Iron sulfide crystals in magnetotactic bacteria: A transmission electron microscopy study

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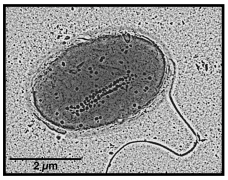
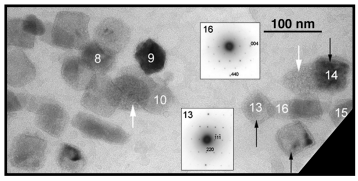
Abstract

Magnetotactic bacteria comprise a number of aquatic species that orient and migrate along geomagnetic field lines. This behavior results from the presence of magnetosomes - intracellular ferrimagnetic mineral grains of magnetite (Fe_3O_4) or greigite (Fe_3S_4). Whereas the structural and magnetic properties of magnetite magnetosomes have been studied extensively, the properties of greigite magnetosomes are less well understood. Here, we present a transmission electron microscopy study of the magnetic microstructures, chemical compositions, three-dimensional morphologies, orientations and positions of greigite crystals in air-dried cells of magnetotactic bacteria. Our results, which are obtained using electron holography, energy-filtered imaging, high-angle annular dark-field electron tomography and selected-area electron diffraction, are compared with similar results obtained from magnetite-containing cells.

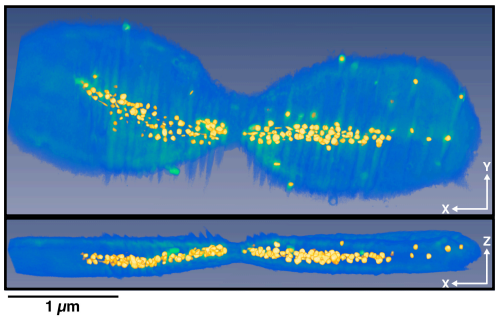
Greigite (Fe_3S_4) containing bacteria

Rod-shaped, iron sulfide containing bacteria were collected at Morro bay, California. Each cell contains multiple chains of magnetosomes. The greigite crystals are ~60 nm in size, approximately equidimensional and have no preferred orientations. The chains also contain elongated magnetite crystals (e.g., No. 16), which are interspersed between the greigite crystals and elongated along both [100] and the axis of the magnetosome chains.

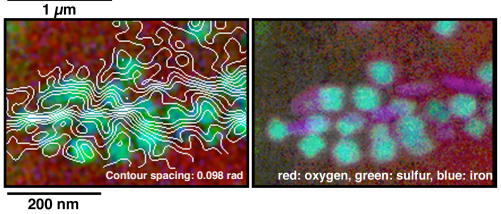




High-angle annular dark-field electron tomography was used to determine the three-dimensional positions, shapes and orientations of the crystals, which are more disorganized than in strains that contain only magnetite crystals. The aspect ratios of the greigite crystals range from 0.7 to 1.

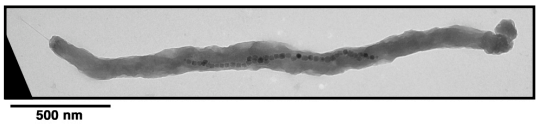


Off-axis electron holography was used to measure the magnetic properties of the crystals, which are consistent with those expected for greigite and magnetite. Although the average magnetization direction of the cell is parallel to the chain axes, the local magnetization direction in each crystal is determined by its shape and by interactions between adjacent crystals.

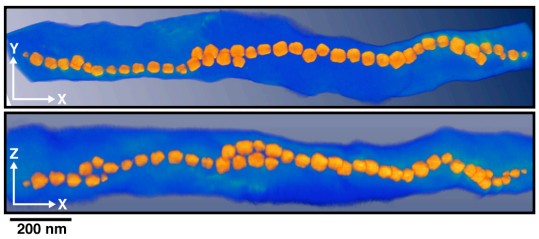


Magnetite (Fe_3O_4) containing bacteria

In contrast, magnetite crystals in a cell of *Magnetospirillum magnetotacticum* are formed in a straight chain. The average crystal size is 44 nm and the chain length is 1660 nm. The chain axis is parallel to magnetite [111]. The sample was provided by Herve Cadiou and prepared using cryofixation by Jeremy Skepper.



High-angle annular dark-field electron tomography reveals the positions, arrangements and equidimensional shapes of the crystals.



Off-axis electron holography shows that the magnetization of the chain follows the positions of the crystals. The contour spacing is 0.098 radians.

Magnetic moments of individual cells and migration speeds

Magnetic moments of cells can be calculated from electron holographic phase images using the equation:

$$m \approx +\left(\frac{\hbar}{e}\right)\int_{chain} \Delta\phi_{mag}(x,y)\,dl$$

where $\Delta\phi_{mag}$ is the step in the magnetic contribution to the phase shift across the chain and l is a direction along the chain axis.

Bacterium	Moment (Am^2)	mB/k_BT	Migration speed in direction of B as a fraction of swimming speed
Greigite containing cell*	9×10^{-16}	10.8	0.91
Magnetite containing cell*	3×10^{-16}	3.1	0.69
Magnetite containing MV-1 cell†	7×10^{-16}	8.4	0.88
Magnetite containing MS-1 cell†	5×10^{-16}	6.0	0.83

*This study
†Dunin-Borkowski et al. (1998) *Science* **282**, 1868-1870.

Even though the crystals in the greigite containing cells are less well organized with respect to their crystallography, morphology and position than in most magnetite-producing cells, collectively they result in a magnetic moment that is sufficient for magnetotaxis.