

## **Magnetite biomineralization in magnetotactic bacteria: insights from iron isotopes and iron biochemistry**

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Magnetotactic bacteria (MTB) produce magnetite [Fe(II)Fe(III)<sub>2</sub>O<sub>4</sub>] nanoparticles in a genetically controlled way. In MTB, magnetite is produced in organelles called magnetosomes, consisting of a bi-layered lipid membrane surrounding the magnetite crystals. Although tremendous advances have been made to understand magnetite biomineralization in MTB, the precise biological and chemical pathways leading to magnetite precipitation are still a matter of debate. Here, we assessed Fe distribution and Fe isotope fractionation by the magnetotactic strain *Magnetospirillum magneticum* AMB-1 cultivated with various Fe(III) and Fe(II) sources to better constrain Fe cycling in MTB.

Growth media before and after AMB-1 culture, bacterial lysates (i.e. cells devoid of magnetosomes), and magnetite were analyzed for their Fe content and isotope composition. In all conditions, growth media after AMB-1 cultures were depleted in heavy isotopes relative to initial Fe sources. A significant fraction of Fe was identified in the bacterial lysates, suggesting that magnetite is not the sole Fe reservoir in AMB-1 cells. No significant amount of Fe adsorbed on cell membranes could be identified, implying that Fe in the lysates is contained in cytoplasm and/or periplasm. Lysates were enriched in the heavy Fe isotopes by 0.3 to 0.8‰ in  $\delta^{56}\text{Fe}$  relative to Fe sources, while magnetite samples were enriched in the light Fe isotopes by 1.5 to 2.5‰ relative to Fe sources. Moreover, mass-independent fractionations in odd (<sup>57</sup>Fe) but not in even isotopes (<sup>54</sup>Fe, <sup>56</sup>Fe and <sup>58</sup>Fe) were evidenced, highlighting a magnetic isotope effect. Magnetite samples were significantly enriched in <sup>57</sup>Fe by 0.23‰ relative to <sup>54</sup>Fe, <sup>56</sup>Fe and <sup>58</sup>Fe. We finally propose an integrative biogeochemical model for magnetite biomineralization in AMB-1.