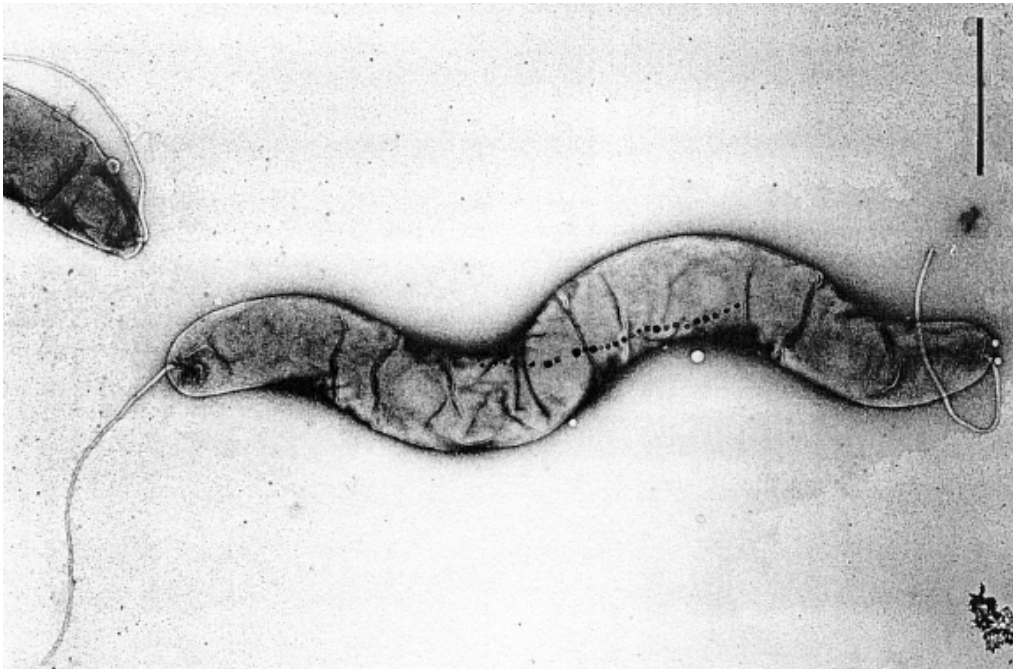


# **Animal Magnetoreception**

**- Models, Physiology and Behaviour**



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**Introductory Paper No 128**

**Department of Ecology**

**Animal Ecology**

**Lund University**

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**- Models, Physiology and Behaviour**

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## 1. Introduction

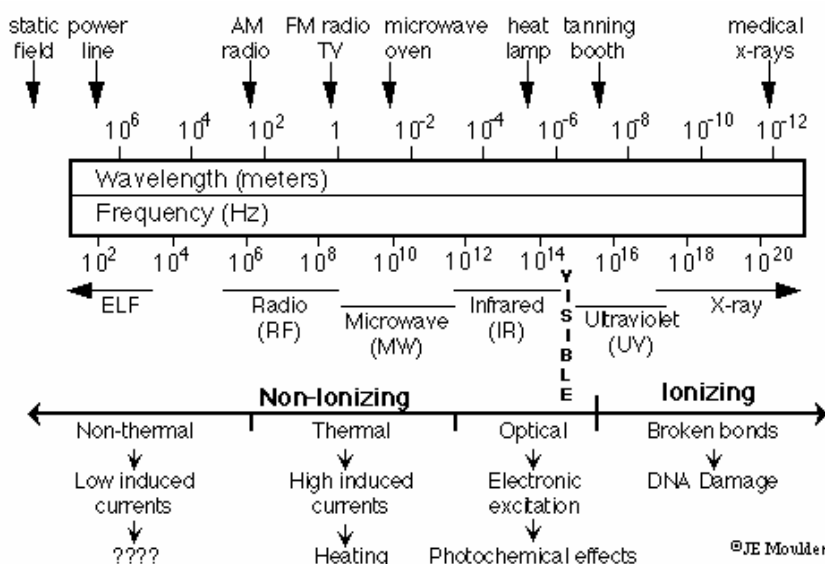
Many animal and plant species have been shown to react to electric, magnetic and/or electromagnetic fields. Natural as well as man-made static and time-varying fields have been shown to interact with biological systems. Especially the effect of high-frequency electromagnetic radiation on life forms is the subject of an agitated scientific and public debate concerning health effects.

Despite intensive research, the biophysical mechanisms of magnetoreception are not entirely known yet. Magnetobiological effects comprise processes at different hierarchical levels of a living organism, from molecular biochemical processes, leading to mutagenic, morphological and developmental effects, to complex adaptive biological processes including magnetic alignment and orientation of whole animals (see Frankel 1986, Tenforde 1991 for review).

In this introductory paper, I give an overview over the existing models and theories concerning the perception of magnetic fields and discuss available empirical results from physiological as well as behavioural studies in some selected animals in relation to these models.

## 2. The Electromagnetic Spectrum

The electromagnetic spectrum can be divided into different regions according to the frequency of the electromagnetic field (Fig. 1, Box 1). It is the energy per particle (photon) that determines the possible biological effects of electromagnetic energy. Electromagnetic fields at frequencies higher than  $10^{15}$  Hz are called ionizing radiation and include vacuum UV, X-ray and  $\gamma$ -ray fields. These ionizing forms of electromagnetic radiation are very energetic and can directly damage living organisms by breaking chemical bonds in biological molecules. But also the non-ionizing electromagnetic fields (static fields at 0 Hz to UV fields at ca.  $10^{15}$  Hz) can affect biological and physiological processes. Within the optical radiation part of the spectrum (UV, visible light, IR) electron excitation can occur. At microwave and high-frequency radiowave frequencies, where the wavelength is smaller than body size, induced currents can cause heating of tissues. Electromagnetic frequencies below  $10^6$  Hz, which include extremely low frequency (ELF) fields, are very inefficient at inducing electric currents or causing heat, but can still cause bioelectromagnetic effects.



**Fig. 1.** The electromagnetic spectrum characterized by frequency and wavelength. Source: <http://www.mcw.edu/gcrc/cop/powerlines-cancer-FAQ/QandA.html>.

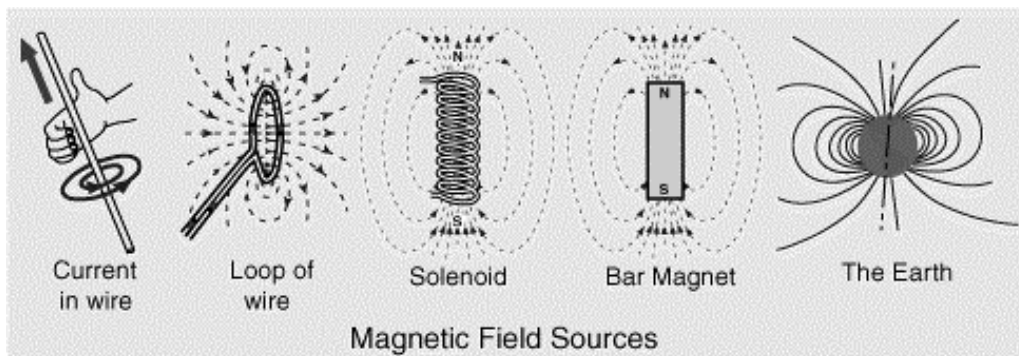
In the following I will restrict myself to the biological effects of non-ionizing fields and concentrate on ELF and static electromagnetic fields because this is the wavelength range relevant to geomagnetic field effects. Man-made static and ELF magnetic fields are found under DC high-voltage transmission lines (magnetic field up to 0.02 mT) and in general near electric appliances (up to 0.15 mT in house-holds), but also within the range of small magnets in audio speaker components, battery-operated motors or simple refrigerator magnets (1-10 mT). The strongest magnetic fields humans are exposed to occur in magnetic resonance imaging (MRI) used in medicine and range from 0.15 to 2 T (Deno and Carpenter 1994, Tenforde 1995).

**Box 1: Physical Properties of Electric, Magnetic and Electromagnetic Fields**

An **electric field** results from the separation of charged particles and is a form of stored energy, characterized by the electric field strength or intensity vector **E** in V/m. There are two distinct types of electrical currents we encounter in everyday life. A **direct current (DC)**, like the one coming from a flashlight battery, is a current that always flows in one particular direction, producing a static field. An **alternating current (AC)**, like the one coming from a household plug, is one that alternately flows in one direction and then the other, producing an alternating electromagnetic field.

A **magnetic field** is a form of stored energy as well, but comes from the motion of charged particles in an electric current or from microscopic currents associated with electrons in atoms of permanently magnetic material. The magnetic-field intensity is defined by the vector **H** in A/m. Another measure is the magnetic-flux density vector **B**= $\mu\mathbf{H}$  in Tesla (T), where  $\mu$  denotes the magnetic property of the material that couples the flux density to the magnetic field.

An **electromagnetic field** is a propagating coupled form of a changing electric field **E** and a magnetic-field intensity **B**. At low frequencies the two components contribute little to each other and can therefore be viewed at separately. These electromagnetic fields are called quasi-static fields and include ELF to low frequencies (0-10<sup>5</sup> Hz). Electromagnetic fields alternating at frequencies higher than 10<sup>6</sup> Hz are called propagating fields.



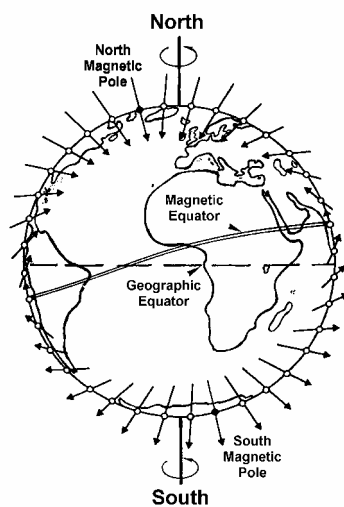
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**3. Natural Magnetic and Electric Fields**

Natural fields include both static and time-varying electric and magnetic fields. They originate from the Earth's core, electric discharges in the atmosphere and solar and lunar influences on ion currents in the upper atmosphere (Tenforde 1995). The magnetic field near the Earth is composed by 97-99% of the main field from electric currents in the outer core, by 1-2% of the crustal field from magnetized rock in the crust and by 1-2% of external fields from ionised particles in the upper atmosphere and solar wind.

### 3.1. Geomagnetic Field

The ambient geomagnetic field is an axially more or less geocentric dipole field, aligned approximately with the Earth's axis of rotation (Skiles 1985). It originates most probably from a so-called self-generating geodynamo, where fluid motion moves electrically conducting material across an existing field (Bloxham and Gubbins 1989). The intensity of the geomagnetic field ranges from maximally 68  $\mu\text{T}$  at the magnetic poles, where the field lines stand vertically (inclination angle is  $90^\circ$ ), to about 23  $\mu\text{T}$  around the magnetic equator, where the field lines are parallel to the Earth's surface (inclination angle is  $0^\circ$ ; see Fig. 2). Because of changes in the non-stationary flow patterns generated in the Earth's liquid outer-core and boundary processes in the core-mantle, the Earth's main geomagnetic field is constantly drifting (Skiles 1985). The poles are wandering several tenths of a degree annually (secular variation), and for instance the total intensity of the Earth's magnetic field has been decreasing by about 10% since 1900. At irregular intervals the poles of the geomagnetic field change, which is called a magnetic field reversal.



**Fig. 2.** The Earth's magnetic field. The length of the arrows indicates the magnetic field intensity at a particular site and the steepness of the arrows in relation to the surface of the Earth gives the angle of inclination. From R. Wiltshcko & W. Wiltshcko (1995).

### 3.2. Natural AC Magnetic Fields from Sun Activity

Solar electromagnetic radiation includes charged particles such as electrons, protons and  $\text{He}^{2+}$  ions, as well as some heavier, highly charged ions that are constantly emitted by the sun. The area where the charged particles emitted from the sun interact with the Earth's magnetic field is called magnetosphere. As a result of this solar activity and thunderstorms, large time-varying magnetic fields (at 60 Hz) are produced in the atmosphere (Tenforde 1995), which are especially strong on the sunward side of the Earth. Normal diurnal changes are in the order of 10 nT to 30 nT, and can reach 500 nT during magnetic storms.

### 3.3. Ambient Atmospheric Electric Fields

The time-varying atmospheric electric fields have relatively small amplitudes of between 90 and 120 V/m and are directed vertically downward into the Earth's surface in fair weather (Deno and Carpenter 1994). They consist of many different low frequencies ( $<30$  Hz), primarily originating from atmospheric conditions and pulsations in the geomagnetic field that produce currents within the Earth (Tenforde 1995). Such electric fields vary over the course of a day in a more or less predictable way and can be as high as 5 to 20 kV/m in the vicinity of thunderstorms (Deno and Carpenter 1994).

## 4. Magnetoreception Models

In this chapter I am presenting the principles of the currently most widely discussed magnetoreception models. The different models are not exclusive, because several different magnetoreception systems can, at least in theory, simultaneously play a role in detecting magnetic fields (see chapter 5).

At least three different principles of how animals detect magnetic fields of the strength of the Earth's magnetic field can be distinguished. Proposed mechanisms are based on permanent magnetic material like magnetite, on magnetically sensitive chemical reactions or on the detection of electromotive forces generated through magnetic induction. The main problem of all three principles is that the geomagnetic field is very weak and that a magnetoreceptor needs to be able to detect small variations in both intensity and direction (Edmonds 2001). The magnetic field detection mechanisms also have to overcome the following problems:

1. The number of receptors must be high enough to overcome the signal-to-noise ratio ( $S/N \geq 1$ ). This means a magnetic field can only be perceived when its effect is higher than any background noise of the reception system (Weaver et al. 2000).
2. The thermal noise limit is defined by a simple physical thermodynamic law and implies that any (electro)magnetic field interaction with biological systems must at least overcome the effects of thermal fluctuations due to random events (Weaver and Astumian 1990, Walleczek 1995). This means that the interaction energies from the maximum change in membrane potential caused by an applied magnetic field must be greater than the thermally induced fluctuations in membrane potential.

Theoretical calculations show that both restrictions can be overcome for static fields as weak as the Earth magnetic field as well as for 50-60 Hz fields with existing magnetoreception models (Ritz et al. 2000, Weaver et al. 2000).

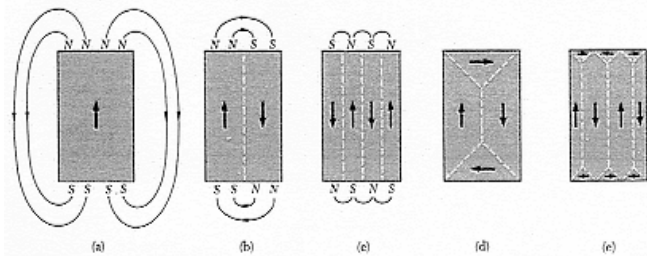
### 4.1. Biogenic Magnetite

In 1962, Lowenstam first discovered biochemically-produced magnetite in the radula of chitons (Lowenstam 1962). Prior to his discovery, magnetite was only known to occur in rocks, formed under high pressure and temperature (Kirschvink 1989). Later, the role of magnetite in orientation behaviour could be shown in magnetotactic bacteria (Blakemore 1975; see below for more details). Up to date magnetite has been found as a biochemical precipitate in three of the five kingdoms, Monera (Bacteria), Protista and Animalia (Chang and Kirschvink 1989). It is assumed that its biomineralization evolved about 2.5-2 billion years ago as a consequence of the increase of the oxidation state of the Earth's surface and the resulting decrease in the availability of dissolved iron. Later on, magnetotactic bacteria have probably been involved in the endosymbiosis when the eucaryotic cells were formed (Chang and Kirschvink 1989).

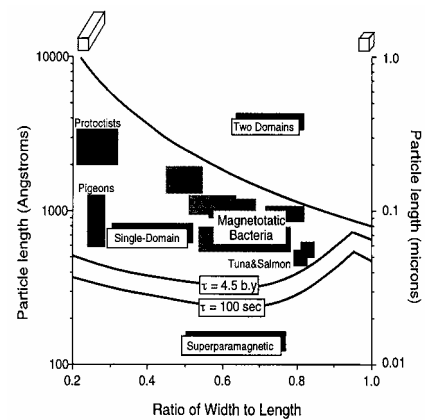
For a magnetoreception system based on magnetite to work several conditions should be met (see Kirschvink 1989): (1) the ferromagnetic material involved in magnetoreception should be biochemically precipitated by the organism itself since incorporated external material is usually too contaminated with Ti, Al, Mg and Mn as the most frequent impurity cations (Banerjee and Moskowitz 1985), (2) the particles must fulfil a variety of magnetophysical properties, like a specific magnetization and size and (3) the ferromagnetic particles must be mechanically coupled to sensory organelles, or another mechanism must allow to sensor the position of the particle.

### Box 2: Properties of Magnetite

Magnetite ( $\text{FeO}\cdot\text{Fe}_2\text{O}_3$  or  $\text{Fe}_3\text{O}_4$ ) is the most frequently occurring of the known biogenic materials that are ferro(i)magnetic at room temperature (Kirschvink 1989). Ferro(i)magnets have a spontaneous magnetic moment, even without the application of an outer magnetic field (Yosida 1996). A magnetite crystal is composed of small regions called domains. Within a domain the magnetization is saturated, i.e. the domain is maximally magnetized, which is a temperature-dependent process. Crystals composed of only one domain are called single-domain (SD) crystals. They are fine, usually elongated particles and have their magnetic moment directed towards one of the two ends (Banerjee and Moskowitz 1985, Yosida 1996). SD particles have larger magnetic energies and are more stable than multi-domain particles. However, in response to a particle's attempt to minimize its magnetic energy, the domain in a SD particle begins to split into several domains with increasing size, which leads to two-domain and multi-domain particles. Multi-domain particles contain different domains whose magnetization need not be equally directed. Applying a strong external magnetic field, however, redirects the single domains in the direction of the external field (Yosida 1996). In contrast to SD particles, multi-domain particles are thought to be not important in a magnetoreception process because their different internal domains have magnetic moments aligned in random directions (Kirschvink and Walker 1986). Magnetite particles which are sufficiently small or exposed to high temperatures become superparamagnetic and persistently reverse the particle magnetization (Banerjee and Moskowitz 1985, Kirschvink and Walker 1986, Yosida 1996; see also Box 4).



A) Ferromagnetic domains: a) single-domain, b) two-domain, c-e) multi-domain, d+e) the magnetic energy is zero, cancelled out. From Yosida (1996).



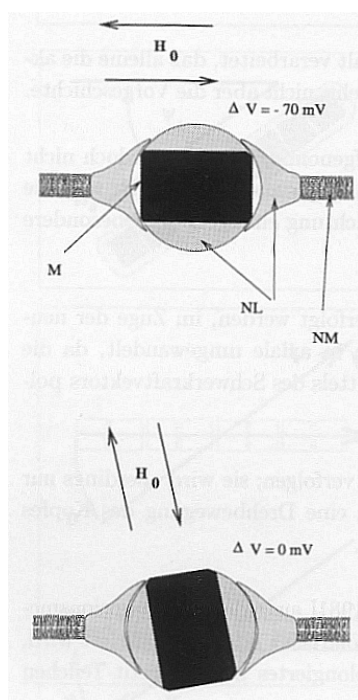
B) Size and shape of biogenic magnetite particles as found in different organisms. From Butler (1998).

#### 4.1.1. Models based on Single-domain Magnetite

The simplest magnetic compass involving magnetic material would be based on SD magnetite particles that align along an external magnetic field like **compass needles**. The magnetic orientation energy of SD magnetite in the geomagnetic field is at least as large as that of the thermal background energy (Polk 1994, but see Adair 1994). The arrangement in chains as found in bacteria (Blakemore 1975, Gould et al. 1978) imparts the magnetite crystals an even larger magnetic moment because of additive effects (Yorke 1985, Kirschvink and Walker 1986). The torque acting on such a receptor can in theory be perceived by two physically different principles (Winklhofer 1999): (1) the torque can be transformed into a free rotation like in an ordinary compass needle, or (2) the torque can produce some sort of elastic resistance or pressure on neighbouring physiological structures like a hair cell or another mechanoreceptor (Kirschvink and Walker 1986).

### Freely rotating compass needle magnetoreceptors

Kirschvink and Gould (1981) proposed a so-called ‘**membrane-short model**’ (Fig. 3) where a SD magnetite crystal is incorporated into a small organelle, held by hydrophobic protein groups across the membrane of a sensory-nerve ending. Because of the partial isolation of the magnetite particle (Fig. 3, top), the normal membrane potential of about -70 mV is maintained in the insulating position. Since magnetite is a good electrical conductor, an orientation of the organelle as shown in the conducting position (Fig. 3, bottom) would lead to a depolarization of the membrane and to a nerve signal. Kirschvink and Gould (1981) proposed that three such organelles in an orthogonal arrangement would give an estimate of the magnetic field direction, whereas the firing frequencies would give information about the intensity of the external field. However, it is not known whether a magnetic field of the strength of the geomagnetic field could overcome the dominating electrical forces in the membrane and whether magnetite would not be chemically changed when exposed to an ion rich protein liquid (Winklhofer 1999). Furthermore, the depolarization of a nerve cell is always connected to an ion transport through openings of the membrane, which is not taken into account in the ‘membrane-short model’ (Winklhofer 1999).



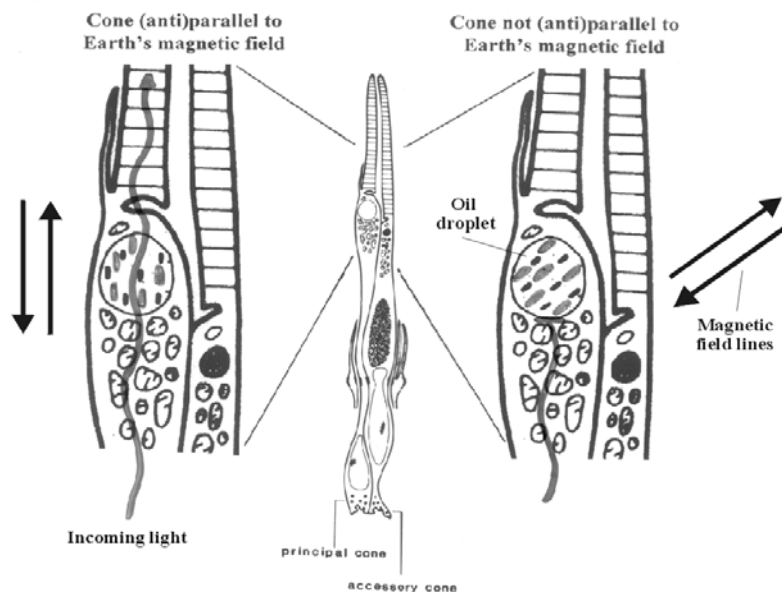
**Fig. 3.** Membrane-short model.

M = SD magnetite particle, NL = organic insulation, NM = nerve membrane

Top: Insulating position: The magnetite particle is insulated and the membrane maintains its usual membrane potential of -70mV between its interior and exterior.

Bottom: Conducting position: Since magnetite is a good electric conductor, the membrane potential is reduced and the nerve membrane depolarized. From Winklhofer (1999).

To account for the observation that the magnetic-field detector of several animals seems to be light sensitive (for a review see Deutschlander et al. 1999b, Phillips et al. 1999; see chapter 5 for more details), Edmonds (1996) developed a **sensitive optically detected magnetic compass** formed by ferro(i)-magnetic crystals, like magnetite, located in the oil droplets of the avian retina (Fig. 4). According to his model, freely moving magnetite particles located in the oil droplets interact with large dye molecules such as  $\beta$ -carotene and align parallel to the geomagnetic field, letting light enter to specialized photoreceptors when the position of the bird's head is oriented parallel or antiparallel to the geomagnetic field lines (Edmonds 1996).



**Fig. 4.** Edmonds' sensitive optically detected magnetic compass model (Edmonds 1996). The photoreceptor cell gets excited only when the cone is positioned parallel or antiparallel to the geomagnetic field (left). Otherwise the dye molecules in the oil droplet act as cut-off filters and absorb the light (right).

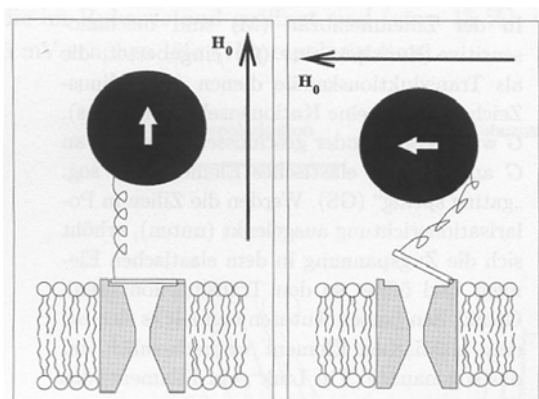
Arrows = direction of geomagnetic field

In oil droplets:  
light-grey spheres = dye molecules,  
small dark spheres = ferro(i)magnetic particles

### Mechanically coupled magnetic torque magnetometers

A **simple torque magnetometer** would contain SD magnetite particles ordered in a chain and connected to a hair cell or another mechanoreceptor. When exposed to an external magnetic field, the whole rod would be bent and impair the hair cell or mechanoreceptor (Kirschvink and Gould 1981).

The '**ferromagnetic transduction model**' proposed by Kirschvink (1992) is based on the idea that an electric potential can also be varied by opening or closing ion channels within the nerve membrane. It suggests that an applied magnetic field would produce a torque on a magnetite particle, mechanically coupled to an ion gate (Fig. 5). The application of ELF, pulsed, square wave as well as DC fields would open these ion gates and allow  $\text{Ca}^{2+}$  ions to pass through and elicit a nerve signal (Dobson and Pierre 1996).



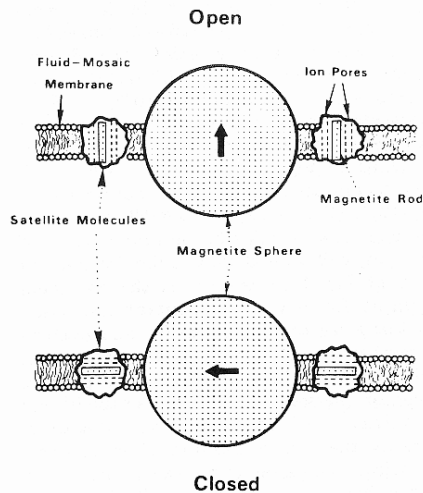
**Fig. 5.** Ferromagnetic transduction model. Ion channels in the nerve membrane open or close depending on the magnetic torque acting at magnetite particles connected to the ion gates and thereby let  $\text{Ca}^{2+}$  ions pass through. From Winklhofer (1999).

Edmonds (1992) suggested that a **magnetite torque detector** might be located in the macula of the lagena, a part of the avian cochlea, where gravity and the magnetic field could be detected simultaneously. In this model, SD magnetite particles would be incorporated within or between the cilia of the gravity detectors. The different responses of magnetite-loaded torque detectors and normal torque detectors would allow to directly determine the position of the north-south plane as well as the angle between gravity and the magnetic field (Edmonds 1992).

#### 4.1.2. Models based on Superparamagnetic Magnetite

Superparamagnetic (SP) materials have no spontaneous magnetic moment, but align with an external magnetic field. They can therefore not produce a torque, but can theoretically detect magnetic fields by other mechanisms (Kirschvink and Gould 1981, Winklhofer 1999).

Kirschvink and Gould (1981) suggested a **'sympathetic satellite model'**, based on the same idea as the 'ferromagnetic transduction model' (Kirschvink 1992; Fig. 6). Large, SP magnetite spheres were suggested to be located in a membrane, surrounded by smaller, membrane-sized molecules with an elongated magnetite core that would align parallel to the larger sphere and open or close ion pores (Kirschvink and Gould 1981).



**Fig. 6.** Sympathetic satellite model. Ion pores open or close depending on the direction of an external magnetic field influencing the spheres containing SP magnetite particles. From Kirschvink and Gould (1981).

Kirschvink and Gould (1981) also developed a magnetic torque model for an axial magnetoreceptor capable of detecting the inclination angle of a magnetic field. In their **'elastic torque rod transducer model'** elongated SP magnetite particles are arranged in a row and connected to a hair cell or some other mechanoreceptor. Under the influence of a magnetic field the neighbouring superparamagnetic crystals either attract or repulse each other, depending on the orientation of their dipole moments and thereby expand or contract the rod (Kirschvink and Gould 1981). Winklhofer (1999) criticized the physical rationale of this model and introduced a new model based on **superparamagnetic particles in an elastic matrix**, which for example would be realized if the (SP) particles were attached to the cytoskeleton of a receptor cell. Under the influence of an external magnetic field the elastic matrix would change its shape symmetrically along the axis of the magnetic field (Winklhofer 1999). However, Winklhofer (1999) also showed that it is energetically more efficient to distribute the SP magnetite particles over a so-called **ferromembrane** (cell membrane, membrane of the endo-plasmatic reticulum).

Stimulated by the discovery of SP magnetite in the upper beak area of homing pigeons (Holtkamp-Rötzler et al. 1997, Winklhofer et al. 2001), Shcherbakov and Winklhofer (1999) presented the **'osmotic magnetometer model'** based on ferovesicles. They showed theoretically that a cluster of SP magnetite particles dispersed in a liquid and enclosed by a biological membrane changes their shape under magnetic field strengths as small as the geomagnetic field. Such clusters connected to a mechanoreceptor would provide axial information about the applied field and the magnetic-field-induced shape of the clusters could be amplified as well as counterbalanced by osmotic pressure regulation, thus providing magnetic intensity information (Shcherbakov and Winklhofer 1999).

## 4.2. Biochemical Magnetoreception Models

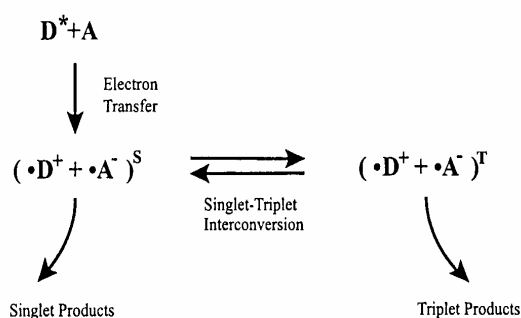
Several different models have been proposed based on magnetic-field perception by specific biochemical reactions (for review see Adey 1993, Grissom 1995, Binhi et al. 1999). Some of them are presented below.

### 4.2.1. Radical-pair Reactions

Magnetic-field interactions based on radical-pair recombination (see box 3) are one of the better-understood magnetic effects on biological systems. The **'radical-pair reaction model'** has been proposed as the underlying mechanism for many magnetic-field effects on various catalytic and enzymatic reactions, on the photosynthetic reaction center or signal transduction (Grissom 1995, Eichwald and Walleczek 1998, Adair 1999). Walleczek (1995) proposed a two-stage model of magnetic-field coupling to biological systems based on the idea that, as a primary physical interaction, static or time-varying magnetic fields would influence magnetically sensitive cellular radical pairs or biradicals and form free-radical intermediate states. These in turn can in a secondary interaction bring about a biological change, for example alter cell-signalling events, which leads to the observed cellular effect. Like this, the magnetic field can affect multiple-cellular targets, and the effect can be amplified by reaction chains (Walleczek 1995). However, the same principle can also alter molecules directly and cause a magnetic-field effect. A similar model examined the biological sensing of small field differences by magnetically sensitive chemical reactions, like radical-pair reactions producing ligands that bind to neural receptors (Weaver et al. 2000).

#### Box 3: Concept of Radical-pair Mechanisms

A radical is any atom or molecule with one or more unpaired electrons. Electrons possess an angular spin momentum, and radicals are therefore paramagnetic (see box 4). Radical pairs are formed in many biochemical transformations as reaction intermediates, either as singlet or triplet pairs, depending on the precursor molecule or the splitting conditions. In the singlet state, the total angular momentum of a radical pair is zero and the electron spins are oppositely directed and paired. In the triplet state, the electron spins are parallel and no bonding is possible. Radical pairs are very reactive and a radical pair in a singlet state can recombine. The presence of an external magnetic field influences the formation of triplet pairs with parallel spin, which prevents the reformation of a bond. Depending on the reaction yield of such single and triplet products, specific bioelectromagnetic effects can be observed.

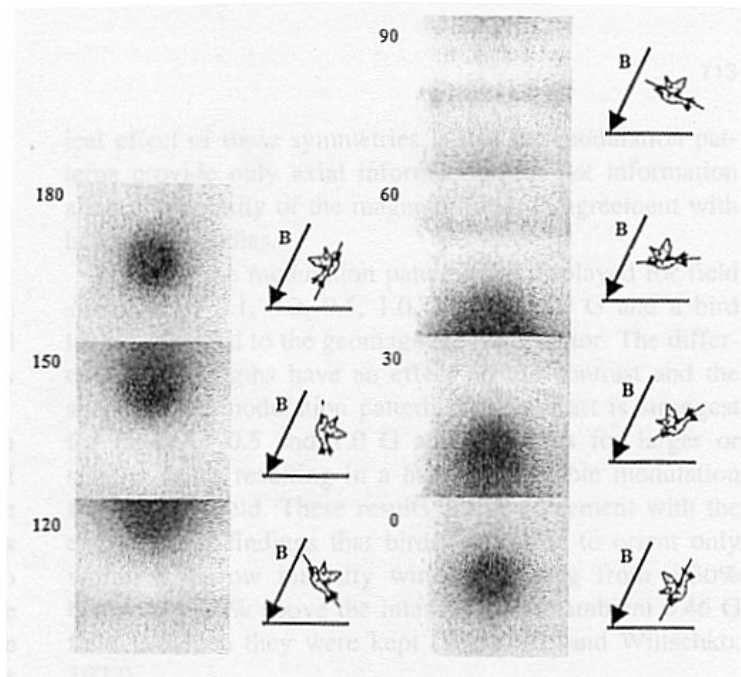


Magnetic-field-dependent radical-pair reaction. A donor molecule  $D^*$  transfers an electron to an acceptor molecule  $A$ . Two radicals, called a radical pair, with each an unpaired electron are formed  $(\bullet D^+, \bullet A^-)$ . An external magnetic field enhances singlet-triplet interconversions and thereby influences the composition of the reaction products. From Ritz et al. (2000).

The radical-pair mechanism has been proposed as a possible chemical sensor for magnetic compass orientation (Schulten 1982, Schulten and Windemuth 1986, Ritz et al. 2000). Schulten (1982) demonstrated that an external magnetic field can influence photon-induced processes which involve bimolecular reactions. In this process the radical pairs are formed by photon excitation through light absorption similar to the photosynthetic reactions. Based on this theory, Schulten & Windemuth (1986) proposed a model for a physiological magnetic compass with rhodopsin or iodopsin as likely organic reactants.

The animals would perceive the magnetic field as an apparent light intensity or colour variation in their visual field. Just recently, this ‘**vision-based magnetic compass model**’ has been refined by Ritz et al. (2000) and a newly discovered class of photoreceptors, the cryptochromes, were proposed as the magnetosensors (Fig. 7). It was shown theoretically that magnetic fields with intensities in the range of the geomagnetic field can produce a significant increase of the triplet yield which also depends on the relative orientation between the magnetic field and the radical pairs (Ritz et al. 2000).

The radical pair reaction model has also been suggested as a possible underlying mechanism for the magnetic-field sensitivity of the human visual system. Human visual sensitivity was shown to be influenced by periodic inversion of an artificial magnetic field of the strength of the Earth’s magnetic field (Thoss et al. 1999, 2000).

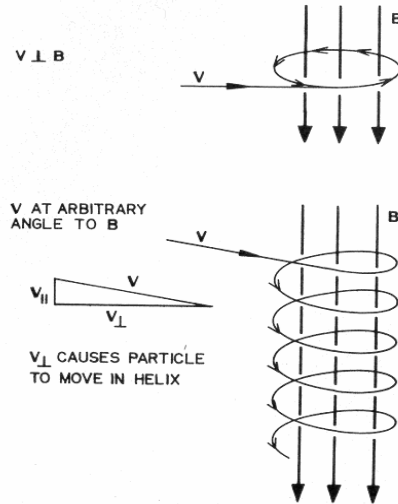


**Fig. 7.** Vision-based magnetic compass model. Proposed visual patterns perceived by a bird looking into different directions (0°: parallel; 90°: perpendicular; 180°: antiparallel) relative to the geomagnetic field vector with an inclination angle set to 68°. From Ritz et al. (2000).

#### 4.2.2. Resonance Models

Resonance models describe the reaction of charged particles, like  $\text{Ca}^{2+}$  ions, when absorbing electromagnetic energy of a weak magnetic field. Two resonance models have been described. The **cyclotron resonance model** describes the resonance effects of ions exposed to a DC and an AC magnetic field (Liboff 1985). A resonance effect is observed when the frequency of the oscillating field matches the gyrofrequency of the charged particle, determined by its mass, charge and the intensity of the static field (see box 4). The charged particle will be forced into circular orbits at right angle to the two imposed fields (Liboff 1985; Fig. 8) and change functional properties of the biosystem it is linked to, for example move  $\text{Ca}^{2+}$  through channels of a cell membrane (Smith et al. 1987). The cyclotron resonance effect has been suggested to be of importance since in a DC magnetic field of the intensity of the Earth’s magnetic field several biologically important ions have their cyclotron resonance frequencies in the ELF range between 10 and 100 Hz (Smith et al. 1987). However, a drawback of the model is that unhydrated ions (ions without their hydration shell) are required which are relatively rare in living systems (Liboff 1985, Adey 1993). The resonance effects for the same ions, but in the hydrated state, would be considerably reduced (Liboff 1985) and might become negligible.

The first proposed magnetoreception model depending on a biochemical mechanism is based on cyclotron resonances in the radio frequency (Leask 1977). This ‘**optical pumping**’ mechanism is a double resonance process and involves the lowest excited triplet state of the rhodopsin molecule in the retina. However, the radio frequency required for a resonance process to occur probably does not exist in living systems and therefore the model does not seem very likely (Phillips et al. 1999).



**Fig. 8.** Circular and helical paths of a charged particle with a velocity  $v$  in a magnetic field  $B$ . From Liboff et al. (1985).

Liboff and Jenrow (2000) proposed a new ‘**avian compass model**’ where magnetoreception takes place in the optic tectum of the brain that receives spatially separable visual signals from the retina. There, a radial electric field is generated by  $\gamma$ -oscillations in sensory processing during visual stimulation. Cyclotron resonance effects would occur when these internal electric fields meet a DC magnetic field, like the geomagnetic field, with maximal effects when arranged perpendicular to each other (Liboff 1997, Liboff and Jenrow 2000). Different intensities of stimulation in the optic tectum would so inform the bird about the orientation of the brain relative to the geomagnetic field and enable it to select a compass course.

The ‘**iron parametric resonance model**’ is a refined and more general version of the ion cyclotron resonance model and specifically predicts magnetic-field effects in a frequency window near 50-60 Hz (Lednev 1991). The model predicts how charged, unhydrated ions can influence the energy structure in a biochemical system, such as a protein complex, in the presence of low-frequency AC and DC magnetic fields (Lednev 1991, Blanchard and Blackman 1994, Adair 1998). The magnetic-field effects observed are not linearly dependent on amplitude or frequency of the applied magnetic fields, but the dependence is resonance-like and the effects are maximal at defined frequencies and amplitudes (Prato et al. 2000). Several experimental outcomes have been explained by the parametric resonance model including the response of nerve-growth-factor stimulated PC-12 cells exposed to magnetic fields at resonant conditions for the different ions (Trillo et al. 1996, Blackman et al. 1999) or the effects of magnetic fields on analgesia (loss of pain sensation) in land snails (*Cepaea nemoralis*; Prato et al. 1995, 1996, 1997, Kavaliers et al. 1998). However, other authors have strongly criticized the model and refuted its biological effects (Adair 1998).

#### 4.3. Induction

Electromagnetic induction is based on Faraday’s law according to which a conductor moving through a magnetic field generates an electric voltage. Moving a permanent magnet into or out of a coil wire also induces a current as long as the magnet is in motion. The strength of the induced current depends on the intensity of the magnetic field involved as well as on its angle relative to the conductor. The polarity of the induced field depends on the relative orientation and direction between conductor and magnetic field

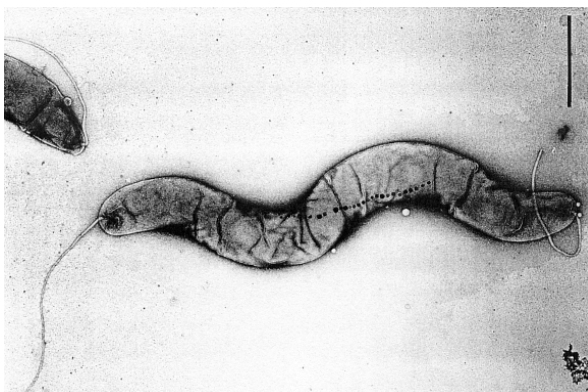
(Tenforde 1989). Electric and magnetic detection through induction has been suggested in Elasmobranch fishes, like sharks, rays and skates (e.g. Smith 1985, Feng 1991). Behavioural evidence suggests that they use their electromagnetic sense both in detecting prey and in spatial orientation (Kalmijn 1982, Feng 1991). They perceive the induced currents by specialized sensory organs, the **ampullae of Lorenzini**, which consist of jelly-filled canals with receptor cells at the end of the canal in an enlarged ampullary lumen (Feng 1991).

Animals can detect the Earth's magnetic field either by inducing electric currents by themselves when swimming through the Earth's magnetic field or by passively sensing induced electric fields from tidal and wind-driven ocean currents moving through the Earth's magnetic field (Kalmijn 1985, Smith 1985). The use of electromagnetic induction is restricted by the need of a good low-resistance return medium for the induced current, which is the case for salt- or freshwater. For terrestrial animals, an induction-based system would require a specialized internal transduction organ of several millimetres in diameter, like for example the labyrinth of the inner ear, since air is a very bad conductor (Jungerman and Rosenblum 1980, Edmonds 2001).

## 5. Behavioural and Physiological Evidences for Magnetoreception

Studies on magnetic sensitivity and magnetoreception in animals have been concentrating on (1) behavioural experiments manipulating magnetic-field components and observing the animals response, (2) physiological studies searching for sensory structures or organs involved in magnetoreception or containing magnetic materials and (3) neurophysiological recordings in order to study the neuronal pathways of nerves sensitive to magnetic stimulations. A multitude of other studies examining electromagnetic-field effects on cells, organs or whole organisms exposed to different other types of magnetic fields, like ELF and RF magnetic fields, powerline fields, ionizing or X-ray fields has also been collected over the years (for reviews see Grundler et al. 1992, Adey 1993, Blank 1995, Grissom 1995). I will restrict myself to effects of magnetic fields of the type of the geomagnetic field and try to relate the findings to the presented magnetoreception models discussed in the previous section. Thereby, only a selection of species or species groups that have been examined thoroughly enough to allow discrimination between the different models will be discussed. Other effects of magnetic fields on animals are reviewed by R. Wiltschko and W. Wiltschko (1995).

### 5.1. Magnetotactic Bacteria



**Fig. 9.** Magnetotactic bacteria with a magnetosome containing magnetite crystals arranged in a chain. From Blakemore and Frankel (1981).

Since the discovery of biogenic magnetite in Chitons by Lowenstam (1962), much effort has been invested in searching for magnetite or other magnetic materials in living organisms. The best studied organisms are magnetotactic bacteria (e.g. *Magnetospirillum magnetotacticum*; Fig. 9), first discovered in

the early 1970s in marine sediments by Blakemore (1975) and later found among different species in a variety of habitats, like freshwater, brackish marine sediments (Esquivel and De Barros 1986), river sediments (Frankel et al. 1979) and soil (Fassbinder et al. 1990). Their magnetotaxis is the only orientation behaviour using the geomagnetic field that can be considered as well understood. The magnetotactic bacteria actively swim along the field lines of an external magnetic field. Individuals collected in the Northern Hemisphere are mostly so-called 'north-seeking', thus swim consistently towards the geomagnetic North and their movements are thereby directed downwards into the anaerobic mud on the bottom because of the inclination of the Earth's magnetic field (Blakemore and Frankel 1981). Bacteria living in the Southern Hemisphere, on the other hand, are preferably 'south-seeking', moving opposite to the polarity of the magnetic field, which also leads them downwards deeper into the sediment (Blakemore et al. 1980). This is an adaptive behaviour since magnetotactic bacteria are either anaerobic or microaerophilic (surviving best in an environment with little oxygen) and thrive in anaerobic conditions (Blakemore and Frankel 1981). Hence, at the geomagnetic Equator, both types of bacteria have been found in roughly equal numbers (Frankel et al. 1981).

The ultrastructure of magnetotactic bacteria has been thoroughly studied and it has been shown that they contain chains of so-called magnetosomes, that are single crystals of magnetite or seldom greigite ( $\text{Fe}_3\text{S}_4$ ) or pyrrhoite ( $\text{Fe}_7\text{S}_8$ ) enclosed by a membrane (Blakemore 1975, Balkwill et al. 1980, Mann et al. 1984). The magnetite particles were identified as SD crystals, between 40 and 100 nm long (Frankel and Bazylinski 1995, Hanzlik et al. 1996, Shcherbakov et al. 1997, Dunin-Borkowski et al. 1998). The magnetosomes are usually arranged in intracellular chains (Hanzlik et al. 1996, Shcherbakov et al. 1997), which act as permanent magnetic dipoles and thereby aligning the organisms along the geomagnetic field lines.

## 5.2. Salmonid and Thunnid Fishes

In behavioural studies it has been demonstrated that Anadromous Rainbow Trout (other name: Steelhead, *Salmo gairdneri*) align along an external magnetic field, but become disoriented in a null magnetic field (Chew and Brown 1989). Rainbow Trout (*Oncorhynchus mykiss*) can discriminate between superimposed magnetic fields, but only when the conditional response allows movement and when the magnetic fields are spatially distinctive (Walker et al. 1997). Experiments with Yellowfin Tuna (*Thunnus albacares*) showed that they reacted to differences in intensity, but not to differences in direction (Walker 1984). Neurophysiological recordings on Rainbow Trout supported these findings. Single neurons in the superficial ophthalmic ramus of the trigeminal nerve have been shown to respond to changes in intensity, but not to the direction of an imposed magnetic field (Walker et al. 1997). Near the basal lamina of the olfactory epithelium, the area innervated by the trigeminal nerve, magnetite has been located in Sockeye Salmon (*Oncorhynchus nerca*; Mann et al. 1988, Walker et al. 1988, Walker et al. 1997). In adult Chinook Salmon (*Oncorhynchus tshawytschna*) and in one year old Yellowfin Tuna SD magnetite particles were located in the dermethmoid cartilage of the skull (Walker et al. 1984, Kirschvink et al. 1985). Based on the findings of iron-rich crystals in the olfactory lamellae in Rainbow Trout (Walker et al. 1997), Diebel et al. (2000) suggested a vertebrate magnetoreceptor in form of a multi-lobed cell, located in the basal lamina of an olfactory lamella and containing chains of magnetite particles. However, the existence of chains could not be shown microscopically, but inferred only from atomic-force and magnetic-force microscopical observations (Diebel et al. 2000). Furthermore, the exact mechanism how this magnetoreceptor cells should work has not been given.

### 5.3. Eastern Red-spotted Newt

North American Eastern Red-spotted Newts (*Notophthalmus viridescens*) are assumed to use two different orientation systems: (1) an axial compass mechanism for simple shoreward orientation based on the angle of inclination and (2) a map and polarity compass mechanism for homeward orientation and navigation responding to the polarity of the Earth's magnetic field (for review see Phillips 1986, Phillips 1987, Deutschlander et al. 2000). Both orientation systems have been shown to be light-dependent.

The axial compass used for shoreward orientation has been shown to reveal expected shoreward directions under short-wavelength light (peak 400-450 nm), but disorientation under 475 nm of light (Phillips and Borland 1992a, b). When tested under long-wavelength light (peak 550-560 nm), newts oriented 90° counter-clockwise to the shore. This suggests that either each receptor cell contains two antagonistic spectral mechanisms or that two different receptors with each a spectral mechanism give antagonistic inputs to a second-order neuron (Phillips and Borland 1992a). Complete disorientation of newts tested under the intermediate wavelength of 475 nm supports these models (Phillips and Borland 1992a). It could be shown that newts probably use a photosensitive extraocular photoreceptor in the pineal complex and hypothalamus as part of this shoreward orientation mechanism (Deutschlander et al. 1999a).

The newts' homeward orientation system reacts to changes in the horizontal component, but not to an inversion of the vertical component of a magnetic field, thus it seems to be a polarity compass (Phillips 1986). Newts tested under the full spectrum and under 400 nm light oriented towards home whereas newts tested under long-wavelength light (550+600 nm) were disoriented (Phillips and Borland 1994). It was therefore proposed that the newts' homeward orientation system receives input from both an intensity detector not dependent on light as well as from the light-dependent magnetic compass (Phillips and Borland 1994). This hybrid magnetoreception system is supported by the presence of magnetic material of the size and property of SD/SP maghemite-magnetite in newts (Brassart et al. 1999), implying that the newts' homing response is comparable to the birds' intensity map sense (see next chapter).

### 5.4. Birds

Two models for magnetoreception are currently discussed in birds: (1) a magnetite-mediated process detecting the intensity of the geomagnetic field and providing magnetic map information (intensity map sense) and (2) a light-dependent process detecting the inclination angle of the geomagnetic field and providing magnetic compass information (inclination compass: for review see Semm and Beason 1990, R. Wiltschko and W. Wiltschko 1995).

Recent behavioural and physiological studies support both models of magnetoreception and suggest that independent mechanisms are used to detect the different parameters of the geomagnetic field. They all suggest that young and adult birds partly rely on different orientation systems on migration. Inexperienced, young birds on their first migration rely on innate compass information for orientation (Berthold 1996). They use the inclination angle of the geomagnetic field to derive compass information and to select a migratory direction (Wiltschko and Wiltschko 1972). Adult birds instead seem to rely on some sort of map information registered on their previous migration(s) to locate already known stopover or wintering areas (Perdeck 1958). However, adults still seem to use inclination compass information, at least in certain situations.

The receptor of the avian inclination compass has been shown to be light-dependent. Young, inexperienced pigeons have shown to be disoriented when displaced in darkness or under red light, but not under green light (Wiltschko and Wiltschko 1981, 1998). Behavioural experiments with passerines performed under different wavelengths of light showed that both young and adult birds were disoriented under red (630 nm) and yellow (590 nm) light, but oriented into the seasonally expected migratory directions under white (full spectrum), blue (443 nm) and green (565 nm) light (Wiltschko et al. 1993, W. Wiltschko and R. Wiltschko 1995, 1999, Munro et al. 1997b, Rappl et al. 2000). Extracellular recordings in the nucleus of the basal optic root (nBOR) as well as in the optic tectum in pigeons have resulted in responses to changes in the direction of the magnetic field (Semm et al. 1984) and magnetic

responsiveness under wavelengths of 503 nm and 582 nm (Semm and Demaine 1986). At the moment, the model proposed by Ritz et al. (2000) seems to best explain these experimental findings.

The receptor of the intensity map sense is proposed to contain magnetite particles and lie in the ethmoid region of the upper beak area in the head of birds. For several bird species magnetic measurements in the head, neck and beak area both indicate the presence of magnetic material in these regions (Walcott et al. 1979, Beason and Nichols 1984, Beason 1986, Beason and Brennan 1986, Edwards et al. 1992, Holtkamp-Rötzler et al. 1997, Hanzlik et al. 2000, Winklhofer et al. 2001). The particles involved have been at least partly identified as SD or SP magnetite crystals and their magnetic characteristics seem to allow discrimination of sufficiently small magnetic-field variations necessary for an intensity map sense (Yorke 1985, Beason 1986, Beason and Brennan 1986, Holtkamp-Rötzler et al. 1997, Hanzlik et al. 2000, Winklhofer et al. 2001). Most recent findings of SP magnetite in homing pigeons in form of dense clusters adjacent to nerve material (Hanzlik et al. 2000, Winklhofer et al. 2001) suggest a model like the 'osmotic magnetometer model' (Shcherbakov and Winklhofer 1999) as the most realistic one. The application of short, high-intensity magnetic pulses of 0.5 T for 4-5 ms resulted in disorientation or deflection in the migratory orientation of passerines which had some migration experience (Wiltschko et al. 1994, 1998, Beason et al. 1995, W. Wiltschko and R. Wiltschko 1995, Beason and Semm 1996). Completely inexperienced birds seemed to be immune to such treatments (Munro et al. 1997a, b). Such pulses were designed to temporarily change the polarity of the magnetite particles and irritate the magnetic map sense (c.f. Beason et al. 1995). Electrophysiological recordings from the ophthalmic nerve, a branch of the trigeminal nerve, which innervates the magnetite-rich regions of the beak, have shown responses to changes in the horizontal component of the magnetic field (Beason 1986, Beason and Semm 1987). Blocking this nerve made adult birds unreceptive of magnetic pulsing, but did not inhibit their orientation (Beason and Semm 1996). This observation and the notion that adult birds are also disoriented under long wavelength light supports the suggestion that adult birds use both a magnetic map sense as well as inclination compass for orientation on migration.

## 6. Conclusions

In contrast to most other senses in animals, we know very little about magnetoreception mechanisms. Magnetic fields of the properties of the geomagnetic field penetrate living matter and a receptor can thus be located anywhere in the body. Indeed, there seems to be no large organ specialized in magnetoreception. This fact makes it very difficult to find possible magnetoreceptors and might be one reason for the very limited knowledge in this field. Behavioural experiments have helped to characterize the magnetoreception systems in some animal groups and physiological studies have revealed some indications how animals could perceive the geomagnetic field, but with the exception of the magnetotactic bacteria, we still do not know the details of how magnetoreception works in most animals. The variety of presented magnetoreception models illustrates in how many different ways animals could perceive a magnetic field. In practice, the different models are difficult to separate, especially with behavioural studies and might not be exclusive as well. Physiological studies are therefore an important part in the study of magnetoreception. Once the magnetoreceptor(s) is/are found, it will still be a challenge to fully try to understand how animals use the acquired information for orientation.

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**Box 4: Units and Definitions**

	cgs units		SI units
Magnetic flux density <b>B</b>	1 Gauss (G)	=	$10^{-4}$ Tesla (T)
Magnetic field density <b>H</b>	1 Oersted (Oe)	=	$\frac{1}{4\pi} 10^3$ A/m
Magnetic moment <b><math>\mu</math></b>	1 emu	=	$10^{-3}$ Am <sup>2</sup>

**Magnetic susceptibility** is a quantitative measure of the extent to which a material is magnetized in relation to an applied magnetic field. Magnetic material can be divided into diamagnetic, paramagnetic and ferromagnetic materials on the basis of their susceptibility:

**Diamagnetic materials** have no magnetic moment. All atoms have inherent sources of magnetism because electron spin contributes a magnetic moment and electron orbits act as current loops that produce a magnetic field. When exposed to an external magnetic field these electron orbits are shifted in such a way that the atoms set up their own magnetic field in opposition to the applied magnetic field which results in a weak repulsion. Their susceptibilities are therefore small and negative. If shaped like a rod, the particles line up at right angles to a non-uniform magnetic field. Diamagnetism is present in all materials, but if the atoms have some net magnetic moment as in paramagnetic materials, or if there is long-range ordering of atomic magnetic moments as in ferromagnetic materials, these stronger effects are always dominant.

**Paramagnetic materials** have small magnetic dipole moments that result from unpaired electrons. In the presence of an externally applied magnetic field they partly line up with the field, and thereby slightly increase it. Paramagnetic materials have small, constant, temperature-dependent positive susceptibilities, which are usually less than 1/1000 of the applied field. **Superparamagnetic materials** have a zero net magnetic moment, but in an external field they will show an alignment of magnetic moments.

**Ferromagnetic materials** on the other hand have large positive susceptibilities. They exhibit a long-range ordering phenomenon at the atomic level that causes the unpaired electron spins to line up parallel with each other in a region called a domain. Within the domain, the magnetic field is intense. The magnetization may be more than 1000 times larger than the applied field and occurs even without an external magnetic field. This is due to the properties of the materials and the tendency of the electrons to orient into the same directions, even without an external magnetic field.

The **gyrofrequency** is the magnitude of the angular velocity of a charged particle spinning around a guiding center. The smaller the particle mass and the higher the magnetic field are, the higher is its gyrofrequency and the smaller its gyroradius.