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Magnetic microstructure of iron sulfide crystals in magnetotactic bacteria from off-axis electron holography

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Abstract

Transmission electron microscopy, off-axis electron holography and energy-selected imaging were used to study the crystallography, morphology, and magnetic microstructure of nanoscale greigite (Fe_3S_4) magnetosomes in magnetotactic bacteria from a sulfidic habitat. The greigite magnetosomes were organized in chains, but were less ordered than magnetite magnetosomes in other bacteria. Nevertheless, the magnetosomes comprise a permanent magnetic dipole, sufficient for magnetotaxis.

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Keywords: Greigite; Magnetosomes; Magnetotactic bacteria; Magnetic microstructure

1. Introduction

Magnetotactic bacteria contain magnetosomes, nanometer-scale crystals of magnetite (Fe_3O_4) or greigite (Fe_3S_4), enveloped in membrane vesicles. The magnetosomes comprise a permanent magnetic dipole that causes the cell to orient and migrate along geomagnetic field lines [1]. Different strains of magnetotactic bacteria have different crystal shapes and magnetosome arrangements. Whereas the structural and magnetic properties of magnetite magnetosomes have been studied extensively [2], this is not the case for greigite magnetosomes [3]. Here, we report on the use of transmission electron microscopy (TEM) and off-axis electron holography to study the composition, crystallography, morphology and magnetic microstructure of greigite crystals in uncultured magnetotactic bacteria collected from a sulfidic salt marsh pool.

Magnetotactic bacteria with iron sulfide magnetosomes were first described in 1990 [4,5]. The predominant mineral phase of the magnetosomes was identified as ferrimagnetic greigite (Fe_3S_4) [5,6]. In subsequent studies the structures and compositions of sulfide magnetosomes were analysed in detail, and non-magnetic precursors of greigite (primarily mackinawite, FeS) were also identified in the cells [3,6]. Despite these studies, sulfide-producing magnetotactic bacteria remain enigmatic because they are not yet available in pure culture [1]. The irregular morphologies and disorganized chain arrangements of greigite magnetosomes differ from most magnetite-producing species that exert stricter control over the physical properties of magnetite magnetosomes [1,7,8].

Greigite occurs in sedimentary rocks and is the primary carrier of the paleomagnetic signal in many anoxic environments [9]. Sedimentary greigite is either authigenic, or may originate from magnetotactic bacteria [10]. Studies of the magnetic properties of greigite magnetosomes are thus useful for providing a better understanding of the contribution of bacterial greigite to rock magnetism.

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Whereas the magnetic properties of magnetite magnetosomes have been studied in several bacterial strains [2,11–14], little is known about the magnetic microstructure of sulfide magnetosomes [15]. In addition, some magnetic parameters of greigite, including the effect of crystal size, shape and magnetocrystalline anisotropy on magnetic microstructure, are not satisfactorily known [16]. By studying bacterial sulfides, we hope to obtain useful information about the magnetic properties of greigite in general.

Off-axis electron holography in the TEM [17] can be used to study the magnetic microstructures of nanocrystals [18]. The method has been applied successfully to studies of magnetite magnetosomes, and proved to be extremely useful for assessing the competing effects of crystal shape, magnetocrystalline anisotropy and interparticle interactions in linear chains of magnetosomes [2,14].

2. Experimental

Magnetotactic bacteria were isolated from mud and water samples collected at Morro Bay, California using bar magnets. Water drops enriched in magnetotactic cells were placed on Ni TEM grids; after half a minute the drops were removed and the grids were allowed to dry in air. High-resolution TEM (HRTEM) images and selected-area electron diffraction (SAED) patterns were obtained using JEOL 4000EX electron microscopes (Arizona State and Cambridge Universities) operated at an accelerating voltage of 400 kV. Electron holograms and elemental maps were obtained using a Philips CM300ST electron microscope (Cambridge University) equipped with a Gatan imaging filter.

Off-axis electron holography in the TEM was used to study the magnetic microstructures of greigite magnetosomes in individual cells on the grids. The technique requires the use of a coherent electron source (a field-emission gun), a Lorentz lens for imaging samples in magnetic-field-free conditions, and a positively charged wire (an electron biprism) in the plane of the selected-area aperture. Half of the electron beam travels through the sample, while the other half travels through vacuum; the two beams are overlapped by the biprism, resulting in interference fringes in the image plane. As a result of the presence of electric and magnetic fields in the specimen, the electron beam that passes through the sample experiences a phase shift with respect to the beam that passes through vacuum; this phase shift is recorded in the spacings of the holographic fringes. By processing the recorded holograms digitally, it is possible to extract and separate the contributions of the mean inner potential (MIP) and the magnetic field to the holographic phase [12]. The results allow the quantitative determination of parameters such as magnetic moments and coercive fields for individual magnetosomes and entire magnetosome chains.

In the present study, the measured magnetic microstructure is displayed by adding contours to the magnetic contribution to the holographic phase shift. The magnetic flux enclosed between any two adjacent contours is then the same. It is important to note that in these experiments only the components of magnetic induction **B** in the plane of the specimen, perpendicular to the electron beam direction, are recorded. No information about the component of **B** in the electron beam direction is obtained.

3. Results

Most of the magnetotactic cells in the Morro Bay sample are rod shaped, have a single polar flagellum, and contain multiple chains of iron sulfide magnetosomes (Fig. 1a). The chains are not as well organized as is usual in magnetite-bearing bacteria; many cells contain crystals offset from the chains, apparently scattered throughout the cytoplasm. In some cells, chains are not recognizable, and the magnetosomes form disordered clusters. The cell shown in Fig. 1a was studied in detail.

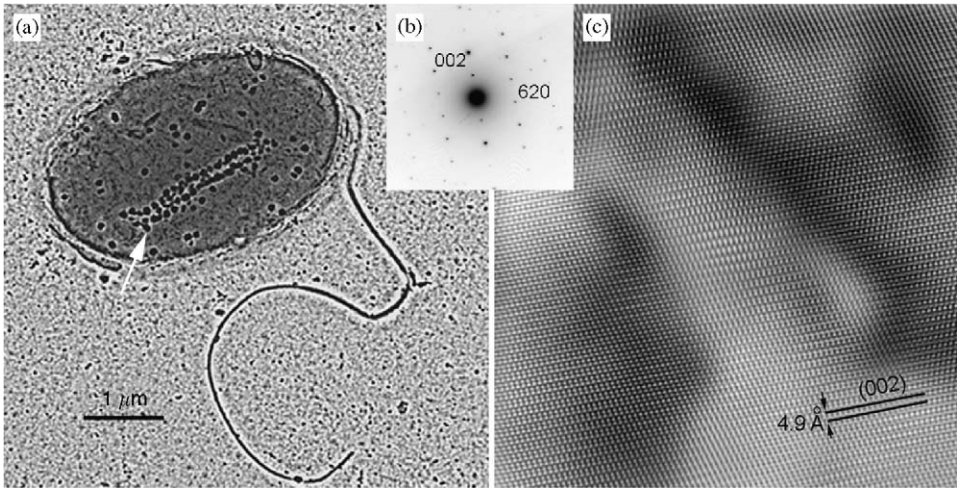

Fig. 1. (a) Bright-field electron micrograph of a rod-shaped single cell containing Fe sulfide magnetosomes. (b) SAED pattern from the crystal indicated by the arrow in (a), which is the same as crystal 2 in Fig. 2 and Table 1. (c) Fourier-filtered high-resolution image of the same crystal, showing non-uniform contrast due to defects or thickness variations arising from the irregular shape of the crystal.