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Stochastic Dynamics of Magnetosomes and a Mechanism of Biological Orientation in the Geomagnetic Field

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The rotations of nanoscopic magnetic particles, magnetosomes, embedded into the cytoskeleton are considered. Under the influence of thermal disturbances, a great number of magnetosomes are shown to move chaotically between two stable equilibrium positions, in which their magnetic moments are neither parallel nor antiparallel to the static Earth's magnetic field (MF). The random rotations attain the value of order of a radian. The rate of the transitions and the probability of magnetosomes to be in the different states depend on the MF direction with respect to an averaged magnetosome's orientation. This effect explains the ability of migratory animals to orient themselves faultlessly in long term passages in the absence of the direct visibility of optical reference points. The sensitivity to deviation from an ''ideal'' orientation is estimated to be 2–4 degrees. Possible involvement of the stochastic dynamics of magnetosomes in biological magnetic navigation is discussed. Bioelectromagnetics 27:58–63, 2006. © 2005 Wiley-Liss, Inc.

Key words: biogenic magnetite; magnetic compass orientation; magnetic navigation; migratory animals

INTRODUCTION

Many migratory birds and other animals annually travel thousands of miles and accurately find the locations of their seasonal habitats. The reason for this is not completely understood in spite of the established involvement of terrestrial magnetism and magnetic biomineralization in organisms [Kirschvink et al., 1985, 2001].

A number of hypotheses have been suggested to account for this phenomenon. In particular, the optical orientation and navigation based on ''maps'' of the terrestrial surface and starry sky have been studied. Also studied has been navigation along the lines of force of the geomagnetic field, which are known to be rigidly bound with the geophysical coordinates of the Earth. There are experimental indications for the latter hypothesis in the numerous observations of the ability of some biological species among microorganisms [Blakemore, 1975], insects [Etheredge et al., 1999], fishes [Walker et al., 1988], birds [Walcott et al., 1979; Wiltschko and Wiltschko, 2002], mammals [Walker et al., 1992; Lohmann et al., 2004], and others [Kirschvink et al., 1985] to orient themselves within a magnetic field (MF) or react to a change in its direction with respect to other acceptable reference marks.

At the same time, there is no recognized explanation for this phenomenon yet [Liboff and Jenrow, 2000; Ritz et al., 2000]. Magnetic orientation is a part of the more general problem of the biological efficacy of weak, less than 1 G (100 μT), magnetic fields (MFs). A brief review of the theoretical works in this area may be found in Binhi and Savin [2003] and a detailed discussion in Binhi [2002].

The problem lies in the fact that the magnetic energy of biologically active molecules in the geomagnetic field is very small. It does not exceed the energy of the electron magnetic moment in the Earth MF, 0.5×10^{-20} erg (0.5×10^{-27} J). This energy is more than seven orders of magnitude less than that of thermal fluctuations, i.e., $\kappa T \approx 4.1 \times 10^{-14}$ erg or 4.1×10^{-21} J at physiological temperatures. It is not clear how such a small ''signal'' could cause a biological reaction on the thermal ''noise'' background.

However, there are submicron particles which have magnetic moments. They have been found in

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many biological species, particularly in those displaying magnetic navigation ability. They consist of magnetite mainly. The magnetic moment μ of the particles exceeds the elementary one by 7–9 orders of magnitude. The energy of their rotation in a weak MF H is essentially larger than that of thermal fluctuations. For single domain magnetite particles of radius $r = 100$ nm (10^{-5} cm) or 70 nm in the geomagnetic field, the energy $\mu H \approx vJH$ equals approximately 24 or 8 κT, respectively, where μ is the magnetic moment of the particle, and v and $J \approx 480$ G (0.48 kA/m in SI units) are the volume and the saturation magnetization. The rotation of such magnetic nanoparticles was considered often to be able to stimulate some specific biochemical reactions.

Particularly interesting are the magnetite particles found in the brain of many animals and in the human brain [Kirschvink et al., 1992b]. The nerve tissue of the brain is separated from the circulatory system by the blood-brain barrier, which is impermeable to most chemicals. In turn, the circulatory system is separated from the digestive system. Therefore, relatively large ferro- or ferri-magnetic particles cannot penetrate into brain tissue as a pollutant. They are found to have a biogenic origin, i.e., they appear over time as a direct result of crystallization in brain matter. Biogenic magnetite particles are often called ''magnetosomes;'' they were first discovered in bacteria that displayed magnetotaxis [Blakemore, 1975]. Biogenic magnetite undoubtedly plays a role in the navigation of migrant birds [Kirschvink et al., 1985] and insects [Etheredge et al., 1999], as well as in other cases.

For an explanation of magnetic navigation, the dynamics of magnetosomes were modeled by using the notion of free rotations in a viscous liquid [Kirschvink et al., 1992a; Adair, 1994]. This regimen was assumed to be most favorable from the viewpoint of the magnitude of possible effects. However, the assumption about free rotations does not match the data of electron microscopy. For example, in some microorganisms, magnetosomes are assembled into firm univariate chains, where rotations are impossible. Another idea was that a rigidly bound magnetosome brings pressure on a closely set receptor. However, in this case, the energy coming from the magnetosome is transferred simultaneously to a number of molecules, which form a molecular link to the receptor, a mechanically sensitive ion channel. Then, the degree of freedom which governs the open/close state of the channel could get just a small amount ($\ll \kappa T$) of that regular energy.

It turns out that taking into account the not-too-tight constraints on the elasticity of the medium enables one to describe qualitatively a new stochastic rotational motion of magnetosomes, where thermal disturbances do not impede but help weak magnetic forces to display themselves. Such nonlinear dynamics is useful in explaining the biological effects of weak MFs, in particular, magnetic navigation.

The mechanism proposed below does not involve mechanosensitive membrane channels as was suggested in Kirschvink et al. [1992a]; instead, the rate of intracellular free-radical biochemical reactions is assumed to be altered by changes in the mT-range magnetosome's MF. The proper MF, $H \sim \mu/x^3$, produced by a 100 nm magnetosome is rather intense: it varies from about 0.2 T on the magnetosome's surface to 0.2 mT at the distance $x \sim 10^{-4}$ cm. So, in a cell, metabolic reactions proceed in mT-level MFs that are many times greater than the geomagnetic field, provided the cell contains a magnetosome. Such MFs, which strongly depend on the orientation of the magnetosome, can appreciably affect the rate of free-radical reactions [Salikhov et al., 1984]. Recent works [Ritz et al., 2004; Thalau et al., 2005] discuss experimental evidence that radical-pair mechanism may underlie the magnetic navigation of migratory birds.

MODEL

This article considers the dynamics of an idealized magnetite particle embedded in the cytoskeleton. The latter consists of a 3D net of elastic protein fibers of 6–25 nm in diameter that include actin filaments, intermediate filaments, and microtubules. The ends of these fibers may be fastened to the membrane surface and to various cell organelles, including magnetosomes [Kirschvink, 1992]. This fixes the position of the magnetosome and constrains its rotation to some extent.

The stationary orientation of the magnetosome generally does not follow the constant MF direction. The balance of the elastic and ''magnetic'' torques determines the orientation. The torque $\mathbf{m}$ affecting a particle of the magnetic moment μ in an MF $\mathbf{H}$ equals $\mathbf{m} = \mu \times \mathbf{H}$. The rotations of the magnetosome in the 3D space occur in a 2D angular potential that has the deepest well as the first idealization for magnetosome's dynamics and an ''easy way'' between two wells as the second one. Since the well-to-well transition probabilities drop exponentially with barrier heights, there is a reason to consider magnetosome's motion only in those two wells. So, putting aside the 3D character of the magnetosome rotations, we consider the magnetosome's motion in the plane of two vectors: the unit vector $\mathbf{n}$ of the x axis, with which the vector of the magnetosome's magnetic moment coincides in the absence of the MF (equilibrium position, $\varphi = 0$), and the MF vector $\mathbf{H}$, Figure 1.

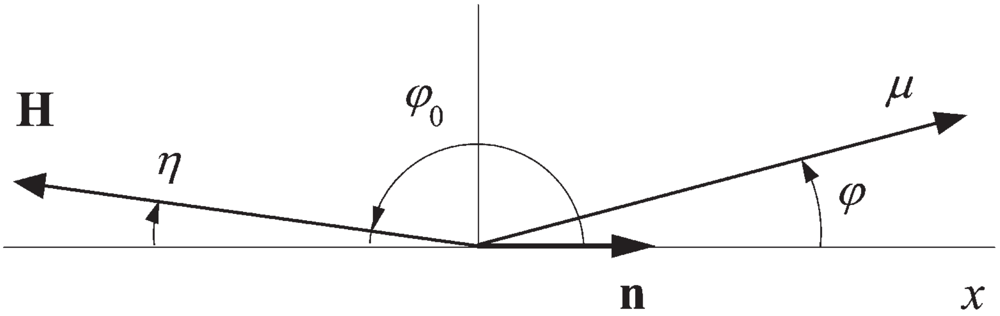

Fig. 1. Relative arrangements of the vectors of magnetic fields (MFs) and the magnetic moment of a magnetosome.

The Langevin equation for rotational oscillations of the particle is as follows:

$$I\ddot{\varphi} + \gamma\dot{\varphi} + k\varphi = -\mu H(t)\sin(\varphi - \varphi_0) + \xi'(t),$$
$$\omega_0 = \sqrt{\frac{k}{I}} \tag{1}$$

where φ is the angular displacement, I is the moment of the particle's inertia, γ is the dissipation coefficient, k is the factor of mechanical elasticity resulting from the cytoskeleton fibers' bending, $\xi'(t)$ is a stochastic torque with the correlation function $\langle\xi'(t)\xi'(t+\Delta t)\rangle = 2\gamma\kappa T\delta(\Delta t)$, while ω_0 is the eigenfrequency, and φ_0 is the MF direction. Then, we will assume that the quantity of fibers fastening the magnetosome to the cytoskeleton may vary from particle to particle and that a significant number of magnetosomes are mobile enough to markedly change their orientation in the geomagnetic field. This means the mechanical elasticity due to the fibers' bending is of the same order as or less than the magnetic elasticity $k \leq \mu H \approx 24\kappa T$. For magnetite Fe_3O_4 particles with the substance density $\rho \approx 5.2$ g/cm^3 and radius $r \sim 10^{-5}$ cm, we derive a value ω_0 in the order of 10^6 rad/s. A resonance, however, is not possible since the inertia forces are much less than viscous forces: $I\omega_0 \ll \gamma$ ($\gamma \sim 10^{-16}$ erg · s or 10^{-23} J · s). Hereafter, the inertia term in the equation of motion may be ignored.

The idea of this work is to study the dynamics of a magnetosome fixed into a visco-elastic cytoskeleton and predominantly oriented in a direction opposite that of a constant MF. We will assume further $\varphi_0 = \pi - \eta$. The angle η should be read as the off-course angle, i.e., the azimuth deviation from an "ideal" or reference direction, which is determined by the mechanical bonds that fasten the magnetosome in an averaged position with regard, for example, to the animal's cranium. In other words, in the frame of reference of the geomagnetic field, η is the deviation of the animal's orientation from an "ideal" one parallel to the MF vector.

For small angles η the nonlinear equation of motion takes the form: $\gamma\dot{\varphi} + k\varphi = \mu H\sin(\varphi) + \mu H\eta\cos(\varphi) + \xi'(t)$. With the designations

$$a = \frac{k}{\mu H}, \quad \tau \equiv \frac{\mu H}{\gamma}t, \quad D \equiv \frac{2\kappa T}{\mu H} \tag{2}$$

the equation is reduced to

$$\dot{\varphi} + \partial_\varphi U(\varphi, \eta) = \sqrt{D}\xi(\tau) \tag{3}$$

with the potential

$$U(\varphi, \eta) = \cos(\varphi) + \frac{a}{2}\varphi^2 - \eta\sin(\varphi). \tag{4}$$

Here, $\xi(\tau)$ is the centered Gaussian process of unit variance (the identity $\delta(\alpha t) = \delta(t)/|\alpha|$ is used).

The potential energy of a magnetosome in terms of μH is shown in Figure 2. As is seen, for not too large angles at $a < 1$ there are two stable equilibrium

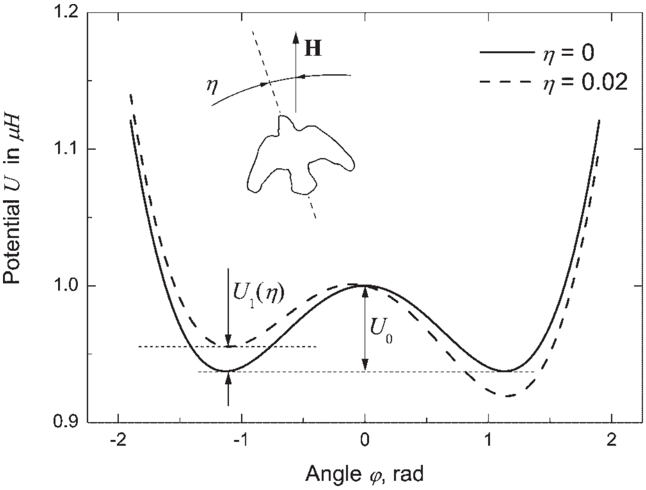

Fig. 2. The potential function of a magnetosome depends on the off-course deviation angle η. U_0 is the potential barrier height, U_1 is the change in the barrier height for $\eta \neq 0$. The elastic parameter a equals 0.8.

positions $\varphi_{\pm}$ and the unstable one $\varphi_0 = 0$. Due to thermal disturbances, there are transitions from well to well, the random turns being of significant value around 2 rad.

In this case, the motion of the magnetosomes in an additional ac MF meets the conditions of the so-called "stochastic resonance" that facilitates explaining the biological effects of low frequency weak MFs [Binhi and Chernavskii, 2005]. Slow variations in the dc MF magnitude were also shown to control the well-to-well transitions effectively. Here, we focus on the effect of variations in the dc MF direction.

Consider the joint influence on a magnetosome of a random torque $\xi(t)$ and a magnetic signal related with the deviation of the organism's orientation from the reference one. The magnetic signal, which varies directly with η, results in the change of the potential function, (Fig. 2). The state of the magnetosome oriented in the direction of the absolute minimum of the potential function becomes a preferred one. So the ratio of the probabilities P and $1-P$ of the magnetosome to locate in the states $\varphi_{\pm}$ equals

$$\frac{P}{1-P} = \exp\left(-2\frac{\delta U}{D}\right) \tag{5}$$

where $\delta U = 2U_1$ is the potential difference of the equilibrium points. It follows

$$P = \frac{1}{1+\exp(4U_1/D)}.$$

The "signal" proportional to the difference of the probability and its equilibrium value 1/2 equals

$$s \equiv \frac{1}{2} - P \approx \frac{U_1}{D}.$$

Since the "noise" is the equilibrium value 1/2, the signal-to-noise ratio in this case is equal to

$$R_{\mathrm{sn}} = 2\frac{U_1}{D}. \tag{6}$$

The quantities U_0, U_1 of the potential (4) have no exact analytical presentation. Here, we derive them as the expansions over the parameter $1-a$, which is assumed to be a small one:

$$\varphi_{\pm}^2 = 6(1-a), \quad U_0 = \frac{3}{2}(1-a)^2, \quad U_1^2 = 6\eta^2(1-a),$$
$$U''(0) = a-1, \quad U''(\varphi_{\pm}) = 2(1-a).$$

The minimally detectable angle of deviation from the reference course follows the equation

$$R_{\mathrm{sn}} = 1. \tag{7}$$

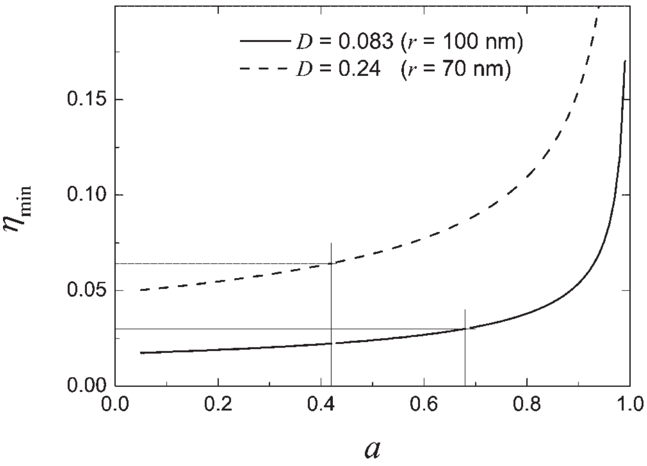

Fig. 3. The minimally detectable off-course angle depends upon the elastic parameter.

From this equation, substituting the derived value U_1 in Equation (6), we arrive to the formula

$$\eta_{\mathrm{min}} = \frac{D}{2\sqrt{6(1-a)}}. \tag{8}$$

This quantity is shown in Figure 3 as the function of the elasticity parameter a. As is seen, the maximum sensitivity takes place at small values a, that is, for "softly" fastened magnetosomes. However, arbitrarily small values of a make no physical sense.

The expression (5) and then expression (8) are valid for the equilibrium probability distribution. This means the changes in the potential have to occur more slowly than the relaxation to a statistical equilibrium. One can separate relaxations within each potential well and between wells. For small values a, when the potential barrier is high, the relaxation time is determined mainly by the well-to-well transitions. The characteristic time here is the mean first passage time (the Kramers time, see for example, Gardiner [2004])

$$\tau_{\mathrm{K}} = \frac{2\pi}{\sqrt{|U''(0)|U''(\pm\varphi)}}\exp\left(\frac{2U_0}{D}\right) = \frac{\pi\sqrt{2}}{1-a}\exp\left[\frac{3(1-a)^2}{D}\right].$$

The equilibrium distribution takes place on condition that

$$\tau_{\mathrm{or}} = \frac{\mu H}{\gamma} t_{\mathrm{or}} \gg \tau_{\mathrm{K}}$$

where τ_{or} is the characteristic time of the reorientation of the animal, the periods of "hunting" around the reference course. Assuming $t_{\mathrm{or}} \geq 1$ s, $\tau_{\mathrm{K}} < 0.1\ \tau_{\mathrm{or}}$, and taking $\gamma \approx 2\pi^2 \nu r^3$ [Landau and Lifshitz, 1976] for the damping coefficient of the rotations in a liquid with viscosity $\nu \approx 10^{-2}$ g/cm · s (water) (10^{-3} Pa · s in SI units), the condition is fulfilled if $a > 0.68$ or $a > 0.42$ for the magnetosome radii 100 and 70 nm, respectively. Therefore, from Figure 3 is seen that the sensitivity to the course deviations is about 0.03 rad and 0.064 rad or 1.7 and 3.7 degrees, respectively, for the magnetosomes of the above gauges.

CONCLUSIONS

We will note that if the signal-to-noise ratio in Equation (7) was n times greater, the minimally detectable angle would be n times less. To explain the observable sensitivity of animals to very weak geomagnetic variations, in Yorke [1985] it was suggested that ensembles rather than single magnetoreceptors detect MF changes. In that case, the averaging of the signals coming from magnetoreceptors, which causes the signal-to-noise ratio to enhance, occurs in the cerebrum. With averaging, the signals of regular rotations are summed; for chaotic rotations, what is summed are just the squares of the chaotic signals. Therefore, enhancement of the signal-to-noise ratio is reached proportionate to the square root of the number of magnetosomes contributing to the endpoint response. Recall that the density of magnetosomes in human brain tissue was measured at around 5×10^6, in brain meninges, more than 10^8 crystals/g [Kirschvink et al., 1992b], and on average, about 50 ng/g [Dobson, 2000]. Some birds have higher orders of concentration of the magnetite crystals.

There is another factor of the signal-to-noise enhancement that apparently was not reported in literature earlier. For the example of birds, if we assume each single bird makes flight-corrective turns during passage in accordance with the flight path of the flock, i.e., the majority of the birds, then the presence of an effective averaging mechanism outside the bird's organism follows. Evidently, this mechanism reduces the level of fluctuations in flight direction in proportion to the square root of the number of birds in the flock.

The derived accuracy of magnetic orientation, 2–4 degrees per unit magnetosome, even though several times better than in Kirschvink et al. [1992a], is not enough for exactly finding seasonal locations. As was repeatedly discussed in literature, corrections may occur by means of visual clues. However, if the signal-to-noise ratio is enhanced due to any of the discussed mechanisms, the accuracy of the orientation could be quite sufficient. This gives a ‘‘compass’’ to an animal to keep the course right.

Even in this case, one still needs explain how the animal could determine where to head for and when to stop. This problem was analyzed, for example, in Walker et al. [2002]. Walker et al. [2002] discussed a magnetic navigation system based on magnetosomes. Magnetosome receptors were assumed to measure both horizontal and vertical components of the geomagnetic field vector. This pair of values is known to be quite uniquely linked to the geophysical coordinates. It provides a ‘‘map’’ for position determination based only on the ‘‘magnetic sense.’’

Developing this idea, we note the possibility of a magnetic navigation that relates to the double-well stochastic dynamics of magnetosomes. It is supposed, of course, that among magnetosomes indirectly bound to animal's cranium, there are groups oriented in a way so as to sense the changes in the MF direction both in horizontal and vertical planes. In other words, the two potential wells should be arranged horizontally or vertically.

As was derived in Binhi and Chernavskii [2005], the sensitivity of the rate of the well-to-well transitions to slow variations in the dc MF magnitude is equal to 200 nT, in order of magnitude. This gives a way to measure the geomagnetic field strength as a signal proportionate to the rate of transitions. The components of the geomagnetic field or its inclination can be measured by the magnetosome system with the potential wells arranged vertically. Since the gradient of the geomagnetic field is very small, on the order of 1–10 nT/km, the animal needs move over a significant distance, about 20–200 km, to be able to feel the difference in 200 nT and correct the course for the goal. To keep the course over relatively short intervals, the animal may use the mechanism of magnetic orientation in horizontal plane.

So the absolute rate of the well-to-well transitions serves as a biological MF magnitude meter and the imbalance in mean populations in the wells as a MF direction meter. In that way, both necessary constituents of the magnetic navigation system, ‘‘map’’ and ‘‘compass,’’ are presented in the stochastic dynamics of one and the same system of magnetosomes with double-well potentials oriented in different planes.

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