the mineral capping of chiton teeth. The abrasion-resistant layer on each of the teeth of the rasping organ of these primitive marine mollusks had been shown by Lowenstam to consist of the dense, hard, mineral magnetite (21).

Impetus for considering that cells might be permanently magnetized came by surprise. In 1975 Blakemore reported a new taxis or behavior type in bacteria (22). The term "magnetotaxis" was used to denote the directed swimming of bacterial cells along magnetic field lines. This behavior is dramatic and unequivocal. When examined with a dark-field microscope at 40–100 X (inexpensive hand-held microscopes may be used), one can see in muds from marshes and lakes, millions of active, highly refractile bacteria. Some move toward one side of their water-drop world and their wobbling motion straightens into nearly uni-directional swimming when a magnetized object is brought near them. If the observer is looking at such magnetotactic bacteria present in northern hemisphere sediments they are observed to swim toward the pole of a magnet which attracts the north-seeking end of a magnetic compass, and away from the pole which attracts the south-seeking end. Magnetotactic bacteria in the southern hemisphere do the opposite; they swim toward the end of a magnet which attracts the south-seeking end of a compass needle (23, 24). Although they cannot swim, dead magnetotactic bacteria are also aligned in a uniform magnetic field. Just as Peregrinus' magnetized needles, living magnetotactic bacteria passively align in the geomagnetic field and consequently swim preferentially along magnetic field lines by ordinary means using their flagella; they act as swimming compass needles. It is important to note that the bacteria are not pulled northward because the Earth has a uniform magnetic field.

THE MAGNETOSOME

The possibility that magnetotactic bacteria were permanently magnetized seemed

likely because each of the dozens of cell types examined by electron microscopy contained cytoplasmic crystals containing iron (22, 23). These regularly shaped, enveloped structures were later shown to consist of crystalline magnetite or lodestone, an iron oxide mineral (25, 26). They were subsequently named “magnetosomes” (27). In forms in which they have been studied, magnetosomes are enveloped single crystals of the iron oxide magnetite (25, 27-29). Each is a single magnetic domain with a crystal size approximately 400–1000 Å, depending upon the species. Consequently, individual magnetosomes are too small to be seen within the cells observed with the light microscope. Their high iron content, however, renders them quite impenetrable by electrons and they are easily visualized even in unstained cells by means of electron microscopy. Recently, magnetotactic algae were discovered in Brazil (30, 31). Each of these single-celled eukaryotic microorganisms possesses thousands of magnetosomes arranged in rows along the long cell axis. Magnetosomes within a given strain or cell type are homogeneous in grain size, and are uniform in shape and arrangement within the cell. This species specificity argues for genetic control of biogenic magnetite formation. The maximum size of the magnetosome within a given bacterial species is limited by an unknown mechanism. The number of magnetosomes per cell, however, can vary in response to culture conditions including iron supply and dissolved oxygen. For instance, the average number of magnetosomes within cells of a magnetic spirillum species varied from 0–17 in response to culture oxygen tension, and optimal numbers were produced under microaerobic conditions (32).

Several morphologically distinct types of magnetosomes have been observed within various types of magneto tactic microorganisms. Magnetosomes within *Aquaspirillum magnetotacticum* are truncated octahedral prisms (33). Magnetosomes within coccoid cells studied by Mann et al. (28, 34) as well as those within an unidentified cell from a pond in Japan (29) were truncated hexagonal prisms. The prismatic crystals of either hexagonal or octahedral type were oriented with their easy axes of magnetization along the chain axis (e.g., [111] faces adjacent). The crystal morphology of tear-drop or bullet shaped magnetosomes found in some bacterial species and in a magnetotactic algal species (see below) is completely unknown.

In some cell types the magnetosomes occur in clusters predominantly at one side of the cell. In others the magnetosomes occur as a string or chain of particles arranged along the axis of cell motility. The magnetosomes situated at ends of such chains are often smaller. This suggests that magnetosome chains grow bidirectionally along their long axis as iron newly transported into the cell is transformed into magnetite. At cell division, whether they exist in chains or not, magnetosomes appear to be partitioned between each daughter cell. Thus, bacteria and algae control the iron biomineralization process thereby determining the magnetosome crystal size, morphology, structure, chemical composition, arrangement and crystallographic orientation within the cell (33, 35). This is a splendid example of natural selection as there are no readily apparent

physical or chemical reasons why constraints on these unique features of biogenic magnetite should exist.

MAGNETOTAXIS

Magnetosomes are unequivocally responsible for the magnetotactic response of microorganisms. Mutants of magnetotactic bacteria have been obtained which do not synthesize magnetosomes. These are fully motile but not magnetotactic. With both bacteria and algae, the arrangement and volume of magnetite present within each cell is more than enough to align it passively in the Earth's field of 0.5 gauss. The ratio of magnetic to thermal energy ($\mu\text{B}/kT$) is greater than 10 for the bacteria and greater than 100 for the algae. Thus, each cell's magnetic moment easily overrides the effect of Brownian motion caused by thermal agitation which tends to randomize cell orientation in water (36, 37). Moreover, the ability to remagnetize the cells by means of a brief, monophasic magnetic pulse of several hundred gauss and thereby instantaneously reverse their swimming direction without cell turning provided unequivocal proof that the magnetotactic behavior of these organisms is due to ferromagnetism (22, 24).

The geomagnetic field over most of the Earth is inclined from the horizontal (e.g. it has an angle of dip). The vertical component of the local geomagnetic field exerts strong selective pressure on natural populations for cells with a direction of magnetization tending to direct them downward along the inclined field lines (23, 24, 36, 38, 39). This was first evident with northern hemisphere monopolarly flagellated forms which persistently swam forward and in the magnetic field direction (e.g. the direction indicated by the north-seeking end of a compass needle), and was further substantiated by field observations which revealed that cells in southern hemisphere natural populations were of opposite magnetic polarity to those in the northern hemisphere. Consequently, magnetotaxis tends to direct unidirectionally swimming cells *downward* in each hemisphere. Some magnetotactic bacteria are bipolarly flagellated and swim principally along the inclined geomagnetic field lines but in either direction. The direction actually taken at any instant depends not only upon magnetism but also upon other taxes. Aerotaxis, for instance, has been shown to override magnetotaxis in bipolarly flagellated magnetotactic spirilla (40). The observed effect of Earth's magnetic field in orienting cells so that they may swim preferentially downward is consistent with their observed natural distribution. They are found in sediments and in the sediment-water interface, not in surface films or the surface micro-layer.

FORMS OF IRON IN MAGNETIC BACTERIA

The most intensively studied magnetotactic organism is the bacterium *A. magnetotacticum* (41, 42). This chemoheterotroph is a microaerophilic denitrifying (43,

44) nitrogen fixer (45). On the basis of extensive spectroscopic analysis, cells of *A. magnetotacticum* are known to contain ferrous ions, a low-density hydrous-ferric-oxide, a high-density hydrous-ferric-oxide (ferrihydrite) and Fe_3O_4 . Additional experiments with cell fractions show that ferrihydrite in the magnetotactic cells is associated with the magnetosomes (46). It has been proposed that *A. magnetotacticum* precipitates Fe_3O_4 in the sequence: Fe^{3+} quinate \rightarrow Fe^{2+} low-density hydrous-ferric-oxide \rightarrow ferrihydrite \rightarrow Fe_3O_4 . In non-magnetic cells the process stops with ferrihydrite. In cells of the cloned, nonmagnetotactic strain the process stops with low-density hydrous-ferric-oxide.

In the proposed sequence, iron enters the cell as Fe^{3+} chelated by quinic acid. Reduction to Fe^{2+} releases iron from the chelator. Fe^{2+} is reoxidized and accumulated as the low-density hydrous-iron-oxide. By analogy with the deposition of iron in the micellar cores of the protein ferritin, this oxidation step might involve molecular oxygen, which as noted previously, is required for Fe_3O_4 precipitation in *A. magnetotacticum* (32). Dehydration of the low-density hydrous-ferric-oxide results in ferrihydrite. Finally, partial reduction of ferrihydrite and further dehydration yield Fe_3O_4 .

In high resolution TEM lattice imaging studies (33), no other crystalline phases in addition to Fe_3O_4 were detected. However, in some magnetosomes, noncrystalline material was found contiguous with the Fe_3O_4 . This suggests that the hydrous-ferric-oxide phase is amorphous ferrihydrite, and that final crystallization of Fe_3O_4 occurs as a solution-reprecipitation process, possibly triggered by Fe^{2+} ions.

Additional experiments demonstrate that while the hydrous-ferric-oxide is primarily associated with magnetosomes, Fe^{2+} in the cell is very probably associated with the peptidoglycan wall layer of the cell (47). This association could occur during the conversion from the iron quinate complex outside the cell to ferric iron and ultimately to Fe_3O_4 within the cell.

Fe_3O_4 is thermodynamically stable with respect to hematite and ferrihydrite at low E_H and high pH (48). However, rapid transformation of ferrihydrite to magnetite appears to involve more than simple reduction and dehydration. While the degree of crystallinity of ferrihydrite can vary, in crystalline samples it has a structure related to hematite, with hexagonal close-packed oxygen atoms and Fe^{3+} octahedrally coordinated sites. Fe_3O_4 has a cubic, inverse spinel structure with Fe^{3+} in octahedral and tetrahedral sites, and Fe^{2+} in octahedral sites. This, plus the fact that the precipitation process requires spatial segregation of regions of differing E_H and possibly pH, suggests that the process falls into the biomineralization category described by Lowenstam (35) as "organic-matrix mediated." Thus the magnetosome envelope is probably an integral element in the precipitation process, functioning as a locus for enzymatic activities, compartmentalizing constituents, providing control of E_H and pH, as well as comprising a structural element anchoring the Fe_3O_4 particles to the remainder of the cell.

MAGNETITE IN EUKARYOTES

The unexpected finding that certain bacterial cells were geomagnetically responsive, were permanently magnetized and contained iron-rich structured particles (22), precipitated a search for permanent magnetic material in other organisms; particularly those known from behavioral studies to be able to sense geomagnetism. The results proved extremely rewarding. Gould et al. (49), using sensitive rock magnetometers, discovered magnetite in honeybees as did Walcott et al. in pigeons (50). Other groups of workers have located magnetic material in migratory birds such as bobolinks (10), buntings and sparrows (51), in Monarch butterflies (52), green sea turtles (53), yellowfin tuna (54), woodmice (17), dolphins (55), cetaceans (56), and humans (57, 58). In the case of honeybees, it may be iron deposits discovered within abdominal cells which play a role in magnetic field detection (59). In the yellowfin tuna, single magnetic domain-sized magnetite particles similar to those of magnetotactic bacteria were found in the skull bone (54). Several of these fish were recently trained to discriminate in their swimming response between the presence of one as compared to two Earth-strength magnetic fields in their tanks (16). Despite these encouraging results, a direct connection between the presence of magnetite in animal tissues and geomagnetic responsiveness of animals has yet to be demonstrated as it has for magnetotactic bacteria and algae.

MAGNETOTACTIC ALGAE

TEM of magnetotactic saprozoic (non-photosynthetic) euglenoid algal cells magnetically separated from brackish sediments in Brazil (31) shows that they contain numerous Fe_3O_4 particles arranged in chains oriented more or less parallel to the long axis of the cell. Individual particles are arrowhead or tooth-shaped and are within the single magnetic domain size range for Fe_3O_4 . Hence, each chain is a permanent magnetic dipole. If the moments of all the chains are oriented parallel to each other, a cell would have a geomagnetic dipole moment equal to the sum of the moments of all its particles. An estimate of the total magnetic moment M of algal cells gives $M = 5 \times 10^{-10}$ emu. This is about 1000 times the moment of a typical magnetic bacterium, and corresponds to a total of about 3×10^3 aligned particles of the observed dimensions.

The biological significance of magnetotaxis in these algae (31, 60) is not yet understood. However, highly ordered arrangement of the chains of particles in the cells suggests that they are chains of magnetosomes very much like the chains of magnetosomes in bacteria. Evidence for the presence of membranes enveloping the particles must await TEM of thin sections.

Thus, eukaryotic cells as well as prokaryotic cells can produce biogenic Fe_3O_4 in the form of single magnetic domains as an intracellular biomineralization product. It will be interesting to compare the biomineralization process and the role(s) of membranes in

these fundamentally different types of organisms.

Recent discoveries of biogenic magnetite in deep sea sediments (61, 62) are exciting, suggesting that these particles are the major contributors to the paleomagnetic record of sediments. Because magnetosomes appear to be formed only with O₂ available (32), they may also provide unique fossilized information concerning sedimentation processes which have occurred since the transition on Earth from an anoxic to aerobic atmosphere.

Obviously, much remains to be discovered concerning the manner in which unicellular and multicellular organisms sense, respond to, and use magnetite and the geomagnetic information in which they are constantly bathed. It is ironical though, that lodestone, the very substance used by the twelfth century Chinese to make compasses and also used by the Late Renaissance scholars to understand the magnetic character of Earth, may now help us understand how some living organisms use geomagnetism in their life activities.

ACKNOWLEDGEMENTS

RPB and NAB were partially supported by NSF Grant DMB 85-15540 and ONR Contract N00015-85-K-0502. RBF was partially supported by ONR Grant N000-85-K-0505.

REFERENCES

- (1) Keeton, W.T.: Magnets interfere with pigeon homing. Proc. Natl. Acad. Sci. USA 68: 102-106, 1971.
- (2) Keeton, W.T., Larkin, T.S., Windsor, D.M.: Normal fluctuations in the earth's magnetic field influence pigeon orientation. J. Comp. Physiol. 95: 95-103, 1974.
- (3) Walcott, C. Anomalies in the Earth's magnetic field increase the scatter of pigeon's vanishing bearings. In: Schmidt-Koenig, K. and Keeton, W.T. eds., Animal Migration, Navigation and Homing. Springer, Heidelberg, 1978.
- (4) Gould, J.L.: The map sense of pigeons. Nature 296: 205-211, 1982.
- (5) Lindauer, M., Martin, H. Magnetic effects on dancing bees. In: Galler, S.R., Schmidt-Koenig, K., Jacobs, G.J. and Belleville, R.E. eds., Animal Orientation and Navigation. Special Publication 262. National Aeronautics and Space Administration, Washington DC, 1972.
- (6) Martin, H., Lindauer, M.: Der Einfluss des Erdsagnet-felds auf die Schwereorientierung der Honingbiene (*Apis mellifica*). J. Comp. Physiol. 122: 147-187, 1977.
- (7) De Jong, D.: The orientation of comb-building by honeybees. J. Comp. Physiol. 147: 495-501, 1982.

- (8) Dyer, F.C., Gould, J.L.: Honey bee orientation: a backup system for cloudy days. *Science* 214: 1040-1041, 1981.
- (9) Wiltschko, W., Wiltschko, R.: Magnetic compass of European robins. *Science* 176: 62-64, 1972.
- (10) Beason, R.C., Nicholls, J.E.: Magnetic orientation and magnetically sensitive material in a transequatorial migratory bird. *Nature* 309: 151-153, 1984.
- (11) Brown Jr., F.A.: Responses of the planarium, *Dugesia*, and the protozoan, *Paramecium*, to very weak horizontal magnetic fields. *Biol. Bull.* 123: 264-281, 1962.
- (12) Brown Jr., F.A., Webb, H.M., Barnwell, F.H.: A compass directional phenomenon in mud-snails and its relation to magnetism. *Biol. Bull.* 127: 206-220, 1964.
- (13) Phillips, J.B.: Use of the Earth's magnetic field by orienting cave salamanders (*Eurycea lucifuga*). *J. Comp. Physiol.* 121: 272-288, 1977.
- (14) Kalmijn, A.J.: The electric and magnetic sense of sharks, skates, and rays. *Oceanus* 20: 45-52, 1977.
- (15) Kalmijn, A.J. Experimental evidence of geomagnetic orientation in elasmobranch fishes. In: Schmidt-Koenig, K. and Keeton, W.T. eds., *Animal Migration, Navigation, and Homing*. Springer, Heidelberg, 1978.
- (16) Walker, M.M.: Learned magnetic field discrimination in yellowfin tuna, *Thunnus albacores*. *J. Comp. Physiol.* 155: 673-679, 1984.
- (17) Mather, J.G., Baker, R.R.: Magnetic sense of direction in woodmice for route-based navigation. *Nature* 291: 151-155, 1981.
- (18) Baker, R.R.: Goal orientation by blindfolding humans after long-distance displacement: possible involvement of a magnetic sense. *Science* 210: 555-557, 1980.
- (19) Gould, J.L., Able, K.P.: Human homing: an elusive phenomenon. *Science* 212: 1061-1063, 1981.
- (20) Jungerman, R.L., Rosenblum, B.: Magnetic induction for the sensing of magnetic fields by animals—an analysis. *J. Theor. Biol.* 87: 25-32, 1980.
- (21) Lowenstam, H.A.: Magnetite in denticle capping in recent chitons (*Polyplacophora*). *Gdol. Soc. Amer. Bull.* 73: 435-438, 1962.
- (22) Blakemore, R.P.: Magnetotactic bacteria. *Science* 190: 377-379, 1975.
- (23) Blakemore, R.P.: Magnetotactic bacteria. *Ann. Rev. Microbiol.* 36: 217-238, 1982.
- (24) Blakemore, R.P., Frankel, R.B., Kalmijn, A.J.: South-seeking magnetotactic bacteria in the southern hemisphere. *Nature* 286: 384-385, 1980.
- (25) Frankel, R.B., Blakemore, R.P., Wolfe, R.S.: Magnetite in freshwater magnetotactic bacteria. *Science* 203: 1355, 1979.
- (26) Towe, K.M., Moench, T.T.: Electron-optical characterization of bacterial magnetite. *Earth Planet Sci. Lett.* 52: 213-220, 1981.
- (27) Balkwill, D.L., Maratea, D., Blakemore, R.P.: Ultrastructure of a magnetotactic spirillum. *J. Bacteriol.* 141: 1399-1408, 1980.
- (28) Mann, S., Moench, T.T., Williams, R.J.P.: A high resolution electron microscopic investigation of bacterial magnetite: implications for crystal growth. *Proc. R. Soc. Lond.*

- 221: 385, 1984.
- (29) Matsuda, T., Endo, J., Osakube, N., Tonomura, A., Arai, T.: Morphology and structure of biogenic magnetite particles. *Nature* 302: 411, 1983.
 - (30) Lins de Barros, H.G.P., Esquivel, D.M.S., Danon, J., de Oliveira, L.P.H. Magnetotactic algae, *Acad. Brasileria Nota de Fisica D8PF-NF-48*, 1981.
 - (31) Torres de Araujo, F.F., Pires, M.A., Frankel, R.B., Bicudo, C.E.M.: Magnetite and magnetotaxis in algae. *Biophys. J.* 50: 375-378, 1986.
 - (32) Blakemore, R.P., Short, K.A., Bazylinski, D.A., Rosenblatt, C., Frankel, R.B.: Microaerobic conditions are required for magnetite formation with *Aquaspirillum magnetotacticum*. *Geomicrobiol. J.* 4: 53-71, 1984.
 - (33) Mann, S., Frankel, R.B., Blakemore, R.P.: Structure, morphology and crystal growth of bacterial magnetite. *Nature* 310: 405-407, 1984.
 - (34) Moench, T.T., Konetzka, W.A.: A novel method for the isolation and study of a magnetotactic bacterium. *Arch. Microbiol.* 119: 203-212, 1978.
 - (35) Lowenstam, H.A.: Minerals formed by organisms. *Science* 211: 1126-1131, 1981.
 - (36) Frankel, R.B.: Magnetic guidance of organisms. *Ann. Rev. Biophys. Bioeng.* 13: 85-103, 1984.
 - (37) Frankel, R.B., Blakemore, R.P.: Navigational compass in magnetic bacteria. *J. Magn. Magn. Mater.* 15-18: 1562-1564, 1980.
 - (38) Blakemore, R.P., Frankel, R.B.: Magnetic navigation in bacteria. *Sci. Am.* 245: 58-65, 1981.
 - (39) Frankel, R.B., Blakemore, R.P., Torres de Araujo, F.F., Esquivel, D.M.S., Danon, J.: Magnetotactic bacteria at the geomagnetic equator. *Science* 212: 1269-1270, 1981.
 - (40) Spormann, A.M., Wolfe, R.S.: Chemotactic, magnetotactic and tactile behavior in a magnetic spirillum. *FEMS Lett.* 22: 171-177, 1984.
 - (41) Blakemore, R.P., Maratea, D., Wolfe, R.S.: Isolation and pure culture of a freshwater magnetic spirillum in chemically defined medium. *J. Bacteriol.* 140: 720-729, 1979.
 - (42) Maratea, D., Blakemore, R.P.: *Aquaspirillum magnetotacticum* sp. nov., a magnetic spirillum. *Int. J. Syst. Bacteriol.* 31: 452, 1981.
 - (43) Bazylinski, D.A., Blakemore, R.P.: Denitrification and assimilatory nitrate reduction in *Aquaspirillum magnetotacticum*. *Appl. Environ. Microbiol.* 46: 1118-1124, 1983.
 - (44) Escalante-Semerena, J.C., Blakemore, R.P., Wolfe, R.S.: Nitrate dissimilation under microaerophilic conditions by a magnetic spirillum. *Appl. Environ. Microbiol.* 40: 429-430, 1980.
 - (45) Bazylinski, D.A., Blakemore, R.P.: Nitrogen fixation (acetylene reduction) in *Aquaspirillum magnetotacticum*. *Curr. Microbiol.* 9: 305-308, 1983.
 - (46) Frankel, R.B., Papaefthymiou, G.C., Blakemore, R.P., O'Brien, W.: Fe₃O₄ precipitation in magnetotactic bacteria. *Biochim. Biophys. Acta* 763: 147, 1983.
 - (47) Ofer, S., Nowick, I., Bauminger, E.R., Papaefthymiou, G.C., Frankel, R.B., Blakemore, R.P.: Magnetosome dynamics in magnetotactic bacteria. *Biophys. J.* 46: 57-64, 1984.
 - (48) Garrels, R.M., Christ, C.L.: *Solution, Minerals and Equilibrium*. Harper and Row, New

- York, 1965.
- (49) Gould, J.L., Kirschvink, J.L., Deffeyes, K.S.: Bees have magnetic remanence. *Science* 201: 1026-1028, 1978.
- (50) Walcott, C., Gould, J.L., Kirschvink, J.L.: Pigeons have magnets. *Science* 206: 1027-1029, 1979.
- (51) Ueda, K., Kusunoki, M., Kato, K., Kakizawa, R., Nakamura, T., Yaskawa, K., Koyama, M., Maeda, Y.: Magnetic remanences in migratory birds. *J. Yamashina Inst. Ornith.* 14: 166-172, 1982.
- (52) Jones, D.S., MacFadden, B.J.: Induced magnetization in the monarch butterfly, *Danaus plexippus* (Insecta, Lepidoptera). *J. Exp. Biol.* 96: 1-9, 1982.
- (53) Perry, A., Bauer, G.B., Dizon, A.E.: Magnetite in the green turtle. *EOS Trans. Am. Geophys. Union* 62: 850, 1981.
- (54) Walker, M.M., Kirschvink, J.L., Chang, S.B.R., Dizon, A.E.: A candidate magnetic sense organ in the yellowfin tuna, *Thunnus albacares*. *Science* 224: 751-753, 1984.
- (55) Zoeger, J., Dunn, J.R., Fuller, M.: Magnetic material in the head of the common Pacific dolphin. *Science* 213: 892-894, 1981.
- (56) Bauer, G.B., Perry, A., Fuller, M., Dunn, J.R., Zoeger, J., Herman, L.M. Biomagnetic studies of cetaceans. 5th Biennial Conference on the Biology of Marine Animals; Boston, MA: Soc. Marine Animals; 1983.
- (57) Baker, R.R., Mather, J.G., Kennaugh, J.H.: Magnetic bones in human sinuses. *Nature* 301: 78-80, 1983.
- (58) Kirschvink, J.L.: Ferromagnetic crystals (magnetite?) in human tissue. *J. Exp. Biol.* 92: 333-335, 1981.
- (59) Kuterbach, D.A., Walcott, B., Reeder, R.J., Frankel, R.B.: Iron-containing cells in the honey bee (*Apis mellifera*). *Science* 218: 694-697, 1982.
- (60) Farina, M., Lins de Barros, H., Esquivel, D.M.S., Danon, J.: Ultrastructure of a magnetotactic microorganism. *Biol. Cell* 48: 85, 1983.
- (61) Peterson, N., Dobeneck, T.V., Vali, H.: Fossil bacterial magnetite in deep sea sediments from the South Atlantic Ocean. *Nature* 320: 611-615, 1986.
- (62) Stolz, J.F., Chang, S.B.R., Kirschvink, J.L.: Magnetotactic bacteria and single-domain magnetite in hemipelagic sediments. *Nature* 321: 849-851, 1986.