

BIOLOGICAL EFFECTS OF STATIC MAGNETIC FIELDS

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## I. INTRODUCTION

Claims for the biological effects of magnetism date from the discovery of magnetism in rocks by the ancient Greeks, Chinese, and Central American Olmecs.<sup>1-4</sup> The pre-Homeric Greeks mined  $\text{Fe}_3\text{O}_4$  in the province of Magnesia in Asia Minor, whence comes the names magnet and magnetite. Explanations for the powers of attraction exerted by pieces of magnetite on each other and on iron metal included the notion, thought to originate with Thales of Miletus, that magnets were alive and attracted iron metal by animating it. Both magnetite and the more weakly magnetic hematite  $\alpha\text{-Fe}_2\text{O}_3$  were thought to have medicinal qualities, and were even prescribed for Queen Elizabeth I of England by her physician William Gilbert of Colchester.

In 1600 this same William Gilbert published his monumental treatise, *De Magnete Magneticisque Corporibus et de Magno Magnete Tellure* (On the Magnet and Magnetic Bodies and on the Great Magnet the Earth). In addition to comparing magnetic forces with life forces, he proclaimed that the earth itself is a giant magnet. The publication summarized his 16 years of study of the interactions of small iron needles with spheres of magnetite called terrellas, or “little earths”. In 1570, Robert Norman, a London compass maker, had discovered that magnetized needles made neutrally bouyant with pieces of cork oriented downward at the angle of  $70^\circ$  as well as northward when suspended in water. Gilbert reached his conclusion about the magnetism of earth by comparing the magnetic inclination of the needle with his observations that the iron needles on the surface of the terrella are inclined from the horizontal at angles that increase from  $0$  to  $90^\circ$  as one passes from the equator to the poles.

Gilbert’s work was a triumph of experimental science and provided a mechanism for the operation of the magnetic compass. The fact that magnetized pieces of magnetite would orient in astronomically significant directions had long been used, at least by the Chinese and possibly by the Olmecs, for geomancy and divination, but was apparently not used for navigational purposes until the 11th century A.D. The first western accounts of this use are by Alexander Neckam and Petrus Peregrinus de Maricourt in the 13th century. From this use of magnetite came the name “lodestone” because it indicated the direction of the pole or lodestar. Iron needles magnetized by stroking with magnetite were subsequently employed. The invention and development of the magnetic compass was one of the technological developments that allowed navigation of the oceans and ushered in the great Age of Exploration. Christopher Columbus, in fact, discovered magnetic declination, namely, that magnetic north and geographic north do not coincide, and the difference varies with longitude.

An inversion of the Greek notion that magnets are animate was popularized by Franz Anton Mesmer, an Austrian physician, who arrived in Paris in the 1770s with a radical theory of human health.<sup>5</sup> This theory, referred to as “animal magnetism”, was based on the same medieval Hermetic philosophy that underlies astrology, alchemy, and magic. The theory envisions a human being as a microcosm corresponding to the world macrocosm. Mesmer believed that the human body had magnetic poles that correspond to those of the earth or cosmic, magnetic poles proclaimed by Gilbert. He postulated a subtle or imperceptible fluid that flowed from the cosmic magnetic poles through the body. Smooth, uninterrupted flow constitutes health. Blockage of the flow results in disease. Health can be restored by removing blockages and restoring smooth flow. This was accomplished by rubbing various parts of the body with magnets. This treatment was apparently efficacious because Mesmer became famous and was even immortalized in Mozart’s opera “Cosi Fan Tutti”. Along the way, he and his disciples invented group therapy, and by discovering that painted pieces of wood worked as well as magnets, the placebo. As Mesmer’s fame and fortune increased, the animosity of the French medical establishment increased until the French Royal Academy of Sciences appointed a commission, including Benjamin Franklin

(then the American ambassador to France) and Lavoisier, to investigate him. The commission declared him to be a quack and a fraud. Thus a cloud was cast over animal magnetism that persists to this day. This is in contrast with the brilliant success of "animal electricity", namely the experiments of Galvani and Volta of the same era that underlay the development of the understanding of electrical phenomena.

However, significant discoveries in the last few years require a reevaluation of animal magnetism, although not Mesmer's version. It is now known that many organisms precipitate inclusions of magnetic material. This phenomenon will be a chief focus of this review.

Biological effects of magnetic fields is a subject that includes many different topics. In order to make the treatment tractable, we have arbitrarily separated time-varying from static field effects. Static field effects will be covered here; time-varying field phenomena including magneto-phosphores and effects of induced currents will be covered in a companion chapter.

Even the subject of static field effects covers many topics. These include the use of magnetic fields in spectroscopies of biological material, including nuclear magnetic resonance (NMR), electron paramagnetic resonance (EPR), and recoilless nuclear gamma resonance (Mössbauer effect), and magnetic susceptibility and magnetization measurement. Magnetic fields have also been used to orient cells or cell fragments in suspension. Applications of magnetism in physiology and clinical medicine include NMR imaging, magnetic targeting and modulation of drug delivery, magnetic separation of biological materials, use of magnetism in surgical procedures, and noninvasive measurement of blood flow. A rapidly growing area spanning AC and DC regimes is the measurement of magnetic fields generated by the human body, and the use of those measurements in medicine and physiology. A large area involves mutagenic, mitogenic, metabolic, morphological, and developmental effects of exposure of organisms or biological materials to intense DC magnetic fields or to null field conditions. Another important area includes behavioral effects of magnetic fields, including effects on orientation, migration, and homing and the involvement of the geomagnetic field in the activities of organisms. Biomineralization of magnetic materials is especially significant for this latter topic, but could also play a role in other interactions of organisms with electromagnetic fields.

## II. PHYSIOLOGICAL AND MEDICAL APPLICATIONS OF MAGNETISM

Magnetic properties and spectroscopy of biological materials have been extensively studied. Especially significant advances in NMR have been made in the last few years.<sup>6</sup> These include increased resolution and sensitivity, pulsed programming, Fourier decomposition of complex spectra allowing study of whole organisms or perfused organs, and observation of the time development of chemical intermediates, e.g., metabolites containing phosphorus, in metabolic pathways.<sup>7-9</sup>

Superconducting magnets with bores large enough to accommodate human bodies have allowed development of NMR imaging systems with resolution comparable and even superior to X-ray and positron computerized tomography and ultrasound techniques.<sup>10,11</sup> The basis of the method is that when a magnetic field gradient is superposed on a static, homogeneous magnetic field, nuclei such as protons will resonate at different frequencies at each point along the gradient. The magnitude of the signals at each frequency is proportional to the number of protons at that point. By switching the gradient to different directions and recording the frequency spectra, the three- or two-dimensional proton density map in any plane can be reconstructed by computer. Measurement of relaxation times also allows discrimination of chemical differences, e.g., different types of tissue. Fields of the order of  $5 \times 10^{-2}$  to 1.5 T with gradients of the order of  $10^{-2}$  T/m are used for periods of the order of  $1/2$  hr. Switching of the gradients will involve changing magnetic fields as high as 2 T/sec. Considering the rapid development of this diagnostic method and its enthusiastic reception by

the medical community, it will shortly be the major cause of human exposure to intense magnetic fields (above 1 T).

The development of superconducting quantum interference devices (SQUIDS) with very high sensitivity has spurred the study of the very weak magnetic fields generated by electrical processes in the human body.<sup>12-14</sup> Applications include magnetocardiography, magnetoencephalography, measurement of pulmonary activity, and detection of body iron stores due to asbestos inhalation or diseases such as Thalassemia, which result in hemochromatosis.<sup>15</sup>

Magnetic devices have been used in several surgical procedures including repair of giant retinal tears,<sup>16</sup> bougienage of esophageal atresia in infants,<sup>17</sup> and in the treatment of aneurysms.<sup>18</sup> Magnetic agitation has been used to modulate the release of macromolecules such as insulin from polymers with magnetic inclusions which are implanted in the body.<sup>19</sup>

The voltage induced when an electrolyte flows perpendicular to a magnetic field, known as the magnetohydrodynamic effect, has been used for a number of years to noninvasively meter blood flow.<sup>20,21</sup> The voltage induced across a blood vessel of diameter  $d$  is

$$\epsilon(\text{volts}) = Bvd \quad (1)$$

where  $B$  is the magnetic flux density in tesla and  $v$  is the perpendicular flow velocity. For  $v = 0.6$  m/sec and  $d = 0.025$  m (human aorta), 15 mV would be generated in a 1-T field. These potentials also show up in electrocardiograms of animals in magnetic fields (see Section IV).

Magnetic microcarriers have been used to target drugs to specific locations in the body and in cell separation and immunological assays.<sup>23,24</sup> These applications are based on the translation of magnetic particles relative to the diamagnetic fluid background in magnetic field gradients. The potential energy of a magnetic dipole of moment  $m$  in a magnetic field with flux density  $B$

$$E_m = - \vec{m} \cdot \vec{B} \quad (2)$$

If the field is homogeneous, the dipole tends to align in the field but no translation occurs. If there is a magnetic field gradient in the  $x$  direction, the dipole will experience a force in the  $x$  direction

$$F = m \, dB/dx \quad (3)$$

If the magnetic material is ferromagnetic or ferrimagnetic,  $m$  is generally independent of  $B$  for fields greater than a few tenths of a tesla. For paramagnetic materials at sufficiently high temperatures this is not the case and

$$m = \chi V H \quad (4)$$

where  $\chi$  is the magnetic susceptibility,  $V$  is the volume, and  $H$  is the magnetic field intensity. Then Equation 3 becomes

$$F_x = \chi V H \, dB/dx \quad (5)$$

ignoring the smaller susceptibility of opposite sign of the diamagnetic background fluid. For small particles in a viscous medium (including water at ambient temperatures), viscous forces are more important than inertial forces and the particle quickly reaches its terminal velocity

$$v = F_x / 6\pi\eta r \quad (6)$$

where  $r$  is the radius of the particle and  $\eta$  is the viscosity ( $10^{-3}$  nsec/m<sup>2</sup> = 0.01 poise for water at room temperature). Thus the velocity due to magnetic forces depends on the nature of the material, the magnitude of the field gradient, and the size of the particle. Since  $F_x$  and  $m$  are proportional to volume of the magnetic material and therefore increase as  $r^3$ ,  $v$  increases as  $r^2$ . However, the size of magnetic microcarriers is limited by the need for a large surface-to-volume ratio, and by the tendency of large particles to coagulate due to interparticle forces.

To employ magnetic drug microcarriers, large field gradients must be generated outside the body by suitably shaped, magnetized pole pieces. In the immunological procedures, the microcarriers, to which specific antibodies or antigens are chemically attached, can be separated by the use of high gradient magnetic separation (HGMS) filters consisting of fine stainless steel wires in a magnetic field strong enough to magnetize the wires. Gradients as high as  $10^4$  to  $10^5$  T/m can be generated within a few diameters of the wires. As the fluid flows through the filter the magnetic particles and anything attached to them are trapped on the wires. This method has been applied to the separation of cells and proteins<sup>25-28</sup> and to removal of microorganisms from water.<sup>29,30</sup>

### III. ORIENTATION OF CELLS AND BIOMOLECULES IN INTENSE MAGNETIC FIELDS AND MAGNETIC FIELD EFFECTS ON CHEMICAL REACTIONS

Alignment of molecular aggregates with sufficient diamagnetic anisotropy will occur in intense magnetic fields (see Appendix). The energy of cylindrically symmetric molecular aggregates in an external magnetic field  $B$  is given by

$$E_m = -\frac{1}{2} [\chi_{\parallel} + (\chi_{\parallel} - \chi_{\perp}) \cos^2\theta] V H \cdot B \quad (7)$$

where  $V$  is the volume and  $\chi_{\parallel}$  is the least negative susceptibility ( $\chi_{\parallel} - \chi_{\perp}) > 0$ .  $\theta$  is the angle between the  $\chi_{\parallel}$  direction and the field direction.  $\chi_{\parallel}$  is usually parallel or perpendicular to the axis of cylindrical symmetry. If  $\chi_{\parallel}$  is parallel to the axis, the aggregate will align with the axis perpendicular to the field. If  $\chi_{\parallel}$  is perpendicular to the axis the aggregate will align with the axis parallel to the field. Since the alignment in the field is opposed by the randomizing forces due to thermal energy, the average alignment  $\langle \cos^2\theta \rangle$  of an ensemble of rods in the field at ambient temperatures will be an exponential function of the ratio of magnetic to thermal energies

$$\langle \cos^2\theta \rangle = \frac{\int \cos^2\theta e^{-E_m/kT} dV}{\int e^{-E_m/kT} dV} \quad (8)$$

Experimental results have been reviewed comprehensively by Maret and Dransfeld.<sup>31,32</sup> Muscle fibers,<sup>33</sup> chloroplasts,<sup>34</sup> retinal elements,<sup>35,36</sup> sickled erythrocytes,<sup>37</sup> bacteriophage fibers,<sup>38</sup> membranes,<sup>39,40</sup> and macromolecules including nucleic acids<sup>31</sup> have diamagnetic anisotropy and have been aligned in intense, homogeneous magnetic fields. Highly oriented structures can result from polymerization in an intense field. Torbet et al.<sup>41</sup> produced oriented fibrin gels from fibrin monomers in a field of 11 T. The fibrin monomers were produced by enzymatic cleavage of fibrinogen. Murthy and Yannas<sup>42</sup> prepared oriented collagen films by heat precipitation in a magnetic field. Collagen in solution dissociates into monomers at low temperatures and precipitates at higher temperature ( $\sim 37$  K). The monomers are apparently not aligned. Alignment of dimers, trimers, etc. occurs as they form from monomers with increasing temperature in the field.

In addition to polymer alignment, intense magnetic fields may interact with biomaterials in other ways. Sperber et al.<sup>43</sup> observed oriented growth of pollen tubes in intense fields and suggests redistribution of membrane proteins that regulate intercellular concentrations of  $\text{Ca}^{2+}$ . Audus<sup>44,45</sup> had previously observed oriented growth, or magnetotropism, in oat shoots and cross roots in inhomogeneous magnetic fields, with growth occurring in the direction of decreasing field intensity. Labes<sup>46</sup> and Aceto et al.<sup>47</sup> proposed interaction of magnetic fields with cell membranes as a plausible mechanism for physiological effects. They noted that membranes have liquid, crystal-like properties and are close to phase transitions at physiological temperatures. Magnetic field could affect membrane fluidity or other properties. Magnetic orientation of diamagnetically anisotropic domains in artificial phospholipid bilayers has been reported.<sup>48</sup> Magnetic fields also affect the fluid-gel transition in agarose gels,<sup>49</sup> possibly by alignment of the monomers in the fluid phase.

Magnetic fields of the order of  $10^{-3}$  to  $10^{-2}$  T can affect chemical reactions by influencing the electronic spin states of reaction intermediates.<sup>50-53</sup> These effects can have biological consequences.<sup>54,55</sup> A relatively simple chemical illustration of the effect involves homolytic cleavage of a chemical bond to produce two radicals.\* Since the electrons in the chemical bond are spin-paired in an  $S = 0$  or singlet state,<sup>55a</sup> these electrons on the nascent radicals will also have overall singlet character as the radicals separate. Separation is a diffusion-controlled process and there is a high probability that the two radicals will reencounter each other. If the electrons retain their overall singlet character, a reencounter is likely to produce recombination. If the electrons have overall triplet ( $S = 1$ ) character, the bond will not reform and the radicals will eventually separate and perhaps participate in other chemical reaction. The transition from singlet to triplet can result from the interaction of the odd electrons of the radicals with the nuclear magnetic moment(s) of the atom(s) on which they have high probability density. This interaction, the magnetic hyperfine interaction, is equivalent to a local magnetic field at the electrons produced by the nuclei. Different local magnetic fields cause the electrons on the radicals to precess at different rates, which destroys singlet phasing and results in triplet formation. However, an applied magnetic field will decouple the electrons and the nuclei, suppressing formation of the triplet state. This enhances the recombination rate and suppresses the other chemical reactions. The decoupling of the electrons and the nuclei will occur when the intensity of the applied field exceeds the effective magnetic field produced by the hyperfine interaction. Then the electrons will precess in phase about the applied field rather than at different rates about the local field. This condition is typically satisfied for fields of the order of  $10^{-3}$  to  $10^{-2}$  T.

A variation of this scheme is proposed to account for the effects of magnetic fields on electron transport in photosynthetic, purple bacterial membranes.<sup>51,55,56</sup> The effects are observed when elements of the transport chain are electrochemically reduced, forcing back transfer of the photoexcited electron. The electron transport sequence can be summarized as follows:

1.  ${}^S(\text{A}) + \text{photon} \rightarrow {}^S(\text{A})^*$
2.  ${}^S(\text{A})^* + (\text{B}) \rightarrow {}^S(\text{A}^+ + \text{B}^-)$
3.  ${}^S(\text{A}^+ + \text{B}^-) \rightleftharpoons {}^T(\text{A}^+ + \text{B}^-)$
4.  ${}^S(\text{A}^+ + \text{B}^-) \rightarrow {}^S(\text{A}) + (\text{B})$
5.  ${}^T(\text{A} + \text{B}) \rightarrow {}^T(\text{A}) + (\text{B})$

(A) corresponds to bacteriochlorophyll dimer and (B) corresponds to bacteriopheophytin. S and T stand for singlet and triplet, respectively, and \* stands for the photoexcited state. (1) Bacteriochlorophyll absorbs a photon resulting in electron excitation. (2) Electron transfer

\* Homolytic cleavage is the breaking of a covalent, single bond so that one electron from the bond is left on each fragment, resulting in two free radicals with single, unpaired electrons.

to bacterioopheophytin occurs, resulting in positive and negative charges on donor and acceptor, respectively. (3) The positive ion-negative ion pair are initially in a singlet state which can evolve into a triplet state via the hyperfine interaction mechanism. In the blocked transport chain, the ion pair decays by back transfer of the electron to a less energetic state of bacteriochlorophyll. (4) If the ion pair is in the singlet state, back transfer populates the singlet ground state of bacteriochlorophyll. (5) If the ion pair is in the triplet state, back transfer populates an intermediate energy triplet state of bacteriochlorophyll which is detected by a delayed fluorescence method. It is found that the amount of bacteriochlorophyll triplet produced following flash excitation is magnetic field-dependent. Because the photosynthetic apparatus is highly structured and membrane-bound, exchange interactions between the ions also play a role in the formation of the triplet state in (3). Although the experimental conditions cited above are nonphysiological, mechanisms of this kind could conceivably play a role in electron transport in viable biological systems.

#### IV. MUTAGENIC, MITOGENIC, MORPHOLOGICAL, AND DEVELOPMENTAL EFFECTS OF MAGNETIC FIELDS

A large number of papers have been published on this topic and a number of bibliographies, reviews, and symposia have appeared.<sup>57-75</sup> Moreover, a number of interaction mechanisms have been proposed.<sup>51,76-82</sup> However, at this time this area remains an empirical science with little elucidation of effects in terms of mechanism. Only some of the more recent reports will be cited here.

Mutagenic effects of chronic exposure to DC magnetic fields have been investigated. Mahlum et al.<sup>83</sup> exposed male mice to a magnetic field of up to 1T for 28 days. The mice were subsequently mated to two females per week for up to 8 weeks and the resulting embryos were assayed for viability 10 days later. No significant differences were reported between exposed and sham-exposed (control) groups. Kale and Baum<sup>84</sup> exposed fruitfly (*Drosophila melanogaster*) male eggs, larvae, pupae, and adults to fields up to 3.7 T for up to 7 days. After mating with females, broods were tested for induction of genetic damage by the sex-linked, recessive lethal test. No evidence for induction of mutations under the conditions of exposure were reported. Skopek et al.<sup>84a</sup> exposed *Salmonella* and cultured human lymphoblasts to 10-T magnetic fields for 4 hr. Cells were surveyed for toxic and mutagenic effects with a forward mutation assay. No effects of magnetic field exposure were found for either cell type when compared with sham-exposed controls.

Morphological and developmental effects have been investigated. Sikov et al.<sup>85</sup> reported no effects on the development of mice after intrauterine exposure to 1 T during gestation. An earlier study by Nahas et al.<sup>86</sup> indicated that exposure of rodents to 0.02- to 0.12-T fields for 1 month resulted in no toxic or histopathological effects. Brewer<sup>87</sup> studied guppies (*Lebistes reticulatus*) chronically exposed to a 0.05-T magnetic field and reported reduction in spawn rate and gestation period in successive generations exposed to the field. However, field effects were not permanent; reproduction eventually returned to normal when fish were removed from the magnetic field. Mild et al.<sup>88</sup> studied development of frog (*Xenopus laevis*) embryos exposed at 0.25 T for periods up to 1 week, at temperatures just above the threshold for development in the embryos. If the effect of the magnetic field is equivalent to a reduction in temperature,<sup>47</sup> exposed embryos should not have developed. However, no differences between development of exposed embryos and unexposed controls were reported. Previous studies had indicated effects of magnetic field exposure on development of frog embryos.<sup>89</sup> Strand et al.<sup>89a</sup> report enhancement of fertilization following exposure of trout sperm, ova, or both to 1-T magnetic fields.

Frazier et al.<sup>99</sup> investigated mammalian cell cultures continuously exposed to magnetic fields of 0.1 or 0.3 T through 80 cell doublings. No mitogenic effects of the field were

reported when doubling times of exposed cells were compared to controls. Differences in plating efficiencies between exposed cells and controls were cited and ascribed to an as yet unexplained increased clumping of exposed cells. Exposure of frozen cells at 1 T did not result in changes in cell morphology<sup>90</sup> as reported earlier.<sup>91</sup> Cultured cells from human bronchogenic carcinoma and from Burkitt lymphoma were exposed to DC magnetic fields up to 1.15 T by Chandra and Stefani.<sup>92</sup> They report that growth characteristics were unaffected by exposure. In vivo exposure of mouse tumors did not cause retardation of growth of the tumor. Leitmannova et al.<sup>93</sup> reported changes in morphology of aged red blood cells in magnetic fields.

Moore<sup>94</sup> studied growth of five species of bacteria and a yeast in DC and slowly varying magnetic fields up to 0.09 T. He reports stimulation or retardation of growth depending on the field strength, frequency, and organism. A number of previous studies had indicated that growth of bacteria and yeasts could be altered by static magnetic fields.<sup>95-97</sup>

Electrophysiological effects of static magnetic fields have been investigated. Blatt and Kuo<sup>98</sup> reported no change in the action potential in the interpodal cells of the fresh water alga *Nitella* exposed to fields up to 2 T. These cells have bioelectrical activity and previous studies<sup>98a</sup> had indicated a reduction of the action potential in magnetic fields. Extended exposure at 1.6 T was not toxic for cells. Edelman et al.<sup>99</sup> reported an increase with time in the amplitude of the compound action potential of stimulated frog sciatic nerve when fields up to 0.71 T were applied perpendicular to the nerve. Fields applied parallel to the nerve produced no changes. However, Gaffey and Tenforde<sup>100</sup> report no changes in electrical conduction in frog sciatic nerve in fields up to 2 T and suggest that results of Edelman et al. are due to changes in temperature. Semm et al.<sup>101</sup> reported electrical changes in cells in the pineal glands of guinea pigs when exposed to magnetic fields of the order of  $10^{-4}$  T. Raybourn<sup>101a</sup> reports that  $10^{-3}$  to  $10^{-2}$ -T fields acutely reduce electroretinographic responses in turtle retina, but do not reduce retinal sensitivity. The effect might involve magnetic field effects on chemical reactions (see Section III).

Static, magnetic fields affect electrocardiograms in mammals.<sup>22,102,103</sup> Alterations in the T wave of rats, rabbits, and baboons are reported at exposures above 0.3 T, and are due to the potentials associated with the flow of blood in the magnetic field. There are apparently no chronic physiological effects associated with this phenomenon.

There are reports of alteration of enzyme activity in vitro by magnetic fields.<sup>104,105</sup> For example, Haberditzl<sup>104</sup> claims that fields up to 7.8 T diminished the activity of glutamic dehydrogenase, while a 6-T field enhanced the activity of catalase. Nonuniform fields produced larger effects than uniform fields. Weissbluth and co-workers<sup>106</sup> reported no effects of intense magnetic fields up to 22 T on the activities of several enzymes.

Ripamonti et al.<sup>107</sup> studied the effect of magnetic field exposures up to 12.5 T on the responses of the contractile protozoan *Spirostomum ambiguum* to the toxic substance 2,2'-dipyridyldisulfide. Magnetic field exposure reportedly diminished the ability of the organism to survive the drug and lengthened the extension phase of the contraction cycle. It was hypothesized that interactions of the magnetic field with cellular membranes alters the regulation of  $Ca^{2+}$  transients. There were no toxic effects of exposure to magnetic fields without the drug. Bücking et al.<sup>108</sup> had previously reported that magnetic field exposure affected the force of contraction of isolated muscle, which also involves regulation of intracellular  $Ca^{2+}$ .

deLorge<sup>109</sup> reports that low-intensity magnetic fields have no measurable effects on operant behavior in monkeys. However, experiments at high magnetic fields showed a suppression of a learned response above a threshold between 4.6 and 7.0 T. Davis et al.<sup>109a</sup> report no behavioral alterations in mice exposed to 1.5-T magnetic fields. Further data on the effects of very intense magnetic fields come from NMR studies on perfused, whole organisms. Fossell et al.<sup>9</sup> note that exposure of perfused rat hearts at 6.4 T does not alter either pressure development or heart rate.



A survey of workers exposed to intense magnetic fields was conducted by Beischer<sup>110</sup> who found no adverse effects of short exposures to fields up to 0.5 T. Epidemiological studies of magnetic field effects in humans are presently being conducted by Budinger et al.<sup>111</sup> and by the National Radiological Protection Board in the U.K. Reviews concerned especially with potential hazards of magnetic field exposure associated with NMR imaging have been published.<sup>74</sup> Interim magnetic field exposure guidelines have been discussed.<sup>112</sup>

Finally, nature has conducted an experiment over geologic times on life in a substantial magnetic field. Magnetotactic bacteria<sup>113</sup> are sediment-dwelling bacteria that contain particles of  $\text{Fe}_3\text{O}_4$  that orient them in the geomagnetic field (see Section V). These particles produce strong intracytoplasmic magnetic fields and field gradients in the bacterium. The fields can be as large as several tenths of a tesla near the surface of the particles. Thus these bacteria carry out all of their cellular and metabolic functions in intracellularly generated magnetic fields.

## V. MAGNETIC FIELD EFFECTS ON ORIENTATION AND HOMING

At the end of the last century, Kreidl<sup>114</sup> published an experiment on magnetic field effects on orientation in crabs. The experimental design was contrived to produce an effect and so does not correspond to the natural circumstances of crabs, but provides a paradigm for effects in other organisms. Crabs periodically molt and subsequently form a new exoskeleton. In the process of molting they also lose their statoliths, dense particles that form part of the vestibular system. They subsequently pick up particles of sand to serve as new statoliths. Kreidl took newly molted crabs and placed them in an aquarium in which the only available particles were magnetic. The crabs indeed placed magnetic particles in their ear labyrinths. When Kreidl approached a crab with magnetic statolith with a bar magnet the crab adopted an orientation that could be correlated with the resultant of the magnetic and gravitational forces on the particles. Electrophysiological responses from crayfish with ferrite statoliths stimulated by magnetic fields have subsequently been reported.<sup>114a</sup>

Since Kreidl's experiment, magnetic field effects have been observed in the orienting behavior of a very diverse group of normal organisms, including bacteria,<sup>113</sup> algae,<sup>115</sup> snails,<sup>116</sup> planaria,<sup>117</sup> honeybees,<sup>118</sup> salmon,<sup>119</sup> salamanders,<sup>120</sup> homing pigeons,<sup>121</sup> robins,<sup>122</sup> mice,<sup>123</sup> and humans.<sup>124-126</sup> In addition, training experiments on pigeons,<sup>127</sup> skates,<sup>128</sup> and tuna<sup>129</sup> have demonstrated the ability of these organisms to sense magnetic fields. Two interaction mechanisms have been elucidated: (1) detection by the organism of the electric field induced by Faraday effect as the organism moves through the magnetic field; (2) interaction of the magnetic field with magnetic material in the organism.

The first mechanism is apparently operative in marine sharks, skates, and rays which are sensitive to electric fields as low as  $5 \times 10^{-7}$  V/m in sea water.<sup>130</sup> The animals detect the electric fields through the ampullae of Lorenzini, which are long, conductive channels that connect electrically sensitive cells in the snout with pores on the skin. Flowing ocean currents or motion of the animal through the geomagnetic field induce voltage gradients with sign and magnitude depending on orientation, which are in general above the sensitivity threshold of the animal. Kalmijn<sup>128</sup> demonstrated that skates could be trained to use magnetic fields of the order of the geomagnetic field as an orientational cue. Brown et al.<sup>7131</sup> used electrophysiological measurements to show that the ampullae of Lorenzini can detect variations in the geomagnetic field. Jungerman and Rosenblum<sup>132</sup> have considered the possibility of the magnetic induction mechanism for an animal in air. They concluded that a circular, electrically conducting loop millimeters in diameter, would be required to overcome thermal noise, with voltages induced by changes in magnetic flux in the loop as the animal changes its heading.

Evidence for orientation by the second mechanism was obtained for homing pigeons in

the classical experiment of Keeton.<sup>133</sup> Keeton glued small bar magnets to the backs of the heads of a group of homing pigeons and compared their homing ability with that of a group of control birds carrying brass weights. Under sunny skies both groups oriented and homed equally well when released from unfamiliar sites many miles from the home loft, but under overcast skies when the birds could not see the sun, the orientation of the birds carrying magnets was disrupted, whereas control birds oriented normally. Subsequently, Walcott and Green<sup>134</sup> used Helmholtz coils attached to the heads of pigeons to change the orientation of the birds under overcast conditions. The orientation depended on the direction of the magnetic field, as determined by the direction of current in the coils. Pigeon orientation is also affected by magnetic anomalies and magnetic storms.<sup>135,136</sup> The experimental results suggest that in addition to a magnetic compass, a homing pigeon may have a magnetic "map".<sup>137</sup> The results have been reviewed by Walcott,<sup>121</sup> Gould,<sup>118,137</sup> Able,<sup>138</sup> and Griffin.<sup>138a</sup> Magnetic orientation in migratory birds has been reviewed by Able<sup>138</sup> and by Wiltschko.<sup>139</sup> Although attempts to observe magnetic sensitivity in pigeons by cardiac response have not been successful, Bookman<sup>127</sup> was able to train pigeons to detect the presence of magnetic fields in a flight cage.

Walcott et al.<sup>140</sup> dissected pigeons with nonmagnetic tools and found magnetic material in head and neck sections. Most of the magnetic material was localized in a piece of tissue between the dura and the skull. Each pigeon had an inducible, remanent moment\* of  $10^{-8}$  to  $10^{-9}$  A·m<sup>2</sup>, which disappeared at 575°C, indicating Fe<sub>3</sub>O<sub>4</sub>. Presti and Pettigrew<sup>141</sup> found magnetic material in the neck musculature of pigeons and migratory, white-crowned sparrows but did not find localized magnetic materials in the heads. Although the connection between the magnetic material and magnetic sensitivity has not been established definitely, it is suggested. Elucidation of anatomical structure is clearly required. Yorke,<sup>142</sup> Kirschvink and Gould,<sup>143</sup> and Presti and Pettigrew,<sup>141</sup> have speculated on the role of Fe<sub>3</sub>O<sub>4</sub> in a magnetic sensor. Yorke points out that if a pigeon can somehow measure the total magnetization of its ensemble of magnetic particles, there is enough magnetic material present to indicate the field direction with high accuracy.

A possible connection between Fe<sub>3</sub>O<sub>4</sub> and magnetic field effects on behavior is also found in honeybees. The behavioral effects have been reviewed by Martin and Lindauer<sup>144</sup> and Gould.<sup>118</sup> Honeybee workers communicate the location of a food source to other workers in a hive by means of a "waggle dance" on a vertical honeycomb. The angle between the direction of the dance and the vertical direction indicates the angle between the food source and the sun. Consistent errors in the dance angle occur which vanish when the magnetic field in the hive is nulled by means of external coils. In anomalous situations where bees are made to dance on horizontal surfaces, after an initial period of disorientation they dance along the eight magnetic compass directions (N, NE, E, SE, etc.).<sup>118,144,145</sup> If the geomagnetic field is nulled, the dances become disoriented again. There is also evidence that bees can use the daily variations in the geomagnetic field to set their circadian rhythms.<sup>144</sup>

Gould et al.<sup>146</sup> have found that honeybees also contain Fe<sub>3</sub>O<sub>4</sub>. They measured an average, induced remanent moment of about  $2 \times 10^{-9}$  A·m<sup>2</sup> per bee, distributed between single-domain and superparamagnetic-sized particles, mostly localized to the abdomen. Recently, Kuterbach et al.<sup>147</sup> found bands of cells around the abdominal segments that contain numerous iron-rich granules. The granules are primarily a hydrous iron oxide, which can be a precursor in the precipitation of Fe<sub>3</sub>O<sub>4</sub> (see below).

In addition to pigeons and honeybees, Fe<sub>3</sub>O<sub>4</sub> appears to be widely distributed in the biological world.<sup>148</sup> Magnetic inclusions have been found in organisms as diverse as dolphins,<sup>149</sup> butterflies,<sup>150</sup> tuna,<sup>151</sup> green turtles,<sup>152</sup> marine crustacea,<sup>153</sup> bacteria,<sup>154</sup> and humans.<sup>155</sup> The first identification of Fe<sub>3</sub>O<sub>4</sub> in an organism was by Lowenstam,<sup>156</sup> who found

\* Magnetic dipole moment that persists following exposure to an intense magnetic field (see Reference 163).

it in the tooth denticles of a group of mollusks, called "chitons".  $\text{Fe}_3\text{O}_4$  is very hard as well as magnetic and this is advantageous to chitons as they scrape algae off rocks. This is an illustration of the fact that the presence of  $\text{Fe}_3\text{O}_4$  in an organism does not necessarily mean that the organism has a magnetic detector. In addition to hardness,  $\text{Fe}_3\text{O}_4$  is also apparently the densest material that can be mineralized by organisms, and this might play a role in certain cases.

The best documentation to date for the connection between magnetically sensitive behavior and the presence of  $\text{Fe}_3\text{O}_4$  is for aquatic bacteria that orient and swim along magnetic field lines.<sup>113,157</sup> This behavior is termed "magnetotaxis." Magnetotactic bacteria were discovered serendipitously in the early 1970s by Richard Blakemore.<sup>113</sup> He initially found bacteria from both fresh water and marine muds that accumulated at the north side of drops of water placed on a microscope slide. These bacteria were attracted and repelled by the north and south poles of a bar magnet, respectively. Subsequently, Blakemore and Kalmijn<sup>158</sup> used homogeneous magnetic fields produced by Helmholtz coils to show that New England bacteria swim along magnetic field lines in the field direction, that is, in the direction indicated by the north-seeking end of a magnetic compass needle. When the field produced by the coils is reversed by reversing the direction of current flow, the bacteria respond immediately by executing U-turns and continuing to swim in the field direction. Killed cells orient along the field lines and rotate when the field direction is reversed, but do not move along the field lines. Thus magnetotactic bacteria from New England behave as self-propelled magnetic dipoles and are predominantly north-seeking.<sup>158,159</sup>

Magnetotactic bacteria are easy to find in the sediments of almost any aquatic environment.<sup>157,159</sup> In addition to world-wide dispersion, the diversity of morphological types suggests that the phenomenon is a feature of a number of bacterial species. Two characteristics unify these species. They are apparently all anaerobic or microaerophilic<sup>157</sup> and they all contain magnetosomes,<sup>160</sup> which are unique intracytoplasmic structures consisting of enveloped  $\text{Fe}_3\text{O}_4$ <sup>154,161</sup> (Figure 1). One species, *Aquaspirillum magnetotacticum*, has been isolated and grown in pure culture in a chemically defined medium,<sup>162</sup> In this species there are typically 20 to 25 cuboidal  $\text{Fe}_3\text{O}_4$  particles about 500 Å on a side per cell. The particles are arranged in a chain which is fixed along the axis of motility of the bacterium. Magnetosomes are arranged in one or two chains in most other bacterial species as well. Since only soluble ferric iron is available in the growth medium,<sup>162</sup> the presence of intracytoplasmic  $\text{Fe}_3\text{O}_4$  in *A. magnetotacticum* implies a bacterial biomineralization process. In fact, since total cellular iron is about 2% of the cellular dry weight, these bacteria are prodigious manufacturers of  $\text{Fe}_3\text{O}_4$ . If iron is withheld from the growth medium, these bacteria grow without magnetosomes; these cells are nonmagnetotactic.\* Thus the magnetotactic response is definitely correlated with the presence of the magnetosomes.

$\text{Fe}_3\text{O}_4$  has an inverse spinel structure and is ferrimagnetic with a Curie temperature of 580 °C.<sup>163</sup>  $\text{Fe}_3\text{O}_4$  particles of 500-Å dimensions are single, magnetic domains with a permanent magnetic moment approaching the saturation magnetization of bulk  $\text{Fe}_3\text{O}_4$ ,  $480 \times 10^3$  A/m. Larger ferrimagnetic particles form magnetic domains, reducing the magnetostatic energy and the remanent magnetic moment. The upper size limit for single magnetic domains is approximately the width of a domain wall  $d_w$ , which is a function of the exchange and anisotropy energy of the material

$$d_w = \left( \frac{kT_c}{Ka^3} \right)^{1/2} a \quad (9)$$

\* Nonmagnetotactic cells grow as well as magnetotactic cells in the homogeneous culture medium which provides all essential nutrients.

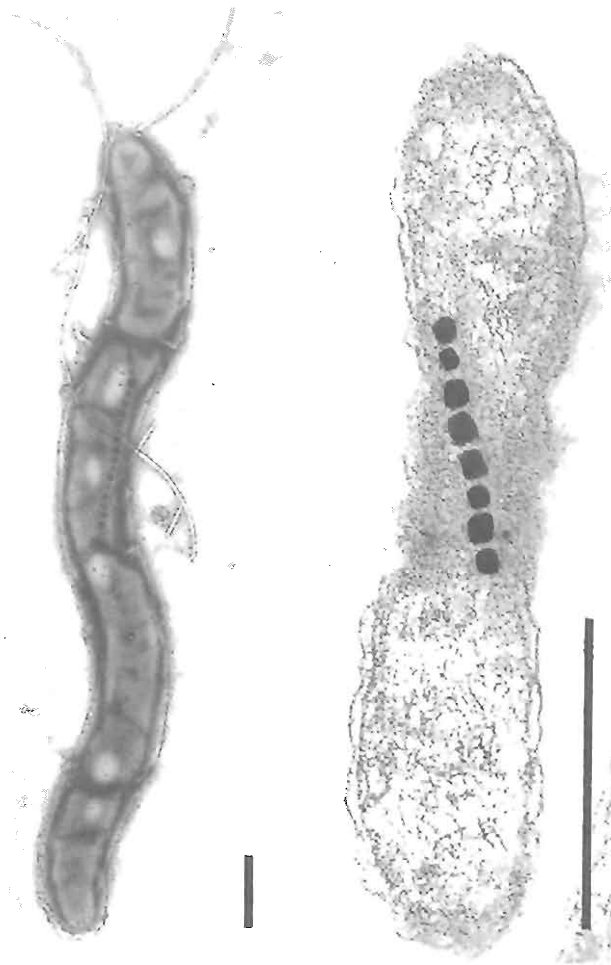


FIGURE 1. Magnetotactic spirillum showing chain of enveloped  $\text{Fe}_3\text{O}_4$  particles. (Left) whole spirillum; (right) thin section. Bar in each photo is  $1\text{-}\mu\text{m}$ .<sup>167</sup>

where  $k$  is Boltzman's constant,  $T_c$  is the Curie temperature,  $K$  is the anisotropy energy per unit volume, and  $a$  is the atomic spacing. Substituting values for  $\text{Fe}_3\text{O}_4$ <sup>163</sup> yields  $d_w \approx 500 \text{ \AA}$ . More precise calculations by Butler and Banerjee<sup>164</sup> for cubic particles yield  $d_w = 760 \text{ \AA}$ . On the other hand, if the particle dimension is less than a certain value  $d_s$ , it will be superparamagnetic at room temperature; i.e., thermal energy will cause transitions of the magnetic moment between equivalent, easy magnetic axes of the particle with a consequent loss of the time-averaged remanent moment.<sup>165</sup> The transition probability is a function of the anisotropy energy and the thermal energy and the most probable transition time between orientations is

$$\tau \sim \tau_0 \exp(KV/2kT) \quad (10)$$

where  $\tau_0$  is a constant of the order of  $10^{-9}$  sec and  $V (= d_s^3)$  is the particle volume. Particles of dimensions  $> 350 \text{ \AA}$  are stable for times  $> 10^6$  years; hence  $d_s < 350 \text{ \AA}$ . Thus particles of  $\text{Fe}_3\text{O}_4$  with dimensions  $350 \text{ \AA} < d < 760 \text{ \AA}$  are permanent, single magnetic domains with remanent magnetization of  $4.8 \times 10^5 \text{ A/m}$ . We can assume that each  $500\text{-\AA}$  particle produced by a bacterium has a moment of  $6.0 \times 10^{-17} \text{ A}\cdot\text{m}^2$ .

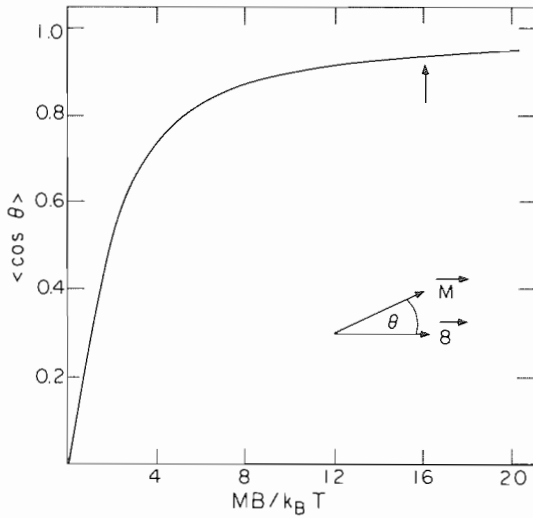


FIGURE 2. Langevin function (Equation 14) plotted as a function of  $mB/kT$ . Arrow indicates the value of the function for typical magnetotactic bacteria.

When the single-domain particles are organized in a chain as they are in *A. magnetotacticum*, the interactions between the particle moments will cause them to be oriented parallel to each other along the chain direction.<sup>166</sup> Thus the moment of the entire chain will be equal to the sum of the individual particle moments. For chains of 22 particles, this gives a total remanent moment  $m = 1.3 \times 10^{-15} \text{ A}\cdot\text{m}^2$ . Since the particles are fixed in the bacterium by the magnetosome envelope, the bacterium is, in effect, a swimming magnetic dipole.

The simplest hypothesis for magnetotaxis is passive orientation of the swimming bacterium along the magnetic field lines by the torque exerted by the field on the magnetic moment.<sup>167,168</sup> Thermal energy, on the other hand, will tend to disorient the bacterium during swimming. The energy of the bacterial moment in a magnetic field  $B$  is

$$\begin{aligned} E_m &= - \vec{m} \cdot \vec{B} \\ &= - mB \cos\theta \end{aligned} \quad (11)$$

where  $\theta$  is the angle between  $\vec{m}$  and  $\vec{B}$ . The thermally averaged orientation of an ensemble of moments, or equivalently, the time-averaged orientation of a single moment

$$\langle \cos\theta \rangle = \frac{\int \cos\theta e^{-E_m/kT} dV}{\int e^{-E_m/kT} dV} = L(\alpha) \quad (12)$$

$L(\alpha)$  is the Langevin function

$$L(\alpha) = \coth(\alpha) - \frac{1}{\alpha}; \quad \alpha = mB/kT \quad (13)$$

and is plotted in Figure 2. If we consider *A. magnetotacticum* in the earth's magnetic field of  $0.5 \times 10^{-4} \text{ T}$  at room temperature, then  $\alpha \sim 16$  and  $\langle \cos\theta \rangle > 0.9$ . Because the

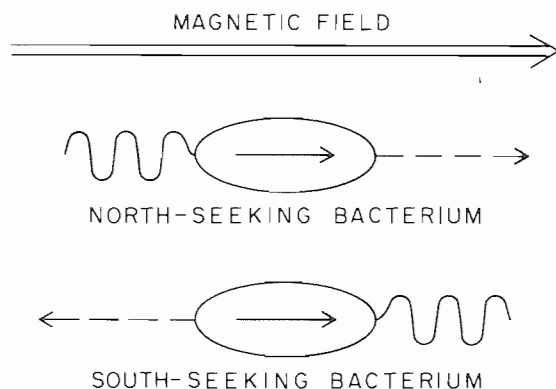


FIGURE 3. Schematic drawings of north- and south-seeking magnetotactic bacteria. The arrow in the cell represents the magnetic dipole moment of the magnetosome chain, with the arrowhead indicating the north-seeking pole.

Langevin function asymptotically approaches 1 as  $\alpha$  increases, the orientation would not improve significantly if there were more particles and the moment per bacterium were larger. Thus each bacterium is in effect a biomagnetic compass optimized to the geomagnetic field at room temperature.<sup>6167</sup>

For passively oriented bacteria, the migration velocity along the magnetic field lines is

$$v_H = v_0 \langle \cos\theta \rangle \quad (14)$$

where  $v_0$  is the forward velocity of the swimming bacterium and  $\theta$  is the angle between the axis of motility and the magnetic field. If  $v_0$  is independent of  $B$  and the magnetic moment is parallel to the axis of motility

$$v_H = v_0 L(\alpha) \quad (15)$$

providing that the velocity is averaged over a time which is long compared to the rotational diffusion time (typically, 1 sec). This is the basis of a method for measuring the magnetic moment of individual bacteria.<sup>169</sup> Determination of the width of the U-turns executed by swimming bacteria following reversal of the magnetic field direction<sup>170</sup> also gives a measure of the magnetic moment.<sup>171</sup> Static light scattering<sup>172</sup> and magnetically induced birefringence techniques<sup>173</sup> have been used to determine the average moment per cell in suspensions of live or dead bacteria. For diverse types of cells the moments range from  $10^{-15}$  to  $5 \times 10^{-13}$   $A \cdot m^2$  per cell.

*A. magnetotacticum* is bipolarly flagellated, i.e., it has a flagellum at each end of the cell and can swim in either direction along the magnetic field lines. However, many other magnetotactic bacterial species one observes in sediments are asymmetrically flagellated and have unidirectional motility. As noted above, these bacteria from New England swim along magnetic field lines in the field direction. Based on the passive orientation hypothesis, this occurs if the bacterial moment is oriented in the cell forward with respect to the flagellum (Figure 3). Then the bacterium will propel itself in the field direction when the moment is oriented in the field, and will be north-seeking in the geomagnetic field. If the bacterial moment were oriented in the cell rearward with respect to the flagellum, the cell would propel itself opposite to the field direction when the moment was oriented in the field, and hence would be south-seeking in the geomagnetic field.

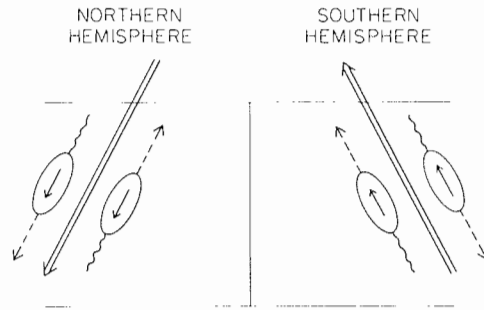


FIGURE 4. Swimming directions of north- and south-seeking bacteria along the inclined geomagnetic field lines in each hemisphere. The arrow in each cell represents the magnetic dipole moment of the magnetosome chain, with the arrowhead indicating the north-seeking pole.

South-seeking bacteria have been produced in the laboratory by subjecting them to magnetic pulses of AC magnetic fields which are strong enough to overcome the magnetic interaction forces between the particles in the chain and cause their moments to rotate and reorient along the chain in the opposite direction.<sup>158</sup> Field strengths of several  $10^{-2}$  T are required, consistent with magnetic measurements on freeze-dried cells<sup>174</sup> and in agreement with estimates based on the "chain of spheres" model of Jacobs and Bean,<sup>166</sup> who considered the magnetic properties of a chain of single-domain particles in a different context before the discovery of magnetotactic bacteria.

The predominance of north-seeking bacteria in the Northern Hemisphere is due to the inclination of the geomagnetic field.<sup>175</sup> Since many sediment-dwelling bacteria are anaerobic or microaerobic,\* it is advantageous for them to have mechanisms that prevent them from swimming up toward the toxic, higher oxygen concentration at the water surface, and keep them in the sediments. Since the geomagnetic field is approximately dipolar, the magnetic field lines at the surface of the earth are inclined at an angle that increases with latitude. The total flux density at geomagnetic latitude  $\theta$  is approximately

$$B_G = 0.3 (\sin^2\theta + 1)^{1/2} \times 10^{-4} \text{ T} \quad (16)$$

and the inclination  $I$  from the horizontal is given by

$$\tan I = 2 \tan\theta \quad (17)$$

In the Northern Hemisphere the field is inclined downwards, pointing straight down at the north magnetic pole. In the Southern Hemisphere the field is inclined upwards, at an angle increasing with latitude, pointing straight up at the south magnetic pole. At the geomagnetic equator the field is horizontal.

Because of the inclination of the field lines, north-seeking bacteria migrate downward in the North Hemisphere and upward in the Southern Hemisphere (Figure 4). South-seeking bacteria migrate upward in the Northern Hemisphere and downward in the Southern Hemisphere. At the equator, both polarity types migrate horizontally. Because downward directed motion is advantageous, north-seeking bacteria should be favored in the Northern Hemisphere

\* Anaerobic bacteria live in the absence of free oxygen. Microaerobic bacteria tolerate or require low concentrations of oxygen.

and south-seeking bacteria should be favored in the Southern Hemisphere. At the equator neither polarity would be favored.

Examination of bacteria in sediments from various places in the world confirms this hypothesis. In contrast to New England (inclination,  $70^{\circ}$  N) and other Northern Hemisphere locales, magnetotactic bacteria in fresh water and marine sediments in Australia and New Zealand (inclination,  $70^{\circ}$  S) are almost exclusively south-seeking.<sup>176,177</sup> These bacteria have chains of particles and can be remagnetized to north-seeking polarity.<sup>176</sup> At the geomagnetic equator in Brazil (inclination,  $0^{\circ}$ ) both north- and south-seeking bacteria are present in roughly equal numbers.<sup>178</sup> Thus the vertical component of the geomagnetic field selects the predominant cell polarity in natural environments, with downward directed motion advantageous for, and upward directed motion detrimental to, survival of the organisms. At the geomagnetic equator where motion is directed horizontally, both polarities benefit because horizontally directed motion reduces harmful upward migration.

The role of the vertical magnetic field component has also been confirmed in laboratory experiments.<sup>176,178</sup> When a sediment sample from New England, initially containing north-seeking bacteria, is placed in a coil that produced a field of twice the magnitude and opposite sign to the ambient vertical field, the polarity of the bacteria in the sample inverted over several weeks, i.e., over many bacterial generations. If a sample is placed in a coil that cancels the vertical component of the ambient magnetic field, the population in the sample tends toward equal numbers of both polarities, again over many generations. Equal numbers of both polarities also result when samples initially containing all north- or all south-seeking bacteria are placed in an enclosure that cancels the ambient magnetic field. Further experiments in null field by Blakemore<sup>157</sup> confirm the role of oxygen. When samples with tight stoppers are placed in the zero field enclosure, bacteria of both polarities are ultimately found in the sediment and in the water column up to the surface. When the sample bottles are loosely stoppered, allowing diffusion of air, bacteria are found in the sediments but not in the water column.

While the ability to synthesize  $\text{Fe}_3\text{O}_4$  and construct magnetosomes is certainly genetically encoded, the polarity of the magnetosome chain cannot be encoded. If a bacterium that lacks magnetosomes starts to synthesize them *de novo*, there is equal probability that when the particles grow to permanent, single-domain size, the chain will magnetize with north-seeking pole forward as with south-seeking pole forward; a population of these bacteria will consist of 1:1 north- and south-seekers. If, however, the daughter cells inherit some of the parental magnetosomes during cell division, they will inherit the parental polarity. As they synthesize new magnetosomes at the ends of their inherited chains, the magnetic field produced by the existing particles will magnetize the new particles in the same direction. Thus, north-seeking bacteria can produce north-seeking progeny and south-seeking bacteria can produce south-seeking progeny. However, there are mechanisms by which some progeny with the opposite polarity can be produced in each generation. For example, if in the cell division process, some of the daughter cells inherit no parental magnetosomes, these cells will synthesize them *de novo* and about one half those cells will end up with the polarity opposite to that of the parental generation. So in New England, where north-seeking bacteria are found and predominate, some south-seekers are produced in each population division. Under normal circumstances, these south-seekers are unfavored by being directed upwards towards the surface when they are separated from the sediments, and their total population remains low compared to the north-seeking population. However, when the vertical magnetic field is inverted, as in the experiment described above, these south-seekers are suddenly favored and their progeny eventually predominate as the previously favored north-seeking population declines in their newly unfavorable circumstances. When the vertical component is set equal to zero, neither polarity is favored and the north- and south-seeking populations eventually equalize.



We can envision a similar process occurring in natural environments during reversals or excursions of the geomagnetic field. During these processes the vertical component changes sign over thousands of years. This would be accompanied by a change in the predominant polarity of the magnetotactic bacteria population in that locale.

Other possible advantages of magnetotaxis to bacteria involve rapid migration along magnetic field lines. This could be useful for population dispersal, as an escape response, or in outrunning chemical diffusion. There are also consequences of magnetotaxis and  $\text{Fe}_3\text{O}_4$  synthesis that may or may not be advantageous. Magnetic bacteria that are within  $4\ \mu\text{m}$  of each other will experience magnetic forces greater than the forces of Brownian motion.  $\text{Fe}_3\text{O}_4$  has a density of 5.1, hence precipitation increases the average density of the bacteria, helping them to stay down in the sediments even when they are not swimming, and may serve some metabolic functions as well.<sup>157</sup>

Finally, as mentioned in Section IV, magnetotactic bacteria live their lives and carry out all their cellular functions in a magnetic field of their own making which varies from over 0.1 T at the surface of the particles to 0.01 T or less at the periphery of the cell, depending on shape of the bacterium, and the location of the particles. The field due to a dipole moment  $m$  at points with coordinates  $r, \theta$ , varies as  $r^{-3}$  and  $(\mu_0/4\pi)(1 + 3\cos^2\theta)^{1/2}$  when  $r \gg \ell$ , the length of the dipole.  $\theta = 0$  corresponds to the dipole moment direction. If we consider the moment  $m = 10^{-15}\ \text{A}\cdot\text{m}^2$  in a magnetotactic bacterium as a point dipole, then the field at the surface of a sphere of radius  $1\ \mu\text{m}$  around the moment would vary from  $2 \times 10^{-4}$  to  $1 \times 10^{-4}$  T as  $\theta$  varies from 0 to  $90^\circ$ .

When  $r < \ell$ , the calculation is more difficult. One approach is to replace the individual  $\text{Fe}_3\text{O}_4$  particles of dimension  $d$  by equivalent current cylinders. This calculation<sup>179</sup> gives fields up to about 0.5 T between the particles and up to 0.3 T at the ends of the particle chain. At points on a line perpendicular to one end of the particle chain the field falls from 0.22 T at the edge of the last particle to 0.03 T at  $d$ , 0.008 T at  $2d$ , 0.003 T at  $3d$ , and 0.002 T at  $4d$ .

Progress has been made in elucidating the  $\text{Fe}_3\text{O}_4$  biomineralization process.<sup>180,181</sup> Mössbauer spectroscopic studies of magnetic and nonmagnetic strains and cell fractions of *A. magnetotacticum* have revealed several iron-containing materials in the cells in addition to  $\text{Fe}_3\text{O}_4$ . One of these is a high-density hydrous iron oxide that is spectroscopically similar to the mineral ferrihydrite. It appears that  $\text{Fe}_3\text{O}_4$  precipitation occurs following partial reduction of a ferrihydrite precursor.

Reduction of a ferrihydrite precursor to  $\text{Fe}_3\text{O}_4$  also occurs in the radular teeth of the marine chiton.<sup>148,182,183</sup> Iron is transported to the superior epithelial cells of the radulae as ferritin. Then iron is transferred to a preformed organic matrix on the tooth surface as ferrihydrite. Finally, the ferrihydrite is reduced to  $\text{Fe}_3\text{O}_4$ . The resulting  $\text{Fe}_3\text{O}_4$  particles have dimensions of the order of  $0.1\ \mu\text{m}$ . Thus the  $\text{Fe}_3\text{O}_4$  precipitation process appears to be similar in magnetotactic bacteria and in chitons, and may be similar in other organisms as well. The facility with which bacteria can be manipulated will allow further elucidation of the precipitation process and eventual understanding of how the bacteria control the size, shape, and number of particles.

## VI. CONCLUSION

Life evolved in the geomagnetic field and it should not be surprising that some and perhaps many species are magnetically sensitive. The discovery of  $\text{Fe}_3\text{O}_4$  in diverse organisms provides a new basis for understanding the interaction of organisms with the geomagnetic field. Inclusions of magnetic materials in organisms could also play a role in the other magnetic field and nonionizing radiation effects.

Effects of high-static fields remains an important area for research, because of increasing

exposure of humans to higher fields in connection with NMR imaging and other technologies involving high magnetic field devices. Epidemiological studies are important for establishing guidelines for human, but more work needs to be done at both the cellular and subcellular levels to elucidate interactive mechanisms. High field alignment of macromolecules and magnetic field interactions with membranes are promising areas but their connection with physiological effects in intact cells and organisms needs to be elucidated.

Finally, there is the question of synergistic effects. Healthy cells or organisms might be able to adapt successfully to the physiological stress imposed by static magnetic fields, but this might not be the case for organisms that are coping with additional stresses, such as disease, environmental factors, etc. This possibility should be considered especially in setting guidelines for high field exposure.

## ACKNOWLEDGMENTS

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## APPENDIX: ELECTROMAGNETIC UNITS AND DEFINITIONS

Purcell<sup>184</sup> gives an excellent discussion of magnetic field concepts; for a review of magnetic measurements see Foner<sup>185</sup> and Morrish.<sup>163</sup> In discussing the interactions of static magnetic fields with materials most workers use the centimeter-gram-second (cgs)-electromagnetic units (emu). In the SI system, the magnetic flux density

$$\vec{B} = \mu_0 \vec{H}$$

and

$$\vec{B} = \mu_0(\vec{H} + \vec{M}) \quad (A1)$$

in vacuum and in a material medium, respectively.  $\vec{H}$  is the magnetic field intensity and the magnetization per unit volume. The permeability of free space

$$\mu_0 = 4\pi \times 10^{-7} \text{ H/m} \quad (A2)$$

where H/m (henry per meter) is equivalent to weber per meter per ampere. The volume magnetization of diamagnetic and paramagnetic materials is related to the magnetic field intensity by the magnetic susceptibility

$$\vec{M} = \chi \vec{H} \quad (A3)$$

In the SI system,  $\chi$  is a dimensionless quantity. In magnetically ordered materials,  $\vec{M}$  is a complex function of H and can have finite values even at  $\vec{H} = 0$ .

In the cgs-emu  $\mu_0 = 1$  and

$$\vec{B} = \vec{H} + 4\pi\vec{M} \quad (A4)$$

Some of the relations between emu and SI units are as follows

Magnetic flux density B	$1 \text{ G} = 10^{-4} \text{ T}$
Magnetic field density H	$1 \text{ Oe} = (10^3/4\pi) \text{ A/m}$
Magnetic moment m	$1 \text{ emu} = 10^{-3} \text{ A}\cdot\text{m}^2$
Magnetization, magnetic moment per unit volume M	$1 \text{ emu/cm}^3 = 10^3 \text{ A/m}$
Magnetic susceptibility $\chi$	$\chi(\text{emu}) = (1/4\pi)\chi(\text{MKS})$

In the emu system, Faraday's law of magnetic induction is

$$\epsilon = -10^{-8} \text{ d}\Phi/\text{d}t \quad (\text{A5})$$

where the emf (electromotive force)  $\epsilon$  (volts) is induced in a conducting loop of area A normal to B, and the magnetic flux

$$\Phi = BA \quad (\text{A6})$$

The emf can be produced by a time-varying field in a stationary loop or by a loop whose normal component is changing with respect to a static magnetic field. The factor of  $10^{-8}$  also appears in the equation for the flow potential when Equation 1 is written with v and d in centimeter per second and centimeter respectively.

Magnetic moments, magnetization, and magnetic susceptibility of materials are expressed on a unit weight, unit volume, per mole, per atom, or molecule basis. Magnetic moments and magnetization have the units emu, gauss, cgs, or ergs per gauss in the emu system, with  $1 \text{ emu} = 1 \text{ G} = 1 \text{ cgs} = 1 \text{ erg/G}$ . For example, the saturation magnetic moment per unit volume, or magnetization, of  $\text{Fe}_3\text{O}_4$  is  $480 \text{ emu/cm}^3$ , or  $92 \text{ emu/g}$ . The conversion factor is the density. Magnetic moments of atoms and molecules are often expressed as Bohr Magnetons ( $\mu\text{B}$ ) with  $1 \mu\text{B} = 0.927 \times 10^{-20} \text{ ergs/G}$ . The electron has a magnetic moment of  $1 \mu\text{B}$ .  $\text{Fe}_3\text{O}_4$  has a magnetic moment of  $4 \mu\text{B}$  per formula unit.

The free energy of magnetic dipoles or of materials with permanent, macroscopic magnetization  $\vec{m}$  oriented at angle  $\theta$  in a magnetic field of flux density B is

$$E_m = -\vec{m} \cdot \vec{B} = -mB \cos\theta \quad (\text{A7})$$

In a homogeneous magnetic field the free energy is a minimum when  $\cos\theta = 1$ , i.e.,  $\vec{m}$  is parallel to  $\vec{B}$ . In an inhomogeneous magnetic field additional lowering of the free energy comes from translational motion of the material toward increasing field strength. The translational force along the gradient is

$$F_x = m \frac{\text{d}B}{\text{d}x} \quad (\text{A8})$$

where x is the magnetic field gradient direction.

For materials without a permanent dipole moment, a magnetic field will induce a moment per unit volume  $\vec{M}$ , where

$$\vec{M} = \overline{\chi} \vec{H} \quad (\text{A9})$$

$\overline{\chi}$  is the susceptibility tensor with units emu/G or ergs/G<sup>2</sup>. For diamagnetic materials  $\overline{\chi}$  is small and negative and is generally independent of temperature. For example, H<sub>2</sub>O has an isotropic volume magnetic susceptibility  $\chi_v = -0.4 \times 10^{-7}$  emu/(G-cm<sup>3</sup>). In paramagnetic materials, i.e., materials with unpaired electrons,  $\chi$  is larger in magnitude, positive in sign, and is generally temperature-dependent. At ambient temperatures typical paramagnets have susceptibilities that follow the Curie Law

$$\chi = N\mu_{\text{eff}}^2/3k_B T \quad (\text{A10})$$

where  $k_B$  is Boltzman's constant,  $N$  is the number density of paramagnetic atoms, and  $\mu_{\text{eff}}$  is the effective magnetic moment per atom. From quantum mechanics, the saturation magnetic moment of an atom or molecule is proportional to the spin and orbital angular momentum

$$\mu = g S \mu_B \quad (\text{A11})$$

where  $\mu_B$  is the Bohr magneton and  $g$  is the proportionality or  $g$ -factor. If we consider spin angular momentum only,  $g \approx 2$ . The effective magnetic moment

$$\mu_{\text{eff}} = [g^2 S (S + 1) \mu_B^2]^{1/2} \quad (\text{A12})$$

In a hypothetical example, if every water molecule had an unpaired electron spin ( $S = 1/2$ ), the magnetic moment per molecule would be  $1 \mu_B$  and the paramagnetic susceptibility per cubic centimeter at 300 K would be  $2.2 \times 10^{-6}$  emu/G. The total susceptibility would be the sum of paramagnetic and diamagnetic contributions of  $2.16 \times 10^{-6}$  emu/G. In some cases the diamagnetic susceptibility contribution can be larger than the paramagnetic contributions. This is often the case in large biological molecules that have a single or a few paramagnetic atoms.

In a magnetic field the free energy is given by

$$E_m = - \frac{1}{2} \vec{H} \cdot \chi \cdot \vec{H} \quad (\text{A13})$$

where the magnitude and direction of the induced moment depends on the orientation of the molecule in the field. If the susceptibility is isotropic, the induced moment is always parallel to  $H$  and

$$E_m = - \frac{1}{2} \chi H^2 \quad (\text{A14})$$

There are no rotational or translational forces in a homogeneous magnetic field. In an inhomogeneous magnetic field, the material will experience a translational force in the direction of increasing or decreasing field strength depending on the sign of  $\chi$

$$F_x = \chi V H \, dH/dx \quad (\text{A15})$$

where  $\chi$  is the susceptibility per unit volume and  $V$  is the volume. Diamagnetic materials move in the direction of decreasing field strength while paramagnetic materials move toward

increasing field strength. As discussed in Section II, this is the basis of a method for separating diamagnetic from paramagnetic materials. In suspensions or solutions, the force depends on the difference in susceptibility between the material and the medium.

Anisotropic materials require two or at most three independent parameters to specify the magnetic susceptibility. In the most general case,

$$E_m = -\frac{1}{2} (\chi_x H_x^2 + \chi_y H_y^2 + \chi_z H_z^2) \quad (\text{A16})$$

where  $x$ ,  $y$ , and  $z$  denote the eigenvectors of the diagonalized susceptibility tensor. These three vectors often correspond to molecular symmetry axes. In addition to translational forces in inhomogeneous fields, there are rotational forces in homogeneous fields. For example, benzene has an inplane susceptibility  $\chi_{\perp} = -4.5 \times 10^{-7} \text{ emu/G-cm}^3$  ( $= -5.7 \times 10^{-6}$  in SI units) and a susceptibility normal to the plane  $\chi_{\parallel} = -12 \times 10^{-7} \text{ emu/G-cm}^3$  ( $= -1.5 \times 10^{-5}$  in SI units).<sup>186</sup> The molecule will experience a torque tending to align its plane parallel to the field direction. In general, any molecule or molecular assembly with anisotropic diamagnetism will tend to align so that the least negative susceptibility direction is parallel to the applied field.

In anisotropic paramagnets the highest (positive) susceptibility direction will tend to align parallel to the field. If  $\chi_{\parallel}$  is the susceptibility along the minimum energy direction and  $\theta$  is the angle between that direction and the applied field

$$E_m = -\frac{1}{2} \chi_{\parallel} H^2 - \frac{1}{2} \Delta \chi H^2 \cos^2 \theta$$

$$\Delta \chi = \chi_{\parallel} - \chi_{\perp} \quad (\text{A17})$$

where by definition  $\Delta \chi > 0$  and  $E_m$  is minimized when  $\theta = 0$ . The degree of orientation of an ensemble of molecules at a given field strength and temperature can be calculated from statistical mechanics. The angular distribution function  $F(\theta)$ , which specifies the probability that a molecule has an equilibrium orientation at angle  $\theta$  with respect to  $H$ , can in general be expanded in terms of  $\cos^n \theta$ . For molecules with cylindrical symmetry, odd terms in  $n$  vanish. Then a convenient measure of the degree of orientation is the average value of the second Legendre polynomial

$$\overline{P_2(\cos \theta)} \equiv \overline{(3/2 \cos^2 \theta - 1/2)} \quad (\text{A18})$$

From statistical mechanics,

$$P_2(\cos \theta) = \frac{\int \left( \frac{3}{2} \cos^2 \theta - \frac{1}{2} \right) \exp \left( -\frac{1}{2} \Delta \chi H^2 \cos^2 \theta / kT \right) d \cos \theta}{Z} \quad (\text{A19})$$

where  $Z$  is the partition function. Complete alignment means  $\overline{\cos^2 \theta} = 1$  and  $\overline{P_2(\cos \theta)} = 1$ . For random orientation in three dimensions  $\overline{\cos^2 \theta} = 1/3$ , hence  $\overline{P_2(\cos \theta)} = 0$ . Even for molecules such as benzene with large diamagnetic anisotropies, thermal excitation will overcome magnetic alignment and the equilibrium alignment will be small. However, if  $N$  molecules are contained in an ordered array or aggregate,  $\Delta \chi$  for the single molecule could be replaced by  $N \Delta \chi$  in the exponential in Equation A17, resulting in substantial alignment.

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