Magnetite and Magnetotaxis in Bacteria and Algae

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Magnetotactic bacteria navigate along geomagnetic field lines. By this means they find and stay in their preferred habitat and avoid the toxic effects of oxygen. Cells contain single-magnetic-domain Fe_3O_4 particles which are responsible for their magnetotactic response. Numerous Fe_3O_4 particle organized in chains have recently been found in eukaryotic cells, euglenoid, motile, magnetotactic algae of the genus Anisonema.

1. Introduction

Magnetotactic bacteria that orient and swim along magnetic field lines are found in freshwater and marine sediments [1]. The diversity of environments and morphological types suggests that magnetotaxis is a feature of many bacterial species [2]. Two characteristics unify these organisms. They are all anaerobic or microaerophilic and they all contain magnetosomes [3] which are unique, intracytoplasmic structures consisting of membrane-bounded particles of magnetite, Fe_3O_4 [4]. One species, Aquaspirillum magnetotacticum, has been isolated and cultured in a chemically defined medium. Iron accounts for 2 per cent of the dry weight of the organism with most of the iron (90%) present as Fe_3O_4 [5]. The particles have linear dimensions of 40-50 nm and are arranged in a chain that longitudinally traverses the cell (Fig. 1). The number of particles per bacterium is variable within a population but typically average 20. Variation of the culture conditions, especially the oxygen tension, affects the number of particles [6].

2. Mechanism Of Magnetotaxis

The particles in A. magnetotacticum are in the single-magnetic-domain size range for Fe_3O_4. Large particles of Fe_3O_4 form magnetic domains that reduce the remanent magnetic moment and hence the magnetostatic energy. The domains are separated by transition regions called domain walls. When the particle length is less than the width of a domain wall, it cannot form domains and will be a single magnetic domain. The upper size limit for single magnetic domains d_{sd} is thus approximately the width of a domain wall d_w, which is a function of the exchange and anisotropy energy of the material. Calculations [7] for equidimensional particles yield d_{sd} = 760 A. d_{sd} increases with the axial ratio (length/width). On the other hand, if the particle dimension is less than a certain value d_s, it will be superparamagnetic at room temperature; that is, thermal energy will cause transitions of the single domain magnetic moment between equivalent easy magnetic axes of the particle with a consequent loss of the time-averaged remanent moment. Particles of dimensions greater than 350 A are stable for times greater than 10^6 years at ambient temperature; hence d_s < 350 A. Thus particles of Fe_3O_4 with dimensions 350 A < d < 760 A are permanent, single magnetic domains with remanent moments of 480 G/cm^3. So each 500-Å particle produced by a bacterium has a magnetic moment of 6.0×10^{-14} emu.

When the single magnetic 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 [8]. Thus, the moment of the entire chain will be equal to the sum of the individual particle moments. For chains of twenty-two particles, this gives a total remanent moment $M = 1.3 \times 10^{-12}$ emu. 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 [9]. Thermal energy, on the other hand, will tend to disorient the bacterium during swimming. In a magnetic field B, the energy E_M is

$$E_M = - M \cdot B = - MB \cos\theta \qquad (1)$$

where θ is the angle between M and B. The thermally averaged orientation of an ensemble of moments $\langle\cos\theta\rangle$ or equivalently, the time averaged orientation of a single moment, is given by the Langevin function

$$\langle\cos\theta\rangle = L(\alpha) \qquad (2)$$

where $\alpha = MB/kT$ and $L(\alpha) = \coth\alpha - 1/\alpha$.

In the geomagnetic field at room temperature, $MB = 6.6 \times 10^{-13}$ erg and $kT = 4.1 \times 10^{-14}$ erg; hence $\alpha = 16$ and $\langle\cos\theta\rangle > 0.9$. That is, each bacterium has a sufficiently large permanent magnetic dipole moment so that it is oriented in the geomagnetic field at ambient temperature. Even cells with 3 or 4 particles will be reasonably well oriented. Thus a bacterium only has to swim straight ahead and the torque exerted by the field on its magnetic dipole moment will cause it to migrate along the magnetic field lines.

In bacteria with unidirectional motility, if the magnetic dipole moment is oriented in the cell so that the North-seeking pole is forward with respect to the flagellum, the cell will propel itself in the field direction or Northward, that is, it will be North-seeking. If the South-seeking pole is forward, the cell will propel itself Southward. Bacteria can be remagnetized [10,11], that is, North-seeking cells turned into South seekers and visa versa by magnetic fields which are larger than the coercive force of the chain of particles [12]. Fields of the order of several hundred gauss are required, which is consistent with theoretical models [8].

3. Biological Advantage Of Magnetotaxis

Because of the inclination of the geomagnetic field lines, North-seeking bacteria migrate downward in the Northern Hemisphere and upward in the Southern Hemisphere. South-seeking bacteria migrate upward in the Northern Hemisphere and downward in the Southern Hemisphere. At the equator, both polarity types migrate horizontally. It is apparently advantageous for anaerobic or microaerophillic, sediment dwelling bacteria to have mechanisms that keep them in the sediments and away from the toxic effects of the high oxygen tension at the water surface. Thus North-seeking bacteria predominate in the Northern Hemisphere and South-seeking bacteria predominate in the Southern Hemisphere [13,14]. At the geomagnetic equator both polarity types coexist [15]. The profound effect of the sign of the vertical component of the geomagnetic field in selecting the predominate polarity is shown by the fact that whereas North-seeking and South-seeking bacteria coexist at the geomagnetic equator, an inclination of the field of only eight degress is sufficient to select one polarity over the other by over 100 to 1 [16]. This is equivalent to a vertical magnetic field of only 0.04 G (for a geomagnetic field of 0.26 G). This result can be understood when one considers an even very small differential survival mechanism operating over many generations.

The role of the vertical magnetic field component has also been confirmed in laboratory experiments [13,15]. When a sediment sample from New England, initially containing North-seeking bacteria, was 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, that is over many bacterial generations. In a sample placed in a coil that canceled the vertical component of the ambient magnetic field, the population in the sample tended toward equal numbers of both polarities, again over many generations. Equal numbers of both polarities also resulted when samples initially containing all North- or all South-seeking bacteria were placed in an enclosure that canceled the ambient magnetic field.

While the ability to synthesize Fe_3O_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-seekers 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 orientation. Thus, North-seeking bacteria can produce North-seeking progeny and South-seeking bacteria can produce South-seeking progeny. This has been cited as an elementary example of "gene-culture transmission" [17]. 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 synthe size 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 previusly 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-seeking and South-seeking populations eventually equalize.

Some magnetotactic bacteria are bipolarly flagellated and can swim in either direction along magnetic field lines. Some of these organisms are also aerotactic and form bands in regions of optimal oxygen concentration [18]. Thus they can use their aerotactic response to decide whether to swim parallel or antiparallel to the field direction. This reduces the biased three-dimensional random walk of chemotactic bacteria to a one-dimensional problem.

4. Fe_3O_4 Precipitation In Magnetosomes

On the basis of extensive spectroscopic analysis. cells of A. magnetotacticum are known to contain ferrous ions, a low-density hydrous-ferric-oxide, a high-density hydrous-ferric-oxide (ferrihydrite) and Fe_3O_4 [5]. Additional experiments with cell fractions show that ferrihydrite in the magnetotactic cells is associated with the magnetosomes. It has been proposed that A. magnetotacticum precipitates Fe_3O_4 in the sequence: Fe^{3+} ⟶ low-density hydrous-ferric-oxide ⟶ ferrihydrite ⟶ Fe_3O_4.

In the proposed sequence, iron enters the cell as chelated Fe^{3+}. Reduction to Fe^{2+} releases iron from the chelator. Fe^{2+} is reoxidized, and accumulated as the low-density hydrous-iron-oxide. By analogy with the deposition of iron in the protein ferritin, this oxidation step might involve molecular oxygen, which is required for Fe_3O_4 precipitation in A. magnetotacticum [6]. Dehydration of the low-density hydrous-ferric-oxide results in ferrihydrite. Finally, partial reduction of ferrihydrite and further dehydration yields Fe_3O_4.

Several morphologically distinct types of magnetosomes have been observed within various types of magnetotactic organisms. Magnetosomes within A. magnetotacticum are truncated octahedral prisms [19]. Magnetosomes within coccoid cells [20] as well as those within an unidentified cell from a pond in Japan [21] were truncated hexagonal prisms. Thus particle morphologies appear to be species specific. In A. magnetotacticum the particles are oriented with [111] planes at the ends of the particles perpendicular to the chain axis. This may be a clue to the growth of the magnetosomes.

Fe_3O_4 is thermodynamically stable with respect to hematite and ferrihydrite at low E_H and high pH [22]. However, rapid transformation of ferrihydrite to magnetite appears to involve more than simple reduction and dehydration because reduction of ferrihydrite in ferritin does not produce Fe_3O_4 [23]. This, plus the fact that the precipitation process requires spatial segregation of regions of differing E_H and possibly pH, suggests that the process falls into the biomineralization category described by LOWENSTAM [24] as "organic matrix mediated." Thus the magnetosome envelope is probably an integral element in the precipitation process, functioning as a locus for enzymatic activities, compartmentalizing constituents, providing control of E_H and pH, as well as comprising a structural element anchoring the Fe_3O_4 particles to the remainder of the cell and determining the particle morphology.

5. Magnetotactic Algae

In addition to bacteria, Fe_3O_4 has been reported as a biomineralization produce in eukaryotes including chitons, honeybees, pigeons, bobolinks, tuna, and others [25]. In these organisms, Fe_3O_4 has been identified magnetically or following extraction from the cell. Recently, Fe_3O_4 has been found in intact, magnetotactic, euglenoid algal cells from brackish sediments in Brazil [26]. The organism was identified as Anisonema platysomum skuja [27]. TEM of these organisms and electron diffraction shows that they contain numerous Fe_3O_4 particles arranged in chains oriented more or less parallel to the long axis of the cell (Fig. 2). Individual particles are arrowhead or tooth-shaped and are within the single magnetic domain size range for Fe_3O_4 (Fig. 3). Hence, each chain is a permanent magnetic dipole. If the moments of all the chains are oriented parallel to each other, a cell would have a magnetic dipole moment equal to the sum of the moments of all its particles. An estimate of the magnetic dipole moment of whole algae was obtained from measurements of the 180° rotation time of killed cells suspended in water, following reversal of the direction of the magnetic field produced by a pair of Helmholtz coils. Using the coefficient of viscous drag for a flat disk, the rotation time τ is related to the magnetic moment M by [28]

$$\tau = \frac{32R^3\eta}{3MB} \ln \frac{2MB}{kT}, \qquad (3)$$

where R is the radius of the cell, η is the viscosity of water, B is the magnetic field and kT is Boltzmann's constant x temperature. Experimental sets of values of τ vs B, fit with Eq. (3), yielded an average, permanent, magnetic moment per cell $M = 6.7 \times 10^{-10}$ emu. This is about 1000 times the magnetic moment of a typical magnetotactic bacterium. The saturation magnetization in magnetite is 480 emu cm^{-3}. Therefore the magnetic moment of an average-sized particle (1400 x 480 x 480 $Å^3$) is 1.5×10^{-13} emu. Hence, each algal cell must contain on the order of 3×10^3 magnetite particles, with the particles occupying about 0.2 percent of the cell volume.

Although the motility of the algae in a magnetic field is more complex than magnetotactic bacteria, the magnetotactic response mechanism of the algae appears to be similar to that in magnetotactic bacteria, i.e., passive orientation of the cell by the torque exerted by the magnetic field on its permanent, magnetic dipole. The fact that the algal magnetic moment is three orders of magnitude larger than typical bacterial moments means that algae and bacteria have similar ratios of magnetic torque to viscous drag, that is, they have similar recovery times following deorientation events [29].

The biological significance of magnetotaxis in these algae is not yet understood. However the highly ordered arrangement of the chains of particles in the cells suggests that they are chains of magnetosomes very much like the chains of magnetosomes in bacteria. Evidence for the presence of membranes enveloping the particles must await TEM of thin sections. However, the fact that the particles are separated from each other and not clumped is evidence that they are not free to move in the cells. Chains of free magnetic particles would lower their energy by moving together and eventually forming clumps.

Thus, eukaryotic cells as well as prokaryotic cells can produce Fe_3O_4 the form of single magnetic domains as an intracellular biomineralization product. It will be interesting to compare the biomineralization process and the role(s) of membranes in these fundamentally different types of organisms.

6. References

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Fig. 1. Transmission electron micrograph of a negatively stained whole cell of the magnetotactic bacterium Aquaspirillum magnetotacticum. Bar = 1 micron. (Photo credit: D. Maratea and R.P. Blakemore).

Fig. 2. Transmission electron micrograph of a negatively stained whole cell of the magnetotactic alga Anisonema platysomum. Bar = 10 microns. (Photo credit: N. Blakemore).

Fig. 3. Transmission electron micrograph of a portion of a cell of A. platysomum. Particles are Fe_3O_4 with dimensions 140 nm by 50 nm.

FIG 1

FIG 3