Chapter

Biology and Physics of Magnetotactic Bacteria

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Abstract

Magnetotactic bacteria are able to align their swimming direction to the geomagnetic field lines because they possess a magnetic moment. These bacteria biomineralize magnetic nanoparticles, magnetite or greigite, inside a membrane. The membrane + nanoparticle set is known as magnetosome and intracellular magnetosomes are disposed in a linear chain. Cytoskeleton-like filaments are resposible for the mechanical stability of this chain. The genes responsible for the magnetosome membrane and for the cytoskeleton proteins have been largely studied: the mam genes. The magnetosome chain also confers to the bacterial body a magnetic moment that can be measured through different physical techniques. Because of their response to magnetic field inversions, magnetotactic bacteria are good models to study bacterial motion. Theoretical and experimental studies show that magnetotactic bacteria swim following a trajectory similar to cylindrical helix. Magnetotactic microorganisms have been observed avoiding regions with UV or violet-blue light of high intensity. If the intensity is lower, magnetotactic microorganims show photokinesis, increasing their velocity in the presence of red light and decreasing their velocity in the presence of green light, both relative to the velocity with blue light.

Keywords: magnetotactic bacteria, magnetosomes, magnetic moment, mam genes, magnetotaxis

1. Introduction

Bacteria are one of the simplest organisms found in nature. They are distinguished from eukaryotes and superior organisms because their genetic material is not contained in a nucleus but is free in the cytoplasm. However, despite their relative simplicity, bacteria inhabit Earth for longer than many other organisms and constitute the most abundant type of cell on our planet [1]. Magnetotactic bacteria (MTB) are microorganisms that biomineralize magnetic nanoparticles inside their cytoplasm. These magnetic nanoparticles are involved by a lipidic membrane, and each "membrane + magnetic nanoparticle" set is known as magnetosome [2]. Magnetosomes are arranged in linear chains in the cytoplasm, conferring a magnetic moment to the bacterial body, being able to interact with the geomagnetic field to orient its navigational direction to the geomagnetic field lines. This response is known as magnetotaxis, resulting from the magnetic torque among the geomagnetic field and the magnetic moment of the magnetosome chain, and for that reason, MTB are described as "living compasses." MTB were discovered

independently by Salvatore Bellini in 1963 and Richard Blakemore in 1975 [3]. The first to observe MTB was Salvatore Bellini, an Italian physician from Pavia, Italy. In 1958, physicians from Pavia were asked to analyze the quality of water for human consume. Bellini was part of the team that studied the water quality, and he observed in water samples some bacteria that consistently accumulate in one side of water drops. After trying different stimuli, he discovered that they were affected by magnets. He called that bacteria as magnetosensitive. The first published observation of MTB was done in 1975 by Richard Blakemore in Massachusetts, USA [4]. His discovery was accidental, because his goal was to isolate *Spirochaeta plicatilis* from marine marsh muds. During his observations, he noted microorganisms migrating to one end of the drop of the mud on the microscope slide, and discover that the presence of magnets altered their swimming direction. He called magnetotaxis as the tactic response to magnetic fields.

2. Biology of magnetotactic bacteria

2.1 Cell biology

MTB comprise a diverse group of prokaryotes that share the ability to synthesize magnetosomes, which are composed by a magnetic nanocrystal, magnetite (Fe_3O_4), or greigite (Fe_3S_4), enclosed by a lipid bilayer (**Figure 1**; [2]). Thus, MTB has no taxonomic meaning regarding phylogeny, morphology, and physiology. The morphology of cultured and uncultured MTB described until now are cocci, spirilla, rods, ovoids, vibrios, and multicellular spherical/ellipsoidal forms [5]. In all morphotypes, magnetosomes are arranged in one or multiple chains along the major axis of the cell, imparting the cell a magnetic moment, as mentioned previously [2]. However, in some uncultured MTB, apparently disorganized chains have already been observed [6, 7]. Besides the magnetosomes, other common features are the Gram-negative cell wall structure, motility by flagella and lipid, polyphosphate and sulfur inclusions [2].

MTB present microaerophilic or anaerobic metabolism and all inhabit aquatic environments characterized by vertical chemical stratification [2]. When observing a drop of environmental sample containing MTB on a light microscope with a magnet next to the slide, MTB tend to accumulate in one of the borders of the drop, which correspond to a magnetic pole, North or South. In the Southern Hemisphere, when MTB are being observed they usually accumulate at the border of the drop of sample corresponding to the magnet's North magnetic pole, swimming to Geomagnetic South pole indicated by a compass. Therefore, these bacteria are

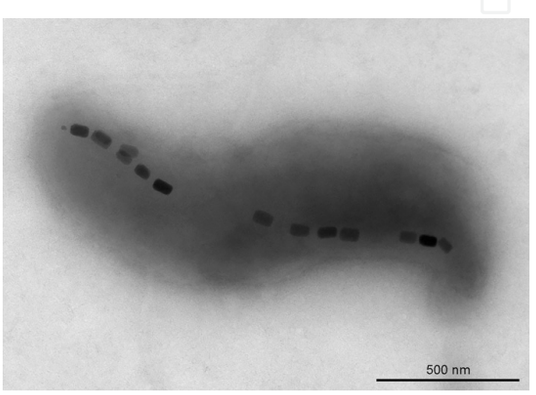

Figure 1.
Transmission electron microscopy of the magnetotactic bacterium Magnetovibrio blakemorei *strain MV-1 showing a single chain of prismatic magnetite magnetosomes.*

called South-seeking. In the Northern Hemisphere, the opposite situation occurs and MTB presenting this behavior are called North-seeking.

The study of MTB movement in an oxygen gradient showed that MTB change flagellar rotation and, consequently, the direction of movement depending on the oxygen concentration, migrating to the optimal conditions [8]. These observations were used to infer MTB dislocation along the vertical chemical gradient in the environment, which is based on the vertical component of the magnetic field and depends on the cellular state regarding oxygen. In the upper layers of the chemically stratified environment, where oxygen is abundant and higher than the optimal for MTB growth, the bacterium is on the oxidized state and rotate flagella to migrate downward, where the environment is more reduced. While in reducing conditions, in which oxygen is not abundant and concentrations are lower than that required for MTB growth, bacteria rotate the flagella in the opposite direction to reach upper layers of the gradient with optimal oxygen concentrations. Therefore, the presence of specific cell structures in MTB, as the magnetosome chain, flagella, and storage inclusions, represent adaptive advantages for dislocation across the chemical gradient to explore resources in the environment. For example, during the day, the oxygen gradient changes among the stratified layers of the environment and microorganisms dislocate across these layers to reach regions with suitable conditions for survival and growth. Because MTB are microaerophilic and/or capable of anaerobic respiration, which means that they are sensitive to high oxygen concentrations, an efficient mechanism to orient and migrate in the environment guarantees species survival.

Only a few species of MTB have been isolated in axenic cultures [9], and fewer type strains are available in cell line repositories. Many uncultured MTB species have been characterized from environmental samples, because it is possible to purify these cells based on their response to an applied magnetic field using a magnet [10]. **Figure 2** shows examples of cultured and uncultured species of MTB and their characteristics according to their phylogenetic affiliation. Note that MTB are spread among different phyla in Bacteria domain and that greigite magnetosomes are only synthesized by MTB belonging to Deltaproteobacteria class.

Magnetospirillum species, which include *M. gryphiswaldense* strain MSR-1, *M. magneticum* strain AMB-1, and *M. magnetotacticum* strain MS-1, among other strains, are spirilla with flagella at each pole of the cell and represent the most characterized MTB. Information about the biomineralization process and magnetosome organization within the cell is mainly based on species belonging to this genus [11]. Cryoelectron tomography studies using *M. magneticum* strain AMB-1 have shown that the magnetosome vesicle is a result of the cytoplasmic membrane invagination, which occurs before the synthesis of the magnetite nanocrystal [11, 12]; forming the magnetosome membrane vesicle in which proteins related to the biomineralization will be anchored. These proteins that are involved in all steps of the magnetosome formation are anchored to this invaginated portion of the membrane and will participate in the process by recruiting other proteins that integrate the process, for example, iron transport, crystal nucleation and growth, size and shape control, and organization of the magnetosomes [11, 13].

According to studies performed in *M. gryphiswaldense* strain MSR-1, mature magnetite magnetosomes are found already organized in a chain within the cytoplasm of the cell 15 min after formation has started [14]. All *Magnetospirillum* species produce a single chain of cuboctahedral magnetite magnetosomes that are 40–45 nm in size [10]. Other MTB species are capable of synthesizing magnetite magnetosomes with cuboctahedral, prismatic, or anisotropic shapes [2] and/or greigite magnetosomes, which are usually classified as irregular. Usually, a magnetotactic bacterium species is capable of producing magnetosomes with one

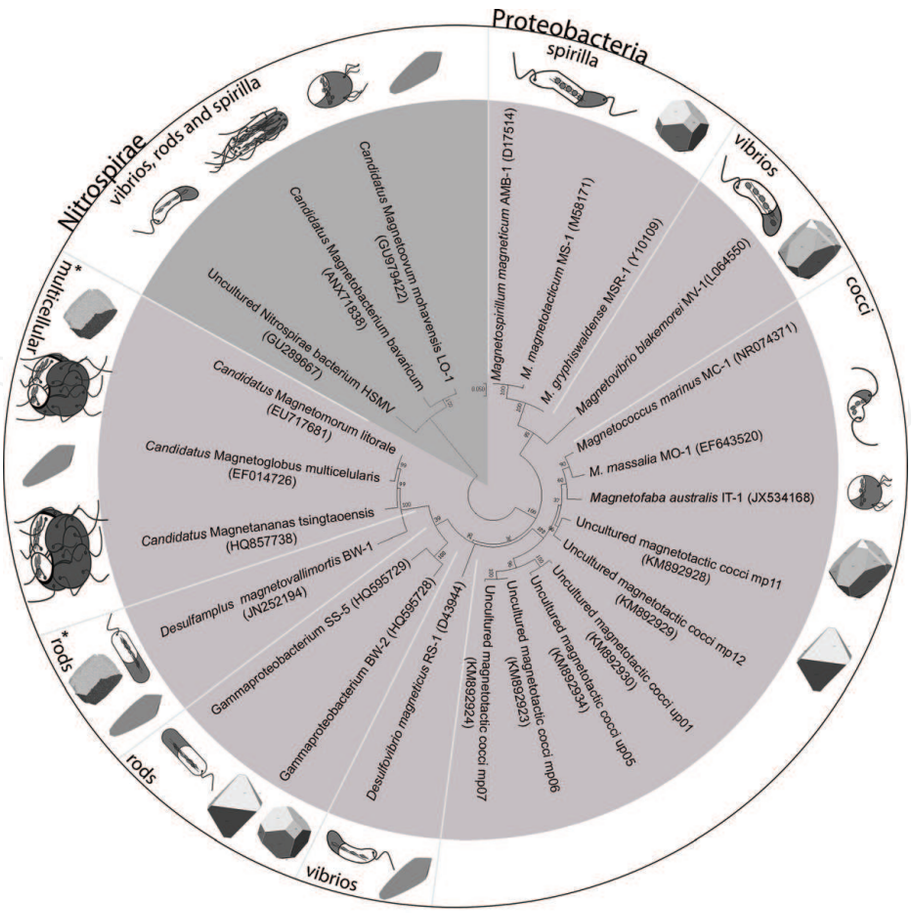

Figure 2.
Phylogenetic tree based on the 16S rRNA gene showing the distribution of some cultured and uncultured MTB in Nitrospirae and Proteobacteria phylum of Bacteria domain. White lines separate morphotypes of MTB in Proteobacteria phylum, showing the distribution of spirilla, vibrios, cocci, including ovoid and fava*-like cells, rods, and multicellular microorganisms. The shape of magnetosomes found in each morphotypes also displayed next to the cells. However, it is important to remember that each MTB species is usually capable of producing only one type of magnetosome (composition and shape). Morphotypes labeled with an asterisk (*) are the only capable of producing greigite magnetosomes; some of them, for example,* Desulfamplus magnetovallimortis *strain BW-1 produces both types of magnetosomes, irregular greigite and bullet-shaped magnetite magnetosomes.*

mineral composition and regular size and shape [15]. Rarely, a magnetotactic bacterium is capable of producing both magnetite and greigite magnetosomes; when it occurs, these magnetosomes with different composition and shape are arranged in the same chain(s) [16, 17]. Although differences have been observed in the formation of magnetosomes in MTB species [12, 18], the process described for bacteria belonging to *Magnetospirillum* genus is considered the model of magnetite biomineralization in MTB.

In the environment, magnetotactic cocci are the most abundant morphotype of MTB and present high phylogenetic diversity and variety of size, shape, and organization of magnetosomes [10, 19]. For example, magnetotactic cocci have been found in marine sediments from Antarctica, suggesting the existence of psychrophilic MTB [7]. Interestingly, these samples presented at least three types of magnetotactic cocci based on the magnetosomes crystal size, shape, and organization [7]. Ultrastructure characterization of cultured magnetotactic cocci showed that these cells present two bundles of flagella and can achieve speed of approximately 300 μm/s, which is extremely high if we consider that the bacterium has nearly 1 μm. Each flagellar apparatus of *Magnetococcus massalia* strain MO-1 is formed by seven flagellar filaments surrounded by a sheath that might interact with the bundle of flagella to decrease the friction of the high-speed rotation of

individual flagella and promote efficient swimming at high speed [20]. One of the most peculiar morphotype of MTB are the multicellular forms, named magnetotactic multicellular prokaryotes (MMP), which can be divided into spherical and ellipsoidal. MMP are formed by Gram-negative magnetotactic cells organized in a sphere that swims as a unit [21]. Cellular organization in MMP is not random and represents the best configuration to optimize the magnetic response of the microorganism [22]. These microorganisms present an exclusive multicellular life cycle in which cells of the microorganisms grow, divide, and rearrange before splitting into two identical multicellular microorganisms [23]. Individual cells of this type of MTB have never been observed and viability assays suggest that when a cell disaggregates from the multicellular structures, it does not remain viable [24]. MMPs are capable of synthesizing irregular greigite or bullet-shaped magnetosomes [21]. MMPs with both types of magnetosomes have already been reported [25].

2.2 Genetics

The origin of magnetotaxis and its distribution among the different phyla of the Bacteria domain are not well understood. Despite the great phylogenetic diversity, MTB have unique genes related to biomineralization, which are located in a generally unstable region in the genome [26]. The genomic and ultrastructure characterizations of nonmagnetotactic spontaneous mutants of *M. gryphiswaldense* strain MSR-1 showed the absence of 130 kb genomic region and complete lack of magnetosomes within these cells [27]. Genomic comparison among MTB affiliated to different phyla showed that genes in this region are conserved within MTB group, even when magnetite- and greigite-producing MTB were analyzed [11]. This region containing the genes responsible for the synthesis of magnetosomes was named magnetosome island and the genes are referred to as *mam* (*magnetosome membrane*), *mms* (*magnetosome membrane specific*), and *mtx* (*m*agneto*t*ax*x*is) genes because proteins encoded by these genes are localized on the magnetosome membrane or participate on the magnetotaxis motility behavior.

The genes for biomineralization are grouped into four operons in *M. gryphiswaldense* strain MSR-1 and other freshwater spirilla, called *mamAB*, *mamGFDC*, *mms6,* and *mamXY* in the magnetosome island [28]. Although species of MTB have different sizes in the region that encompasses the genes involved in biomineralization, some genes are conserved in all species. The content and organization of genes on the magnetosome island vary between magnetotactic species, and often, some genes are deleted or inserted without any change in the formation of the magnetosomes [27]. In general, proteins encoded by *mam* genes are involved in four major steps of magnetosome formation. These steps include: (1) formation of the magnetosome membrane (MamI, MamL, and MamAB); (2) formation of magnetite crystal (MamE, Mms6, MamB, and MamM); (3) maturation of the magnetite crystal (MamE, MmsF, MamGFDC, and Mam P, S, T); and (4) alignment of the chain magnetosome (MamJ and MamK) [29]. The mechanism by which these genes were and can be transferred between species of bacteria is unknown till date. In the past years, hypotheses were elaborated to explain the evolution of magnetotaxis. One of them was based on the observation that the evolution and divergence of the conserved Mam proteins and the 16S rRNA gene among MTB are congruent and support the monophyletic origin, in which all MTB would present a single common ancestor [9]. The other hypothesis states that the present diversity of MTB and magnetotaxis-related gene distribution is a result of multiple events of horizontal gene transfer, possibly with a common ancestral, gene modification and/or loss in different cell lines [26]. Functional analysis of the magnetosome island based on deletion of genes in *Ms. gryphiswaldense* strain MSR-1 indicated that genes

in the *mamAB* operon are sufficient for magnetosome biomineralization [30]. Examples of genes found in this operon and their functions are listed in **Table 1**. Interestingly, the transference of genes from the *mamAB* operon from *M. gryphiswaldense* strain MSR-1 to *Rhodospirillum rubrum* resulted in magnetite magnetosome production within the photosynthetic cell [39]. Because of the magnetic properties of magnetosomes, which will be discussed on the following topic, these nanometric magnetic structures have great importance for the development of new applications and processes in Biotechnology. However, one of the limitations of their use in biotechnological applications is the fastidiousness of MTB, which makes the production of magnetosomes in bioreactors expensive and with low yield. The transference of the ability to synthesize magnetosomes from MTB to

Protein	Function	Effect on cell upon deletion	Reference/ strain used on the study
MamA	Activation of biomineralization	Decrease in the number of magnetosomes	[31] Strain AMB-1
MamB	Transport of iron into the magnetosome vesicle; interacts with PDZ domains (MamE)	Magnetosomes are not produced; no magnetic response	[29] Strain AMB-1; [32] strain MSR-1
MamE	Crystal maturation	Synthesis of magnetosomes smaller than <20 nm; cells without magnetic response	[29, 33] Strain AMB-1
MamH	Balance in the redox state of iron on the magnetosome membrane	Decrease in magnetosome number and size; less efficient magnetic response	[29] Strain AMB-1; [34] strain MSR-1
MamI	Synthesis of the magnetosome membrane	Magnetosomes are not produced; no magnetic response	[29] Strain AMB-1
MamJ	Alignment of the magnetosome chain: it interacts with the surface of the magnetosome and with a structure similar to the cytoskeleton (MamK filament)	Magnetosomes are not aligned in chains; reduced magnetic orientation	[35] Strain MSR-1
MamK	Controls the assembly, segregation, and positioning of the magnetosome chain inside the cell	Alignment of the magnetosomes in short chains and decrease in the number of magnetosomes	[36] Strain MSR-1
MamM	Transport of iron into the magnetosome: magnetite nucleation, crystal growth, and stabilization of MamB	Increase in the formation of polycrystalline particles of magnetite; formation of crystals of hematite; no magnetic response	[29] Strain AMB-1; [32] strain MSR-1
MamO	Nucleation of the magnetite crystal	Magnetosomes are not produced; cells without magnetic response	[29] Strain AMB-1; [37] strain MSR-1
MamP	Magnetite crystal size control	Decrease in the size of magnetosomes; less efficient magnetic response	[29, 38] Strain AMB-1
MamR MamT	Magnetite crystal size control	Decrease in the size of magnetosomes; less efficient magnetic response	[29, 38] Strain AMB-1
MamU	Possibly lipid metabolism	No changes were observed	[29] Strain AMB-1

Table 1.
Proteins encoded by genes within mamAB *operon in* Magnetospirillum *and their function.*

other cells represents a new frontier in Microbiology and greatly expands the use of magnetosomes in nanotechnological and biomedical applications [39].

3. Physical characteristics of magnetosomes

Two different processes of mineral formation by living beings have been recognized. One process of mineral formation is known as biologically induced mineralization (BIM), and is characterized by bulk extracellular and/or intercellular mineral formation, without the elaboration of organic matrices. It produces minerals having crystal habits similar to those produced by precipitation from inorganic solutions. BIM processes are less controlled than organic matrix-mediated mineralization, and looks like a primitive stage in the evolution of biogenic mineral formation. The other process is known as biologically controlled mineralization (BCM). In general, the organism constructs an organic mold into which the appropriate ions are actively introduced to crystallize a mineral. The mineral type, orientation of crystallographic axes, and microarchitectures are under genetic control [40].

Magnetotactic bacteria distinguish from other bacteria because they biomineralize, through BCM, magnetic nanoparticles of magnetite, or greigite. Magnetite is a very interesting iron oxide because it is magnetic and a good conductor. Its free charge density is similar to that of some metals [41]. It is also a hard mineral, being used by chitons for tooth hardening [42]. Several studies show that greigite has similar electrical [43] and hardening use [44] as magnetite. The magnetic properties of nanoparticles have a strong dependence on the size: very small particles have a magnetic moment nonstable in the body, changing randomly its orientation and producing a null average magnetic moment. Those particles are known as superparamagnetic. If the size increases, the anisotropic energy also increases and creates an energy barrier that maintains the magnetic moment in a fixed direction. In that case, the nanoparticles behave as stable magnets and are known as single domains [45]. Magnetosomes are in the size range of magnetic single domains. The magnetic flux lines created by the magnetosome in the chain can be observed using the magnetic electron holography technique [46], showing the flux lines entirely aligned to the chain as corresponds with a dipolar field created by a single magnetic moment. So, it is appropriate to say that the magnetosome chain behaves as a compass needle. The linear arrange of magnetosomes is not energetically stable, because after some number of magnetosomes the best configuration is a ring. To maintain the linear configuration, magnetosomes are attached to the cytoskeletal filaments [47].

The first analysis done in magnetosomes was energy-dispersive X-ray microanalysis (EDS or EDX), showing that they are composed mainly by iron and oxygen [4]. To show that they are the iron oxide magnetite, the Mossbauer technique was used [48], showing that the Mossbauer spectra behave as a mixture of magnetite and maghemite. Also, electron diffraction shows the diffraction patterns corresponding to magnetite [49]. Several studies with EDS show that this magnetite is highly pure. However, in some cases, some metallic ions can be absorbed in the magnetosome structure, depending on the ambient pollution [50]. Studies done with high-resolution electron microscopy show that magnetosomes are produced in specific geometric morphologies [51]. Those morphologies are truncated cuboctahedron, elongated cuboctahedron, and hexagonal prisms. In the case of greigite, the crystalline morphologies are truncated cuboctahedrons and elongated rectangular prisms [51]. This iron sulfide was discovered in magnetosomes of multicellular magnetotactic prokaryotes, and identified through EDX spectroscopy and electron diffraction [52].

4. Determination of bacterial magnetic moment

As the magnetosome chain determines a magnetic moment to MTB, let us talk about the different techniques used to estimate that magnetic moment. The first theoretical estimate for the magnetic moment was done counting the contribution of several nanoparticles arranged in a chain [53]. For a magnetosome chain composed of 22 particles of magnetite with every nanoparticle having 1.25×10^{-16} cm^3 of volume, it is possible to calculate the total magnetic moment as $M = nV_{ind}M_V$, where n is the number of particles in the chain, V_{ind} is the volume of each particle (assuming that all are equal), and M_V is the magnetic moment per unit volume of the magnetic material. For magnetite, $M_V = 480 \times 10^{-3}$ Am^2/cm^3. In this way, a magnetic moment of 1.3×10^{-15} Am^2 is obtained. This magnetic moment value means a magnetic to thermal energy rate of about 16 (assuming a temperature of 300 K). This method can be used whenever is possible to observe and count the number of magnetosomes in the chain. This method is not applied in the case of live bacteria and for bigger microorganisms with lots of magnetosomes, as is the case for "*Candidatus* Magnetobacterium bavaricum" and "*Candidatus* Magnetoglobus multicellularis."

A statistical analysis of the swimming orientation of magnetotactic bacteria, assuming that they behave as paramagnetic particles, produces the orientation to be equivalent to the average of cosθ (<cosθ>), being θ the angle among the bacterial velocity and the magnetic field. Kalmijn showed that <cosθ> is function of the magnetic to thermal energy ratio [54]: $<\cos\theta> = L(MH/kT) = \coth(MH/kT) - kT/MH$, where M is the bacterium magnetic moment, H is the magnetic field intensity, k is the Boltzmann constant, T is the absolute temperature, and L(x) is the Langevin function: coth(x)—1/x. For $MH/kT \approx 10$, the Langevin function is about 0.9, which means that the bacterial trajectory is well oriented to the magnetic field direction. The analysis of the velocity as function of the magnetic field [54] or of the orientation as function of the magnetic field [55] permits the estimative of the bacterial magnetic moment. Kalmijn stressed the fact that this kind of study is valid only for the orientation of a single bacterium and not for the average orientation of several bacteria [54]. Using this method, it has been shown that "*Candidatus* Magnetoglobus multicellularis" shows values of L(x) lower than 0.9 in the presence of the geomagnetic field. A measuring method for the magnetic moment of individual MTB was developed in [56] and consists in the analysis of the U-turn trajectory, which is the form of the trajectory followed by an MTB when the sense of the external magnetic field vector is inverted. The theoretical analysis assumes that the bacteria and the magnetosome chain forms a rigid body, the bacteria following the movement of the magnetic moment. In the low Reynolds number regime and ignoring the flagellar forces, the sum of the magnetic torque and the viscous torque is equal to zero. From that equation, mathematical expressions are obtained for the time τ and diameter L of the reversal trajectory: $L = 8\pi\eta R^3 v/(MH)$ and $\tau = [8\pi\eta R^3/(MH)]\ln[2MH/(kT)]$, where M is the bacterium magnetic moment, H is the magnetic field intensity, k is the Boltzmann constant, T is the absolute temperature, R is the bacterium radius (assuming it is a coccus), v is the velocity, η is the viscosity, and ln is the natural logarithm function. The measurement of those parameters for the U-turn trajectory makes possible to calculate the value of the magnetic moment of magnetotactic bacteria. The experimental measurement of the magnetic moment of bacteria with different sizes and shapes, done by Esquivel and Lins de Barros [56], showed that the magnetic moment can have values from 0.3×10^{-15} to 54×10^{-15} Am^2, generating magnetic to thermal energy ratios from 3 to 326. Those results challenge the idea that the magnetosome contains the sufficient magnetic

nanoparticles, arranged in the proper configuration, to efficiently orient the bacteria in the geomagnetic field direction. A problem with this method is that the U-turn trajectory must be in the focal plane for a good measurement of L, but that is not the case in the general. An alternative is to use only the U-turn time τ because it can be determined well for any U-turn trajectory [57]. The U-turn analysis done by Esquivel and Lins de Barros [56] also assumes that bacteria have spherical geometry, that it is not the general case. When the bacterium is enlarged, as a small cylinder, another approximation must be done. So, assuming that this small cylinder behaves as a set of attached spheres, the contribution to the total torque can be calculated. Doing the experimental analysis in that way, Bahaj et al. [58] calculated a value of 6.1×10^{-16} Am^2 for the magnetotactic spirillum *Magnetospirillum magnetotacticum*. They also calculated the variation of magnetic moment with the growth time, and observed that it grows from 2.8×10^{-16} Am^2 at 35 h to 6.5×10^{-16} Am^2 at 240 h [59]. Another technique widely used to determine the magnetic moment of magnetotactic bacteria is the analysis of the movement in a rotating magnetic field [60]. In that method, a set of four coils (two crossed pairs) is adapted to an optical microscope stage to generate a rotating magnetic field with frequency f. That experimental setup is known as bacteriodrome. The resultant trajectory is a circle, observed clearly by dark-field images. Again, ignoring the flagellar movement and in the low Reynolds number regime, the magnetic torque must be equal to the viscous torque. The magnetic torque depends on the angle among the bacterial magnetic moment and the external magnetic field. That angle increases when the frequency f increases, and its upper limit is 90° meaning that there is a critical value of f_c. For values of f higher than f_c, the trajectory is not more a circle. The determination of f_c permits to calculate the magnetic moment as: $M \approx c\eta 2\pi f_c\, l^3/H$, where M is the bacterium magnetic moment, H is the magnetic field intensity, c is a shape factor, η is the viscosity, and l is the bacterium length. It is difficult to determine the shape factor, and Petersen et al. [60] proposed an approximated value of 8π. Using this technique, Petersen et al. [60] determined the magnetic moment of magnetotactic bacteria, of natural samples from Southern Germany, of about 4×10^{-15} Am^2, and Pan et al. [61] calculated a value of about 1.8×10^{-15} Am^2 for MYC-1, an uncultivated magnetotactic coccus from China.

Other techniques have been used for measuring the magnetic moment of magnetotactic bacteria. Using a SQUID magnetometer, an average magnetic moment of $1.8 \pm 0.4 \times 10^{-12}$ emu for bacteria from natural sediments had been determined [62]. This method is interesting because it is a direct measurement and does not need to assume unknown values for parameters from the studied cell. There are two interesting physical techniques involving light for measuring the magnetic moment of magnetic bacteria. One is the analysis of the birefringence arising in a pull of magnetotactic bacteria when in presence of an external magnetic field [63]. The birefringence transforms an input linear polarized light beam in an output elliptically polarized light beam, with a phase shift between the fast and slow components. This phase shift is measured and it depends on the intensity of the external magnetic field and on the magnetic moment. Experiments were done with live and dead bacteria, killed with drops of formalin. The measured values, at normal concentration conditions, for live bacteria were about 1.21×10^{-13} emu and for dead bacteria about 1.33×10^{-13} emu. Apparently, for dead bacteria, the measured values are higher than for live bacteria. It was assumed that this difference could be an effect of motile behavior in live bacteria and the concept of "effective temperature" T_{eff} was introduced, meaning that live bacteria feels a disorienting thermal energy kT_{eff} higher than the ambient thermal energy in 10–20%. The other technique is the analysis of the light scattered by a pull of magnetic bacteria [64],

based on the fact that the presence of an external magnetic field determines an angular distribution in the orientation of bacteria. This angular distribution affects the structure factor in the scattered light intensity. With this method, the average length and average magnetic moment can be determined. For two different cultures of *Aquaspirillum magnetotacticum* were determined values of $(2.2 \pm 0.2) \times 10^{-13}$ emu and $(4.3 \pm 0.5) \times 10^{-13}$ emu, which are in good agreement with the value obtained by electron microscopy, or about 4.4×10^{-13} emu. Using a similar experimental approach in [65] was determined the magnetic moment of a wild-type *Magnetospirillum gryphiswaldense* strain and obtained a value of about 25.3 $(\pm 1.6) \times 10^{-13}$ emu. Other methods found in literature are based basically in the analysis of the bacterial body rotation caused by the magnetic torque and in the analysis of the equation magnetic torque = viscous torque. For example, in Ref. [66], it was measured the magnetic moment of single *Magnetospirillum gryphiswaldense* cells using magnetic tweezers, observing and analyzing the rotation of the bacterial body after a magnetic field reversion. They observed that the measured magnetic moment has a dependence on the magnetic field intensity, as occurs in magnetization measurements of magnetic materials, starting from a remanence magnetization at zero magnetic field and progressively increasing until the magnetization saturates at higher magnetic fields. They measured for 6 mT < H < 23 mT a magnetic moment of 2.4 $(\pm 1.1) \times 10^{-13}$ emu and for 90 mT < H < 130 mT a magnetic moment of 7.7 $(\pm 3.4) \times 10^{-13}$ emu. **Table 2** resumes the magnetic moment measured with the different techniques, remembering that 1 emu = 10^{-3} Am^2. It can be observed that the magnetic moment obtained by the direct measurement from the magnetosome chain is always bigger than that obtained from indirect physical methods. In the study by Zahn et al. [66], this fact is explained identifying the direct measurement in the magnetosome chain as the saturation magnetization, that is only observed for higher magnetic fields.

Technique	Organism	Magnetic moment (Am^2)	References
Electron microscopy	Magnetotactic spirillum MS1	1.3×10^{-15}	[53]
U-turn analysis	Several microorganisms from fresh to marine water	0.3×10^{-15} to 54×10^{-15}	[56]
U-turn modified	*Magnetospirillum magnetotacticum*	6.1×10^{-16}	[58]
SQUID	Fresh water uncultured bacteria	1.8×10^{-15}	[62]
Light scattering	*Aquaspirillum magnetotacticum*	(live) 2.2×10^{-16} (dead) 4.3×10^{-16}	[64]
Light scattering	*Magnetospirillum gryphiswaldense*	$25.3 \pm 1.6 \times 10^{-16}$	[65]
Birefringence	*Aquaspirillum magnetotacticum*	1.21×10^{-16}	[63]
Rotating magnetic field	Natural samples	4×10^{-15}	[60]
Rotating magnetic field	Uncultivated coccus MYC-1	1.8×10^{-15}	[61]
Magnetic tweezers	*Magnetospirillum gryphiswaldense*	(low H) $2.4 \pm 1.1 \times 10^{-16}$ (high H) $7.7 \pm 3.4 \times 10^{-16}$	[66]

Table 2.
Magnetic moment value for MTB using different physical techniques.

5. The movement of magnetotactic bacteria

Several experimental observations show that magnetotaxis functions together with aerotaxis, determining the so-called magneto-aerotaxis [8, 67]. Basically, two different behaviors have been identified in magneto-aerotaxis: polar magnetotaxis, that consists in the North-seeking or South-seeking behaviors in the search for the better oxygen concentrations; and axial magnetotaxis, in that case, MTB move in the magnetic field direction but without preferential sense. MTB from natural samples always present polar magnetotaxis. Axial magnetotaxis has been observed only in cultured MTB.

MTB are easily identified because of their response to the inversion of the local magnetic field direction: after the inversion bacteria swim following the new magnetic field direction. It can be stated that magnetic field inversions stimulate MTB to swim, making them a model for the study of microorganism swimming. Bacteria swim in the low Reynolds number regime, where viscous forces and torques act to null the resultant force and torque [68]. In that regime, microorganisms swim following an helical trajectory [69] whose parameterization in Cartesian coordinates (x, y, z), considering the helix axis as the z axis, can be written as (Rcos(ωt), Rsin(ωt), Vt), where R is the helix radius, V is the axial velocity, and $\omega = 2\pi f$ being f the helix frequency. In the case of magnetotactic microorganisms, the helical trajectory of the multicellular magnetotactic prokaryote "*Candidatus* Magnetoglobus multicellularis" has been studied for two different applied magnetic fields (3.9 and 20 Oe) [70] and for magnetic fields from 0.9 to 32 Oe [55]. Those studies show that for spherical multicellular magnetotactic prokaryotes, the axial velocity V is about 90 μm/s, the radius R is about 8 μm for lower magnetic fields, and the helix frequency f is about 1.1 Hz. For uncultured magnetotactic coccus, the helical movement has been studied recently (data not published), in the presence of magnetic fields of about 0.7 Oe, and the helical parameters measured were: axial velocity of about 90 μm/s, radius of about 2.5 μm, and helix frequency of about 1 Hz. For other magnetotactic microorganisms, it has been observed that the 2D trajectory is similar to the projection of a 3D helix in the microscope focal plane (for example, see [19, 68, 71].

For the theoretical study of microorganisms, motion in the low Reynolds number regime is necessary to know all the forces and torques acting on the microorganism. Nogueira and Lins de Barros [68] developed a model in that regime, considering a spherical MTB with a single flagellum and a magnetosome chain aligned to the flagellum line. The equations to be considered are $\mathbf{F}_{\text{flagella}} + \mathbf{F}_{\text{viscous}} = 0$ and $\boldsymbol{\tau}_{\text{flagella}} + \boldsymbol{\tau}_{\text{viscous}} + \boldsymbol{\tau}_{\text{magnetic}} + \boldsymbol{\tau}_{\text{body}} = 0$. Using the appropriate expressions for the forces and torques in that model, they were able to calculate numerically the temporal evolution of the center of mass coordinates (x, y, z) and of the Euler's angles for the rigid body (θ, ϕ, ψ), being the trajectory similar to a cylindrical helix. In the other hand, Refs. [72, 73] studied the motion of nonspherical MTB, to include the effect of the bacterial body geometry on the viscous forces. Also, Yang et al. [73] studied MTB with two flagellar bundles. To do that, they calculated numerically the motion using the second Newton's law, considering all the forces and torques and calculating the appropriate inertial terms for the geometrical body form. They also studied the effect of the relative inclination λ between the magnetosome chain and the flagella. Those studies showed that when $\lambda \neq 0$, the velocity decreases when the magnetic field increases, effect also observed experimentally in the work by Pan et al. [74] when studying the circular movement of the MYC-1 strain. In that case, it was measured the velocity in the circular trajectory obtained in a bacteriodrome as function of the applied magnetic field, in the hope to obtain a growing Langevin curve as predicted by Kalmijn [54]. But they observed that the velocity decreases as

the magnetic field increases, in the contrary of a Langevin curve. To explain this, they assumed that the magnetosome chain has an inclination relative to the flagellar bundle. Interestingly, it has been observed that some MTB strains have the magnetosome chain with different inclinations relative to the flagellar bundle, in some cases being almost perpendicular to it, not orienting the magnetic moment to the magnetic field direction during their swimming [73].

The movement of magnetotactic microorganisms also depends on the presence of light, and the response depends on the wavelength and the intensity. This behavior has been studied mainly in multicellular magnetotactic prokaryotes. Negative photo response has been observed when they are illuminated with high-intensity UV light (365 nm), violet-blue light (395–440 nm filter) of about 80 W m^{-2} of intensity, and blue light (450–490 nm filter) of about 200 W m^{-2} of intensity. For longer wavelengths, no photo response was observed, and apparently long exposure to green light is lethal [70, 75]. That negative photo response is not observed when very low intensities are used. Photokinesis has been observed in multicellular magnetotactic prokaryotes, decreasing the velocity when illuminated with green light (517 nm, 0.46 W m^{-2}) and increasing the velocity when illuminated with red light (628 nm, 0.16 W m^{-2}), both respectively to the velocity observed when illuminated with blue light (469 nm, 0.8 W m^{-2}) [76, 77]. Recently, De Melo and Acosta-Avalos [78] showed that the photokinesis in multicellular magnetotactic prokaryotes is related to the combined presence of monochromatic light and a constant magnetic field, and that it can be canceled in the presence of radio-frequency electromagnetic fields oscillating at the Zeeman resonance frequency associated to the constant magnetic field, showing the involvement of a radical pair mechanism, a very well-known magnetoreception mechanism used by migratory birds. Interestingly, magnetotactic microorganisms have the proper physical tools to sense the geomagnetic field with light. Perhaps, magnetotaxis and the radical pair mechanism are involved in a more elaborate magnetic sensing in MTB.

6. Conclusions

Since the discovery of MTB, they attracted the attention of the scientific community for several reasons. Firstly, they show clearly that living beings can interact with the geomagnetic field through magnetic nanoparticles and became a model that has been extensively used in magnetoreception research. The study of the magnetosome synthesis process within MTB is being used to develop new strategies to produce magnetic nanoparticles with potential use in Biotechnology. For example, genes responsible for magnetosome synthesis could be transferred and expressed in a host cell to increase the yield of magnetosomes production in bioreactors. If high amounts of magnetosomes were achieved at low cost, magnetosome use as biotechnological tools would be possible. For physicists, MTB are interesting to apply models of magnetism, used in solid-state theory, in living beings behavior. The different techniques developed to measure the MTB magnetic moment have shown that considering MTB as paramagnetic particles is as insufficient model, defying previous models about MTB magnetotaxis. The study of motion is also giving support to new understandings about magnetotaxis, because new characteristics of the interaction among MTB and the geomagnetic field are arising through the study of the movement as function of the applied magnetic field. There are some evidences that MTB use more than one mechanism to detect the magnetic field direction, and not only through the magnetic torque. So, a new magnetoreception mechanism shall be discovered in MTB in the near future.

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Conflict of interest

The authors declare no conflict of interest.

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