Spatial arrangements and magnetic properties of oxide and sulfide magnetosomes in magnetotactic bacteria

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We have used several advanced transmission electron microscopy techniques to study the physical, chemical and magnetic properties of intracellular ferrimagnetic magnetite (Fe_3O_4) and greigite (Fe_3S_4) crystals in magnetotactic bacteria. The structures, orientations and morphologies of the magnetosomes were identified using electron diffraction, high-resolution electron microscopy and high-angle annular dark field electron tomography. Their compositions were studied using energy-selected imaging. Off-axis electron holography was used to record magnetic induction maps of the cells.

Iron sulfide-containing, rod-shaped cells were collected from salt marshes. Each cell contained multiple chains of greigite magnetosomes, which had random shapes and orientations. Many of the greigite crystals appeared to be only weakly magnetic, presumably because their magnetic induction direction was almost parallel to that of the electron beam. The disordered three-dimensional arrangement of the crystals resulted in the magnetic field in the chain following a meandering path between adjacent crystals. Nevertheless, the magnetosomes were observed to collectively comprise a permanent magnetic dipole moment that is sufficient for magnetotaxis.

Magnetite-producing cocci were collected from lakes and streams. A cell type containing two double chains of magnetite magnetosomes was studied in detail. Within the double chains, the [111] axes of most crystals were approximately parallel to the chain axis. In contrast, the crystallographic directions perpendicular to the chain axis were randomly distributed. Each chain was therefore analogous to beads on a string, in which biological control appeared to be stricter in setting the [111] magnetocrystalline easy axis of the crystals to be parallel to the chain axis than in constraining their orientation about this direction. The magnetic signal was dominated by inter-particle interactions and by the shapes of the individual crystals.

The magnetic microstructures of chains and clusters of magnetite crystals in *Magnetospirillum gryphiswaldense* and its genetically engineered mutants were studied. Wild-type cells contained single chains of cubooctahedral magnetite crystals that were uniformly magnetized along the length of the chain. Mutant _mamJ cells lacked a magnetosome-associated protein that was apparently responsible for assembling the magnetosomes into chains. The magnetite crystals then occurred in clusters in each cell, producing a wide variety of magnetic microstructures, including vortex states with no net magnetic moment. Other mutant cells contained chains of small (~30 nm), irregularly-shaped crystals, many of which were superparamagnetic at room temperature. These observations highlight the delicate balance between crystal size, shape, orientation and chain configuration that determines whether such cells are able to respond to an external magnetic field.