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Magnetic orientation and magnetoreception in birds and other animals

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Abstract Animals use the geomagnetic field in many ways: the magnetic vector provides a compass; magnetic intensity and/or inclination play a role as a component of the navigational ‘map’, and magnetic conditions of certain regions act as ‘sign posts’ or triggers, eliciting specific responses. A magnetic compass is widespread among animals, magnetic navigation is indicated e.g. in birds, marine turtles and spiny lobsters and the use of magnetic ‘sign posts’ has been described for birds and marine turtles. For magnetoreception, two hypotheses are currently discussed, one proposing a chemical compass based on a radical pair mechanism, the other postulating processes involving magnetite particles. The available evidence suggests that birds use both mechanisms, with the radical pair mechanism in the right eye providing directional information and a magnetite-based mechanism in the upper beak providing information on position as component of the ‘map’. Behavioral data from other animals indicate a light-dependent compass probably based on a radical pair mechanism in amphibians and a possibly magnetite-based mechanism in mammals. Histological and electrophysiological data suggest a magnetite-based mechanism in the nasal cavities of salmonid fish. Little is known about the parts of the brain where the respective information is processed.

alien to us, as man cannot consciously sense the geomagnetic field (but see Baker 1989). To fully understand this phenomenon, we must first consider the type of information the geomagnetic field can provide and—even more important—the type of information animals do actually use.

The earth itself is a huge magnet, with its poles situated close to the rotational poles. The magnetic field lines leave the surface of the earth at the southern magnetic pole, run around the globe and re-enter at the northern magnetic pole. As a consequence, the magnetic field lines point upward on the southern hemisphere, run parallel to the earth’s surface at the magnetic equator and point downward in the northern hemisphere. Magnetic inclination or dip, the angle between the local magnetic vector and the horizontal, changes continuously, showing a fairly regular gradient, from -90° at the southern magnetic pole to $+90^\circ$ at the northern magnetic pole, being 0° at the magnetic equator (Fig. 1). The intensity of the geomagnetic field, indicated by the length of the arrows in Fig. 1, is highest at the two poles and lowest near the magnetic equator. It thus forms gradients running from the poles to the equator on each hemisphere (see Skiles 1985 for details). This regular field can be locally distorted by material in the upper crust resulting in magnetic anomalies with slight increases or decreases in intensity. It is temporally altered by electromagnetic radiation originating in the sun causing daily variations, which, in the temperate latitudes, lead to slight decrease in magnetic intensity around noon; occasional magnetic storms may cause more pronounced changes in all magnetic parameters. These changes, however, are mostly small compared to the regular field.

The geomagnetic field thus represents a reliable, omnipresent source of navigational information. This information can be of two kinds: the magnetic vector provides directional information that animals could use as a compass, whereas total intensity and/or inclination may provide information that might be used as a component of the navigational ‘map’ indicating position.

The geomagnetic field

Many animals are able to perceive the magnetic field of the earth; among them are mollusks, arthropods and members of all major groups of vertebrates. This seems

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Magnetic orientation

Animals have been shown to use both types of information for various tasks. However, our knowledge on magnetic orientation differs greatly between the various animals. Birds are by far the best studied group, followed by marine turtles, while little is known about other vertebrates and arthropods. Here, we summarize the findings that are most important in demonstrating how widespread the use of magnetic information is and what types of information the animals utilize.

Magnetic compass orientation

A magnetic compass means that directions can be determined with the help of the magnetic field. In orientation experiments, the observation that an animal responds to shift in magnetic North with a corresponding change in its heading is diagnostic of magnetic compass use.

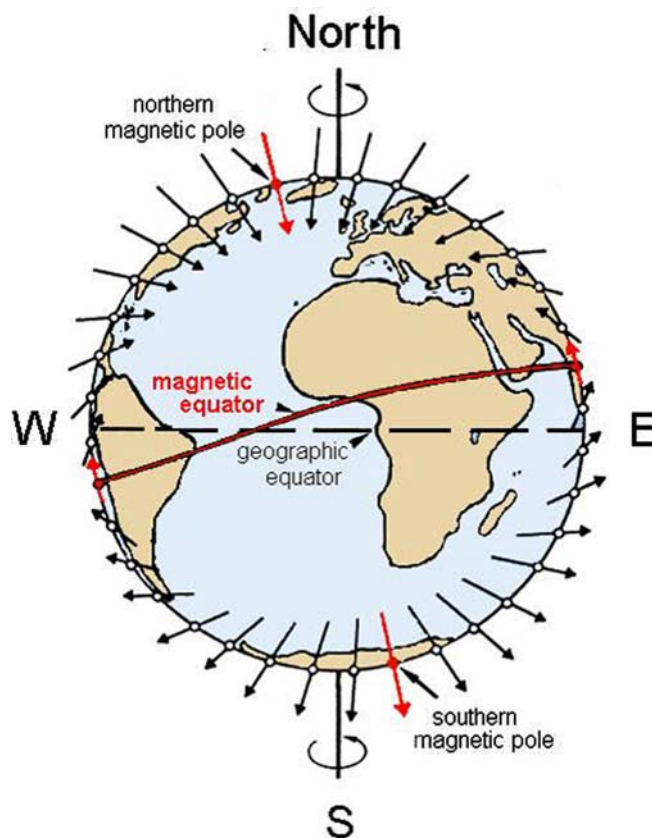


Fig. 1 Magnetic field of the earth. The *arrows* indicate the local magnetic vectors with their lengths proportional to the intensity of the local field. The magnetic poles and the magnetic equator are marked in red (after Wiltschko and Wiltschko 1995)

Demonstrating magnetic compass orientation

A magnetic compass appears to be rather widespread among animals. It was first demonstrated in migratory birds, taking advantage of a spontaneous behavior: during migration season, the urge of migrants to move into migratory direction is so strong that even captive birds head into the respective direction in their cages. When tested in the local geomagnetic field, European robins, *Erithacus rubecula*, but also other species of migrants, showed a strong preference of their seasonally appropriate migratory direction. Tested in an experimental field of equal intensity, but with magnetic North turned by a certain angle with the help of Helmholtz coils, the same birds altered their headings accordingly and preferred the direction that now corresponded to the same magnetic course (Fig. 2, left, center). This clearly shows that robins used the geomagnetic field to orient their movements (see Wiltschko and Wiltschko 1995 for details).

Meanwhile, magnetic compass orientation has been described for a number of other birds, such as several passerine migrants, homing pigeons (Walcott and Green 1974) and a shorebird species (Gudmundsson and Sandberg 2000). A magnetic compass has also been demonstrated in numerous other animals, including members of the other major groups of vertebrates, crustaceans, insects and a mollusk species (see Table 1). The behaviors involved range from spontaneous behavior, like e.g. the headings of sockeye salmon fry, *Oncorhynchus nerka* (Quinn 1980) or building a nest in Zambian mole rats, *Cryptomys* sp. (Marhold et al. 1997a), over directions set by other environmental factors, like in hatchling marine loggerhead turtles *Caretta caretta* heading away from the shore (e.g. Lohmann 1991), y -axis orientation of various arthropods (e.g. Pardi et al. 1988) and the salamander *Notophthalmus viridescens* (e.g. Phillips 1986) at the border land/water, building activities in honeybees, *Apis mellifera* (e.g. DeJong 1982) and compass termites, *Amitermes meridionalis* (Duelli and Duelli-Klein 1978; Jacklyn and Munro 2002) to directional training and other acquired directions (for summary, see R. Wiltschko and Wiltschko 1995).

Functional mode of magnetic compass mechanisms

The functional mode of the magnetic compass was first analyzed in birds, again with the help of migratory orientation. Two unexpected properties became evident.

In contrast to our technical compass, the avian magnetic compass was found to be an '*inclination compass*', based on the inclination of the field lines instead of their polarity. Apparently, birds can only perceive the axial course of the field lines; to derive non-ambiguous directional information, they must interpret the inclination of the field lines with respect to up and down. This was demonstrated in a magnetic field where the vertical component was inverted: birds heading north in

Table 1 Animals demonstrated to use a magnetic compass (numbers in parentheses give the number of species where the respective type of compass is indicated; ??? means that the type of compass has not yet been analyzed)

Systematics	No. of orders	No. of families	No. of species	Type of compass?
Mollusks				
Snails	1	1	1	???
Arthropods				
Crustacean	3	3	5	Polarity compass (1)
Insects	6	7	9	Polarity compass? (1)
Vertebrates				
Cartilaginous fish	1	1	1	???
Bony fish	2	2	4	Polarity compass? (1)
Amphibians	1	2	2	Inclination compass (1)
Reptilians	1	2	2	Inclination compass (2)
Birds	3	11	20	Inclination compass (8)
Mammals	2	2	3	Polarity compass (1)

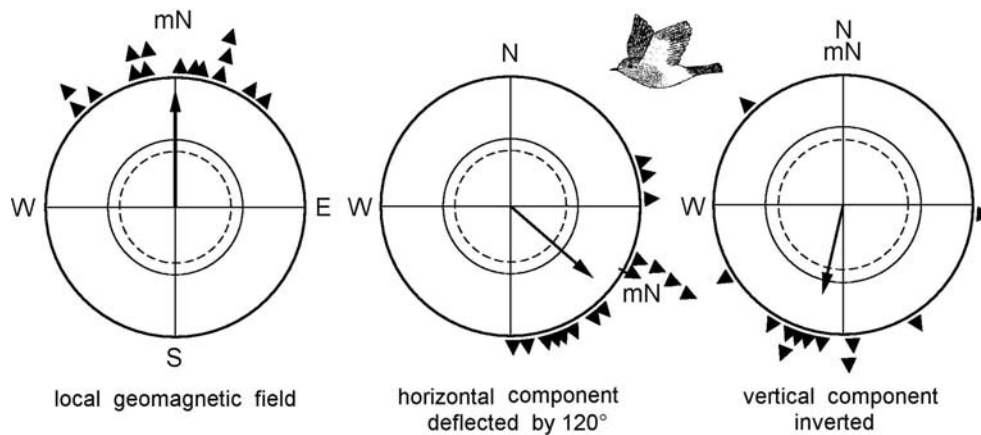


Fig. 2 Orientation behavior of migrating European Robins in spring, tested in the local geomagnetic field and in two experimental fields. *mN*, magnetic North. The *triangles* at the periphery of the circle mark mean headings of individual birds, the *arrows* represent the grand mean vectors with their lengths proportional to the radius of the circle. The two *inner circles* are the 5% (*dashed*) and the 1 % significance border of the Rayleigh test (data from Wiltschko and Wiltschko 1999; Wiltschko et al. 2001)

the geomagnetic field reversed their heading, now preferring magnetic South (Fig. 2, right diagram). Reversing the horizontal component and inverting the vertical component alter the axial course of the field lines in the same way (Fig. 3); an animal not perceiving the polarity of the magnetic field will not realize any difference. Hence birds reverse their headings in both situations alike (Wiltschko and Wiltschko 1972). This means that the avian magnetic compass does not distinguish between magnetic ‘north’ and ‘south’ as indicated by polarity, but between ‘poleward’ where the field lines point to the ground, and ‘equatorward’, where they point upward (Fig. 3).

All bird species studied so far use an ‘inclination compass’. Yet this is not the only type of magnetic compass found in animals. Sea turtles possess an inclination compass like birds (Light et al. 1993; Lohmann and Lohmann 1992), whereas salmon (Quinn and Brannon 1982) and rodents (Marhold et al. 1997a) have a ‘polarity compass’ based on the

polarity of the field lines (see Table 1, last column): they do not reverse their headings when the vertical component is inverted (Fig. 4). The latter seems to apply also for the few invertebrate species analyzed so far (e.g. Lohmann et al. 1995). Salamanders were first reported to use both types of mechanisms, an inclination compass for shoreward orientation and a polarity

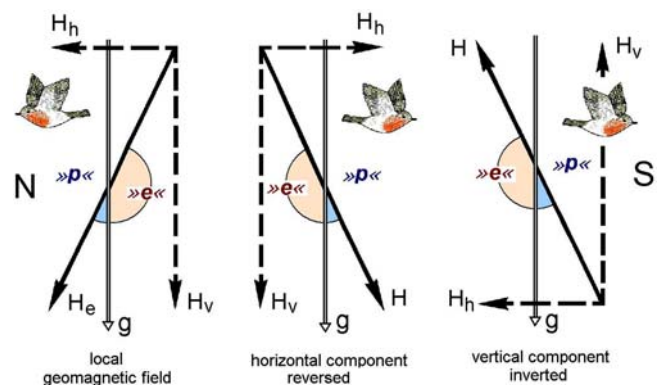
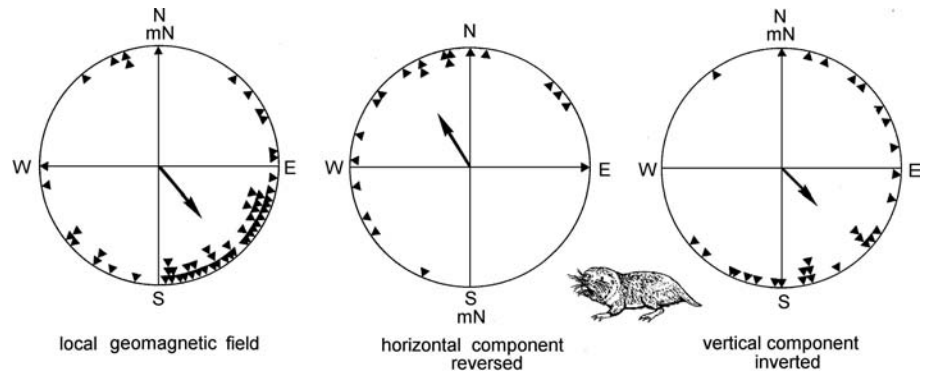


Fig. 3 Vertical section through the geomagnetic field to illustrate the functional mode of the inclination compass. *N*, *S*, magnetic North and South. *H*, magnetic vector, with *H_e*, the vector of the geomagnetic field; *H_h*, *H_v*, horizontal and vertical component, respectively; *g*, gravity vector. » *p* «, » *e* «, ‘poleward’ and ‘equatorward’, the readings of the inclination compass. The *bird* flies ‘poleward’

Fig. 4 Orientation of mole rats *Cryptomys* sp. (Rodentia) in the geomagnetic field and in two experimental fields. The triangles at the periphery of the circle mark the direction of the nest position from the center of the arena; the arrow represents the mean vector proportional to the radius of the circle (data from Marhold et al. 1997a)



compass for homing (Phillips 1986); however, as magnetic parameters are also involved in determining the home course, the data were interpreted to suggest a polarity compass for homing may also reflect an effect on the mechanisms determining this course (Phillips and Borland 1994), leaving the inclination compass as the only compass mechanism demonstrated in salamanders.

Another surprising finding in birds was that their magnetic compass is closely tuned to the total intensity of the ambient field. When the intensity of an experimental field was reduced or increased by 20–30%, birds were no longer oriented, suggesting a rather narrow functional window (Fig. 5). This window is not fixed, however, but adjusts to lower or to higher intensities when birds are exposed to these intensities for three days, but possibly also after a much shorter period of time. At the same time, these birds did not lose their ability to orient in the local geomagnetic field, yet they proved unable to orient in an intermediate field. (see Fig. 5; Wiltschko 1978). This indicates that the newly-gained ability to orient in higher or lower fields represents neither a shift nor an amplification of the functional range. Apparently, birds can orient only in field intensities they experienced before, with this experience possibly forming a new functional range. The magnetic compass of other animals has not yet been analyzed in view of a functional window of limited range.

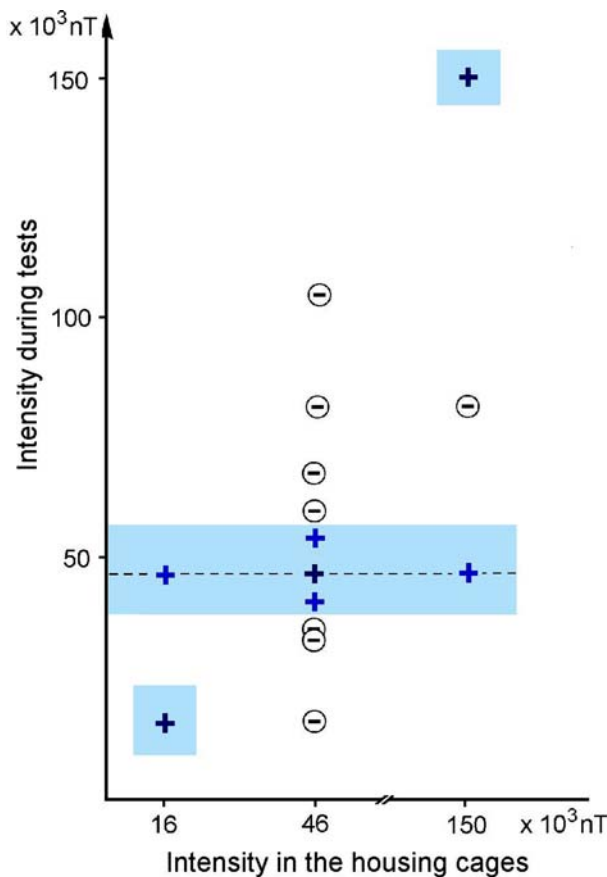


Fig. 5 Orientation responses of robins in magnetic fields of different total intensities indicating the functional window of the avian magnetic compass (shaded in blue). It is narrowly tuned to the intensity in which the bird is living; keeping birds at other intensities gives rise to a new functional window at the respective intensity. The intensity of the local geomagnetic field, 46,000 nT, is marked by a dashed line (data from Wiltschko 1978)

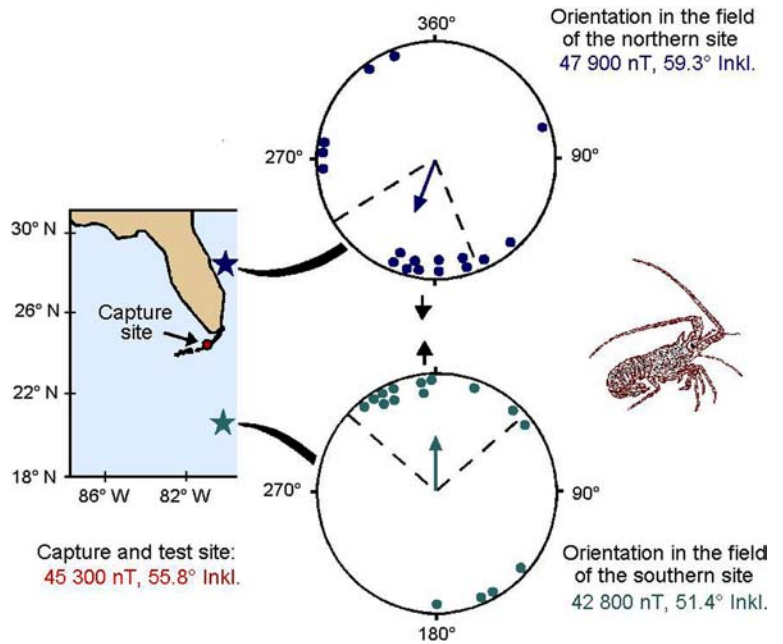
Non-compass use of the magnetic field

Because of their nature as gradients running from north to south, magnetic intensity and inclination can give information on position. Evidence for this use of magnetic information is much rarer than that supporting compass use, and the number of species involved is much smaller.

Magnetic navigation

Magnetic intensity has been discussed as a component of the navigational 'map' of pigeons ever since the late nineteenth century (Viguer 1882). It could be used in the following way: in the northern hemisphere, birds know by experience that magnetic intensity increases towards north; when finding themselves at a location with intensity higher than at home, they would conclude that they are north of home and hence must head south to return. The intensity difference to be detected for magnetic navigation within the home range would be in the order of magnitude of 20 to 100 nT, the

Fig. 6 True navigation by magnetic parameters indicated in spiny lobsters. The lobsters were tested near their capture site in magnetic fields replicating the ones of two distant geographic locations (marked with *asterisks*). In the circular diagrams, the *small arrows* outside the circle indicate the home directions from the simulated sites. *Dots* at the periphery of the circle mark the headings of single lobsters; the *arrow* represents the mean vector proportional to the radius of the circle, with the *dashed radii* indicating the 95% confidence interval of the mean direction (after Boles and Lohmann 2003)

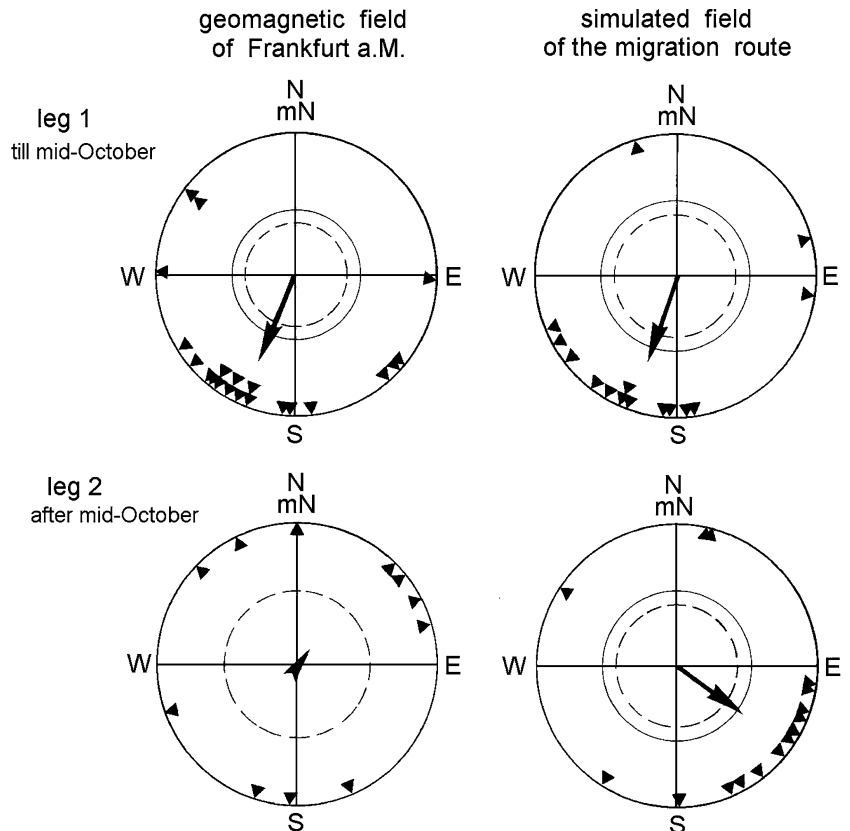


differences in inclination in fractions of a degree, depending on the regional gradients and the distances involved.

First indications that animals use magnetic parameters in their navigational ‘map’ came from correlations of the vanishing bearings of homing pigeons, *Columba*

livia f. domestica, with temporal changes of the magnetic field (e.g. Keeton et al. 1974). Pigeons released in a magnetic anomaly showed an increase in scatter up to disorientation that was strongly correlated with steepness of the local intensity gradient (Walcott 1978). The effects of various magnetic treatments on pigeons’ initial

Fig. 7 Specific magnetic conditions acting as ‘sign posts’ in Pied Flycatchers: orientation of hand-raised birds tested in cages during their first autumn migration. *Left diagrams*: birds tested in the local magnetic field of Frankfurt a.M. (46,000 nT, 66° inclination) during the entire migration season; *right diagrams*: birds tested in magnetic fields simulating in four steps the decrease in intensity and inclination to 34,000 nT, 10° inclination Pied Flycatchers would normally experience during autumn migration. *Symbols* as in Fig. 2 (data from Beck and Wiltschko 1988)



orientation that cannot be attributed to interfering with the magnetic compass also suggested an involvement of magnetic factors in the navigational process (for summary, see Wiltschko and Wiltschko 1995). Migratory Australian Silvereyes, *Zosterops lateralis*, also responded to slight changes in magnetic intensity and inclination (Fisher et al. 2003).

Recently, however, more direct evidence for the use of magnetic factors as navigational parameters became available: When spiny lobsters *Panulirus argus* were captured and exposed at their capture site to magnetic conditions found at a distant site, they headed into the direction that would have brought them home from that distant site (Fig. 6; Boles and Lohmann 2003). Similar results also indicating true navigation by magnetic parameters have now also been reported for subadult green sea turtles, *Chelonia mydas* (Lohmann et al. 2004). In salamanders *Notophthalmus viridescens*, a response to changes in the angle of inclination alone has been described (Phillips et al. 2002a).

Magnetic conditions as 'sign posts' or triggers

Total intensity and/or inclination may also serve as 'sign-posts', marking specific regions where animals must act in a specific way. The respective responses are innate and are elicited when the animals encounter the crucial magnetic conditions. A first example involved passerine birds that change their migration course in order to avoid ecological barriers. The central European population of Pied Flycatchers, *Ficedula hypoleuca*,

heads first southwest to Iberia, then changes to a southeasterly course, in this way travelling around the Alps, the Mediterranean Sea and the central Sahara. Hand-raised birds of this population started autumn migration with southwesterly preferences when tested in cages in the local geomagnetic field of central Europe; however, they showed the change in direction only when they experienced the magnetic field of northern Africa (Fig. 7; Beck and Wiltschko 1988). Apparently, these magnetic conditions serve as a 'sign post' and initiate the second leg of migration. Likewise, in Garden Warblers, *Sylvia borin*, transequatorial migrants, a horizontal field caused a reversal in headings – here, the field of the equator serves as trigger, eliciting the change in magnetic heading from 'equatorward' to 'poleward' that enables these birds to go on into the southern hemisphere (Wiltschko and Wiltschko 1992). The function of magnetic parameters as 'sign post' is not restricted to orientation responses, however; it also includes physiological responses. Thrush nightingales, *L. luscinia*, caught and held in Sweden, showed a slow weight gain during autumn migration; simulation of the specific magnetic condition of northern Egypt induced a much more rapid gain in weight; during real migration, this extra fat load enables these birds to cross the vast ecological barrier of the Sahara (Fransson et al. 2001).

Other well-documented cases of magnetic conditions of certain regions eliciting specific responses have been reported from young loggerhead turtles. Juvenile turtles from Florida spend the first years of their life in the Atlantic gyre; conditions found at the edge of the Atlantic gyre caused them to prefer headings that would lead them back into the gyre and thus prevent them from leaving the normal range of their population. Here, intensity, inclination and a combination of both proved effective (Fig. 8; Lohmann and Lohmann 1994, 1996; Lohmann et al. 2001).

Implications for magnetoreception

The behavioral evidence summarized above clearly shows that magnetoreception is not a uniform phenomenon: animals use different parameters of the geomagnetic field in different tasks. The nature of these parameters makes it rather unlikely that they are detected by the same mechanism. The magnetic compass does not respond to the small differences in intensity whose detection is crucial for using magnetic intensity as component of the navigational 'map'; these small changes are well within the functional window of the compass mechanism and are thus filtered off. Likewise, a mechanism designed to record tiny changes in intensity can, at the same time, hardly measure the direction of the magnetic field with great precision. Hence we must expect animals to have specialized receptors for mediating magnetic intensity and others for mediating information on magnetic direction, just as we use different technical devices – a compass and a magnetometer – to measure

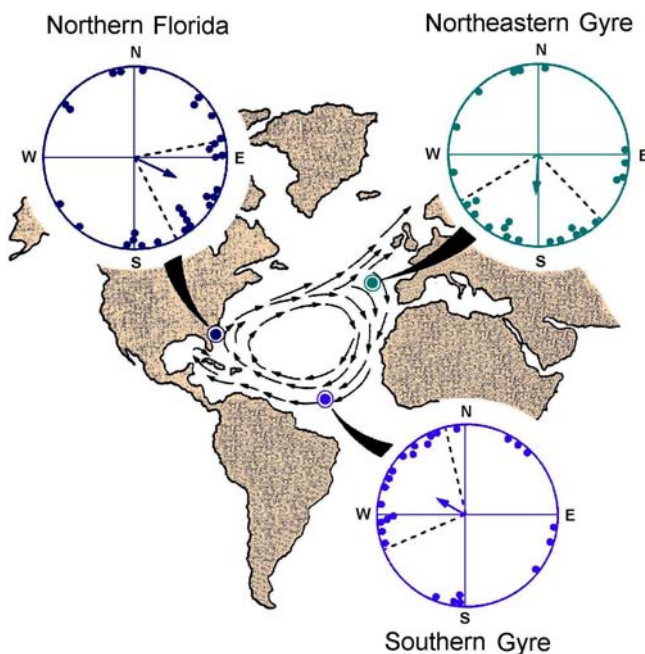


Fig. 8 Orientation of hatchling loggerhead turtles tested in magnetic field characteristic for three locations (marked by dots) at the edge of the Atlantic gyre (indicated by small arrows). Symbols in the circular diagrams as in Fig. 6 (from Lohmann et al. 2001)

the direction and the intensity of the magnetic field. Additionally, the two types of magnetic compass – inclination compass and polarity compass – imply that here, too, different mechanisms may be involved.

Magnetoreception

For a complete understanding of a ‘magnetic sense’, one needs to know (1) details on the primary processes mediating magnetic input, (2) the location of the sensory organ, its structure and its connections to the central nervous system and (3) what parts of the brain are involved in processing magnetic information. Unfortunately, our knowledge on the physiological and neurobiological processes associated with magnetoreception is still rather limited. The various animal groups are not equally represented: birds are by far the best studied group; fish are the only other group where some neuroanatomical and electrophysiological evidence is available.

A number of models for magnetoreception based on fundamentally different principles have been proposed, the three most prominent ones being (1) induction, (2) interactions of chemical processes with the ambient magnetic field and (3) processes involving permanently magnetic material.

Induction would be restricted to marine animals because it requires sea water as a surrounding medium with high conductivity. When skates and rays swim into different directions, they cross the field lines of the geomagnetic field at different angles, thus inducing different voltages at their electric organs (Murray 1962). The ampullary organs of skates and rays are known to be sensitive enough to detect the differences in voltage induced when the fish are heading in different directions (e.g. Kalmijn 1978), but evidence that this information is indeed used to derive compass orientation is still lacking.

The other two models – the ‘radical pair’-model and the magnetite-hypothesis – are more general and would also serve terrestrial animals and those living in fresh water.

Magnetoreception based on ‘radical pair’-mechanisms, and associated findings

The radical pair model, first proposed by Schulten and Windemuth (1986) and later detailed by Ritz et al. (2000), postulates a ‘chemical compass’ based on direction-specific interactions of radical pairs with the ambient magnetic field. It is supported by experimental evidence in birds and amphibians.

The model

In the initial step, the radical pair model assumes that specialized photopigments absorb a photon and are

elevated to the singlet excited state. They form singlet radical pairs with antiparallel spin, which, by singlet–triplet interconversion, may turn into triplet pairs with parallel spin (Fig. 9). The magnetic field alters the dynamics of the transition between spin states; as a consequence, the triplet yield depends on the alignment of the macromolecule in the ambient magnetic field (for details, see Ritz et al. 2000) – it can thus convey information on magnetic directions. As receptor molecule, Ritz and colleagues (2000) suggested cryptochromes, a class of photopigments known from plants and related to photolyases (Sancar 2003); they possess chemical properties crucial for the model, including the ability to form radical pairs (Giovani et al. 2003).

To obtain magnetic compass information by a radical pair mechanism, animals must take advantage of the fact that triplet products are chemically different from singlet products and compare the triplet yields in different directions. This requires an orderly array of photopigments oriented in the various spatial directions. These conditions could be met by the more or less spherical arrangement of receptors in the eyes – radical pair processes would generate characteristic patterns of activation across the retina (Ritz et al. 2000). These patterns whose specific manifestations depend on magnetic intensity, would be centrally symmetric around the axis of the field lines, that is, axial rather than polar, and would enable animals to detect the direction of the ambient field. At the same time, the initial photon absorption would make magnetoreception a light-dependent process.

Evidence supporting the radical pair model

Because of the axial pattern of activation, a radical pair mechanism would provide an inclination compass.

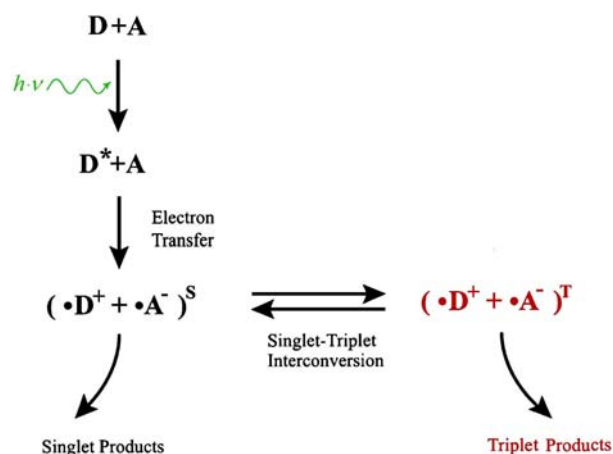


Fig. 9 Schema of a radical pair mechanism: a donor absorbs a photon and, by electron transfer, a singlet radical pair is formed. Singlet–triplet interconversion leads to triplet pairs, with the triplet yield depending on the alignment of the molecules in the ambient magnetic field. Triplet products are chemically different from the singlet products and thus may play a role in magnetoreception (modified from Ritz et al. 2000)

Hence the radical pair model can only apply to the magnetic compass of birds, amphibians and marine turtles (see Table 1). In birds, this model also provides an explanation for the narrow functional window of the magnetic compass that can be altered by exposing them to magnetic intensities outside the normal functional range (see Fig. 5): when tested under intensities that differ markedly from that of the local geomagnetic field, the birds would be faced with a novel activation pattern (Ritz et al. 2000). This may confuse them at first, yet the pattern retains its central symmetry around the axis of the field lines. Given sufficient time, the birds may become familiar with the novel pattern and learn to interpret it, thus regaining their ability to orient.

The radical pair model predicts that magnetoreception is light-dependent. Light is indeed required for magnetic compass orientation in birds and salamanders. First evidence came from behavioral experiments with young homing pigeons that use their magnetic compass to record the direction of displacement: displaced in total darkness, they were disoriented (Wiltschko and Wiltschko 1981), just as young pigeons displaced in a distorted magnetic field had been (Wiltschko and Wiltschko 1978). Disorientation in the absence of visible light was also observed in the salamander *Notophthalmus viridescens* (Phillips and Borland 1992a). Later tests revealed a wavelength-dependency of the magnetic compass in amphibians (Phillips and Borland 1992b), migratory birds and pigeons (see Wiltschko and Wiltschko 2002). Marine turtles, on the other hand, proved well oriented in total darkness (Lohmann 1991; Lohmann and Lohmann 1993). Although an inclination compass is involved here, magnetoreception as proposed by the radical pair model appears unlikely, unless there is a yet unknown way that radical pairs could be generated in total darkness.

Demonstrating a radical pair mechanism

A diagnostic test based on magnetic resonance aimed at obtaining direct evidence for a radical pair mechanism underlying the avian magnetic compass. If the triplet yield is crucial for magnetoreception, interfering with the singlet-triplet interconversion should alter the output of the receptors markedly and thus disrupt magnetoreception. The singlet-triplet interconversion rate can be significantly affected by oscillating fields of specific frequencies in the MegaHertz range (Ritz et al. 2000). The intensities required for these resonance effects are so low that they would not affect any of the magnetite-based mechanisms currently considered (as explained below), so that a disruption of magnetic orientation would be diagnostic for the involvement of a radical pair mechanism.

At present, it is not easy to predict exactly which specific frequencies will interfere with the radical pair mechanisms underlying magnetoreception, because the chemical composition and the geometric structures of molecules involved are not yet known; theoretical

considerations and in vitro studies indicate that they are to be expected in the 0.1–10-MHz range. The effect of the oscillating fields should depend on their orientation with respect to the static background field (Cranfield et al. 1994). These resonances are generally very broad and might therefore lead to disturbing effects at virtually all frequencies within this range, provided the intensity of the oscillating field is sufficiently strong (Henbest et al. 2004). However, a special resonance occurs when the frequency of the oscillating field matches the energetic splitting induced by the static geomagnetic field; here, one expects a marked effect regardless of the structure of the molecules forming the radical pairs. For the 46,000 nT geomagnetic field of Frankfurt, this frequency is 1.315 MHz (see Thalau et al. 2005).

First tests with a weak broad band noise field of frequencies from 0.1 MHz to 10 MHz added to the geomagnetic field indeed showed that this disrupted the orientation of migratory birds (Ritz et al. 2004). Further tests used the single frequencies of 1.315 and 7.0 MHz with an intensity of about 480 nT. When these fields were presented parallel to the geomagnetic vector, the birds were oriented in their migratory direction, whereas they were disoriented when the same fields were presented at an angle of 24° or 48° to the geomagnetic field (Fig. 10; Ritz et al. 2004; Thalau et al. 2005). This is in agreement with the radical pair model and clearly shows that the observed effect of high-frequency field is a specific one. Together, these findings indicate that the primary process of magnetoreception in birds involves a radical pair mechanism.

Interactions of at least two receptors

If photopigments were involved, these pigments can hardly be expected to absorb light over the entire range of the visual spectrum – hence magnetoreception should

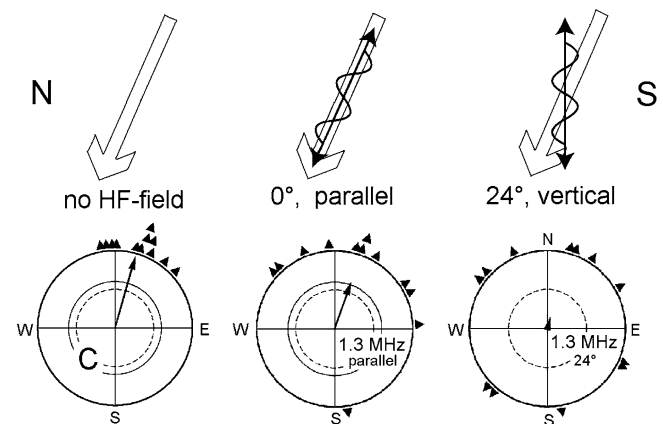


Fig. 10 Orientation of European Robins in the geomagnetic field (Control, C) and in high-frequency fields added to the geomagnetic field in two different orientation. The upper part of the diagram illustrated the orientation of the geomagnetic field and the high-frequency field in the three test conditions; symbols in the circular diagrams as in Fig. 2 (data from Thalau et al. 2005)

depend on the wavelength of light. A wavelength-dependency of magnetic compass orientation was reported for salamanders, passerine birds, and homing pigeons. In the respective experiments, salamanders and birds were tested under monochromatic lights of various wavelength and intensities. By reflecting the absorption ranges of the crucial pigments, these studies may indicate the number of receptors involved and how they interact.

Salamanders Salamanders show a wavelength dependency that is characterized by normal orientation only in a rather narrow wavelength band at the short-wavelength end of the spectrum and a variety of responses induced by long-wavelength light, with the specific manifestations of these responses attributed to different motivational stages. Salamanders manipulated to head shoreward showed normal orientation only up to 450 nm; at 475 nm, they were disoriented; and under wavelength of 500 nm and beyond, their headings were shifted by approximately 90° counterclockwise. When the animals were kept under long wavelength light with $\lambda > 500$ nm, they showed a mirror-image clockwise shift under ‘white’ light, but headed shoreward under long-wavelength light (Phillips and Borland 1992b). To explain these findings, the authors suggested two antagonistic spectral mechanisms indicating directions perpendicular to each other. Only the short wavelength receptor was to indicate the correct magnetic directions, while the long-wavelength receptor activated by most of the visual spectrum indicated shifted ones. To reconcile these findings with the normal orientation observed under ‘white’ light, where both receptors are stimulated, the authors postulate that the signal of the short-wavelength dominates over the contradicting input (Phillips and Borland 1992b; Phillips et al. 2001). Since a spectral mechanism providing animals with false information is

difficult to accept, Phillips and Deutschlander (1997) speculated about the two spectral mechanisms being connected, possibly being essential components of the same biochemical process.

When the salamanders were manipulated to head homeward, however, they were normally oriented only under 400 nm light and disoriented under wavelength of 450 nm and beyond (Phillips and Borland 1994). The authors attributed this disorientation to the false compass readings under long-wavelength light, which no longer allow the ‘map’-receptors to work properly and determine the home course. Held under long-wavelength light, the salamanders now preferred an axis that roughly corresponded with the magnetic north-south axis under both, ‘white’ and long-wavelength light (Phillips et al. 2002b). This response was discussed as being related to alignments and possibly controlled by tiny magnetite particles in the heads of the salamanders.

Birds Most tests with birds used migratory orientation as a criterion whether or not normal directional information from the magnetic field could be obtained in a given situation. Migratory birds have not only been tested under different wavelengths, but also under different intensities and under combinations of two monochromatic lights. Their responses under the various light regimes indicate highly complex interactions between at least two, possibly more, receptors.

Wavelength-dependency: European Robins were tested under monochromatic light produced by light-emitting diodes (LEDs) with a half band-width of 30–50 nm. Their behavior at various wavelengths revealed the following pattern: magnetic orientation was possible under 424 nm blue, 510 nm turquoise and 565 nm green light, whereas under 590 nm yellow and 635 nm red, the birds were disoriented (Fig. 11; Wiltschko and Wilt-

Fig. 11 Orientation behavior of European robins in spring under monochromatic lights of different wavelength (indicated in the circles); symbols as in Fig. 2. (after W. Wiltschko and Wiltschko 2002)

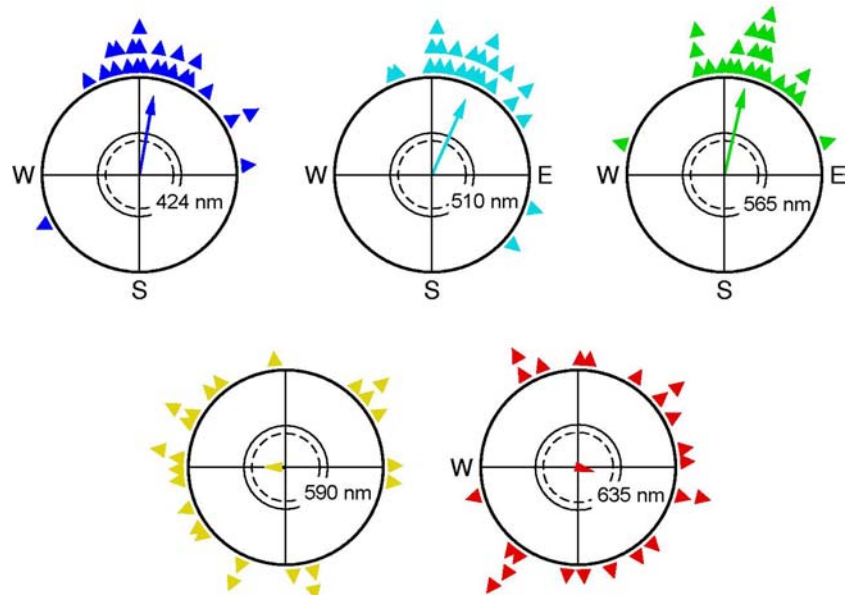
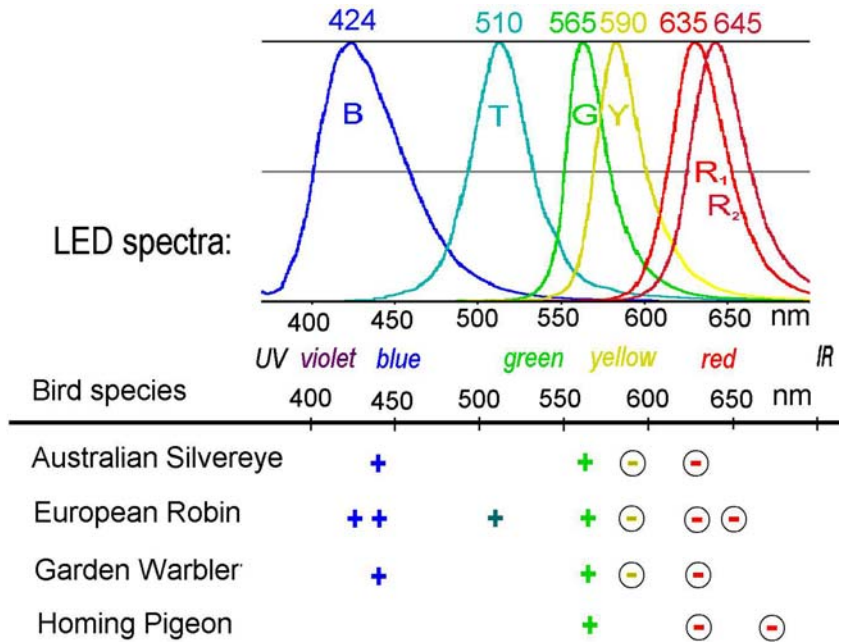


Fig. 12 Oriented behavior of four birds species tested under monochromatic light produced by light-emitting diodes (LEDs). *Upper part* of the diagram: spectra of the test lights; *lower part*: (+) oriented behavior or (−) disoriented behavior observed at the respective wavelengths (after W. Wiltschko and Wiltschko 2002)



schko 1999). Experiments using interference filters with a half-band width of only 10 nm could narrow down the onset of disorientation in robins even further to between 561 nm and 568 nm (Muheim et al. 2002). This pattern seems to be common to passerine species and homing pigeons (Fig. 12; see Wiltschko and Wiltschko 2002). That is, in contrast to salamanders, the spectral range where birds obtain normal magnetic compass

information includes the larger part of the visual spectrum. At the same time, this wavelength dependency of magnetoreception shows no relationship to the peaks of the four color cones of the birds' visual system (see Maier 1992) and thus speaks against their involvement in mediating magnetic directions, suggesting the existence of another type of receptor. The birds' response looked like an 'all-or-none'-response that could be attributed to one receptor, yet the rather abrupt transition to disorientation, which persisted under increased intensity of the yellow or red light (Wiltschko and Wiltschko 2001; Wiltschko et al. 2004a), seems to suggest an antagonistic interaction with a second receptor.

A second receptor with peak absorption at long wavelengths is also indicated by another finding. Although normally disoriented under long wavelengths, birds could orient under 645 nm red light after they had been exposed to this wavelength for 1 h prior to the critical test (Möller et al. 2001; Wiltschko et al. 2004a). The orientation induced this way proved to be normal migratory orientation. This ability to orient after having been pre-exposed to the test condition shows an interesting parallel to the ability to adjust the functional window to magnetic intensities outside the normal functional range (Wiltschko 1978) and may be based on similar mechanisms, namely learning to interpret a novel pattern of activation. The disorientation normally observed under red light suggests that under 'white' light, the long-wavelength receptor forms the minor component of a complex response pattern. Presented by itself, it would seem novel, but it would also be centrally symmetric to the axis of the field lines. Birds suddenly faced with this pattern alone might need a certain time until they are able to recognize its general characteristic and interpret it to derive magnetic directions (for a more detailed discussion, see Wiltschko et al. 2004b).

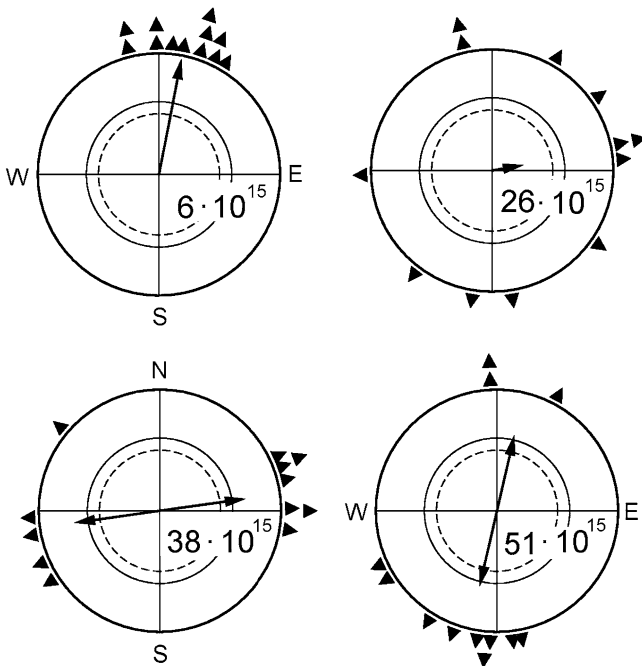


Fig. 13 Orientation behavior of European robins under the same 565 nm green light at different intensities; the respective quantal flux (in quanta m^{−2} s^{−1}) is indicated in the circular diagrams. Symbols as in Fig. 2

Effect of higher intensities: The findings mentioned so far were obtained under rather low light levels of $6\text{--}9 \times 10^{-15}$ quanta $\text{s}^{-1} \text{m}^{-2}$, an intensity found in nature more than half an hour after sunset or before sunrise. This seemed to be appropriate, because the passerine species tested were either nocturnal migrants or migrating during the twilight hours. When the light intensity was increased six times, birds were still disoriented under yellow and red light (see above), but under light from the blue-to-green part of the spectrum, a marked change in behavior was observed: passerine migrants no longer preferred their natural migratory direction, but instead showed axial preferences or odd unimodal tendencies (Wiltschko et al. 2000, 2003b; Wiltschko and Wiltschko 2001). Tests at the same wavelength of light showed that changes in intensity led to different responses: e.g. under 565 nm green light, robins first showed normal migratory orientation, then disorientation, followed by preference of the east–west-axis and finally a preference of the north–south-axis, depending on intensity (Fig. 13; R. Wiltschko and R. Wiltschko, unpublished data). The unimodal preferences observed at higher intensities were ‘fixed directions’ in the sense that they did not show the normal seasonal change between spring and autumn (Wiltschko et al. 2000). They were found to be fundamentally different from migratory orientation, as they also did not depend on the inclination compass normally used by birds (Wiltschko et al. 2003b).

The nature of these odd responses is not yet clear. The axial preferences show some similarities to alignments, but unimodal tendencies in directions other than the migratory direction (e.g. Wiltschko et al. 2000, 2004b) are hard to explain. As motivational differences can largely be excluded, they imply that the magnetic receptors no longer provide information that can be used to locate the migratory course. Yet the light with identical spectral compositions, but lower intensity, allows excellent migratory orientation. The light levels of these brighter lights were still fairly low – on a sunny day, the natural light is brighter by powers of ten. Hence saturation of the receptors appears highly unlikely. Because ‘white’ light of high intensity allows normal orientation, the reason for the odd responses seem to lie in the near monochromatic nature of the light consisting of a narrow band of wavelengths only. Speculating on why this should matter leads to considerations about the interaction of the input of various receptors at higher centers. The number of receptors involved in magnetoreception is still unclear, but if they were more than one or two, monochromatic light would stimulate one receptor strongly, while others are not stimulated at all. This could result in an imbalance of input at higher units where the input of these receptors converge. The other receptors may also be specialized on magnetic input, or they may involve the cones of color vision which might provide background information of the general light level. Possibly, as long as the quantal flux is so low that the cones are not activated, monochromatic light from the blue-to-green part of the spectrum allows normal

orientation; if the monochromatic lights are strong enough to activate the cones, however, the resulting imbalance might affect the processing of magnetic input in a way that the information content of magnetic input changes its general characteristics.

Bichromatic test lights: A combination of light from the blue-to-green part of the spectrum with 590 nm yellow light also leads to unimodal responses that no longer coincided with the natural migratory direction. These responses were likewise ‘fixed directions’, as they failed to show the normal seasonal change (Wiltschko et al. 2004b). The responses to bichromatic light combined from wavelengths where birds normally show excellent orientation, and yellow light, where they are disoriented when it is presented alone, clearly show that yellow light is not neutral, also pointing out interactions between at least two receptors that have not yet been fully understood. Interestingly, the specific response depended on the wavelength from the blue-to-green part of the spectrum: robins preferred northerly headings under green-and-yellow, southeasterly headings under turquoise-and-yellow and southerly headings under blue-and-yellow (Wiltschko et al. 2004b; Stapput et al. 2005). Apparently, the receptor(s) activated by light from the blue-to green part of the spectrum, although no longer providing magnetic compass information for locating the migratory direction, are active and determine the specific directions of the ‘fixed’ headings.

Similar patterns in birds and amphibians? The findings described above indicate that certain light regimes drive the reception mechanisms for compass information towards their limits, leading to odd responses that cannot yet be explained. In birds, specific combinations of wavelengths as well as monochromatic light above a certain quantal flux result in such responses. To what extent this is also true for salamanders is unclear, because salamanders have not yet been tested under the same wavelengths at different intensities. It is interesting to note that the odd shifts in directions of salamanders heading shoreward and the disoriented behavior of salamanders heading homeward observed from 500 nm onward (Phillips and Borland 1992b, 1994; Phillips et al. 2002b) were recorded at light intensities where birds no longer prefer their migratory direction; at 400 nm, where salamander always showed normal orientation, the light intensity was markedly lower. Unfortunately, it is still unknown how salamanders would respond to long wavelengths at this lower light intensity. The manifestations of the responses under higher intensity – unimodal preference of unexplained directions, axial preferences and disorientation – are very similar in salamanders and birds. Hence it appears possible that the odd responses in these two animal groups represent related phenomena, which in salamanders depend not only on wavelength, as described by Phillips et al. and colleagues (e.g. 2001), but also on the intensity of light, reflecting a magnetoreception system functioning under borderline conditions. Future studies will have to clarify this question.

The site of the light-dependent magnetoreceptors

Another question concerns the location of the magnetoreceptors. Theoretical considerations favored the eyes as site of magnetoreception because of their almost spherical shape (Ritz et al. 2000) – this prediction has also been confirmed in birds, with the surprising finding that magnetoreception seems to be restricted to the right eye. Passerine migrants tested with their left eye covered were just as well oriented as binocular birds, whereas the same birds failed to show oriented behavior when their right eye was covered (Wiltschko et al. 2002a, 2003a). In salamanders, however, the receptors were found to be located in the pineal, the ancient third eye of vertebrates, which in amphibians is directly sensitive to light. Critical tests in which the skull above the pineal was covered with a color filter, but the eyes were open to the natural light, clearly showed that the magnetic compass in salamanders depended solely on the spectral properties of the light reaching the pineal (Deutschlander et al. 1999; Phillips et al. 2001).

Cryptochromes, first known from plants, but recently also discovered in animals (see Sancar 2003 for review) have been suggested to form the radical pairs involved in magnetoreception (Ritz et al. 2000). These photopigments have been found in the retina of vertebrates, first in mammals (Miyamoto and Sancar 1998), but also in chicken (Haque et al. 2002) and recently in migrating passerine birds. In Garden Warblers, *Sylvia borin*, cryptochromes are located in the large displaced

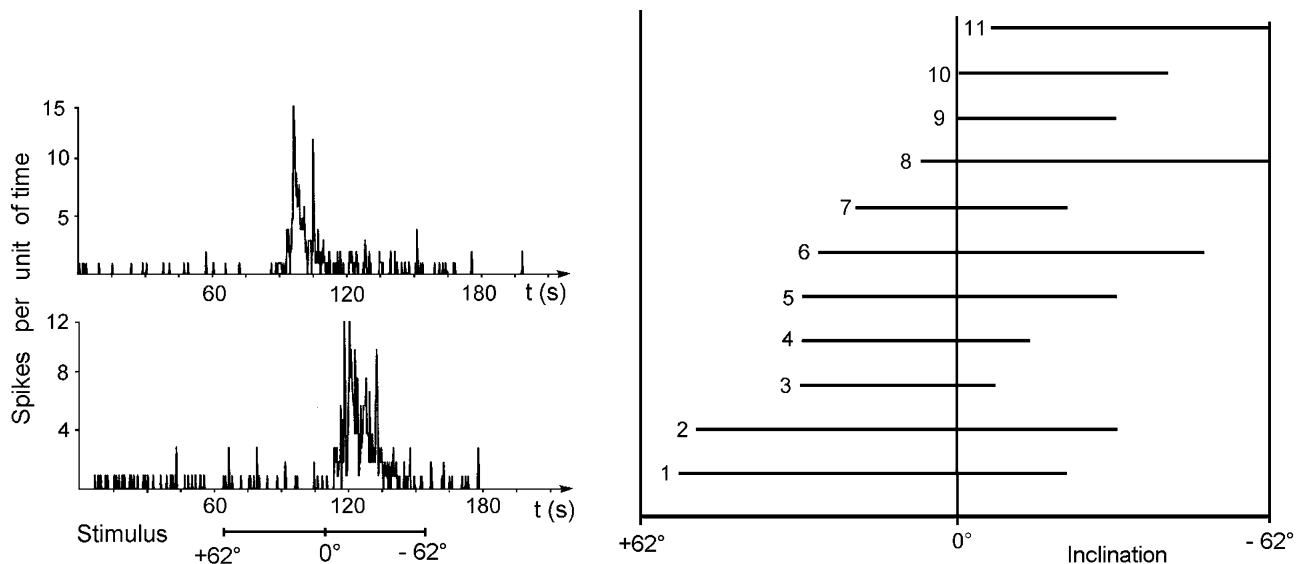
ganglion cells (Mouritsen et al. 2004). In European robins, two forms of cryptochrome 1, splice product of the same gene, were identified, with the novel C-terminal of the second form implying a novel function (Möller et al. 2004). These findings support the idea that cryptochromes may be involved in the radical pair processes underlying the avian magnetic compass, yet direct evidence for their crucial role is still lacking.

Neuronal pathways associated with the avian magnetic compass

Our knowledge on the neural pathways and the parts of the brain processing magnetic compass information is rather limited; the available evidence comes entirely from studies with birds. Electrophysiological recordings in pigeons suggest that magnetic input is processed in parts 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 (Semm et al. 1984; Semm and Demain 1986). These responses are in accordance with the predictions of the radical pair model, as they were observed only in the presence of light; they seem to originate in the retina, as they depended on an intact retina and optic nerve. When the eyes were illuminated with monochromatic light of various wavelengths, units with a peak of responsiveness around 503 nm and others with a peak beyond 580 nm were identified, thus suggesting the two types of receptors with different absorption maxima, a finding that is in agreement with the behavioral studies likewise indicating two types of receptors with absorption peaks in the blue-to-green and in the long-wavelength range (e.g. Möller et al. 2001; Wiltschko et al. 2004b).

Individual neurons in the nBOR as well as the *tectum opticum* showed distinct peaks of response at particular alignments of the magnetic field (Fig. 14). These varied between cells so that the input of a number of units

Fig. 14 Electrophysiological responses recorded from direction-selective cells in the nucleus of the basal optic root (nBOR) of pigeons; the stimulus was a gradual change of magnetic inclination from 62° downward to 62° upward (= vertical component inverted). *Left*: responses of to individual units; *right*: different neurons responding to different spatial directions of the magnetic vector, with the horizontal bars indicating the range of augmentation of electrical activity of representative neurons (data from Semm et al. 1984)



would represent the various directions in space model (Semm et al. 1984; Semm and Demaine 1986). Processed collectively and integrated, it would thus provide a suitable basis for a compass as predicted by the radical pair model.

The finding that magnetic input is mediated exclusively by the right eye (Wiltshcko et al. 2002a) indicates a strong lateralization of the magnetic compass that appears to be rather widespread among birds (see Wiltshcko et al. 2003a; Prior et al. 2004). Because of the very few connections between the two hemispheres, it means that magnetic information is processed almost exclusively by the left hemisphere of the brain. This is intriguing, as a number of morphological asymmetries have been described in the tectofugal system, a part of the visual system (Güntürkün 1997) which, aside from the *tectum opticum*, comprises the *nucleus rotundus*, where activation by magnetic stimuli was indicated by the glucose method (Mai and Semm 1990). Together, the few findings available suggest that magnetic input originating in the right eye shares neuronal pathways with the visual system, being processed in the tectofugal system of the left hemisphere of the brain. Other parts of the brain involved in processing magnetic compass information are yet to be determined.

Magnetoreception based on magnetite, and associated findings

Magnetite is a specific form of iron oxide Fe_3O_4 whose general properties depend on the size and shape of the particles (Fig. 15). 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 $1.2 \mu\text{m}$ and $0.05 \mu\text{m}$ consist of a *single domain* and have a stable magnetic moment, acting as tiny permanent magnets. Even smaller particles are *superparamagnetic*: at room temperature, their magnetic moment fluctuates as a result of thermal agitation, but it can easily be aligned by an external magnetic field (see Kirschvink et al. 1985 for details).

The model

In the 1970s, certain bacteria were discovered to contain chains of single domain magnetite (Blakemore 1975) that act as magnets and align these bacteria along the field lines of the geomagnetic field. Magnetic information mediated by tiny magnets was an attractive idea, and the existence of magnetic material of biogenic origin caused authors to speculate about its potential role in the orientation of higher animals.

Based on theoretical considerations, the magnetite hypotheses propose a variety of models on how magnetite particles might mediate magnetic information,

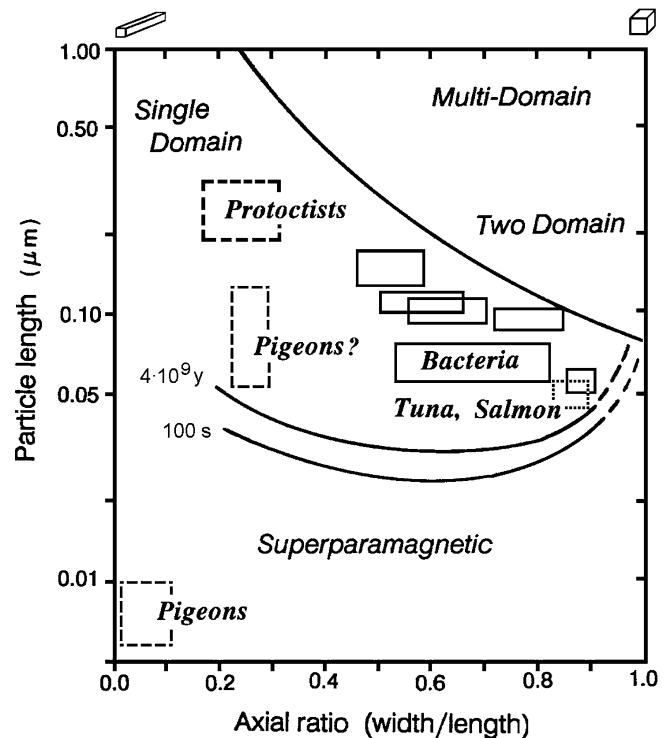


Fig. 15 Magnetic properties of magnetite particles: domain stability field diagram indicating how the magnetic moments of particles of a given shape differ with size; size of particles found in various living beings is indicated (after Kirschvink and Gould 1981, with the superparamagnetic particles identified by Fleißner et al. 2003 added)

some of them involving single domains (e.g. Yorke 1979; Kirschvink and Gould 1981; Kirschvink and Walker 1985; Edmonds 1996), others superparamagnetic particles (e.g. Kirschvink and Gould 1981; Shcherbakov and Winklhofer 1999). A uniform concept on how magnetite-based magnetoreceptors might work does not yet exist. Interestingly, some of the models predict polar, others axial responses. Model calculations showed that magnetite-based receptors could convey directional information or information on magnetic intensity, depending on their specific structure and on the amount

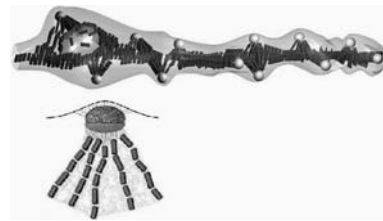


Fig. 16 Schematic reconstruction of structures found in the skin of upper beak of pigeons, based on ultrathin section series. *Above*: the terminal region of a nerve containing a scaffold of iron platelets and numerous spherules of superparamagnetic magnetite particles; *below*: a spherule of superparamagnetic particles and the structures surrounding it (from Fleißner et al. 2003)

of magnetite included; they could account for the sensitivities indicated by behavioral evidence.

Histological findings

Magnetite has been discovered in a large number of species belonging to all major phyla, mostly by measuring the natural and induced remanence with highly sensitive SQUID-magnetometers. In honey bees, *Apis mellifera*, magnetic material was described in the front part of the abdomen (Gould et al. 1978); in vertebrates, it appears to be located mostly in the ethmoid region in the front of the head (see Kirschvink et al. 1985).

In salmonid fish, chains of single domain magnetite have been isolated from ethmoid tissue (Mann et al. 1988). A histological study showed magnetite particles embedded in specific cells in the basal lamina within the olfactory lamellae of rainbow trout, *Oncorhynchus mykiss* (Walker et al. 1997). These particles were identified as single domains; applying a strong external magnetic field could change the direction of their magnetization (Diebel et al. 2000). In birds, histological and electron-optic studies revealed magnetite particles in the orbital and in the nasal cavity, where single domains were reported (Beason and Nichols 1984; Beason and Brennon 1986; William and Wild 2001), and at specific locations in the skin of the upper beak of pigeons, where clusters of very small crystals were described, with the particles identified by crystallographic means as superparamagnetic magnetite (Hanzlik et al. 2000). These clusters were located within nervous tissue and associated with a remarkable framework of platelets consisting of elementary iron (Fig. 16); the authors speculate about possible functions in a magnetoreceptor (Fleissner et al. 2003). Altogether, the magnetite-containing structures found in birds and fish do not seem to be identical, implying that the respective magnetite-based receptors might differ in their general characteristics.

Effects of a strong, short magnetic pulse

The first behavioral tests were designed to generally demonstrate an involvement of magnetite in magneto-reception. They aimed at interfering with the potential receptors by altering the magnetization of the magnetite crystals. This was expected to change the output of receptors in a dramatic way and thus cause a lasting after-effect on orientation behavior. A popular method was to apply a brief, strong magnetic pulse to the head of the test animal – the pulse had to be strong enough to remagnetize the magnetite particles but, at the same time, short enough to prevent these particles from rotating into the pulse direction and thus to escape remagnetization. In most studies, a 0.5 T pulse with 3–5 ms duration was used.

Behavioral tests Tests with migratory birds again use the preference of the migratory direction as a criterion

whether pulse treatment affected behavior. A pulse prior to the critical tests caused a marked 90° change in direction: Australian Silvereyes, *Zosterops lateralis*, preferred easterly headings, and that when they had been heading northward in autumn as well as southward in spring (Fig. 17, left). This effect of the pulse lasted for about 3 days; after that, the birds became disoriented and, about 10 days after pulse treatment, resumed their original orientation in migratory direction (Wiltshcko et al. 1994, 1998). Interestingly, this effect of pulsing was restricted to experienced migrants that had completed at least one migratory trip; young birds that had been captured immediately after fledging proved to be unaffected and continued in their normal migratory direction (Fig. 17, right; Munro et al. 1997). This suggests that the pulse affected a mechanism that is based on experience, and points to the position-finding system of the ‘navigational map’. The same pulse also caused experienced pigeons to deviate from the mean of untreated control birds (Beason et al. 1997).

In further tests, the protocol of the pulse treatments was modified to identify specific properties of the receptor. An identical pulse applied in two different orientations – e.g. ‘south anterior’, the induced south pole towards the beak, and ‘south left’, the induced south pole towards the left side of the head - lead to deflections to different sides of the control birds (Fig. 18). This was true for passerine migrants like bobolinks, *Dolichonyx oryzivorus*, as well as for homing pigeons (Beason et al. 1995, 1997). It implies that the pulse does not simply deactivate the receptors altogether, but instead causes them to provide altered information, which causes birds to head in different directions. In other tests, the same pulse was applied together with a strong, 100 μ T biasing field. It had been argued the pulse alone would remagnetize only an unknown portion of the particles of the receptor; the biasing field was to align movable particles in one direction so that a pulse affected them all. A pulse applied parallel would not change their magnetization,

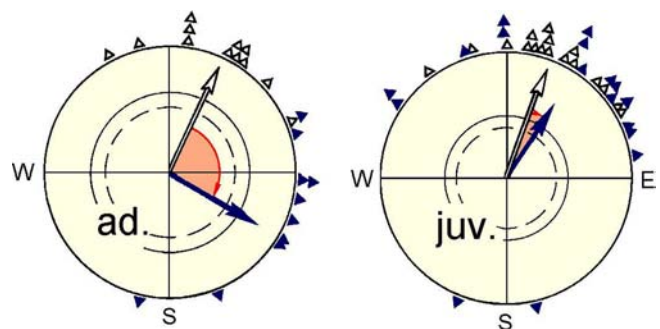


Fig. 17 Effect of a short, strong magnetic pulse on the orientation behavior of Australian Silvereyes in Australian autumn. *ad.*, old, experienced birds tested; *juv.*: young, inexperienced birds tested. *Open symbols* indicate control data recorded before, *solid symbols* data recorded after pulse treatment. Symbols as in Fig. 2 (data from W. Wiltshcko et al. 1994, Munro et al. 1997).

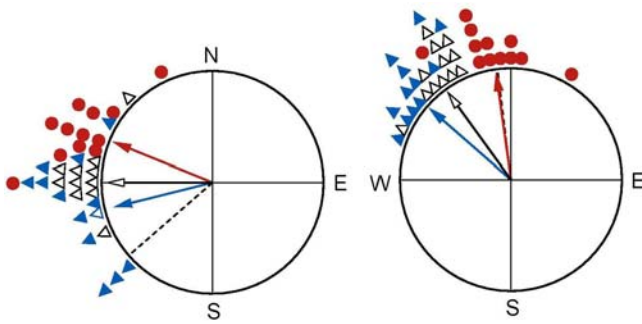


Fig. 18 The effect of a magnetic pulse on the orientation of homing pigeons released at sites 129 km and 108 km from the loft; the home directions 229° and 353° are indicated by a *dashed radius*. The *symbols* at the periphery of the circle mark the vanishing bearings of individual pigeons: *open symbols*, untreated control birds; *blue symbols*, birds treated with a pulse oriented 'south anterior'; *red symbols*: birds treated with a pulse oriented 'south left'; the *arrows* represent the respective mean vectors (data from Beason et al. 1997)

whereas the pulse applied in an antiparallel direction should have a maximum effect. In critical tests, however, both groups of birds showed the same deflections (Wiltchko et al. 2002b). These results largely exclude single-domain particles free to move as part of a polarity-sensitive receptor.

Treating mammals with the same pulse also induced noticeable deflections. Zambian molerats shifted the position of their nest by about 75° from the south-south-east to east. Retesting the same animals showed that this altered preference, in contrast to the one observed in birds, was stable for three months until the end of the experiments (Marhold et al. 1997b).

Single domains or superparamagnetic particles? Since none of the other reception mechanisms would show an after-effect following treatment with a magnetic pulse, the observation that the pulse had an effect is diagnostic for magnetite particles involved in the receptor

controlling the observed behavior. The response to pulse treatment can also be interpreted in view of the type of magnetite particles involved – single domains or superparamagnetic particles.

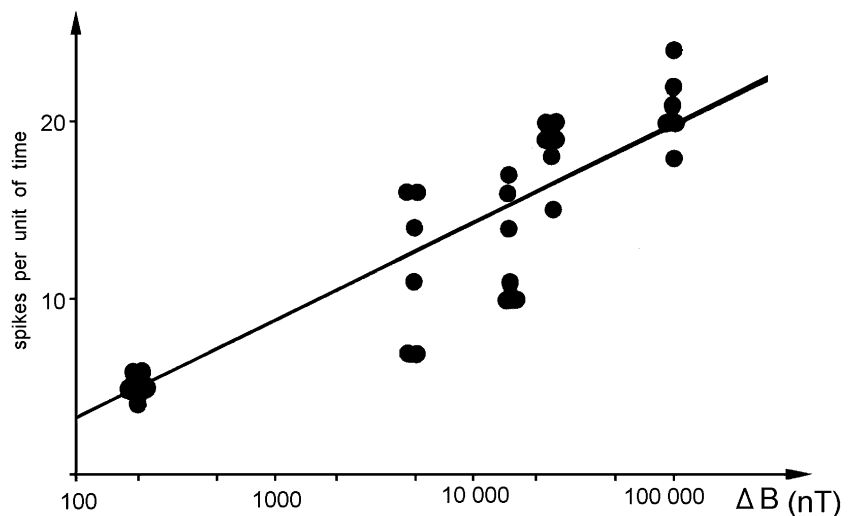
In birds, where both types have been described, the short duration of the pulse effect seems to speak against single domains. Remagnetization of single domain particles should be just as stable and lasting as the original one. Yet in birds, a clear pulse effect was observed only on the day of pulsing and the following two days (Wiltchko et al. 1994, 1998; Beason et al. 1997). The behavior of birds after pulse treatment thus indicates magnetite-based receptors, but these receptors do not seem to be based on single domains. This leaves superparamagnetic particles. Single superparamagnetic particles are not affected by a magnetic pulse as used in the experiments described above, but clusters and chains of clusters are. A strong pulse might break up the clusters and disrupt the chains, but they rearrange themselves, with a time rate in the order of several days, depending on the specific structure of the clusters, the angle with which they are hit by the pulse etc. (Davila et al., *in press*).

In rodents, the situation is different insofar as anatomical and histological data are entirely lacking. The pulse effect indicates a receptor based on magnetite, and the long duration of the pulse effect would be in accordance with single domains.

Neuronal pathways associated with magnetite-based receptors

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 in passerine birds used stimuli produced by a coil system that in some experiments was set up in a way that the axis of the coils was aligned with the magnetic vector so

Fig. 19 Electrophysiological recordings from a trigeminal ganglion cell of a bobolink, responding to different changes in the intensity of the geomagnetic field (after Beason and Semm 1991)



that intensity alone could be modified. Units responding to magnetic stimuli modified their spontaneous activity by changes in magnetic intensity, showing a logarithmic characteristic. The minimum intensity difference tested was 200 nT (Fig. 19), where the birds still showed a clear response. Similar recordings are reported from the trigeminal ganglion (Semm and Beason 1990). Electrophysiological recordings from the corresponding nerve in rainbow trouts produced likewise responses to changes in intensity (Walker et al. 1997).

Two other findings provide more direct evidence that the input from magnetite-based receptors in birds is mediated by the ophthalmic nerve: behavioral experiments showed that deactivating the ophthalmic nerve with a local anesthetic suppressed the pulse effect (Beason and Semm 1996); the bobolinks treated this way continued in their migratory direction, which clearly shows that the pulse does not affect the compass mechanism. In conditioning experiments, pigeons trained to respond to changes in intensity failed to respond correctly after deactivation of the ophthalmic nerve (Mora et al. 2004). Together, these findings suggest that in birds and probably also in fish, magnetite-based receptors mediate information on intensity rather than compass information.

In rodents, a study using c-Fos identified the *superior colliculus* as a site of neural activity caused by magnetic stimulation (Němec et al. 2001). The origin of this activity is unclear; an involvement of the magnetite-based receptor indicated by the pulse effect seems possible.

Two types of receptors for different tasks

In recent years, the number of publications on the aspects of reception and processing magnetic information has greatly increased, but it is only in case of birds, that the various pieces of the puzzle begin to form a consistent picture, although many questions still remain unanswered. The available data indicate the existence of two magnetoreceptor systems in birds for different types of information (see Beason and Semm 1991): a radical-pair mechanism in the right eye provides directional information, and magnetite-based receptors in the upper beak records differences in magnetic intensity – one might say: birds have a compass in their eye and a magnetometer in their beak. The input of the former appears to be mediated and processed by parts of the visual system, involving the nBOR, the *tectum opticum* and the *nucleus rotundus*; the input of the latter by the ophthalmic nerve and the trigeminal ganglion. It is still unknown as to where these two types of information finally converge to form crucial components of the ‘map and compass’ system used for navigation (for review, see Wiltschko and Wiltschko 2003).

In other vertebrates, our knowledge is limited to certain aspects of magnetoreception. In marine turtles,

the various uses of magnetic information are well documented, yet magnetoreception has not yet been analyzed. The nature of the primary processes of magnetoreception are indicated by behavioral data in salamanders, where the light-dependency of an inclination compass suggests magnetoreception based on a radical pair mechanism, and in mammals, where the pulse effect points to magnetite-based receptors. The position of the receptors and anatomical details about their structure are known in fish, where they are found in the olfactory lamellae; in salamanders, behavioral studies identified the pineal as site of the receptors. Some of the neuronal pathways are known in fish, where electrophysiological recordings indicate that information on magnetic intensity is mediated by the trigeminal system; in mammals, an involvement of the *superior corniculus* is suggested, but neither the origin nor the type of the respective magnetic information is entirely clear.

At the same time, the mechanisms employed by fish, mammals and several arthropods in their polarity compass are entirely unknown. Magnetite-based receptors are an option, as they could theoretically provide information on direction as well as on intensity. Here, the lasting pulse effect on nest building in mole rats is interesting: since the direction of the nest would involve only a compass, we may speculate that this compass might be based on single domain magnetite, but direct evidence is still lacking.

In view of the many open questions, we can only hope that the ‘magnetic sense’ continues to meet with great interest and that further research in the coming years will lead to a better understanding of reception and processing of magnetic information.

References

- Baker RR (1989) Human navigation and magnetoreception. Manchester University Press, Manchester and New York
- Beason RC, Brennon WJ (1986) Natural and induced magnetization in the bobolink (*Dolichonyx oryzivorus*). *Ethology* 91:75–80
- Beason RC, Nichols JE (1984) Magnetic orientation and magnetically sensitive material in a transequatorial migratory bird. *Nature* 309:151–153
- Beason RC, Semm P (1991) Two different magnetic systems in avian orientation. In: Bell BD, Cossee RO, Flux JEC, Heather BD, Hitchmough RA, Robertson CJR, Williams MJ (eds) *Acta XX Congr Intern Ornithol, New Zealand Ornithological Congress Trust Board, Wellington*, pp 1813–1819
- Beason RC, Semm P (1996) Does the avian ophthalmic nerve carry magnetic navigational information? *J Exp Biol* 199:1241–1244
- 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
- Beason RC, Wiltschko R, Wiltschko W (1997) Pigeon homing: effects of magnetic pulses on initial orientation. *Auk* 114:405–415
- Beck W, Wiltschko W (1988) Magnetic factors control the migratory direction of Pied Flycatchers (*Ficedula hypoleuca* Pallas). In: Ouellet H (ed) *Acta XIX Congr Int Ornithol Vol II*. University of Ottawa Press, Ottawa, pp 1955–1962
- Blakemore RP (1975) Magnetotactic bacteria. *Science* 190:377–379

- Boles LC, Lohmann KJ (2003) True navigation and magnetic map in spiny lobsters. *Nature* 421:60–63
- Cranfield J, Belford R, Debrunner P, Schulten K (1994) A perturbation treatment of oscillating magnetic fields in the radical pair mechanism. *Chem Phys* 182:1–18
- Davila AF, Winklhofer M, Sheherbakov V, Petersen N Magnetic pulse affects a putative magnetoreceptor mechanism. *Biophys J* in press
- DeJong D (1982) Orientation of comb building by honeybees. *J Comp Physiol* 147:495–501
- Deutschlander ME, Phillips JB, Borland SC (1999) The case for light-dependent magnetic orientation in animals. *J Exp Biol* 202:891–908
- Diebel CE, Proksch R, Green CR, Neilson P, Walker MM (2000) Magnetite defines a vertebrate magnetoreceptor. *Nature* 406:299–302
- Duelli P, Duelli-Klein R (1978) Die magnetische Nestausrichtung der australischen Kompaßtermiten *Amitermes meridionalis*. *Mitt Schweiz Entomol Ges* 51:337–342
- Edmonds DT (1996) A sensitive optically detected magnetic compass for animals. *Proc R Soc Lond B* 263:295–298
- Fisher JH, Munro U, Phillips JB (2003) Magnetic navigation in an avian migrant? In: Berthold P, Gwinner E, Sonnenschein E (ed) *Avian migration*. Springer, Berlin Heidelberg New York, pp 423–432
- Fleissner G, Holtkamp-Rötzler E, Hanzlik M, Winklhofer M, Fleissner G, Petersen N, Wiltshcko W (2003) Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. *J Comp Neurol* 458:350–360
- Fransson T, Jakobsson S, Johansson P, Kullberg C, Lind J, Vallin A (2001) Magnetic cues trigger extensive refuelling. *Nature* 414:35–36
- Giovani B, Byrdin M, Ahmad M, Brettel K (2003) Light-induced electron transfer in a cryptochrome blue-light photoreceptor. *Nature Struct Biol* 6:489–490
- Gould JL, Kirschvink JL, Deffeyes KS (1978) Bees have magnetic remanence. *Science* 201:1026–1028
- Gundmundsson GA, Sandberg R (2000) Sanderlings (*Calidris alba*) have a magnetic compass: orientation experiments during spring migration in Iceland. *J Exp Biol* 203:3137–3144
- Güntürkün O (1997) Morphological asymmetries of the *tectum opticum* in the pigeon. *Exp Brain Res* 116:561–566
- Hanzlik M, Heunemann C, Holtkamp-Rötzler E, Winklhofer M, Petersen N, Fleissner G (2000) Superparamagnetic magnetite in the upper beak tissue of homing pigeons. *BioMetals* 13:325–331
- Haque R, Charausia SS, Wessel JH, Iuvone PM (2002) Dual regulation of cryptochrome I mRNA expression in chicken retina by light and circadian oscillators. *Neuroreport* 13:2247–2251
- Henbest KB, Kukura P, Rodgers CT, Hore PJ, Timmel CR (2004) Radio frequency magnetic field effects on a radical recombination reaction: a diagnostic test for the radical pair mechanism. *J Am Chem Soc* 126:8102–8103
- Jacklyn PM, Munro U (2002) Evidence for the use of magnetic cues in mound construction by the termite *Amitermes meridionalis* (Isoptera, Termitinae). *Austr J Zool* 50:357–368
- Kalmijn AJ (1978) Electric and magnetic sensory world of sharks, skates, and rays. In: Hodgson FS, Mathewson RF (eds) *Sensory biology of sharks, skates and rays*. Office Naval Res, Arlington, VA, pp 507–528
- Keeton WT, Larkin TS, Windsor DM (1974) Normal fluctuation in the earth's magnetic field influence pigeon orientation. *J Comp Physiol* 95:95–103
- 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 (eds) *Magnetite biomineralization and magnetoreception in organisms*. Plenum, New York, London, pp 243–256
- Kirschvink JL, Jones DS, MacFadden BJ (eds) (1985) *Magnetite biomineralization and magnetoreception in organisms*. Plenum, New York
- Light P, Salmon M, Lohmann KJ (1993) Geomagnetic orientation of loggerhead sea turtles: evidence for an inclination compass. *J Exp Biol* 182:1–10
- Lohmann KJ (1991) Magnetic orientation by hatchling loggerhead sea turtles (*Caretta caretta*). *J Exp Biol* 155:37–49
- Lohmann KJ, Lohmann CMF (1992) Orientation to oceanic waves by green turtle hatchlings. *J Exp Biol* 171:1–13
- Lohmann KJ, Lohmann CMF (1993) A light-independent magnetic compass in the leatherback sea turtle. *Biol Bull* 185:149–151
- Lohmann KJ, Lohmann CMF (1994) Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitudes. *J Exp Biol* 194:23–32
- Lohmann KJ, Lohmann CMF (1996) Detection of magnetic field intensity by sea turtles. *Nature* 380:59–61
- Lohmann KJ, Pentcheff ND, Nevitt GA, Stetten GD, Zimmer-Faust RK, Jarrard HE, Boles LC (1995) Magnetic orientation of spiny lobsters in the ocean: experiments with undersea coil systems. *J Exp Biol* 198:2041–2048
- Lohmann KJ, Cain SD, Dodge SA, Lohmann CMF (2001) Regional magnetic fields as navigational markers for sea turtles. *Science* 294:364–366
- Lohmann KJ, Lohmann CMF, Erhart LM, Bagley DA, Swing T (2004) Geomagnetic map used in sea-turtle navigation. *Nature* 428:909–910
- Mai JK, Semm P (1990) Patterns of glucose utilization following magnetic stimulation. *J Hirnforsch* 31:331–336
- Maier EJ (1992) Spectral sensitivities including the ultraviolet of the passeriform bird *Leiothrix lutea*. *J Comp Physiol A* 170:709–714
- Mann S, Sparks NHC, 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
- Marhold S, Burda H, Wiltshcko W (1997a) A magnetic polarity compass for direction finding in a subterranean mammal. *Naturwissenschaften* 84:421–423
- Marhold S, Burda H, Kreilos I, Wiltshcko W (1997b) Magnetic orientation in the common mole-rat from Zambia. In: *Orientation and navigation—birds, humans and other animals*. Royal Instit of Navig, Oxford, 5-1–5-9
- Miyamoto Y, Sancar A (1998) Vitamin B₂-based blue-light photoreceptors in the retinohypothalamic tract as the photoactive pigments for setting the circadian clock in mammals. *Proc Natl Acad Sci USA* 95:6097–6102
- Möller A, Gesson M, Noll C, Phillips J, Wiltshcko R, Wiltshcko W (2001) Light-dependent magnetoreception in migratory birds previous exposure to red light alters the response to red light. In: *Orientation and navigation—birds, humans and other animals*. Royal Institute of Navigation, Oxford, 6-1–6-6
- Möller A, Sagasser S, Wiltshcko W, Schierwater B (2004) Retinal cryptochrome in a migratory passerine bird: a possible transducer for the avian magnetic compass. *Naturwissenschaften* 91:585–588
- Mora CV, Davison M, Wild JM, Walker MM (2004) Magnetoreception and its trigeminal mediation in the homing pigeon. *Nature* 432:508–511
- Mouritsen H, Janssen-Bienhold U, Liedvogel M, Feenders G, Stalleicken J, Dirks P, Weiler R (2004) Cryptochromes and neuronal-activity markers colocalize in the retina of migratory birds during magnetic orientation. *Proc Nat Acad Sci USA* 101:14294–14299
- 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
- Munro U, Munro JA, Phillips JB, Wiltshcko R, Wiltshcko W (1997) Evidence for a magnetite-based navigational 'map' in birds. *Naturwissenschaften* 84:26–28
- Murray RW (1962) The response of the ampullae of Lorenzini of elasmobranchs to electrical stimulation. *J Exp Biol* 39:119–128

- 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
- Pardi L, Ugolini A, Faqi AS, Scapini F, Ercolini A (1988) Zonal recovering in equatorial sandhoppers: Interaction between magnetic and solar orientation. In: Chelazzi G, Vannini M (eds) Behavioral adaptation to intertidal life. Proc of the NATO Sci, Plenum, New York, London, pp 79–92
- Phillips JB (1986) Two magnetoreception pathways in a migratory salamander. *Science* 233:765–767
- Phillips JB, Borland SC (1992a) Magnetic compass orientation is eliminated under near-infrared light in the eastern red-spotted newt *Notophthalmus viridescens*. *Anim Behav* 44:796–797
- Phillips JB, Borland SC (1992b) Behavioral evidence for use of a light-dependent magnetoreception mechanism by a vertebrate. *Nature* 359:142–144
- 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
- Phillips JB, Deutschlander ME (1997) Magnetoreception in terrestrial vertebrates: implications for possible mechanisms of EMF interaction with biological systems. In: Stevens RG, Wilson BW, Andrews LE (eds) The melatonin hypothesis: electric power and the risk of breast cancer. Battelle Press, Columbus Ohio, pp 111–172
- Phillips JB, Deutschlander ME, Freake MJ, Borland SC (2001) The role of extraocular photoreceptors in newt magnetic compass orientation: parallels between light-dependent magnetoreception and polarized light detection in vertebrates. *J Exp Biol* 204:2543–2552
- Phillips JB, Freake MJ, Borland SC (2002a) Behavioral titration of magnetic map coordinates. *J Comp Physiol A* 188:157–160
- Phillips JB, Borland SC, Freake M, Brassart J, Kirschvink JL (2002b) ‘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
- Prior H, Wiltschko R, Stapput K, Güntürkün O, Wiltschko W (2004) Visual lateralization and homing in pigeons. *Behav Brain Res* 154:301–310
- Quinn TP (1980) Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. *J Comp Physiol* 137:243–248
- Quinn TP, Brannon EL (1982) The use of celestial and magnetic cues by orienting sockeye salmon smolts. *J Comp Physiol* 147:547–552
- Ritz T, Adem S, Schulten K (2000) A model for vision-based magnetoreception in birds. *Biophys J* 78:707–718
- 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
- Sancar A (2003) Structure and function of DNA photolyase and cryptochrome blue-light photoreceptors. *Chem Rev* 103:2203–2237
- Schulten K, Windemuth A (1986) Model for a physiological magnetic compass. In: Maret G, Boccara N, Kiepenheuer J (eds). Biophysical effects of steady magnetic fields. Springer, Berlin Heidelberg New York, pp 99–106
- Semm P, Beason RC (1990) Responses to small magnetic variations by the trigeminal system of the Bobolink. *Brain Res Bull* 25:735–740
- Semm P, Demaine C (1986) Neurophysiological properties of magnetic cells in the pigeon’s visual system. *J Comp Physiol A* 159:619–625
- Semm P, Nohr D, Demaine C, Wiltschko W (1984) Neural basis of the magnetic compass: interaction of visual, magnetic and vestibular inputs in the pigeons’s brain. *J Comp Physiol* 155:283–288
- Shcherbakov VP, Winklhofer M (1999) The osmotic magnetometer: a new model for magnetite-based magnetoreceptors in animals. *Eur Biophys J* 28:380–392
- Skiles DD (1985) The geomagnetic field: its nature, history and biological relevance. In: Kirschvink JL, Jones DS MacFadden BJ (eds) Magnetite biomineralization and magnetoreception in organisms. Plenum, New York, London, pp 43–102
- Stapput K, Gesson M, Wiltschko R, Wiltschko W (2005) Light-dependent magnetoreception: behavior of migratory birds under monochromatic and bichromatic lights. In: Orientation and Navigation. Proc RIN 05 Conf, Royal Institute of Navigation, Reading (in press)
- 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
- 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’Étranger* 14:1–36
- Walcott C (1978) Anomalies in the earth’s magnetic field increase the scatter of pigeons’ vanishing bearings. In: Schmidt-Koenig K, Keeton WT (eds) Animal migration, navigation and homing. Springer, Berlin Heidelberg New York, pp 143–151
- Walcott C, Green RP (1974) Orientation of homing pigeons altered by a change in the direction of an applied magnet field. *Science* 184:180–182
- 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
- Williams MN, Wild JM (2001) Trigeminally innervated iron-containing structures in the beak of homing pigeons and other birds. *Brain Res* 889:243–246
- Wiltschko W (1978) Further analysis of the magnetic compass of migratory birds. In: Schmidt-König K, Keeton WT (eds) Animal migration, navigation and homing. Springer, Berlin Heidelberg New York, pp 302–310
- Wiltschko W, Wiltschko R (1972) Magnetic compass of European Robins. *Science* 176:62–64
- Wiltschko R, Wiltschko W (1978) Evidence for the use of magnetic outward-journey information in homing pigeons. *Naturwissenschaften* 65:112
- Wiltschko W, Wiltschko R (1981) Disorientation of inexperienced young pigeons after transportation in total darkness. *Nature* 291:433–434
- 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
- Wiltschko R, Wiltschko W (1995) Magnetic Orientation in Animals. Springer, Berlin Heidelberg New York
- Wiltschko W, Wiltschko R (1999) The effect of yellow and blue light on magnetic compass orientation in European Robins, *Erithacus rubecula*. *J Comp Physiol A* 184:295–299
- 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
- Wiltschko W, Wiltschko R (2002) Magnetic compass orientation in birds and its physiological basis. *Naturwissenschaften* 89:445–452
- Wiltschko R, Wiltschko W (2003) Avian navigation: from historical to modern concepts. *Anim Behav* 65:257–272
- Wiltschko W, Munro U, Ford H, Wiltschko R (1993) Red light disrupts magnetic orientation of migratory birds. *Nature* 364:525–527
- 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
- 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

- 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
- Wiltschko W, Gesson M, Wiltschko R (2001) Magnetic compass orientation of European robins under 565 nm green light. *Naturwissenschaften* 88:387–390
- Wiltschko W, Traudt J, Güntürkün O, Prior H, Wiltschko R (2002a) Lateralization of magnetic compass orientation in a migratory bird. *Nature* 419:467–470
- Wiltschko W, Munro U, Wiltschko W, Kirschvink JL (2002b) Magnetite-based magnetoreception in birds: the effect of a biasing field and a pulse on migratory behavior. *J Exp Biol* 205:3031–3037
- Wiltschko W, Munro U, Ford H, Wiltschko R (2003a) Lateralization of magnetic compass orientation in silvereyes, *Zosterops lateralis*. *Austr J Zool* 51:1–6
- Wiltschko W, Munro U, Ford H, Wiltschko R (2003b) Magnetic orientation in birds: non-compass responses under monochromatic light of increased intensity. *Proc R Soc Lond B* 270:2133–2140
- Wiltschko W, Möller A, Gesson M, Noll C, Wiltschko R (2004a) Light-dependent magnetoreception in birds analysis of the behaviour under red light after pre-exposure to red light. *J Exp Biol* 207:1193–1202
- 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
- Yorke ED (1979) A possible magnetic transducer in birds. *J Theor Biol* 77:101–105