COMMENTS

Comments are short papers which criticize or correct papers of other authors previously published in the **Physical Review**. *Each Comment should state clearly to which paper it refers and must be accompanied by a brief abstract. The same publication schedule as for regular articles is followed, and page proofs are sent to authors.*

Comment on "Constraints on biological effects of weak extremely-low-frequency electromagnetic fields"

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In a recent paper, Adair [Phys. Rev. A **43**, 1039 (1991)] concludes that weak extremely-low-frequency (ELF) electromagnetic fields cannot affect biology on the cell level. However, Adair's assertion that few cells of higher organisms contain magnetite (Fe_3O_4) and his blanket denial of reproducible ELF effects on animals are both wrong. Large numbers of single-domain magnetite particles are present in a variety of animal tissues, including up to a hundred million per gram in human brain tissues, organized in clusters of tens to hundreds of thousand per gram. This is far more than a "few cells." Similarly, a series of reproducible behavioral experiments on honeybees, *Apis mellifera,* have shown that they are capable of responding to weak ELF magnetic fields that are well within the bounds of Adair's criteria. A biologically plausible model of the interaction of single-domain magnetosomes with a mechanically activated transmembrane ion channel shows that ELF fields on the order of 0.1 to 1 mT are capable of perturbing the open-closed state by an energy of kT. As up to several hundred thousand such structures could fit within a eukaryotic cell, and the noise should go as the square root of the number of independent channels, much smaller ELF sensitivities at the cellular level are possible. Hence, the credibility of weak ELF magnetic effects on living systems must stand or fall mainly on the merits and reproducibility of the biological or epidemiological experiments that suggest them, rather than on dogma about physical implausibility.

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Recently, Adair [1] presented a well-argued case covering the constraints on biological effects of weak extremely-low-frequency (ELF) electromagnetic fields, and concludes that many biological effects that have been reported could not possibly be real. His paper includes numerous statements such as "Hence, any biological effects of weak ELF fields on the cellular level must be found outside the scope of conventional physics," and "$\cdots$ there are very good reasons to believe that weak ELF fields can have no significant biological effect at the cell level—and no strong reason to believe otherwise."

Although it is clear that many of the mechanisms considered by Adair are implausible on first principles, there is a gaping hole in the discussion concerning the biological precipitation of ferromagnetic minerals (e.g., magnetite, Fe_3O_4). Adair's discussion implies that only the magnetotactic bacteria are able to precipitate single-domain crystals of magnetite, and he states, "Hence, with the aid of ferromagnetic materials, a cell can—barely—sense a 50-μT field. But Fe_3O_4 is found in few other cells. And without the crafting of such compasses, we cannot expect the effects of magnetic fields on cells to compete with thermal fluctuations."

This is an unfortunate flaw in an otherwise reasonable discussion. *Humans and many other organisms also precipitate magnetite* in a wide variety of tissues [2]. And in the nervous system or immune system, signals transduced by a minute fraction of the total cells can have global consequences.

Three goals of this present comment are as follows: First, for background, I review briefly the evidence for magnetite biomineralization in higher organisms. Second, Adair asserts that there are no good reasons to believe weak ELF fields have biological effects at the cellular level in terrestrial animals. I therefore review the recent literature which links incontrovertibly weak magnetic fields and behavior, providing a clear counterexample to his assertion. Of the eight magnetic effects on bees described in the literature, six have been replicated independently, and three by more than one other group. Good evidence links the transduction mechanism to the motion of magnetite in specialized receptor cells. Finally, a simple calculation shows that the motions of magnetosomes in response to a weak ELF magnetic field would be capable of opening or closing transmembrane ion channels. This provides one plausible mechanism for triggering a number of significant biological effects.

Magnetite biomineralization. Lowenstam [3] discovered the process of magnetite biomineralization in the teeth of a primitive group of mollusks, the chitons, and

his subsequent work has provided one of the clearest examples of this mineralization process in any higher organism [4,5]. Each tooth contains up to 1 mg of single-domain magnetite [6], enough so that the entire tongue plate (the radula) will stick to an ordinary hand magnet [3]. So far, chiton radulae are the only macroscopic biological structures known to contain visible quantities of biogenic magnetite, although as discussed below it is present commonly in the ppm to ppb levels in a variety of other species and tissues.

Adair's discussion of the magnetotactic bacteria, while technically correct, is based largely on the analysis of one species, *Aquaspirillum magnetotacticum,* which has been studied extensively because it can be grown in pure culture [7]. This organism makes relatively small magnetosomes (membrane-bound structures containing a single-domain crystal of magnetite [8]), the chains of which have total magnetic-to-thermal energy ratios between about 10 and 20 [9] in the earth's field. Other natural magnetotactic bacteria have been discovered which contain hundreds of magnetosomes, and have magnetic-to-thermal energy ratios of several thousand [10]. Similar magnetotactic abilities also exist in the eukaryotic kingdom Proctista (the protists). Torres de Araujo *et al.* [11] describe an algae of the genus *Anisonema (Euglenophyceae)* which makes several thousand magnetosomes aligned in hundreds of magnetosome chains, which collectively give the cell a magnetic-to-thermal energy ratio of several thousand. Hence, Adair's [1] statement that magnetite-containing cells can barely detect the 50-μT geomagnetic field is not generally true. Many of these cells are not just "barely" detecting the field, they are responding *strongly* to it.

In higher animals other than the chitons, the discovery of magnetite biomineralization was made largely through the use of moment magnetometers based on superconducting quantum interference devices developed initially for use in rock and mineral magnetism [12]. If these are used in clean-lab conditions, the threshold sensitivity for the detection of magnetite can be a few parts in 10^{12}. The initial detection of magnetite in honeybees [13] and homing pigeons [14] triggered a flurry of discoveries in other animal groups (reviewed in Ref. [2]), and led eventually to the development of gentle extraction techniques which did not disrupt the chainlike organization of the magnetosomes. Magnetosome chains extracted from the anteriordorsal (ethmoid) region of salmon [15,16] possess many of the features also found in the magnetotatic bacteria, including size and shapes within the single-domain stability region, and the alignment of the {111} crystallographic axes along the chain length. Hence, in direct contradiction to the assertion of Adair [1], some cells of higher animals do indeed craft biological bar magnets which enable them to respond strongly to weak ELF magnetic fields.

Related studies of other tissue types often reveal lower but reproducible levels of background ferromagnetic material [2]. Although efficient techniques for extracting the ferromagnetic crystals and identifying them are only now being perfected, the results are intriguing. Soft tissues of the human brain, for example, contain the equivalent of several million magnetosomes per gram [17], serving as-yet unknown biological functions. Although this implies that less than 0.1% of brain cells contain magnetite, the potential number of such cells is quite large. Two strains of mouse tumor, YC-8 lymphoma and Lewis lung carcinoma, make between five and ten crystals per cell [18].

No ELF effects on living systems? A counter example. Adair's [1] assertion that "After 20 years of experimentation, no significant effect of weak ELF fields at the cell level has been firmly established" is also inaccurate. In neurobiology, all known sensory modalities transduce their signals in specialized sensory cells. Hence, if an animal responds behaviorally to an external magnetic field, the stimulus to neural activity will originate at the cellular level, presumably in cells specialized for its transduction. Thus, a convincing demonstration of behavioral sensitivity to weak magnetic fields in *any* animal is enough to falsify Adair's assertion. The honeybee *(Apis mellifera)* is one of several animals which exhibit magnetically influenced behavior.

Table I shows a summary of the known magnetic effects on honeybee behavior, as well as the independent attempts to replicate them. I know of no attempts to replicate these effects that were not eventually successful (some apparently took practice). As Towne and Gould [19] provide a thorough and critical review of this literature prior to 1985 [effects (1)–(4) in Table I], a complete discussion of them is not necessary here. However, note that the horizontal dance experiment of Lindauer and Martin [20] and Martin and Lindauer [21] [effect (2) in Table I] has proven to be particularly easy to replicate [22]. Kirschvink [23] noted that the accuracy of the dance orientation data in varying strength background fields published by Martin and Lindauer [21] followed closely the Langevin function, and from the least-squares match to it predicted that the average honeybee compass receptor had a magnetic-to-thermal energy ratio in the geomagnetic field of about 6, equivalent to a single-domain cube of magnetite about 0.1 μm in size in the 50-μT geomagnetic field.

In a series of papers, Walker and Bitterman [24–26] and Walker, Baird, and Bitterman [27] have shown recently that individual foraging honeybees will learn to discriminate weak magnetic anomalies superimposed against the background geomagnetic field [effects (5)–(7) in Table I]. Given the appropriate experimental situation, honeybees learn to discriminate magnetic cues as easily as they do visual cues [27]. In addition to our replication of the Walker-Bitterman extinction test [(5) in Table I] [28], we have recently replicated their two-choice paradigm as well [29]. We have also discovered that it can be used to map out the frequency response of the honeybee magnetoreceptor, and that honeybees will condition to powerline frequency magnetic fields [29]. The basic experiments are simple and direct.

The measurement of Walker and Bitterman [25] of the threshold sensitivity of the bees to a small static anomaly superimposed upon the background field is the most dramatic result of such conditioning experiments. By starting with a moderately strong anomaly (3 mT) in the two-choice training experiment, and by reducing the am-

TABLE I. Summary of magnetic effects on honeybee behavior.

Effect	Original reports	Similar replications
(1) Misdirection in the waggle dance influenced by weak magnetic fields	Lindauer and Martin [51,20] Martin and Lindauer [21]	Hepworth *et al.* [52] Towne and Gould [19], Kilbert [53]
(2) Dances on horizontal comb align with points of magnetic compass	Lindauer and Martin [20] Martin and Lindauer [21]	Brines [54]; Gould *et al.* [22] (Also see Kirschbink [23])
(3) Magnetic orientation of comb building	Lindauer and Martin [20] Martin and Lindauer [56]	De Jong [55]; Towne and Gould [19]
(4) Time sense of bees influenced by geomagnetic variations	Lindauer [57]	Partially by Gould [58]
(5) Extinction test conditioning experiment	Walker and Bitterman [24]	Kirschvink and Kobayashi-Kirschvink [28]
(6) Two-choice threshold conditioning experiment	Walker and Bitterman [25]	Kirschvink *et al.* [29]
(7) Small magnets on anteriordorsal abdomen interfere with conditioning experiments	Walker and Bitterman [26]	No attempts reported yet
(8) Pulse remagnetization converts north-seeking into south-seeking bees	Kirschvink and Kobayashi-Kirschvink [28]	No attempts reported yet

plitude of the anomaly in small exponential steps, the threshold sensitivity could be determined by the point at which the bees were no longer able to discriminate correctly. Nine bees were tested in this procedure; the median threshold was 250 nT *in the presence of the earth's field,* a relative sensitivity of 0.6%. Their best bee lost the ability to discriminate in fields *below* 25 nT (0.06% of background). Similar, but less direct, estimates of the magnetic sensitivity of bees were obtained from both the misdirection and circadian rhythm experiments (effects (1) and (4) in Table I, reviewed by Towne and Gould [19]). This astounding sensitivity, however, is not physically unreasonable for a magnetite-based sensory system. Estimates for the number of discrete sensory organelles per bee, based on the measured magnetic moments, are on the order of several million [13,23]. Several analyses have shown that the ultimate sensitivity of such an array will improve by the square root of the number of receptors, and that nT-level sensitivity should be obtained easily [30–32]. Similar neurological averaging schemes are well known in the auditory and electroreception systems of many other animals.

Two of the experiments listed in Table I have a direct bearing on the nature of the magnetic sensory receptors in the honeybee. First, Walker and Bitterman [26] found that small magnetized wires glued to the anteriordorsal abdomen interfered with the ability of the bees to discriminate magnetic anomalies, whereas copper wires had no effect. Magnetic wires in other locations similarly had no effect. Magnetite biomineralization in the anteriordorsal abdomen was discovered previously by Gould, Kirschvink, and Deffeyes [13]. Second, Kirschvink and Kobayashi-Kirschvink [28] were on occasion able to elicit magnetic north-seeking behavior in bees trained to visit a simple T maze. A short magnetic pulse with a peak amplitude of 100 mT (stronger than the coercivity of most biogenic magnetities) was able to convert north-seeking exit responses into south-seeking ones. This same experiment works on the magnetotactic bacteria [33,34], and is a unique fingerprint of a ferromagnetic compass receptor.

It is thus clear that the initial reports of magnetic behavioral effects on honeybees, although met with intense skepticism, have survived the acid tests of replication. They have led progressively to more refined experiments which illuminate the nature and sensitivity of the receptor system. The honeybee data provide clear and reproducible evidence that at least one terrestrial animal is influenced at the cellular level by weak ELF magnetic fields. Hence, the existence of similar effects in other magnetite containing cells cannot be dismissed *a priori* as done by Adair [1].

A biophysical model of magnetite and ELF magnetic fields. Adair [1] is correct to stress that biophysical models of interaction must be examined *quantitatively.* Thus, it is necessary to present here a biologically plausible but quantitative sketch model showing how ELF magnetic effects at the cellular or subcellular levels might lead to

significant effects; the model presented here is adapted from a similar biophysical analysis developed for the magnetite-based sensory system of honeybees [29]. The existence of this sketch shows that it is wrong to reject the ELF bioeffect data, including recent epidemiological [35–37] studies, merely because Adair [1] could not construct a physically plausible linkage.

Several biological constraints are as follows. First, studies of biogenic magnetities indicate that they are coated usually by a thin veneer of organic material [2,16], which is usually a thin phospholipid membrane [8,10]. Only in the chiton teeth is there evidence for magnetite crystals embedded in a larger, more rigid structure [3–5]. Second, many of the particles in fresh tissues move relatively freely *in situ*, as shown by the poor ability of unfixed or unfrozen tissues to hold a remanent magnetization [2]. Third, because most intracellular components in eukaryotic cells are held in place relative to cellular membranes by proteinaceous filaments of the cytoskeletal system, similar attachments probably exist for the magnetosomes, as they do in magnetotactic bacteria [10].

Hence, it is reasonable to suggest that magnetic ELF biological effects could arise from membrane deformations produced by magnetosome-induced cytoskeletal tension. In fact, mechanically sensitive *trans*-membrane ion channels are present in almost every organism and tissue, including bacteria, yeast, invertebrates, higher plants, and vertebrates, and are known from oocytes, epithelia, endothelial cells, skeletal muscles, smooth muscles, and neurons [38]. In higher organisms there is good evidence that they are linked to the cytoskeletal system through spectrinlike proteins, and their number densities can be many per square μm [39]. Biophysical properties of such channels are understood fairly well, largely through their identification on the stereocilia of hair cells. Opening of a single channel for a few milliseconds can lead to the firing of an action potential, and the sensitivity of these structures is such that they can sense the Brownian motion of the ciliary bundles [40]. Howard and Hudspeth [41] have made estimates of the single-channel gating force, the difference between the force exerted on the ionic gate when it is open and that when it is closed, which are in the range between 0.2 and 0.4 pN. Similarly, the gating distance for these channels is about 4 nm [41]. These structures operate essentially at the kT limit, and an external input of mechanical energy of ΔE will change the probability of a channel being open or closed by a Boltzmann factor of $\exp(-\Delta E/kT)$. If coupled perfectly, a magnetosome with a magnetic-to-thermal energy ratio of 10 in the geomagnetic field (which "barely" responds to the field according to Adair [1]) could act to change the probability of a gate being closed by a factor of $\exp(-10)$ (e.g., the probability at any time of the gate being closed could shift from a value near 0.999 99 to a value of 0.000 05). Ca^{2+} ions, in particular, move easily through this type of channel, and this ion also controls many phosphorylation cascades which are chemical systems of very high "gain." Hence, the question posed above reduces to finding the level of external ELF magnetic fields that would be required to supply enough torque on a magnetosome to allow it to open a mechanically sensitive ion channel.

Figure 1 is a sketch of a configuration which fits these biological constraints. A cytoskeletal filament anchors a magnetosome to the membrane via a mechanically sensitive ion channel as shown. The background geomagnetic field, B_{earth}, of 50 μT is aligned perpendicular to the membrane, and we apply an ELF magnetic field, $B_{\text{ELF}}\cos(\omega t)$, parallel to the membrane and perpendicular to B_{earth}. We wish to determine the minimum strength of the ELF magnetic field (as a function of fre-

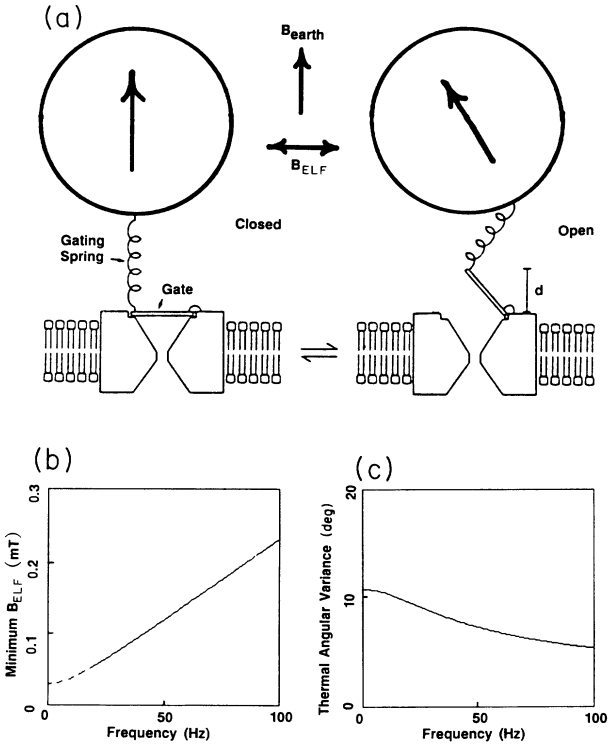

FIG. 1. A schematic diagram for how a magnetosome might act to open or close a mechanically sensitive *trans*-membrane ion channel, and order-of-magnitude estimates of the field levels required. (a) shows a magnetosome connected to an ion channel gate via a cytoskeletal filament (a gating spring), adapted from Howard and Hudspeth [41], but not drawn to scale as the magnetosome should be larger than shown. The geomagnetic field B_{earth} is perpendicular to the plane of the membrane, whereas the ELF component, $B_{\text{ELF}}\cos(\omega t)$, is parallel to it. As discussed in the text, rotation of the magnetosome in response to the oscillating external field should be capable of opening and closing the ion gate. (b) shows an order-of-magnitude estimate for the minimum fields to switch the gate as a function of frequency for a magnetosome of 0.1-μm radius in a fluid with a viscosity of 1 poise, and (c) shows the magnitude the rms angular deviation produced by Brownian motion; this is below the 16° needed to open the gate. This rms angular deviation decreases slightly with increasing frequency because the minimum value of B_{ELF}, shown in (b), increases. These calculations are made assuming that other cytoskeletal links prevent the magnetosome from drifting sideways while allowing it to rotate freely. Note also that this model should not apply at frequencies below about 10 Hz due to the phasic nature of mechanically sensitive ion channels and the elastic properties of membranes.

quency) necessary to open periodically the ionic gate. To be conservative, assume that the gate opens through the distance, d of 4 nm with an applied force, F, of 1 pN. To open the gate using a spherical magnetosome of radius, r, equal to 0.1 μm, this grain will need to rotate through an angle θ_{min} of $\arccos(1-d/r)$, or about 16°. A magnetosome of this size and shape will be a single magnetic domain [42]. Although somewhat larger than the *A magnetotacticum* particles considered by Adair [1], magnetite crystals of this size have been extracted from the human brain and other organisms [2,10,43].

Under most circumstances, a magnetosome in a fluid medium will be overdamped critically by viscous forces (e.g., the low Reynolds number intracellular environment described by Purcell [44]). Hence, inertial terms can be neglected, and the equation of motion is similar to that of a forced, over-damped torsional pendulum. In the situation shown in Fig. 1, the torque on the magnetosome from the cytoskeletal filament (the "gating spring" [41]) acts with the same $\sin(\theta)$ dependence as does the magnetic torque from the earth's field. The equation is then

$$C\dot{\theta}+(Fr+\mu B_{earth})\sin(\theta)=\mu B_{ELF}\cos(\theta)\cos(\omega t)\ , \qquad (1)$$

where C is the coefficient of rotational friction about the center of the magnetosome, θ is the angle between the static background field and the magnetic moment of the magnetosome, $\dot{\theta}$ is the angular velocity, μ is the total magnetic moment of the particle, ω is the frequency, and t denotes time. The magnetic moment for a magnetite particle of this radius is 2×10^{-15} A m^2. For a sphere of this size, the coefficient of rotational friction is given by $6\eta V$, where V is the volume and η is the viscosity of eukaryotic cellular protoplasm, which is about 100 times more than water [45]. The stochastic rotations produced by Brownian motion are not included here, as they act independently of the other forces; for our purposes we note that the angular variance of motion, $\langle\theta_{therm}\rangle^2$ is given by the thermal-to-magnetic energy ratio, $kT/\mu B_{total}$, and its rms value should be less than the 16° estimated above for opening the ionic channel gate.

Although Eq. (1) is a first-order equation, it does not have closed-form solutions for $\theta(t)$ due to the presence of the $\sin(\theta)$ and $\cos(\theta)$ terms, and the small angle approximation is not always appropriate in this situation. However, a close approximation can be found easily by the following approach. In the case where θ is small, $\sin(\theta)$ and $\cos(\theta)$ are approximately θ and 1, respectively. Equation (1) then becomes linear, and the solution for long times becomes

$$\theta(t)=\theta_{max}\cos(\omega t+E)\ , \qquad (2)$$

where

$$\theta_{max}=\frac{\mu B_{ELF}}{\sqrt{(rF+\mu B_{earth})^2+c^2\omega^2}} \qquad (3)$$

and E is a small phase delay. Although this works for small θ, if the value of B_{ELF} is much larger than B_{earth}, θ_{max} may become much larger than its maximum possible value of $\pi/2$. In the low-frequency limit where ω approaches zero, θ_{max} should reduce simply to the arctangent of B_{ELF}/B_{earth}, so it is reasonable to replace θ_{max} with $\mathrm{Arctan}(\theta_{max})$. This modification also works for low values of θ because $\mathrm{Arctan}(\theta)$ is also θ in this limit. Numerical approximations for Eq. (1) confirm that this modification gives the correct values for θ_{max} to within a few percent for a wide range of frequencies and field strengths.

Figure 1(b) shows the minimum values for B_{ELF} needed to make θ_{max} just equal to the 16° rotation for opening the ion gate as a function of frequency, and Fig. 1(c) shows the expected angular deviation of the particle produced by Brownian motion, $\langle\theta\rangle_{therm}$. At the powerline frequency of 60 Hz, the critical ELF field for opening the channel is 0.14 mT (1.4 G), and $\langle\theta\rangle_{therm}$ is well below 16°.

One obvious problem with the sketch model as shown is that a 90° rotation of the magnetic field would cause the gate to open permanently. Humans move around in the magnetic field and natural selection would have removed any harmful effect of such motion long ago. However, two factors should act to mitigate this at very low frequencies. First, mechanically sensitive *trans*-membrane ion channels are phasic, closing on their own with an exponential time constant of about 0.1 s after sudden onset of a unidirectional membrane stress [46]. Second, a small force on a biological membrane will cause it to deform, with a characteristic time constant also of about 0.1 s [47]. These effects may be related, as closure of the channels may be a result of membrane deformation relieving stress in the cytoskeleton. Hence, at frequencies below about 10 Hz there should be minimal effects of alternating fields of virtually any strength, as the ion channels and membranes have enough time to respond. At higher frequencies the membranes and channels should behave in the manner assumed in the model. Because humans do not typically spin themselves at 60 Hz in the geomagnetic field for extended periods of time, alternating fields of earth strength are not something which cells have been exposed to during most of the past 3.5 billion years of organic evolution.

Hence, in direct contradiction to the statements of Adair [1], it may indeed be possible for weak, ELF magnetic fields to produce biological effects at the cellular level through a nonsensory process. If sensory processes are involved which integrate over large numbers of magnetosomes, effects at lower-field strengths are possible [29]. Although the minimum threshold field levels required for this type of nonsensory effect at 60 Hz are well above the 0.3-μT (3-mG) levels inferred from some of the early epidemiological correlations between electric power wiring configurations and leukemia, those levels have not withstood subsequent replication attempts [37]. On the other hand, the studies of Savitz, John, and Kleckner [36] and London *et al.* [37] (and several others) show a consistent pattern of increased risk from the regular use of household electrical appliances, like electric blankets and hair dryers, which do expose users to fields of this strength [48]. Because the mechanically sensitive ion channels allow Ca^{2+} to pass easily when opened, and intracellular Ca^{2+} orchestrates many aspects of the cell-division process [49], the model outlined above could lead

plausibly to occasional chromosome nondisjunction and consequences of this sort [50].

In summary, there are very good reasons to believe that weak ELF fields can and do have significant biological effects at the cell level, and the process of magnetite biomineralization provides at least one viable mechanism through which such things can happen. The credibility of weak ELF magnetic effects on living systems must therefore stand or fall mainly on the merits and reproducibility of the biological or epidemiological experiments which suggest them, rather than on dogma about physical implausibility.

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