Magnetite-based magnetoreception

Joseph L Kirschvink*, Michael M Walker† and Carol E Diebel‡

Orientation, navigation, and homing are critical traits expressed by organisms ranging from bacteria through higher vertebrates. Sensory systems that aid such behavior have provided key selective advantages to these groups over the past 4 billion years, and are highly evolved; magnetoreception is no exception. Across many species and groups of organisms, compelling evidence exists that the physical basis of this response is tiny crystals of single-domain magnetite (Fe_3O_4). It is the opinion of the authors that all magnetic field sensitivity in living organisms, including elasmobranch fishes, is the result of a highly evolved, finely-tuned sensory system based on single-domain, ferromagnetic crystals.

Addresses
*Division of Geological and Planetary Sciences, California Institute of Technology, Pasadena, California 91125, USA;
e-mail: Kirschvink@Caltech.edu
†Experimental Biology Research Group, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, NZ;
e-mail: m.walker@auckland.ac.nz
‡Marine Biology Department, Auckland Museum, Private Bag 92018, Auckland, NZ; e-mail: cdiebel@akmuseum.org.nz

Current Opinion in Neurobiology 2001, **11**:462–467

0959-4388/01/$ – see front matter

Abbreviations

SD	single-domain
SO	superficial opthalmic
SPM	superparamagnetic
TN	trigeminal nerve

Introduction

> "Addition to the known roster of sensory systems, not merely of a new organ or example, but of a new class or major modality, is a rare event."
>
> Bullock and Szabo [1] (with reference to electric field perception in fish)

Several factors have made magnetoreception one of the most controversial topics in the behavioral and neural sciences. First, and foremost, it is not a sensory modality that humans are consciously aware of, and so we do not have *a priori* experience with which to guide experimentation and theory. Second, the general field of magnetic effects on organisms has traditionally been something of a romping ground for quacks and charlatans, dating at least to the French Mesmerists in the late 18th century [2]. Part of this particular problem was the lack of a clear and simple transduction mechanism, leading to a plethora of competing biophysical hypotheses [3], many of which were simply implausible. The few that did seem plausible assumed that magnetic direction was perceived as a by-product of another sensory modality (e.g. electroreception [4] or vision [5]); as we note below, this assumption is unlikely from an evolutionary perspective. The most plausible mechanism — that animals might have a built-in 'compass needle' — was rejected initially on the assumption that animals "had no physiological ferromagnetic materials" [6]. Third and finally, prior to the 1970's, behavioral evidence for the existence of magnetoreception was difficult to reproduce and virtually all laboratory-based attempts to train animals to discriminate magnetic cues had failed.

Despite these controversies, the reports of Earth-strength magnetic effects on behavior did not die away, and it remained an attractive hypothesis to explain long-distance animal migration. Because animals are able to navigate they must first determine their position and then set a compass course towards a goal. Earth's magnetic field is the only geophysical signal that gives consistent information about position and direction at virtually all times and in all environments. Further, the discovery that some mollusks and bacteria can biologically precipitate the mineral magnetite [7,8], and that the magnetotactic bacteria [8] use it for orientation provides both a simple biophysical mechanism for magnetoreception and an unambiguous example of an Earth-strength magnetic effect on biology. Work during the past two decades has led gradually to success with conditioning experiments and improved laboratory and experimental techniques have reduced the reproducibility problems to minimal levels (see [9–14] for discussions).

As illustrated in Figure 1, research over the past 20 years has progressed steadily from the initial discoveries of biogenic magnetite in magnetically-sensitive insects and vertebrates [15–19] to a rudimentary understanding of the neurophysiology and function of this sensory system [12,20,21••,22,23] as well as the biophysical constraints on its function [24–28]. Our goal here is to focus primarily on important developments during the past ~10 years with the deliberate intent of stimulating interest in the field; by our count, fewer than ten research groups are seriously involved in the study of magnetoreception (including in bacteria). Our central thesis is that the magnetic sense should share many of the common attributes of other sensory systems, as outlined by Block [29], including a 'primary transducer', detectors, and neural amplification and transmission pathways to convey signals to the brain. We argue that the magnetic sense will approach the thermal (kT) limit, but that it does not need to be either large or complex. We conclude this contribution by identifying key areas for future study.

Evolution, biophysics, and receptor cells

Evolution of the magnetic sense

The widespread distribution of organisms (bacteria through higher vertebrates) that are magnetoreceptive argues that this sensory modality evolved prior to the radiation of the animal phyla and shares a common origin. In microorganisms, magnetoreception solves the problem of the random walk induced by Brownian motion, as the magnetic orientation energy is typically a factor of 10 or more than the background thermal energy, kT. Swimming along magnetic field lines allows them to stay at the oxygen gradient near the mud/water transition. As the early metazoans also lived in an aqueous environment, navigational abilities ought to have been selected for strongly (for recent reviews see [14,30]). Thus, we propose that the biophysical mechanisms for magnetoreceptive transduction in the nervous system have evolved as ancestral traits, common to all animals, and not as separate entities between groups.

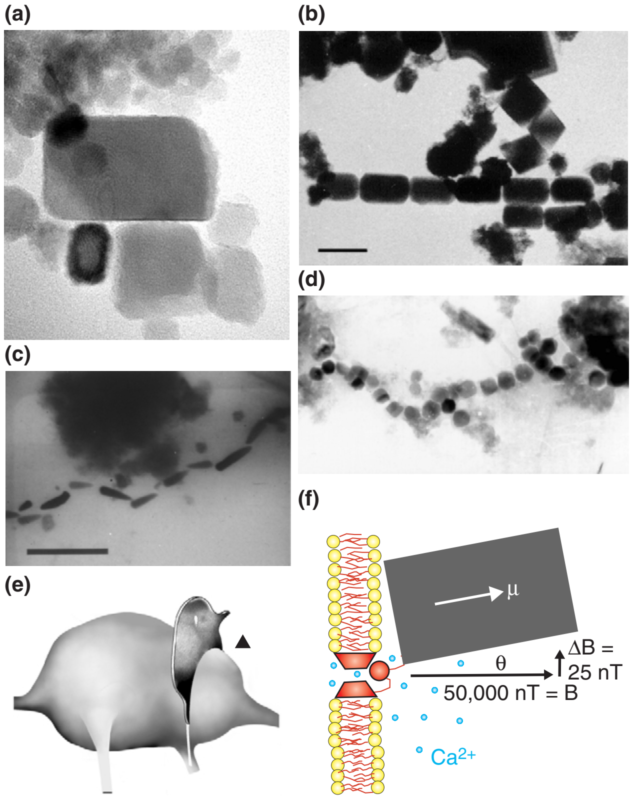
Furthermore, any magnetic sensory system will be subjected to the same forces of evolution as any other genetically-controlled biological process. We suggest that magnetoreception has evolved through the process of 'exaptation', as described by Gould and Vrba [31]. This process involves the elaboration of a biological system as an ancillary survival tool to existing modalities, until eventually the new system evolves independently and distinctly from its ancestor. Hence, the magnetic sense has increased its sensitivity, through evolutionary processes, down to the thermal noise limit (as has happened for the other senses). We reject the idea that magnetoreception is purely a by-product of electroreception or photoreception, as has been proposed [4,5].

As a result of its distinct evolution, we would expect the magnetic sense, like ~50 known sensory systems, to have developed its own complement of essential engineering features, as summarised by Block [29]. These include, first, a highly sensitive initial detection stage or primary transducer, high selectivity and minimal cross-talk with the other modalities. Transduction machinery would also be evident, as well as receptor specializations. Second, an amplification step, characterised by high gain and low noise, would boost received signals, through feedback and filtering steps. Third, signals would be encoded for transmission in a robust, faithful and efficient manner. These are characteristics of all the other sensory systems, and we propose that exaptation and natural selection have moulded the magnetic sense similarly. As a further analogy to other sensory systems we postulate that magnetoreceptive receptors are specialised for discrete functions: some monitor the direction of the magnetic field, others respond to variations in field intensity [25].

Magnetoreception is distinct from vision and electroreception

Some authors report that magnetic compass orientation is a function of other sensory systems in particular vision and electroreception. Indeed, experiments altering the colour of light presented to animals in orientation cages or arenas changes the magnetoreceptive effects on their behaviour [32–34].The authors interpret these data as support for the optical pumping hypothesis of Leask [5], which notes that photosensitive molecules, like rhodopsin, are subject to magnetic influences which might lead to chemical effects. However, other experiments have shown that light is not necessary for manetoreception in bees, turtles or birds [13,14,35]. This rules out the dependence of magnetoreception on optical pumping. Tiny magnets attached near the measured region of magnetite concentration in honey bees (and far from the eyes) interfere with magnetic discrimination in choice experiments [11]. In addition, the nature of light-induced behavioral changes in the compass orientation response of *Drosophila* [34], the newt [36] and birds [14] varies greatly. Visual cues undoubtedly have profound

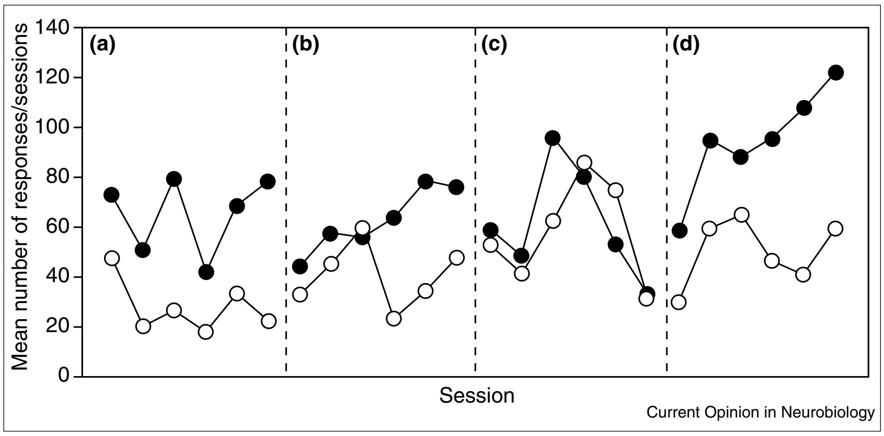
Figure 1



Current Opinion in Neurobiology

Critical advances in the evolution and understanding of magnetite-based magnetoreception. **(a)** Oldest reported magnetofossils from 4.0 billion-year-old carbonate blebs in the Martian meteorite ALH84001 [50••,51•,52•]; the oldest Earth magnetofossils are 2.1 billion years old. **(b)** Typical chains of biogenic magnetite from magnetotactic bacteria (courtesy H Vali). **(c)** Bullet-shaped magnetosomes in eukaryotic algae [56]. **(d)** Magnetosome chains from the frontal tissues of chinook salmon [19]. **(e)** Three- dimensional reconstruction of the candidate magnetite-based sensory cell in the trout [21••], imaged by confocal microscopy. A single optical slice that contains the magnetosome chain (arrowhead) is offset from the rest to show its placement within the cell. **(f)** Model of how a magnetosome chain could act to open a trans-membrane ion channel. The grey rectangle represents a magnetosome that is anchored via a cytoskeletal filament to a mechanically activated trans-membrane ion channel [24,26,28]. Torque from the magnetosome, if properly applied, could cause the transient opening of the channel and lead to membrane depolarization.

Figure 2



Current Opinion in Neurobiology

Impairment of learned magnetic discrimination by short-tailed stingrays (data from [40]). An attached magnet, moving with an animal, should not impair an induction-based sensory system, whereas it should disable any other receptor within its field of influence. Experiments were performed following the general magnetic training technique of Walker [57] for tuna, in which two magnetic stimuli are presented: one with the uniform background magnetic field; the other with the field altered by application of non-uniform gradients from a large coil system. Each point represents the mean number of responses per session made by the experimental animals in the presence of the reinforced stimulus (filled circles) and the non-reinforced stimulus (open circles). Panels **(a)** and **(b)** show the discrimination performance before and after the insertion of brass weights into the nasal cavities of the animals. Panel **(c)** shows impairment of discrimination by replacement of the brass weights by neodymium-iron-boron magnets of the same size as the brass weights. Panel **(d)** shows the recovery of discrimination after removal of the magnets.

effects on all aspects of behavior, including those influenced by magnetism. However, these cues do not need to act at the receptor level.

Electrical induction has also been proposed as the mechanism for magnetic compass orientation in elasmobranch fish [4,37], although this system would be inefficient in terrestrial animals and navigating sharks [38] without large structures [39]. Conditioning experiments suggest an adequate electrical sensitivity for a compass response, but observed behaviour in sharks and rays indicates electroreception to be primarily used for locating prey. As induction in the geomagnetic field generates unwanted noise for the electrical sense, a separate magnetic sense would enable elasmobranchs to filter out this unwanted noise, and concentrate on prey location. Recent experiments rule out electroreception as the basis of magnetoreception in elasmobranchs: magnets attached to rays impaired their performance in discrimination tasks (Figure 2). Furthermore, to achieve the magnetic sensitivity needed to explain migratory behavior and navigation [20,38] with these other sensory systems, elasmobranchs would require extremely long ampullary canals and birds would need extremely large photoreceptor structures. Neither of these has yet been demonstrated.

Experimental evidence for a ferromagnetic-based receptor

All magnetotactic microbes, both bacteria and eukaryotic algae, contain internal chains of either single-domain (SD) magnetite or greigite (Fe_3S_4) [41] that produce a magnetic moment large enough to rotate the cells passively into alignment with the geomagnetic field. A simple pulse-remagnetization experiment that turns north-seeking organisms into south-seekers, and *vice versa* [42] demonstrates that this behavior is ferromagnetic. Elongate SD magnetite crystals can only be magnetized parallel to their long axis, but in one of two polarities. A magnetic pulse applied antiparallel to the magnetization direction causes the moment to reverse direction, making a bacterium swim south instead of north. This is a unique property of ferromagnetic materials. The short time duration and moderate strength of this magnetic pulse can be applied without affecting any other physiological function. The controlled application of a weak DC-biasing field rules out other magnetic effects (such as induced electric fields and paramagnetism) as the mechanism.

Similar pulse-remagnetization experiments on bees and birds also affect animal behavior, a finding only compatible with the existence of SD ferromagnetic magnetoreceptors [13,32,33,43–45]. In birds, results show a clear effect of pulse treatment on directional choice in orientation experiments, although pulses were applied perpendicular, rather than antiparallel, to the background field. Hence, the results are not as easy to predict or interpret as those in microorganisms or bees.

Suggestions have been made that deposits of superparamagnetic (SPM) magnetite detected in some animals [24,46,47] may be involved in magnetoreception. These magnetite crystals are so small that the magnetic effects that normally pin the magnetic moment to the crystal are below thermal noise, thus allowing the moments to track the direction of the local magnetic field without moving the crystal. However, our early suggestion [24] that these small crystals might actually be the primary coupling agents between the magnetic field and membrane depolarization is probably wrong, as they are far less efficient at this than are the larger, more stably magnetized particles. Forces between adjacent magnetized particles vary as the inverse fourth power of distance, implying that evolutionary pressures noted above should drive them to employ the more energetic SD particles, as found in the candidate receptor cells in fish [12,21••]. Transmission electron microscopy images of SPM extracts in bees show them in ordered sheet-like arrays [46], clearly not free to deform or move, as suggested recently for SPM material in pigeon beaks [48]. In retrospect, our attempt to 'demagnetize' honeybees [49], which we interpreted as supporting a SPM receptor, probably failed because the alternating-field frequency used (60 Hz) caused the magnetosome chains to rotate rather than remagnetize as in the Kalmijn-Blakemore experiment [42]. Short magnetic pulses have a reversing effect on bees [13], indicating that their primary receptors are SD. SPM magnetite, however, will locally amplify the flux density of the local geomagnetic field, and could enhance the frequency response and sensitivity of nearby SD receptors [28]. Rough estimates for SD receptors indicate that the high sensitivity to small geomagnetic fluctuations displayed by bees [9] and migratory animals [20] can be achieved by the integration of intensity-dependent signals from only a few million receptor cells [25].

Neurophysiology of magnetite and magnetoreceptors

Although early work on the distribution of biogenic magnetite in birds and fish hinted at a role for the trigeminal nerve system in magnetoreception [16,17], Semm and Beason [20] were the first to obtain clear recordings of responses to weak magnetic stimuli. They found that single units in the superficial ophthalmic (SO) branch and ganglion cells of the trigeminal nerve (TN) system responded to changes in the intensity of the earth's magnetic field as small as 200 nT, or ~0.4% variation in background strength. They also showed that the firing rates of units increased as the logarithmic function of field intensity, and that units fired in phase with a weak sinusoidal magnetic stimulus at very low frequencies. Apparently, however, the units locked on to one phase of the wave cycle and not to its anti-phase. A similar observation was made by Walker *et al.* [12] who reported that units in the SO branch of the TN of rainbow trout responded to either the onsets or offsets of step changes in magnetic intensity, but not to both. These results point to a common locus of magnetic field detection in vertebrates.

If magnetite-containing cells are used in magnetoreception, it is reasonable to predict that they should be linked to magnetically responsive nerves. Nerve-tracing studies in the trout [12,21••] have used Di-I placed on the cut ends of the SO branch of the TN at the site where electrophysiological recordings of responses to magnetic field stimulation were made. The Di-I migrated in both anterograde and retrograde directions along myelinated and unmyelinated fibres in the TN. Posterior to the orbit, the SO branch joined other branches of the TN, terminating in cell bodies of the anterior ganglion. From the ganglion, labeled nerve tracts entered the anterior dorsal area of the medulla oblongata. Anterior to the orbit, the SO branch has rami that innervate the skin, surround the olfactory nerve and olfactory capsule, and that surround as well as penetrate the olfactory capsule. Fine branches of the SO also penetrated the olfactory lamellae from the top and the base. The top branches terminated in finer processes at the distal end of the olfactory lamellae. Diebel *et al.* [21••] then used the crystal and magnetic properties of SD magnetite to identify candidate magnetoreceptor cells in the nose despite the small size (<100 nm) and extreme rarity (<5 ppb by volume) of the magnetite crystals. Reflection of laser light off the crystal surfaces permitted detection of chains of magnetite crystals in a confocal laser-scanning microscope that were then imaged and uniquely identified as magnetite using atomic and magnetic force microscopy. The chains of magnetite crystals were 1 μm long (range 0.5 μm–1.5 μm) giving a magnetic to thermal energy ratio of ~4, which is appropriate for magnetoreception [25•].

The multi-lobed cells containing magnetite particles were 10–12 μm long and were consistently located near the basal lamina of the olfactory epithelium. The location of the magnetite crystals chains within each cell suggests that a mechanical linkage could transduce its movement in response to external magnetic fields into changes in the membrane potential of the cell. This may be achieved by opening mechanically-activated transmembrane ion channels, as depicted in Figure 1f, and the biophysical properties of such a system are well understood [24,26,28]. The way is thus open for detailed ultrastructural studies to determine how the magnetite chains are coupled to the cell and to search for afferent synaptic links to the SO branch of the TN.

Conclusions and future prospects

Magnetoreception may well have been among the first sensory systems to evolve, as suggested by the presence of magnetosomes and magnetosome chain structures in the 4.0 billion year old carbonate blebs of the Martian meteorite ALH84001 [50••,51•,52•]. Although this is nearly half a billion years older than the oldest microbial fossils on Earth, it suggests that this genetic ability was brought here from Mars via the process of panspermia [53•]. In terms of the evolutionary arguments presented above, the striking similarity in magnetosome structure and organization in bacteria, protists, and vertebrates, and the deep fossil record, supports the hypothesis that magnetite biomineralization system arose initially in the magnetotactic bacteria and was incorporated into eukaryotic cells through endosymbiosis; later, it may even have been used as a template to drive the widespread biomineralization events during the Cambrian explosion [54•]. Bertani *et al.* [55] have shown this year that the genome of *Magnetospirillum magnetotacticum* is only ~4.3 Mb in size, and the US Department of Energy has recently completed shotgun sequencing of both it and a *Magnetococcus* (MC-1); final assembly is now in progress. Understanding the genetic basis of magnetite biomineralization through these organisms will provide molecular tools for testing the hypothesis of common descent, and for testing magnetite's role in magnetoreception of all animal groups.

References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Bullock TH, Szabo T: **Introduction.** In *Electroreception*. Edited by Bullock TH, Heiligenberg W. New York: Wiley; 1986:1-12.

2. Kirschvink JL: **Magnetoreception: homing in on vertebrates.** *Nature* 1997, **390**:339-340.

3. Adair RK: **Constraints on biological effects of weak extremely-low frequency electromagnetic fields.** *Phys Rev* 1991, **43**:1039-1048.

4. Kalmijn AJ: **Biophysics of geomagnetic field detection.** *IEEE Trans Magn* 1981, **17**:1113-1124.

5. Leask MJM: **A physiochemical mechanism for magnetic field detection by migratory birds and homing pigeons.** *Nature* 1977, **267**:144.

6. Griffin DR: **The sensory basis of bird navigation.** *Q Rev Biol* 1944, **19**:15-31.

7. Lowenstam HA: **Magnetite in denticle capping in recent chitons (*Polyplacophora*).** *Bull Geol Soc Am* 1962, **73**:435-438.

8. Blakemore RP: **Magnetotactic bacteria.** *Science* 1975, **190**:377-379.

9. Walker MM, Bitterman ME: **Honeybees can be trained to respond to very small changes in geomagnetic field intensity.** *J Exp Biol* 1989, **145**:489-494.

10. Walker MM, Bitterman ME**: Conditioned responding to magnetic fields by honeybees.** *J Comp Phys* 1985, **157**:67-73.

11. Walker MM, Bitterman ME: **Attached magnets impair magnetic field discrimination by honeybees.** *J Exp Biol* 1989, **141**:447-451.

12. Walker MM, Diebel CE, Haugh CV, Pankhurst PM, Montgomery JC, Green CR: **Structure and function of the vertebrate magnetic sense.** *Nature* 1997, **390**:371-376.

13. Kirschvink JL, Kobayashi-Kirschvink A: **Is geomagnetic sensitivity real? Replication of the Walker-Bitterman conditioning experiment in honey bees.** *Am Zool* 1991, **31**:169-185.

14. Wiltschko R, Wiltschko W: *Magnetic Orientation in Animals*, vol 33. Berlin: Springer; 1995.

15. Gould JL, Kirschvink JL, Deffeyes KS: **Bees have magnetic remanence.** *Science* 1978, **201**:1026-1028.

16. Walcott C, Gould JL, Kirschvink JL: **Pigeons have magnets.** *Science* 1979, **205**:1027-1029.

17. Walker MM, Kirschvink JL, Chang SBR, Dizon AE: **A candidate magnetic sense organ in the Yellowfin Tuna *Thunnus albacares*.** *Science* 1984, **224**:751-753.

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

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

20. Semm P, Beason RC: **Responses to small magnetic variations by the trigeminal system of the bobolink.** *Brain Res Bull* 1990, **25**:735-740.

21. •• Diebel CE, Proksch R, Green CR, Nielson P, Walker MM**: Magnetite defines a magnetoreceptor.** *Nature* 2000, **406**:299-302.

Following up on previous work [12], the authors used confocal and magnetic force microscopy to demonstrate that the iron oxide crystals in cells near the terminus of the trigeminal neurons were SD magnetite crystals. They also made a preliminary three-dimensional reconstruction from optical sections of a candidate receptor cell as shown here in Figure 1e.

22. Lohmann KJ, Willows AOD, Pinter RB: **An identifiable molluscan neuron responds to changes in earth–strength magnetic-fields.** *J Exp Biol* 1991, **161**:1-24.

23. Wang JH, Cain SD, Lohmann KJ: **The identification and characterization of magnetically sensitive neurons in the marine mollusc *Tritonia diomedea*.** *Am Zool* 1999, **39**:252.

24. Kirschvink JL, Gould JL: **Biogenic magnetite as a basis for magnetic field sensitivity in animals.** *Biosystems* 1981, **13**:181-201.

25. Kirschvink JL, Walker MM: **Particle-size considerations for magnetite-based magnetoreceptors.** In *Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism*. Edited by Kirschvink JL, Jones DS, McFadden B. New York: Plenum Press; 1985:243-254.

26. Kirschvink JL: **Constraints on biological effects of weak extremely low-frequency electromagnetic fields comment.** *Phys Rev* 1992, **46**:2178-2184.

27. Kirschvink JL: **Microwave absorption by magnetite: a possible mechanism for coupling nonthermal levels of radiation to biological systems.** *Bioelectromagnetics* 1996, **17**:187-194.

28. Kirschvink JL, Padmanabha S, Boyce CK, Oglesby J: **Measurement of the threshold sensitivity of honeybees to weak, extremely low frequency magnetic fields.** *J Exp Biol* 1997, **200**:1363-1368.

29. Block SM: **Biophysical principles of sensory transduction.** In *Sensory Transduction*. Edited by Corey DP, Roper SD. New York: The Rockefeller University Press; 1992:1-18.

30. Lohmann KJ, Johnsen S: **The neurobiology of magnetoreception in vertebrate animals.** *Trends Neurosci* 2000, **23**:153-159.

31. Gould SJ, Vrba ES: **Exaptation — a missing term in the science of form.** *Palaeobiology* 1982, **8**:4-15.

32. Wiltschko W, Wiltschko R: **Migratory orientation of European robins is affected by the wavelength of light as well as by a magnetic pulse.** *J Comp Physiol* 1995, **177**:363-369.

33. Munro U, Munro JA, Phillips JB, Wiltschko W: **Effect of wavelength of light and pulse magnetization on different magnetoreception systems in a migratory bird.** *Aust J Zool* 1997, **45**:189-198.

34. Phillips JB, Sayeed O: **Wavelength-dependent effects of light on magnetic compass orientation in *Drosophila melanogaster*.** *J Comp Physiol* 1993, **172**:303-308.

35. Lohman K, Lohman C: **Acquisition of magnetic directional preference in hatchling loggerhead sea turtles.** *J Exp Biol* 1994, **190**:1-8.

36. Phillips JB, Borland SC: **Use of a specialized magnetoreception system for homing by the eastern red-spotted newt *Notophthalmus viridescens*.** *J Exp Biol* 1994, **188**:275-291.

37. Paulin MG: **Electroreception and the compass sense of sharks.** *J Theor Biol* 1995, **174**:325-339.

38. Klimley AP: **Highly directional swimming by scalloped hammerhead sharks, sphyrna-lewini, and subsurface irradiance, temperature, bathymetry, and geomagnetic-field.** *Mar Biol* 1993, **117**:1-22.

39. Rosenblum B, Jungerman RL, Longfellow L: **Limits to induction-based magnetoreception.** In *Magnetite Biomineralization and Magnetoreception in Organisms: A New Biomagnetism*. Edited by Kirschvink JL, Jones DS, MacFadden BJ. New York: Plenum Press; 1985:223-232.

40. Walker MM, Diebel CE, Kirschvink JL: **Detection and use of the earth's magnetic field by aquatic vertebrates.** In *Proc SPAE Conference, 2000*; 2001:in press.

41. Schuler D, Frankel RB: **Bacterial magnetosomes: microbiology, biomineralization and biotechnological applications.** *Appl Microbiol Biotechnol* 1999, **52**:464-473.

42. Kalmijn AJ, Blakemore RP: **The magnetic behavior of mud bacteria.** In *Animal Migration, Navigation and Homing*. Edited by Schmidt-Koenig K, Keeton WT. Berlin: Springer-Verlag; 1978:354-355.

43. Beason RC, Wiltschko R, Wiltschko W: **Pigeon homing: effects of magnetic pulses on initial orientation.** *Auk* 1997, **114**:405-415.

44. Munro U, Munro JA, Phillips JB, Wiltschko R, Wiltschko W: **Evidence for a magnetite-based navigational map in birds.** *Naturwissenschaften* 1997, **84**:26-28.

45. Wiltschko W, Munro U, Beason RC, Ford H, Wiltschko R: **A magnetic pulse leads to a temporary deflection in the orientation of migratory birds.** *Experientia* 1994, **50**:697-700.

46. Kirschvink JL, Brassart J, Nesson MH: *Magnetite-Based Biological Effects in Animals*, vol TR-111901. Edited by Rafferty C. Palo Alto, CA: Electrical Power Research Institute; 1998.

47. Hanzlik M, Heunemann C, Holtkamp-Rotzler E, Winklhofer M, Petersen N, Fleissner G: **Superparamagnetic magnetite in the upper beak tissue of homing pigeons.** *Biometals* 2000, **13**:325-331.

48. Shcherbakov VP, Winklhofer M: **The osmotic magnetometer: a new model for magnetite-based magnetoreceptors in animals.** *Euro Biophys J* 1999, **28**:380-392.

49. Gould JL, Kirschvink JL, Deffeyes KS, Brines ML**: Orientation of demagnetized bees.** *J Exp Biol* 1980, **86**:1-9.

50. •• Thomas-Keprta KL, Bazylinski DA, Kirschvink JL, Clemett SJ, McKay DS, Wentworth SJ, Vali H, Gibson EK, Jr, Romanek CS: **Elongated prismatic magnetite crystals in ALH84001 carbonate globules: potential martian magnetofossils.** *Geochim Cosmochim Acta* 2000, **64**:4049-4081.

See annotation [52•].

51. • Thomas-Keprta KL, Clemett SJ, Bazylinski DA, Kirschvink JL,McKay DS, SJ W, Vali H, Gibson EKJ, McKay MF, Romanek CS: **Truncated hexa-octahedral magnetite crystals in ALH84001: presumptive biosignatures.** *Proc Natl Acad Sci USA* 2001, **98**:2164-2169.

See annotation [52•].

52. • Friedmann IE, Wierzchos J, Ascaso C, Winklhofer M: **Chains of magnetite crystals in the meteorite ALH84001: evidence of biological origin.** *Proc Natl Acad Sci USA* 2001, **98**:2176-2181.

These three papers [50••,51•,52•] report the presence of bacterial magnetosomes – indistinguishable from those produced in living magnetic bacteria – in carbonate blebs within the ALH 84001 Martian meteorite. The carbonate blebs are 4.0 billion years old. If these are biological in origin, not only does magnetite biomineralization provide the oldest evidence of life anywhere (500 million years older than the oldest fossils on Earth), but it implies that magnetoreception is truly the ‘primal’ sensory system. But this debate will surely continue.

53. • Weiss BP, Kirschvink JL, Baudenbacher FJ, Vali H, Peters NT, MacDonald FA, Wikswo JP: **A low temperature transfer of ALH84001 from Mars to Earth.** *Science* 2000, **290**:791-795.

If magnetotactic bacteria did evolve first on Mars (see [52•]), this paper demonstrates that they could have traveled to Earth on meteorites without being killed in the process (e.g. panspermia).

54. • Kirschvink JL, Hagadorn JW: **A grand unified theory of biomineralization.** In *The Biomineralization of Nano- and Micro-structures*. Edited by Bäuerlein E, Berlin: Wiley-VCH Verlag GmbH; 2000:139-150.

This paper argues that all matrix-mediated biomineral systems in higher animals could have evolved from the magnetite system during the Cambrian explosion.

55. Bertani LE, Weiko J, Phillips KV, Gray RF, Kirschvink JL: **Physical and genetic characterization of the genome of *Magnetospirillum magnetotacticum*, strain MS-1.** *Gene* 2001, **264**:257-263.

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

57. Walker MM: **Learned magnetic field discrimination in yellowfin tuna, *Thunnus albacares.*** *J Comp Physiol* 1984, **155**:673-679.