The Puzzle of Magnetic Resonance Effect on the Magnetic Compass of Migratory Birds

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Experiments on the effect of radio-frequency (RF) magnetic fields on the magnetic compass orientation of migratory birds are analyzed using the theory of magnetic resonance. The results of these experiments were earlier interpreted within the radical-pair model of magnetoreception. However, the consistent analysis shows that the amplitudes of the RF fields used are far too small to noticeably influence electron spins in organic radicals. Other possible agents that could mediate the birds' response to the RF fields are discussed, but apparently no known physical system can be responsible for this effect. Bioelectromagnetics, 2009. © 2009 Wiley-Liss, Inc.

Key words: magnetoreception; spin relaxation; radical pair; magnetic nanoparticle

INTRODUCTION

Hundreds of publications are devoted to the hypothetic magnetic sense of animals [for a review, see Able, 1994; Wiltschko and Wiltschko, 1995, 1996, 2005; Johnsen and Lohmann, 2005], yet the phenomenon remains elusive and is often regarded with skepticism. As we humans are apparently deprived of this sense, and other animals cannot tell us whether they feel magnetic fields or not, nearly all the available information has been obtained from behavioral experiments. These experiments are rarely quite unambiguous and normally require outstanding skills and experience in working with the animal species in question, to exclude the influence of innumerable interfering factors. However, some results obtained lately in experiments with migratory birds allow quantitative interpretation, and might become the basis for a conclusive physical theory of magnetoreception.

Birds are certainly a ''privileged'' class of animals regarding studies of the magnetic sense, for two main reasons. Firstly, the ability of migratory birds to find their way over great distances has been known to mankind for ages; the analogy with the methods of human navigators brought about the idea of birds' using a magnetic compass as long ago as in the 19th century.[1] Second, and more important for modern science, is the genetically prescribed *circannual rhythm* of the bird's life, that gives a great advantage to the experimentalist. In certain periods of the year when the bird should migrate, its physiology and behavior dramatically changes [Berthold, 1996]. In particular, the bird, even kept in a cage, demonstrates increased locomotory activity. Very often this *migratory restlessness* is accompanied by attempts to move in the direction corresponding to the seasonal migration route. The preferential direction of movements of caged birds, recorded by various technical means, was shown to be determined from celestial cues like the sun or stars (including artificial ones demonstrated to the bird in a planetarium) [Emlen, 1967a,b]. Many bird species, when deprived of the possibility to take bearing from any visible object, still show seasonally appropriate direction of movements. This direction was reported to change when the laboratory magnetic field was deflected with electromagnets. Though directional preference of caged birds in magnetic fields is faint, and its registration requires accumulation of large statistical samples, a few leading research groups developed accurate methods for detecting this effect [for review, see Able, 1994, 1995]. The possibility of studying the orientation behavior of birds in the laboratory allowed the accumulation of a considerable amount of exper-

[1]According to Wiltschko and Wiltschko [1996], by A. von Middendorff [1859] and C. Viguier [1882].

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imental information on the dependence of orientation ability on various external physical factors [Wiltschko and Wiltschko, 1995, 1996, 2005; Wiltschko et al., 2001, 2004; Mucheim et al., 2002; Ritz et al., 2004; Johnsen and Lohmann, 2005; Thalau et al., 2005; Stapput and Wiltschko, 2006].

THE PHYSIOLOGICAL AND EXPERIMENTAL BASIS FOR CURRENT MAGNETORECEPTION MODELS

Several models of magnetoreception have been proposed [for a review, see Johnsen and Lohmann, 2005]. Most of them, however, are not supported by any physiological or experimental evidence. For this reason, two hypotheses having some (though not decisive) factual confirmation are now most popular: one involving magnetic minerals [Kirschvink and Gould, 1981], and another based on spin chemistry [Ritz et al., 2000]. The latter, so-called radical-pair model will be discussed in the next section.

The magnetic-mineral theory is largely based on the universal presence of iron-containing compounds in living organisms. Recently, the finding of a candidate magnetoreceptor structure in birds has been reported [Fleissner et al., 2003, 2007]. A complex structure attached to a nerve ending was found in the upper beak of the homing pigeon; remarkably, this structure contains large amounts of iron in various forms (mainly oxides Fe_2O_3 and Fe_3O_4 in different crystalline modifications, some of the crystals probably carrying macroscopic magnetic moments). In principle, the torque experienced by magnetic microcrystals in the external magnetic field can be detected by biological mechanoreceptors [Adair, 2000]; however, the question as to how exactly this specific structure might work remains open (a theoretical model has been proposed in Solov'yov and Greiner [2007]; see also critical comments in Winklhofer and Kirschwink [2008]).

Many experimental results indicate that a different mechanism of magnetoreception is responsible for determining the magnetic-field *direction*, that is, for functioning of the bird's magnetic compass. It is believed that the compass receptor is situated in the bird's eye; this location is derived from the observed sensitivity of the bird's orientation ability to the intensity and spectral composition of the ambient light [Wiltschko et al., 2001, 2004; Mucheim et al., 2002], and from experiments with blindfolded birds. For instance, European Robins with covered right eye were shown to lose the ability to orient by the magnetic field, while those with covered left eye retained this ability [Wiltschko et al., 2002]. Though this lateral asymmetry may be related to the structure of the bird's brain, the very fact that blocking vision of one or other eye disrupts orientation suggests that some structures in the eye are involved in magnetoreception. Accordingly, it was supposed that the magnetoreception is realized via a photochemical reaction sensitive to magnetic fields [Ritz et al., 2000].[2]

THE RADICAL-PAIR MODEL OF MAGNETORECEPTION

The radical-pair model [Ritz et al., 2000] assumes that the geomagnetic field changes the rate of radical-pair chemical reactions, affecting certain (so far unknown) receptors. Reactions of this type are well known in chemistry [Turro, 1983; Salikhov et al., 1984]. In such a reaction, an organic molecule is transferred into an excited state by absorption of a photon, and then splits into two radicals with spins of the two electrons forming a triplet state. The destiny of the molecule now depends on its spin state: if it remains a triplet, a chain of reactions, involving each of the two radicals separately, follows; if it transforms into a singlet, the radicals rapidly recombine. The triplet-to-singlet transition may result from the hyperfine interaction: one of the electrons flips its spin under influence of magnetic fields created by nuclear spins nearby. The probability of this process depends on the external magnetic field. Therefore, the yield of the photoinduced reaction may be, to a degree, controlled by the magnetic field. Calculations show that certain (though rather weak) sensitivity to magnetic fields of the order of the geomagnetic one (50 μT) may be expected [Adair, 1999]. The sensitivity to the *direction* of the magnetic field is attributed to the anisotropy of the hyperfine interaction with respect to structural axes of the molecule: the molecules are assumed to be spatially fixed and oriented uniformly, in order to make the overall reaction yield a function of the field direction [Ritz et al., 2000]. Recently, an argument in favor of this hypothesis was gained by biochemical methods: cryptochrome, a protein able to undergo a chain of photoinduced transformations affected by magnetic fields, was found in the birds' retina [Mouritsen et al., 2004].

EXPERIMENTS ON THE INFLUENCE OF RADIO-FREQUENCY MAGNETIC FIELDS ON MAGNETIC ORIENTATION OF BIRDS

In an attempt to prove the radical pair model, a series of experiments was conducted that gave very

[2]This is a modification of an earlier proposal, not involving photoexcitation [Schulten et al., 1978].

remarkable results, which will be discussed in the rest of the article. These are the experiments on the effect of weak oscillating magnetic fields on the work of the birds' magnetic compass [Ritz et al., 2004; Thalau et al., 2005; Stapput and Wiltschko, 2006; Wiltschko et al., 2007]. In these experiments, the ability of caged birds to show the seasonally appropriate direction of movements was tested under application of alternating magnetic fields with amplitudes of the order of less than 0.01 of the constant geomagnetic field. The results may be summarized as follows:

(1) A broadband "noise" magnetic field with the frequency range 0.1–10 MHz and average amplitude of 85 nT, applied at 24° to the local geomagnetic field of 46 μT [Ritz et al., 2004; Wiltschko et al., 2007], disrupted the orientation of birds.
(2) Orientation of birds was also disrupted by monochromatic oscillating fields of the amplitude of 485 nT in the frequency range, approximately, from 1 to 7 MHz (experiments at 1.315 [Thalau et al., 2005; Stapput and Wiltschko, 2006], 2.63 [Stapput and Wiltschko, 2006], and 7 MHz [Ritz et al., 2004] have been so far reported). The oscillating field was applied vertically (i.e., at an angle of 24° to the local geomagnetic field).
(3) A higher sensitivity to the oscillating field was observed at 1.315 MHz: the orientation ability was disrupted by RF fields 10 times weaker than at other frequencies [Stapput and Wiltschko, 2006].[3]
(4) Oscillating fields with the same amplitude, but applied parallel to the geomagnetic field, did not affect the orientation of birds, with the only exception of 1.315 MHz, at which frequency a marginally weak effect was observed [Ritz et al., 2004; Thalau et al., 2005].

In the original articles, these findings were interpreted as the electron paramagnetic resonance in the radicals undergoing the radical-pair reaction. Given the frequency range and strength of the AC magnetic field, it is indeed impossible to explain these effects by its influence on nuclear spins or motion of charges [Adair, 1991, 2000]. However, the analysis given in the next section shows that these results are not explainable in terms of the electron spin resonance in organic radicals either.

[3]It is erroneously stated in Thalau et al. [2005] and Stapput and Wiltschko [2006] that 1.315 MHz is the exact frequency of the paramagnetic resonance of unperturbed electron spins in the local geomagnetic field of 46 μT; in fact, this frequency is 1.289 MHz.

EXPERIMENTS WITH THE RF FIELD: GENERAL PHENOMENOLOGY

The following estimates are based on the general theory of magnetic resonance, which can be found in many textbooks and monographs [see, for instance, Abragam, 1961; Abragam and Bliney, 1970]. A brief qualitative introduction to the physics of spin with explanation of the main terms used is given in the Appendix.

We start with estimating the rate of electron spin transitions induced by the RF fields applied in the experiments. This can be most easily done for the experiment with the 0.1–10 MHz broadband field, because in this case we should not assume a specific resonance frequency (which is not known a priori). The general expression for the transition rate between quantum states i and j under a random magnetic field B_1 reads:

$$W_{\mathrm{B}} = \frac{1}{\hbar^2}|\langle i|M_{\mathrm{B}}|j\rangle|^2 \int_0^\infty \langle B_1(t)B_1(t-\tau)\rangle \mathrm{d}\tau = \frac{1}{\hbar^2}|\langle i|M_{\mathrm{B}}|j\rangle|^2 \langle B_1^2\rangle \tau_{\mathrm{c}} \quad (1)$$

where $\langle i|M_{\mathrm{B}}|j\rangle$ is the matrix element of the projection of the electron magnetic moment on the direction of the RF field, and the correlation time of the random field is determined as $\tau_{\mathrm{c}} = \frac{1}{\langle B_1^2\rangle}\int_0^\infty \langle B_1(t)B_1(t-\tau)\rangle \mathrm{d}\tau \approx (2\pi\Delta f)^{-1}$, where Δf is the bandwidth of the random field. Equation (1) is valid if the transition frequency ω_{ij} satisfies the condition $\omega_{ij}\tau_{\mathrm{c}} \ll 1$ (approximation of short correlation time). In terms of the bandwidth this condition reads $\omega_{ij} \ll 2\pi\Delta f$, which is indeed the case in the discussed experiments. Taking the transition matrix element equal to one of a free electron spin (this gives an upper estimate of W_{B}):

$$\langle i|M_{\mathrm{B}}|j\rangle = \mu_{\mathrm{B}} g B_1 \sin\alpha \quad (2)$$

we obtain, for $\Delta f = 10$ MHz, $\alpha = 24°$, and $B_1 = 85$ nT, the transition probability $W_{\mathrm{B}} \approx 1\ \mathrm{s}^{-1}$. Here μ_{B} is the Bohr magneton, α the angle between the RF and constant fields, and $g \approx 2$ is the electron g-factor.

Since the component of the RF field parallel to the constant one produces almost no effect, we should conclude that i and j are states with definite electron spin projections on the constant field B_0. For the RF field to induce a noticeable change in population of these states the transition probability should be of the same order as,

or larger than, T_1^{-1}, where T_1 is the longitudinal spin relaxation time. Thus, we are coming to the following lower estimate of T_1:

$$T_1 > 1\,\mathrm{s} \tag{3}$$

Now we can use the experiments with monochromatic RF fields to estimate other characteristics of the spin system in question. With the exception of 1.315 MHz, the frequencies used in the experiment are not associated with any known transition. As the RF fields applied at 2.63 and 7 MHz gave the effect comparable to that of 1.315 MHz field, and it is very unlikely that they hit some other resonances by chance, we should consider these experiments as off-resonant, with the detuning of at least 1 MHz. The probability of such transitions is given by the quantum-mechanical perturbation theory [Landau and Lifshits, 1973]:

$$W_{\mathrm{OR}} = \left(\frac{\mu_{\mathrm{B}} g B_1 \sin\alpha}{\hbar\Delta\omega}\right)^2 T_2^{-1} \tag{4}$$

where B_1 is again the amplitude of the RF field, $\Delta\omega$ the detuning, and T_2 the dephasing time of the periodic perturbation. Since, as noted above, the transition goes between the states with definite projections of the electron angular momentum, the dephasing time T_2 can be interpreted in the usual manner for EPR as the transversal relaxation time.

Once again, the RF field inducing a noticeable change in population of these states means that the transition probability W_{OR} is of the same order as, or larger than, T_1^{-1}. This condition results in the following relation of relaxation times:

$$\frac{T_2}{T_1} < \left(\frac{\mu_{\mathrm{B}} g B_1 \sin\alpha}{\hbar\Delta\omega}\right)^2 \approx 10^{-6} \tag{5}$$

from which we readily find $T_2 \approx 10^{-6}$ s.

Close to the exact resonance (that is, when $\Delta\omega \ll T_2^{-1}$), the transition probability equals

$$W_{\mathrm{R}} = \frac{1}{2\hbar^2}(\mu_{\mathrm{B}} g B_1 \sin\alpha)^2 T_2 \tag{6}$$

It becomes larger than T_1^{-1} under the condition

$$\frac{1}{2\hbar^2}(\mu_{\mathrm{B}} g B_1 \sin\alpha)^2 > (T_1 T_2)^{-1} \tag{7}$$

With the values of relaxation times that we have found, this condition is satisfied if $B_1 > 10$ nT, in qualitative agreement with the experimental result obtained for 1.315 MHz [Stapput and Wiltschko, 2006].

To conclude this section, we have found that the observed disruption of the birds' orientation by the broadband noise magnetic field with the amplitude 85 nT and frequency range of 0.1–10 MHz implies the longitudinal relaxation time T_1 of the electron spin system in question, approximately equal to 1 s. This result does not depend on the specific energy spectrum of the system, provided the transition frequencies fall within the bandwidth of the RF field. The results of experiments with monochromatic RF fields at different frequencies can be qualitatively explained suggesting that the transversal relaxation time of the system, T_2, equals 10^{-6} s.

RESTRICTIONS IMPOSED BY THE DETERMINED RELAXATION TIMES ON THE SPIN SYSTEM IN QUESTION

Analysis of the experimental data performed in the previous section reveals two unusual facts: a very long longitudinal relaxation time $T_1 \approx 1$ s of the spin system in question, and a very large ratio of longitudinal and transversal relaxation times, $T_1/T_2 \approx 10^6$.

The first fact immediately rejects the hypothesis that the observed disruption of birds' orientation is due to the effects of RF fields on radical pairs: typical lifetimes of such pairs are $10^{-9} - 10^{-7}$ s [Turro, 1983; Adair, 1999], and even the most optimistic estimates do not give lifetimes longer than 10^{-5} s [Cintolesi et al., 2003]. Moreover, to the best of my knowledge, the time T_1 as long as 1 s was never observed in electronic spin systems of condensed matter.

The second finding, the large T_1/T_2, leads to even stronger conclusions. Large T_1/T_2 ratios in weak magnetic fields are typical for crystalline solids; they are never met in liquids or soft organic matter. The origins of this fact are the following. The longitudinal time T_1 is normally longer than the transversal time T_2 for two reasons. One is the suppression of relaxation of the spin component along the constant magnetic field B. However, one can easily estimate that the constant field of 50 μT cannot suppress relaxation to the required degree. Indeed, the suppression factor reads

$$T_1/T_2 \approx 1 + (\mu_{\mathrm{B}} g B \tau_{\mathrm{c}}^*/\hbar)^2 \tag{8}$$

where τ_{c} is the shortest of the two correlation times: one of effective random magnetic fields causing spin relaxation, and one of the electron spin itself. Without going into details of the spin relaxation mechanism, one can only say that $\tau_{\mathrm{c}} \le T_2$. By substituting this inequality into Equation (8) and neglecting 1 in the right-hand side, one gets $T_1/T_2 \le (\mu_{\mathrm{B}} g B/\hbar)^2 T_2^2$. With $B = 50$ μT and $T_2 = 10^{-6}$, this gives $T_1/T_2 \le 10^2$, which is far below the observed value of 10^6.

The second possible reason for a large T_1/T_2 is that the relaxation of the longitudinal spin component is accompanied by dissipation of the Zeeman energy $\mu_B g B$, which requires coupling of spin with the motion of atoms. This process is indeed strongly suppressed in solids with rigid crystal structure, but not in liquids or in soft matter, where thermal agitation of molecules is much less restricted. For this reason, such large values of T_1/T_2 are met only in crystals, and even there they typically occur at low temperatures.

Therefore, we should conclude that the observed effects of RF magnetic fields on the magnetic orientation of birds could not result from the influence of these fields on electron spins in organic radicals.

EXTERNAL RF FIELD VERSUS INTERNAL RANDOM NUCLEAR FIELDS

This conclusion is further confirmed by a comparison of the RF fields applied in the experiment with magnetic fields created by nuclear magnetic moments in the media surrounding the radical.

Each magnetic nucleus produces the field $\vec{B}_N = \frac{\mu_N}{Ir^3}\left(\vec{I} - 3\frac{(\vec{I}\cdot\vec{r})\vec{r}}{r^2}\right)$, where μ_N and I are nuclear magnetic moment and spin, respectively. The squared field is $B_N^2 = \frac{\mu_N^2}{I^2 r^6}\left(I^2 + 3\frac{(I\cdot\vec{r})^2}{r^2}\right)$.

The mean squared field produced by all the nuclei inside a spherical layer with radius r and thickness dr at the center of the sphere is

$$\left\langle B_{Nr}^2 \right\rangle = \frac{\mu_N^2}{I^2 r^6}\left(I^2 + 3\frac{\left\langle (I\cdot\vec{r})^2 \right\rangle}{r^2}\right) 4\pi n_I r^2 \mathrm{d}r = \frac{\mu_N^2}{I^2 r^6}\left(I^2 + 3I^2\langle\cos^2\theta\rangle\right) 4\pi n_I r^2 \mathrm{d}r = \frac{8\pi\mu_N^2}{r^4} n_I \mathrm{d}r \tag{9}$$

where θ is the angle between $\vec{r}$ and $\vec{I}$, and n_I is the concentration of magnetic nuclei.

Integrating over r from R to infinity, we obtain the field produced by all the nuclei outside a ''bubble'' with radius R at its center:

$$\left\langle B_{NR}^2 \right\rangle = \int_R^\infty \frac{8\pi\mu_N^2 n_I}{r^4}\,\mathrm{d}r = \frac{8\pi\mu_N^2 n_I}{3r^3} \tag{10}$$

For protons, $\mu_N = 1.141\ \ 10^{-26}\ J/T$. In water, $n_I \approx 6\times 10^{22}\ \mathrm{cm}^{-3}$. We can use this value also as a rough estimate for n_I in organic substances. So we get,

$$\left\langle B_{NR}^2 \right\rangle^{1/2} = 30\,\mu\mathrm{T}\cdot\sqrt{1/R^3} \tag{11}$$

where R is in nm. Assuming $R = 1$ nm, we get $\left\langle B_{NR}^2 \right\rangle^{1/2} = 30\,\mu$T, that is, the random nuclear field is 400 times stronger than the broadband RF field (85 nT) applied in the experiment! However, the correlation time of the nuclear field, τ_{cN}, can be different from that of the RF field. In water, it is determined by molecular motion and is of the order of 10^{-11} s [Abragam, 1961]. This means that typical frequencies of electron spin transitions are within the bandwidth $\Delta\nu_N$ of the random field created by water protons, and we can calculate the transition rate as $W_N = \frac{\gamma_e^2\left\langle B_N^2\right\rangle}{2\pi\cdot\Delta\nu_N} = \gamma_e^2\left\langle B_N^2\right\rangle\tau_{cN} \approx 3\times 10^2\ \mathrm{s}^{-1}$, that is, more than 2 orders of magnitude faster than that induced by the broadband RF field.

If the radical is surrounded by soft matter (lipids or proteins), the correlation time of the nuclear field is longer because the molecular motion is much slower, while its amplitude is nearly the same as in water. As a result, the transition rate under random nuclear fields is in this case even faster.

Therefore, external RF fields applied in the discussed experiments exert a much weaker effect upon electron spins in radicals than internal nuclear magnetic fields inevitably present in biological systems; under these conditions, external RF fields are not expected to affect radical pair reactions.

OTHER POSSIBLE ORIGIN OF THE EFFECT: MAGNETIC NANOPARTICLES

If organic radicals cannot be responsible for the observed effect of RF fields on the bird's compass, what other object can? According to the results of Restrictions Imposed by the Determined Relaxation Times on the Spin System in Question and External RF Field Versus Internal Random Nuclear Fields Sections, it should be a piece of crystalline solid, which does not contain magnetic nuclei. In addition, it should be large enough to diminish penetration of nuclear magnetic fields from protons contained in the organic matter in which it is immersed. Using Equation (11), it is easy to estimate that its radius should be not less than 20–30 nm. Finally, this object should carry an electron spin moment. Seemingly, this is the portrait of an iron oxide magnetic nanocrystal!

However, spin relaxation times presently known for magnetic nanoparticles are far shorter than those estimated in Experiments With the RF Field: General Phenomenology Section. For example, in a recent work [Noginova et al., 2007] superparamagnetic γ-Fe_2O_3 particles were studied by magnetic resonance in the external magnetic field of about 0.3 T. The longitudinal

relaxation time was measured to be just 10 ns, instead of the 1 s required.

On the other hand, experimental data on spin relaxation in magnetic nanocrystals are sparse, leaving some room for speculation. For instance, I am unaware of any such experiment performed in magnetic fields as weak as the geomagnetic field. Possibly, small Zeeman splitting together with a modification of the spectrum of lattice vibrations by size effects in the nanocrystal [Goupalov and Merkulov, 2001] can suppress energy transfer from electron spins to the crystal lattice and, correspondingly, make T_1 longer. Still, gaining in T_1 by 8 orders of magnitude does not seem realistic. I would like to stress once again that the electron spin relaxation time of 1 s at the temperature of 310 K is unheard of in condensed matter.

CONCLUSIONS

As our analysis has shown, the radical pair model is unable to explain the results of the experiments [Ritz et al., 2004; Thalau et al., 2005; Stapput and Wiltschko, 2006; Wiltschko et al., 2007] on disruption of the bird magnetic compass by radio-frequency (RF) magnetic fields. The main reasons are that (i) this would require longitudinal spin relaxation times of the order of 1 s, which is much longer than the lifetime of the radical pair, and (ii) internal stochastic magnetic fields produced by magnetic nuclei around the radicals exert a much stronger effect on their spins than the external RF fields applied in the experiments. Moreover, the properties of the hypothetic object that would give the required response to magnetic fields of amplitudes and frequencies used in those experiments, are so unusual that they can hardly be attributed to any known physical system.

The experimental procedure of Ritz et al. [2004], Thalau et al. [2005], Stapput and Wiltschko [2006], and Wiltschko et al. [2007] looks adequate for a biological experiment, and the conclusions would have been quite reasonable if they were purely biological. But it follows from these experiments that the compass magnetoreceptor of birds incorporates an unknown object with physical properties that have not yet been realized in physical laboratories. Therefore, the methodological requirements of experimental physics should also be applied to these experiments. One of these requirements is that if an experimental result contradicts the general theory, the experiment should be repeated with special attention to all imaginable parasitic effects that could give the same result—until all of them are, one by one, excluded. Only then the new phenomenon can be believed to exist. This was concisely expressed by Adair [1999]: ''Remarkable conclusions, which seem to violate well considered principles, require remarkably strong evidence.'' Adair's maxim seems fully appropriate here.

If further research confirms the so far obtained results, they may lead to a breakthrough in condensed-matter physics, where systems with long spin relaxation times are hunted because of their envisaged technical applications (''spintronics'' [Dyakonov, 2004]). This would mean that Nature has by far outperformed the attempts of physicists and engineers to make practical use of long-lived spin states in condensed matter.

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REFERENCES

Able KP. 1994. Magnetic orientation and magnetoreception in birds. Prog Neurobiol 42:449–473.

Able KP. 1995. Orientation and navigation: A perspective of fifty years of research. Condor 97:592–604.

Abragam A. 1961. Principles of nuclear magnetism. Oxford: Clarendon Press.

Abragam A, Bliney B. 1970. Electron paramagnetic resonance of transition ions. Oxford: Clarendon Press.

Adair RK. 1991. Constraints on biological effects of weak extremely-low-frequency electromagnetic fields. Phys Rev A 43:1039–1048.

Adair RK. 1999. Effects of very weak magnetic fields on radical pair reformation. Bioelectromagnetics 20:255–263.

Adair RK. 2000. Static and low-frequency magnetic field effects: Health risks and therapies. Rep Prog Phys 63:415–454.

Berthold P. 1996. Control of bird migration. London: Chapman and Hall.

Cintolesi F, Ritz T, Kay C, Timmel C, Hore P. 2003. Anisotropic recombination of an immobilized photoinduced radical pair in a 50 μT magnetic field: A model avian photomagnetoreceptor. Chem Phys 294:385–399.

Dyakonov MI. 2004. Spintronics? In: Luryi S, Xu J, Zaslavsky A, editors. Future trends in microelectronics. The Nano, The Giga, and The Ultra: Wiley. p 157. Available also from arXiv:cond-matt/0401369.

Emlen ST. 1967a. Migratory orientation in the indigo bunting, Passerina cyanea. Part I: Evidence for use of celestial cues. Auk 84:309–342.

Emlen ST. 1967b. Migratory orientation in the indigo bunting, Passerina cyanea. Part II: Mechanism of celestial orientation. Auk 84:463–489.

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

Fleissner G, Stahl B, Thalau P, Falkenberg G, Fleissner G. 2007. A novel concept of Fe-mineral-based magnetoreception: Histological and physicochemical data from the upper beak of homing pigeons. Naturwissenschaften 94:631–642.

Goupalov SV, Merkulov IA. 2001. Confinement of acoustic phonons in CuCl nanocrystal quantum dots. Phys Status Solidi B 224:649–653.

Johnsen S, Lohmann KJ. 2005. The physics and neurobiology of magnetoreception. Nature Reviews Neuroscience. AOP 6:703–712.

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

Landau LD, Lifshits EM. 1973. Quantum mechanics. London: Pergamon Press.

Mouritsen H, Janssen-Bienhold U, Liedvogel M, Feenders G, Stalleicken J, Dirks P, Weiler R. 2004. Cryptochromes and neuronal-activity markers colocalize in the retina of migratory birds during magnetic orientation. Proc Natl Acad Sci 101:14294–14299.

Mucheim R, Bäckman J, Åkesson S. 2002. Magnetic compass orientation in European robins is dependent on both wavelength and intensity of light. J Exp Biol 205:3845–3856.

Noginova N, Chen F, Weaver T, Giannelis EP, Bourlinos AB, Atsarkin VA. 2007. Magnetic resonance in nanoparticles: Between ferro- and paramagnetism. J Phys Condens Matter 19 246208 (15 p).

Ritz T, Adem S, Schulten K. 2000. A model for photoreceptor-based magnetoreception in birds. Biophys J 78:707–718.

Ritz T, Thalau P, Phillips J, Wiltschko R, Wiltschko W. 2004. Resonance effects indicate a radical-pair mechanism for avian magnetic compass. Nature 429:177–181.

Salikhov KM, Molin YuN, Sagdeev RZ, Buchachenko AL. 1984. Spin polarization and magnetic effects in radical reactions. Amsterdam: Elsevier.

Schulten K, Swenberg CE, Weller A. 1978. A biomagnetic sensory mechanism based on magnetic field modulated coherent electron spin motion. Z Phys Chem Neue Folge 111:1–5.

Solov'yov IA, Greiner W. 2007. Theoretical analysis of an iron mineral-based magnetoreceptor model in birds. Biophys J 93:1493–1509.

Stapput K, Wiltschko R. 2006. Behavioral evidence for the radical pair model of magnetoreception. J Ornithol 147 (Suppl 1):49.

Thalau P, Ritz T, Stapput K, Wiltschko R, Wiltschko W. 2005. Magnetic compass orientation of migratory birds in the presence of a 1.315 MHz oscillating field. Naturwissenschaften 92:86–90.

Turro N. 1983. Influence of nuclear spin on chemical reactions: Magnetic isotope and magnetic field effects (a review). Proc Natl Acad Sci USA 80:609–621.

Wiltschko R, Wiltschko W. 1995. Magnetic orientation in animals. Springer. Berlin.

Wiltschko W, Wiltschko R. 1996. Magnetic orientation in birds. J Exp Biol 199:29–38.

Wiltschko W, Wiltschko R. 2005. Magnetic orientation and magnetoreception in birds and other animals. J Comp Physiol A 191:675.

Wiltschko W, Gesson M, Wiltschko R. 2001. Magnetic compass orientation of European robins under 565 nm green light. Naturwissenschaften 88:387–390.

Wiltschko W, Traudt J, Güntürkün O, Prior H, Wiltschko R. 2002. Lateralization of magnetic compass orientation in a migratory bird. Nature 419:467–470.

Wiltschko W, Gesson M, Stapput K, Wiltschko R. 2004. Light-dependent magnetoreception in birds: Interaction of at least two different receptors. Naturwissenschaften 91:130–134.

Wiltschko R, Stapput K, Ritz T, Thalau P, Wiltschko W. 2007. Magnetoreception in birds: Different physical processes for two types of directional responses. HFSP J 1:41–48. Available from: http://dx.doi.org/10.2976/1.2714294.

Winklhofer M, Kirschwink J. 2008. Does avian magnetoreception rely on both magnetite and maghemite? Available from: arXiv:0805.2249v1 [phys.bio-ph].

APPENDIX: INTRODUCTION TO THE SPIN PHYSICS FOR BIOLOGISTS

The *spin* is the internal angular momentum (''quantity of rotation'') of an electron or another particle. It is a vector which can point, in principle, anywhere. The length of this vector is fixed for any elementary particle. It is usually measured in units equal to the Planck constant: the electron spin being 1/2 means that the electron carries the angular momentum of $\hbar/2 \approx 5 \times 10^{-28}\,\mathrm{g\,cm^2/s}$. For a complex particle, the total spin is equal to vector sum of the spins of constituent particles and may have different length depending on their mutual orientation. For an ensemble of particles, one can speak about their *mean spin*, equal to the vector sum of all the spins divided by the number of particles. Alternatively, one can introduce the *spin polarization* as the length of the vector sum of all the spins divided by the maximal total spin of these particles. If the polarization is equal to 1, all the spins point in the same direction.

A vector of the magnetic moment is often associated with the spin. It is parallel to the spin vector, but its value and sign are different for different particles. For example, spins of the electron and the proton are equal, but the magnetic moment of the proton is $-1/657$ of the electron magnetic moment. Each magnetic moment creates magnetic field around it, exactly as a bar magnet does.

In a magnetic field, the energy of a magnetic moment depends on its direction: it is minimal when it is directed along the field and maximal when it takes the

opposite direction. In other words, there exists a force that tries to turn the spin so that its magnetic moment would come closer to the field direction. However, a free spin will never do this because it is a gyroscope: subjected to a force, it turns perpendicular to the force. As a result, the spin placed in a magnetic field rotates about the field direction with the frequency called *Larmor frequency* and proportional both to the field strength and to the value of the magnetic moment. The spin projection onto the magnetic field remains constant. This phenomenon is called *Larmor precession*.

If, in addition to the constant field, the spin is subjected to weak alternating magnetic fields perpendicular to the constant one, the direction of the total magnetic field slightly changes with time. As a result, the trajectory of the spin vector is no longer a circle; it deflects by greater and greater angle from the initial orbit. After many revolutions, the spin direction becomes impossible to predict precisely: it becomes a random vector. If the alternating fields are created by surrounding magnetic moments or by thermal motion of charges, the distribution function of the spin direction soon becomes determined by thermal equilibrium in the spin ensemble. The spin polarization will then take the value prescribed by thermodynamics for the given magnetic field: the stronger the field, the larger is the spin polarization. The process, which brings a spin ensemble to equilibrium, is called *spin relaxation*. It is characterized by a *spin relaxation time*, usually denoted as τ_s. If we create a non-equilibrium spin polarization and leave it alone, it will disappear during the spin relaxation time. The term "*spin lifetime*" is sometimes also used, meaning the shortest of all the times determining the existence of spin polarization (e.g., the spin lifetime in a radical is determined either by spin relaxation or by recombination of the radical, whichever process is faster). Some spin systems are characterized by more than one relaxation time. For example, the relaxation time of the spin component parallel to the external static magnetic field is called the *longitudinal relaxation time* and denoted T_1. The components of the mean spin, perpendicular to the static field (they rotate about this field with the Larmor frequency), decay with the *transversal relaxation time*, T_2, which is often shorter than T_1.

If the experimentalist applies an external RF magnetic field perpendicular to the constant one, it depolarizes spins, so that its projection on the constant field decreases. This process is accompanied by changing the spin energy at the expense of absorbed RF power. The effect of the RF field is especially strong if its frequency is close to the Larmor frequency in the constant magnetic field. This is called *magnetic resonance*. To observe the magnetic resonance, one should first have some spin polarization. For example, magnetic resonance tomographs use thermodynamically equilibrium polarization of spins of hydrogen nuclei; this is why they incorporate huge electromagnets capable of producing strong fields. Though absorption of the RF power by the spin system, usually registered in magnetic-resonance spectrometers, can be observed for arbitrary weak AC fields (if you have a very sensitive detector), the RF field will induce a noticeable change to the mean spin only if the field is strong enough to depolarize spins faster than does spin relaxation.

It is known from quantum mechanics that the spin 1/2 placed in a magnetic field may occupy two discrete energy levels. These levels correspond to certain spin projections on the magnetic field (for an electron they are $+1/2$ and $-1/2$). This does not mean, as some people erroneously believe, that the spin can point only up or down the field. The spin, as any vector, can point anywhere. However, as mentioned above, the spin, being inclined to the magnetic field direction, rotates about it. Only in the case when it points up or down the field, the spin can remain stationary. It is no coincidence that the energy difference between the spin levels in a magnetic field is equal to the Larmor frequency multiplied by the Planck constant. This is just the way by which quantum mechanics accounts for the spin rotation. Quantum and classical descriptions of the spin dynamics in magnetic fields give exactly the same results, but the terminology is different. For instance, the spin polarization in quantum mechanics is interpreted as a difference of electron populations on the two spin levels. Correspondingly, spin relaxation is a result of quantum transitions between stationary spin states, induced by alternating magnetic fields. The *transition rate* between a pair of spin levels (i.e., the average number of transitions per second) is equal to $1/\tau_s$.

Spins can be coupled by spin–spin interactions. Most of these interactions are of magnetic origin: the magnetic moment of one particle creates a magnetic field that affects the magnetic moment of the other (the only exception is the *exchange interaction* between two quantum particles of the same kind, which is mediated by electric fields). Magnetic fields of spin–spin interactions can bring about spin relaxation. For example, magnetic fields created by nuclear spins cause spin relaxation of electrons.

While the dynamics of non-interacting spins in magnetic fields can be qualitatively and even quantitatively described within the classical mechanics of angular momenta, the properties of interacting spins cannot be fully understood without using quantum mechanics. According to quantum mechanics, the

energy of interacting spins also takes discrete values. For example, the exchange interaction of two electrons forms two energy levels corresponding to their total spin equal to 1 and 0. These levels are called *triplet* and *singlet*, respectively, because the former can be further split into three sublevels by applying a magnetic field, while the latter is not affected by magnetic fields and remains a single level. Triplet and singlet states play a key role in formation of chemical bonds: spins of two electrons forming a covalent bond are in the singlet state. Their transfer into the triplet states would break the bond. The energy difference between adjacent triplet sublevels is again Larmor frequency times Planck constant. This corresponds to Larmor precession of the total spin of the two electrons. It is worth noting that a homogeneous magnetic field cannot cause transitions between the singlet and the triplet states; it just induces rotation of the total spin without changing its value. To induce such a transition (also called the singlet–triplet interconversion), an inhomogeneous field is needed, which would have different strength at the positions of the two electrons. Inhomogeneous fields can be created by nearby magnetic moments, notably those associated with nuclear spins. Hence, the important role played by nuclear spins in spin-dependent chemical reactions. External fields can also affect the rate of such reactions by changing energy intervals between different spin levels.