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A new model for a magnetoreceptor in homing pigeons based on interacting clusters of superparamagnetic magnetite

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Abstract

We present a new model of magnetic-field reception in magnetite-containing nerve terminals, which have recently been identified in the upper-beak skin of homing pigeons. The potentially magnetoreceptive nerve cells comprise chain-like aggregates with up to 20 closely spaced clusters of superparamagnetic (SP) magnetite. We designed experiments on superparamagnetic model systems to simulate the behaviour of the aggregates in varying magnetic fields. Magnetic-field induced interactions between the clusters in an aggregate gives rise to attractive and repulsive forces between the clusters. The resulting stress on the surrounding cellular structures varies with field direction and intensity. Our model is able to explain the principal features of the magnetic sense in homing pigeons as derived from behavioural experiments.

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1. Introduction

Diverse animals are known to be capable of using the Earth's magnetic field for their orientation, e.g. several migratory birds (Wiltschko and Wiltschko, 1972), honey bees (Lindauer and Martin, 1968), amphibians (Phillips, 1977), sea turtles (Lohmann and Lohmann, 1996) and fish (Kalmijn, 1975; Quinn, 1980; Walker et al., 1997). Yet, apart from magnetic bacteria (Blakemore, 1975) and elasmobranch fish (sharks and rays; Kalmijn, 1981), neither the underlying magnetoreceptor system nor the physical properties of its functioning are known with certainty.

When discussing possible mechanisms of biological magnetic-field reception, it seems likely that nature has followed different strategies for developing the appropriate organs. One hypothesis about the physical nature of magnetic-field receptor assumes ferrimagnetic material—biogenic magnetite—to be involved in the trans-

formation of the magnetic-field stimulus into a physiologically exploitable signal (Lowenstam, 1962; Gould et al., 1978; Walcott et al., 1979). Lowenstam (1962) first discovered biochemically precipitated magnetite in the denticle capping of a coastal mollusc (chitons, or Coat-of-Mail shells). Magnetic bacteria were the second group of organisms found to contain biogenic magnetite and the first group known to use magnetic particles for passive orientation by the Earth's magnetic field (Blakemore, 1975).

The present study is centred on homing pigeons, *Columba livia*, which are well known examples of birds that use the Earth's magnetic field as a cue for orientation (for a review see Wiltschko and Wiltschko, 1995). Homing pigeons use among other mechanisms both a so-called *inclination compass* and a *navigational map* for magnetic orientation. According to Wiltschko and Wiltschko (1972) the *inclination compass* system provides directional information based on the axial direction of the geomagnetic field lines (declination $\pm 180^\circ$) in combination with the absolute value of the inclination (dip angle). Thus, the Earth's magnetic field in the northern and southern hemisphere at equivalent magnetic longitudes and latitudes provides the same information: in both cases, the birds recognise only a

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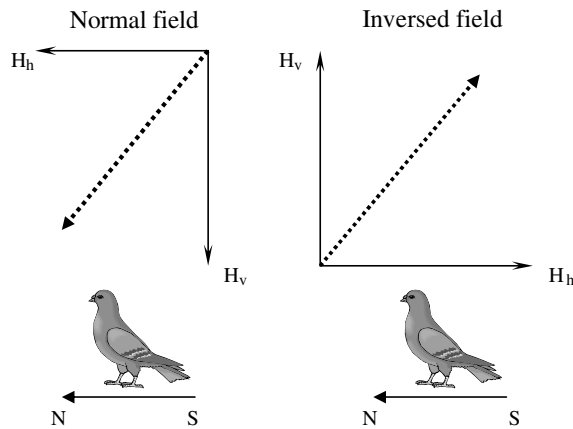


Fig. 1. Principle of the *inclination compass* according to Wiltschko and Wiltschko (1995). Both experimental situations are equivalent in terms of the information that a test bird can receive from a magnetic field: It can detect the axis of the geomagnetic field lines, but not their polarity.

polewards and equatorwards direction, instead of northwards and southwards (Fig. 1). In particular, the *inclination compass* is not affected by changes in polarity (field reversals). The *navigational map* on the other hand is a “mental” representation of the spatial distribution of different parameters like the position of the sun, geomagnetic intensity, odours and landmarks, which pigeons are able to memorise and use for orientation and navigation (see Wiltschko and Wiltschko, 1995, for a review of the functioning of the *inclination compass* and the *navigational map*). Any model proposed for a magnetoreceptor in homing pigeons has to be able to explain the *inclination compass* or the *navigational map* system. If there is only one kind of magnetoreceptor realised in homing pigeons, the model has to be able to explain both systems.

Walcott et al. (1979) reported the discovery of a magnetic remanence in the pigeon head concentrated in a particular region. They identified the magnetic material by Curie-temperature measurements as magnetite. However, similar experiments by Presti and Pettigrew (1980) showed that magnetic remanence was diffuse and spread uniformly throughout the entire skull rather than concentrated in a particular region.

Electrophysiological studies on birds suggest that the ophthalmic branch of the trigeminal nerve (in the head of the birds, see Fig. 2(a)) might be involved in magnetoreception, since this nervous tissue is sensitive to small changes in the intensity of an applied magnetic field (Beason and Semm, 1987, 1996; Semm and Beason, 1990). This makes the upper-beak skin as the sensory input region of the ophthalmic branch a likely site for a magnetic-field receptor.

Following this idea, Hanzlik et al. (2000) could localise Fe^{3+} accumulations in exactly this region of the upper-beak skin of homing pigeons, *Columba livia*, and identified the material by transmission electron micros-

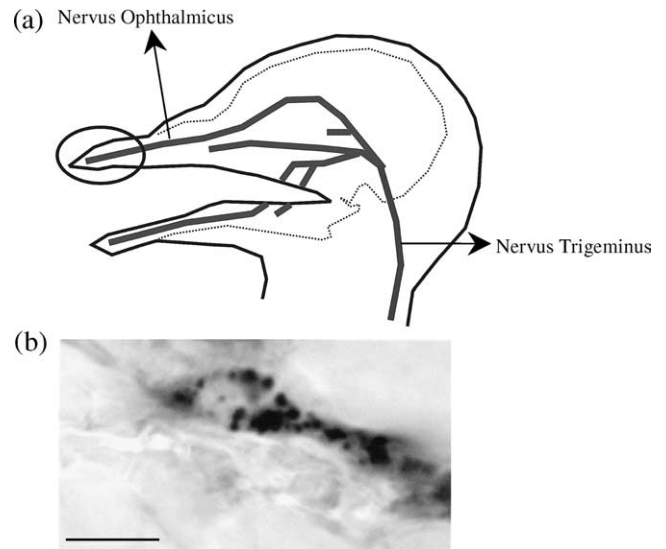


Fig. 2. Scheme of a pigeon skull showing the projections of the trigeminal nerve with the ophthalmic branch, which extends through its sensory input region, the upper-beak skin (ellipse) (a). Light-microscopic view of a nervous terminal (tissue stained by the Prussian blue reaction) with clusters of superparamagnetic particles distributed along the cell membrane in a coherent elongated arrangement (stack reconstruction of 10 confocal planes of the same microscopic section; scale bar 10 μm) (b).

copy (TEM) and low-temperature magnetic measurements as aggregates of magnetite nanocrystals (grain size between 1 and 5 nm), i.e. in a grain-size range where superparamagnetic (SP) behaviour occurs at normal temperature (Butler and Banerjee, 1975; Winklhofer et al., 1997). Under the light microscope, these SP aggregates appear symmetrically arranged inside the inner skin of the upper beak along its lateral rim, always occurring in the stratum laxum of the subcutis within strands of connective tissue and between fat cells. At higher magnification, these aggregates are resolved into intracellular groups of discrete particle clusters, arranged in coherent elongated structures (Hanzlik et al., 2000) (Fig. 2(b)). No evidence of single-domain (SD) magnetite, as known from magnetic bacteria, was found in their study.

Following the studies of Hanzlik et al. (2000), Fleissner et al. (2003) could demonstrate that the SP clusters occur always inside nervous terminals and are arranged alongside the cell membrane, possibly connected to it by tiny fibers.

The SP-grain size of the magnetic minerals, their arrangement into spherical clusters that form coherent elongated structures, and the location within nervous cells is a common pattern in all the individuals studied by Hanzlik et al. (2000) and Fleissner et al. (2003); this makes the SP clusters in the upper-beak skin a promising candidate for primary transducers of the magnetoreceptor system in homing pigeons.

2. Interacting clusters of superparamagnetic magnetite

Based on the special properties of magnetotactic bacteria, where single-domain magnetite particles play a key role for magnetic-field orientation, several theoretical models have been proposed for a magnetoreceptor system in higher organisms using a similar principle. In all these models it is assumed that the mechanical torque acting on an individual SD-magnetite particle or on a chain of SD-magnetite particles by their interaction with the Earth's magnetic field is somehow transformed into an electrical signal, which then could be used for orientation. Such models however, do not seem to account for the properties of the above mentioned *inclination compass*, which does not distinguish between magnetic north and south. It is also important to note that neither Hanzlik et al. (2000) nor Fleissner et al. (2003) could detect any SD magnetite in the tissue, only superparamagnetic material.

A first consistent model for magnetoreception based on clusters of SP particles has been proposed by Shcherbakov and Winklhofer (1999). They consider a single cluster of SP particles in connection with strain receptors as primary magnetoreceptors: such a cluster, polarised in the presence of a magnetic field, undergoes a change in shape as the magnetic field changes and deforms into a prolate ellipsoid with the long axis parallel to the magnetic-field direction.

Here we go a step further and take into account the observation that the SP clusters described above do not occur isolated from each other, but form well-structured aggregates of up to 20 clusters (see Fig. 2(b)). The close spacing between the clusters within an aggregate means that magnetic interactions between clusters will play an important, if not decisive, role in the response of an aggregate to changes in the external magnetic field. Our new model therefore is based on magnetic interactions between the clusters, leading to attraction and repulsion forces and, consequently, to mechanical stress in the surrounding tissue. Similar to most of the magnetite-based receptor models, our model requires mechanoreceptors to transform field-induced deformation into nerve impulses.

3. Tissue observations

The spatial arrangement of the SP clusters plays an essential role for the model proposed here. Therefore we carried out first light-microscopy analysis of biological samples from homing pigeons, bred and kept in the lofts of the Zoological Institute at the University in Frankfurt am Main. Since there are no chemical methods known to directly identify magnetite ($\text{Fe}_2^3+\text{Fe}^{2+}\text{O}_4$) particles in tissue, we first looked histochemically for concentrations of Fe^{3+} in the light microscope using the Prussian blue

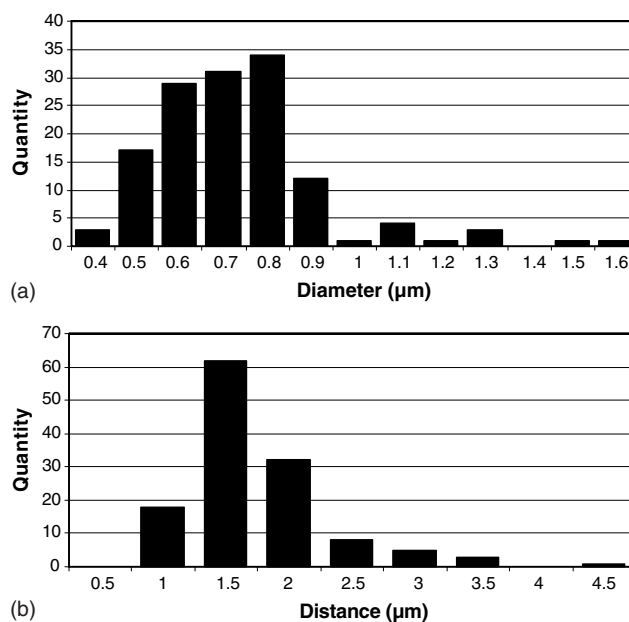


Fig. 3. Size distribution of the SP clusters found in the upper-beak skin of homing pigeons (a) and distance between adjacent clusters (b).

(PB) reaction on fixed tissue. In the presence of Fe^{3+} and HCl potassium hexacyanoferrate turns into the dark-blue ferric ferrocyanide. To map the iron enrichments, we used horizontal and sagittal sections (10 μm thick) of paraffinum-embedded skin; the clusters of SP magnetite in the sections under the light microscope can then be identified as dark-blue spherules inside the cells (see Fig. 2(b)). The analysis of the sections revealed an average cluster diameter of $0.8 \pm 0.2 \mu\text{m}$ (Fig. 3(a)). The average distance between the centre of two adjacent clusters was determined as $1.6 \pm 0.5 \mu\text{m}$ (typically two times the mean diameter of the clusters) (Fig. 3(b)). Within a cell, the clusters are arranged in the form of chain-like aggregates. In most cases, there are more than 10 clusters per chain and nervous terminal.

The sections were studied under a Reichert Polyvar microscope (Reichert, Vienna, Austria) with an attached digital microscope camera (Spot; Diagnostic Instruments, Sterling Heights, IL) and Metaview software (version 3.6; Universal Imaging Corporation, West Chester, PA).

4. Model experiments

We test here this model by experiments based on the assumption that the SP particles found in the upper-beak skin are not embedded in an elastic matrix but dispersed in a liquid. With this assumption, the clusters of SP particles may physically be described as droplets of a magnetic fluid. Shcherbakov and Winklhofer (1999) used the same analogy in their theoretical model for the single-cluster receptor.

Table 1
Composition and chemical and physical properties of the ferrofluid used in our model experiments

Composition (by volume)	Magnetite: 3–15%; oil soluble dispersant: 6–30%; carrier liquid: 55–91%
Grain size of the magnetic crystals (nm)	2–12
Boiling point (°F)	401–491
Solubility in water	Negligible
Saturation magnetisation at 25 °C	900 G
Carrier liquid	Benzine

So far, it has not been possible to extract the SP clusters from the upper-beak skin of the pigeons, or to study the response of the SP clusters to magnetic fields directly in the tissue. Therefore, we have designed a set of experiments to model a hypothetical magnetoreceptor system based on magnetically interacting SP clusters. For this purpose we employed microdroplets of ferrofluid, which potentially have the same magnetic response as the natural SP clusters in an applied magnetic field.

The ferrofluid used in our model experiments is a colloidal suspension of magnetite nanoparticles in benzene; composition, chemical and physical properties are summarised in Table 1. When brought into an aqueous environment, the suspension forms separate macrodroplets of variable size. The macrodroplets were then treated with ultrasonic for a couple of minutes to obtain microdroplets (radius between 1 and 50 μm) for our model experiments.

The manipulation and observation of the microdroplets in magnetic fields were conducted in our *bacteriodrome* (Petersen et al., 1989), which consists of a light microscope with video camera (SONY CCD Video Camera) surrounded by two independent Helmholtz-coil systems. Two inner Helmholtz pairs produce a planar magnetic field in two perpendicular directions. Three outer Helmholtz pairs, arranged perpendicular to each other, are used to compensate for the external Earth's magnetic field. A magnetic field of controlled direction and intensity is applied and the response of the droplets to the applied field is recorded by the video camera.

The studies of Fleissner et al. (2003) also show that the SP clusters are not freely dispersed within the cell but seem to be aligned alongside the cell membrane. It can therefore be assumed that the movement of every single SP cluster is restricted to the direction of the long axis of the chain. To simulate this alignment in our model experiments we engraved microgrooves into microscope slides (Plexiglas) similar in size to the microdroplets and placed there several microdroplets with a micropipette. The droplets could then move along one axis only.

In our model experiments we applied magnetic fields ranging from 0 to 25 Oe. The resulting movement of the

droplets was then recorded with the video camera attached to the microscope.

When exposed to an external magnetic field, a dipole–dipole interaction between neighbouring SP cluster can be expected, since each single cluster will be polarised in the presence of a magnetic field (Fig. 4). The interaction between adjacent clusters in a chain-like arrangement strongly depends on the direction of the long axis of the chain relative to the direction of the magnetic field. A magnetic field applied parallel to the chain axis polarises every cluster in a way that an attractive force between adjacent clusters arises, since opposite poles of adjacent clusters face each other (Fig. 4(a)); on the other hand, if the direction of the applied field is perpendicular to the axis of the chain, induced dipoles will now lie side by side rather than one behind each other. Such a configuration is energetically not favourable and gives rise to repulsive forces. Being constrained to move along-axis only, the clusters will separate (Fig. 4(b)).

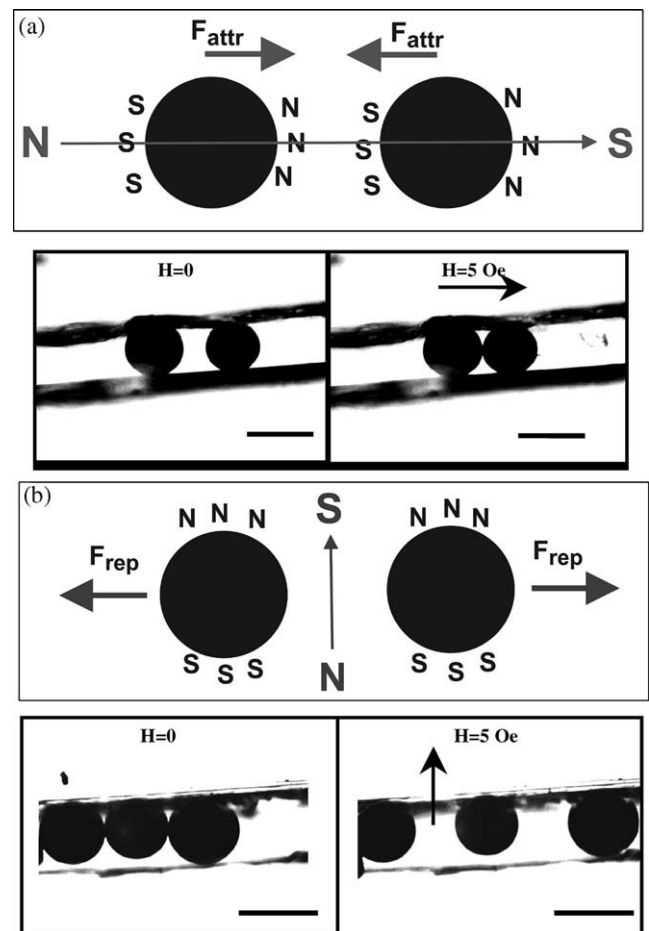


Fig. 4. Microscopic observations of ferrofluid droplets in magnetic fields. (a) Attraction between a pair of ferrofluid droplets oriented parallel to an applied magnetic field (arrow). (b) Repulsion between ferrofluid droplets when aligned perpendicular to the magnetic field (arrow). The droplets are framed so that they can only move in a direction parallel to the axis of the chain. Scale bar 50 μm .

Contrary to the response of an isolated SP cluster in a magnetic field, a chain of clusters will shrink parallel to the magnetic-field axis and stretch perpendicular to it. On first thought, our result appears to tally with the one derived by Kirschvink and Gould (1981): For their “elastic-rod-transducer” model, they predict contraction along the field axis and expansion perpendicular to it. However, their model is based partly on physically wrong assumptions, leading to questionable results (Winklhofer et al., 2001). For the sake of clarity, we here emphasise again that the magnetic-field induced deformation of an ordered array of SP particles (as the elastic-rod-transducer) would be similar to that of an isolated cluster, but opposite to that of a chain of interacting clusters.

5. Theoretical analysis of the model

The observed ferrofluid microdroplets are roughly spherical. Therefore, we can use the dipole–dipole approximation to describe their magnetic interaction. The force between two adjacent droplets then writes

$$F_{\text{attr}} = -\frac{6 \cdot m_1 \cdot m_2}{d_{12}^4}, \quad F_{\text{rep}} = \frac{3 \cdot m_1 \cdot m_2}{d_{12}^4} \quad (1)$$

for the one-behind-another (F_{attr} , Fig. 4(a)) and the side-by-side position (F_{rep} , Fig. 4(b)), respectively, where m_1 , m_2 are the induced magnetic moments of two droplets and d_{12} their centre-to-centre distance. The induced magnetic moment of a droplet, m is given by

$$m = \frac{\chi \cdot H_0 \cdot V}{1 + N \cdot \chi}, \quad (2)$$

where V is its volume and χ its intrinsic susceptibility; H_0 denotes the applied magnetic field and N the demagnetisation factor, which for a pair of spherical droplets can be approximated by that of a suitably chosen prolate ellipsoid of revolution. In the case of magnetic attraction, N is smaller than the demagnetisation factor of a single sphere, $4\pi/3$ (cgs units) and correspondingly larger than $4\pi/3$ in the case of repulsion. If we chose a prolate ellipsoid with the same axial ratio as the pair of spheres and the same volume, we obtain for two-spheres in contact, $N_{\text{attr}}/4\pi = 0.17$ and $N_{\text{rep}}/4\pi = 1 - 2N_{\text{attr}}/4\pi = 0.65$. For that example, we can now approximate the attractive force by

$$F_{\text{attr}} \approx -6 \cdot (\chi \cdot H_0 \cdot R)^2, \quad (3)$$

where we have assumed $\chi < 1$ (cgs units). For a cluster size of radius $R \sim 0.5 \mu\text{m}$, Eq. (3) yields $F_{\text{attr}} \sim \chi^2 \cdot 10^{-8}$ dyn in the geomagnetic field ($H_0 \approx 0.5$ G). We are not in a position yet to give a better estimate as the actual value of the susceptibility remains to be determined. Since 10^{-8} dyn (0.1 pN) may appear small, we want to emphasise that this force acts on microscopic structures

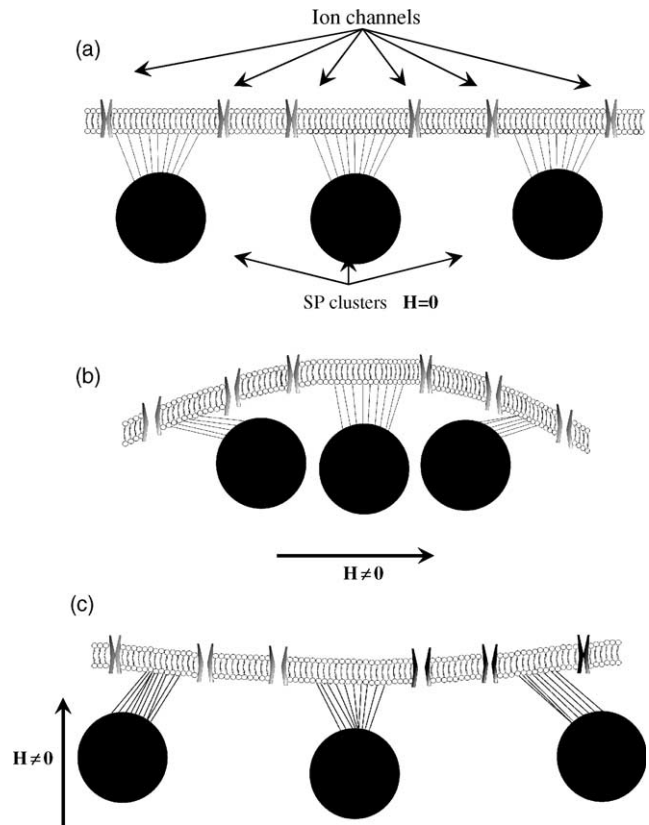


Fig. 5. Model for a magnetoreceptor based on the interaction of SP clusters: A chain of SP clusters attached to the membrane of a nervous cell by tiny fibers (see also Fig. 2 (b)), which allow the magnetic interaction force to be transferred to the nerve system. (a) No deformation occurs in zero magnetic field. (b) The clusters attract each other when the chain axis is oriented parallel to the magnetic field, (c) but repel each other when the magnetic field is perpendicular to the chain axis. As the clusters are linked with the nervous membrane, stress due to magnetic interactions can be transferred to the membrane. Depending on its magnitude, that stress may induce opening (or closing) of mechanosensitive ion channels in the membrane. Such an event on the cellular basis would represent a local early receptor potential. The model is able to explain the *inclination compass* as the reaction of the chain of clusters only depends on the orientation of the field with respect to the chain axis, but not on the polarity.

on the cellular or subcellular level. For instance, this force is comparable to the weight of a cell’s nucleus ($\sim 2 \cdot 10^{-8}$ dyn in water according to Sachs and Morris, 1998), which suggests that the attraction or repulsion forces between the clusters are able to cause local deformations on the cellular level. A possible physiological realisation of the magnetoreception mechanism is shown in Fig. 5.

It is important to note that the nature (i.e. liquid-viscous or solid-elastic) of the matrix around the magnetic nanocrystals will not affect the principal magnetic behaviour of the SP clusters, but may well have an influence on the amount of deformation and on the response time of the SP clusters to changes in magnetic field.

6. Summary and conclusions

A candidate structure of a magnetoreceptor in homing pigeons has recently been identified inside terminals of the ophthalmic branch of the trigeminal nerve (Hanzlik et al., 2000; Fleissner et al., 2003). The structure contains clusters of superparamagnetic magnetite arranged in chain-like aggregates with typically more than 10 clusters per terminal. Using light-microscopy techniques, we determined the average diameter of the clusters as $0.8 \pm 0.2 \mu\text{m}$, and the average centre-to-centre distance between adjacent clusters as $1.6 \pm 0.5 \mu\text{m}$. This close spacing suggests that magnetic interactions between the clusters determine the response of such an aggregate to an applied external magnetic field. To confirm our hypothesis, we designed model experiments with microdroplets of ferrofluid (suspensions of superparamagnetic particles). From our experiments and theoretical analysis, we conclude that a chain-like aggregate of SP clusters in the nerve cells will shrink parallel to the magnetic-field axis and stretch perpendicular to it. We therefore consider magnetic-field induced attraction and repulsion forces between the clusters as a plausible mechanism to pick up directional information from the Earth's magnetic field. As the response of the system to an externally applied magnetic field does not depend on its polarity, our model is able to explain the *inclination compass* as observed in behavioural experiments. The response of the system depends also on the field strength, and therefore in principle can account for the magnetic part of the *navigational map* system. As the physical properties of the system are not well known, we are not in a position yet to state the sensitivity of such a magnetoreceptor.

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References

Beason, R.C., Semm, P., 1987. Magnetic responses of the trigeminal nerve system of the bobolink (*Dolichonyx oryzivorus*). *Neurosci. Lett.* 80, 229.

Beason, R.C., Semm, P., 1996. Does the avian ophthalmic nerve carry magnetic navigational information? *J. Exp. Biol.* 199, 1241–1244.

Blakemore, R.P., 1975. Magnetotactic bacteria. *Science* 19, 377–379.

Butler, R.F., Banerjee, S.K., 1975. Theoretical single-domain grain-size range in magnetite and titanomagnetite. *J. Geophys. Res.* 80, 4049–4058.

Fleissner, G., Holtkamp-Rötzler, E., Hanzlik, M., Winklhofer, M., Fleissner, G., Petersen, N., Wiltschko, W., 2003. Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. *J. Comp. Neurol.* 458, 350–360.

Gould, J.L., Kirschvink, J.L., Deffeyes, K.S., 1978. Bees have magnetic remanence. *Science* 201, 1026–1028.

Hanzlik, M., Heunemann, C., Holtkamp-Rötzler, E., Winklhofer, M., Petersen, N., Fleissner, G., 2000. Superparamagnetic magnetite in the upper-beak tissue of homing pigeons. *Biometals* 13, 325–331.

Kalmijn, A.J., 1975. Electro-perception of sharks and rays. *Nature* 212, 1232–1233.

Kalmijn, A.J., 1981. Biophysics of geomagnetic field detection. *IEEE Trans. Magn.* 17, 1113–1224.

Kirschvink, J.L., Gould, J.L., 1981. Biogenic magnetite as a basis for magnetic field detection in animals. *Biosystems* 13, 181–201.

Lindauer, M., Martin, H., 1968. Die Schwereorientierung der Bienen unter dem Einfluß des Erdmagnetfeldes. *Z. Vergl. Physiol.* 60, 219–243.

Lohmann, K.J., Lohmann, C.M.F., 1996. Detection of magnetic field intensity by sea turtles. *Nature* 380, 59–61.

Lowenstam, H.A., 1962. Magnetite in denticle capping in recent chitons polyplacophora. *Geol. Soc. Am. Bull.* 73, 435–438.

Petersen, N., Weiss, D.G., Vali, H., 1989. In: Lowes, F.J. et al. (Eds.), *Geomagnetism and Paleomagnetism*. Kluwer Academic Press, Dordrecht, Netherlands, pp. 231–241.

Phillips, J.B., 1977. Use of the Earth's magnetic field by orienting cave salamanders (*Eurycea luifuga*). *J. Comp. Physiol.* 121, 273–288.

Presti, D., Pettigrew, J.D., 1980. Ferromagnetic coupling to muscle receptors as a basis for geomagnetic field sensitivity in animals. *Nature* 285, 99–101.

Quinn, T.P., 1980. Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. *J. Comp. Physiol.* 137, 243–248.

Sachs, F., Morris, E., 1998. Mechanosensitive ion channels in non-specialized cells. In: Blaustein, M.P. et al. (Eds.), *Rev. Physiol. Biochem. Pharmacol.*, 1–78.

Semm, P., Beason, R.C., 1990. Response to small magnetic variations by the trigeminal system of the bobolink. *Brain Res. Bull.* 25, 735–740.

Shcherbakov, V.P., Winklhofer, M., 1999. The osmotic magnetometer: a new model for magnetite-based magnetoreceptors in animals. *Eur. Biophys. J.* 28, 380–392.

Walcott, C., Gould, J.L., Kirschvink, J.L., 1979. Pigeons have magnets. *Science* 205, 1027–1029.

Walker, M.M., Diebel, C.E., Haugh, C.V., Pankhurst, P.M., Montgomery, J.C., Green, C.R., 1997. Structure and function of the vertebrate magnetic sense. *Nature* 390, 371–376.

Wiltschko, W., Wiltschko, R., 1972. Magnetic compass of European robins. *Science* 176, 62–64.

Wiltschko, W., Wiltschko, R., 1995. Magnetic orientation in animals. In: *Zoophysiology*, vol. 33. Springer, Berlin, Heidelberg, New York.

Winklhofer, M., Fabian, K., Heider, F., 1997. Magnetic blocking temperatures of magnetite calculated with a three-dimensional micromagnetic model. *J. Geophys. Res.* 102, 22695–22709.

Winklhofer, M., Holtkamp-Rötzler, E., Hanzlik, M., Fleissner, G., Petersen, N., 2001. Clusters of superparamagnetic magnetite particles in the upper-beak skin of homing pigeons: evidence of a magnetoreceptor. *Eur. J. Miner.* 13, 659–669.