

Magnetoreception

Roswitha Wiltschko and Wolfgang Wiltschko*

Summary

The vector of the geomagnetic field provides animals with directional information, while intensity and/or inclination provide them with positional information. For magnetoreception, two hypotheses are currently discussed: one proposing magnetite-based mechanisms, the other suggesting radical pair processes involving photopigments. Behavioral studies indicate that birds use both mechanisms: they responded to a short, strong magnetic pulse designed to change the magnetization of magnetite particles, while, at the same time, their orientation was found to be light-dependent and could be disrupted by high-frequency magnetic fields in the MHz range, which is diagnostic for radical pair processes. Details of these findings, together with electrophysiological and histological studies, suggest that, in birds, a radical pair mechanism located in the right eye provides directional information for a compass, while a magnetite-based mechanism located in the upper beak records magnetic intensity, thus providing positional information. The mechanisms of magnetoreception in other animals have not yet been analyzed in detail. *BioEssays* 28:157–168, 2006. © 2006 Wiley Periodicals, Inc.

Introduction

In contrast to humans, many animals are able to perceive the geomagnetic field. It represents a reliable, omnipresent source of navigational information (see Ref. 1 for details) which is of two kinds: the magnetic vector provides directional information and can be used as a compass, while total intensity and/or inclination show gradients between the magnetic poles and the magnetic equator and may thus be used as a component of a system indicating position.

Animals have been shown to use both types of magnetic information.⁽²⁾ However, magnetoreception is not included in the classic senses—although speculations about a possible magnetic sense date back as far as the 19th century,^(3,4) first reports on experiments indicating magnetically controlled behavior were only published in the 1960s.^(5–7) Meanwhile, the navigational use of magnetic information and its behavioral

and ecological aspects are fairly well understood,⁽²⁾ yet our knowledge on the physiological and neurobiological aspects of magnetoreception is still rather limited. A systematic analysis of magnetoreception has only just begun and, in spite of recent progress, crucial questions are still open. This review represents an interim report summarizing the present state of knowledge.

The use of magnetic information for orientation and navigation

First indications that animals can use magnetic information for orientation came from behavioral experiments with migratory birds: caged European robins, *Erithacus rubecula* (Turdidae) changed their heading accordingly when magnetic North was experimentally altered, demonstrating that they oriented with respect to the magnetic field and thus the use of a magnetic compass.⁽²⁾ Meanwhile, magnetic compass orientation has been demonstrated in numerous other animals involving members of the phyla molluscs, arthropods and all major groups of vertebrates; Table 1 gives an overview.¹ The tasks involved are manifold and include spatial scales ranging from less than a meter to thousands of kilometers. The magnetic compass is used for orientation within the animals' home range and homing, but also for building activity e.g. by honey bees and compass termites. Magnetic compass orientation is involved when animals move shoreward or waterward at the borderline of land and water and in the extended migrations of eels and salmon, marine turtles and birds. The compass courses located with the magnetic compass range from innate courses as in migratory birds to acquired courses set by other environmental factors, as in young marine turtles, and courses within the home range based on local knowledge. For a detailed summary on magnetic compass use see Ref. 2.

Interestingly, two types of magnetic compass mechanisms have been described, with fundamental differences in their functional characteristics, a *polarity compass* and an *inclination*

Fachbereich Biowissenschaften der J.W. Goethe-Universität Frankfurt am Main, Germany.

*Correspondence to: Wolfgang Wiltschko, Fachbereich Biowissenschaften der J.W. Goethe-Universität Frankfurt am Main, Germany.

E-mail: wiltschko@zoology.uni-frankfurt.de

DOI 10.1002/bies.20363

Published online in Wiley InterScience (www.interscience.wiley.com).

¹Certain anaerobic or microaerophil bacteria are 'magnetotactic': when they are stirred up from the ground, they rely on the magnetic field to guide them from the oxygen-rich open water back down to the sediments with more favorable conditions.^(8,9) These bacteria contain chains of crystals of the permanently magnetic material magnetite, so-called magnetosomes, that mediate their responses to the magnetic field. With the help of their magnetosomes, 'magnetotactic' bacteria are passively aligned along the field lines, i.e. they make direct use of the magnetic force and do not process magnetic information, which makes their 'orientation' fundamentally different from that of animals.

Table 1. Animals demonstrated to use a magnetic compass

Systematic group				Type of compass
Molluscs				
Snails	1 order	1 family	1 species	???
Arthropods				
Crustaceans	3 orders	3 families	5 species	polarity compass ⁽¹¹⁾
Insects	6 orders	7 families	9 species	polarity compass ⁽¹⁵⁾
Vertebrata				
Cartilaginous fish	1 order	1 family	1 species	???
Bony fish	2 orders	2 families	4 species	polarity compass ⁽¹⁶⁾
Amphibians	1 order	2 families	2 species	inclination compass ⁽¹³⁾
Reptilians	1 order	2 families	2 species	inclination compass ⁽¹⁴⁾
Birds	4 orders	12 families	21 species	inclination compass ⁽¹²⁾
Mammals	2 orders	2 families	3 species	polarity compass ⁽¹⁰⁾

compass (Fig. 1). The *polarity compass* works similar to our technical compass, using the polarity of the magnetic field to distinguish between magnetic ‘North’ and ‘South’. The *inclination compass*, in contrast, ignores polarity and relies instead on the axial course of the field lines, obtaining unimodal directional information by interpreting the inclination of the field lines with respect to up and down; it thus distinguishes between ‘poleward’, where the field lines run downward, and ‘equatorward’, where they run upward. The

response of animals in a magnetic field with the vertical component inverted (see Fig. 1, right) is diagnostic: rodents⁽¹⁰⁾ and spiny lobsters⁽¹¹⁾ maintain their headings, indicating that their magnetic compass is a *polarity compass*, while birds,⁽¹²⁾ salamanders⁽¹³⁾ and marine turtles⁽¹⁴⁾ reverse theirs, revealing the use of an *inclination compass* (Fig. 2). The functional mode of the magnetic compass is indicated in Table 1 where it is known; in most cases, however, only few species of the respective group have been tested.

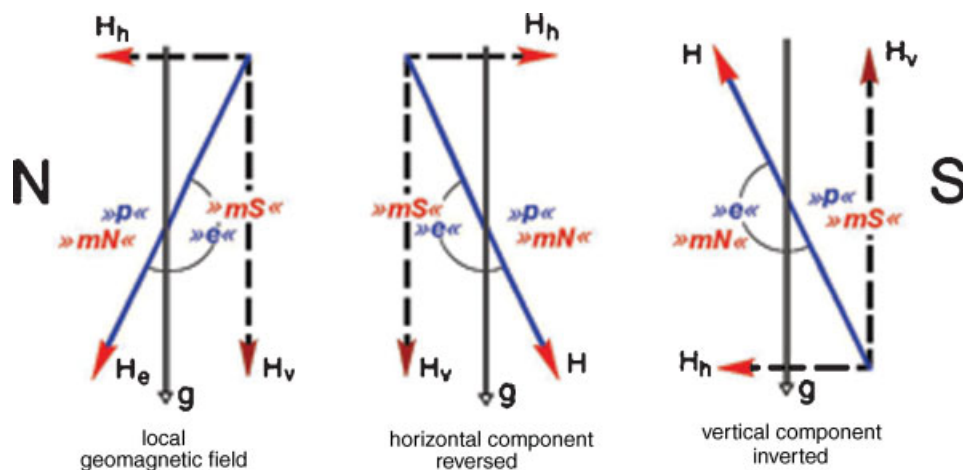
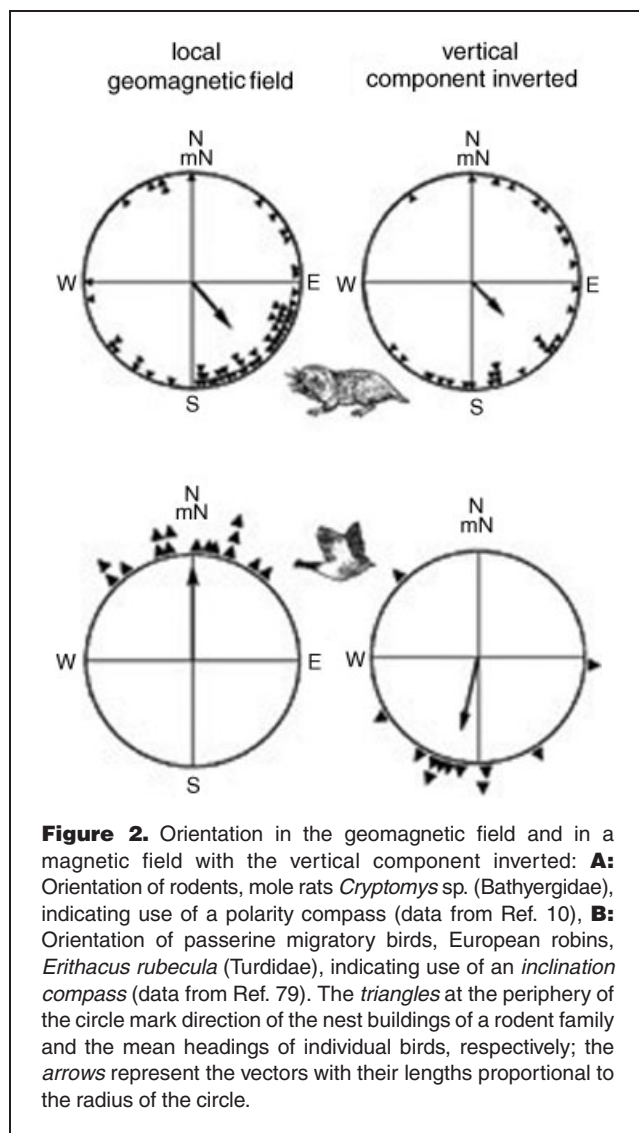


Figure 1. Schematic view of a cross section of the geomagnetic field and two experimental fields viewed from west to east, demonstrating the two types of magnetic compass identified in animals. The arrows indicating the polarity of the field are given in red, the course of the field lines is given in blue.; N, S, geographic North and South, respectively; H_e , vector of the geomagnetic field, H vector of the experimental fields; H_h , H_v , horizontal and vertical component, respectively; g , gravity vector indicating up and down. **Left:** geomagnetic field at Frankfurt, Germany, with northward polarity and field lines running south-up/north-down; **center:** horizontal component reversed by Helmholtz coils, with southward polarity and field lines running north-up/south-down; **right:** vertical component inverted, with polarity remaining northward, but the field lines running south-down/north-up. The “polarity compass” is based on the polarity of the field lines, its readings $\gg N \ll$, magnetic north, i.e. in the direction of polarity, and $\gg S \ll$, magnetic south, in the opposite direction, are given in red. The “inclination compass” is based on the course of the field lines and their inclination; its readings $\gg p \ll$, poleward, i.e. where the field lines point downward, and $\gg e \ll$, equatorward, where they point upward, are given in blue. Note that inverting the vertical component is diagnostic, because in this situation, a *polarity compass* indicates the same directions as in the geomagnetic field, while an *inclination compass* indicates reversed directions.



In birds, another unexpected characteristic of the magnetic compass became evident: it is closely tuned to the total intensity of the ambient field. Reducing or increasing the intensity by 20–30% led to disorientation.⁽²⁾ This seemingly narrow functional window is not fixed, but adjusts to lower or to higher intensities when birds are exposed to these intensities for a certain period of time. Birds adjusted to higher intensities did not lose their ability to orient in the local geomagnetic field, yet proved unable to orient in an intermediate field.⁽²⁾ This indicates that the newly gained ability to orient in higher or lower fields represents neither a shift nor amplification of the functional range. Apparently, birds can orient only in field intensities that they have directly experienced before, with this experience possibly forming a new functional range. Comparable data from other animals are not available.

The geomagnetic field not only provides directional information, however. Magnetic intensity and/or inclination can be used to obtain positional information. This is less well documented and the available evidence comes only from a small number of species. When spiny lobsters⁽¹⁷⁾ and marine turtles⁽¹⁸⁾ were tested in magnetic fields characteristic for sites hundreds of kilometers away from the location where they actually stayed, the animals chose headings that would have led them to their home site if they had been displaced to the respective sites. This clearly shows that these animals can use magnetic intensity and inclination to derive information on their position relative to a goal; it is part of a navigational process determining the home course. The same is suggested for birds⁽¹⁹⁾ and salamanders.⁽²⁰⁾

Total intensity, inclination or a combination of both may also serve as 'sign-posts' or 'triggers', marking certain regions on the earth where animals must respond in a particular way. Here, specific magnetic parameters elicit orientation responses like changes in heading in migrating birds^(21,22) and marine turtles⁽²³⁾ as well as physiological responses like gaining body weight.⁽²⁴⁾

The magnetic parameters required for navigation and the trigger function are fundamentally different from the vector quality used for compass orientation. This implies that we will have to look for different types of magnetoreceptors. In the technical world, very different instruments based on different physical principles—magnetometers and compasses—are used for measuring magnetic intensity and magnetic directions. Nature must also be expected to have developed senses optimized for detecting these qualities, just as there are, for example, different types of mechanoreceptors for tactile and auditory input. At the same time, the two types of magnetic compass mechanisms found among different animals (see Table 1) suggest that we may even have to expect more than one type of receptor for directional information.

Possible primary processes

To understand magnetoreception, one must start out to look for processes that allow magnetic information to be mediated to the nervous system. A number of mechanisms have been suggested as potential primary processes. One of the obvious ones is induction. A magnetic compass based on induction was postulated for cartilaginous fishes with electroreceptors: their ampullary organs can be stimulated in a direction-dependent way when they move through the geomagnetic field.⁽²⁵⁾ This type of magnetoreception would be restricted to marine animals because it requires sea water as a surrounding medium with high conductivity. The ampullary organs of skates and rays are indeed sensitive enough to respond to the differences in voltage induced when the fish are heading in different directions, but evidence that the information obtained this way is indeed used for compass orientation is still lacking.

Other models not subject to these restrictions are listed in Ref. 2; more recent ones involve a combination of permanent magnetic material and photopigments⁽²⁶⁾ or assume interactions of electric field ion cyclotron resonances with the geomagnetic field in certain brain areas.⁽²⁷⁾ The current discussion focuses on the two models that are supported by experimental evidence: the *magnetite hypothesis* proposing a primary process involving tiny crystals of permanently magnetic material, and the *radical pair model* suggesting a 'chemical compass' based on singlet-triplet transitions in photopigments. These two models are briefly summarized below.

Magnetite is a specific form of iron oxide Fe_3O_4 whose general properties depend on the size and shape of the particles (Fig. 3). Spin interactions cause the spins of adjacent atoms to align, thus forming *domains* with all spins parallel. Large particles include multiple domains with their magnetic moments largely canceling each other; particles in the range between about 1.2 and $0.05 \mu\text{m}$ consist of a *single domain* and have a stable magnetic moment, thus acting as tiny magnets. Even smaller particles are *superparamagnetic*; their magnetic moment fluctuates as a result of thermal agitation, but it can be aligned by an external magnetic field (see Ref. 28 for details).

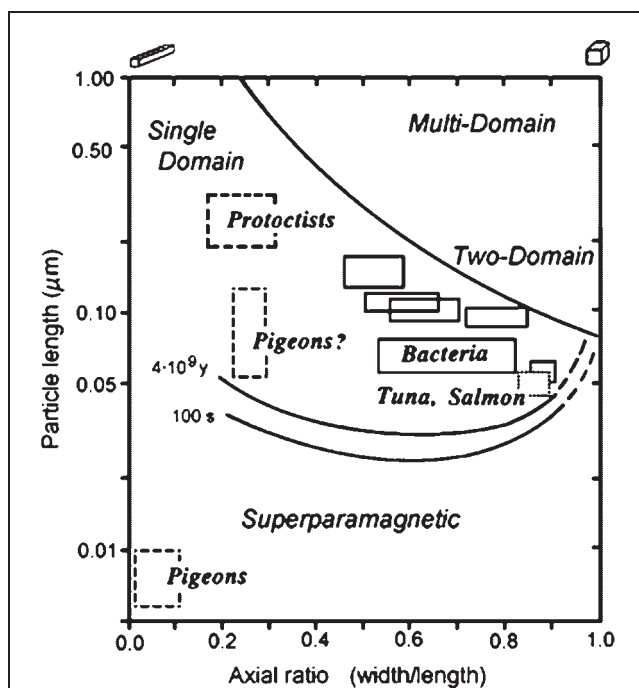
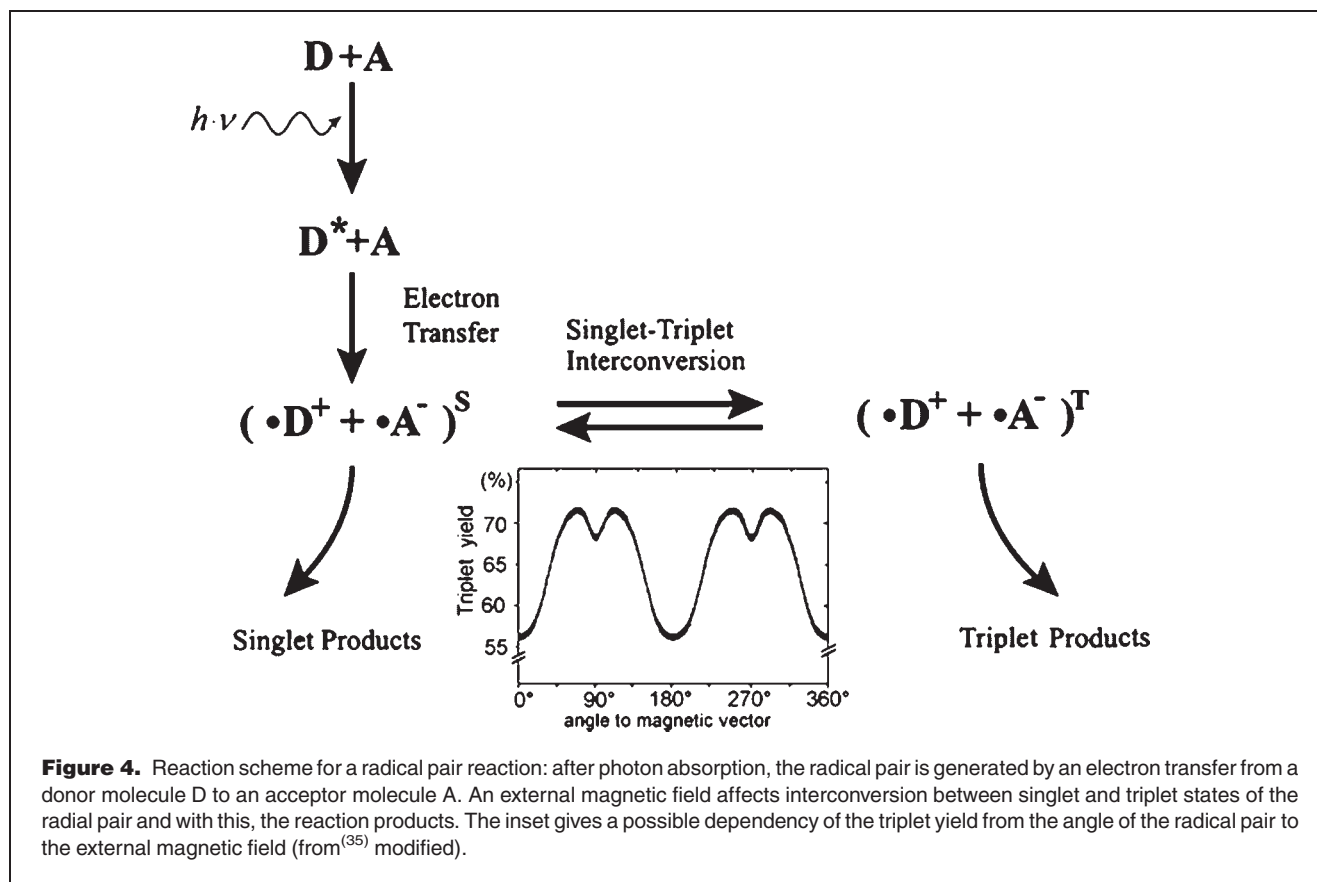


Figure 3. Magnetic properties of magnetite particles as a function of their size and shape. Domain stability field diagram showing the size of particles of the various types of particles and indicating the size of particles found in various organisms (after⁽³¹⁾ modified). Note that for pigeons, *single domains*^(38,39) as well as *superparamagnetic particles*⁽⁴¹⁾ have been described.

In the 1970s, certain bacteria were discovered to contain chains of single domain magnetite⁽⁸⁾ that act as magnets and align the bacteria along the field lines. The resulting 'orientation' observed in bacteria and some algae is a direct result of the magnetic force acting upon the magnetite particles, without involving an active part of the organism (see Ref. 9 for review). Magnetic fields being mediated by tiny magnets was an attractive idea, and the existence of magnetic material of biogenic origin caused authors to speculate about a potential role of magnetite in the orientation of higher animals. A variety of models on how such magnetite-based magnetoreceptors might work has been suggested, some of them involving single domains,^(29–31) others superparamagnetic particles.^(30,32,33) Interestingly, some of these models would produce polar, others axial responses. Model calculations showed that such receptors could convey directional information or information on magnetic intensity, depending on their specific structure and on the amount of magnetite included; they could account for the sensitivities indicated by behavioral evidence.⁽³¹⁾

The *radical pair model*^(34,35) proposes an entirely different mechanism based on specialized photopigments. In the initial step, these macromolecules absorb a photon and are elevated to the singlet excited state. They form singlet radical pairs, i.e. two molecules or parts of a molecule with an unpaired electron each. By singlet–triplet interconversion, singlet pairs with their free electrons in antiparallel spin turn into triplet pairs with their free electrons in parallel spin. The magnetic field alters the dynamics of this transition between the spin states (Fig. 4); as a result, the triplet yield depends on the alignment of the macromolecules in the ambient magnetic field and can thus convey information on magnetic directions. As receptor molecule, cryptochromes were suggested,⁽³⁵⁾ a class of photopigments first known from plants, but later also found in animals (see Ref. 36 for review). They belong to the flavins and possess chemical properties that are crucial for the model, including the ability to form radical pairs.⁽³⁷⁾

To obtain magnetic compass information by a radical pair mechanism as suggested above, animals must take advantage of the fact that triplet products are chemically different from singlet products and compare the triplet yields in different spatial directions. This requires an orderly array of photo-pigments oriented in the various directions. The required conditions could be met by the more or less spherical arrangement of receptors in the vertebrate eyes—radical pair processes would generate characteristic response patterns across the retina, which would allow animals to detect the direction of the ambient field.⁽³⁵⁾ These patterns would be centrally symmetric around the axis of the field lines, that is, axial rather than polar, which means that a compass based on radical pair processes would have to be an inclination compass. At the same time, the initial step of photon absorption would make magnetoreception light-dependent.



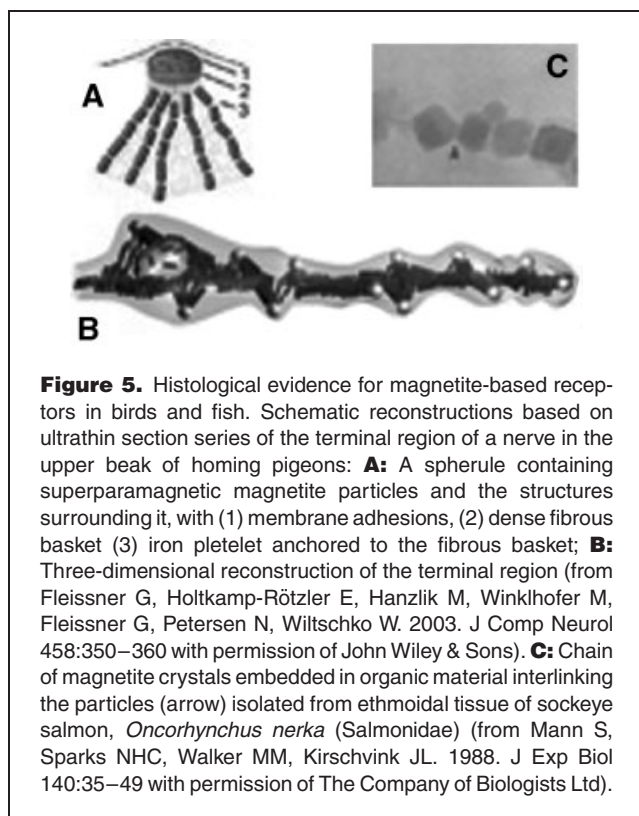
When first suggested, the *magnetite hypothesis* and the *radical pair model* were considered alternatives that largely exclude each other. However, an increasing body of evidence indicates that both mechanisms can exist side by side, at least in birds. Unfortunately, the number of groups that have so far been tested for their magnetoreception mechanisms is still very limited, with birds being by far the best-studied group. Birds and fish are the only groups where some neuroanatomical and electrophysiological evidence associated with magnetoreception is available. Behavioral experiments designed to distinguish between the two models are only known from birds.

Anatomical and electrophysiological findings supporting the magnetite hypothesis

Magnetite has been discovered in a large number of animals, mostly by measuring the natural and induced remanence with highly sensitive SQUID magnetometers. In vertebrates, it was mostly found in the ethmoid region of the head.⁽²⁸⁾ Histological and electronoptical studies in birds revealed iron-rich particles in the orbital and the nasal cavities, some of them reported to be single domain magnetite.^(38–40) A recent study⁽⁴¹⁾ described clusters of very small crystals at specific locations in the skin of the upper beak of pigeons, *Columba livia f. domestica*, with the particles identified by crystallographic means as superpar-

amagnetic magnetite. The clusters were located within nervous tissue and associated with a remarkable framework of platelets consisting of noncrystalline iron (Fig. 5A,B); the authors speculate about possible functions in a magnetoreceptor.^(33,41) In salmonid fish, chains of single domain magnetite have been isolated from ethmoid tissue (Fig. 5C).⁽⁴²⁾ A histological study showed magnetite particles embedded in specific cells within the basal lamina in the olfactory lamellae of rainbow trouts, *Oncorhynchus mykiss* (Salmonidae). These particles were identified as single domains; applying a strong external magnetic field could change the direction of their magnetization.^(43,44) This means that the potential magnetoreceptors found in birds and fish need not necessarily be identical in their general characteristics.⁽⁴⁰⁾ In addition, although some details of the structures surrounding magnetite in situ in the potential receptor cells have been described, the functional characteristics of magnetite-based receptors have yet to be determined.

The region of the head where magnetite particles were found in birds and fish is innervated by the *ramus ophthalmicus*, a branch of the *nervus trigeminus*. Electrophysiological recordings from the ophthalmic nerve and from the trigeminal ganglion in passerine birds revealed units responding to magnetic stimuli, with the spontaneous activity of these



neurons modified by changes in magnetic intensity. The units showed a logarithmic characteristic. The minimum intensity differences tested were 200 nT, where the birds still showed a clear response;⁽⁴⁵⁾ in some cases, even responses to 20 nT differences could be recorded. Magnetic intensity can convey positional information; the electrophysiological recordings suggests a magnetite-based receptor with sensitivity as one would expect for a mechanism that allows birds to fix their position within a few tens of kilometers. Recordings from the corresponding branch of the trigeminal nerve in rainbow trout produced similar responses to changes in intensity⁽⁴³⁾ originating in the cells containing magnetite. In this respect, a parallel between birds and fish is suggested.

Behavioral tests indicating magnetite-based magnetoreceptors in birds

Behavioral tests designed to demonstrate a role of magnetite in magnetoreception aimed at interfering with the potential receptors by altering the magnetization of single domain magnetite crystals. By changing the output of the receptors, this should affect orientation. A popular method was to apply a brief, strong magnetic pulse—the pulse had to be strong enough to remagnetize single domain particles but, at the same time, short enough to prevent these particles from rotating into the pulse direction and thus escape remagnetization.

First tests were performed with migratory birds, using the preferred migratory direction as a criterion of whether or not pulse treatment had an effect. A 0.5 Tesla pulse of 3 to 5 ms duration prior to the critical tests caused approx. 90° change in direction: Australian Silvereyes, *Zosterops l. lateralis*, now preferred easterly headings (Fig. 6, left), which was true for birds heading northward in autumn and southward in spring.^(46,47) Interestingly, this effect of pulsing was restricted to experienced migrants that had completed at least one migratory journey; young birds that had been captured immediately after fledging proved to be unaffected and continued in their normal migratory direction (Fig. 6, right).⁽⁴⁸⁾ These findings suggest two conclusions: (1) the observation that young birds continued in migratory direction after pulse treatment shows that the avian magnetic compass was not affected, indicating that the compass is not based on magnetite, and (2) the effect of the pulse solely on experienced migrants suggests that the magnetite-based receptors are part of a mechanism that is based on experience - this points to the position-finding system of the 'navigational map', which, in contrast to the innate magnetic compass, has to be learned by individual experience.^(48,49) This interpretation is in agreement with the electrophysiological recordings mentioned above.⁽⁴⁵⁾

Findings with homing pigeons also fit this interpretation.⁽⁵⁰⁾ Even when the sun was visible and the pigeons could use the sun compass, pulse treatment had an effect on the directions in which displaced pigeons left the release site: pulsed birds deviated from untreated control birds. Yet these deflections became evident only at greater distances from home and, with 20° to 50°, were considerably smaller than the ones observed in migrants. In contrast to the caged migrant, the pigeons had access to a multitude of environmental factors; the multifactorial nature of their 'navigational map' would reduce any deflection induced by the altered magnetite-based sensor, in particular in the largely familiar area near home.

Modifications in the protocol of pulse treatment revealed some interesting properties of the receptor. An identical pulse applied in different orientations with respect to the bird—e.g. 'south anterior' with the south pole to the beak or 'south left' with the south pole to the left side of the head—led to different responses, with the birds deviating to different sides of the untreated control birds. This was true for passerine migrants as well as homing pigeons^(50,51) and implies that pulse treatment does not totally deactivate the magnetite-based receptors, but instead causes them to provide altered information, indicating false positions which resulted in altered headings.

Treating the ophthalmic nerve with a local anesthetic was found to suppress the pulse effect in migrants: the birds were no longer deflected, but headed in their normal migratory direction.⁽⁵²⁾ This is another strong indication that the pulse does not affect the compass, but a different system. At the same time, it shows that the information causing the birds to

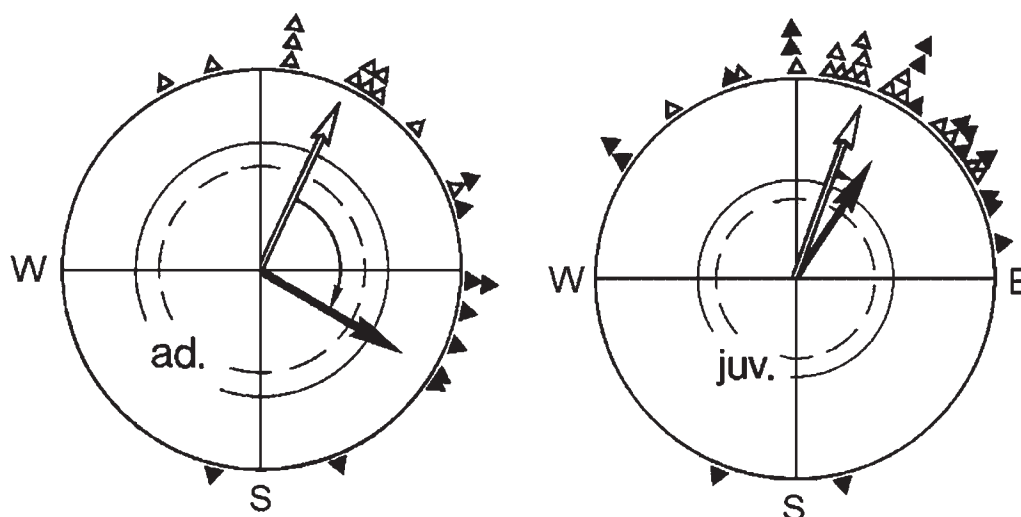


Figure 6. Effect of a short, strong magnetic pulse on the orientation of migratory birds, Australian Silvereyes, *Zosterops l. lateralis*. *ad.*, old, experienced birds; *juv.*: young, inexperienced birds. Symbols as in Fig. 1, with *open symbols* indicating control data recorded before, *solid symbols* data recorded after pulse treatment. The two inner circles represent the 5% (dashed) and the 1% significance border of the Rayleigh test (data from Refs 46,48).

change their headings indeed originates in the ethmoid region that is innervated by this nerve, that is, in the region where magnetite had been located. Additional evidence indicating a crucial role of the ophthalmic nerve in mediating information on magnetic intensity comes from recent conditioning experiments:⁽⁵³⁾ pigeons were trained to choose between two feeders according to whether a magnetic stimulus was present or absent, with the stimulus consisting of a local 'anomaly' with a strong increase in intensity. After the pigeons had learned the task, the ophthalmic nerve was bilaterally sectioned, and their performance broke down to chance level.

The findings mentioned above tell us little about the type of magnetite crystals that are involved—single-domains or superparamagnetic particles. Both types have been described in birds.^(38–41) To learn details about the particles included in the avian receptor, in particular to test whether single domains free to move to a certain extent were involved, passerines were subjected to the same pulse as before in the presence of a strong biasing field. The 100 μ T field was to align any movable particles in one direction; a pulse applied parallel should not change their magnetization and thus not have an effect, whereas a pulse applied in antiparallel direction should have a maximum effect. In critical tests, however, both groups of birds showed the same deflection.⁽⁵⁴⁾ These results exclude single-domains free to move as part of a polarity-sensitive receptor.

In view of the type of particles involved, another observation deserves attention, namely the transient nature of the pulse

effect. Since the magnetization of single domain particles is stable (see Fig. 3), the remagnetization should be just as stable and lasting as the original one. Yet in pulse experiments with migrants, a clear pulse effect was observed only on the day of pulsing and the following two days. Then, after a short period of disorientation, the birds returned to their original headings and continued to prefer their migratory direction.^(46,47) In homing pigeons, the duration of the pulse effect was even shorter lived.⁽⁵⁰⁾ Together, the behavioral experiments with birds mentioned here indicate the involvement of magnetite-based receptors, because magnetite is the only mechanism where after-effects of a pulse are to be expected; yet other aspects of the same findings seem to argue against single-domains, or would require auxiliary hypotheses. This leaves superparamagnetic particles, but because of their lack of stable magnetic moment, they were believed not to be affected by a pulse. A recent model study on ferrofluids,⁽³³⁾ however, showed that short, strong pulses could affect ordered arrays of superparamagnetic particles by rearranging them. Rearrangement of these arrays was reported to occur in a time frame similar to the time required for migrants to overcome the pulse effect. Hopefully, the various findings on magnetite-controlled responses in birds will soon be reconciled by a unifying model on how magnetite-based receptors might work.

Aside from birds, only a few animals have been subjected to pulse treatment. In mammals, the same type of strong magnetic pulse had a more lasting effect. Mole rats changed

the orientation of their nest building from southsoutheast by about 75° to east, and this new orientation proved stable over an observation period of three months.⁽⁵⁵⁾ This finding would be compatible with a mechanism based on single domain magnetite. In baby loggerhead turtles, *Caretta caretta* (Cheloniidae), a series of five short strong pulses applied perpendicular to each other had a disorienting effect.⁽⁵⁶⁾ The hatchlings were still oriented towards a light, but were disoriented in the dark where they had to rely on their magnetic compass. The duration of this effect is not known. These latter two cases are of particular interest, because here, in contrast to birds, the pulse appears to affect compass responses. However, considerations on magnetite-based compass mechanisms are still rather speculative, because so far, magnetite has not been documented in either molarats or marine turtles.

Evidence supporting the radical pair model

The radical pair model was proposed for mediating magnetic information on directions. Since the responses are axial rather than polar, it would only apply to animals that possess an inclination compass—birds, amphibians and marine turtles (see Table 1). Considering birds, this model was rather attractive, because it also provides an explanation for the narrow functional window of the avian magnetic compass: the specific patterns of activation postulated to form on the retina also depend on magnetic intensity.⁽³⁵⁾ In intensities that differ markedly from that of the local geomagnetic field, birds would be faced with a novel pattern, but this pattern would retain its central symmetry. The novel pattern may confuse the birds at first, but after becoming familiar with it, they may learn to interpret it, thus regaining their ability to orient.

The radical pair model, as detailed in 2000,⁽³⁵⁾ allows four predictions that can be experimentally tested. The first two predictions directly derived from the involvement of a radical pair mechanism are: (1) because the first step is assumed to be photon absorption, magnetoreception should be light dependent, and (2) high-frequency fields in the MHz range that interfere with the singlet/triplets interconversion should disrupt the detection of magnetic directions. Two more follow from the considerations on the circumstances of magnetoreception: (3) the eyes should be the site of the receptors perceiving magnetic directions, and (4) cryptochromes, the photopigment assumed to form the radical pairs, should be present in the eyes. All four predictions were found to be true in birds.

A light dependency of magnetoreception was first indicated by behavioral experiments with homing pigeons. When very young inexperienced pigeons are displaced, they derive their home course by reversing the direction of the outward journey.⁽⁵⁷⁾ Displaced in total darkness, they were disoriented, apparently unable to use their magnetic compass for detecting the direction of displacement.⁽⁵⁸⁾ Disorientation in darkness

was also found in the salamander *Notophthalmus viridescens* (Salamandridae).⁽⁵⁹⁾ Further experiments revealed a wavelength dependency of magnetoreception in both these groups.^(60–64) Marine turtles, however, proved well oriented in total darkness^(65,66)—here, although an inclination compass is involved, magnetoreception as proposed by the radical pair model appears rather unlikely, unless there is a yet unknown way that radical pairs could be initiated without light. Considerations on the radical pair model thus mainly focus on birds and amphibians.

High-frequency fields provide a diagnostic test for the involvement of a radical pair mechanism: weak fields of certain frequencies in the MHz range can interfere with the singlet–triplet interconversion, which should alter the output of the receptors markedly and thus disrupt orientation. At the same time, the effect of these fields should depend on their orientation with respect to the static background field. In critical tests, European robins were disoriented under the influence of weak high-frequency fields—a broad band noise field, a 7.0 MHz and a 1.3 MHz field—when these fields were presented at an 24° or 48° angle to the static geomagnetic field, whereas the same 7.0 MHz or 1.3 MHz field did not interfere with orientation when presented parallel to the geomagnetic vector.^(67,68) This clearly shows that the observed effect of high-frequency fields is a specific one. The intensity of the applied high-frequency fields was much too low to affect, for example, particles of magnetite. It suggests interfering resonance processes and thus indicates a radical pair mechanism underlying magnetoreception in birds, providing direct support for the radical pair model.

Further questions concern the location of the receptors providing magnetic compass information. Theoretical considerations favored the eyes as the site of magnetoreception because of their almost spherical shape.⁽³⁵⁾ In birds, the crucial processes of magnetoreception indeed take place in the eyes, but they seem to be restricted to the right eye. Passerine migrants tested with their left eye covered were found to be just as well oriented as binocular birds, whereas the same birds failed to show oriented behavior when their right eye was covered,^(69,70) suggesting that magnetic input is mediated exclusively by the right eye. This strong lateralization of the magnetic compass in favor of the right eye may be rather widespread among birds.^(69–71) Cryptochrome, the photopigment suggested to form the crucial radical pairs, has recently been extracted from the retina of two species of passerine migrants,^(72,73) where two types of cryptochrome 1, one of them with a novel C terminus, were identified.⁽⁷²⁾ In salamanders, however, the receptors were found to be located in the pineal gland,⁽⁷⁴⁾ the ancient third eye of vertebrates which is still directly sensitive to light.

Electrophysiological studies in pigeons also support a connection between magnetoreception and vision, suggesting that magnetic compass information is processed in part of the

visual system. Recordings from the nucleus of the basal optic root (nBOR) and from the *tectum opticum* revealed units that responded to changes in magnetic direction.^(75,76) These responses depended on the presence of light and an intact retina and optic nerve. Individual neurons in the nBOR as well as the *tectum* showed distinct peaks of response at particular alignments of the magnetic field, which varied between cells. The input of a number of such units would represent all directions in three-dimensional space; processed collectively and integrated, it could thus provide a suitable basis for a compass.⁽⁷⁵⁾

Taken together, the available findings from birds indicate the following pathways of magnetic compass information: it is mediated by a radical pair mechanism in the right eye, possibly involving cryptochromes, and it is processed in the nBOR and the *tectum opticum*, a part of the tectofugal system, which also comprises the *nucleus rotundus*, where an activation by magnetic stimuli was indicated using the glucose utilization method.⁽⁷⁷⁾

Responses under various light regimes

The responses of birds and amphibians under the various wavelengths of light are of interest because they should reflect the absorption ranges of the crucial pigments. Indirectly, they may also indicate the number of receptors involved and the way these are interconnected. In view of these questions, birds and salamander were tested under monochromatic light of different wavelengths.

A wavelength dependency of magnetic compass orientation, reflecting a wavelength dependency of magnetoreception was indeed observed in migratory birds and homing pigeons:^(60,78) magnetic orientation was observed under 424 nm blue, 502 nm turquoise and 565 nm green light, whereas under 590 nm yellow and 635 and 645 nm red light, birds were disoriented (Fig. 7). Experiments with interference filters could narrow down the onset of disorientation even further to between 561 and 568 nm.⁽⁶¹⁾ That is, the spectral range where birds obtain magnetic compass information includes the entire blue-to-green part of the spectrum. The orientation observed under monochromatic blue, turquoise and green light was normal migratory orientation, showing the seasonal reversal between northerly headings in spring and southerly headings in autumn; it was controlled by the avian inclination compass and was based on radical pair processes.^(60,79,80)

At a first glimpse, this relationship between orientation and wavelength of light may look like an 'all-or-none'-response reflecting the absorption range of a photopigment, yet the abrupt transition from orientated behavior to disorientation when the wavelength increased only a few nm^(60,61) suggest an antagonistic interaction with a second receptor activated by longer wavelength. A second such receptor was also indicated by an electrophysiological study that had identified two different types of units, one with a peak near 500 nm, the

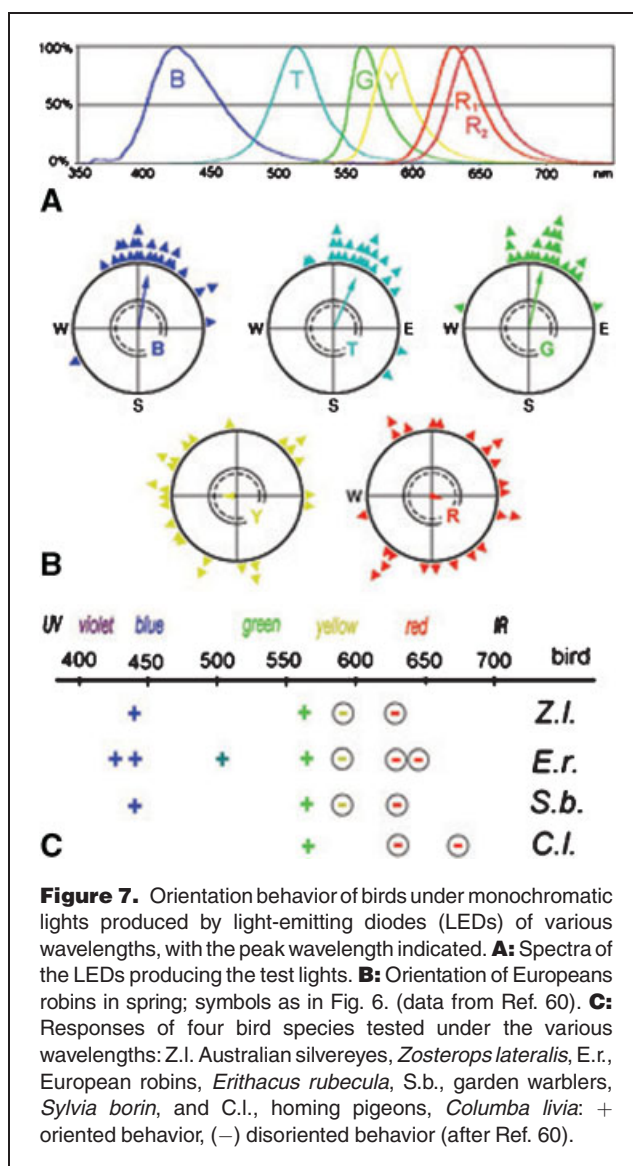


Figure 7. Orientation behavior of birds under monochromatic lights produced by light-emitting diodes (LEDs) of various wavelengths, with the peak wavelength indicated. **A:** Spectra of the LEDs producing the test lights. **B:** Orientation of European robins in spring; symbols as in Fig. 6. (data from Ref. 60). **C:** Responses of four bird species tested under the various wavelengths: Z.I. Australian silvereyes, *Zosterops lateralis*, E.r., European robins, *Erithacus rubecula*, S.b., garden warblers, *Sylvia borin*, and C.I., homing pigeons, *Columba livia*: + oriented behavior, (-) disoriented behavior (after Ref. 60).

other with a peak beyond 580 nm.⁽⁷⁴⁾ Further behavioral tests under long-wavelength light showed that birds could orient under monochromatic light of 645 nm, provided they had been exposed to this wavelength for at least 1 hour prior to the critical tests.^(81,82) This orientation was normal migratory orientation, but its origin and the possible role of the long-wavelength receptor is not yet clear (for a detailed discussion, see Ref. 82).

The experiments with birds under monochromatic light mentioned so far were performed under rather low light levels of $6-8 \times 10^{-15}$ quanta $s^{-1}m^{-2}$, an intensity found in nature more than half an hour before sunrise or after sunset. Under monochromatic light of 7 times higher intensities, which still corresponded to intensities found well before sunrise or after sunset so that saturation of the receptors can be excluded,

migratory birds showed a marked change in behavior: they no longer preferred their migratory direction. Instead, they showed axial preferences or headed into 'odd' directions.^(83–85) Directions different from the migratory direction were also observed under bichromatic lights, when low intensity 590 nm yellow light—a wavelength that, when presented alone, caused disorientation—was combined with low intensity light from the blue-to-green part of the spectrum.⁽⁸⁶⁾ In all these cases, the specific manifestation of the 'odd' directions was dependent on the light regime, with e.g. bright turquoise leading to northerly headings,⁽⁸⁰⁾ bichromatic turquoise-and-yellow light to easterly headings etc. A detailed analysis revealed some unexpected characteristics of these responses: they turned out to be 'fixed' in the sense that they did not show the normal seasonal change between spring and autumn^(80,83,86) and, most surprisingly, they were found to be polar responses, not involving the inclination compass.^(80,85) Tests with high frequency fields showed that they are not based on radical pair processes.⁽⁸⁰⁾ These findings show that certain light regimes, like monochromatic light above a certain intensity, or those leading to specific interaction of short wavelengths and the long-wavelength receptor, drive the avian magnetoreception systems towards its limits, leading to responses of fundamentally different nature. This suggests highly complex interactions of several receptors in the avian magnetoreception system, which require further analysis to be fully understood.

Tests with amphibians under monochromatic light revealed a different wavelength dependency: normal orientation was found only in a rather narrow wavelength band at the short-wavelength end of the spectrum up to 450 nm; under longer wavelength from 500 nm onward, a variety of responses, ranging from a 90° shift to disorientation, was observed, with different aftereffects of pre-exposure to long-wavelength light, which were attributed to different motivational stages.^(62–64,87) The observed differences in orientation between short-wavelength light and wavelength beyond 500 nm lead to speculations about two antagonistic spectral mechanisms indicating directions perpendicular to each other, with only the dominant receptor activated by the short wavelengths indicating correct magnetic directions (see Refs 62–64,87 for a detailed discussion). However, although the change in behavior between normal orientation and the responses under

longer wavelengths was described as wavelength dependent, it has to be noted that the longer wavelengths were presented at a higher intensity, namely at an intensity where migratory birds no longer show migratory orientation, but the 'odd' responses described above. Assuming that the magnetoreception systems of birds and amphibian are similar, it seems possible that the responses observed under wavelength beyond 500 nm represent a related type of behavior, involving fixed directions and polar responses. The same may also apply to the axial response along the north–south axis recently described and discussed as an alignment response possibly controlled by magnetite.⁽⁸⁷⁾ So far, the behavior of salamanders under long-wavelength light has not been analyzed in detail, so that further experiments are needed to clarify its nature.

Conclusion

Any attempt to summarize our knowledge on how animals perceive magnetic fields faces the problem that magnetoreception is no uniform phenomenon. Firstly, there is more than one type of magnetic information used implying more than one type of receptor, with even different types of receptors for compass information indicated. Secondly, the extent to which magnetoreception has been analyzed varies greatly among the various groups of animals—in some groups, different aspects have been analyzed, in others, we know practically nothing. Birds are by far the best studied group, and here data from different fields fall together to produce a largely consistent picture. Behavioral as well as electrophysiological studies indicate in birds the existence of two magnetoreceptor systems that provide them with two different types of information for different tasks (see also Ref. 49), as is summarized in Table 2: receptors based on radical pair processes in photopigments in the right eye for recording magnetic directions, and magnetite-based receptors in the upper beak for recording differences in magnetic intensity. In short, birds have a compass in the eye and a magnetometer in their beak.

In other vertebrates, our knowledge is much more limited. In amphibians, light-dependent mechanisms in the pineal provide a compass,⁽⁷²⁾ but whether they are based on radical pair processes and details on where the input of that receptor is processed are still unknown. In fish, anatomical details about a

Table 2. The two types of magnetoreceptors in birds

Parameter of the geomagnetic field:	Magnetic vector	Intensity gradients
Task in which it is used by birds:	compass orientation	Indicating position and/or as 'sign post' or 'trigger'
Primary processes of magnetoreception:	Radical pair processes involving photopigments	Magnetite-based processes
Site of reception:	Retina of the right eye	Upper beak and/or ethmoid region
Nerves and brain structures involved:	optic nerve, nBOR, <i>tectum opticum</i> ,	Ophthalmic branch of the <i>nervus trigeminus</i> , trigeminal ganglion

magnetite-based receptor have been described,^(43,44) but what type of information it provides is not entirely clear—electrophysiological studies suggest that it may also be a receptor for magnetic intensity. In mammals, a study using c-Fos identified the *nucleus superior colliculus* in the brain as a site of neural activity resulting from magnetic stimulation,⁽⁸⁸⁾ but neither the location of the respective receptors nor the type of information mediated is known. Fish, turtles, mammals and several arthropods have been shown to use the magnetic field as a compass without requiring light, but the reception mechanisms that they employ are not yet known. Magnetite-based processes are an option, as they could theoretically provide information on direction as well as on intensity. However, we would expect that these animals, too, possess different receptors for different tasks. We can only hope that future studies will focus on magnetoreception in some of the groups that have been neglected so far, leading to new insights and providing answers to many of the questions that still remain unanswered today.

References

- Skiles DD. 1985. The geomagnetic field: its nature, history and biological relevance. In: Kirschvink JL, Jones DS, MacFadden BJ, editors. *Magnetite Biomineralization and Magnetoreception in Organisms*. New York, London: Plenum Press. p 43–102.
- Wiltschko R, Wiltschko W. 1995. *Magnetic Orientation in Animals*. Berlin, Heidelberg, New York: Springer Verlag.
- von Middendorff A. 1859. Die Isepiptesen Rußlands. *Mém Acad Sci St Petersburg VI Ser, Tome 8*:1–43.
- Viguier C. 1882. Le sens de l'orientation et ses organes chez les animaux et chez l'homme. *Revue Philosophique de la France et de l' Etranger* 14:1–36.
- Brown FA, Webb HM, Barnwell FH. 1964. A compass directional phenomenon in mud-snails and its relation to magnetism. *Biol Bull* 127:206–220.
- Wiltschko W, Merkel FW. 1966. Orientierung zugunruhiger Rotkehlchen im statische Magnetfeld. *Verh Dtsch Zool Ges* 59:362–367.
- Lindauer M, Martin H. 1968. Die Schwereorientierung der Bienen unter dem Einfluß des Erdmagnetfelds. *Z Vergl Physiol* 60:219–243.
- Blakemore RP. 1975. Magnetotactic bacteria. *Science* 19:377–379.
- Mann S, Sparks NCH, Board RG. 1990. Magnetotactic bacteria: microbiology, biomineralization, palaeomagnetism and biotechnology. *Adv Microb Physiol* 31:125–181.
- Marhold S, Burda H, Wiltschko W. 1997. A magnetic polarity compass for direction finding in a subterranean mammal. *Naturwissenschaften* 84:421–423.
- Lohmann KJ, Pentcheff ND, Nevitt GA, Stetten GD, Zimmer-Faust RK, et al. 1995. Magnetic orientation of spiny lobsters in the ocean: experiments with undersea coil systems. *J Exp Biol* 198:2041–2048.
- Wiltschko W, Wiltschko R. 1972. Magnetic compass of European robins. *Science* 176:62–64.
- Phillips JB. 1986. Two magnetoreception pathways in a migratory salamander. *Science* 233:765–767.
- Light P, Salmon M, Lohmann KJ. 1993. Geomagnetic orientation of loggerhead sea turtles: evidence for an inclination compass. *J Exp Biol* 182:1–10.
- Arendse MC, Vrins JCM. 1975. Magnetic orientation and its relation to photic orientation in *Tenebrio molitor* L. (Coleoptera, Tenebrionidae). *Neth J Zool* 25:407–437.
- Quinn TP, Brannon EL. 1982. The use of celestial and magnetic cues by orienting sockeye salmon smolts. *J Comp Physiol* 147:547–552.
- Boles LC, Lohmann KJ. 2003. True navigation and magnetic map in spiny lobsters. *Nature* 421:60–63.
- Lohmann KJ, Lohmann CMF, Erhart LM, Bagley DA, Swing T. 2004. Geomagnetic map used in sea-turtle navigation. *Nature* 428:909–910.
- Walcott C. 1978. Anomalies in the earth's magnetic field increase the scatter of pigeons' vanishing bearings. In: Schmidt-Koenig K, Keeton WT, editors. *Animal Migration, Navigation and Homing*. Berlin, Heidelberg, New York: Springer Verlag. p 143–151.
- Phillips JB, Freake MJ, Borland SC. 2002a. Behavioral titration of magnetic map coordinates. *J Comp Physiol A188*:157–160.
- Beck W, Wiltschko W. 1988. Magnetic cues control the migratory direction of Pied Flycatchers, (*Ficedula hypoleuca* Pallas). In: Ouellet H, editor. *Acta XIX Congr Int Ornithol Vol II*. ed; Ottawa: University of Ottawa Press. p 1955–1962.
- Wiltschko W, Wiltschko R. 1992. Migratory orientation: magnetic compass orientation of garden warblers (*Sylvia borin*) after a simulated crossing of the magnetic equator. *Ethology* 91:70–79.
- Lohmann KJ, Cain SD, Dodge SA, Lohmann CMF. 2001. Regional magnetic fields as navigational markers for sea turtles. *Science* 294:364–366.
- Fransson T, Jakobsson S, Johansson P, Kullberg C, Lind J, et al. 2001. Magnetic cues trigger extensive refuelling. *Nature* 414:35–36.
- Kalmijn AJ. 1978. Electric and magnetic sensory world of sharks, skates and rays. In: Hodgson FS, Mathewson RA, editors. *Sensory Biology of Sharks, Skates and Rays*. Arlington, VA: Office Naval Res. p 507–528.
- Edmonds DJ. 1996. A sensitive optically detected magnetic compass for animals. *Proc R Soc Lond B* 263:295–298.
- Liboff AR, Jenrow KA. 2000. New model for the avian magnetic compass. *Bioelectromagnetics* 21:55–565.
- Kirschvink JL, Jones DS, MacFadden BJ, editors. 1985. *Magnetite Biomineralization and Magnetoreception in Organisms*. New York, London: Plenum Press.
- Yorke ED. 1979. A possible magnetic transducer in birds. *J Theor Biol* 77:101–105.
- Kirschvink JL, Gould JL. 1981. Biogenetic magnetite as a basis for magnetic field detection in animals. *BioSystems* 13:181–201.
- Kirschvink JL, Walker MM. 1985. Particle-size considerations for magnetite-based magnetoreceptors. In: Kirschvink JL, Jones DS, MacFadden BJ, editors. *Magnetite Biomineralization and Magnetoreception in Organisms*. New York, London: Plenum Press. p 243–256.
- Shcherbakov VP, Winklhofer M. 1999. The osmotic magnetometer: a new model for magnetite-based magnetoreceptors in animals. *Eur Biophys J* 28:380–392.
- Davila AF, Winklhofer M, Shcherbakov V, Petersen N. 2005. Magnetic pulse affects a putative magnetoreceptor mechanism. *Biophys J* 89:56–63.
- Schulten K, Windemuth A. 1986. Model for a physiological magnetic compass. In: Maret G, Boccara N, Kiepenheuer J, editors. *Biophysical Effects of Steady Magnetic Fields*. Berlin, Heidelberg, New York: Springer Verlag. p 99–106.
- Ritz T, Adem S, Schulten K. 2000. A model for vision-based magnetoreception in birds. *Biophys J* 78:707–718.
- Sancar A. 2003. Structure and function of DNA photolyase and cryptochrome blue-light photoreceptors. *Chem Rev* 103:2203–2237.
- Giovane B, Byrdin M, Ahmad M, Brettel K. 2003. Light-induced electron transfer in a cryptochrome blue-light photoreceptor. *Nature Struct Biol* 6:489–490.
- Beason RC, Nichols JE. 1984. Magnetic orientation and magnetically sensitive material in a transequatorial migratory bird. *Nature* 309:151–153.
- Beason RC, Brennon WJ. 1986. Natural and induced magnetization in the bobolink (*Dolichonyx oryzivorus*). *Ethology* 91:75–80.
- Williams MN, Wild JM. 2001. Trigeminally innervated iron-containing structures in the beak of homing pigeons and other birds. *Brain Research* 889:243–246.
- Fleissner G, Holtkamp-Rötzler E, Hanzlik M, Winklhofer M, Fleissner G, et al. 2003. Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. *J Comp Neurol* 458:350–360.
- Mann S, Sparks NCH, Walker MM, Kirschvink JL. 1988. Ultrastructure, morphology and organization of biogenic magnetite from sockeye salmon, *Oncorhynchus nerka*: implications for magnetoreception. *J Exp Biol* 140:35–49.

43. Walker MM, Diebel CE, Haugh CV, Pankhurst PM, Montgomery JC, Green CR. 1997. Structure and function of the vertebrate magnetic sense. *Nature* 390:371–376.
44. Diebel CE, Proksch R, Green CR, Neilson P, Walker MM. 2000. Magnetite defines a vertebrate magnetoreceptor. *Nature* 406:299–302.
45. Semm P, Beason RC. 1990. Responses to small magnetic variations by the trigeminal system of the bobolink. *Brain Res Bull* 25:735–740.
46. Wiltschko W, Munro U, Beason RC, Ford H, Wiltschko R. 1994. A magnetic pulse leads to a temporary deflection in the orientation of migratory birds. *Experientia* 50:697–700.
47. Wiltschko W, Munro U, Ford H, Wiltschko R. 1998. Effect of a magnetic pulse on the orientation of Silvereyes, *Zosterops l. lateralis*, during spring migration. *J Exp Biol* 201:3257–3261.
48. Munro U, Munro JA, Phillips JB, Wiltschko R, Wiltschko W. 1997. Evidence for a magnetite-based navigational 'map' in birds. *Naturwissenschaften* 84:26–28.
49. Beason RC. 2005. Mechanisms of magnetic orientation in birds. *Integr Comp Biol* 45:565–573.
50. Beason RC, Wiltschko R, Wiltschko W. 1997. Pigeon homing: effects of magnetic pulse on initial orientation. *Auk* 114:405–415.
51. Beason RC, Dussourd N, Deutschlander M. 1995. Behavioural evidence for the use of magnetic material in magnetoreception by a migratory bird. *J Exp Biol* 198:141–146.
52. Beason RC, Semm P. 1996. Does the avian ophthalmic nerve carry magnetic navigational information? *J Exp Biol* 199:1241–1244.
53. Mora CV, Davison M, Wild JM, Walker MM. 2004. Magnetoreception and its trigeminal mediation in the homing pigeon. *Nature* 432:508–511.
54. Wiltschko W, Munro U, Wiltschko W, Kirschvink JL. 2002a. Magnetite-based magnetoreception in birds: the effect of a biasing field and a pulse on migratory behavior. *J Exp Biol* 205:3031–3037.
55. Marhold S, Burda H, Krellos I, Wiltschko W. 1997. Magnetic orientation in the common mole-rat from Zambia. In *Orientation & Navigation—Birds, Human & other Animals*. Oxford: Royal Inst of Navig. p. 5–1–5–9.
56. Irwin WP, Lohmann KJ. 2005. Disruption of magnetic orientation in hatchling loggerhead sea turtles by pulsed magnetic fields. *J Comp Physiol* 191:475–480.
57. Wiltschko R, Wiltschko W. 1978. Evidence for the use of magnetic outward-journey information in homing pigeons. *Naturwissenschaften* 65:112.
58. Wiltschko W, Wiltschko R. 1981. Disorientation of inexperienced young pigeons after transportation in total darkness. *Nature* 291:433–434.
59. Phillips JB, Borland SC. 1992. Magnetic compass orientation is eliminated under near-infrared light in the eastern red-spotted newt, *Notophthalmus viridescens*. *Anim Behav* 44:796–797.
60. Wiltschko W, Wiltschko R. 2002. Magnetic compass orientation in birds and its physiological basis. *Naturwissenschaften* 89:445–452.
61. Muheim R, Bäckman J, Åkesson S. 2002. Magnetic compass orientation in European robins is dependent on both wavelength and intensity of light. *J Exp Biol* 205:3845–3856.
62. Phillips JB, Borland SC. 1992. Behavioral evidence for use of a light-dependent magnetoreception mechanism by a vertebrate. *Nature* 359:142–144.
63. Phillips JB, Borland SC. 1992. Wavelength specific effects of light on magnetic compass orientation of the eastern red-spotted newt *Notophthalmus viridescens*. *Ethol Ecol Evol* 4:33–42.
64. Phillips JB, Borland SC. 1994. Use of a specialized magnetoreception system for homing by the eastern red-spotted newt *Notophthalmus viridescens*. *J Exp Biol* 188:275–291.
65. Lohmann KJ. 1991. Magnetic orientation by hatchling loggerhead sea turtles (*Caretta caretta*). *J Exp Biol* 155:37–49.
66. Lohmann KJ, Lohmann CMF. 1993. A light-independent magnetic compass in the leatherback sea turtle. *Biol Bull* 185:149–151.
67. Ritz T, Thalau P, Phillips JB, Wiltschko R, Wiltschko W. 2004. Resonance effects indicate a radical-pair mechanism for avian magnetic compass. *Nature* 429:177–180.
68. Thalau P, Ritz T, Stapput K, Wiltschko R, Wiltschko W. 2005. Magnetic compass orientation of migratory birds in the presence of a 1.315 MHz oscillating field. *Naturwissenschaften* 92:86–90.
69. Wiltschko W, Traudt J, Güntürkün O, Prior H, Wiltschko R. 2002. Lateralization of magnetic compass orientation in a migratory bird. *Nature* 419:467–470.
70. Wiltschko W, Munro U, Ford H, Wiltschko R. 2003. Lateralisation of magnetic compass orientation in silvereyes, *Zosterops lateralis*. *Austr J Zoo* 51:1–6.
71. Prior H, Wiltschko R, Stapput K, Güntürkün O, Wiltschko W. 2004. Visual lateralization and homing in pigeons. *Behav Brain Res* 154:301–310.
72. Möller A, Sagasser S, Wiltschko W, Schierwater B. 2004. Retinal cryptochrome in a migratory passerine bird: a possible transducer for the avian magnetic compass. *Naturwissenschaften* 91:585–588.
73. Mouritsen H, Janssen-Bienhold U, Liedvogel M, Feenders G, Stalleicken J, et al. 2004. Cryptochromes and neuronal-activity markers colocalize in the retina of migratory birds during magnetic orientation. *Proc Nat Acad Sci USA* 101:14294–14299.
74. Deutschlander ME, Borland SC, Phillips JB. 1999. Extraocular magnetic compass in newt. *Nature* 400:324–325.
75. Semm P, Nohr D, Demaine C, Wiltschko W. 1984. Neural basis of the magnetic compass: interaction of visual, magnetic and vestibular inputs in the pigeon's brain. *J Comp Physiol* 155:283–288.
76. Semm P, Demaine C. 1986. Neurophysiological properties of magnetic cells in the pigeon's visual system. *J Comp Physiol A* 159:619–625.
77. Mai JK, Semm P. 1990. Patterns of glucose utilization following magnetic stimulation. *J Hirnforsch* 31:331–336.
78. Wiltschko W, Munro U, Ford H, Wiltschko R. 1993. Red light disrupts magnetic orientation of migratory birds. *Nature* 364:525–527.
79. Wiltschko W, Gesson M, Wiltschko R. 2001. Magnetic compass orientation of European robins under 565 nm green light. *Naturwissenschaften* 88:387–390.
80. Wiltschko R, Ritz T, Stapput K, Thalau P, Wiltschko W. 2005. Two different types of light-dependent responses to magnetic fields in birds. *Curr Biol* 15:1518–1523.
81. Möller A, Gesson M, Noll C, Phillips J, Wiltschko R, et al. 2001. Light-dependent magnetoreception in migratory birds previous exposure to red light alters the response to red light. In *Orientation and Navigation—Birds, Humans & other Animals*. Oxford: Royal Inst of Navig. p. 6–1–6–6.
82. Wiltschko W, Möller A, Gesson M, Noll C, Wiltschko R. 2004. Light-dependent magnetoreception in birds analysis of the behaviour under red light after pre-exposure to red light. *J Exp Biol* 207:1193–1202.
83. Wiltschko W, Wiltschko R, Munro U. 2000. Light-dependent magnetoreception in birds: the effect of intensity of 565-nm green light. *Naturwissenschaften* 87:366–369.
84. Wiltschko W, Wiltschko R. 2001. Light-dependent magnetoreception in birds: the behavior of European robins, *Erithacus rubecula*, under monochromatic light of various wavelengths. *J Exp Biol* 204:3295–3302.
85. Wiltschko W, Munro U, Ford H, Wiltschko R. 2003. Magnetic orientation in birds: non-compass responses under monochromatic light of increased intensity. *Proc R Soc Lond B* 270:2133–2140.
86. Wiltschko W, Gesson M, Stapput K, Wiltschko R. 2004b. Light-dependent magnetoreception in birds: interaction of at least two different receptors. *Naturwissenschaften* 91:130–134.
87. Phillips JB, Borland SC, Freake M, Brassart J, Kirschvink JL. 2002. 'Fixed-axis' magnetic orientation by an amphibian: non-shoreward-directed compass orientation, misdirected homing or positioning a magnetite-based map detector in a consistent alignment relative to the magnetic field? *J Exp Biol* 205:3903–3914.
88. Némec P, Altmann J, Marhold S, Burds H, Oelschläger HHA. 2001. Neuroanatomy of magnetoreception: the *superior colliculus* involved in magnetic orientation in a mammal. *Science* 294:366–368.