Theoretical Evaluation of Magnetoreception of Power-Frequency Fields

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Several effects of power-frequency (50/60 Hz) magnetic fields (PF-MF) of weak intensity have been hypothesized in animals and humans. No valid mechanism, however, has been proposed for an interaction between PF-MF and biological tissues and living beings at intensities relevant to animal and human exposure. Here we proposed to consider PF-MF as disrupters of the natural magnetic signal. Under exposure to these fields, an oscillating field exists that results from the vectorial summation of both the PF-MF and the geomagnetic field. At a PF-MF intensity (rms) of 0.5 µT, the peak-to-peak amplitude of the axis and/or intensity variations of this resulting field exceeds the related discrimination threshold of magnetoreception (MR) in migrating animals. From our evaluation of the 50/60 Hz responsiveness of the putative mechanisms of MR, single domain particles (Kirschvink's model) appear unable to transduce that oscillating signal. On the contrary, radical pair reactions are able to, as well as interacting multidomain iron–mineral platelets and clusters of superparamagnetic particles (Fleissner/Solov'yov's model). It is, however, not yet known whether the reception of 50/60 Hz oscillations of the natural magnetic signal might be of consequence or not. Bioelectromagnetics, 2010.   © 2010 Wiley-Liss, Inc.

INTRODUCTION

Several effects of exposure to power-frequency (50/60 Hz) magnetic fields (PF-MF) of weak intensity have been hypothesized and studied in animals (mostly mammals) and humans. No valid mechanism, however, has been proposed for an interaction between PF-MF and biological tissues and living beings at exposure intensities relevant to animals and humans [WHO, 2007]. To date, the question of a possible influence from PF-MF on living beings through the disruption they cause on the natural magnetic signal—the geomagnetic field (GMF)—has still not been asked. Such mechanism of interaction might, however, be relevant only in magnetosensitive animals. The sense of magneto-reception (MR) has been observed in most migrating and homing animals and provides an obvious orienta-tional tool [Walker et al., 2002; Wiltschko and Wiltschko, 2005]. But it has also been observed in different mammal species, of which several have no obvious orientational use for it (e.g., hamster, mice, cattle, and deer) [Marhold et al., 1997; Deutschlander et al., 2003; Muheim et al., 2006; Begall et al., 2008; Holland et al., 2008]. Consequently, it might be that MR is a more general feature of the animal kingdom, including mammals [Muheim et al., 2006].

We address here the question of the possible reception by magnetosensitive animals of the 50/60 Hz oscillations of the natural magnetic signal that are caused by PF-MF at exposure intensities relevant to animal and human. Two arguments motivate us to consider that possibility. First, most of sensory systems have operating time scales on the order of the millisecond [Butts et al., 2007]. Second, no low-pass filter is required for MR to be efficient on earth. Indeed, the intensity of the fastest time variations of the natural signal (erratic periodicity ranging from 0.1 s to a few minutes) is always ≤ 10 nT, which is lower then the accepted discrimination threshold of MR [Wiltschko and Wiltschko, 2005].

Under exposure to 50/60 Hz sinusoidally varying MF, the resulting field is the sum of both the GMF vector

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(mainly static) and the PF-MF vector (Fig. 1). The axis of the resulting field will thus oscillate at a frequency of 50/60 Hz between the angles $(-\beta_o; +\beta_o)$ relative to the GMF axis, and its intensity will also oscillate. Adopting a reference value of 0.5 μT for the PF-MF rms intensity (i.e., a 0.7 μT peak amplitude), results in the following respective magnitudes for the angular oscillations $2\beta_o$ and for the intensity variations, if φ is the angle between the two field vectors: 1.6° and 5 nT for $\varphi = 90°$; 1.1° and 1.0 μT for $\varphi = 45°$; and 0° and 1.4 μT for $\varphi = 0°$. As the thresholds of sensitivity of migrating animals are thought to be close to a fraction of a degree for axis variation and about 0.1–0.2 μT for intensity variation, one can conclude that under exposure to a 0.5 μT PF-MF and according to the relative directions of the PF-MF and the GMF, the magnitude of the oscillations of the magnetic signal can be larger than the discrimination thresholds of MR [Wiltschko and Wiltschko, 2005].

THEORETICAL CONSIDERATIONS OF TRANSDUCTION MECHANISMS

Identified Mechanisms

Behavioral, electrophysiological, and histological studies focus on two mechanisms that are considered as putative transducers for the magnetic signal: iron-
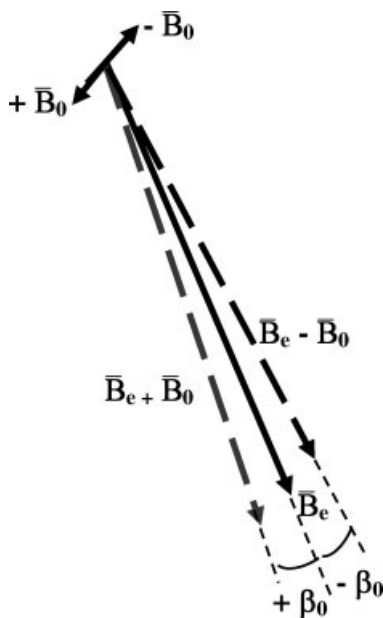

Fig. 1. At any place on earth (B_e is the geomagnetic field) and under exposure to a 50/60 Hz sinusoidally varying field whose peak value is B_o, a resulting field (vector in dotted line) will exist whose intensity oscillates at the same frequency between $||B_e + B_o||$ and $||B_e - B_o||$ and whose axis oscillates between $-\beta_o$ and $+\beta_o$.

mineral particles (IMP) and spin-correlated radical pair reactions (RPR) [Wiltschko and Wiltschko, 2005].

Iron mineral particles. NMR or histological studies and magnetic pulse experiments allow identifying IMP, presumably involved in MR, in fish, insects, birds, and rodents (mole rats and bats) [Kirschvink et al., 2001; Wiltschko and Wiltschko, 2005; Fleissner et al., 2007; Holland et al., 2008].

Single domain (SD) particles, on the one hand, have been identified in rainbow trout in the form of chains of particles or "magnetosomes" [Walker et al., 1997]. They have also been identified in honeybees, other insects, newts, and birds, where, contrary to fish, their precise arrangement as well as their actual function has not yet been specified [Kirschvink et al., 2001; Desoil et al., 2005; Wiltschko and Wiltschko, 2005; Wiltschko et al., 2009]. SD particles are ferrimagnetic particles (40–120 nm sized) of magnetite (Fe_3O_4) with a typical volumic magnetization M of 4.8×10^5 A/m that determines a permanent magnetic moment m (in A m^2, $m = MV$ with V the particle volume). If allowed to freely rotate, the particles will be subjected to a mechanical torque from an external MF (of magnitude B in Tesla), possibly providing a suitable mechanism for a polarity-compass sense (sensitivity to both the axis and the direction of the GMF) if the magnetic interaction energy (mB) in the GMF exceeds the characteristic thermal energy kT, where k is the Boltzmann constant, and T, the absolute temperature in K. Kirschvink's model assumes a direct connection of the SD particle chain with the ion channels that they open/close according to their relative orientation (Fig. 2).

On the other hand, chains of multidomain (MD) maghemite (γFe_2O_3) crystals ($0.1 \times 1 \times 1$ μm^3) associated to clusters (1 μm sized) of superparamagnetic (SPM) nanoparticles (2–4 nm sized) have been recently identified by Fleissner et al. [2007] in endings of three pairs of orthogonally oriented populations of dendrites of the ophthalmic nerve in the upper beak skin of homing pigeons (Fig. 3). These structures have also been identified in several other bird species and appear to be a common feature of all birds [Fleissner et al., 2007; Wiltschko et al., 2009]. Each ending contains 10–15 units that are, respectively, constituted of one chain of 10 (presumably fixed) MD platelets and one cluster, both types of particle having inducible but no remnant magnetic moment. On the basis of their observation, Fleissner et al. [2007] did propose a transducer mechanism that has been then developed by Solov'yov and Greiner [2007, 2009]. The Fleissner/Solov'yov model is based on the amplification of the GMF intensity (up to 20 times) by the chain of MD
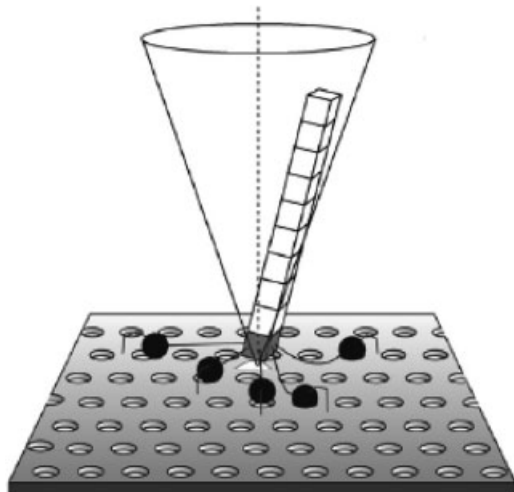
Fig. 2. Schematic illustration of Kirschvink's model of a chain of single domain particles connected by cytoskeletal filaments to mechanosensitive ion channels, whose mean orientation is imposed by the geomagnetic field. The movement of the chain causes the gates of channels to open/close [reproduced with permission from Walker, 2008].

particles along their axis of easy magnetization. A consecutive attractive force then acts on the cluster that lies in its vicinity, the *mB* value of it reaching there 160 kT. That attractive force depends on firstly, the magnetic moment of the chain of MD platelets—this depends on both the GMF intensity and the orientation of the chain in the GMF—and secondly, on the relative location of the cluster with respect to the chain. Both a map sense (sensitivity to the GMF intensity) and a polarity-compass sense are thus achievable [Fleissner et al., 2007; Solov'yov and Greiner, 2007, 2009; Wiltschko and Wiltschko, 2009]. Mechanical transduction would be provided either through imposed deformation of the nerve cell membrane or through opening/closing of ion channels to which clusters of SPM particles would be connected through cytoskeletal filaments. Spatial summation is achieved over the 10–15 units per ending, the different dendrites of each pair of ending populations, and the three orthogonally oriented ending populations [Fleissner et al., 2007].
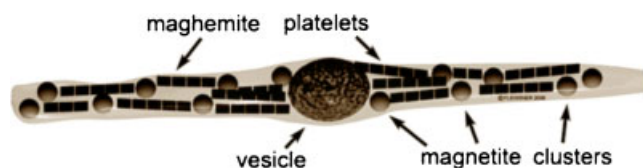

Fig. 3. Drawing of a single dendrite of the upper beak skin of homing pigeon with two different ferrimagnetic components and the iron-coated vesicle, whose function is yet unknown [reproduced with permission from Solov'yov and Greiner, 2007]. [The color figure for this article is available online at www.interscience. wiley.com.]

Radical pair reactions. Magnetosensitive spin-correlated RPR have their recombination yield and their reversibility influenced by an external MF [Schulten and Windemuth, 1986]. Being sensitive to MF axis, but not polarity, RPR can provide an inclination compass if they take place in orientationally ordered structure with consecutive anisotropic hyperfine coupling [Ritz et al., 2000]. Their role in orientation of birds has been confirmed by the perturbations caused, through resonance effects, by radiofrequency MF. In accordance with the dependence of the inclination compass in birds on short-wavelength light, the accepted candidate is a cryptochrome photoreceptor, a protein of the retina, presumably paired with molecular oxygen as a reaction partner [Ritz et al., 2009; Rodgers and Hore, 2009]. A light-dependent compass possibly similar to that in birds has been described in amphibians and might also exist in insects [Wiltschko and Wiltschko, 2005]. From both theoretical considerations and behavioral observations, the possibility of the involvement in other animals of enzymatically driven and not light-driven RPR cannot be excluded [Weaver et al., 2000]. Indeed, an inclination compass similar to that in birds, although independent of light, has been reported in sea turtles [Johnsen and Lohmann, 2005]. Finally, the possibility exists theoretically of a coupling of RPR with any IMP in their immediate proximity but at fixed relative locations [Scaiano et al., 1997].

Magnetotransduction at 50/60 Hz

Both the oscillations of axis and intensity that are caused by the 0.5 µT PF-MF are considered here. It must, however, be kept in mind that fast variations of intensity have no physiological equivalent, as indeed a variation of 1.0 µT is only obtained for ≥200 km north–south travel. On the contrary, fast variations of axis, at least up to a certain intensity of PF-MF, do have a physiological equivalent. As an example, under 0.5 µT of rms intensity in a GMF intensity of 50 µT, the angular velocity of the resulting field does not exceed 200°/s, which still lies within the range of velocity of head rotations.

Kirschvink's model. Kirschvink's model assumes the involvement of (chain of) SD-IMP. Due to thermal agitation, SD particles oscillate around the mean orientation imposed by the GMF, with a mean angular amplitude θ_{kT} that is given by the Langevin function [Kirschvink and Walker, 1985; Bryant et al., 2007]

$$\overline{\text{Cos}\,\theta_{kT}} = L(x) = \coth(x) - \frac{1}{x} \qquad (1)$$

where $x = mB/kT$. An mB/kT value of about 4 (between 2 and 6) has been adopted from theoretical considerations

and also from histological and experimental observations [Kirschvink and Walker, 1985; Diebel et al., 2000; Kirschvink et al., 2001]. We consider two models of SD particles (supposedly involved in Kirschvink's model) for which $m = 3.6 \times 10^{-16}$ A m^2, and so as to fulfill the condition of $mB/kT = 4$ in $B = B_e$ (the GMF) $= 50$ µT at 310 K. The first model is a parallelepipedic crystal with a 105 nm length and a transverse square section (square side 85 nm, so that the width/length ratio is 0.8, similar to fish), and the second is a chain binding seven rectangular parallelepipedic crystals 55 nm in length, with the same width/length ratio. The magnetic grains embedded in the chain are anchored to each other [Kobayashi et al., 2006], and each of them has a magnetic interaction with its neighbors much larger than its own coupling with the GMF. As a consequence, the chain may be treated as a unique particle.

Axis oscillations. Under exposure to a PF-MF of frequency ω ($= 2\pi$f) that causes a resulting field B ($= B_e + B_o \cos \omega t$) to oscillate between ($-\beta_o; +\beta_o$) (see Fig. 1), the mean orientation of an SD particle will oscillate between ($-\theta_o; +\theta_o$) by being submitted to a torque Γ (in Nm) that is given by Adair [1994]

$$\Gamma = mB \sin(\beta - \theta) \cos \phi - C\theta - \frac{\gamma \mathrm{d}\theta}{\mathrm{d}t} \qquad (2)$$

where β and θ are, respectively, the angles (in radians) between the resulting field and the reference direction of the GMF, and between the chain axis and the same reference direction, and ϕ is the angle between the imposed torque and the final acceleration. The first term at the right is the magnetic torque. The second term is the elastic torque imposed by the surrounding structures, where $C = \kappa VG$ is the elastic constant, κ, the shape factor of the particle or chain, V, the hydrodynamic volume (in m^3), and G, the shear modulus of the medium in Pa. This last also accounts for the cytoskeletal filaments that link the SD particles with the ion channels. The third term is the viscous torque, where $\gamma = \kappa V \eta$ is the dissipative constant of the medium, and η is the viscosity in Pa s.

We pose $B_e = 50$ µT, $B_o = 0.7$ µT (for $B_{rms} = 0.5$ µT) $\perp B_e$ ($\beta_o = 0.8°$) and $\omega = 346$ rad/s (for $f = 55$ Hz). Concerning the shape factor, and accounting for the presence of a membrane of 5 nm thickness surrounding the particles, $\kappa = 7.5$ for the single particle. For the chain, $\kappa = 10.7$, accounting also for a ~10 nm interparticle gap [Kobayashi et al., 2006]. Regarding the shear modulus, its value must allow the magnetic torque from B_e to surpass the elastic and viscous ones, which is the condition for Kirschvink's model to be valid. Thus, under the least restrictive condition of

$\mathrm{d}\theta/\mathrm{d}t = 0$, as $\sin(\beta - \theta) \le \theta$, then $C < mB$. We thus pose $G = 1$ Pa as a worst-case hypothesis. With regard to the viscosity of the surrounding medium, the uncertainty about its actual value causes the largest margin of error in the present model. The intracellular value of η is highly heterogenous and is related to the required molecular mobility in each considered cell compartment. While $\eta = 0.002$–0.003 Pa s in the aqueous phase of the cytoplasm, it can reach up to 0.14 Pa s in some specialized organelles [Luby-Phelps et al., 1993; Kuimova et al., 2008]. Similar to a discussion by Adair [1994], we pose $\eta = 0.005$ Pa s and also discuss the case of $\eta = 0.05$ Pa s. In the discussion that follows, the models used are for bodies rotating about their center of mass, which is the case for a single particle but not a chain of particles where one end is fixed (see Fig. 2). For the latter, the calculated results are corrected by taking the value of the moment of inertia relative to the one of a body that rotates about its center of mass (ratio $= 4/1$).

Wilhelm et al. [2003] developed a theoretical model that has been experimentally confirmed and that allows for the calculation of the relative amplitude θ_o/β_o of the oscillations of chains of SPM particles submitted to an oscillating field. Applying Wilhelm's model to a chain of SD particles for small angular displacement in a Maxwell fluid—a valid approximation for the cytoplasm in the case of small deformations—we obtain the amplitude θ_o of the oscillations of this chain relative to the ones (β_o) of the MF oscillations [Wilhelm et al., 2003]

$$\frac{\theta_o}{\beta_o} = \left[\frac{[1 + (\omega\tau)^2]}{\left\{ 1 + [\omega\tau (1 + C/m\mathrm{B})]^2 \right\}} \right]^{1/2} \qquad (3)$$

where $B = B_e$, the time-averaged value of the oscillating field, and $\tau = \eta/G$ (in s), the viscoelastic relaxation time. For $\eta = 0.005$ Pa s, $\theta_o/\beta_o = 0.75$ for the single particle, and $\theta_o/\beta_o = 0.28$ for the chain. For $\eta = 0.05$ Pa s, the respective values are 0.70 and 0.24. Under exposure to a 0.5 µT PF-MF, θ_o is thus always much smaller than θ_{kT}; a signal summation is thus required for it to be detected.

Intensity oscillations. According to Equation (1), any variation of the intensity of B will cause a variation of θ_{kT} [Walker, 2008]. For $x = 4$, $L(x)$, the mean value of $\cos \theta_{kT}$, is equal to 0.75, and for $\sqrt{\mathrm{d}L/\mathrm{d}x}$, the rms variation of $\cos \theta_{kT}$ is equal to 0.25. Taking $B = 50$ µT, a variation of about 1.0 µT, as under exposure to a 0.5 µT PF-MF ($\varphi = 45°$) will thus cause variations of θ that are much smaller than the mean value of θ_{kT} ($= 41°$) and also much smaller than the value of the rms deviation of θ_{kT}.

It will also cause maximal variations of *mB* of 0.08 kT, requiring a signal summation for it to be detected.

Signal summation. Signals transduced by several different receptors will presumably be summed by downstream neural processing. Yet at the level of each receptor, the full magnetic signal will, in principle, only be transduced at the end of a complete Brownian revolution of the SD particle around the direction of *B* (Fig. 2). The time *t* (in s) required for characteristic Brownian movement angular excursion θ_{Br} (in radians) is given by Adair [1994]

$$t = \theta_{Br}^2 \tau_{Br} \qquad (4)$$

where $\tau_{Br} = 3V\eta/kT$ is the Brownian relaxation time. By equating θ_{Br} to π we obtain the time required for a complete revolution. For $\eta = 0.005$ Pa s, this time is equal to 36 ms for the single particle and 183 ms for the chain. Those values are multiplied by 10 for $\eta = 0.05$ Pa s. In some units of the superficial ophthalmic branch in trout, in which they identified chains of SD particles, Walker et al. [1997] registered neural responses (increased firing rate) that persisted over 100 ms, on average, after a single step change of MF intensity. This observation supports our assumption of a likely low viscosity value.

As a conclusion, and at least under exposure to a 0.5 μT PF-MF, no signal transduction appears to be possible by Kirschvink's model because the required signal summation lengthens the processing time scale beyond the PF-MF period.

Fleissner/Solov'yov's model. The Fleissner/Solov'yov model is based on interacting MD-IMP and SPM particles.

Axis oscillations. Due to their vanishing coercive force, (in directions parallel to their plane), the MD platelets show negligible alternating losses up to frequencies well beyond power frequencies at body temperature [Fleissner et al., 2007]. And, as even ferrofluids do not show losses at that frequency, clusters of SPM particles also would not show losses at 50/60 Hz [Wang and Huang, 2006]. Thus, under exposure to a 50/60 Hz oscillating field, the induced magnetization in both MD and SPM particles will oscillate in phase with the external field. Under the axis oscillations that are caused by a 0.5 μT PF-MF, the average magnitude of the variations of the value of *mB* for $\varphi = 45°$ and $90°$ will, respectively, be equal to 1.0 kT (between 0 and 2.0 kT, according to the orientation of the chain of MD platelets in the GMF)

and 1.5 kT (between 0 and 2.9 kT) [Solov'yov and Greiner, 2009].

Intensity oscillations. For axis oscillations, the intensity of induced magnetization will oscillate in phase with the one of the external field. Under exposure to a 0.5 μT PF-MF, the average magnitude of the variations of the value of *mB* that are caused by intensity oscillations will, respectively be equal to 3.3 kT (between 0 and 6.7 kT) and 4.7 kT (between 0 and 9.4 kT) for $\varphi = 45°$ and $0°$ [Solov'yov and Greiner, 2007, 2009]. Therefore, following the evaluations by Solov'yov and Greiner, the signal that is received under intensity oscillations has the same nature as the one received under axis oscillations, but has a larger magnitude.

As a conclusion, because both the magnitude of *mB* in each case and the spatial summation that otherwise exists, no time summation is required and the signal oscillations will be transduced and transmitted in phase with the external signal.

Radical pair reactions

Axis oscillations. The lifetime of the radical pairs (≥ 100 ns and < 1 μs) is much shorter than the period of the 50/60 Hz oscillations [Rodgers and Hore, 2009]. Hence under exposure to PF-MF, RPR will be influenced by any instantaneous vector of the oscillating MF as they are by the same vector of a static field. According to their reaction rate, they will thus transmit the time variations of the MF axis in phase with the ones of the external signal.

Intensity oscillations. Only the case of birds is considered here because it is the only one documented. A rather narrow functional window of intensity has been observed, with a complete loss of anisotropy for variations of only $\pm 25\%$ of the operating intensity (the one of the GMF at the current location of the bird). Contrary to axis oscillations, which will cause oscillations of the retinal coordinates of the area of activated RPR, the oscillations of the signal intensity will cause oscillations of the size of that area. And under a 0.5 μT PF-MF, the amplitude of these size oscillations might be quite large as, indeed, a large loss of anisotropy is observed for only a few microteslas above or below the operating intensity [Rodgers and Hore, 2009].

COMPARISON WITH EXPERIMENTAL DATA OR OBSERVATIONS

Two studies have been published to date on the perception of PF-MF, and the orientational behavior under exposure to PF-MF in magnetosensitive animals.

Kirschvink et al. [1997] studied the sensitivity threshold of the perception of time-varying MF in honeybees in a pilot study that was based on behavioral observations (recognition, between two cavities, of the one where food is situated, thanks to the systematic association with it of the presence of time-varying MF). They reported the following approximative threshold values according to the MF frequency: 200 µT at 10 Hz, and 1 mT at 60 Hz. These values are, respectively, 3 and 4 orders of magnitude above the one of the threshold value of 0.2 µT that they previously reported for static MF in the same animals. Assuming MR mechanism in bees to be based on SD-IMP, the authors have suggested that the increase of threshold with frequency is due to viscous damping of the motion of the particles. According to the present evaluation, their observation might also reflect the time summation required by the Kirschvink's model, in case it actually applies to bees. Furthermore, and whichever the involved mechanism, such increase, if confirmed, could also be due to one of the possible obstacles opposed, at the step of the neural transmission, to the conscious perception of a time-varying signal.

Following the observation by Begall et al. [2008] of magnetic alignment of resting and grazing cattle and deer along the geomagnetic north–south direction, Burda et al. [2009] recently reported that the magnetic alignment was disrupted in the proximity of high power lines, an effect they evaluated to be due to the presence of the PF-MF only. Analyzing the case of cattle situated immediately under power lines, they observed a randomization of their orientation with a mean angular shift relative to the north–south direction that depends on the orientation of the power line. That shift was ∼13°, on average, for a north–south orientation of the line, corresponding to a resulting MF of which only the azimuth oscillates (peak-to-peak amplitude evaluated to be about 69°). By contrast, the shift was ∼85°, on average, and thus much larger, for an east–west orientation of the line, corresponding then to a resulting MF of which only the intensity and the inclination oscillate (peak-to-peak amplitude of about 13 µT and 31°, respectively). Should that effect be confirmed to be caused by PF-MF, then that observation might be usefully compared with the relative magnitude of the signal that is transduced by the Fleissner/Solov'yov model, as a function of the nature of the signal oscillations that are caused by PF-MF. That magnitude is indeed the largest when mainly the intensity oscillates.

DISCUSSION

From the present evaluation, the transduction and transmission of the oscillating signal that exists under exposure to a 0.5 µT (rms) PF-MF appears not to be possible by SD particles, according to the model of Kirschvink. On the contrary, it appears to be effective, at least in migrating animals, by mechanisms that are based either on RPR or on a combination of MD iron–mineral platelets and clusters of SPM particles, according to the model of Fleissner and Solov'yov.

Considering magnetosensitive mammals, two conditions are required for reception of a 0.5 µT PF-MF to be effective: (1) the mechanism of MR must be based on RPR and/or on IMP with inducible moment, and (2) their discrimination threshold must allow for effective reception. Though the precise MR mechanism is not yet known for any considered species—with the exception of IMP in mole rats and bats—the first condition is presumably fulfilled. On the one hand, indeed, cryptochrome is a ubiquitous protein in the animal kingdom. On the other hand, one can presume that the particles involved in IMP-based MR in mammals are particles with inducible moment rather than SD particles, because evolution, in principle, would have preserved the former instead of the latter. Indeed, in comparison with the model of Fleissner and Solov'yov, the one of Kirschvink is characterized by a much lower precision (lower isotropy and lower signal/noise ratio) and a much higher energy cost (rate of events of ion channel activation) [Niven and Laughlin, 2008]. In support of this are experimental observations in migratory silvereyes and honeybees, in which, while both SD and SPM particles have been identified, MR has been reported to be based on SPM particles only [Desoil et al., 2005; Hsu et al., 2007; Wiltschko et al., 2009]. According to the second condition, however, it is not certain whether non-migrating magnetosensitive mammals might be able to transduce the oscillations caused by a 0.5 µT PF-MF. Indeed, the discrimination threshold of MR might be higher in them than in migrating animals. However, considering intensity variations and the IMP-based mechanism of Fleissner/Solov'yov, one notes that under a 0.5 µT PF-MF, these variations cause the transduction of an oscillating signal of which the magnitude is, on average ($\varphi = 45°$), comparable to the one caused by axis oscillations of 3.6° of amplitude. This should be compared with the abovementioned observations by Burda et al. [2009] of a disruption that is much larger for intensity oscillations than for axis oscillations. Things are less clear concerning RPR, and variations of anisotropy might possibly deserve further consideration in view of their magnitude.

Downstream of the transduction of any sensory signal, a transmission first occurs that allows for intermediate signal processing through interactions between simultaneous and successive spikes before
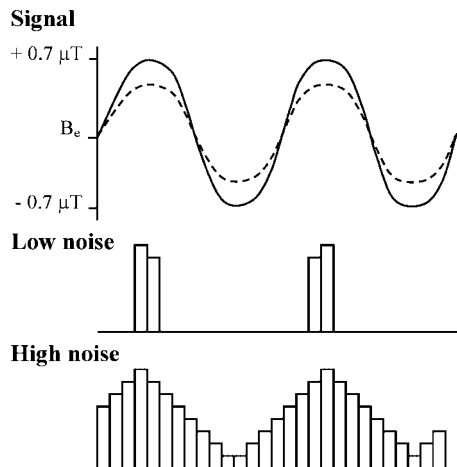
Fig. 4. Intensity of the signal transmitted by RPR and by Solov'yov and Greiner's model, as a function of time, under exposure to a 50/60 Hz field of 0.5 µTrms intensity ($B_o = 0.7$ µT). The sinusoids in plain and dotted lines are for angles 0° and 45°, respectively, between B_o and B_e (the geomagnetic field)—the same reasoning is valid for axis variations. According to the noise level, the neural transmission will either lose (low noise) or preserve (high noise) the shape of the inputs (the height of each bar in the lower part represents the spike probability) [adapted from Stein et al., 2005].

possible perception. In migrating birds, the neural pathways thought to be involved in the RPR-based inclination compass are the right eye and optical nerve [Wiltschko and Wiltschko, 2005]. In different species, the signal transmission of the IMP-based compass and/or map sense has been identified in neurons of the trigeminal pathway : neurons of the ophthalmic branch in rainbow trout, bobolink and homing pigeon, and innervation of the cornea in mole rat [Beason and Semm, 1996; Walker et al., 1997; Mora et al., 2004; Wegner et al., 2006]. In mole rats, the processing of the magnetic signal has been reported in the superior colliculus, a structure of the midbrain where visual, auditory and somatosensory inputs are integrated [Němec et al., 2001].

Under exposure to PF-MF, if the time variations of the signal are actually transduced they will cause a sustained increase of the firing rate, as in response to any sustained change in sensory stimulation. One condition, however, for a sinusoidally varying sensory signal to be actually transmitted is that a certain "noise" exists. Without noise, such signal, in principle, induces a cyclic, phase-fixed, entrainment of the firing rate (Fig. 4), which thus cancels the signal perception [Stein et al., 2005]. In the case of the considered magnetic signal, a noise can be caused by a temporal variability of the rms intensity and/or the axis of the PF-MF. As a consequence, an effective transmission might only exist under real circumstances of exposure, thanks to enough temporal variability (Fig. 5), unlike experimental ones where the PF-MF intensity is mostly stable.

Even if they are transduced and transmitted, it is, however, uncertain whether power-frequency oscillations of the magnetic signal can be consciously perceived. On the one hand, a signal filtering might exist. First, as is the case in vision and mechanoreception, a filtering might exist downward of peripheral transmission that prevents the perception of the oscil-
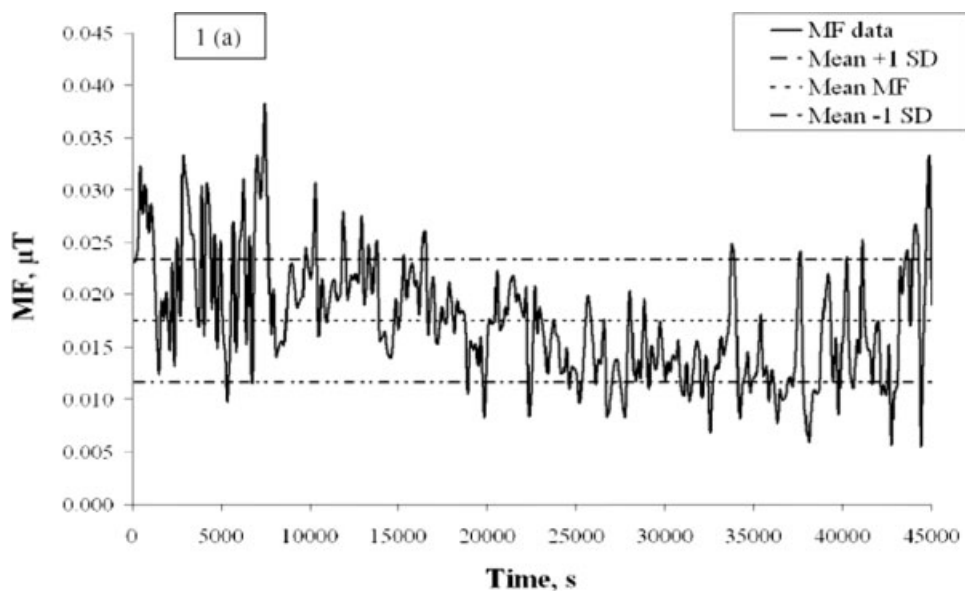

Fig. 5. Fifty Hz magnetic field (MF) rms intensity overnight in a residence from 8:00 p.m. to 8:30 a.m. [reproduced with permission from Ainsbury and Henshaw, 2006].

lating nature of the signal above a certain frequency [Butts et al., 2007]. Second, as the oscillating magnetic signal under PF-MF is comparable to the one that is transmitted upon oscillatory motions of the head, a filtering might exist at the level of the sensory integration because that signal is in conflict with other somatosensory inputs [Wallace and Stein, 2007]. On the other hand, the transmission of the signal to the level of the cortex might be dampened by the lack of selective attention [VanRullen and Thorpe, 2002]. All these considerations might possibly help to explain the abovementioned observations by Kirschvink et al. [1997]. Nevertheless, whether perceived or not, MF oscillations can, in principle, be of no consequence on MR-based orientation because the time-averaged deviation of the resultant field is nul. Such assertion might, however, be challenged if the observation by Burda et al. [2009] is confirmed to be caused by PF-MF.

CONCLUSION

The hypothesis of MR of PF-MF appears to be worth consideration, not only in migrating animals but also in magnetosensitive mammals and, possibly, all mammals. And in mammals, that hypothesis might constitute an alternative way of searching for a possible mechanism of interaction between PF-MF and health. Presumably, no conscious perception exists of the oscillations of the magnetic signal under exposure to PF-MF, and possible consequences of the reception of these oscillations might, for example, be searched for at the sub-cortical level where multiple interactions are known to occur between the multiple sensory inputs and the regulation of homeostatic and neurovegetative functions.

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