Magnetic properties, microstructure, composition, and morphology of greigite nanocrystals in magnetotactic bacteria from electron holography and tomography

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ABSTRACT

Magnetotactic bacteria comprise several aquatic species that orient and migrate along geomagnetic field lines. This behavior is based on the presence of intracellular ferrimagnetic grains of the minerals magnetite (Fe3O4) or greigite (Fe3S4). Whereas the structural and magnetic properties of magnetite magnetosomes have been studied extensively, the properties of greigite magnetosomes are less well known. Here we present a study of the magnetic microstructures, chemical compositions, and three-dimensional morphologies and positions of Fe-sulfide crystals in air-dried cells of magnetotactic bacteria. Data were obtained using several transmission electron microscopy techniques that include electron holography, energy-filtered imaging, electron tomography, selected-area electron diffraction, and high-resolution imaging. The studied rod-shaped cells typically contain multiple chains of greigite magnetosomes that have random shapes and orientations. Many of the greigite crystals appear to be only weakly magnetic, because the direction of their magnetic induction is almost parallel to the electron beam. Nevertheless, the magnetosomes collectively comprise a permanent magnetic dipole moment that is sufficient for magnetotaxis. One of the cells, which is imaged at the point of dividing, contains multiple chains of both equidimensional Fe-sulfide and elongated Fe-oxide crystals. The equidimensional and elongated crystals have magnetic properties that are consistent with those of greigite and magnetite, respectively. These results can be useful for obtaining a better understanding of the function of magnetotaxis in sulfide-producing cells, and they have implications for the interpretation of the paleomagnetic signals of greigite-bearing sedimentary rocks.

Keywords: Greigite, magnetotactic bacteria, transmission electron microscopy, electron holography, electron tomography, magnetic properties, biomineralization

INTRODUCTION

Iron-sulfide magnetosomes in magnetotactic bacteria were first described in 1990 (Farina et al. 1990; Mann et al. 1990). The primary mineral in the magnetosomes was identified as greigite (Fe3S4) (Heywood et al. 1990, 1991; Bazyliński et al. 1990, 1993), which is ferrimagnetic and isomorphic with magnetite (Fe3O4). In subsequent studies, the structures and compositions of sulfide magnetosomes were analyzed in detail, and non-magnetic precursors of greigite (primarily mackinawite, FeS) also were identified (Pósfai et al. 1998a, 1998b). Despite these studies, sulfide-producing magnetotactic bacteria remain enigmatic because they are not available in pure culture (Bazyliński and Frankel 2004). Whereas the magnetic properties of magnetite magnetosomes have been studied from many perspectives for several bacterial strains (Diaz-Ricci et al. 1991; Moskowitz et al. 1993; Proksch et al. 1995; Dunin-Borkowski et al. 1998, 2001; McCartney et al. 2001; Weiss et al. 2004; Simpson et al. 2005), little is known about the magnetic microstructure of sulfide magnetosomes (Diaz-Ricci and Kirschvink 1992). The magnetic parameters of greigite, including the critical particle size for single-domain behavior, and the effects of shape and magnetocrystalline anisotropy on magnetic microstructure, are not known satisfactorily (Hoffmann 1992; Roberts 1995; Dekkers et al. 2000; Peters and Dekkers 2003; Chen et al. 2005). In the present study, we characterize Fe-sulfide magnetosomes comprehensively, with the aim of providing measurements that may shed light on sulfide biomineralization processes and on the biological functions of sulfide magnetosomes, as well as on the contribution of biogenic greigite to the paleomagnetic signal in sedimentary deposits.

Off-axis electron holography is a transmission electron microscopy (TEM) technique that can be used to study the magnetic microstructures of nanocrystals (Dunin-Borkowski et al. 2004). The method has been applied successfully to studies of magnetite magnetosomes, and it has been extremely useful for assessing the competing effects of shape and magnetocrystalline anisotropy and interparticle interactions on the magnetic properties of linear chains of magnetosomes (Dunin-Borkowski et al. 1998,