
Magnetoreception in mammals and birds: a comparison (Mammalia, Aves)

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received on 10 October 2022

Abstract. The magnetic compass systems of birds and mammals differ in their functional modes and are based on different physical principles: The inclination compass of birds is not sensitive to polarity; it is light-dependent; with the direction indicated by spin-chemical processes in the photo-pigment cryptochrome. The polarity compass of mammals works also in total darkness and is based on magnetite, a biogenic iron-containing substance. Aside from the compass, birds include magnetic components in their navigational ‘map’; these components are based on magnetic intensity and are perceived by magnetite-containing receptors. Mammals probably also have a ‘map’, but its components are unclear. Reception based on magnetite particles appears to be the primary form of sensing the magnetic field, which, in the course of evolution, developed in different ways in the various animal groups: in mammals into a compass system to determine directions and in birds into parts of the ‘map’ to determine position.

Key words. Magnetoreception, inclination compass, polarity compass, light-dependency, radical pair mechanism, magnetite, radio frequency fields, pulse treatment

The use of the magnetic navigational information was first discovered in birds in the mid-1960s, when European robins, *Erithacus rubecula* (Turdidae) were found to use the magnetic field for compass orientation (WILTSCHKO W. & MERKEL 1966). This finding was initially met with great skepticism, because it seemed hard to believe that birds should have a sensibility so alien to us humans. Meanwhile, responses to the magnetic field have been described in a wide variety of animals: in all classes of vertebrates, among arthropods in crustaceans as well as in insects, in mollusks and even in some worms (see e.g., WILTSCHKO R. & WILTSCHKO W. 1995) – it seems most wide-spread among moving animals. In many cases, however, these responses were not analyzed in detail, and it often remained open to what component of the magnetic field the animals respond, how the magnetic field is perceived, how it is used and what exactly the magnetic input effects.

Magnetic compass orientation indicated by spontaneous behaviors

In mammals and birds, however, responses to the magnetic field could be analyzed and provide insight in the use of magnetic information. Both these vertebrate classes have a magnetic com-

doi: 10.37520/lynx.2022.014

pass, i.e. they can derive directions from the geomagnetic field. This has been demonstrated in laboratory experiments based on spontaneous behaviors, and important characteristics of their compass mechanisms could be identified.

During the migration season in spring and autumn, migratory birds have a strong urge to move into their migratory direction, and they do so even in suitable cages. When the North direction of the ambient magnetic field around the cage was shifted, the birds changed their directional preferences accordingly. This, first observed in European robins (WILTSCHKO W. 1968), has now been demonstrated in more than twenty avian species from five orders. Among them are also a few non-migrating species like homing pigeons (*Columba livia domestica*), domestic chickens (*Gallus gallus*, Phasianidae), mallards (*Anas platyrhynchos*, Anatidae), and zebra finches (*Taeniopygia guttata*, Estrildidae); here, the magnetic compass was demonstrated by directional training (see WILTSCHKO W. & WILTSCHKO R. 2020).

In the beginning of the 1980s, first indications for the use of magnetic information in mammals came from displacement experiments, when wood mice, *Apodemus sylvaticus* (Muridae) were transported in an altered magnetic field (MATHER & BAKER 1981). In 1990, however, BURDA and colleagues discovered that a subterranean rodent species, Ansell's mole-rat *Fukomys ansellii* (formerly referred to as *Cryptomys hottentotus*, Bathyergidae), when housed in a round arena, build their nests predominantly at the south-southeastern side (BURDA et al. 1990); the mole-rats shifted their nests accordingly when magnetic North of the ambient magnetic field was altered. This and a related type of experimental approach was also used to demonstrate magnetic compass orientation in other rodent species, like the blind mole-rat, *Spalax ehrenbergi* (MARHOLD et al. 2000, KIMCHI & TERKEL 2001), Siberian hamster, *Phodopus sungorus* (Cricetidae; DEUTSCHLANDER et al. 2003), the epigeic bank vole, *Clethrionomys glareolus* (Cricetidae; OLIVERIUSOVÁ et al. 2014), and laboratory mice (Muridae; e.g. MUHEIM et al. 2006, PAINTER et al. 2018). This resting behavior in a specific direction is not restricted to rodents: bats as the Chinese noctule, *Nyctalus plancyi* (Vespertilionidae) were found to preferably roost in the north-northeastern end of their roosting basket (WANG et al. 2007).

The functional properties of the magnetic compass systems

Testing the birds and mammals in various magnetic fields revealed characteristic properties of their magnetic compass mechanisms:

When birds were tested in a magnetic field with the vertical component inverted, i.e. pointing upward instead of downward like in the local geomagnetic field, they reversed their directional preference. They thus have a so-called 'inclination compass', that is, they are not sensitive to the polarity of the field, but only perceive the axial course of the field lines and decide between its two ends by its inclination in space (WILTSCHKO W. & WILTSCHKO R. 1972). As a result, they do not distinguish between magnetic North and South, as we do with our technical compass, but between 'poleward' where the field lines point downward, and 'equatorward', where they point up. Another characteristic of the avian magnetic compass is its response to magnetic intensity: it works spontaneously only in a limited functional range around the intensity of the ambient magnetic field; a decrease or increase in intensity of about 20% leads to disorientation. Yet, it can adjust to intensities outside this range, when the birds experience this other intensity for some time. The respective process is neither a shift nor an enlargement of the functional range: Birds are not able to orient in intermediate intensities, yet they do not lose the ability to orient in the previous experienced magnetic field (WILTSCHKO W. 1978). Furthermore, the magnetic

compass of birds requires light from the short-wavelength end of the spectrum, from UV to about 565 nm green. For a more detailed summary of the avian magnetic compass, see WILTSCHKO R. & WILTSCHKO W. (2021). This type of magnetic compass was found in all bird species tested to far: It was found in several passerine birds as well as in pigeons and chickens. Passerines and chicken belong to two different avian lineages – Neoaves and Galloanseres – that separated already in the mid-Cretaceous more than 100 million years ago (ERICSON et al 2006), so that the inclination compass appears to be common to all birds and possibly was already developed by their common ancestors.

The magnetic compass of mammals has been analyzed in few species only. The mole-rat *Fukomys anselli* as well as the bat *Nyctalus plancyi* did not change their preferred directions when the vertical component of the magnetic field was inverted – they obviously sense the polarity of the magnetic field, having a ‘polarity compass’ (MARHOLD et al. 1991, 1997a, WANG et al. 2007). Ansell’s mole-rats could not orient in an extremely weak field (MARHOLD et al 1997b), but studies suggest that the bat *N. plancyi* can spontaneously orient in strong field of about twice the local intensity and in weak fields of only 10 μ T (microTesla), $1/5$ of the local field (WANG et al. 2007, TIAN et al. 2015) – a spontaneous functional range around the local geomagnetic field, if it exists, seems to be much wider than in birds. The magnetic compass of mole-rats as well as that of the hamster *P. sungorus* does not require light; it also works in complete darkness (MARHOLD et al. 1997b, KIMCHI & TERKEL 2001, MALEWSKI et al. 2018). The same applies to the magnetic compass of the bat *N. plancyi* (WANG et al. 2007).

Reception of directional information from the magnetic field

These principal differences in the functional mode of the magnetic compass between birds and mammals suggest very different reception mechanisms. And indeed, there is evidence that they are based on different physical processes:

For birds, RITZ et al. (2000) proposed the ‘Radical Pair Model’, which suggests magnetoreception based on spin-chemical processes. By absorbing a photon, a special type of photo-pigment forms a radical pair of electrons, which can occur in two states, namely singlet with antiparallel spin and triplet with parallel spin. The ratio singlet/triplet depends on the directional relation of the radical pair to the ambient magnetic field. Since the singlet and triplet products show different properties, this ratio could indicate magnetic directions. The eyes were proposed as site of magnetoreception, because light is available and, due to their more or less round shape, the receptor cells are arranged in all spatial directions. The latter would result in a specific activation pattern across the retina that is centrally symmetric to the direction of the magnetic vector and thus can mediate the axis of the field lines. As a crucial photo-pigment, RITZ et al. (2000) suggested cryptochrome, the only photo-pigment known in animals that forms radical pairs. This model can explain the specific properties of the avian magnetic compass: Since the relationship of the radical pair to the field lines and thus the singlet/triplet ratio is not sensitive to the polarity of the field, the consequence is an inclination compass as found in birds. The fact that the activation pattern would change with intensity explains the flexible functional window: Birds experiencing a sudden change in intensity are faced with a novel activation pattern, which is confusing at first; yet because the pattern retains its central symmetry to the magnetic vector, birds can eventually learn to interpret it (see e.g. WILTSCHKO R. & WILTSCHKO W. 2021). The dependency of magnetic compass orientation on short-wavelength light is in agreement with the absorbance spectrum of cryptochrome (see, e.g., MÜLLER & AHMAD 2011), a photo-pigment of

which several types are found in the avian retina (e.g. NIESSNER et al. 2011, 2013, 2016, BOLTE et al. 2016, GÜNTHER et al. 2018; for review, see WILTSCHKO R. et al. 2021).

Radio-frequency fields in the MHz (MegaHertz) range interfere with the singlet/triplet transition; hence they can be used to indicate whether radical pair processes are involved (RITZ 2001, HENBEST et al. 2004). Birds were indeed disoriented when exposed to broad band fields with frequencies from 0.1 to 10.0 MHz and single frequencies between 0.5 and 7 MHz, but only when the radio frequency fields were presented at an angle to the vector of the ambient static field (RITZ et al. 2004, 2009, THALAU et al. 2005), with the Larmor frequency, the frequency of the electron in the local field, being disruptive even at intensities of a few nanoTesla only (RITZ et al. 2009, KAVOKIN et al. 2014, PAKHOMOV et al. 2017).

In mammals, the sensitivity to the polarity of the magnetic field suggests an involvement of permanently magnetic material. Magnetite, a specific form of iron oxide, $\text{Fe(II)Fe(III)}_2\text{O}_4$, is a biogenic magnetic substance produced by a variety of animals, among them several rodents (see MATHER et al. 1982). Magnetic particles are also found in the heads of several bats species (BUCHLER & WASILEWSKI 1982, TIAN et al. 2010). It was suggested that these animals sense the direction of the magnetic field by such particles exerting a torque that acts on receptors etc. (for a detailed discussion, see WINKLHOFFER & KIRSCHVINK 2010).

A test for the involvement of permanently magnetic material is the treatment with a short, strong magnetic pulse that can re-magnetize the magnetic moment of such particles. In the mole-rat *Fukomys anselli*, such a pulse led to a shift in the direction of the nest-building. The duration of the effect – it was still present after 3 months – suggests an involvement of single domain magnetite, i.e. particles with a permanent magnetic moment that is altered by the pulse (MARHOLD et al. 1997b). A pulse also changed the homing orientation of displaced big brown bats, *Eptesicus fuscus* (Vespertilionidae) (HOLLAND et al. 2008). In mole-rats, the crucial particles are located in the cornea of the eyes, as anesthesia of the cornea or a surgical removal of the eyes led to nest building in random directions (WEGNER et al. 2006, CASPAR et al. 2020). An effect of a magnetic pulse was also observed in Nathusius' bat, *Pipistrellus nathusii* (Vespertilionidae): The bats departed randomly when the corneas of both eyes were anesthetized (LINDECKE et al. 2021).

The experimental evidence thus indicates two rather different compass mechanisms in the two vertebrate groups, birds and mammals. Whereas all birds tested so far seem to use the same mechanism (at least there is no evidence contradicting this assumption), this is not necessarily true for mammals, where the magnetic compass of only very few species has yet been analyzed. For mole-rats and bats, the findings suggest identical mechanisms so far, but mammals of other orders, man included, have been reported to also respond to magnetic stimuli (for a list, see BURDA et al 2020), and whether they use the same mechanism is unclear. A wide-spread use of a magnetic compass is to be expected, however, and it probably provides the basis of the alignments and other oriented behaviors described in several mammalian groups (e.g. BEGALL et al. 2008, ČERVENÝ et al. 2011, 2016, for reviews, see BEGALL et al. 2013, BURDA et al. 2020).

Some findings, however, indicate that the situation is even more complex: There is evidence that mammals are also affected by radio frequency fields and that birds are also affected by pulse magnetization: The same radio frequency fields that disrupted the compass orientation in birds did not affect the nest building direction of Ansell's mole-rats (THALAU et al. 2006), but the nest building of wood mice *Apodemus sylvaticus* (Muridae) was altered by a weak 28 to 100 nT broad band field in the range of 0.9–5.0 MHz, whereas a stronger field of the Larmor frequency had no effect (MALKEMPER et al. 2015). The alignment behavior of cattle and deer

was also disrupted by the low frequency electromagnetic field of 50–60 Hz of high voltage power lines (BURDA et al. 2009). PHILLIPS et al. (2022) even suggest that frequent failures to find magnetic compass orientation in laboratory tests with mice might be caused by low-level radio frequency fields originating from the apparatus in laboratories etc. – On the other hand, a magnetic pulse led to a significant deflection of the headings of migratory birds in cage tests (e.g. WILTSCHKO W. et al. 1994, WILTSCHKO W. & WILTSCHKO R. 1995, MUNRO et al. 1997) and it also affected the orientation of free flying migrants released after pulsing, but not in all cases (e.g. HOLLAND & HELMS 2013, KARWINKEL et al. 2022). A pulse also altered the departure directions of displaced homing pigeons at sites at greater distances (BEASON et al. 1997), indicating an involvement of permanent magnetic material like magnetite.

Magnetite-based magnetoreception

In birds, this seeming contradiction has been solved: Aside from a radical pair-based magnetic compass, they have a second reception mechanism for magnetic fields based on magnetite, which allows them to record the local magnetic intensity as a component of their navigational ‘map’.

Small magnetite particles have been detected with the Prussian blue staining technique in the ethmoid region (BEASON & NICHOLS 1984) and in the skin of the upper beak of birds (HANZLIK et al. 2000, FLEISSNER et al. 2003, TIAN et al. 2007, FALKENBERG et al. 2010). The role of the latter as magnetoreceptors has been questioned, claiming that they are macrophages (TREIBER et al. 2012), although selected-area electron diffraction (HANZLIK et al. 2000) and micro-XANES (microscopic X-ray absorption near-edge structure; FALKENBERG et al. 2010) measurements had identified them as clusters of superparamagnetic magnetite and maghemite ($\text{Fe(III)}_2\text{O}_3$), both forms of iron unusual for macrophages. Clusters of superparamagnetic magnetite are also affected by a magnetic pulse (see DAVILA et al. 2005); the shorter duration of the pulse effect in birds – only about 10 days (WILTSCHKO W. et al. 1994, HOLLAND & HELMS 2013) – is in agreement with an involvement of clusters of such particles.

The region of the upper beak is innervated by the ophthalmic nerve, a branch of the trigeminal nerve, where electrophysiological recordings and immediate early gene expression showed activation by magnetic stimuli (BEASON & SEMM 1987; see also MORA et al. 2004, HEYERS et al. 2010); this activation continued when the direction was held constant, indicating that magnetite-based sensors mediate not direction, but magnetic intensity (SEMM & BEASON 1990). Anesthesia of the ophthalmic nerve in migrants (BEASON & SEMM 1996) as well as local anesthesia of the upper beak (WILTSCHKO W. et al. 2009) eliminated the pulse effect, with the birds again preferring their migratory direction. On the one hand, this supports the location of magnetite receptors in the upper beak and their innervation by the ophthalmic nerve; on the other hand, it shows that the avian magnetic compass is not impaired by the pulse, indicating that magnetite is not involved in the compass. – The latter is also supported by the observation that the pulse affects only experienced migrants, i.e. birds that have migrated before and are familiar with the goal, while first-time migrants (whose migration is controlled by the innate migration program, see e.g. BERTHOLD 1988) are not affected (MUNRO et al. 1997, HOLLAND & HELMS 2013). This suggests that a learned system is involved and points to the navigational ‘map’, a system established by experience.

A most impressive experiment indicating an important role of the magnetite-based receptors in the navigational ‘map’ comes from displacements experiments: During spring migration, migrants head toward their breeding area; when they are displaced, they change their course

accordingly, heading towards that goal (CHERNETSOV et al. 2008). They do so also when they are not physically displaced, but when the displacement is magnetically simulated by testing them in the magnetic field of the distant site, showing that the magnetic field of that site was the basis of their goal-oriented change in headings (KISHKINEV et al. 2015). However, they did not compensate for the real or the magnetically simulated displacement when the trigeminal nerve was sectioned (KISHKINEV et al. 2013, PAKHOMOV et al. 2018), indicating magnetite-based receptors in the beak area as origin of the underlying information.

Yet another behavior of birds has been described that seems to involve the magnetite-based receptors in the ethmoid region. Under light conditions where the magnetic inclination compass cannot work, i.e. total darkness, red light or monochromatic light of higher intensity, migrants showed directional preferences that were different from their migratory direction and did not change between spring and autumn. Local anesthesia of the upper beak abolished this ‘fixed direction’ behavior, leading to random orientation, indicating magnetite-based receptors in the upper beak as origin of the respective information (for an overview and discussion, see WILTSCHKO R. et al. 2010). We can only speculate about the significance of this behavior – it does not seem helpful for the birds because they cannot link it with their migratory direction. Possibly, it is an ancient relict that is brought forward anew by the unnatural light conditions.

With mammals, there are more open questions. The basis of the effect of oscillating field is unclear – is it caused by radical pair mechanisms being affected or has other reasons? Do different orders of mammals possibly have different compass mechanisms? It has been argued that mole-rats, living underground, and bats, being nocturnally active, need to have a light-independent compass, which does not necessarily apply to epigeic rodents and day-active mammals. However, many of the avian migrants that have been shown to use the light-dependent inclination compass use it also during their nocturnal migration flights. The possibility of a ‘magnetic map’ must also be considered. Mammals do home after displacement (for an overview, see BURDA et al. 2020), but the mechanisms involved still await a detailed analysis. Experiments with displaced big brown bats (*Eptesicus fuscus*) exposed to altered magnetic fields or to a magnetic pulse before release clearly showed that the magnetic field is involved in homing (HOLLAND et al. 2006, 2008), but it is still open whether the compass, a ‘map’ or both have been affected, or possibly something else. This also applies to other magnetic effects in mammals. A magnetic ‘map’ has not yet been conclusively demonstrated in this animal group. The different ways of moving result in home ranges that are normally much smaller in mammals than in birds, which applies also to the distances covered during migration (maybe with the exception of cetaceans). Displaced homing pigeons were significantly affected by the magnetic pulse only at sites 80 km and beyond (BEASON et al. 1997) and the successful magnetic displacement of migrants returning to their breeding site mentioned above (KISHKINEV et al. 2015) involved a distance of 1000 km. Hence it is unclear whether there was a strong selective pressure for mammals to develop a magnetic ‘map’.

It is striking, however, that both – birds and mammals – use orientation mechanisms based on magnetite, even if these involve different forms of magnetite and different mechanisms. Magnetite is found in many living beings, starting from bacteria (e.g. BLAKEMORE 1975) through most animal groups to all classes of vertebrates (see KIRSCHVINK et al. 1985). KIRSCHVINK et al. (2001) suggested that magnetoreception based on magnetite was the primary form of magnetoreception and the starting point for the development of sensory systems providing magnetic information. Mobile animals must be expected to have evolved specialized mechanism adapted to their need. In birds, this led to a magnetic ‘map’ that allows navigation and steering directly to

distant goals over hundreds and thousands of kilometers, whereas to detect magnetic directions, they developed another mechanism, independent of magnetite, utilizing another physical principle, namely the reaction of radical pair in the magnetic field (RITZ et al. 2000). – Mammals, in contrast, at least rodents and bats, developed a light-independent compass mechanism based on single domain magnetite; whether this is also true for other mammalian groups is still open. During an early phase of their development, when in the Mesozoic age the dinosaurs dominated the earth during daytime, mammals were predominantly nocturnally active, which has shaped their sensory world: They have senses that are well suited for living in the dark. Mammals have an excellent sense of smell, and they have outstanding hearing abilities, being the only group with movable outer ears, while their visual sense is partly reduced, as they have lost two of the four original color receptors of vertebrates. Their magnetic compass sense may also be an adaptation to that situation, having developed an elaborated magnetite-based sense for magnetic directions that does not require light.

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