

Magneto-Aerotaxis

Richard B. Frankel¹ (✉) · Timothy J. Williams² · Dennis A. Bazylinski³

¹Department of Physics, California Polytechnic State University, 1 Grand Avenue,
San Luis Obispo, CA 93407, USA
rfrankel@calpoly.edu

²Department of Biochemistry, Biophysics and Molecular Biology, Iowa State University,
Ames, IA 50011, USA

³School of Life Sciences, University of Nevada, Las Vegas, 4505 Maryland Parkway,
Las Vegas, NV 89154-4004, USA

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Abstract Magnetotactic bacteria orient and migrate along geomagnetic field lines. Magneto-aerotaxis increases the efficiency of respiring cells to efficiently find and maintain position at a preferred microaerobic oxygen concentration. Magneto-aerotaxis could also facilitate access to regions of higher nutrient and electron acceptor concentration via periodic excursions above and below the preferred oxygen concentration level.

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Introduction

1.1

History

The terms “magnetotaxis” and “magnetotactic bacteria” were first used by Richard P. Blakemore in his landmark 1975 paper (Blakemore 1975) announcing the discovery of aquatic bacteria from Woods Hole, Massachusetts that migrated northward in water drops along magnetic field lines. Using transmission electron microscopy he found that the cells were roughly coccoid with two bundles of seven flagella each on one side of the cell. He also found the cells contained chains of elongated, electron-dense, iron-rich crystals, later shown to consist of magnetite (Fe_3O_4) (Frankel et al. 1979). The crystals were contained in intracytoplasmic vesicles arranged adjacent to the cytoplasmic membrane in the cell. He noted the probable relationship of the chains of crystals and magnetotaxis in the cocci and other magnetotactic bacteria recovered from aquatic sediments in Woods Hole. Blakemore (1975) postulated “Perhaps the iron-rich cell inclusions serve as magnetic dipoles which convey a magnetic moment on the cells, thus orienting the cells in magnetic fields. Magnetotaxis would result if, within each cell, a fixed spatial relationship existed between the orienting mechanism and cell propulsion”. In a sense, all subsequent research on magnetotactic bacteria follows from these and other original observations in that paper. In this review, we describe and discuss recent work on magnetotaxis.

1.2

General Features of Magnetotactic Bacteria

Magnetotactic bacteria inhabit water columns or sediments with vertical chemical concentration stratification, where they occur predominantly at the oxic–anoxic interface (OAI) and the anoxic regions of the habitat or both (Bazylinski et al. 1995; Bazylinski and Moskowitz 1997; Simmons et al. 2004). All known magnetotactic bacteria phylogenetically belong to the domain Bacteria and are associated with different subgroups of the Proteobacteria and the Nitrospira phylum (Spring and Bazylinski 2000; Simmons et al. 2004). They represent a diverse group of microorganisms with respect to morphology and physiology (Bazylinski and Frankel 2004).

The magnetotactic bacteria are difficult to isolate and cultivate (Bazylinski and Frankel 2004) and thus there are relatively few axenic cultures of these organisms. Most cultured strains belong to the genus *Magnetospirillum*. Currently recognized species include *M. magnetotacticum* strain MS-1 (Blakemore et al. 1979; Maratea and Blakemore 1981; Schleifer et al. 1991), *M. gryphiswaldense* (Schleifer et al. 1991) and *M. magneticum* strain AMB-1

(Matsunaga et al. 1991). Several other freshwater magnetotactic spirilla in pure culture have not yet been completely described (Schüler et al. 1999). Other species of cultured magnetotactic bacteria include a variety of as yet incompletely characterized organisms: the marine vibrios, strains MV-1 (Bazylinski et al. 1988) and MV-2; a marine coccus, strain MC-1 (DeLong et al. 1993; Meldrum et al. 1993a); and a marine spirillum, strain MMS-1 (formerly MV-4) (Bazylinski and Frankel 2000; Meldrum et al. 1993b). There is also an anaerobic, sulfate-reducing, rod-shaped magnetotactic bacterium named *Desulfovibrio magneticus* strain RS-1 (Sakaguchi et al. 1993, 2002). These cultured organisms, except *D. magneticus*, are facultatively anaerobic or obligate microaerophiles. All are chemoorganoheterotrophic although the marine strains can also grow chemolithoautotrophically (Bazylinski et al. 2004; Williams et al. 2006). The genomes of several strains, including *M. magnetotacticum* strain MS-1 and strain MC-1, have been partially sequenced while that of *M. magneticus* strain AMB-1 (Matsunaga et al. 2005) has been recently completed.

Several uncultured, morphologically conspicuous, magnetotactic bacteria have also been examined in some detail. A very large, rod-shaped bacterium, *Candidatus Magnetobacterium bavaricum*, has been found to inhabit the OAI in the sediments of calcareous freshwater lakes in Bavaria (Spring et al. 1993; Spring and Bazylinski 2000). Cells of this organism biomineralize multiple chains of tooth-shaped crystals of magnetite. A multicellular bacterium, referred to as the many-celled magnetotactic prokaryote (MMP) (Rogers et al. 1990), biomineralizes crystals of iron sulfides (Mann et al. 1990; Farina et al. 1990; Pósfai et al. 1998) and is comprised of about 20–30 cells in a roughly spherical arrangement that moves as an entire unit. There is evidence that suggests that the MMP is a sulfate-reducing bacterium (DeLong et al. 1993) and organisms like it have been found in marine and brackish aquatic habitats around the world.

All studied magnetotactic bacteria are motile by means of flagella and have a cell wall structure characteristic of Gram-negative bacteria (Bazylinski and Frankel 2004). The arrangement of flagella varies between species/strains and can be either polarly monotrichous, bipolar, or in tufts (lophotrichous). The MMP is peritrichously flagellated as a unit but not as individual cells, which are multi-flagellated on only one side (Rogers et al. 1990). It is the only magnetotactic bacterium whose external surface is covered with flagella. Like other flagellated bacteria, magnetotactic bacteria propel themselves through the water by rotating their helical flagella. Because of their magnetosomes, magnetotactic bacteria passively orient and actively migrate along the local magnetic field **B**, which in natural environments is the geomagnetic field. Reported swimming speeds (Table 1) vary between species/strains, from ca. 40 to 1000 $\mu\text{m/s}$. In general, the magnetotactic spirilla are at the slower end ($<100 \mu\text{m/s}$) (Maratea and Blakemore 1981) and the magnetotactic cocci are at the faster end of the range at $>100 \mu\text{m/s}$ (Blakemore 1975; Moench 1988; Cox et al. 2002).

Magnetoreception and Magnetosomes in Bacteria

Schüler, D. (Ed.)

2007, VIII, 319 p., Hardcover

ISBN: 978-3-540-37467-1