Q&A

ANIMAL BEHAVIOUR

Magnetic-field perception

Kenneth J. Lohmann

The ability to perceive Earth's magnetic field, which at one time was dismissed as a physical impossibility, is now known to exist in diverse animals. The receptors for the magnetic sense remain elusive. But it seems that at least two underlying mechanisms exist — sometimes in the same organism.

What is the evidence that animals perceive magnetic fields?

The evidence for magnetoreception is mainly behavioural. The most common approach has been to alter the magnetic field around animals and watch for corresponding changes in orientation or navigation behaviour. Usually this has been done in the lab, where carefully calibrated magnetic fields can be produced. But experiments have also been done in the field on unrestrained animals that are migrating or homing. For example, standard bar magnets produce much stronger magnetic fields than Earth's naturally occurring field, and placing these on homing pigeons and sea turtles disrupts navigation under some conditions. Neurobiological techniques have also provided evidence; in several cases, electrophysiological recordings and activity-dependent gene expression have revealed neurons, nerves and brain areas that show altered electrical activity in response to changes in the ambient field.

What information can animals extract from Earth's field?

Two types of information are potentially available. The simplest is directional information, which enables an animal to maintain a consistent heading, for example towards the north or south. Animals with this ability are said to have a 'magnetic compass' (Fig. 1). By contrast, at least a few animals can also derive positional information from Earth's field; in other words, they can use magnetic cues to assess their approximate geographical location, or where they are located relative to a goal. Animals that derive positional information from the field are said to have a 'magnetic map' (Fig. 1). This term is used as a convenient shorthand, and does not imply that the map is necessarily detailed or organized in the same way as a human map.

Figure 1 | Animal magnetism. Diverse species have magnetic compasses, including (clockwise from top left) the European robin, the loggerhead sea turtle, the brown bat, the Caribbean spiny lobster and the red-spotted newt. A few, including turtles, lobsters and newts, also have magnetic maps.

E. OLSEN/FLPA; T. PUSSER/NATUREPL.COM; B. MANSELL/NATUREPL.COM; N. PROBST/PHOTOLIBRARY.COM; T. PUSSER/NATUREPL.COM

How can the geomagnetic field be used as a map?

Several geomagnetic parameters, such as field intensity (strength) and the inclination of field lines, vary predictably across Earth's surface in ways that make them suitable for position-finding (Fig. 2). Sea turtles, lobsters and a few other animals can perceive these elements. By learning the features of the field that exists at a particular destination, as well as the surrounding magnetic topography, these animals can use the geomagnetic field to navigate towards specific locations. In effect, they have a low-resolution biological equivalent of the Global Positioning System, but one that is based on Earth's field instead of satellite signals.

Is magnetoreception restricted to migratory species?

No. Although much magnetoreception research has focused on long-distance migrants, magnetic sensitivity is phylogenetically widespread; it exists in all major groups of vertebrate animals, as well as in some molluscs, crustaceans and insects. The list includes groups such as flies, chickens and mole rats, none of which migrate. Some evidence even suggests that cattle align themselves with Earth's field, although why is not known. But even though diverse animals evidently perceive magnetic fields, locating the receptors that underlie this ability has proven to be quite difficult.

Why is it so challenging to identify magnetoreceptors?

Magnetic fields are unlike other sensory stimuli in that they pass freely through biological tissue. Whereas receptors for senses such as olfaction and vision must make contact with the external environment, magnetoreceptors might be located almost anywhere inside an animal's body. In addition, large accessory structures for focusing and manipulating the field — the analogues of eardrums and lenses — are unlikely to exist because few materials of biological origin affect magnetic fields. Magnetoreceptors might also be tiny and dispersed throughout a large volume of tissue, or the transduction process might occur as a set of chemical reactions, which means that no obvious organ or structure devoted to this sensory system necessarily exists. If you imagine trying to locate a small number of submicroscopic, possibly intracellular, structures scattered in unknown places throughout an animal's body, you can begin to appreciate the challenge.

How do animals detect magnetic fields?

No one knows for certain, although numerous ideas have been proposed. At present, the three leading hypotheses invoke electromagnetic induction, a system that involves magnetite, and chemical magnetoreception.

How might electromagnetic induction operate?

Imagine a small bar composed of an electrically conductive material. If the bar moves through a magnetic field in any direction other than parallel to the field lines, positively and negatively charged particles migrate to opposite sides of the bar. This results in a constant voltage that depends on the speed and direction of the bar's motion relative to the magnetic field. If the bar is immersed in a conductive medium that is stationary relative to the field, an electric circuit is formed and current flows through the medium and the bar. This same basic principle of electromagnetic induction might explain how elasmobranch fish (sharks, skates and rays) perceive magnetism. The bodies of these animals are conductive, and the fish have highly sensitive electroreceptors with which they might detect the voltage drop of the induced current that arises as they swim through Earth's field. But whether these fish actually perceive magnetic fields in this way is not known.

Could a similar induction mechanism work for lots of animals?

Probably not. Such a mechanism requires highly sensitive electroreceptors, which most species lack. In addition, sea water is strongly conductive, but air is not. Thus, birds and other terrestrial animals cannot accomplish magnetoreception in the way that has been proposed for electrosensitive marine fish. Two mechanisms seem more likely for other animals: magnetite and chemical magnetoreception.

What is the magnetite hypothesis?

The hypothesis is that crystals of the magnetic mineral magnetite (Fe_3O_4) provide the physical basis for magnetoreception. The idea was inspired in part by the discovery that some bacteria produce magnetite crystals; as a result, the bacteria are physically rotated into alignment with geomagnetic field lines and can move along them. Magnetite has been detected in several magnetically sensitive animals, but particularly detailed studies have been done with salmon and rainbow trout. In trout, magnetite exists in a region of the nose near a nerve that responds to magnetic stimuli. Magnetite isolated from fish and other animals has mainly been in the form of single-domain crystals closely resembling those in bacteria. Single-domain crystals are tiny (about 50 nanometres in diameter), permanently magnetized magnets that twist into alignment with Earth's magnetic field if allowed to rotate freely. Such crystals might provide the physical basis for magnetic sensitivity.

How might this work?

The simplest possibility is that magnetite crystals exert torque or pressure on secondary receptors (such as stretch receptors, hair cells or mechanoreceptors) as the particles attempt to align with the geomagnetic field. Alternatively, the rotation of intracellular magnetite crystals might open ion channels in nerve cells directly if, for example, cytoskeletal filaments connect the crystals to the channels. Opening these channels allows ions to flow across nerve-cell membranes and produce electrical signals used in communication by the brain and nervous system.

Are all magnetite crystals in animals identical?

No. In some animals they are smaller than single-domain size and have different magnetic properties. These 'superparamagnetic' crystals, unlike single-domain crystals, do not have a permanent magnetic moment. Instead, the magnetic axis of a superparamagnetic crystal tracks the axis of the ambient field, even though the crystal itself remains stationary. In Earth-strength magnetic fields, such crystals can generate fields that are strong enough to attract or repel other nearby crystals, a process that might be sufficient to deform a matrix containing a cluster of such crystals (Fig. 3, overleaf). In principle, the nervous system might be able to detect the expansion or contraction of either a single cluster or an array of clusters, providing a possible means of detecting the direction of the field, its intensity, or both. In pigeons, arrays of superparamagnetic magnetite crystals have been detected in the upper beak, where clusters of these crystals are located inside nerve terminals and along the cell membrane. They seem to be well situated for transducing geomagnetic stimuli to the nervous system.

What is chemical magnetoreception?

The principle here is that magnetoreception occurs through unusual biochemical reactions that are influenced by Earth's magnetic field. The proposed reactions involve pairs of free radicals as fleeting intermediates, so the idea is also known as the radical-pairs hypothesis.

And how might it work?

The details are complex, but the putative process begins with an electron transfer from a donor molecule to an acceptor molecule.

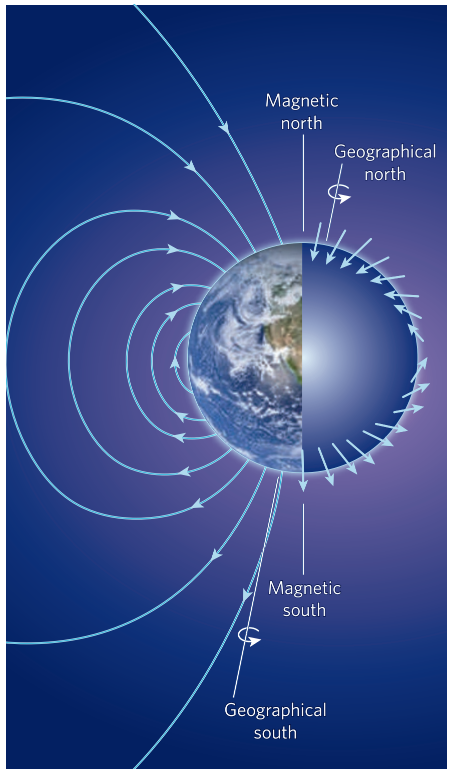

Figure 2 | Earth's magnetic field. Field lines emerge from the Southern Hemisphere, wrap around the globe, and re-enter Earth in the Northern Hemisphere. Field lines are parallel to Earth's surface at the geomagnetic equator, but become progressively steeper as an animal migrates towards the poles. Field intensity also varies predictably across Earth's surface. Thus, different geographical regions often have unique 'magnetic signatures' consisting of specific combinations of field-line inclination and intensity, as indicated by the angle and length of the arrows on the right. Animals that have magnetic maps can exploit such information when navigating to particular areas. (Reproduced from T. Alerstam *Nature* 421, 27–28; 2003.)

This leaves each molecule with an unpaired electron. For a brief instant, the spin of each electron precesses at a rate determined by its unique local magnetic environment, which depends on the combined magnetic fields generated by the spins and orbital motions of unpaired electrons and magnetic nuclei, plus the orientation and strength of any external field. Back-transfer of the electron can occur only if the spins are oppositely aligned. Alignment depends in part on the difference in precession rates that the two spins undergo. Because the external field can influence the precession rate, it can, under the correct set of conditions, influence reaction rates or the chemical products that ultimately result.

Are magnetically sensitive chemical reactions known to exist?

Yes. It has been known since the 1970s that certain chemical reactions involving free radicals are influenced by applied magnetic fields, so the idea is not merely hypothetical. But the reactions that are best understood require fields that are much stronger than Earth's field. An active area of 'spin chemistry' now involves efforts to determine whether fields of geomagnetic strength might exert an effect — and, if so, how.

Where might chemical magnetoreceptors be located?

Quite possibly in the visual system. Many of the best-known radical-pair reactions begin with electron transfers that are induced by the absorption of light. This has led to the suggestion that chemical magnetoreceptors, if they exist, might also be photoreceptors. The connection with photoexcitation has also led to interest in blue-light-sensitive photoreceptive proteins known as cryptochromes. Cryptochromes are attractive candidates for magnetoreceptors because they exist in diverse animals and have a chromophore that forms radical pairs after photoexcitation.

What evidence is there that cryptochromes are involved?

Cryptochromes seem to have the required chemical properties and, in migratory birds, they are concentrated in retinal cells that show high levels of neural activity when birds orient magnetically. Moreover, these retinal cells connect with a forebrain region known as cluster N, and ablating cluster N disrupts magnetic orientation without disrupting other navigation behaviour. The most direct evidence for cryptochrome involvement, however, comes from experiments with the fruitfly *Drosophila*, in which the flies were trained to enter one arm of a simple maze on the basis of magnetic-field conditions. Mutant flies lacking genes for cryptochrome were unable to perform this task, but magnetic sensitivity was restored when cryptochrome genes were inserted into the flies.

What would it be like to perceive magnetic fields visually?

One idea is that, as magnetically sensitive animals look out at the world, they see superimposed on the normal (for a human) visual field an additional signal consisting of a pattern of lights or colours, which changes depending on the direction the animal faces. If so, the animal might learn to associate a particular visual signal with a particular magnetic direction.

Are the magnetite and chemical-magnetoreception hypotheses mutually exclusive?

No. Many researchers think that birds have a compass based on chemical magnetoreception in the eye and a map based on magnetite receptors in the beak. According to this idea, two mechanisms are needed because each detects a different element of the field. The compass detects field direction, whereas the map detects field strength, inclination or both.

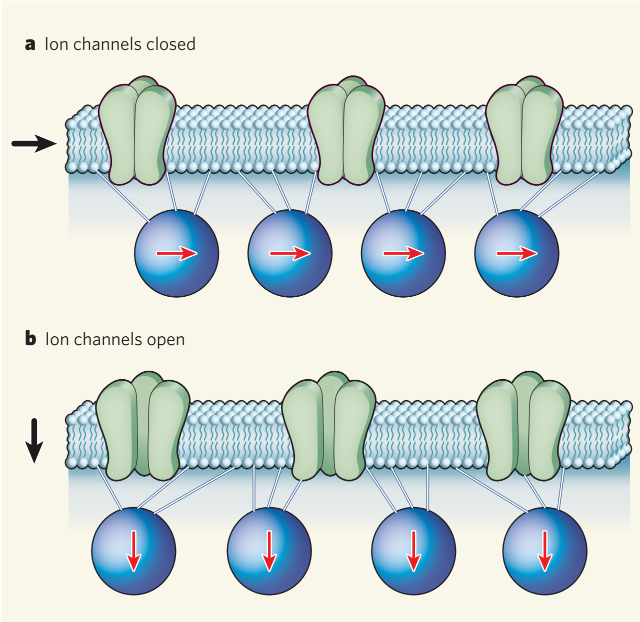

Figure 3 | Hypothetical model of magnetite-based magnetoreception. The conceptual principle involves interacting clusters of superparamagnetic crystals (blue balls) anchored to neuronal membranes by cytoskeletal filaments. Depending on the orientation of the external field, the clusters either attract or repel each other, deforming the membrane and opening or closing ion channels (green). **a,** When the external field (black arrow) is parallel to the cell membrane, the fields in each crystal (red arrows) align in such a way that adjacent clusters attract one another like a row of bar magnets aligned end to end, compressing the membrane slightly and closing ion channels. **b,** By contrast, a 90° change in the orientation of the external field causes adjacent clusters to behave like a row of bar magnets aligned side by side; thus, they repel one another, stretch the membrane and open ion channels. (Modified from A. F. Davila *et al. Phys. Chem. Earth* 28, 647–652; 2003.)

Does everyone agree with this 'dual receptor' hypothesis?

No. Some researchers argue that all magnetoreception is based on magnetite, and that the putative connection between cryptochromes, the visual system and magnetoreception is illusory. According to this view, cryptochromes and other visual pigments function in maintaining biological rhythms and informing birds or other animals when conditions are right for travel, but photopigments are not actually involved in detecting magnetic fields. Impairing or eliminating cryptochrome function may disrupt navigation behaviour, but only through indirect means, such as by disturbing normal activity rhythms or confusing the animal about whether it is the right time to migrate.

Is this viewpoint reasonable?

It depends on who you ask. Opinions differ.

So where do things stand?

Considerable progress has been made, and a few candidate magnetoreceptors have now been identified. But investigators have not yet successfully delineated, on a physiological level, the basic events that presumably occur; there has been no clear demonstration of a stimulus eliciting an electrical response in a receptor, for example. In the absence of such findings, all the proposed mechanisms must be considered hypothetical. This situation seems unlikely to change until a way is found to identify primary magnetoreceptors unequivocally — or to confirm the function of the putative ones — through some combination of electrophysiological, neuroanatomical and other techniques.

Is there a prospect of further progress?

Yes, but new techniques and systems might be needed to pave the way. Magnetoreception research began with behavioural studies on relatively large migratory animals, but these are not necessarily the best systems for investigating transduction processes. A promising development is that three model organisms (*Drosophila*, zebrafish and the neurobiological model mollusc *Tritonia*) are now known to respond to magnetic stimuli. Regardless of the system used, the solution to the magnetoreception mystery will almost certainly come from a fascinating interplay of biology, chemistry and physics. ■

Kenneth J. Lohmann is in the Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599, USA.
e-mail: klohmann@email.unc.edu

FURTHER READING

Gegear, R. J., Casselman, A., Waddell, S. & Reppert, S. M. Cryptochrome mediates light-dependent magnetosensitivity in *Drosophila*. *Nature* **454,** 1014–1018 (2008).
Johnsen, S. & Lohmann, K. J. Magnetoreception in animals. *Phys. Today* **61** (3), 29–35 (2008).
Kirschvink, J. L., Winklhofer, M. & Walker, M. M. Biophysics of magnetic orientation: strengthening the interface between theory and experimental design. *J. R. Soc. Interface* **7,** S179–S191 (2010).
Lohmann, K. J., Lohmann, C. M. F. & Putman, N. F. Magnetic maps in animals: nature's GPS. *J. Exp. Biol.* **210,** 3697–3705 (2007).
Ritz, T., Ahmad, M., Mouritsen, H., Wiltschko, R. & Wiltschko, W. Photoreceptor-based magnetoreception: optimal design of receptor molecules, cells, and neuronal processing. *J. R. Soc. Interface* **7,** S135–S146 (2010).
Rodgers, C. T. & Hore, P. J. Chemical magnetoreception in birds: the radical pair mechanism. *Proc. Natl Acad. Sci. USA* **106,** 353–360 (2009).
Wiltschko, W. & Wiltschko, R. Magnetic orientation and magnetoreception in birds and other animals. *J. Comp. Physiol. A* **191,** 675–693 (2005).