

Magnetoreception in animals

Sönke Johnsen and Kenneth J. Lohmann

Determining how animals orient themselves using Earth's magnetic field can be even more difficult than finding a needle in a haystack. It is like finding a needle in a stack of needles.

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Like the theory of plate tectonics, the idea that animals can detect Earth's magnetic field has traveled the path from ridicule to well-established fact in little more than one generation. Dozens of experiments have now shown that diverse animal species, ranging from bees to salamanders to sea turtles to birds, have internal compasses. Some species use their compasses to navigate entire oceans, others to find better mud just a few inches away. Certain migratory species even appear to use the geographic variations in the strength and inclination of Earth's field to determine their position. But how animals sense magnetic fields remains a hotly contested topic. Whereas the physical basis of nearly all other senses has been determined, and a magnetoreception mechanism has been identified in bacteria, no one knows with certainty how any animal perceives magnetic fields. Finding this mechanism is thus the current grand challenge of sensory biology.

The problem is difficult for several reasons. First, humans do not appear to have the ability to sense magnetic fields. Whereas most nonhuman senses, such as polarization detection and UV vision, are relatively straightforward extensions of human abilities, magnetoreception is not. As a result, neither intuitive understanding nor the medical literature on human senses provides much guidance. Another complicating factor is that biological tissue is essentially transparent to magnetic fields, which means that magnetoreceptors, unlike most other sensory receptors, need not be located on an animal's surface and might instead be anywhere in the body. That consideration transforms a routine two-dimensional visual inspection into a three-dimensional search requiring advanced imaging techniques. Another impediment is that large accessory structures for focusing and otherwise manipulating the field—the analogs of eardrums and lenses—are unlikely to exist because few materials of biological origin affect magnetic fields. Indeed, magnetoreception might be accomplished by a small number of microscopic, possibly intracellular structures scattered throughout the body, with no obvious structure devoted to magnetoreception. Finally, the weakness of the interaction between Earth's field and the magnetic moments of electrons and atoms, roughly one five-millionth of the thermal energy kT at body temperature, makes it difficult to even suggest a feasible mechanism.

The weakness of the field does provide one major advantage to researchers: It greatly limits the list of possible physical detection mechanisms. Any suitable mechanism

would presumably have to involve a very sensitive detector, amplification of magnetic interactions, or isolation from the thermal bath. Interestingly, the three main mechanisms that have so far been proposed—electromagnetic induction, ferrimagnetism, and chemical reactions involving pairs of radicals—are each based on one of those designs. The electromagnetic induction hypothesis, for example, is based on the extremely sensitive electroreceptive abilities of some marine species. The various hypotheses involving magnetite or other ferrimagnetic materials are based on the powerful interaction of such materials with magnetic fields. Finally, the radical-pair mechanism relies on the relatively efficient isolation of electron and nuclear spins from other degrees of freedom.

Different animals may detect magnetic fields in different ways, and behavioral experiments and microscopic examinations of possible magnetoreceptors have both yielded results that are consistent with all three mechanisms. Nevertheless, a magnetoreceptive organ has not yet been identified with certainty in any animal. In this article we discuss the physics of the three main mechanisms that have been proposed and highlight some of the critical evidence in support of each.

Electromagnetic induction

The Lorentz force causes a conducting rod moving through a magnetic field to develop a nonuniform charge distribution. If the rod is immersed in a conductive medium that is stationary relative to the field, an electrical circuit is formed. As far back as 1832, Michael Faraday noted that ocean currents should generate electric fields as they move through Earth's magnetic field. Indeed, some modern profiling systems that detect and map ocean currents are based on that principle.

Electroreception is relatively common and found in animals ranging from aquarium fish to duck-billed platypuses. Due to the weakness of Earth's magnetic field, however, the electromotive force induced in an animal moving at a realistic speed can be detected only by a highly sensitive electroreceptive system. In 1974, Adrianus Kalmijn suggested that sharks and their close cousins, rays, possess such a system. Those fish, collectively known as elasmobranchs, possess several hundred long canals that begin at tiny pores in the skin and end blindly inside the body (figure 1a). The canals, which feature exceptionally resistive walls and an interior filled with a highly conductive "jelly," essentially function as electrical cables. At the ends of the canals are the ampullae of

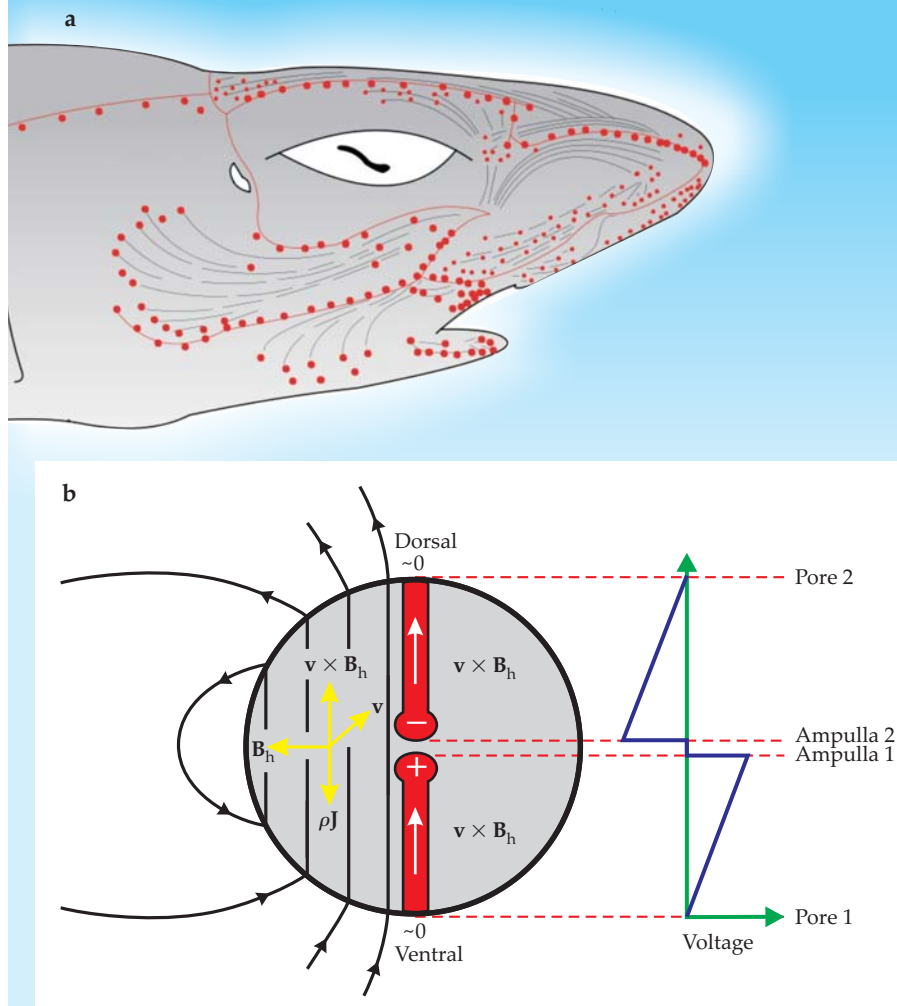


Figure 1. Inductive magnetoreception. (a) Side view of a shark's head, showing the ampullae of Lorenzini electroreceptors (red dots) and jelly-filled conductive canals (gray lines). The red lines are so-called lateral lines, used to detect vibrations in the surrounding water. (Image courtesy of Chris Huh.) (b) Schematic showing two ampullae with their canals. As the shark swims east and into the page with a velocity $\mathbf{v}$, its movement across the horizontal component of Earth's field, $\mathbf{B}_h$, causes a vertical electromotive force of magnitude vB_h . Because the shark's body and especially its skin are highly resistive, the voltage drop due to the current density ρJ results in no potential difference between the dorsal and ventral surfaces of the animal. The high conductivity of the canals, however, results in a large voltage drop across the ampullae. The thick black lines illustrate the electric field surrounding and permeating the shark. (Adapted from A. Kalmijn, *IEEE Trans. Magn.* **17**, 1113, 1981.)

Lorenzini—collections of cells that are extremely sensitive to small changes in voltage. Because the canals are highly conductive, almost all the induced voltage drop occurs at the ampullae (figure 1b). The ampullae's exact detection threshold has been debated, but a conservative estimate is $2 \mu\text{V/m}$, the field that would be produced by a 1.5-V battery with one electrode in New York Harbor and the other off Cape Hatteras, North Carolina, 750 km south! Given that extraordinary sensitivity, magnetoreception using induction is theoretically possible. Depending on its compass direction, a shark or ray moving horizontally through the ocean at 1 m/s (about 2 miles per hour) could generate a voltage gradient at the receptor as high as $25 \mu\text{V/m}$, well above the detection threshold.

In the several decades since the hypothesis was first proposed, however, several findings have emerged that compli-

cate matters. First, although they are exquisitely sensitive to changes in voltage, the electroreceptors of elasmobranchs were found to be incapable of detecting DC voltages. In addition, ocean currents are also conductors moving through Earth's magnetic field and thus create electric fields of their own. Michael Paulin addressed both problems in 1995 by suggesting that sharks and rays might pay attention only to the oscillating electric fields that arise as their heads sway rhythmically back and forth during swimming. In addition to creating AC voltages that the animals can detect, the head motion might function as a high-pass filter, removing irrelevant stimuli associated with ocean currents.

As one might guess, sharks (and even rays) are not ideal experimental animals, and the evidence for their magnetic sense is not as complete as for that in many other species. The few experiments that have been done mostly involved training captive animals to respond to the presence of local magnetic field gradients generated by an electromagnet. Given their extremely sensitive electroreception, however, it is unclear whether the animals responded to the magnetic field or to the electric fields induced as the magnet was turned on and off. In addition, it has never been demonstrated that electromagnetic induction is responsible for any of the observed magnetic behavior. In a 2001 experiment by Michael Walker, rays lost their ability to detect magnetic field gradients when small magnets (but not nonmagnetic brass bars) were inserted into their nasal cavities. Since a magnet that moves with the detector should not affect an induction-based system, Walker and his colleagues interpreted the results to mean that induction was not involved. But because the bodies of rays are flexible, the possibility remains that the magnets moved slightly relative to the electroreceptors and thus affected an induction-based system.

It is also possible that freshwater and terrestrial animals have induction-based mechanisms based on internal conducting rods or loops such as neural circuits. However, electromagnetic induction appears unlikely to be a widespread mechanism for magnetoreception because only elasmobranchs are known to have the extreme electrical sensitivity required. Most animals with electroreceptors have electric thresholds two to five orders of magnitude higher—too high for magnetoreception. For example, the electric fish *Eigenmannia* (glass knifefish), a relatively electrosensitive



Figure 2. Bacterial magnetoreceptors. Transmission electron micrograph of the bacterium *Magnetospirillum magnetotacticum* showing the chain of magnetosomes inside the cell. The magnetite crystal incorporated in each magnetosome is about 42 nm long. (Image courtesy of Dennis Bazylinski.)

animal, would need to swim at 400 mph (nearly 180 m/s) to detect Earth's field using induction.

Ferrimagnetism

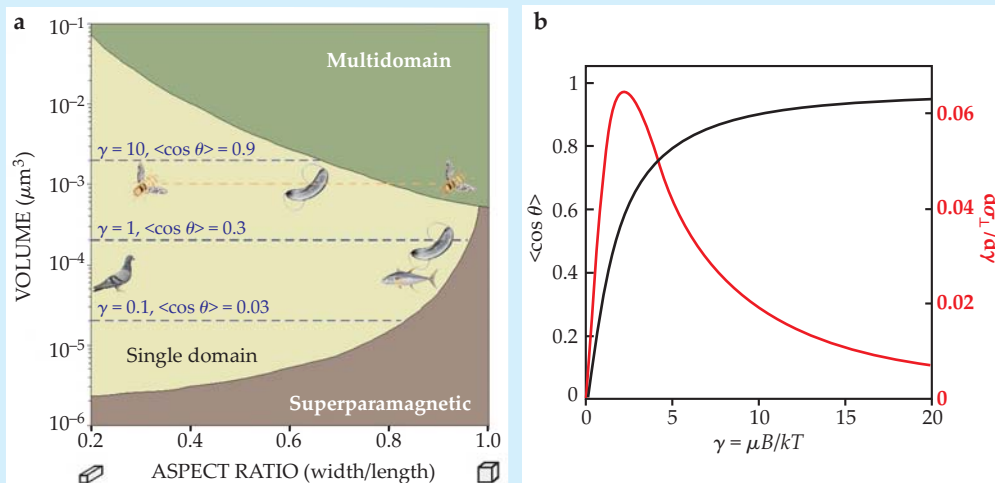
The only conclusively demonstrated magnetoreceptors are found in various phytoplankton and bacteria, which contain chains of crystals of ferrimagnetic minerals, either magnetite (Fe_3O_4) or greigite (Fe_3S_4), as shown in figure 2 and on the cover. The torque on the chain is so large that it rotates the entire organism to align with Earth's field. The field generally has a vertical component, and some of those organisms use magnetoreception to sense what direction is "down" and to move toward the deeper, less oxygenated mud they prefer. The 1963 discovery by Salvatore Bellini of magnetotaxis

in certain bacteria, followed by Richard Blakemore's 1975 description of the crystals, led to the detection of magnetite in a diverse array of magnetoreceptive species, including honeybees, birds, salmon, and sea turtles.

Ferromagnetic and ferrimagnetic minerals are natural choices for a compass mechanism, due to their powerful interaction with magnetic fields caused by spontaneous ordering of electron spins. Certain compounds of ferromagnetic elements, including magnetite, maghemite (Fe_2O_3), and greigite, are ferrimagnetic, meaning that although neighboring spins are antiparallel, the material still has a net moment because the moments in one direction are larger than those in the other. In both ferro- and ferrimagnetic minerals, the minimization of energy that comes from spin alignment is superseded at larger distances by other contributions to the total energy primarily magnetostatic energy. Thus larger volumes of those minerals are broken up into clearly defined domains on the order of 0.1–1 μm in diameter, each of which has a powerful magnetic moment in the absence of an external field. A single cuboidal domain 60 nm on a side has an interaction with Earth's field roughly equal to kT .

In the presence of moderately strong external fields, energetically favorable domains expand at the expense of neighboring domains, and the material as a whole becomes a magnet. Lacking a source for such fields, however, animals' internal compass needles are limited to their minerals' original domain size. Particles larger than the typical domain will develop multiple domains with moments in different directions (figure 3a). Particles smaller than a certain size (about 30 nm for magnetite, depending on the aspect ratio) have their moments randomized by thermal energy, even though the local spins are still aligned. In the single-domain range, the magnetic interaction μB , where μ is the magnetic moment of the particle and B is Earth's field strength, must be about six times greater than kT ; otherwise even a tethered compass will be tumbled too much by thermal interactions

Figure 3. Magnetite properties. (a) The behavior of magnetite crystals depends on their volume and aspect ratio. Large particles separate into multiple domains, while small particles are superparamagnetic, their moments tumbled by thermal fluctuations. In the yellow region, crystals are single domain. The dashed blue lines show three different values of the ratio γ of the magnetic energy μB to the thermal energy kT , and the associated average cosine of the angle θ between Earth's field and the crystal as it is buffeted by thermal agitation. The average cosine is given by the Langevin function, $\langle \cos \theta \rangle = \coth(\gamma) - 1/\gamma$. The animal symbols indicate the geometric parameters of the crystals found within them. (b) Alignment of the crystal (black) requires the magnetic coupling to be roughly six times the thermal energy. But its sensitivity to changes in the field strength, as determined by the derivative with respect to γ of the standard deviation of the component perpendicular to field (red), peaks for ratios near 2. (Adapted from J. L. Kirschvink, M. M. Walker, in J. L. Kirschvink et al., eds., *Magnetite Biomineralization and Magnetoreception in Organisms*, Plenum Press, New York, 1985.)



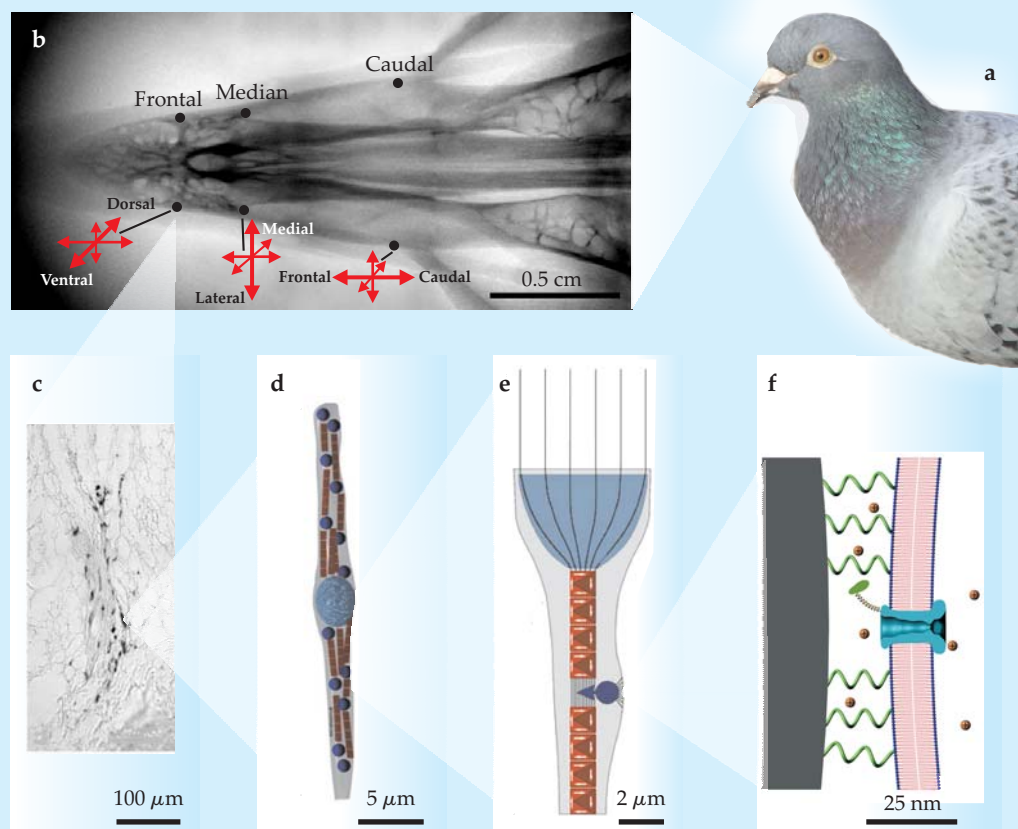


Figure 4. Evidence for magnetite-based magnetoreception. (a) The homing pigeon *Columba livia* provides some of the best evidence. (b) X-ray image of the upper beak of *C. livia*, showing the three pairs of iron-containing areas and the prevailing orientations of their neurons. (c) Stained section of the dendritic region in one of the areas. Dark areas are iron deposits. (d) Schematic of a single neuron, showing the centrally located, iron-coated vesicle (light blue) and the clusters of magnetite crystals (dark blue) alternating with rows of maghemite plates (red). (e) Hypothesized concentration of magnetic flux in a neuron and its effect on the position of one of the magnetite clusters. (f) Magnetite cluster pulling away from a membrane, which bends and opens a mechanically stimulated ion channel. (Panel a courtesy of Andreas Trepte; panels b–c adapted from G. Fleissner et al., *Naturwissenschaften* **94**, 631, 2007; panels d–e adapted from G. Fleissner et al., *J. Ornithol.* **148**, 643, 2007; panel f adapted from I. Solov'yov, W. Greiner, *Biophys. J.* **93**, 1493, 2007.)

to be reliable (figure 3b). Bacteria thus may have found the best strategy: long chains of single-domain particles. However, the most sensitive measurements of magnetic field strength are found when the ratio of μB to kT is about 2.

Exactly how the rotation of a single-domain particle creates an action potential in a neuron is not known, but the existence of diverse mechanical sensors in cells offers many possibilities. One is that the particles strain or twist hair cells, stretch receptors, or other mechanical receptors as they attempt to align with the geomagnetic field. Another is that the rotation of intracellular magnetite crystals might open ion channels directly if cytoskeletal filaments connect the crystals to the channels.

The small size and ferric nature of those putative compasses make them almost impossible to unambiguously locate in a body. They are below the resolution limit of light microscopy and are dissolved by many common tissue preservatives. In addition, iron is one of the most common metals found in organs and accumulates in a number of degenerative processes, including hemochromatosis, Parkinson's disease, and blood coagulation. Iron is also widespread in both outdoor and lab environments. Thus searching for a

magnetite-based compass is even worse than finding a needle in a haystack—it is like finding a needle in a stack of needles.

Evidence for magnetite receptors

Numerous techniques, including superconducting quantum interference device magnetometry, x-ray fluorescence, and atomic force microscopy, have been used in efforts to localize magnetite-based receptors. So far, the best evidence has come from trout and homing pigeons. In trout, confocal and atomic force microscopy have found single-domain magnetite crystals in cells near a nerve that responds to magnetic stimuli. In pigeons, a complex array of magnetic minerals has been found in a part of the beak coupled to a nerve that responds to magnetic field changes. Six clusters of such minerals have been found, three on each side of the beak (figure 4). The apparent functional unit, found in the branches of nerve cells, consists of a vesicle 3–5 μm in diameter that is coated with a noncrystalline iron compound and surrounded by about 10 to 15 1- μm -diameter spherical clusters, each containing approximately 8 million 5-nm-diameter crystals of magnetite that alternate with chains of about 10 plates, each roughly $1 \times 1 \times 0.1 \mu\text{m}$, of maghemite. The functional units

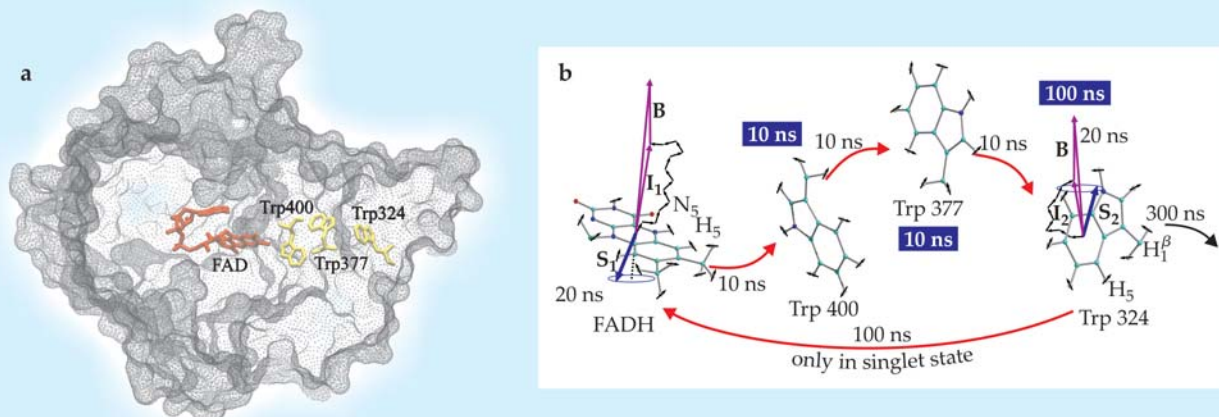


Figure 5. Cryptochrome is a candidate magnetoreceptor based on pairs of radicals. **(a)** The key components, illustrated on this electron density image, are the chromophore flavin adenine dinucleotide and three tryptophan residues involved with the chromophore's reduction to the hydrogenated FADH. **(b)** Following cryptochrome excitation by a blue photon, holes transfer from FADH through the chain of tryptophan residues (the reaction steps are labeled by their time constants, and the tryptophans by their radical-state lifetimes). The resulting unpaired electron spins S_1 and S_2 precess about the local magnetic field produced by the addition of the external magnetic field B and the contributions I_1 and I_2 from the nuclear spins on the two radicals. Hole back-transfer from tryptophan-324 to FADH quenches cryptochrome's active state but can occur only when the radicals' electron spins are in a singlet state. (Adapted from I. A. Solov'yov, D. E. Chandler, K. Schulten, *Biophys. J.* **92**, 2711, 2007.)

are regularly spaced at roughly 100- μm intervals in each of the six locations. Interestingly, the orientation of the units in each of three pairs of magnetic regions is perpendicular to the other two pairs, which suggests a triaxial system.

Gerta Fleissner, Gunther Fleissner, and their colleagues have proposed that the three different elements of the functional unit have different functions (figure 4d–f). The maghemite platelets, which are large enough to have approximately four magnetic domains, are thought to act as soft magnets that locally amplify Earth's field in the same way that a soft iron core increases the strength of an electromagnet. The amplified field then interacts with the clusters of tiny magnetite crystals. Those crystals are too small to have a stable magnetic moment at body temperature. An applied field will align the moments to a degree that depends on the field's strength and the temperature, but it will not rotate the particles themselves like compass needles. Termed superparamagnetic, such small particles of ferrimagnetic minerals have magnetic moments that are weak compared with those of single-domain particles. Nevertheless, Earth's field, concentrated by the platelets, may be able to move or deform a large enough cluster of the particles. Calculations based on the morphology of the system suggest that when aligned with Earth's field, the maghemite platelets increase the local field strength 20-fold, producing a force of about 0.2 piconewtons on the 2.6-picogram magnetite clusters. The resulting movement of the clusters might then open membrane channels either through direct physical connections or by deforming the nerve cell membrane. The function of the coated vesicle is uncertain, though iron storage and additional field concentration have been suggested.

Because finding magnetic minerals in tissue is hard and proving that they function in magnetoreception is harder, some researchers have tested the hypothesis indirectly using strong pulsed magnetic fields (about 500 μT for 5 ms) to alter the direction of magnetization in single-domain magnetite particles. After the pulses were applied, the magnetic orientation of certain birds and sea turtles either vanished or was slightly altered. However, given the high strength of the field and the even larger induced electric field, it is impossible to

rule out effects on other compass mechanisms or even general physiology.

Radical pairs

The third proposed magnetoreception mechanism involves biochemical reactions. Although magnetic-field-dependent chemical reactions are known, a magnetoreception system based on chemistry must clear some high hurdles. First, in Earth's 50 μT field, energy shifts of molecular states due to Zeeman splitting are only one five-millionth of kT at body temperature (10^{-27} versus 5×10^{-21} joules); thus product yields and rates of most chemical reactions will not be sensitive to weak magnetic fields. But a class of chemical reactions involving pairs of radicals shows an unusual sensitivity to the strength and orientation of magnetic fields. For example, the rates of certain redox reactions involving horseradish peroxidase are slightly increased in fields of 1 mT. However, no room-temperature reaction of any kind has shown a measurable effect at geomagnetic field strengths. Second, any such reaction used for a compass requires immobilization of at least one of the reactants, so that a constant orientation relative to the field is maintained. With the exception of structural components, biological molecules continually rotate and move. Even proteins bound in cell membranes are in constant motion.

Assuming that spins are relatively isolated from thermal effects, researchers interested in the possibility of chemically mediated magnetoreception have focused on the correlated spin states of paired radical ions. The reaction, first proposed by Klaus Schulten in 1982 and then developed by Thorsten Ritz, begins with an electron transfer between two molecules, leaving two unpaired electrons in a pure singlet state. Over what is assumed to be a relatively long period (about 100 ns), the spins interact with the nuclear spins and precess at different rates that depend on the local magnetic neighborhood and the orientation and strength of the geomagnetic field. Back-transfer of the electron can only occur if the spins are oppositely aligned, and their alignment depends on the length of the reaction and the difference in precession rates. Because the geomagnetic field can influence the precession rate, it may be able, under the right set of

conditions, to influence reaction rates or products.

In quantum mechanical terms, the initial singlet state is coupled to a nearly degenerate triplet state via the hyperfine interactions between the electron spins and the nuclear spins, the coupling strength depends on the magnetic field, and the rate at which the state acquires triplet character is thus field dependent. If one assumes that the radical pair in the triplet state forms a chemical product that differs from that of singlet pairs, one has a potentially viable detector for weak magnetic fields. It's important to note that the radical-pair mechanism can detect only the field's axis, not its polarity. However, few animals appear to be able to detect the polarity of Earth's magnetic field (exceptions are lobsters, salamanders, and mole rats). Instead, they define "poleward" as the direction along Earth's surface in which the angle formed between the magnetic-field vector and the gravity vector is smallest.

Because the influence of the geomagnetic field on singlet-to-triplet conversion is very weak, the lifetime of the singlet state due to other decay modes—such as fluorescence, decoherence of the quantum state, and intramolecular conversion—must be quite long for any appreciable magnetic effects to develop. Quantum mechanical calculations of model systems, using plausible parameters, have shown that the conditions can be met. In addition, the relationship between the reaction time and the internal magnetic interactions must be precise, and the molecules must contain few hydrogen or nitrogen atoms, whose relatively strong magnetic moments will overwhelm any effects due to Earth's field. Furthermore, the formation of the initial state must not randomize the spin relationship of the two unpaired electrons. In general, that requirement is met only in reactions begun by photoexcitation.

The cryptochrome hypothesis

The connection with photoexcitation has led to interest in a group of blue-sensitive photoreceptive proteins known as cryptochromes (figure 5a). Those molecules, which are quite different from the usual proteins involved in vision, are often involved in timing and biological rhythms in plants and animals and were recently shown to cue the mass coral spawnings on the Great Barrier Reef. They are attractive candidates for magnetoreceptors because they are found in the eyes of magnetoreceptive birds during migration and have a chromophore that forms radical pairs after photoexcitation. In the proposed reaction, an electron is donated to the chromophore FAD (flavin adenine dinucleotide) from one of the tryptophan amino acids in the protein (figure 5b).

Surprisingly, the best evidence that cryptochromes function in magnetoreception has come from plants. Intrigued by persistent but controversial reports of weak magnetic fields affecting plant growth, a group of researchers led by Margaret Ahmad studied the growth of the small mustard plant *Arabidopsis thaliana*, the botanists' equivalent of the laboratory rat. Plants raised in a magnetic field of 500 μT grew much more slowly than did control plants raised in the 50- μT geomagnetic field, but the inhibitory effect of the field occurred only when the plants were raised under blue light (the color that cryptochromes detect). Similar experiments in darkness, in red light, and with mutant plants that had no cryptochrome gene showed no growth inhibition in either field. The finding demonstrated that cryptochrome mediates a field-affected process, though not necessarily that cryptochrome itself mediates the magnetic effect.

The photoexcitation possibility has inspired a large number of experiments—mostly performed by Wolfgang Wiltschko, Roswitha Wiltschko, and John Phillips—that have examined animals' magnetic orientation behavior under dif-

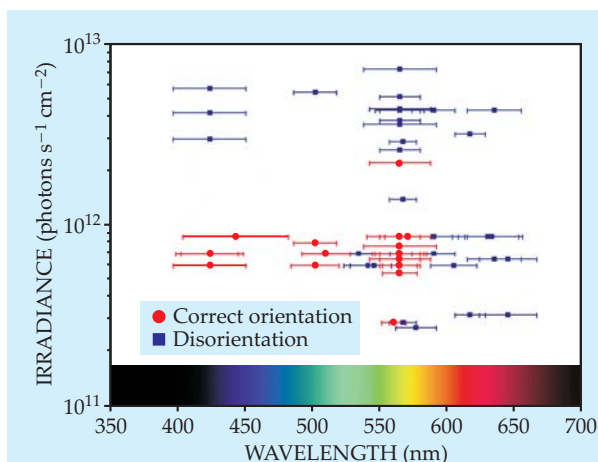


Figure 6. Photoexcitation experiments have explored a possible connection between photoreceptors and magnetoreception. The 40 different magnetoreception experiments plotted here exposed three different migratory birds (28 used the European robin, *Erethacus rubecula*; 9 the silvereye, *Zosterops lateralis*; and 3 the garden warbler, *Sylvia borin*) to single-wavelength LEDs. The error bars denote the light's full width at half maximum. Magnetic orientation was inhibited (blue points) by high intensity or long-wavelength light. (Adapted from S. Johnsen et al., *J. Exp. Biol.* **210**, 3171, 2007.)

ferent wavelengths of light, on the assumption that the candidate molecules are in the visual system. The orientation behavior of many species has been found to change under specific wavelengths and intensities, but the results have been bewildering, with different intensities and wavelengths of lights leading to orientation in the correct direction in Earth's field, to random movements, or to orientation in the wrong direction. The data are difficult to interpret, since they do not fit the absorption spectra of any known photoreceptive molecule. An examination of the experiments on birds reached only two general conclusions: Magnetic orientation is disrupted when animals are exposed to light levels above 10^{12} photons/(s·cm²) or to light at wavelengths greater than 565 nm (figure 6). Because dimmer, blue light occurs after sunset, the time when the birds begin to migrate, it is possible that the ambient light simply signals the birds that it is time to begin orienting in the appropriate migratory direction rather than affecting any compass mechanism (twilight has a visible irradiance less than 10^{12} photons/(s·cm²) and is, of course, blue). However, the pattern of responses is also consistent with the cryptochrome hypothesis because long-wavelength light temporarily deactivates the molecule.

A frequency of 1.315 MHz matches the electron spin resonance in the geomagnetic field. Hence, RF fields of that frequency should interfere with the radical-pair mechanism. In 2005 Peter Thalau and his colleagues found that an oscillating magnetic field of that frequency, with an intensity of 0.48 μT , disrupted the orientation of the European robin. That followed work by Ritz that showed that a 7-MHz field (0.47 μT) and RF noise (0.085 μT at 0.1–10 MHz) both disrupted orientation in the same animal. But in each case, the effect might be attributable to the induced electric field. Both Ritz and Thalau found that the RF fields did not disrupt magnetic orientation when the oscillating field was parallel to the

geomagnetic field, which appears to be a good control for nonspecific effects. One caveat, however, is that RF experiments on known radical-pair reactions found effects regardless of how the RF field was aligned relative to the ambient field.

Where next?

Biological systems often make ingenious use of physical principles, and magnetoreception appears to be no exception. All three proposed mechanisms can, in principle, get useful information from the weak geomagnetic field. However, with the exception of magnetotactic bacteria, no mechanism has been conclusively established.

Electromagnetic induction is based on straightforward principles and appears to be within the capabilities of sharks and rays, but its use has not been directly demonstrated. The hypotheses based on ferrimagnetic minerals have the best morphological evidence and a solid theoretical background. The most recent work in homing pigeons also appears to get past the concern that the magnetic minerals are just contaminants.

The radical-pair mechanism is fascinating but enigmatic. The conditions for its success are extremely strict. However, evolution has built some equally improbable chemical factories, including the photosynthesis reaction center, which can split water molecules using visible light. The biggest hurdle for the radical-pair mechanism is not theoretical but how to find the actual molecules involved. Through no fault of the investigators, the current evidence for the radical-pair hypothesis is maddeningly circumstantial. Cryptochrome is photosensitive, is found in migratory birds, and forms radical pairs, but it has no direct links to magnetoreception. The RF data are certainly suggestive, but they will be more so if future experiments reveal an action spectrum in which some, but not all, frequencies have an effect. In theory, such specificity should exist.

Magnetoreception research began with behavioral studies on relatively large migratory animals, but those animals may not be ideal for understanding the mechanism. It may be better to continue the work with zebrafish or fruit flies, two magnetoreceptive species that are also model systems for studying cellular and molecular processes. Regardless of the experimental system used, the solution to the long-standing mystery of magnetoreception in animals will almost certainly come from a fascinating interplay of biology and physics.

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