BIOGENIC MAGNETITE AND MAGNETIC SENSITIVITY IN ORGANISMS – FROM MAGNETIC BACTERIA TO PIGEONS

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Introduction. A large number of animals across all major animal phyla use the Earth's magnetic field for orientation, long-distance migration and homing (see [1], for a review of the behavioral evidence). Despite three decades of research in the field, astonishingly little is known about the nature of the underlying magnetic sense, the main reason for its elusiveness being that magnetic sensory cells – the postulated morphological correlates of the magnetoreceptor – have not yet been identified with certainty. It was only in the last five years that candidate magnetoreceptor cells have been detected, on which hypothesis can now be tested and specific theoretical models be elaborated to answer the following questions:

1. What is the nature of magnetic sensory cells?
2. By what physical mechanism is the external magnetic field coupled into the organism (reception)?
3. How sensitive is the mechanism to small changes in the magnetic field (detection threshold)?
4. What physical mechanisms or chemical pathways convert the received magnetic energy into a nervous signal (transduction)?

This paper gives an overview over the recent progress in tackling those crucial questions. Current research into magnetoreception is driven by two different hypotheses, which first were introduced in the late 1970's [2, 3] and have been developed further recently [4, 5]. The "radical-pair hypothesis" [2, 5] invokes magnetically sensitive biochemical reactions involving spin-correlated radical pairs such as produced by photoexcitation in the retina. The magnetic field interacting with the radical pair controls the reaction yields and so is transduced into a chemical stimulus. The "magnetite hypothesis" [3, 4], on the other hand, assumes that the external magnetic field interacts with inclusions of magnetite (Fe_3O_4) in tissue, which convert the received magnetic energy into a mechanic stimulus (strain) to be detected by adjacent mechanoreceptors, which eventually generate a nervous signal (receptor potential). Thus magnetoreception is connected to chemoreception in the first case and to mechanoreception in the second case. The two hypotheses are equally plausible at this stage of experimental evidence and it is due to the scope of the conference that this review is mainly focussed on the magnetite hypothesis. Relying on completely different physical principles, the two hypotheses do not mutually exclude each other. On the contrary, there is good experimental evidence that both types of magnetoreceptor principles may be realized, even in one and the same animal, although the primary magnetic information provided by each mechanism appears to be used differently. Examples will be given further below.

Radical-pair mechanism. Magnetic fields can influence biochemical reactions involving spin-correlated radical pairs by altering the dynamics of transitions between spin states [2]. The transitions between the spin states, in turn,

affect reaction rates and products. The Heisenberg principle requires that the transient state live long enough (at least 0.1 μs) in order to exchange magnetic energy with the comparatively weak geomagnetic field ($\sim$0.5 Oe). The magnetic interaction energy is much smaller than the randomising thermal energy kT. Nevertheless, the magnetic-field effects might well be amplified beyond the level of random fluctuations in a sufficiently large array of receptors, then making the radical-pair mechanism a feasible basis of a biological compass. Under the assumption that evolutionary pressure has optimized the system, an array of some $4 \cdot 10^8$ and $4 \cdot 10^{10}$ receptors is needed to detect field changes of the order of 0.01 Oe and 0.001 Oe, respectively [6]. Spin-correlated radical pairs can be generated by electron transfer from a photo-excited donor molecule to an acceptor molecule. Photo-excitation is in accord with the fact that magnetic compass orientation in some migratory birds depended on the wavelength of the light they were offered in behavioural experiments. While red light alone impaired the orientation, green or blue light did not [7]. Photoreceptor molecules such as cryptochromes in the inner retina or rhodopsin in the rods or color opsins in the cones in the outer retina are possible key proteins for a light-dependent magnetoreception mechanism. Moroever, since such a mechanism is related to vision, affecting visual transduction pathways, the magnetic field would modulate visual patterns [5]. In that way, the direction of the magnetic field could literally be seen.

Testing the radical-pair hypothesis. Although a chemically based biological compass is theoretically feasible, the specific transducing processes are not understood yet nor have the receptive structures been identified with certainty. Nevertheless, Ritz et al. [8] have recently provided firm evidence that the radical-pair mechanism is realized in migratory birds. They had designed a series of experiments to selectively affect the radical pair mechanism by using monochromatic 565 nm green light combined with radio-frequency (rf) fields of low intensity (0.5 μT) superimposed on the local geomagnetic field. Theory [9] predicts that a rf-field in resonance with the splitting between radical-pair states (singlet and triplet) can directly drive transitions between the spin states, thereby perturbing a radical-pair mechanism. Since this effect is anisotropic, it can be tested experimentally by varying the direction of the DC field with respect to the rf-magnetic-field vector. Indeed, when the rf-field (7 MHz) was aligned parallel with the DC field, birds displayed normal migratory orientation; however, in the rf-field aligned at a 24 deg or 48 deg angle to the DC field, the birds were disoriented, indicating that the rf-field interfered with magnetoreception [8]. These findings are in agreement with theoretical predictions about the resonance effects of oscillating magnetic fields in a radical pair mechanism and support the assumption of a radical-pair mechanism underlying the processes mediating magnetic compass information in the birds.

Magnetite-based magnetoreception. Conceptually more straightforward than the radical-pair hypothesis, the magnetite hypothesis is often considered the most plausible mechanism. The magnetite hypothesis assumes that some specialized sensory cells contain accumulations of ferrimagnetic material, such as biogenic magnetite, through which the external magnetic field is coupled into the nerve system. In its simplest realisation, the ferromagnetic material would act like a compass needle, being rotated into the direction of the magnetic field, thereby exerting a torque on the neighbouring tissue. A torque produces mechanical deformation, which in combination with a mechanoreceptor such as a Pacinian corpuscle can create a receptor potential and hence trigger a nerve signal. Such a torque mechanism is theoretically well-understood [10] and of course plausible, as

it is already realised in magnetotactic bacteria [11, 12], which can be considered as microscopic compass needles, swimming along the magnetic field lines. What makes this hypothesis so attractive is the fact that magnetic single-domain (SD) crystals of magnetite have indeed been found in animal tissue and closely resemble bacterial magnetite crystals. The most impressive example in this context are magnetite crystals extracted from ethmoid tissue of the sockeye salmon, with grain-sizes between 25-60 nm and a mean of 48 nm; the crystal morphology was described as cubo-octahedral [13]. Such a narrow grain-size range is typical of biologically controlled mineralisation processes. Due to the extraction procedure, however, there was no information left on the in-situ disposition of crystals and their histological context. Chains of crystals were observed in the magnetic extracts but most likely are artefacts from the extraction procedure: ethmoid tissue was ground and dissolved; the released magnetic particles centrifuged, washed, aggregated magnetically, and resuspended ultrasonically [13]. Likewise, it is not known if the ethmoid tissue is involved in the magnetic sense of sockeye salmon. So far, however, chains of magnetite crystals have not been identified in situ. Besides, the presence of SD magnetite in tissue does not automatically make a case for magnetite-based magnetoreception. So has SD magnetite been identified in radula teeth in recent chitons (Mollusca, Polyplacophora), where it is forming denticle cappings [14]. Apart from being magnetic, magnetite is also quite hard (between calcite and quarz), thus allowing chitons to scrape encrusting algae from intertidal rocks without having their tooth cusps abraded. As an ore mineral, magnetite has a high density (5 g/ccm), which can be utilised to design more sensitive gravity receptors than on the basis of calcium carbonate (3 g/ccm), which otoconiain otolithic organs are normally made of. Indeed, magnetite particles in sand ingested by rays (guitarfish) were incorporated as otoconia in the vestibular organ, alongside calcitic otoconia [15]. Even though the magnetite particles are exogenous, they may well interact with the geomagnetic field and produce a mechanical torque on the sensory cells in the otolithic organs [16]. There may be additional physiological or metabolic functions of endogenously mineralised magnetite that have not been unearthed yet. Magnetite has been identified in the human brain, meninx [17], and hippocampus [18], but also in heart, spleen and liver [19]. Magnetite may, therefore, be an iron dump for the body, or a by-product from iron metabolism, or may even be diagnostic for uncontrolled metabolism in tumour cells. Magnetic remanence measurements on two mouse tumours have revealed large concentrations of ferromagnetic mineral, presumably magnetite [20]. Taken together, those findings prompted the necessity of new approaches to verify the magnetite hypothesis: first, magnetite (or some other ferrimagnetic) crystals have to be localized in-situ in or next to nerve fibres, which convey magnetic-field modulated impulses to the brain. Detection of magnetic remanence can only be taken as a first hint where to search more closely. After describing the disposition of the crystals with respect to each other and to the cellular elements, a definite biophysical model can be developed to the point of making quantitative predictions testable by experiment.

Magnetite in homing pigeons   The only examination thus far that met all these requirements was on the upper beak skin of homing pigeons, where a putative magnetite-based magnetoreceptor has been identified and its subcellular organization and ultrastructure been characterized [21, 22, 23, 24].The putative magnetoreceptive structures were consistently found at six particular sites in the subcutis and contained groups of clusters of ultra-fine-grained magnetite crystals (grain sizes around 5 nm). There was no evidence of magnetite particles larger than 10 nm. Preliminary magnetic measurements on pigeon beaks at low temperature

had already pointed to tiny amounts of super paramagnetic material, which is in accord with the grain-sizes determined under the transmission electron microscope (TEM) [21]. Importantly, the magnetite clusters were found to be contained in free nerve endings (FNE), that is ,bare, unmyelinated dendrites as opposed to dendrites enclosed in a connective-tissue capsule. While magnetite was only found in FNE, not all FNE were found to contain magnetite [23]. The magnetite-bearing structures are innervated by the ophthalmicnerve, which conveys the sensory input from the beak skin to the brain [23]. This finding is consistent with electrophysiological recordings showing that the avian ophthalmicnerve carried magnetic information [25].

Physical mechanisms. The magnetic nanocrystals in the pigeon beak are super paramagnetic (SP), that is, the individual particles cannot carry a magnetization stably fixed in the particle's crystallographic reference frame. They can, therefore, not be physically twisted by the external magnetic field. Nevertheless, a cluster of SP crystals behaves as a statistical collective in an external magnetic field and takes on an induced magnetization. In such a way, the external magnetic field can be coupled into the FNE containing the clusters (reception). The next step to be done is to convert the magnetic energy into a physiologically exploitable stimulus that can eventually be transduced into a nerve signal. It isimportant to recall here that the magnetite clusters occur in FNE. FNE detect temperature, pain, and, more importantly, touch, that is, they are sensitive to mechanical stimulation. Thus, a mechanism, which converts the received magnetic field energy into deformation will stimulate the FNE. There are several ways of producing deformation in clusters of SP magnetite. An individual cluster will deform into a prolate ellipsoid of revolution with its long axis pointing along the applied magnetic field axis, regardless of wether the SP particles are dispersed in liquid or in a soft elastic matrix like the cytoskeleton [4, 22]. This behaviour is well known from ferrofluids, a technical representation of a super paramagnetic (SP) system. A second transducer model is based on magnetic interactions between clusters. As can be seen in Fig. 1, roughly 20 clusters occur in one terminal, loosely arranged in a coherent elongated structure. A detailed analysis shows that the spacing between two adjacent clusters is roughly twice their diameter [24]. Thus, the clusters will interact magnetically, thereby attracting or repelling each other in dependence of
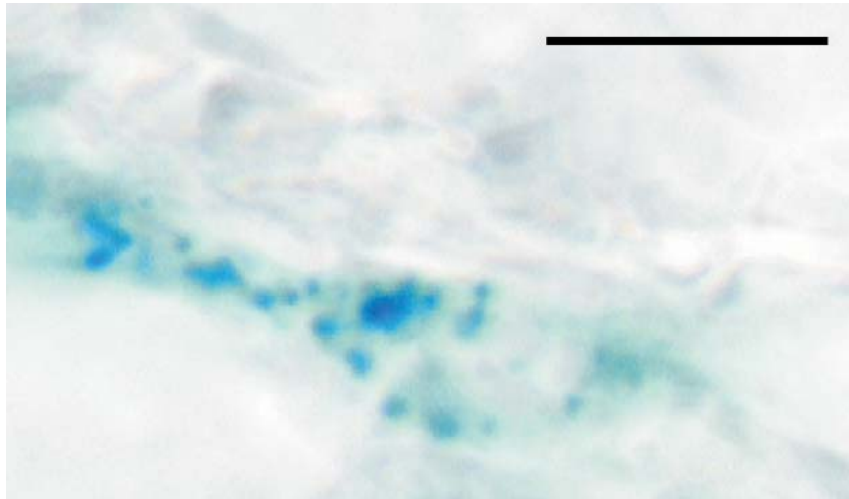

Fig. 1. Light-microscopic view of free nerve endings (FNE) containing clusters of SP magnetite (dark). Scale bar is 10 μm (from [24]).
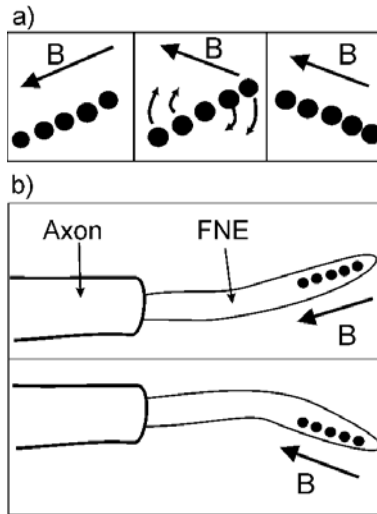
Fig. 2. (*a*) Dynamics of interactingSP clusters, and (*b*) suggested realization of the SP torque transducer mechanism, after [26].

the direction of the magnetic field with respect to the imaginary axis joining the clusters. In that way, mechanical forces arise that can stimulate the FNE, too. More precisely, an elongated group of SP clusters will experience a mechanical torque [26] in an external field applied at an angle ϕ with respect to the long axis of the group,

$$T \approx N \frac{16\,\pi^2\,\chi^2\,H_0^2\,R^3}{9\,avgr}\sin(2\phi)\,, \tag{1}$$

where N is the number of clusters in the group, χ is the magnetic susceptibility, H_0 is the strength of the external field, R is the radius of the cluster, and $avgr$ is the center-to-center distance of two adjacent clusters normalized by R. For the sake of simplicity, it was assumed in the derivation of Eq. 1 that the clusters are all of the same size and arranged in a linear chain. An exact expression for arbitrary dispositions is given in [26]. Anyway, as long as the clusters group in an elongated arrangement, they will behave macroscopically (Fig. 2a) like a compass needle and rotate into the axial direction of an applied field. On a microscopic scale, the clusters do not rotate but display translatory motion ($\mathbf{F} = \mathbf{m} \cdot \nabla \mathbf{B}$) caused by the stray fields of the other clusters in the group. The clusters in the FNE are of course not completely free to rotate, but confined by the nerve membrane. They will, therefore, exert a torque on the FNE. The torque, in turn, will bend the dendrite [27] and so may trigger transduction (Fig. 2b).

Theoretical calculations show that transducer mechanisms based on the clusters of SP magnetite are feasible [22, 4, 24, 26]. Although the models do make quantitative predictions, it is not yet possible (without ad-hoc assumptions based on evolutionary optimization arguments) to give a numerical estimate of the field sensitivity of the proposed mechanisms and the resulting detection threshold. This requires measurements of the physical model parameters such as magnetic susceptibility of SP clusters as well as viscosity and shear modulus of the medium containing the nanocrystals. Likewise, the threshold sensitivity of FNE to mechanical stimuli has to be determined. Still, the FNE containing SP clusters are excellent structural candidates for a magnetoreceptor, on which the theoretical models can be tested.

Experiments with pulsed fields. In several behavioural experiments test birds were subjected to a brief but strong magnetic pulse (0.5 T, 3 millisec) to

specifically test if ferromagnetic material is involved in magnetoreception (see [1], for an overview). The pulse intensity was chosen high enough to remagnetize stable single-domain magnetite. The minimum duration of the pulse was dictated by the coil geometry used in the experiments. A duration of less than 5 millisec was widely considered short enough to solely remagnetize ferromagnetic material, without affecting SP particles and without triggering any unwanted side effects such as electrondynamically induced nerve pulses. A positive test, i.e., misorientation after pulse treatment, was prematurely taken as evidence of single-domain magnetite being involved in magnetoreception. The problem with those pulse studies, however, was that there was no specific prediction how the pulse experiments may be less specific for single-domain magnetic without having made any specific predictions Davila et al. [26] simulated the effect of a magnetic pulse using the theoretical framework they developed to describe the dynamics of a group of interacting SP clusters under time-dependent magnetic fields. It turns out that SP clusters will be affected by a pulse, too: if applied at an angle $\phi > 45$ deg with respect to the chain axis, a strong magnetic pulse will disrupt the chain, causing temporal impairment of the magnetoreceptor mechanism and misorientation [26]. Interestingly, the chain will re-assemble on a time scale of hours to days after the pulse treatment, which is in good agreement with behavioural experiments, showing that normal orientation behavoir is recovered after 4 to 10 days. Interestingly, the pulse would only affect experienced birds, but not young birds before their first migration. Compass orientation in young birds, on the other hand, is affected by rf-magnetic fields. This led to the paradigm that compass orientation is based on a radical-pair mechanism, while magnetite forms the basis of a magnetic-intensity sensor, which is likely to be used in the so-called magnetic map sense for determining geographic position by means of local magnetic field variations, as caused by spatial variations in the magnetization of the Earth's crust.

Not only pigeons have magnets. Interestingly, accumulations of SP magnetite particles have also been reported in the abdomen of honey bees [28]. SP magnetite has been extracted from the abdomen and thorax of two species of termites [29] and of *Pachycondyla marginata*, a migratory ant [30]. The presence of SP magnetite in social insects has also been inferred from electron paramagnetic resonance [31, 32] and remanence measurements [33, 34]. On the other hand, TEM investigations on bees have not come so far as to reveal magnetite in its histological context; instead of magnetite, hydrous iron-oxides (ferrihydrite) were identified [35]. It is important to compare the candidate magnetoreceptor in pigeons with a structure described in a rainbow trout (*Oncorhynchus mykiss*) [36]. Using electrophysiological recordings, Walker et al. [36] were able to identify single neurons in the ophthalmic branch of the trigeminal nerve that respond to changes in the intensity but not the direction of an imposed magnetic field. To localize the magnetoreceptor, they used a staining technique to trace the magnetically responsive nerves back to the endings of the individual nerve cells. The candidate magnetoreceptor cells were eventually detected in the olfactory lamellae (nose). Using confocal laser scanning microscopy, TEM and EADX, they found iron-rich crystals (grain size 50 nm) in low volume concentrations, which by means of magnetic-force microscopy were later shown to have a permanent magnetism with magnetic properties similar to SD magnetite [37]. Surprisingly, the putative SD magnetite particles are located within a cell rather than in unmyelinated dendrites (FNE) or other mechanosensitive nerve structures. This raises questions on the possible transducer mechanism. It is not clear either if the magnetic particles are coupled to any potentially mechanosensitive elements and if they are arranged in the form of a chain or a cluster, necessitating detailed ultrastructural investi-

gations. Nevertheless, like theSP-magnetite-containing FNE in the beak-skin of pigeons, the presumably SD-magnetite-bearingnerve cells in the nose of trout are excellent candidates for a magnetoreceptor, too.

Biomineralization of magnetite. A question so far unanswered concerns magnetite biomineralisation in vertebrates. In the radula teeth of chitons (molluscs), the iron-oxyhydroxide ferrihydrite ($5\ Fe_2O_3 \cdot 9H_2O$) was identified as a precursor mineral to magnetite [38]. Ferritin may be the key protein in magnetite biomineralisation in vertebrates. Ferritins comprise a class of iron storage molecules ubiquitous among living systems. Each molecule of ferritin consists of 24 subunits which are assembled to form an approximately spherical cage-like structure of external diameter 12 nm; the cavity has a diameter of 8 nm [39]. Ferritin transforms highly toxic Fe(II) into the less toxic Fe(III) iron, to be sequestered in the cavitiy in the form of an iron mineral similar to ferrihydrite with varying amounts of phosphate incorporated [40]. Interestingly, the SP magnetite particles inhoming pigeons have grain sizes below 8 nm and, therefore, may well have been originated in ferritin, with ferrihydrate as a precursor to magnetite. At this stage, this is just a working hypothesis and further investigations are clearly warranted to elucidate the cellular and molecular pathways of magnetite biomineralisation.

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