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Magnetoreception in microorganisms and fungi

Alexander Pazur[1*], Christine Schimek[2], Paul Galland[3†]

[1] *Department of Biology I*
Ludwig-Maximilian University München,
D-80638 München, Germany

[2] *Department of General Microbiology and Microbial Genetics*
Friedrich-Schiller-University Jena
D-07743 Jena, Germany

[3] *Faculty of Biology*
Philipps-University Marburg
D-35032 Marburg, Germany

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Abstract: The ability to respond to magnetic fields is ubiquitous among the five kingdoms of organisms. Apart from the mechanisms that are at work in bacterial magnetotaxis, none of the innumerable magnetobiological effects are as yet completely understood in terms of their underlying physical principles. Physical theories on magnetoreception, which draw on classical electrodynamics as well as on quantum electrodynamics, have greatly advanced during the past twenty years, and provide a basis for biological experimentation. This review places major emphasis on theories, and magnetobiological effects that occur in response to weak and moderate magnetic fields, and that are not related to magnetotaxis and magnetosomes. While knowledge relating to bacterial magnetotaxis has advanced considerably during the past 27 years, the biology of other magnetic effects has remained largely on a phenomenological level, a fact that is partly due to a lack of model organisms and model responses; and in great part also to the circumstance that the biological community at large takes little notice of the field, and in particular of the available physical theories. We review the known magnetobiological effects for bacteria, protists and fungi, and try to show how the variegated empirical material could be approached in the framework of the available physical models.

Keywords: magnetic field, magnetoreception, ion-cyclotron resonance, magnetosomes, quantum coherence, radical-pair mechanism, ecology, climate change

* E-mail: a.pazur@lrz.uni-muenchen.de
† E-mail: galland@staff.uni-marburg.de

Abbreviations

B	magnetic flux density (magnetic induction)
BAC	alternating magnetic field (generated by alternating current)
BDC	static magnetic field (generated by directed current)
CD	coherent domain
ELF	extremely low frequency (i.e. magnetic field, ∼3-300 Hz)
EMF	electromagnetic field
H	magnetic field strength
IIM	ion interference mechanism
ISC	intersystem crossing
ICR	ion cyclotron resonance
IPR	ion parametric resonance
LF	low frequency (i.e. magnetic field)
MF	magnetic field

1 Introduction

The earliest studies on the influence of electromagnetism on organisms date back to the late 19^{th} century, probably beginning in St. Petersburg [1]. A larger, more general interest arose only some decades later, coinciding with worldwide electrification and telecommunication. Although microorganisms play a major role in the global ecosystem, the number of publications covering magnetoreception in fungi, protists and non-magnetotactic bacteria is small compared to similar reports on humans and animals [1–6]; and is perhaps comparable to the state of knowledge in plants [7]. The magnetoorientation of magnetotactic bacteria [8], as well as that of migrating birds and insects, belongs to the best understood and most intensely studied phenomena of magnetoreception [6, 9, 10]. Recently Ritz *et al.* [11, 12] suggested a light-driven, radical-pair mechanism for the magnetoreception of birds mediated by cryptochrome [13, 14]. There is evidence that even plant cryptochromes are involved in the magnetoreception of *Arabidopsis* [15]. Bacterial magnetotaxis is based on the magnetoorientation of magnetite crystals; thus representing the only magnetoreception mechanism completely elucidated up to now [8, 16–18].

The two central questions in this context: (i) whether or not microorganisms are able to perceive geomagnetic fields, and (ii) whether or not magnetoreception is an essential and vital environmental factor for survival, have remained largely unanswered, even though magnetoreception must be regarded as an established fact. Furthermore, we contend that the recent discussion regarding the mechanisms of climate change and global warming should consider other, non-anthropogenic contributions, e.g. the altered gas exchange of microorganisms as a consequence of the steadily changing geomagnetic field.

Despite the numerous magnetobiological effects that have been described in the pertinent literature, there is an apparent lack of model organisms, model responses and genetic approaches; tools that are typical for modern research strategies commonly found

in other biological fields. The problem is compounded by the fact that magnetic effects are observed for a huge range of magnetic flux densities, which cover more than 10 orders of magnitude. To come to grips with such a huge dynamic range, that is similar to that of human vision, one would expect the study of dose-response relationships to be of paramount importance. It thus comes as a surprise that there exists only one dose-response curve for a biomagnetic effect in DC fields [19], and only a limited number of dose-response studies for AC-fields. Despite the limited information it is nevertheless apparent that magnetobiological dose-response relationships differ drastically from the ones usually found in physiology, where one typically finds exponential rise or decay curves, and in some cases optimum curves. Magnetoresponses, in contrast, show certain "windows" of magnetic flux densities, or, in the case of AC-fields, windows of frequencies for which a response is obtained. Applying a higher field strength may thus not necessarily guarantee a stronger response. As a consequence, some of the apparent contradictory results in the magnetism literature could be explained by the fact that different authors often used different magnetic flux densities that were within or outside these windows.

Research on biological magnetoresponses can be roughly divided into experiments that employ static magnetic fields (B_{DC}), or alternating fields (B_{AC}), or as in most cases, a combination of both (B_{AC}+ B_{DC}). The body of literature on AC fields and their concomitant effects dominates by far that of DC fields. This appears surprising in view of the fact that DC experiment is required to find out how geomagnetic fields influence life.

Most experiments with AC fields are done with frequencies near 50 or 60 Hz, i.e. frequencies akin to that of ubiquitous electric appliances. Much of this type of research was historically motivated by the wish to find out whether or not our electric environment influences life, and specifically, human health. Even though this line of research may not directly contribute to the understanding of how static geomagnetic fields influence life, it nevertheless represents a powerful technical tool to investigate the involvement of specific ions in a given biomagnetic response. It had earlier been noticed that AC fields elicit responses most prominently at the cyclotron resonance frequencies (including their harmonics and subharmonics) of biologically important ions, in particular Ca^{2+}. This pattern gives rise to dose-response curves with several minima and maxima. Therefore it is not difficult to understand why explaining this type of dose-response relationship is the subject of several theories (ion-cyclotron resonance, ion-parametric resonance, ion-interference mechanism, coherence mechanism; see below).

One of the reasons that magnetobiological responses frequently meet with reservations is based on the fact that the energy content of biologically actinic magnetic fields can be several orders of magnitude below their thermal energy content (kT problem). We will show how the problem can be addressed within the framework of modern theories. Also the hunt for "the" magnetoreceptor remains presently an unresolved task (with the exception of magnetite in bacterial magnetotaxis, see below). As function of fact, it is contested as to whether or not there exists only one type of magnetoreceptor; the requisite literature rather indicates that in prokaryotic and eukaryotic cells several

magnetosensitive molecules, and physically distinct mechanisms, exist that could mediate magnetoreception. Because cell membranes do not constitute barriers for magnetic fields, magnetoreception could in theory occur on many different levels. For example, DNA itself, and the transcription and translation machineries, have been proposed as targets. It is thus noteworthy that even cell-free systems of protein biosynthesis are receptive to magnetic fields (see below).

2 Magnetic effects on solutes

Magnetic fields can affect organisms not only directly, but also indirectly, by changing the physical properties of solutes and growth media. For example, a 1 minute magnetic pretreatment of culture media stimulated the subsequent growth of Escherichia coli in a geomagnetic field [20]. Magnetically treated water inhibits the germination of the microfungus *Alternaria alternata* [21], and treatment of nutritional media affects the subsequent growth of *Saccharomyces fragilis*, *Brevibacterium* and *Bacillus mucilaginosus* [22]. Such effects are possible because magnetic treatments alters solutes, for example the formation of calcium carbonate [23], water vaporization [24], ion hydration and resin absorption [25]. Indeed effects on Ca^{2+} hydration after short treatment with a weak magnetic field or pulses, applicable, for example, to organismal growth stimulation, is reported by Goldsworthy *et al.* [26]. As these effects were usually achieved with very strong magnetic fields in the mT to T range, they may not be pertinent for experiments done in very weak or geomagnetic fields.

3 Bacterial magnetotaxis

3.1 Magnetosomes and their role in magnetoreception

Apart from the general effects of all types of magnetic fields on growth and morphogenesis, some organisms have succeeded in employing the directional qualities of magnetic fields for orientation purposes. Animals using geomagnetic fields for navigation are either long-distance travellers, such as migratory birds, whales, sharks, turtles and butterflies, or depend for other reasons on the ability for exact orientation, e.g. honeybees. Clearly, microorgansims do not fall into a category where magnetoorientation would be expected. Nonetheless this behaviour, known as magnetotaxis, is the best studied of the magnetoresponses [27–29]. This reaction has been globally observed in a number of marine [30, 31] and freshwater bacteria [32–34], as well as in several types of unicellular eukaryotic microorganisms. The latter are rarely observed, probably because they are easily overlooked in samples teeming with bacteria. Due to their overall high fragility and sensitivity, eukaryotic laboratory strains usable for detailed analyses have not yet been established; yet the occurrence of magnetoperception in eukaryotes may be rather widely distributed, as magnetotactic species have been detected in a number of major groups, such as dinoflagellates, ciliates, cryptophytes [35, 36].

3.2 Magnetotactic microorganisms

Research into magnetoresponsive prokaryotes began with the discovery that certain bacteria consistently preferred one geomagnetic pole over the other, and therefore always swam to the same side of a water droplet on microscopic slides [16]. Magnetotaxis, although biased for fast-swimming organisms, provided a handy tool for the isolation of several similar species [4, 37–39, 41–45]; and moreover also allows for the enrichment and studies of unculturable strains and communities [46, 47]. Magnetotactic bacteria are flagellated chemolithoautotrophs exhibiting various morphotypes; to date cocci, spirilla, rod-shaped, and vibroid or helical forms have been described [47, 48]. They inhabit the oxygen-anoxygen transition zone of marine or freshwater sediments or chemically stratified water columns, where they occasionally occur in high cell densities [31, 49] and are either obligate anaerobes [30, 45] or facultatively anaerobic microaerophils [50–53]. Although likely to be of polyphyletic origin [54], most of the characterized morphotypes have been grouped into the Proteobacteria, with a distinct subcluster present in its alpha subgroup [32, 42, 46, 55, 56] (Table 1). Genome data are available from *Magnetospirillum magnetotacticum* MS-1 (GenBank accession AAAP00000000, *Magnetospirillum gryphiswaldense* MSR-1A [57]; GenBank acc. BX571797) and *Magnetospirillum magneticum* AMB-1 (GenBank acc. AP007626). Highly organized aggregates of magnetotactic cells have also been described from a variety of other locations [28, 58–61].

3.3 Magnetotaxis

Magnetotaxis is defined as movement parallel to the field lines of an external magnetic field. Nevertheless it is not a taxis in the strictest sense as the organisms are not following the direction of the magnetic field itself, but rather ultilize the directional information to support other orientation mechanisms. It was generally assumed that they navigate along the inclination of the magnetic field lines to locate a suitable environment within an oxygen (magneto-aerotaxis), or other chemical, gradient; thus reducing search movement in turbid surroundings to just one dimension - up and down [62]. The key benefit of magnetotaxis in this process is the enhancement of the bacterium's ability to detect oxygen, not an increase in average speed of reaction [29]. Movement along a straight path allows for earlier detection of an existing oxigen gradient, and thus enhances the flight from oxygen. One study suggests a role for magnetosome formation in mediating the response to gravity, as magnetosomes and magnetotaxis were shown to be completely absent in prolonged microgravity [63]. In magnetotaxis, polar and axial magnetotactic strains can be discriminated between. Bipolar flagellated cells display axial behavior by swimming back and forth within a local applied magnetic field. In polar magnetotaxis, the cells follow a preferential direction and swim away when the local field is reversed [64]. This classification apparently results from cellular morphology, and has no impact on orientation efficiencies in natural environments. The observation that polar magnetotactic cells in the southern hemisphere predominantly exhibited a south-seeking behavior in

laboratory tests was taken as support for the importance of the magnetic field line for magnetotaxis [65]. The recent discovery of seasonally occurring, predominantly south-seeking polar bacteria, in populations from the northern hemisphere call this explanation into question. Instead, the oxidation-reduction potential at any given position of a water column seems to influence the polarity of movement [31, 49].

3.4 Magnetosomes

All magnetotactic cells contain magnetosomes. These organelles consist of a ferrimagnetic crystal surrounded by a specialized membrane. In prokaryotes, the magnetosome crystals result from the controlled biomineralization of either magnetite (Fe_3O_4), or greigite (Fe_3S_4) [66–69]. Additionally one single strain has been found that contains iron pyrite (FeS_2) [67]. A few morphotypes mineralize magnetite and greigite within the same cell, and even within the same crystal aggregate [70, 71].

In both magnetite and greigite, crystal structures follow the spinel type, consisting of two interlocking grid systems with different numbers of grid coordinates (nodes). Magnetite, as well as greigite, contains a mixture of two- and three-valent iron, with each form occupying specific nodes. This leads to the complete extinction of the atomic magnetic dipol moments of Fe^{3+}. The magnetic properties, therefore, are solely attributed to Fe^{2+}. Each morphotype is usually associated with a particular crystalline habit of magnetite, whereas greigite crystals of different shapes may occur simultaneously [48, 72–74]. Cuboid, bullet-, tooth- and drop-shaped crystals have been described [45, 73, 75, 76].

Besides eukaryotic microorganisms, magnetite crystals that are similar in appearance and structure to those of bacteria were also found in animal cells [77]; however no information exists on their origin and biosynthesis. Ferrimagnetic crystals interact in excess of a million times more strongly with magnetic fields than do diamagnetic or paramagnetic materials. If a ferrimagnetic nanocrystal were fixed to an ion channel - an assumption that has not been verified yet - it would generate torque in a weak geomagnetic field that would suffice to alter ion movement across a membrane. Such considerations show that magnetites hold, at least in theory, the potential to directly influence ion transport [77]. It has also been pointed out that trace amounts of magnetite may be ubiquitous, and that a single 100-nm magnetite crystal, exposed to a 60 Hz, 0.1 mT magnetic field, could absorb sufficient energy to supersede several times the thermal background noise [78]. Magnetite particles can have dramatic effects on the dynamics of photogenerated free radicals [79]. It is thus pertinent to reckon with a modulating effect of magnetites if present, particularly in context of the radical pair mechanism (see below).

Fossil records of magnetosome crystals date back to the Precambrian time; while similar crystals have been detected in 4 billion year-old carbonate blebs of martian meteorite fragments [80–82]. Although controversely discussed [83, 84], it appears possible that the martian magnetites are of a biogenic origin. This would also imply that these martian minerals constitute the oldest fossils on Earth, and at the same time provide evidence for the possibility of panspermia [85].

The number of magnetosomes within a single cell ranges from a few large structures in cryptophyte cells [35] to several hundred [73, 86], with $10 - 20$ the average number in magnetotactic spirilla [8, 16, 72]. Crystal sizes range from 35 to 200 nm, which indicates their single-domain status [86–88]. The size of a magnetic domain depends on the material, and can be roughly calculated. According to such estimations, a domain of magnetite corresponds to a size between 35 and 75 nm, and in elongated crystals up to 120 nm [89–91]. As single domain crystals, the magnetosome cystals are especially susceptible to efficient magnetization and alignment, and they produce stable magnetic fields. Exceptions have been published by Farina *et al.* [92] and Spring *et al.* [56], who demonstrated that at least two strains isolated from the Itaipu lagoon in Brazil contained magnetosomes with dimensions up to, and even exceeding, 200 nm, a size that could easily harbour two magnetic domains. In such large crystals a metastable, single-domain state is only possible when the crystals are aligned within a chain [93]. The extracellular formation of single-domain magnetite for biotechnological applications has also been performed by a biologically-induced, biomineralization process of non-magnetotactic bacteria [94, 95]; and by the aerobic fungi *Fusarium oxysporum* and *Verticillium* sp. [96].

3.5 Magnetosome organization and synthesis

In some morphotypes magnetosomes form loose aggregates within the cell [60, 97], however in the majority of strains studied they are arranged in one or more chains spanning the cytoplasm. The magnetosomes within a given chain are separated by a gap containing no particulate structures, as observed in transmission electron micrographs [98]. In *Magnetospirillum* species, the single magnetosome chain is usually located close to the inner membrane [98, 99]. The combination of disposition in chains, and size control, results in a high magnetic to thermal energy ratio. The total magnetic moment of a magnetosome chain equals the sum of the individual particle moments [100], and substantially surpasses thermal noise [73, 101].

Organization into chains implicates the crystals in magnetizing each other, and aligning their magnetic dipole moments with each other. These processes start at synthesis, thus each newly formed magnetosome crystal is influenced by the pre-existing chain. Biologically controlled biomineralization is a highly precise process, and is necessarily subject to very exacting control. Therefore the organism first creates a matrix, delimiting the space within which the mineral will grow. The form and size of the nascent crystals depend on the interactions between organic and inorganic phases, and are influenced by parameters such as pH, redox conditions, ionic strength, lattice geometry, polarity, stereochemistry and topography. The biomineralization of greigite is less well studied than that of magnetite. It seems to be less organized, and to require considerably more time [102]. Similar to magnetite biomineralization, it requires several mineralization steps, leading from the non-magnetic precursors, mackinawite and cubis FeS [103], to the final product over a transition period of several days or weeks. During this latter period, iron atoms

are rearranged between adjacent sulfur layers, and some of the iron is lost and likely deposited as amorphous iron oxide aggregates.

The processes leading towards the formation of magnetite have been reviewed by Schüler [64, 72, 76, 104–106]. At the onset, a low oxygen potential is likely to be a regulatory signal for metabolic induction of biomineralization, as in *Magnetospirillum gryphiswaldense, M. magnetotacticum* and *Magnetospirillum sp.* AMB-1. Thus biomineralization only occurs at pO_2 values below a threshold of 20 mbar [107]. Biomineralization occurs inside a specialized organella, the magnetosome, providing a scaffold organized by membrane proteins which ensures the spatial and temporal accuracy of the process. The scaffold need not be proteinaceous: it can also be thought of as a matrix of amporphous mineral precursors [108]. Indeed amorphous iron oxide has been found to form a layer surrounding maturing crystal [102]. Magnetosomes are enmeshed in a network of cytoskeletal filaments [99], and provides a surrounding for the precise coordination of events involved in magnetite biomineralization [109]. The whole complex consists of several structural entities: the magnetite crystal, magnetosome membrane, surrounding matrix, and, as described for *Magnetospirillum magnetotacticum* MS-1, an interparticle connection [110]. It has been assumed that magnetosomes are invaginations of the cell membrane; indeed proteins probably involved in such an invagination process have in fact been identified in the magnetosome membrane [111]. Recently electron cryotomography revealed that the membrane surrounding magnetite crystals is continuous with the inner membrane [99]. Nevertheless, some questions remain. The process of iron acquisition and biomineralization would require a closed compartment. Also, in the electron cryotomography picture series, the connection of magnetosomes with the inner membrane was only visible for the innermost structures; the largest magnetosomes seemingly already contained finished crystals. The small, incomplete magnetosomes at the chain ends were completely inside the cytoplasm, with no apparent contact with the inner membrane. Moreover, the lipid and protein composition of the magnetosome membrane differed from all of the other membrane systems of the cell [112]. If it really does originates from the inner membrane, then it is at the very least least subject to extensive modifications. The hitherto identified proteins are apparently involved in iron import, iron conversion and in magnetite synthesis [57, 113, 114].

These membrane vesicles precede magnetite biomineralization and may exist independently [109]. When cells grown under iron limitation are changed to iron sufficiency, biomineralization occurs simultaneously in many pre-formed vesicles, and from the same location within each vesicle. In cells with sufficient iron supply, new magnetite crystals are formed in vesicles at the end of the fully developed magnetosome chain [109]. Usually, the magnetosome chain is distributed to daugther cells at the point of cell division, and during cellular growth. However complete *de novo* synthesis is also possible [71].

As a prerequisite for biomineralization, iron needs to be imported into the cell. This is a very fast process, for example in iron depleted cells of *Magnetospirillum sp.* AMB-1 iron uptake is complete within 10 minutes [115], and in *Magnetospirillum gryphiswaldense* an increase in magnetite measured as intracellular insoluble iron can also be found within

10 minutes [116]. Indeed a recent microarray analysis of iron-inducible genes demonstrated the up-regulation of Fe^{2+} transporters in iron-rich conditions [115].

Soluble Fe(II) may be taken up by the cells by unspecific mechanisms. In these cells, Fe^{2+} was found asssociated with the cell envelope, whereas the free Fe^{3+} was associated with the magnetosomes [117]. Other strains use Fe(III), and require more complicated translocation systems. Magnetospirillum magnetotacticum, which has an iron content approaching 2% of its total dry weight, incorporates iron as Fe^{3+} [37] using a siderophore transport system [118]. A ferric iron reductase was purified and characterized by Noguchi *et al.* [119] and may well be involved in the subsequent periplasmatic reduction of Fe^{3+}. Iron oxidation in Magnetospirillum magnetotacticum MS-1 is an aerobic respiratory process, and is also necessary for magnetite synthesis [120]. In a generalized scheme, Fe(III) becomes reduced upon entering the cell. The resulting Fe(II) is then incorporated into empty magnetosome vesicles, already possessed of its specific protein components. Inside the magnetosome Fe(II) becomes oxidized again. From this process hydratized Fe(III)-oxides result, which are dehydratized step by step. Just before the last dehydration step, at the final position within the crystal, one third of all of the Fe(III) is reduced again to form Fe(II). The final dehydration step then leads to the product, magnetite [121].

The magnetosome is connected via a membrane protein to the cytoskeleton, and is thus fixed at a distinct postion within the cell [99, 122]. The chain results from the magnetosomes being attached to filaments of the actin homologon, MamK [99, 122]. This close contact between magnetosomes and the cell membrane may provide additional stability to the chain [123].

The genes encoding proteins of the magnetosome membrane, or those otherwise involved in magnetosome formation, are concentrated in several clusters [124–126]. Within the magnetotoactic bacteria, the homology of individual genes is high, and their positions within clusters are well conserved. Some of the genes have been identified and are comprised of several that would encode proteins with protein-protein interaction domains, e.g. tetratricopepetide-repeat-proteins. Thus protein complexes may be necessary for events in the biomineralization process.

Other groups encompass genes specifying proteins involved in: metal transport, other forms of transport, and those for protein processing, e.g. chaperones or specific proteases. Within these clusters the gene for the actin homolog is also present. The magnetosome gene clusters are themselves concentrated on a genomic island, a region of about 130 kb existing exclusively in magnetotactic bacteria. Deletion of this region leads to the complete loss of magnetosomes and magnetotaxis [57, 124, 126]; yet curiously the functional magnetosome island alone is insufficient for magnetosome formation. Thus orthologs present outside of this discrete genetic island are also necessary for this process [126]. Within this region, a conspicuous number of insertion elements, transposases, integrases and other phage - associated genes abounds [124]. This accumulation, and the high and retained homology between different strains, hints at the probability that the magnetosome gene island was acquired via phage-mediated, horizontal gene transfer. The region

was also found to be hypervariable, as spontaneous mutations displaying various phenotypes often occur, especially during stationary growth.

Within the magnetosome chains, the individual units attract each other via their immanent magnetic forces. This implies that their opposite magnetic poles are facing each other, and thus their magnetic dipole moments are mutually enhancing each other. Chain formation is influenced by the shape of the crystals, with rigid chains more easily maintained by cubic shapes, as compared to tear-shaped magnetite [123]. In fact, a chain of magnetosomes corresponds to an equivalently sized bar magnet spanning the whole cell which generates a permanent magnetic dipole moment [100]. The magnetic field within a magnetite crystal chain can even be visualized using modern electron microscopical techniques [91, 127].

The crystal chain is rigid within the cell, and is fixed in position. As a bar magnet, the magnetic moment is sufficiently large to align with the geomagnetic field. The cell is drawn with the magnetosome chain, and thus becomes aligned passively and parallel to geomagnetic field lines [100]. This phenomenon also occurs with dead cells, although only living ones may move along magnetic field lines. Passive attraction to a magnetic pole is also possible [128].

4 Zero and weak magnetic fields

To asses the role of magnetic fields in nature, one depends on investigations done at geomagnetic field strengths (75 μT at the poles - 25 μT at the equator), and, in addition, also under conditions without a magnetic field (zero field = magnetic vacuum). Apart from studies on bacterial magnetotaxis, such investigations are, however, extremely rare; and it remains largely unknown what role geomagnetic fields plays in nature.

Weak static MFs ($0 - 110$ μT) affect the "anomalous viscosity time dependence" of *E. coli*, a parameter that reflects the status of DNA-protein complexes [19]. Interestingly, dose-response curves for this effect show several minima and maxima. These observations were explained using the framework of the ion interference mechanism, and were linked to the dissociation of ion-protein complexes that rotate at a speed of about 18 revolutions per second. The authors believe that the carrier for the rotating, ion-protein complexes is DNA [19]. *E. coli, Pseudomonas* and *Enterobacter* display, in a zero-magnetic field, modified resistance to various antibiotics [129, 130]. Surprisingly, even the extremely low magnetic flux densities generated by the human body can affect bacteria, because *E. coli* and *Staphylococcus aureus* have altered functional activities [131]. For fungi and protists no studies on the effect of zero magnetic fields are presently available.

Geomagnetic storms can lead to a small increase in geomagnetic fields by some $1-5\%$. This increase seems to be sufficient to prolong the photobioluminescence of *Photobacterium* [132]. In the slime mold, *Physarum polycephalum*, a weak field of 100 μT elicits a mitotic delay, and decrease of respiration [133]. At a magnetic flux density of 100 μT, the growth of the phytopathogenic fungi, *Alternaria alternata, Curvularia inaequalis* and

Fusarium oxysporum, decreased by some 10%. At the same time the MF caused an increase of conidia formation in *A. alternata* and *C. inaequalis* by some 68 – 133% [134].

5 Effects on growth and cell division

5.1 DC-fields

Very strong magnetic fields (5.2 – 6.1 T) are able to delay cell death in stationary cultures of *Bacillus subtilis* [135]. A field of 14.1 T had, however, no substantial effect on the growth of *Shewanella oneidensis*, even though several genes were up- or down-regulated [136]. The latter result shows that growth can be highly inappropriate for evaluating the magnetosensitivity of an organism.

Moderate static magnetic fields (0.1 – 1 mT) stimulated, both in liquid and solid media, the growth and metabolism of *Pseudomanas fluorescens, Staphylococcus albus* and *Aspergillus niger* [137]. In contrast, three species of *Acanthamoeba* responded with a growth decrease at modest static fields of 71 and 106 mT [138]. A weak static field (400 μT, i.e. about 8 times the geomagnetic field) elicits, in *Saccharomyces cerevisiae*, a 30% inhibition of bud formation [139]. Colonial growth of *Alternaria alternata* and *Curvularia inaequalis* decreased by a mere 10% during exposure to weak magnetic fields between 0.1 and 1 mT [140]. An inhibition of growth was reported for *Anabaena doliolum* for a moderate DC field of 300 mT [141].

5.2 AC-fields

Numerous investigators have reported magnetic effects on development of bacteria, which includes an increase in mass and / or cell division. *Escherichia coli*, for example, when exposed to an AC field (0–22 mT, 16 and 50 Hz), shows a shortened generation time [142]. The dose-response relationships for this effect were complex, they occurred only at certain flux densities between 0 and 22 mT. AC fields (0.8, 2.5 mT, 0.8 and 1 kHz) and increased the growth of *Bacillus subtilis*, as it caused a growth increase and interestingly also a loss of intercellular cohesion, which is characteristic for cells raised in a geomagnetic field [143].

Whether or not an AC magnetic field exerts an inhibitory or else a stimulatory mode of action depends in a complex manner on the frequency and the field strength. For example, Moore [144] observed elevated or even diminished growth rates for *Bacillus subtilis, Candida albicans, Halobacterium, Salmonella typhimurium,* and *Staphylococci* in dependence of AC frequencies ranging from 0 - 0.3 Hz and magnetic flux densities of 5 – 90 mT. In contrast, magnetic square wave signals (0.05 – 1 mT, 50 Hz) had no effect on the growth of *E. coli* [145]. The viability of *Escherichia coli, Leclercia adecarboxylata* and *Staphylococcus aureus* was negatively affected by prolonged exposures to AC fields of 10 mT, 50 Hz) [146].

In *Paramecium tetraurelia*, AC fields (1.8 mT, 72 Hz) caused increased cell division rates, a response that was Ca^{2+} specific, and absent in the presence of a Ca^{2+} blocker.

The magnetic treatment also caused alterations in membrane fluidity [147]. *Physarum polycephalum* responds to weak AC fields (0.2 mT, 60, 75 Hz) with a delay in its mitotic cycle [133, 148], exhibited by an increased mitotic cycle length at 0.2 mT and 75 Hz [149–151].

The mechanism for magnetotactic effects at ELF-frequencies (e.g. 50, 60, or 75 Hz) is not completely clear, however energy conversion to heat can likely be ruled out because of the low induction of living matter. Conversely higher frequency, long wave band fields (160 mT, 62 kHz) are in fact lethal for *E. coli* [152]. After an exposure time of 16 h only a small fraction (10^{-4} organisms) survive. Under these conditions, the dissipation to heat is likely not to be increasingly negligible, and, in general, these results are not comparable with findings for the ELF band in any case.

6 Effects on DNA: mutagenicity, repair, transposition

Weak, static magnetic fields ($0-110\ \mu$T) affect DNA-protein conformations in *E. coli* [19]. This analysis represents the only dose-response curve for a static magnetic field. The peculiarity of this curve stems from the fact that it has three prominent maxima, a feature that makes it very different from other dose-response curves in nature that often follow rising or decaying exponential functions. The shape of this curve is explained in the context of the ion interference mechanism [19].

AC fields (14.6 mT, 60 Hz) have been shown not to cause DNA breaks in a *Salmonella* test system [153]. Various strains of *Escherichia coli*, including DNA-repair mutants, showed no evidence of increased DNA damage when exposed to very strong magnetic fields (0.5 and 3 T) [154].

The transposition frequency of Tn10 in *E. coli* is enhanced by pulsed, square-wave AC fields [145], but is diminished by sinusoidal AC fields [155]. Increased transposition activity was also obtained for Tn5, after the exposure of *E. coli* to AC magnetic fields (1.2 mT, 50 Hz). Concomitantly, DNA repair was enhanced [156], an event that was seemingly mediated by the overexpression of DnaK/J [157].

AC fields (0.2 mT, 60 Hz) can increase in *Salmonella typhimurium*, azide-induced revertants [158]. The enhanced DNA repair of hydroxylamine-mutagenized plasmid pUC8 occurred in *E. coli* in AC magnetic fields ($0 - 1.2$ mT, 50 Hz) via the induction of heat-shock proteins Hsp 70 and Hsp 40 (DnaK and DnaJ) [156]. Since it is known that DnaK can upregulate UvrA, it is understandable that magnetic field stress causes improved DNA repair. An AC magnetic field also (120 μT, 50 Hz) caused a reduction in the survival of *Saccharomyces cerevisiae* after UV irradiation, whilst sustaining no effect on cell cycle kinetics [159].

Most of the effects listed in Tables 2–5 are generally modest, i.e. often amounting to a response of some 10% to maximally 50%. A notable exception is the response of *E. coli* to strong unhomogenous fields ($5.2 - 6.1$ T); in the presence of glutamic acid, stationary phase cells display up to a 100,000 times survival elevation in comparison to cells maintained in the geomagnetic field. Concurrently, strong fields also cause an

increase in expression of the sigma factor, Sigma S (*rpoS*) [160]. As glutamic acid causes cell death in stationary phase, it appears likely that the magnetic field is modulating glutamic acid metabolizing enzymes.

7 Effects on gene expression: transcription and translation

AC MFs of moderate flux density ($200 - 660$ μT, 50 Hz) alter the transcription rate of the lac operon in *E. coli* [161]. Sharp "amplitude windows" are observed for this effect, which are a hint on a non-linear dose dependence. Furthermore while a field strength of 300 μT suppresses transcription, a field strength of 550 μT results in a substantial increase. These antagonistic interactions have been attributed to the involvement of different ions, i.e. Ca^{2+} and Mg^{2+} competing for protein-binding sites [162, 163].

AC magnetic fields can induce specific sets of genes. In *E. coli* an increase in σ^{32} mRNA (transcription factor) was found for 1.1 mT and 60 Hz [164]. Pulsed square fields (1.5 mT) elicit an increase in the α subunit of RNA polymerase, and also NusA, in *E. coli*. The protein biosynthesis was studied by gel electrophoresis. Thirty proteins were identified, which were up- or down- regulated by approximately a factor of two [165]. An important observation in this context is the fact that AC fields can enhance translation, even in an *in vitro* system [166]. This shows that the translation machinery itself must be magnetosensitive, and is not, for example, dependent on the existance of a biomembrane. Investigations using HeLa cells, though of human origin, generated data that was highly pertinent to the problem of magnetically induced gene expression. Lin *et al.* [167] were able to show that weak, alternating, magnetic fields (8 and 80 μT, 60 Hz) increased the transcription of mouse or human c-*myc* genes. This effect was dependent on the presence of specific electromagnetic response elements located between -353 and -1257 bp relative to the promoter [168]. Similar response elements were also detected in the promoter region of the heat shock gene *hsp70* [169].

Strong magnetic fields (14.1 T) caused the transcriptional up-regulation of 21 genes, and the down-regulation of 44 genes, in *Shewanella oneidensis*; while at the same time causing no substantial alterations in growth [136]. No alteration in the profile of stress proteins occurred after exposing *E. coli* to AC fields ($7.8 - 14$ mT, $5 - 100$ Hz) [170]. Furthermore, no changes in differential gene expression (microarray analysis) or protein profile (2-D gel analysis) were obtained with *Saccharomyces cerevisiae* exposed to AC magnetic fields ($10 - 300$ mT, 50 Hz) [171].

In the photosynthetic bacterium, *Rhodobacter sphaeroides*, magnetic fields of $0.13 - 0.3$ T induced a 5-fold increase in porphyrin synthesis, and enhanced expression of the enzyme 5-aminolevulinic acid dehydratase, which may be caused by elevated gene expression [172]. AC MFs can modulate the activity of enolase in *E. coli*; at 16 Hz a stimulation is observed, while at 60 Hz a suppression of enolase activity occurs [173]. Propionylcholinesterase activity in the amoebae *Dictyostelium* was lowered upon exposure to an AC magnetic field of 200 μT and 50 Hz [174]; while at the same time the fission rate was reduced. This magnetoresponse was, interestingly, adaptive, as it dis-

appeared after a 24-h, lasting exposure. Very strong DC fields (0.13 – 0.3 T) induce, in *Rhodobacter sphaeroides*, an increase of 5-aminolevulinic acid dehydratase concentration predominantly at the magnetic North pole, an effect that was paralleled by increased porphyrin production [172].

8 Effects on enzyme activity

The fact that MFs can modulate enzyme activities *in vitro* is a crucial observation, because it indicates that enzymes may function as magnetoreceptors. Even though several of the studies listed in Table 6 used enzymes derived from animals or plants, they nevertheless show that enzymes have the potential to function as magnetoreceptors. For example, a static MF of 20 μT alters the *in vitro* activity of Ca^{2+}/calmodulin-dependent cyclic nucleotide phosphodiesterase in a Ca^{2+}-dependent manner. This effect shows that the earth's magnetic field could be biologically relevant in calcium-dependent reactions [175]. Weak MFs ranging from 0−200 μT modulate the phosphorylation rate of the 20 kDa light chain of myosin by affecting Ca^{2+}/calmodulin-dependent myosin light chain kinase [176–179], an observation that remains, however, unconfirmed by other researchers [180]. A moderate increase or decrease in the geomagnetic field modulates, *in vivo* and *in vitro*, the activity of hydroxyindole-O-methyltransferase (HIOMT, EC 2.1.1.4) and N-acetylserotonin transferase (NAT, EC 2.3.1.5); two key enzymes in the biosynthesis of melatonin in the pineal gland and retina [181]. A 50% increase or decrease in the geomagnetic field strength caused a decrease of HIOMT activity. NAT responded differently in that a 50% increase in magnetic field increased activity in the pineal organ, but not in the retina. The enzyme was unresponsive to a decrease in field strength. These observations are particularly pertinent in view of a series of investigations on the effects of static and alternating magnetic fields on human and animal behaviour, and melatonin synthesis. Numerous studies have shown that magnetic fields can substantially alter circadian melatonin levels [182–185]. One such example is the brook trout (*Salvelinus fontinalis*), in which AC-fields (40 mT, 1 Hz) elicit an increased night-time, pineal and serum melatonin levels [186]. In pigeons the activity of the melatonin-synthesizing enzyme NAT was substantially reduced in the pineal glands of pigeons exposed, for 30 min at midnight, to a 50 degree rotation in the horizontal component of the earth's magnetic field [187].

The threshold for stimulation of the Na, K-ATPase by electromagnetic fields is extremely low, i.e. 0.2 - 0.3 μT [188], a value close to the threshold for transcriptional stimulation in human cell cultures [189].

Strong MFs (6 T, uniform field) reduced the activity of L-glutamic dehydrogenase by some 10%, whilst in a non-uniform field of 7 T it was reduced up to 93% [190]. Catalase was similarly modulated by strong magnetic fields [190]. The activity of carboxydismutase from spinach chloroplasts exposed to a strong magnetic field of 2 T was substantially enhanced [191]. The activities of trypsin [192] and ornithine decarboxylase [193] can be enhanced in strong magnetic fields. Weak and moderate, static and alternating, magnetic fields (50 Hz) influence the redox activity of cytochrome-C oxidase [194]. *Triticum*

responds to treatment with 30 mT (50 Hz) with increased esterase activity and proton extrusion [195]. The activity of horseradish peroxydase (1 mT, 50 – 400 Hz) depends substantially on the frequency of the applied magnetic field [196].

9 Effects on metabolism

AC fields (14.6 mT, 60 Hz) can provide protection for *Salmonella typhimurium* from heat stress [153]. This observation is particularly interesting in view of the fact that magnetic field exposure can induce the heatshock protein HSP70 in *Drosophila* [197].

Magnetic fields can exert substantial effects on the metabolic rates of organisms. For example, *Saccharomyces cerevisiae*, when exposed to an AC field (0.5 μT, 100 – 200 Hz), responded with a 30% reduction in respiration [198]. *Corynebacterium glutamicum* increases ATP levels by about 30% in an AC field (4.9 mT, 50 Hz) [199]. In the cyanobacterium, *Spirulina platensis*, a DC field of moderate strength (10 mT) enhanced growth, O_2 evolution, and pigment synthesis; at 70 mT however, a repression, rather than stimulation, was observed [200]. AC fields (0.1 mT, 60 Hz) caused lower ATP levels in *Physarum polycephalum*, but no decreased respiration [201]. Reduced respiration was, however, found with 0.2 mT and 60 and 75 Hz [133]. *Tetrahymena pyriformis* responds to an AC field (10 mT, 60 Hz) with delayed cell division and increased oxygen uptake [202].

10 Effects on differentiation: growth patterns and germination

The dimorphic fungus *Mycotypha africana* can exist in a myceliar or yeast-like form. Weak ELF magnetic fields shift development towards the yeast form [203]. Weak AC fields (0 – 1.2 nT, 0.8 – 50 Hz) further increase this germination rate [204]. Very strong DC fields (5.2 – 6.1 T) suppress spore formation from vegetative cells of *Bacillus subtilis*, an effect that was paralleled with the diminished activity of alkaline phosphatase [135].

11 Effects on behaviour: gravitaxis and bioluminescence

AC fields (0.5 – 2.0 mT, 50 Hz) elicit in the ciliates *Paramecium biaurelia, Loxodes striatus* and *Tetrahymena thermophila* increased swimming velocities and a decrease in the linearity of cell tracks. At least in the case of *Paramecium*, this response must be Ca^{2+} specific as it is abnormal in Ca^{2+}-channel mutants [205]. *Paramecium multimicronucleatum* transiently responds to an AC field (600 mT, 60 Hz) with an enhanced gravitaxis [206]. Nakaoka *et al.* [207] found no effect of an AC field (650 mT, 60 Hz) on swimming orientation of *Paramecium tetraurelia*. The fact that some of these responses are Ca^{2+}-specific and -dependent is highly relevant in view of the observation that several magnetic phenomena in animals, such as morphine-induced analgesia in mice [208, 209] and pineal melatonin synthesis in teleost fish [186], are also related to Ca^{2+} channels. Contradictory data exist regarding magnetic effects on bioluminescence. No effect was found for AC fields for *Vibrio fisheri* [210], while enhanced bioluminescence was described

for *Vibrio quinghaiensis* after exposure to AC fields (0.1 – 9.6 mT, 50 Hz) [211]. Geomagnetic storms were reported to prolong bioluminescence in *Photobacterium* [132].

12 Effects on ecology: aquatic systems

The migration and distribution of magnetotactic bacteria in marine and freshwater aquatic systems is dependent on the magnetization of the local environment [212]. On one hand this is determined by the petromagnetic properties of benthic deposits, reflecting the paleo-ecological history of this aquatic biotope [213]. On the other hand, short- and medium-term variations of the geomagnetic field, e.g. caused by increased solar activity, are superimposed. A variation of biological productivity, which correlates with the occurrence of biogenic magnetite, was found in the Rybinsk Reservoir [214]. In the littoral of the same artificial biotope, a correlation between geomagnetic activity, water transparency and photosynthesis intensity of phytoplankton was investigated [215]. The ecological role of magnetotactic bacteria in coastal salt ponds, whose spatial and temporal distribution is affected by the geomagnetic field, is described by Sakaguchi *et al.* [31].

Liquids, in organisms and natural waters, generally contains colloids, consisting of dissolved gases, dispersed biological material, small soluble carbonates and other similar components; all of which contribute to a multitude of boundary layers with concomitant zeta potentials that originate from these space-charge areas. Exposure of such solutes to weak MF and EMF caused altered solvation properties for carbonates and gases, and, in addition, also affected surface tension, viscosity and pH [216, 217]. Furthermore, the observation that pH alterations in soils, which always contain a wide spectrum of biocolloids, correlate with geomagnetic events [218] could be explained along these lines. These findings could be highly relevant for assessing the consequences of the decreases in main geomagnetic field strength [219] that has been occurring for about 150 years. This could also likely affect the solubility of CO_2, O_2, and CH_4, as well as the solution equilibrium of carbonates in the oceans [220–222]. Thus it would be an essential factor regarding marine carbon cycles.

13 Mechanisms and models for magnetoreception

Models of magnetoreception need to explain sensitivity to: (i) static magnetic fields, (ii) alternating magnetic fields; and (iii) resolve the paradox that the thermal energy content of (living) matter exceeds, by many orders of magnitudes, that of the magnetic field. Chemical reaction rates depend on temperature, and the existence of liquid water, and occur typically at temperatures of $T > 273$ K (0°C), which correspond to a thermal energy of $E > 3.76 \cdot 10^{-21}$ J. Weak magnetic fields of far lower energies can nevertheless affect life processes, which implies that they generate molecular order and overcome the thermal barrier, i.e. entropy. A theoretical limit for the threshold of a biomagnetic response is determined by the fact that the magnetic flux is always quantized [223], the magnitude of the magnetic flux quantum being $2.07 \cdot 10^{-15}$ Tm^{-2}. The lowest thresholds that have

been reported for magnetobiological responses approach this value, an observation that represents a formidable challenge to any theory of magnetoreception [142].

13.1 Ferrimagnetism

Ferrimagnetic magnetoreceptors consist of magnetic minerals like magnetite (Fe_3O_4) and greigite (Fe_3S_4), and act as the magnetoreceptors for bacterial magnetotaxis. In contrast to ordinary magnets (ferromagnetism), in which the individual magnetic moments of the electron spins are aligned in parallel, the magnetic moments are antiparallel for ferrimagnetic materials. Magnetite, which is more precisely written as $(Fe^{3+}Fe^{2+})\ Fe^{3+}\ O_4^{2-}$, is characterized by a spinell type of crystal structure, i.e. it possesses two unequivalent lattice positions, tetraedrically coordinated A-positions and octaedrically coordinated B-positions. The A-positions are occupied exclusively by Fe^{3+}-ions, while the B-positions are equally occupied by Fe^{3+}- and Fe^{2+}-ions (inverse spinell). In this structure the magnetic moments of the Fe^{3+}-ions cancel each other and the residual magnetic moments derive from the Fe^{2+}-ions. Ferrimagnetism is thus much weaker than that observed for ferromagnetic materials. On the other hand, the force generated by ferrimagnetic materials exceeds those of dia- or paramagnetic materials by more than 6 orders of magnitude.

Magnetite crystals are organized in magnetosomes, which assemble chains along the motility axis of the bacterium, generating a permanent magnetic dipole moment and aligning the cells parallel to the geomagnetic field lines (see above). Magnetites are able to transport electrons, and thus to conduct current. Whether or not this property plays a role in biology remains presently unknown. Because magnetite is ubiquitous in the animal kingdom, it is possible that ferrimagnetic nanocrystals also play a vital role in organisms other than magnetotactic bacteria. One possibility could be that nanocrystals fixed to ion channels modulate ion movement across membranes [77]. The energy that would be absorbed by a single 100-nm magnetite crystal exposed to 0.1 mT at 60 Hz is, in theory, sufficient to exceed the thermal noise [78].

13.2 Radical-pair mechanism

When two radical molecules stay, for a short time, in close proximity displaying spin correlation, they form a radical pair. This spin correlation of radical pairs implies a normally forbidden state of equal spin quantum numbers ("parallel spins", Figure 1), resulting in a net paramagnetic momentum. There exists a multitude of ways to generate radical pairs. One possible way is through homolysis of a molecule of 1A-D that is split into two radicals, $A^\bullet$ and $D^\bullet$, creating at first a pair $^1[A^\bullet\ D^\bullet]$ in the singlet state (Wigner conservation rule; the single bond in 1A-D also being in a singlet state). Under the influence of such a magnetic field (including the weak field of a nuclei), the radical pair undergoes intersystem crossing (ISC) to form a pair $^3[A^\bullet\ D^\bullet]$ in the triplet state. Singlet and triplet radical pairs have different fates: while the singlet pair can recombine directly to the

original donor ^{1}A-D, the triplet cannot and will often take indirect routes. Since a magnetic field induces the generation of triplet pairs, the magnetic field effectively causes a longer lifespan for the radicals. A donor molecule ^{1}A-D may also give rise to a radical pair made up of cationic and anionic radicals, as shown in Figure 1. Other modes of radical-pair formation may involve other reaction partners, and redox reactions, as in the case of cryptochrome (see below). A great advantage of the radical-pair mechanism is the fact that magnetically modulated ISC and radical pair recombination are inherently temperature independent, so that no kT-problem arises.

Figure 1 shows an example how homolysis of a donor molecule, ^{1}A-D, leads, via the excited singlet state ^{1}A-D*, to the formation of a cation-anion radical pair $^1[A^{\bullet+}\ D^{\bullet-}]$. As a rule, the mobility of the single radicals - in the specific case $A^{\bullet+}$ and $D^{\bullet-}$ - is, immediately after its generation, restricted, because of their size and the viscosity of the environment. Remaining close together, the partners exist in the singlet state, $^1[A^{\bullet+}\ D^{\bullet-}]$, and have antiparallel spins. ISC provides a paramagnetic state by the spin-orbit coupling of electrons, with the consequence that it can be modulated by an external magnetic field (MF). This isoenergetic, radiationless transition between two electronic states has different multiplicities, and enables the interconversion of the pair to the triplet state, $^3[A^{\bullet+}\ D^{\bullet-}]$, in which the single radicals can have parallel and antiparallel spins, implying four possible states with a probability of 25% each ($\uparrow\downarrow, \downarrow\uparrow, \uparrow\uparrow, \downarrow\downarrow$). Here, only the hyperfine-niveaus, with parallel spins, are paramagnetic and can interact with a moderate magnetic flux. In the presence of a MF ($B > 0$), the triplet states, with parallel spins T_{+1}, T_{-1}, have a probability of 50%, and do not contribute to the subsequent reaction.

As long as the external MF is zero or very weak, the three triplet states: T_0, T_{+1}, T_{-1}, of the radical pair $^3[A^{\bullet+}\ D^{\bullet-}]$ can recombine to ^{3}AD. In bacterial photosynthetic reaction centers this allows for the conversion of $^3O_2$ to $^1O_2$ (Figure 1). With increasing magnetic field strength ($B >$ hyerfine interaction), and concomitant Zeeman splitting, the probability for recombination of the T_{+1} or T_{-1} states decreases, and only the T_0 state recombines (Figure 2). For very weak magnetic fields, in the range of the hyperfine interaction, the yield of the singlet state decreases, while it increases for elevated magnetic flux densities (Figure 3).

In the framework of the radical-pair mechanism magnetobiological effects are explained in the following way: (i) external magnetic fields shift the equlibria of singlet and triplet radical pairs, (ii) the primary magnetobiological response occurs either from the singlet or else from the triplet radical pair, and (iii) because the fates of the singlet and the triplet radical pairs are different (Figure 1), it is expected that the requisite biological responses are equally different, i.e. dependent on the magnetic flux density. It is irrelevant in this context whether or not the magnetobiological response occurs from the singlet or else from the triplet state of the radical pair.

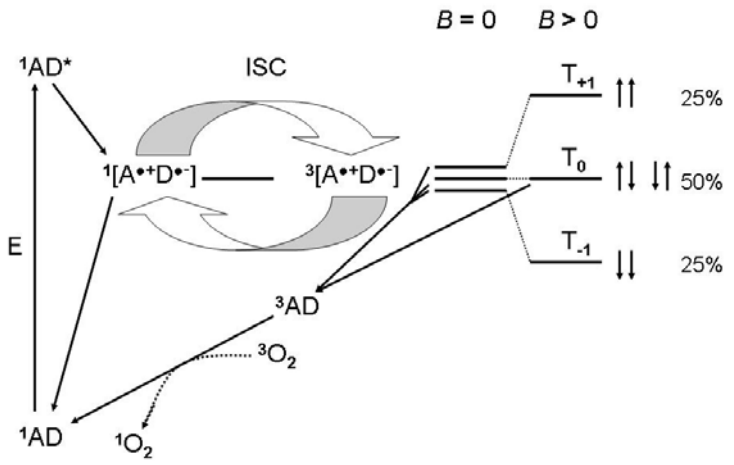

Fig. 1 Generation of cation-anion radical pairs, and ISC (intersystem crossing) under the influence of a magnetic field. Without a MF (B = 0) the three triplet states may recombine to the triplet radical ^{3}AD. For B > 0 (Zeeman splitting) only the T_0 pairs can recombine to ^{3}AD, while T_{+1} and T_{-1} are excluded from recombination. In photosynthetic reaction centers this leads to the formation of singlet-oxygen ($^3O_2 \longrightarrow {}^1O_2$). Other radical-pair reactions do not, of course, necessarily lead to the generation of $^1O_2$, and the singlet and triplet radical pairs can have different fates and decay products. Modified after Liu *et al.* [237].

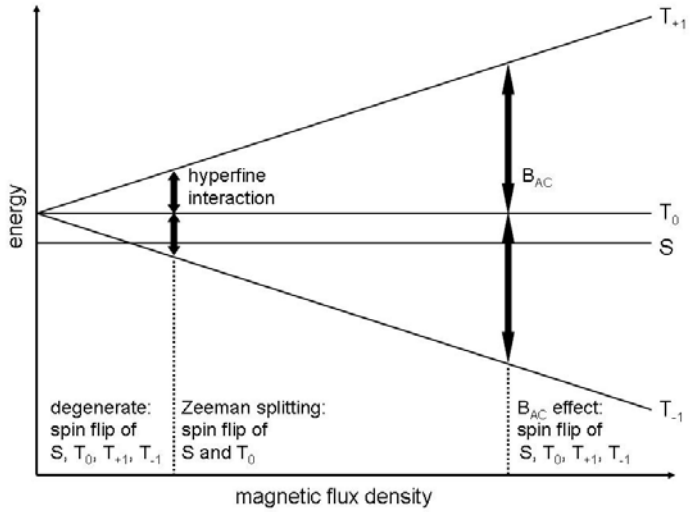

Fig. 2 Energy states and spin multiplicities in dependence of the magnetic flux density. When the energy separation exceeds that of the hyperfine interaction, radicals in the T_{-1} and T_{+1} state are excluded from the spin flip, and as a consequence, the singlet yield increases (Figure 3).

The MF-dependent interconversion rate between the singlet and triplet radical pairs can be described by the Zeeman interaction. The energy difference ΔE for the two splitting Zeeman niveaus by a MF (B > 0) is given by the equation:

$$\Delta E = g\beta B \tag{1}$$

where g is the Lande factor (near 2 for free electron radicals), B is the magnetic flux density, and β is the Bohr magneton (9.274×10^{-24} J T^{-1}) [224].

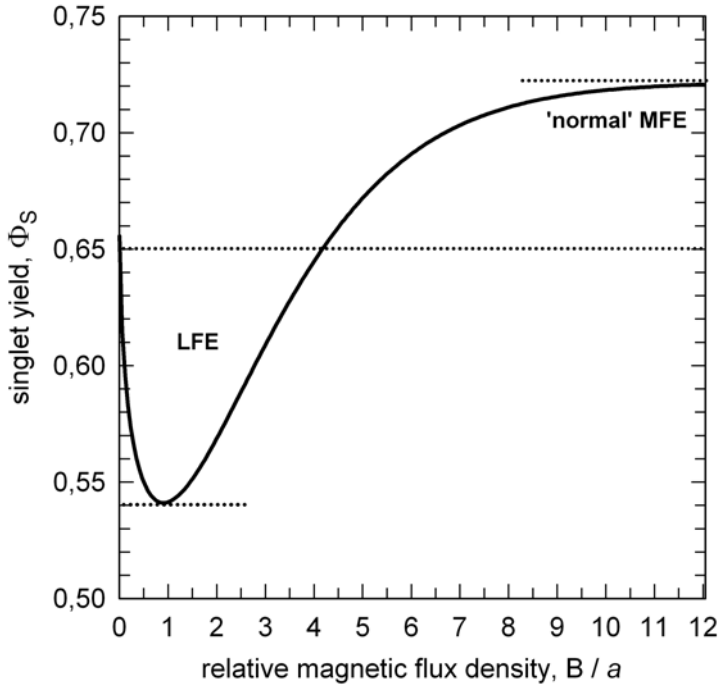

Fig. 3 Dependence of the singlet yield of radical pairs in dependence of the magnetic field. The magnetic flux density, B, is expressed in relative units as multiples of a, the average strength of the hyperfine interaction. Modified after Timmel and Henbest [354]. LFE: low-field effect; 'normal' MFE: normal magnetic field effects often occur in the mT-range.

Depending on external MF strengths, lifetimes of the occurring spin dynamics (spin flip) may last up to some μs, and compete with radical separation [225]. ISC is furthermore influenced by hyperfine coupling of the MF with the nucleic magnetic momentum. Because of the spin relaxation times of about 1 μs, the effects of ELF magnetic fields are frequency independent up to a few MHz. For a MF of 50 μT to be biologically effective one requires a cage time of about 50 ns, during which the two partners stay in close proximity. During this time the hyperfine field of the radicals must allow at least one precession period; in addition, also the recombination time must be of the same order as the cage time [226]. Cage times critically depend on the molecular environment; macromolecules with cavities or pockets such as nucleic acids or proteins extend the cage times of radical pairs, and contribute in this way to sensitizing living matter to magnetic fields

of moderate strength [227]. For lower magnetic fluxes, these time windows become still more critical, so that MFs substantially smaller than the geomagnetic field can hardly mediate biological effects solely by this mechanism [226]. On the other hand a relief of MF impacts, by partial thermal decoupling of the electron spins, is suggested by several authors [226, 228, 229].

In some cases photogenerated radical pairs seem to be involved in magnetoreception, e.g. for bird orientation [11, 12]. The magnetoreception of migratory birds depends on the presence of cryptochrome, a FAD-containing, blue-light receptor in the retina [13, 14], that probably undergoes a photoreduction with concomitant generation of $FADH^{\bullet}$ radicals, and radical-pair formation. Blue light-mediated, hypocotyl shortening of Arabidopsis thaliana is clearly influenced by a weak MF of 400 μT [15]. Because double mutants lacking cryptochromes 1 and 2 do not respond to such fields, this magnetoresponse also depends on functioning cryptochrome (Figure 4). Because Arabidopsis cryptochrome generates, upon blue-light absorption, a [$FADH^{\bullet}$ $Trp^{\bullet}$] radical pair [230], it is very likely that cryptochrome operates as a magnetoreceptor only in its radical-pair state [15]. In line with this assumption is the observation that Arabidopsis reacts to a magnetic field only upon blue-light irradiation, but not, however, in darkness [15].

In the reaction centers of photosynthetic bacteria or plants, absorption of light leads to the formation of ^{1}Chl, and subsequent charge separation, which includes electron transfer to a second pigment (PheoChl), thus forming a radical pair in the singlet state, i.e. ^{1}[$Chl^{+\bullet}$ $Pheo^{-\bullet}$]. Only relatively strong magnetic fields in the range of several hundred mT can affect the singlet-triplet mixing of the radical pair, because the pair is rather shortlived. The short half-live of the radical pair is due to the fact that the pair rapidly donates an electron to a quinone. Technically the described magnetic effects are monitored by measuring the triplet yield and the fluorescence emission intensity of the bacterial photosynthetic reaction center [231, 232]. Because the magnetically modulated charge separation processes of bacterial photosynthesis [231, 233], or photosystems I and II of green plants [234–236], require rather high magnetic flux densities between 10 to several hundred mT, one can conclude that the geomagnetic field does not influence photosynthetic electron transport.

A very elegant system to study the radical-pair mechanism is a mutant of the purple bacterium *Rhodobacter sphaeroides* that lacks carotenoids, so that photosynthetically generated singlet oxygen is longer lived than in the wild-type strain ($^1O_2$ being quenched by carotenoids). At magnetic flux densities between 0 to 100 mT, the yield of $^1O_2$ decreases in the mutant from 100% to about 50% [237]. The response is predicted by the model shown in Figure 1. Because of the magnetically-induced *Zeeman* splitting for $B > 0$, only the T_0 state is available for recombination and formation of $^1O_2$, while the triplet states T_{+1} and T_{-1} do not contribute (Figure 1). Flash-induced bleaching of the photosynthetic reaction centers is likewise dependent on magnetic flux densities; for example, the bleaching at 800 nm at 15 mT is 45% smaller than that in a zero field [237].

Evidence for radical-pair mechanisms were also obtained for some retinoids and porphyrins involved in the mitochondrial respiratory chain, where radical pairs could enhance the synthesis of reactive oxygen species (ROS) [238]. Intermediates of enzyme reactions may involve the formation of radical pairs. An enzyme that has been investigated in detail is B_{12} ethanolamine ammonia lyase [224, 239, 240]. Further cases of radical pair mechanisms include ionizing radiation damage, and its concomitant repair. Dicarlo *et al.* [241] report increased repair rates after ultraviolet light (UV) exposure and subsequent treatment with a 60 Hz EMF of only 8 μT field strength, an observation that confirmed earlier results [242–244]. Magnetic fields also substantially influence antioxidant scavenging of ROS [245].

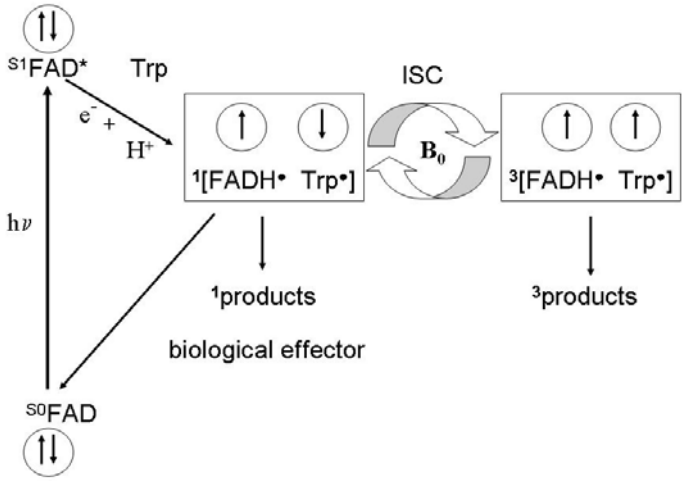

Fig. 4 Radical-pair formation of the blue-light receptor cryptochrome upon absorption of near-UV or blue light. The excited chromophore, ^{S1}FAD, undergoes a photoreduction to form, with a tryptophanyl residue (Trp) from the apoprotein, a radical pair; the electron and proton donors are omitted. The radical pairs can recombine to form ^{S0}FAD, or triplet products. The biological effector molecule may be derived either from the singlet radical pair (as shown in the figure) or else from the triplet radical pair (not shown). Modified after Ahmad *et al.* [15].

13.3 Ion cyclotron resonance

In the mid eighties it became increasingly clear that numerous biomagnetic responses display characteristic dose-response relationships, with distinct amplitudes and frequency "windows". To explain these results, a physical phenomenon was taken into account, which was long known from vacuum physics, and thinned gases. Charged particles moving perpendicularly to a magnetic field are deflected by the Lorentz force on a circular path perpendicular to the magnetic field lines. An electron orbiting around the nucleus has a magnetic momentum, which is proportional to its angular momentum, L (Figure 5).

An external MF affects L by an additional torque, ΔL, and forces the electron to precess around the magnetic field, B_0. The resulting precession angular velocity, ω_{Larmor} (Larmor precession), can be written as:

$$\omega_{Larmor} = \frac{d\phi}{dt} = \frac{B_0 e}{2m_e} \tag{2}$$

where e is the charge and m_e, the mass of the electron. There is substantial experimental evidence that magnetobiological effects are maximal when the frequency of an alternating MF B_{AC}, which is superposed to a static magnetic field, coincides with the Larmor frequency of a biological relevant ion such as Ca^{2+} or Na^{+}. Because of this fundamental relationship, dose-response curves display the characteristic presence of "windows".

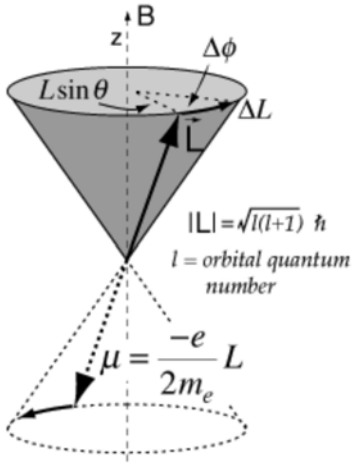

Fig. 5 The Lamor precession of a charged particle around a magnetic field, **B**, having a rotating angular momentum vector, **L**, that circumscribes the surface of a cone. For further explanation see text.

The field strength B_{DC} of the MF, the charge Q, and mass m of the involved ion, as well as the corresponding frequency (f) of the additional superimposed ELF-EMF can be described by the "ion cyclotron resonance" (ICR) formula":

$$f = \frac{B_{DC} Q}{2\pi m} \tag{3}$$

Here, the specific charge (Q/m) of ions like Ca^{2+}, K^{+}, Mg^{2+} is a unique material constant, determining its circulation frequency on a forced orbit.

One of the first ICR models [246, 247] described Ca^{2+} ions moving helically along the geomagnetic field lines. A superposed ELF magnetic field of suitable frequency accelerates the movement, purportedly resulting in an increase of Ca^{2+} influx via calcium channels that are aligned with the geomagnetic field. Biological relevant effects, and *in vitro* effects, have been obtained for nearly any ion of characteristic ELF frequency, e.g. [248–250]. Significantly, the globally used powerline frequencies of 50 and 60 Hz are pertinent in this context [251, 252], as they provide ICR for Ca^{2+} and many other important ions. Relevant effects can be obtained, for example, if a 50 Hz AC field of a moderate flux density of 65 μT

superposes with a static field, BDC, that is comparable to the geomagnetic field [253]. One thus has to reckon with the possibility that ICR conditions, for Ca^{2+} and other ions, are ubiquitous in our technical environment, with an innate ability to influence health and biological experiments. Further consequence are found with very weak natural AC fields caused by the atmospheric *Schumann*-resonance [254], the circumpolar *Birkeland* currents [255] from the auroral zones, and the van Allen radiation belts, each of which have putatively been persistent ecological and evolutionary factors.

The criticism of earlier ICR models [256, 257] hinges on the problem, that the thermal energy of biological matter (kT) is too high, by several orders of magnitude, to allow the undisturbed movement of charged particles on classical Lorentzian orbits [251, 258, 259]. To resolve this dilemma, theoretical attempts were made to decouple micro-regions, controlled by weak magnetic fields, from the thermal equilibrium. A possible decoupling mechanism could consist in a transition zone between molecular layers of decreasing refraction numbers, for example, water to oil interfaces. All ICR theories imply such transition zones, typically lipid membranes, tertiary protein structures, cell organells, or the two-phase state of water (Chapter 13.5 Quantum coherence).

It should be stressed, however, that ICR constitutes a phenomenon that exists even in the absence of macromolecular structures, such as interface-forming proteins, lipid membranes or microtubuli, as it occurs even in amino acid solutions exposed to suitable combination of $\mathbf{B}_{DC}$ and $\mathbf{B}_{AC}$ fields [260]. The effect of such fields manifests as an increase in electric conductivity when the ICR condition for the amino acid is met. Interestingly, a splitting, in two closely adjacent conductivity bands, became apparent when the magnitude of $\mathbf{B}_{DC}$ was scanned and the conductivity was monitored by an AC synchronous to the frequency of $\mathbf{B}_{AC}$; an observation that could indicate a multi-term energy scheme for the underlying process [261]. These experiments can be understood in the framework of quantum electrodynamic models, which provide for coherence, and collision-free movements of small ions [262].

To overcome the kT-problem interactions with electric fields were also taken into account [263]. It was proposed, for example, that not only a parallel combination of $\mathbf{B}_{DC}$ and $\mathbf{B}_{AC}$, but also a perpendicular arrangement, allows for ICR [264]; an observation that could indicate rather stable energy states brought about by intrinsic alternating electric fields, and the geomagnetic field. ICR could be the physical basis for perception of weak EMF in biological matter, it could furthermore explain substrate specificity, high sensitivity and unusual dose-response relationships, i.e. "effective windows", that are usually absent in other biological dose-response curves. It can also be helpful for the interpretation of the effects caused by static MF; this would require, however, the displacement or rotation of charged particles [265], to generate a local $\mathbf{B}_{AC}$. An example for such a mechanism is the magnetoresponse "anomalous viscosity time dependence" of *E. coli* in static magnetic fields ($0 - 110\ \mu$T). The dose-response curve for this response shows several prominent maxima and minima ("windows"), which can be explained by the rotation of ion-protein complexes [19].

13.4 Ion parametric resonance, ion interference mechanism

The original ICR theory of Liboff [246, 247] was later modified by the ion paramagnetic resonance (IPR) model. The former predicts ELF magnetic effects at the cyclotron frequencies and their harmonics [266], the latter at the cyclotron frequencies and their subharmonics [257, 267]. IPR, a generic name for a number of theoretical models based on classical electrodynamics, as well as quantum electrodynamics, views biomagnetic effects largely as magnetically modulated ion binding, and thus provides a description for ion-ligand interactions in MFs. The IPR model also applies to experimental situations in which a static magnetic field ($\mathbf{B}_{DC}$) is superposed to a parallel ELF magnetic field ($\mathbf{B}_{AC}$); but theoretical considerations predict low sensitivities in the range of several hundred μT

range [259, 264]. An experimental confirmation of the IPR model was attempted by Smith *et al.* [249] with germination experiments, and by Berden *et al.* [268] using bioluminescence of the dinoflagellate, *Gonyaulax scrippsae*.

Ions caged in a protein domain can be described by a superposition of quantum states, in which the contribution of quantum mechanical interference becomes relevant because it results in uneven distribution of the ion inside the cage [162, 269]. According to this ion interference mechanism (IIM), a static magnetic field induces an inhomogeneous density pattern that begins to rotate with the cyclotron frequency. The addition of an AC MF results in the cessation of rotation, and finally in the release of the bound ion; a process that may elicit a biological response. IIM relates the magnetic field parameters to those of dissociation of ion-protein complexes, and is able to explain a number electromagnetic phenomena that also include the effect of MF on rotating ion-protein complexes, and the concomitant dose dependency [19], as well as the effects of pulsed magnetic fields [163].

13.5 Quantum coherence

The quantum coherence mechanism can explain several paradoxical observations, among which the so-called kT-problem stands most precipitously. The energy content, E, of an EMF that elicits ICRs is several orders of magnitude smaller than the thermal energy content (kT) of the molecules in the EMF. In the case of water, for example, the thermal energy content at 278.5 K is $1.17 \cdot 10^9$ J m^{-3}, while the magnetic energy content at 0.8 μT amounts to only $2.6 \cdot 10^{-7}$ J m^{-3}. For fermions, i.e. particles, the relation between kT and magnetic fields can be expressed as:

$$k \cdot T >> E = \mathbf{B} \cdot \mathbf{v} \cdot l \cdot Q \tag{4}$$

where Q is the charge moving along distance l, with speed $\mathbf{v}$, inside a magnetic flux, $\mathbf{B}$. For bosons, i.e. photons, or likewise ELF-EMF, the relation can be expressed as:

$$k \cdot T >> E = v \cdot h \tag{5}$$

where T is the absolute temperature, k the Boltzmann constant, v the frequency and h the Planck constant. It is a well-known principle in physiology that a stimulus needs to

exceed the kT limit in order to elicit a response. The probability (W) for overcoming the Boltzmann-distributed thermal equilibrium at temperature $T > 0$ K, by an external energy (E) is approximated by:

$$W(E) \approx 1 - e^{-\frac{E}{kT}} \tag{6}$$

In photobiology, for example, the energy content of a single photon surpasses, many times, kT, thus resulting in a value for W near unity; which in turn means that a response is elicited. In magnetobiology, however, one encounters quite a different situation. If one calculates $W(E)$ for T = 293 K, and a MF of $\mathbf{B} = 40$ μT (i.e. geomagnetic field), one obtains for the spin-related energy of an electron a value for W as low as $\sim 10^{-7}$. This means that statistically only one out of ten million free electrons contributes to a charge transfer caused by MF interactions. It is apparent that such a low particle fraction could not possibly elicit a biological reaction. Since weak fields do, however, elicit biological reactions, it appears on the grounds of eq. 6, as if living matter behaves in a MF like a subcooled gas at a temperature of $\sim 5 \cdot 10^{-6}$ K; which would result in a conduction band of $\geq 99\%$ occupation, i.e. $W(E)$ is approaching unity. Such behaviour is known for Bose-Einstein-condensates, which represent matter states near 0 K, and that appear at first sight to be incompatible with living matter. The coherence mechanism nevertheless provides the possibility to resolve this paradoxical situation by providing a mechanism by which the magnetic field action is thermally decoupled from its environment.

Particle properties (e.g. the spin) are described by quantum mechanics by wavefunctions, which express the probability for a certain quantum state with respect to location and time. If several similar particles (e.g. photons or electrons), are related to the same wavefunction in a fixed phase ratio (by analogy to synchronously swinging pendulums) their state is said to represent "coherence". The De Broglie equation describes the wavelength λ of such a matter-wave for a fermion particle (e.g. an electron). Because the probability of location of the particle inside a distance (l) must be 1, it is the minimum coherence length (zero order) for the particle at the same time. With the matter wavelength $\lambda \geq l$, particle mass m, and kinetic energy E, it will be written as:

$$\lambda = \frac{h}{\sqrt{E \cdot 2m}} \tag{7}$$

If the location probabilities of at least two particles are coherently superimposed, one obtains one common wavefunction, i.e. a loss of the individual (e.g. fermion) properties which leads to Schrödinger's "entanglement" [270]. In this way a newly condensed matter state originates in which individual particles appear to be "glued" together by transposition forces like phonons or solitons (*Cooper* pairs in superconductivity theory).

At this point of the coherence mechanism, the universal mediator of biological processes, water, comes into play. Water dipoles assemble spontaneously into self-organizing, ordered clusters. Quantum electrodynamics predicts two-state aggregates for water consisting of: (i) a bulk phase, which is determined by the thermal equilibrium (water in Brownian motion), and (ii) ordered clusters (Figures 6–8) [262, 271, 272]. Clusters orig-

inate spontaneously by an in-phase propagation of the oscillating quantum field of delocalized orbitals of water molecules [273]. Ordered water clusters generate a 12.06 eV (resp. $2.9 \cdot 10^{15}$ Hz) (Figure 6) superradiation-transition [274, 275], which corresponds to an electromagnetic wavelength of approximately 100 nm, and a quantum coherence over $\sim 1.36 \cdot 10^7$ water molecules which is likely mediated by excitons [272]. These "coherence domains" (CD) should be spheres (Figures 6–8) with a uniform, zero-dimensional wavefunction, i.e. they should be quantum dots. Seen from the surrounding environment the CD appears as supramolecular structure with a molecular mass of 217.6 MDa; the inside is inaccessible to ions except the hydronium-ion (H_3O^+), considered by energetic relations. The oscillation strength is expected to reach $8.4 \cdot 10^{10}$ V m^{-1} at the center [275], a value which is two orders of magnitude in excess of that of biological membranes; assuming thereby a potential of 100 mV across the lipid bilayer. The spherical interface region (Figures 6, 8) explains the sudden drop of dielectricity from the interior of the CD ($\varepsilon_r \sim 160$) to the incoherent domain ($\varepsilon_r < 80$). This results in a mean in these values that closely mirrors that found experimentally for water ($\varepsilon_r \sim 80$).

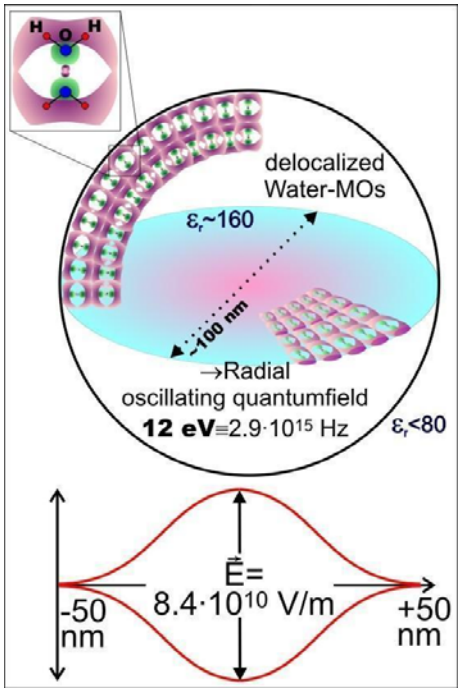

Fig. 6 Model of a water phase organized in spherical coherence domains (CD). Delocalized molecule orbitals generate a radially oscillating quantum field with 12 eV, which leads to a 100 nm spherical superradiation with an amplitude of $8.4 \cdot 10^{10}$ V m^{-1} in the center. Further explanations in the text.

The $2-4$ nm thick interface region of the CD (Figures 6–8) appears in many respects akin to the water transition zone of lipid membranes. A potential trough of about 0.26 eV, which is predicted by the Born-equation, constitutes a circular ion trap that is responsible for the experimentally-observed, ICR effects in water. These ions are assembled in this interface in a plane perpendicular to MF lines, up to a critical density that is reached when

their Debye-Hückel radii interact (Figure 8, left). This "ring" of ions, around the water CD, represents a one-dimensional coherent particle system, in effect a quantum wire. For glutamate solutions at 293 K such a quantum wire is composed of approximately 330 glutamate anions [260, 272]. Ionic current measurements have shown that about 36% of the glutamate anions are organized in this coherent state. The Eigenvalue of the water CD (eq. 8) matches the total rotation energy of the ion-ring mediated by the $\mathbf{B}_{DC}$. Such a coupling of a bosonic (CD) and fermionic (ions) quantum system is known as Freshbach-resonance, which can be described by the Hartree-Fock-Bogoliubov equations [276, 277].

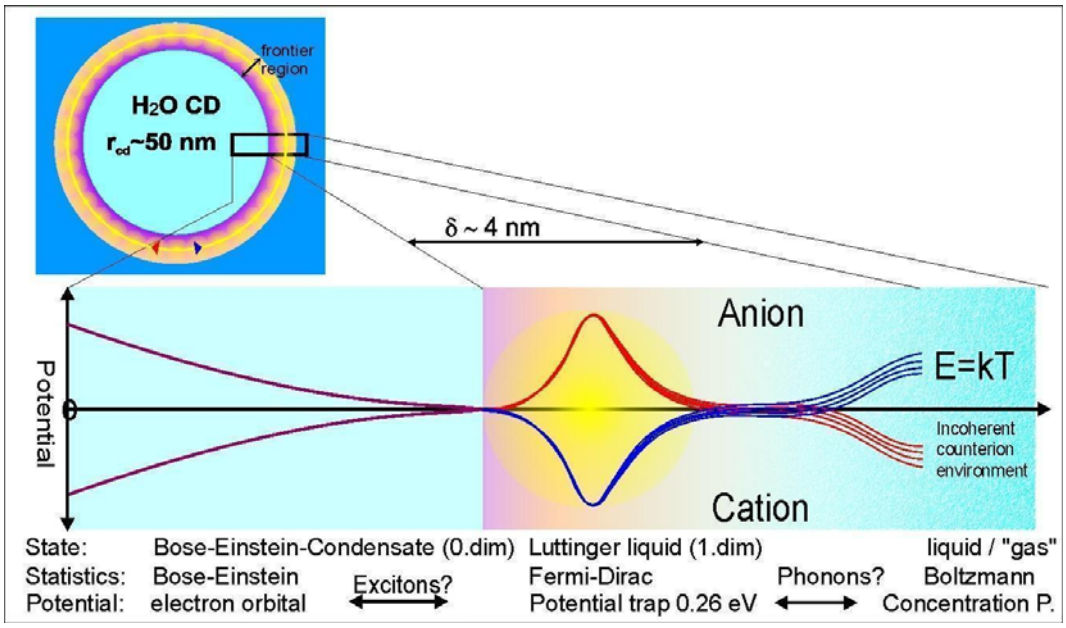

Fig. 7 Schematic diagram of the coupling of a ring of ions to a water coherence domain (CD): The zero dimensional water CD is a quantum dot and represents a Bose-Einstein-condensate; the ions behave like a Luttinger liquid, settling around as (1-dimensional) quantum wire, in a plain perpendicular to the direction of an external MF. Possible quantum statistics, and exchange forces of the states, are demarcated below the pictogram.

Figure 7 sketches the potential interaction at the frontier region of the water CD, leading to a Freshbach-resonance. The potential trough that generates the ion ring (quantum wire) surrounds the CD in its immediate vicinity, without any discontinuity or jump. As a result the trap is constructed by the ions itself; the polarity of the potential depends on the sign of the ion charge. This potential will be increasingly influenced by thermic noise in the transition zone to the outer environment. The coherence mechanism also allows for an alternative structure of the "quantum wire" as there is no absolute requirement for the synchronous circulation of each ion. Alternatively, an equivalent effect could be achieved by impulse-perturbation that would circulate along the ion-ring with the ICR frequency, e.g. mediated by phonons. The ion-ring could also be stabilized by an equivalent number of counterions (e.g. H_3O^+), which concentrate in the same plane outside in the surrounding, incoherent environment, comparable with the Stern-layer of lipid membranes. The coherence condition inside the quantum wire itself will be given by the Debye-Hückel radii

r_i (h = Planck constant, m_{ion} = ion mass, E_{chem} = electrochemical energy given by the potential, $\varepsilon = \varepsilon_r \cdot \varepsilon_0$ = permitivity of the solvent (water), N_A = Avogadro constant, the ion strength $\prod$ is given by the ion-concentration c_i and -charge z_i):

$$\frac{h}{\sqrt{2 \cdot m_{ion} \cdot E_{chem}}} \sim \sqrt{\frac{\varepsilon \cdot k \cdot T}{2 \cdot N_A \cdot e^2 \cdot \prod}} \text{ ion - strenght } \prod = \frac{1}{2} \sum_i c_i z_i^2 \tag{8}$$

With glutamate anions one obtains a radius r_i of 1.04 nm using the conditions in the *in vitro* ICR experiments of Zhadin *et al.* [260, 261]. How does the coherence mechanism account for the observed biological effects of alternating MFs? Ions can access the interface region of the water clusters (Figures 6, 8) and orbit (orbit frequency ω) as long as their Lorentz-radius, specified by the external magnetic flux density $\mathbf{B}_{DC}$, matches (Figure 8, left). The superimposed, though substantially weaker, EMF $\mathbf{B}_{AC}$ with frequency ω, interferes constructively for $\omega = \Omega$, or one of its harmonics (Figure 8, middle). This way it causes an interfering distortion of the trap geometry, which becomes time-invariant for the ICR frequency ω and its harmonics n, increasing the probability for decoherence (Figure 8. center). Such a mechanism could explain the ICR effect for EMF-amplitudes $\mathbf{B}_{AC}$, down to some nT. An additional electric field, E, amplifies this effect (Figure 8, right), which causes transitions of the ions to the incoherent environment (Figure 8, right). Such effects can be measured electrochemically by increases in the ionic current through the electrolyte solution [261]. The release of ions to the incoherent environment could elicit subsequent biological reactions. The coherence mechanism provides a good approximation for the results of *in vitro* ICR experiments [256, 260–262].

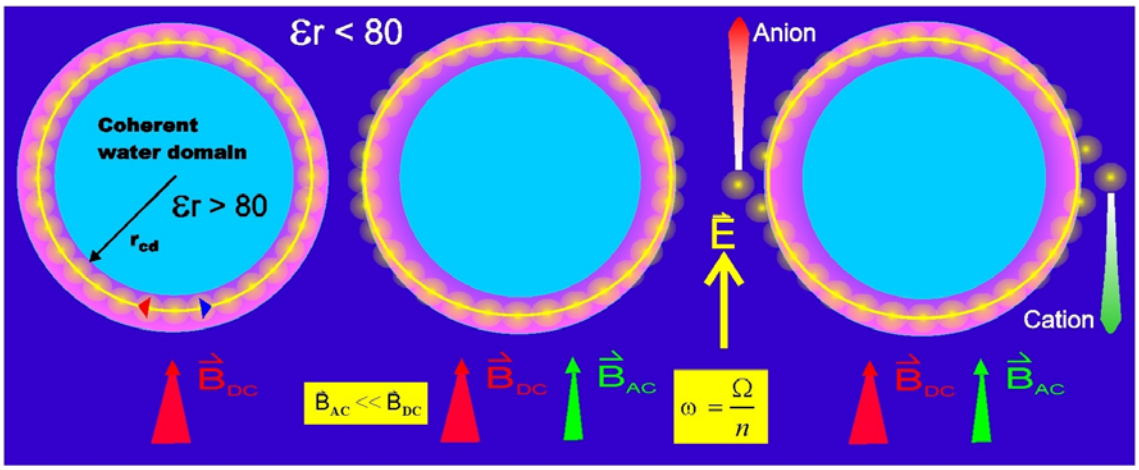

Fig. 8 The coherent-domain model of water. B_{DC} = static magnetic field, B_{AC} = *a* much weaker, superimposed electromagnetic field with frequency ω. Ω is the orbit frequency of the ion in the frontier region of the coherent region. Left: ICR in the undisturbed circular ion trap without a superimposed field B_{AC}. Center: a superimposed field B_{AC} with frequency distorts the circular ion trap, so that ions can "break out" to the incoherent water phase. Right: complete decoherence and emptying of the ion trap by an additional local electric field **E.** Modified after [262]; further explanations in the text.

There remain open questions with respect to the fate of the CDs in ultra pure water, and in the absence of any magnetic field. Also in pure water at room temperature, some water molecules are dissociated by auto-protolysis, known as the "ion product of water". It is possible that these products serve as ions in order to sustain the Freshbach resonance mechanism of the CDs. At a zero MF, the ICR frequency likewise reaches zero. Even though a description for this case is not presently available, it is quite possible that CDs cannot exist in the absence of a MF.

In addition to the coherent "water spheres" described above, cellular macromolecules were also considered as coherence mediators for biological EMF effects. For example, microtubules [278], as well as DNA [279], may function as one-dimensional, anisotropic "quantum wires". One should, however, keep in mind that the assumptions of these authors were too specific to derive an ICR model of general applicability for living matter and aqueous solutions. An ICR effect could also be possible at the boundary layers of collodial solved particles. If the Lamor radii would approach the particle size, the Lorentz forces would become parallel to the boundary charge layer, forcing it by the additional magnetic pressure. Findings for the disappearance of the ICR effect in thoroughly degassed, and ultrafiltrated solutions [280], suggest the existence of such a mechanism.

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Organism	environment	magnetic mineral	major group (phylum)	reference
Magnetospirillum magnetotacticum MS−1 =*magnetotacticum Aquaspirillum*	microaerophilic	Magnetite	α-proteobacteria	[281] [24, 40]
Magnetospirillum gryphiswaldense	microaerophilic	Magnetite	α-proteobacteria	[42]
Magnetospirillum magneticum AMB−1	facultative anaerobic	Magnetite	α-proteobacteria	[42]
Magnetospirillum sp. MGT−1	facultative anaerobic	Magnetite	α-proteobacteria	[42]
Rod		Greigite	γ-proteobacteria	[31]
Magnetotactic multicellular aggregate		magnetite, greigite		
Marine magnetic coccus MC−1	microaerophilic			
MSM−6				[46]
Bilophococcus magnetotacticus	microaerobic	magnetite, sulfur containing		[282]
Desulfovibrio magneticus	sulfate reducing		δ-proteobacteria	[283]
magnetotactic many-celled prokaryote MP			δ- proteobacteria	[58] [54, 60]
chain-forming marine coccus “barbell’			δ- proteobacteria	[49]
Magnetobacterium bavaricum	microaerophilic	giant magnetotactic rod, up to 1000 magnetosomes/cell	*Nitrospira* phylum	[33] [284]
MHB−1 magnetotactic rod			*Nitrospira* phylum	[47]
magnetotactic vibrio MV−1				[285]
magnetotactic vibrio MV−2				[285]
small vibroid/helicoids				[38]

Table 1 Magnetotactic bacteria.

Organism	magnetic flux density	response	reference
Acetobacter xylinum	$0.05 - 1.8\ T$	induction of atypical cellulose material	[286]
Actinomycetes		spores, inhibition of germination	[287]
Agrobacterium tumefaciens	magnet	reduced ability for tumor induction	[288]
Anabaena doliolum	300 mT, magnet	growth inhibition	[141]
Aquaspirillum magnetotacticum	50 μT, geomagn. field	magnetotaxis caused by magnetosomes	[8]
Bacillus subtilis	0.8, 2.5 mT	growth stimulation, altered cell morphology	[143]
Bacillus subtilis	15, 30 mT	increase and decrease of growth	[144]
Bacillus subtilis	5.2 – 6.1 T, inhom. field	suppression of cell death in stationary phase	[135]
Enterobacter	zero MF	modified resistance to various antibiotics	[130]
Escherichia coli	zero MF	antibiotic resistance; strains sensitive to zero MF	[129]
Escherichia coli	field of human body	changed properties of liquid water	[131]
Escherichia coli	0 – 110 μT	DNA: anomalous viscosity time dependence	[19]
Escherichia coli	1.35 mT	enhanced mechanosensensitive ion channel	[289]
Escherichia coli	8 – 60 mT, magnet	increased piperazine resistance	[290]
Escherichia coli	80 mT	altered ion channel activity in liposomes	[291]
Escherichia coli	30 – 100 mT	decrease of growth rate	[292]
Escherichia coli	300 mT	increased cell growth, gene expression, transposase	[293]
Escherichia coli	300 mT	no inhibitory effect on growth	[294]
Escherichia coli	0.5, 3 T	no increased DNA damage	[154]
Escherichia coli	0.5 – 4 T	no effects on growth & antibiotic sensitivity	[295]
Escherichia coli	1.4 T	growth unaffected	[296]
Escherichia coli	2, 5 T	increased mutagenicity, Ames test	[297]
Escherichia coli	5.2 – 6.1 T, inhom. MF	10^5-fold lowered cell death, stimul. of sigma factor	[160]
Escherichia coli	5.2 – 6.1 T	stimulation of growth and transcription	[298, 299]
Escherichia coli	7 T	suppression of cell death	[300]
Escherichia coli	11.7 T	growth stimulation	[301]
Escherichia coli	magnet	1-min pretreatment, growth stimulation	[20]
Leptospira interrogans	140 mT	lowered immunoreactivity, abnormal morphology	[302]
Micrococcus denitrificans	0.5 – 0.8 T	stimulation of growth and respiration	[303]
Photobacterium spec.	geomagnetic storms	prolonged bioluminescence after storms	[132]

Table 2 Effect of static magnetic fields on bacteria.

Organism	magnetic flux density	response	reference
Pseudomonas	zero MF	modified resistance to various antibiotics	[130]
Pseudomonas aeroginosa	$0.5 - 2$ mT	enhanced activity of gentamycin	[230]
Pseudomonas fluorescens	$0.1 - 1$ mT	stimulation of growth and metabolism	[137]
Rhodobacter sphaeroides	$0.13 - 0.3$ T	increased porphyrin production	[172]
R. sphaeroides mutant R-26	$1 - 100$ mT	reduction of photosynthetic $^1O_2$ yield	[237]
Salmonella typhimurium	$1.5 - 7$ T	no mutagenic effect; Ames test	[304]
Serratia marcescens	8 mT	growth inhibition, reduced virulence	[305]
Serratia marcescens	1.49 T, inhom. field	inhibition and stimulation of growth	[306]
Shewanella oneidensis	14.1 T	21 up-, 44 downregulated genes, no growth effect	[136]
Spirulina platensis	10 mT	enhanced growth, O_2 evolution, pigments	[200]
	70 mT	decreased growth, O_2 evolution, pigments	[200]
Staphylococcus albus	$0.1 - 1$ mT	stimulation of growth and metabolism	[137]
Staphylococcus aureus	MF of human body	changed properties of liquid water	[131]
Staphylococcus aureus	5.08 mT	decrease of colony size and number	[307]
Staphylococcus aureus	$30 - 100$ mT	growth inhibition under aerobiosis	[292]
Staphylococcus aureus	$30 - 100$ mT	growth stimulation under anaerobiosis	[292]
Staphylococcus aureus	$0.5 - 4$ T	no effects on growth & antibiotic. sensitivity	[295]
Staphylococcus aureus	1.49 T, inhom. MF	inhibition and stimulation of growth	[306]
Staphylococcus aureus	1.49 T	growth inhibition, exposure-time dependent	[296]
Streptococcus mutants	$30 - 100$ mT	aerobiosis = growth inhibition unaerobiosis = growth stimulation	[292]
Streptomyces claviforme	$60 - 70$ mT	altered coremia formation and rhythm	[308]
Streptomyces marinensis	$3 - 15$ mT	increase of neomycin synthesis	[309]
bacteria from Brazilean lagoon	$25 - 930$ μT	magnetotaxis caused by magnetosomes	[58, 310, 311]
bacteria	homogeneous MF	growth, shape, colony size unaltered	[312]
bacteria	1.5 T	growth inhibition	[306]
multicellular prokaryote	higher than geomagnetic field	complex swimming pattern; suggesting magnetoreception, not torque	[61]
sludge microbes	$80 - 300$ mT	enhanced sedimentation of activated sludge	[313]
waste water microbes	$0.35 - 0.63$ T	enhanced oxidation of phenol	[314]

Table 2 continued Effect of static magnetic fields on bacteria.

Organism	magnetic flux density	response	reference
Aspergillus giganteus mut alba	150 mT	reduction of myceliar mass	[315]
Aspergillus puniceus	200 mT	morphological changes in conidia	[316]
Aspergillus niger	200 mT	colony pigmentation	[316]
Aspergillus niger	$0.1 - 1$ mT	stimulation of growth and metabolism	[317]
Alternaria alternata	200 mT	morphological changes in conidia	[316]
Alternaria alternata	$0.1 - 1$ mT	growth inhibition	[314]
Alternaria alternata	$0.1 - 1$ mT	promotion of conidia formation	[134]
Alternaria alternata	0.1, 0.5, 1 mT	growth inhibition	[140]
Alternaria alternata	0.1, 0.5, 1 mT	promotion of conidia formation	[140]
Candida	15 mT	growth stimulation	[144]
Candida	$30 - 60$ mT	growth inhibition	[144]
Curvularia inaequalis	0.1, 0.5, 1 mT	growth inhibition	[140]
Curvularia inaequalis	0.1, 0.5, 1 mT	promotion of conidia formation	[140]
Curvularia inaequalis	$0.1 - 1$ mT	promotion of conidia formation	[134]
Fusarium oxysporum	$0.1 - 1$ mT	inhibition of conidia formation	[134, 311]
Fusarium culmorum	0.3 T	inhibition of mycelial growth reduced viability and conidia germination	[317]
Penicillium claviforme	$60 - 70$ mT	altered coremia formation and rhythm	[308]
Saccharomyces cerevisiae	400 μT	30% inhibition of bud formation	[139]
Saccharomyces cerevisiae	460 mT	growth inhibition	[318]

Table 3 Effect of static magnetic fields on fungi and protists.

Organism	magnetic flux density	response	reference
Saccharomyces cerevisiae	$0.5 - 0.8$ T	stimulation of growth and respiration	[303]
Saccharomyces cerevisiae	1.5 T	no effect on growth	[319]
Saccharomyces cerevisiae	0.35, 2.45 mT	no effect on growth	[320]
Saccharomyces cerevisiae	homogeneous	modification of radiation damage	[242]
Saccharomyces cerevisiae	7.28 T	pre-exposure: increased UV-survival rate	[321]
Saccharomyces cerevisiae	7.28 T	post-exposure: decreased UV-survival rate	[321]
yeasts, molds	magnet	growth inhibition	[312]
Acanthamoeba, 3 species	71, 106 mT	$14 - 71\%$ decrease of growth	[138]
Colpidium colpoda	$500 - 800$ mT	movement and growth inhibition	[322]
Loxophyllum	$500 - 800$ mT	movement and growth inhibition	[322]
Paramecium	$< 100\ \eta$T	growth acceleration	[323]
Paramecium		enhanced lethality in presence of dyes	[324]
Paramecium	126 mT	reduced velocity, disorganized movements	[325]
Paramecium tetraurelia	680 mT	magnetotaxis perpendicular to field lines	[207]
P. multimicronucleatum	680 mT	diamagnetic anisotropy of cilia	
Paramecium caudatum	field gradient 4.3 T/m	$10 - 15\%$ decrease in population	[326]
Paramecium	magnet	weak horizontal magnetic field	[327]
Paramecium caudatum	15.9, 1.9 mT, magnet	avoidance of the north pole	[328]
Paramecium caudatum	> 3 T	alignment with field lines, diamagnetism	[329]
Spirostomum ambiguum	12.5 T	less tolerance of 2,2'-dipyridyldisulfide	[330]
Trichomonas vaginalis	46, 120 mT	growth stimulation	[331]
Trichomonas vaginalis	220, 320, 420 mT	growth inhibition	[331]

Table 3 continued Effect of static magnetic fields on fungi and protists.

Organism	magnetic flux density	response	reference
Bacillus subtilis	0.8, 2.5 mT, 0.8, 1 kHz	altered growth pattern, increased growth	[143]
Bacillus subtilis	$5-90$ mT, $0-0.3$ Hz	growth inhibition or stimulation	[144]
Corynebacterium glutamicum	4.9 mT, 50 Hz	30% increase of ATP level	[199]
Escherichia coli	65, 97 ηT, 16, 60 Hz	modulation of enolase activity	[173]
Escherichia coli	21 μT, $2-24$ Hz	altered DNA-protein complexes	[332]
Escherichia coli	30 μT, 9 Hz	altered DNA-protein complexes	[333]
Escherichia coli	$0.1-1$ mT, 50 Hz	reduced transposition activity of Tn10 enhanced viability	[145]
Escherichia coli	1.1 mT, 60 Hz	increase of σ^{32} mRNA, transcription factor	[164]
Escherichia coli	0.07 - 1.1 mT, 72 Hz	enhanced translation in cell-free system	[166]
Escherichia coli	1.5 mT, pulsed square	more α subunit RNApolymerase, NusA	[165]
Escherichia coli	$0-22$ mT, 16 & 50 Hz	shortened generation time	[142]
Escherichia coli	$1-10$ mT, $2-50$ Hz	no effect on protein synthesis and growth	[334]
Escherichia coli	$0.2-0.66$ mT, 50 Hz	altered synthesis of β-galactosidase	[161]
Escherichia coli	$0.1-1$ mT, 50 Hz sinusoidal	reduction of Tn 10 transposition activity no effect on growth	[155]
Escherichia coli	$0.05-1$ mT, 50 Hz pulsed square wave	enhanced Tn 10 transposition no effect on growth	[145]
Escherichia coli	1.2 mT, 50 Hz	enhanced Tn5 transposition by DnaK/J	[157]
Escherichia coli	$0.4-1.2$ mT, 50 Hz	enhanced DNA repair, DnaK/J synthesis	[156]
Escherichia coli	$7.8-14$ mT, $5-100$ Hz	no alteration of stress proteins	[170]
Escherichia coli	10 mT, 50 Hz	decreased viability	[146]
Escherichia coli	150 mT, 50 Hz	cell killing, flow through magnetic field	[335]
Escherichia coli	160 mT, 62 kHz	decreased survival	[152]
Escherichia coli	weak field, low Hz	generates partial diploids during conjugation affects recombination and growth	[336]
Escherichia coli	ELF	growth stimulation	[20]

Table 4 Effect of alternating magnetic fields on bacteria and bacteriophages.

Organism	magnetic flux density	response	reference
Flavobacterium spec.	$0.1\mu T - 4\mu T$, 1, 10 Hz	enhanced growth, changed metabolism	[337]
Halobacterium halobium	$5 - 90$ mT, $0 - 0.3$ Hz	growth inhibition or stimulation	[144]
Lactobacterium acidophilum	1 Hz, 10 Hz	stimulated growth	[338]
Listeria innocua	$30 - 50$ kV/m	inactivation, skim milk	[339]
Leclercia adenocarboxylata	10 mT, 50 Hz	decreased viability	[146]
Photobacterium phosphoricum	$1 - 10$ mT, $2 - 50$ Hz	no effect on protein synthesis, growth and bioluminescence	[334]
Propionibacterium acnes	$200\mu T$, 50 Hz	no effect on internal Ca^{2+} and viability	[340]
Proteus vulgaris	$1 - 10$ mT, $2 - 50$ Hz	no effect on protein synthesis and growth	[334]
Pseudomonas aeroginosa	$5 - 90$ mT, $0 - 0.3$ Hz	growth inhibition or stimulation	[144]
Salmonella typhimurium	0.2 mT, 60 Hz	increase of azide-induced revertants	[158]
Salmonella typhimurium	14.6 mT, 60 Hz	protection from heat stress	[153]
Salmonella typhimurium	$5 - 90$ mT, $0 - 0.3$ Hz	growth inhibition or stimulation	[144]
Salmonella typhimurium	6.3 T, 0.5 Hz	no mutagenic effect	[341]
Salmonella typhimurium	27.12 MHz; 2.45 GHz	stimulation of growth	[342]
Serratia marcescens	8 mT	growth inhibition, reduced virulence	[305]
Staphylococcus aureus	10 mT, 50 Hz	decreased viability	[146]
Staphylococcus epidermidis	$5 - 90$ mT, $0 - 0.3$ Hz	growth inhibition or stimulation	[144]
Vibrio fischeri	1.3 mT, 60 Hz	no effect on bioluminescence	[21]
Vibrio qinghaiensis	$0.1 - 9.6$ mT, 50 Hz	enhanced luminescence in 'dose windows'	[21]
RNA-phage MS2 host: *Escherichia coli*	0.5 mT, 60 Hz 2.5 mT, 60 Hz	delay in phage yield impeding replication, increased yield	[343]

Table 4 continued Effect of alternating magnetic fields on bacteria and bacteriophages.

Organism	magnetic flux density	response	reference
Candida albicans	$5-90$ mT, $0-0.3$ Hz	growth inhibition or stimulation	[144]
Mycotypha africana	weak field, ELF	more yeast-like form, better germination	[203]
Mycotypha africana	$0-1.2$ nT, $0.8-50$ Hz	increase in germination	[20]
Pisolithus tinctorius	0.025, 0.1 mT, 50 Hz	stimulation of growth and ergosterol	[344]
Saccharomyces cerevisiae	0.5 μT, $100-200$ Hz	30% depression of respiration	[198]
Saccharomyces cerevisiae	120 μT, 50 Hz	reduced survival after UV irradiation	[159]
Saccharomyces cerevisiae	1 mT, 60 Hz	no additional mutation rates	[345]
Saccharomyces cerevisiae	0.35, 2.45 mT, 50 Hz	no effect on growth	[320]
Saccharomyces cerevisiae	$10-300$ mT, 50 Hz	no differential gene expression	[171]
Saccharomyces cerevisiae		stimulation of respiration	[346]
Saccharomyces cerevisiae	$2-620$ μT, 100 kHz	up to 30% growth stimulation	[347]
Saccharomyces cerevisiae	0.11 mV/m, 80 Hz	stimulated CO_2 production	[348]
Sclerotium rolfsii	$0.5-20$ Hz	reduction of growth and germination	[349]

Table 5 Effect of alternating magnetic fields on fungi and protists.

Organism	magnetic flux density	response	reference
yeast, cold-stressed		fermentation	[348]
Dictyostelium discoideum	200 μT, 50 Hz	decrease of fission rate, modulation of propionylcholinesterase activity	[174]
Dictyostelium discoideum	0.4 mT, trains of 2 ms pulses gated at 20 ms	damping of adenine nucleotide oscillations changes in phase relationship	[350]
Gonyaulax scrippsae	1.2, 11.5 mT, 50 Hz	bioluminescence	[268]
Loxodes striatus	0.5 – 2.0 mT, 50 Hz	increased swimming velocity	[250]
Paramecium biaurelia	0.5 – 2.0 mT, 50 Hz	increased swimming velocity, abnormal response in Ca^{2+}-channel mutant	[205]
P. multimicronucleatum	600 mT, 60 Hz	enhanced gravitaxis, transient response	[206]
Paramecium tetraurelia	1.8 mT, 72 Hz	increased cell division rate, Ca^{2+}-specific decreased membrane fluidity	[147]
Paramecium tetraurelia	650 mT, 60 Hz	no effect on swimming orientation	[207]
Physarum polycephalum	0.2 mT, 60, 75 Hz	delay of mitotic cycle	[148]
Physarum polycephalum	0.2 mT, 60, 75 Hz	mitotic delay; decreased respiration	[133]
Physarum polycephalum	0.1 mT, 60 Hz	lower ATP level; no decreased respiration	[201]
Physarum polycephalum	0.2 mT, 75 Hz	increase of mitotic cycle length	[151]
Physarum polycephalum	0.2 mT, 75 Hz	increase of mitotic cycle length	[149, 150]
Tetrahymena thermophila	0.5 – 2.0 mT, 50 Hz	increased swimming velocity	[205]
Tetrahymena pyriformis	10 mT, 60 Hz	delayed cell division, increased oxygen uptake	[202]

Table 5 continued Effect of alternating magnetic fields on fungi and protists.

substrate enzyme	magnetic flux density	response	reference
Na, K-ATPase	$0.2 - 2$ μT	threshold for stimulation	[188]
cyclic nucleotide	20 μT	50% activation, pure enzyme	[175]
phosphodiesterase Ca^{2+}		and calmodulin dependent	
hydroxyindole-O-methyltransferase	~ 25 μT	20% decrease of activity, crude extract	[181]
N-acetyl-serotonin transferase	~ 25 μT	10% decrease of activity, crude extract	[181]
hydroxyindole-O- methyltransferase	~ 70 μT	50% decrease of activity, crude extract	[181]
myosin light chain kinase	$0 - 200$ μT	activation, Ca^{2+} and calmodulin dependent	[177–179]
myosin light chain kinase	$0 - 400$ μT	kinase from chicken, no effect	[180]
B12 ethanolamine-ammonia lyase	0.1 T	radical-pair mechanism; 25% enzyme inhibition	[239]
trypsin	0.5 T	activity stimulation, pure enzyme	[192]
carboxydismutase	2 T	20% stimulation, purified enzyme	[191]
catalase	6 T	stimulation $16 - 52$%	[190]
L-glutamate dehydrogenase	6 T	10% inhibition in a uniform field	[190]
L-glutamate dehydrogenase	7 T	93% inhibition in a non-uniform field	[190]
adenylate kinase of the	250 μT, 75 Hz	bovine retina; decrease of activity	[351]
rod outer segment			
cytochrome-C oxidase	10 or 50 mT, 50 Hz	90% change of activity	[194]
from beef heart	300 μT or 10 mT	90% change, no changes at other fields	[194]
horseradish peroxydase	1 mT, $50 - 400$ Hz	activity is frequency dependent	[196]
horseradish peroxydase	$0 - 0.25$ T, static field	no effect	[224]
ornithine decarboxylase	5 mT, 60 Hz	50% stimulation of activity	[193]
from L929 fibroblasts	exposure of cells	threshold ~ 5 μT	
respiratory enzymes	constant	effects on activity	[352]
enzyme kinetics		radical pair recombination	[240]
esterases, *Triticum*	30 mT, 50 Hz	*in vivo* treatment, increased activity	[195, 353]
		increased proton extrusion	

Table 6 Effects of static and alternating magnetic fields on enzymes.