Towards understanding of birds magnetoreceptor mechanism

Ilia A. Solov’yov and Walter Greiner

Frankfurt Institute for Advanced Studies, Johann Wolfgang Goethe University,
Max-von-Laue Str. 1, 60438 Frankfurt am Main, Germany

In the present letter we suggest a new theoretical model for a quantitative description of the magnetoreception mechanism in birds. The considered mechanism involves two types of iron minerals (magnetite and maghemite) which were found in subcellular compartments within sensory dendrites of the upper beak of several bird species. The analysis of forces acting between the iron particles shows that the orientation of the external geomagnetic field can significantly change the probability of the mechanosensitive ion channels opening and closing. The performed theoretical analysis shows that the suggested magnetoreceptor system might be a sensitive biological magnetometer providing an essential part of the magnetic map for navigation.

A large variety of animals possess a magnetic sense. The best-studied example is the use of the geomagnetic field by migratory birds for orientation and navigation during migration. Reviews of these studies are given in Refs. [1, 2]. In the present letter we address this problem from the theoretical point of view. Based on the known experimental observations we develop a physical model which we use for the description of magnetoreception phenomena in birds. The suggested model is based on the interaction of magnetic particles consisting of ferrimagnetic iron-minerals magnetite (Fe₃O₄) and maghemite (γ-Fe₂O₃), which were observed in the beak of different bird species [3, 4, 5]. Based on the analysis of forces which act between these particles we show that the considered iron-mineral system can serve as a magnetoreceptor with distinct orientational properties. We demonstrate that- depending on the orientation of the external magnetic field- the probability of opening of mechanosensitive ion channels significantly changes, thus leading to different nerve signals. The nerve signals are delivered to the brain causing a certain orientational behavior of the bird.

The histology studies of the upper beak of homing pigeons [4, 5] showed that iron minerals are concentrated in six symmetrical spots near the lateral margin of the skin of the
FIG. 1: Magnetoreceptor unit consisting of ten maghemite platelets (boxes) and a magnetite cluster (sphere). The coordinate frame shown here is used in the computations. The direction of the external magnetic induction vector $\vec{B}$ is characterized by two polar angles $\Phi$ and $\Theta$. The magnetic moments of the maghemite platelet $i$, $\vec{m}_i$, and of the magnetite cluster $\langle \vec{M} \rangle$ are indicated.

The geometry of the magnetoreceptor unit is determined from the experimental observations [5]. Thus, the maghemite platelets have the dimensions $1 \times 0.1 \times 1 \mu m$ and the magnetite cluster has the diameter of $1 \mu m$. The maghemite platelets are located in the (xz)-plane being aligned along the x-axis (see Fig. [I]). The distance between two neighboring upper beak inside the dendrites of nerve cells. For the study of the magnetoreception function of the dendrite a primary magnetoreceptor unit has been defined, being the smallest structure possessing the magnetoreception properties of the whole dendrite. The magnetoreceptor unit consists of ten maghemite platelets and one magnetite cluster as shown in Fig. [I]. Experimental observations [4, 5] suggest that the dendrite contains about 10-15 magnetoreceptor units, which should have similar behavior in the external magnetic field. Therefore, if the entire dendrite is subject to the external magnetic field the repetition of the magnetoreceptive units increases the functional safety of the dendrite magnetoreception.

The geometry of the magnetoreceptor unit is determined from the experimental observations [4]. Thus, the maghemite platelets have the dimensions $1 \times 0.1 \times 1 \mu m$ and the magnetite cluster has the diameter of $1 \mu m$. The maghemite platelets are located in the (xz)-plane being aligned along the x-axis (see Fig. [I]). The distance between two neighboring
platelets is equal to 0.1 µm.

The size of a single maghemite platelet (MP) is sufficient for the formation of magnetic domains in the (xz)-plane of the platelet (see Fig. 1). Thus, the MPs have a magnetic moment in this plane even in the absence of the external magnetic field. The magnetic moment of a platelet has the same direction as that of the total magnetic field at its site, \( \vec{H}_i \):

\[
\vec{m}_i = M l_x l_y l_z \vec{H}_i / |\vec{H}_i|, \tag{1}
\]

where \( M \) is the remanent magnetization of maghemite, \( l_x, l_y \) and \( l_z \) are the dimensions of a platelet along the \( x, y \) and \( z \) axes respectively. With \( M = 50 \text{ emu/cm}^3 \), \( l_x = l_z = 1 \mu \text{m} \) and \( l_y = 0.1 \mu \text{m} \) one obtains: \( m_i \approx 3.121 \text{ eV/G} \).

The magnetite cluster (MC) consists of nanoparticles which are 5 nm in diameter. In the case of finite temperature and finite magnetic field, the mean total moment of the MC, \( \langle \vec{M} \rangle \), is:

\[
\langle \vec{M} \rangle \approx \frac{n \mu^2}{3kT} \vec{H} = \chi \vec{H}, \tag{2}
\]

where \( n \) is the number of nanomagnets in the cluster, \( \mu \) is the magnetic moment of an individual nanomagnet, \( \vec{H} \) is the magnetic field strength at the site of the MC, \( T \) is the temperature and \( k \) is the Bolzmann constant. With \( R_0 = 0.5 \mu \text{m} \) and \( r_0 = 2.5 \text{ nm} \), being the radii of the MC and of the nanoparticle respectively, one obtains \( n \approx 8 \cdot 10^6 \).

The proportionality constant between the magnetic moment and the field strength, \( \chi \), is the magnetic susceptibility. Dividing it by the volume of the MC one obtains the volume susceptibility of the MC, \( \chi_v \), which at 300 K is equal to 0.12 CGS units. With \( H = 10 \text{ Oe} \), which is the typical value of the total field at the site of the MC, one obtains: \( \langle \vec{M} \rangle \approx 0.392 \text{ eV/G} \). Note that this value is about an order of magnitude smaller than the magnetic moment of a single MP.

The potential energy of the MC reads as:

\[
E(\vec{R}) = -\chi_v \frac{4}{3} \pi R_0^3 \left| \frac{\vec{B}}{\mu_{med}} + \sum_{j=1}^{N} \vec{H}_j(\vec{R}) \right|^2, \tag{3}
\]

where \( \vec{R} \) defines the position of the MC, \( \vec{B} \) is the induction vector of the external magnetic
field, \( \mu_{med} \approx 1 \) is the permeability of the medium, \( N \) is the number of MPs, \( \vec{H}_i(\vec{R}) \) is the magnetic field created by the \( i \)-th MP at the site of the MC, which is known to be \( \vec{H}_j(\vec{R}) = \frac{3 \left( \vec{R} - \vec{r}_j \right) \left( \vec{m}_j \left( \vec{R} - \vec{r}_j \right) \right) - \vec{m}_j \left| \vec{R} - \vec{r}_j \right|^2}{\left| \vec{R} - \vec{r}_j \right|^5} \). (4)

Here \( \vec{r}_j \) describes the position of the \( j \)-th platelet and \( \vec{m}_j \) is its magnetic moment defined in Eq. (1). The total magnetic field at the site of the \( i \)-th MP is:

\[
\vec{\mathcal{H}}_i = \frac{\vec{B}}{\mu_{med}} + \sum_{j=1}^{N} \vec{H}_j(\vec{r}_i). \tag{5}
\]

The first term describes the external magnetic field while the second term describes the magnetic field created by all MPs except the \( i \)-th one.

It follows from Eq. (5) that the total magnetic field \( \vec{\mathcal{H}}_i \) is determined by the magnetic moments of the platelets. Thus Eqs. (1) and (5) have to be treated iteratively. In the zeroth-order of approximation \( \vec{m}_i \) are aligned along the x-axis, what is energetically the most favorable configuration of the system. The magnetic moment of a platelet is then \( \vec{m}_i^{(0)} = M l_x l_y l_z \vec{I} \), where \( \vec{I} \) is the unit vector along the x-axis. The total magnetic field in the first-order approximation at the site of the \( i \)-th MP reads as:

\[
\vec{\mathcal{H}}_i^{(1)} = \vec{B} + 2 M l_x l_y l_z \xi_i \vec{I}, \tag{6}
\]

where \( x_i \) is the x-coordinate of the \( i \)-th platelet and \( \xi_i = \sum \frac{1}{\left| x_i - x_j \right|^3} \). Substituting Eq. (6) into Eq. (11) one yields the first-order approximation for \( \vec{m}_i \):

\[
m_{i_x}^{(1)} = \frac{M l_x l_y l_z (B_x + 2 M l_x l_y l_z \xi_i)}{\sqrt{(B_x + 2 M l_x l_y l_z \xi_i)^2 + B_y^2 + B_z^2}} \tag{7}
\]
\[
m_{i_y}^{(1)} = 0 \tag{8}
\]
\[
m_{i_z}^{(1)} = \frac{M l_x l_y l_z B_z}{\sqrt{(B_x + 2 M l_x l_y l_z \xi_i)^2 + B_y^2 + B_z^2}}. \tag{9}
\]

Here \( B_x \) and \( B_z \) are the x- and z-components of the external magnetic induction vector respectively. In [1] we demonstrated that the first-order approximation can be used to calculate the interaction energy with accuracy higher than 1%.
FIG. 2: Potential energy surfaces of the MC calculated as a function of x and y coordinates, while z=0 μm (see Fig. 1) at different orientations of the external magnetic field vector: plot a): magnetic field vector directed along the x-axis; plot b): magnetic field vector directed along the y-axis; plot c): magnetic field vector directed along the z-axis. The MPs are shown with black rectangles. The gray rectangle in the center of the potential energy surfaces shows the region, where the MC can not be placed, due to its finite size.

Figure 2 shows the potential energy surfaces of the MC as a function of its coordinates x and y, while z=0 μm (see Fig. 1), calculated at different orientations of the external magnetic field vector. Because of the MC size and because of the MPs there exists a forbidden region on the potential energy surface, where the MC can not be placed. The MPs are shown in Fig. 2 with black rectangles. The gray rectangle in the center of the potential energy surfaces defines the forbidden region for the MC.

In our calculations the external magnetic field strength is 0.5 G, being a typical value of the Earth magnetic field strength. The potential energy surfaces (Fig. 2) were calculated using Eq. (3). The potential energy surfaces calculated for the external magnetic field directed along the x-, y- and z-axes are shown in plots a), b) and c) of Fig. 2 respectively. The
three potential energy surfaces are similar, although some differences can be observed. The potential energy surfaces corresponding to the x- and z- orientations of the external field have axial symmetry along the y=0, z=0 axis, while the potential energy surface corresponding to the orientation of the external field along the y-axis has point symmetry with respect to the point (5.45,0) µm. There are two minima with energies about -8.5 eV at the tips of the maghemite chain. These minima are the global energy minima, being the spots of energetically most favorable attachment of the MC to the chain of MPs. This fact is in agreement with experimental observations, where the MC was observed at the tip of the chain [5].

To illustrate the effect of the external magnetic field on the magnetoreceptor system we have calculated the differences in forces acting on the MC due to the 90° change of the direction of the external magnetic field. The force differences are shown in Fig. 3. The thin line shows the force difference arising due to the change of external magnetic field direction from x to z, and the thick line shows the force difference arising due to the change of the external magnetic field direction from x to y. The force differences were calculated as a function of x-coordinate of the MC, while y=0.8 µm and z=0 µm. Fig. 3 shows that the force change, caused by the 90° change of the direction of the external field is 0.1-0.2 pN in both cases.

It was experimentally demonstrated [4, 5] that the MCs are connected to the nerve cell membrane. Depending on the magnetic field strength the magnetite cluster exerts forces on the membrane and activates mechanosensitive ion channels increasing the flux of ions into the cell. The ions change the membrane potential. If the potential is reduced to the threshold voltage [8], an action potential is generated in the cell, which opens up hundreds of voltage-gated ion channels in the membrane. During the millisecond that the channels remain open, thousands of ions rush into the cell [8], producing a nerve signal to the brain. The mechanosensitive ion channels influence the time needed for the membrane potential to reach the threshold value, and thus influence the birds behavior.

A typical example of a mechanosensitive ion channel is the transduction channel of a hair cell (for review see Refs. [9, 10, 11]). The opening/closing of the mechanosensitive ion channel is regulated by the so-called gate, which is a large biological complex (protein or complex of proteins) at the edge of the ion channel [9, 10, 11, 12]. The gate is connected to an elastic element, the gating spring [9, 10, 11, 12], transmitting the force to the gate.
FIG. 3: Difference in force acting on the MC and arising due to the 90° change of the direction of the external magnetic field. The thin line shows the force difference arising due to the change of external magnetic field direction from x to z, and thick line shows the force difference arising due to the change of external magnetic field direction from x to y. The force differences were calculated as a function of the x-coordinate of the MC, while y=0.8 µm and z=0 µm.

The ion channel has two conformations: closed and open. Because the gate swings through a distance λ upon opening, an external force f changes the energy difference between open and closed states and can bias the channel to spend more time in its open state. The gating springs are connected to the magnetite cluster which produces an external pull on the gates. As follows from our calculations the magnitude of this pull is about 0.2 pN, when the direction of the external magnetic field is changed on 90°. The work done in gating the channel is \[ \Delta E = \Delta \varepsilon - f \lambda \], where the first term represents the change of the intrinsic energy between the open and the closed states of the channel and the second term shows the work of external force required for opening the channel. \( \lambda \) is the displacement of the gate. For the mechanosensitive ion channels in hair cells \( \lambda \approx 4 \text{ nm} \) [9, 12]. The probability for the ion channel to be open in the presence of external force is:

\[
p = \frac{1}{1 + \exp \left( \frac{\Delta \varepsilon - f \lambda}{k_B T} \right)}.
\]  

If no external force is applied then \( f = 0 \) and the corresponding probability for the channel to be open is \( \tilde{p}_0 \). Thus, the change of channel opening probability due to the applied force

\[
p - \tilde{p}_0 = \frac{1}{1 + \exp \left( \frac{\Delta \varepsilon - f \lambda}{k_B T} \right)} - \frac{1}{1 + \exp \left( \frac{\Delta \varepsilon}{k_B T} \right)}.
\]
is:

$$\eta = \frac{p - \tilde{p}_0}{\tilde{p}_0} = \frac{\exp\left(\frac{\Delta \varepsilon}{kT}\right) \left(\exp\left(\frac{f \lambda}{kT}\right) - 1\right)}{\exp\left(\frac{f \lambda}{kT}\right) + \exp\left(\frac{\Delta \varepsilon}{kT}\right)}.$$  \hspace{1cm} (11)

The value of $\Delta \varepsilon$ is not known. Usually \[12\], it is assumed that $\Delta \varepsilon = 0$, but in general it is not because the gate can form hydrogen bonds with the membrane, which break when the gate is opened. Thus $\Delta \varepsilon > 0$.

Fig. 4 shows the dependence of the change of channel opening probability, $\eta$ on $\Delta \varepsilon$ (thick line). From Fig. 4 and from Eq. (11) it follows that the change of channel opening probability saturates at large values of $\Delta \varepsilon$. The limiting value is $\eta_{\text{max}} = \exp\left(\frac{f \lambda}{kT}\right) - 1$. For the given $f$, $\lambda$ and $T$: $\eta_{\text{max}} = 0.21$, being the maximal change of channel opening probability possible in the suggested mechanism. If $\Delta \varepsilon = 0$ then $\eta_0 = 0.096$. If $\Delta \varepsilon$ is positive then $\eta$ is somewhere between $\eta_0$ and $\eta_{\text{max}}$.

Another possible transducer mechanism of the geomagnetic field is based on the elastic deformation of the membrane. The deformation mechanism might arise in addition to the gating mechanism or be an alternative to it. The work performed on membrane deformation is given by \[1\]:

$$A = \gamma \Delta S = \frac{f^2}{\pi \gamma},$$  \hspace{1cm} (12)

where $\Delta S$ is the change of the membrane surface area and $\gamma$ is the membrane surface tension coefficient. Substituting $A$ instead of $f \lambda$ in Eq. (11) one obtains the change in channel opening probability caused by the membrane deformation.

Fig. 4 shows the dependence of the change of channel opening probability caused by the membrane deformation, on $\Delta \varepsilon$ (thin line) obtained for $f = 0.2$ pN and $\gamma = 0.01$ dyn/cm=$10^{-5}$ N/m, being the typical surface tension coefficient of a membrane \[13, 14\]. The maximal value of $\eta^\text{def}$ is $\eta^\text{def}_{\text{max}} = 0.36$, being 1.7 times greater than in the case of the gate-spring mechanism discussed above. If $\Delta \varepsilon = 0$ then $\eta^\text{def}_0 = 0.15$. Since $\Delta \varepsilon$ is expected to be positive then $0.15 < \eta^\text{def} < 0.36$.

In the present paper a possible mechanism of avian orientation in a magnetic field is discussed. It was shown that in the external magnetic field the MCs experience an attractive (repulsive) force leading to their displacement, which induces a primary receptor potential
FIG. 4: Change of the mechanosensitive ion channel opening probability calculated as the function of change of the intrinsic energy between the open and the closed states of the channel. The thick line corresponds to the gating-spring transducer mechanism and thin line corresponds to the mechanism based on the elastic deformation of the membrane.

via mechanosensitive membrane channels leading to a certain orientation effect of a bird. We believe that the suggested magnetoreception mechanism is a realistic candidate for the magnetoreception mechanism in birds. It might also be responsible for magnetosensation in other animals like fishes, salamanders, bees (for review see Ref. [1]). Unfortunately, lack of sufficient information about magnetic particles in these species hinders us to draw conclusions about their precise magnetoreception mechanism. However, we believe, that the magnetoreception mechanism should be universal, i.e. the same for all kinds of animals with, probably, minor alternations. Therefore, after more experimental data regarding the magnetic particles in animals become available the present investigation can be easily extended to a more general description.

We thank Professors Gerta and Günther Fleissner for many helpful discussions. We
also thank Professors Klaus Schulten and Andrey Solov’yov, as well as Mr. Alexander Yakubovich for many insightful comments. We acknowledge support of this work by the NoE EXCELL.

* On leave from the A.F. Ioffe Institute, St. Petersburg, Russia.; Email address: ilia@fias.uni-frankfurt.de

[1] I. A. Solov’yov and W. Greiner, Submitted to Biophys. J. (2007).
[2] I. A. Solov’yov, D. Chandler, and K. Schulten, Biophys. J. 92, 2711 (2007).
[3] M. Hanzlik et al., BioMetals 13, 325 (2000).
[4] G. Fleissner et al., The Journal of Comparative Neurology 458, 350 (2003).
[5] G. Fleissner et al., Naturwissenschaften pp. DOI: 10.1007/S00114–007–0236–0 (2007).
[6] J. Kirschvink and J. Gould, Biosystems 13, 181 (1981).
[7] V. Mathé and F. Léveque, 56, 737 (2005).
[8] D. L. Nelson and M. M. Cox, Principles of Biochemistry (W.H. Freeman and Company, New York, 2005).
[9] A. J. Hudspeth, Y. Choe, A. Mehta, and P. Martin, Proc. Natl. Acad. Sci. USA 97, 11765 (2000).
[10] V. S. Markin and A. Hudspeth, 24, 59 (1995).
[11] O. P. Hamill and B. Martinac, Physiol. Rev. 81, 685 (2001).
[12] D. P. Corey and J. Howard, Biophys. J. 66, 1254 (1994).
[13] R. M. Hochmuth, J.-Y. Shao, J. Dai, and M. P. Sheetz, Biophys. J. 70, 358 (1996).
[14] J. Dai, M. P. Sheetz, X. Wan, and C. E. Morris, J. Neurosci. 18, 6681 (1998).