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RESEARCH ARTICLE

Electroactivity of the magnetotactic bacteria *Magnetospirillum magneticum* AMB-1 and *Magnetospirillum gryphiswaldense* MSR-1

Mathias Fessler, Qingxian Su, Marlene Mark Jensen (✉), Yifeng Zhang (✉)

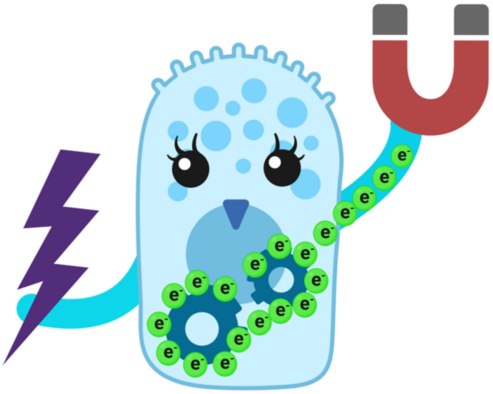
Department of Environmental and Resource Engineering, Technical University of Denmark, Copenhagen, DK-2800, Denmark

HIGHLIGHTS

- The first study of electrochemically active magnetotactic bacteria.
- Two magnetotactic species are able to generate current in microbial fuel cells.
- Electron shuttle resazurin enables both species to reduce the crystalline Fe_2O_3.
- *M. magneticum* can reduce poorly crystalline iron oxide (FeOOH).
- Electroactivity might be common for magnetotactic bacteria.

GRAPHIC ABSTRACT

Are Magnetotactic Bacteria Electroactive?



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ABSTRACT

Magnetotactic bacteria reside in sediments and stratified water columns. They are named after their ability to synthesize internal magnetic particles that allow them to align and swim along the Earth's magnetic field lines. Here, we show that two magnetotactic species, *Magnetospirillum magneticum* strain AMB-1 and *Magnetospirillum gryphiswaldense* strain MSR-1, are electroactive. Both *M. magneticum* and *M. gryphiswaldense* were able to generate current in microbial fuel cells with maximum power densities of 27 and 11 μW/m^2, respectively. In the presence of the electron shuttle resazurin both species were able to reduce the crystalline iron oxide hematite (Fe_2O_3). In addition, *M. magneticum* could reduce poorly crystalline iron oxide (FeOOH). Our study adds *M. magneticum* and *M. gryphiswaldense* to the growing list of known electroactive bacteria, and implies that electroactivity might be common for bacteria within the *Magnetospirillum* genus.

1 Introductions

The growing interest in replacing fossil fuels with renewable energies has increased the development of sustainable biotechnological processes. Microbial fuel cells (MFCs) are transducing devices where microorganisms use an anode as an electron acceptor for their anaerobic respiration of organic compounds, converting chemical energy into electrical energy (Logan et al., 2019). Although the feasibility of MFCs for electric energy production requires significant improvement, MFCs have been successfully applied to treat wastewater and remove toxic compounds (Wang and Ren, 2013; Fernando et al., 2019). Numerous microorganisms specia-

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✉ Corresponding authors
E-mails: mmaj@dtu.dk (M. Jensen); yifz@dtu.dk (Y. Zhang)

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lize in extracellular electron transfer (EET), i.e., electron transfer reactions beyond the cell surface, which is central to the function of MFCs (Logan et al., 2019) The generation of current in MFCs depends on electroactive microorganisms (EAM) that use their unique ability to export electrons to solid-state electron acceptors, such as iron oxides (Reguera et al., 2005) or electrodes (Logan et al., 2019) The microorganisms with EET abilities used in studies of MFC technologies are often based on axenic cultures. Some of the commonly used axenic cultures are *Geobacter sulfurreducens*, *Shewanella putrefaciens*, and *Rhodoferax ferrireducens*. Several mixed bacterial cultures are being employed in MFCs. Overall, EAM used in axenic and mixed cultures are phylogenetically diverse and found in all three domains of life (Logan et al., 2019).

Bacteria from the *Geobacteraceae* and *Shewanellaceae* families are the most used in MFCs due to their well-documented EET mechanisms and ability to generate high power densities (Coursolle et al., 2010; Logan et al., 2019; Lovley and Walker, 2019 ; Gu et al., 2021). The deduction of different EET mechanisms mainly derives from studies with different wild-type strains of *Geobacter* or *Shewanella* species, e.g., *Geobacter sulfurreducens* PCA and *Shewanella oneidensis* MR-1 (Reguera et al., 2005; Coursolle et al., 2010). During direct long-range EET, often found in *Geobacter* species, cells establish physical contact with the solid electron acceptor through electrically conductive nanowires extending from the cell surface (Filman et al., 2019; Lovley and Walker, 2019); Yalcin et al., 2020). On the other hand, *Shewanella* species usually rely on direct cell-electrode contact (Sun et al., 2021). Common for both types of EET are conductive proteins, such as outer-membrane multiheme *c*-type cytochromes and conductive nanowires. During indirect EET, electron transfer is mediated by flavins, which are diffusible redox-active molecules produced by the bacteria themself (Marsili et al., 2008). It is possible to mimic this EET mechanism artificially and enhance the current output of MFCs by adding synthetic redox mediators, such as resazurin, Anthraquinone-2,6-disulfonate (AQDS), neutral red, and humic acids to the reactor medium (Sund et al., 2007; Fathey et al., 2016; Yamasaki et al., 2018).

Bacteria with electroactive properties are not limited to metal-reducers (Holmes et al., 2016; Koch and Harnisch, 2016; Logan et al., 2019). The phylogenetic diversity of new EAM is continuously expanding. The search and finding of new EAM is important as it broadens the potential applications of microbial electrochemistry (Yee et al., 2020). Identifying and mapping EET mechanisms in bacteria outside the *Geobacter* and *Shewanella* genera will broaden our understanding of the phenomenon. Unveiling novel electroactive microorganisms can clarify how representative the different EET mechanisms are, leading to the identification of new electron transfer pathways and potentially increasing the success of microbial electrochemical technologies.

Magnetotactic bacteria (MTB) contain intracellular magnetic nano-crystal particles, which function as biological compasses, allowing MTB to migrate along redox gradients according to the Earth's geomagnetic field (Lefèvre et al., 2014). The so-called magnetosomes are membrane-enclosed vesicles containing iron oxide and/or iron sulfide in the form of magnetite (Fe_3O_4) or greigite (Fe_3S_4), respectively (Wang et al., 2020). To synthesize magnetosomes, MTB sequester soluble iron from the surroundings (Uebe and Schüler, 2016). Therefore, they play an essential role in global iron cycling (Moisescu et al., 2014; Amor et al., 2020). Magnetite biomineralisation relies on the precipitation of soluble Fe^{2+} and Fe^{3+}. However, the exact mechanism for uptake of extracellular iron for magnetite formation remains unclear, even though several genes, such as *mamB*, *mamM,* and *nirS*, are known to be important (Uebe and Schüler, 2016).

Magnetotactic bacteria are a phylogenetically and metabolically diverse group of prokaryotes, and many MTB remain uncultured (Lin et al., 2018). In this study, *Magnetospirillum magneticum* strain AMB-1 and *Magnetospirillum gryphiswaldense* strain MSR-1 were selected as model MTB to explore their potential for electroactive behavior. Both bacterial strains have been isolated from freshwater sediments and belong to the *Alphaproteobacteria* class in the *Proteobacteria* phylum (Matsunaga et al., 1991; Schüler and Köhler, 1992). *M. magneticum* has previously been shown to generate electricity by electromagnetic induction (Smit et al., 2018). In that study, mechanical energy is converted into electrical energy by pumping *M. magneticum* or purified magnetosomes through a solenoid by applying Faraday's law of electromagnetic induction. The heterotrophic and microaerophilic anaerobic lifestyle of *M. magneticum* and *M. gryphiswaldense* together with their strong dependence on iron for the production of their magnetosome led us to examine their potential for EET to electrodes and solid iron oxides. The purpose of this study was to screen these two MTB for their electroactive abilities in MFCs.

2 Materials and methods

2.1 Strains and medium

The strain *Magnetospirillum magneticum* AMB-1 was kindly supplied by Dennis Bazylinski (UNLV, Las Vegas). *Magnetospirillum gryphiswaldense* MSR-1 was purchased from the German Collection of Microorganisms and Cell Cultures (Braunschweig, Germany). Both species were cultivated in *Magnetospirillum* medium unless otherwise stated in the different experimental setups described below. The growth medium contained 0.68 g/L KH_2PO_4, 0.85 g/L Sodium succinate·$6H_2O$, 0.575 g/L Sodium tartrate·$2H_2O$, 0.05 g/L sodium acetate, 0.17 g/L $NaNO_3$, 0.11 g/L NH_4Cl, 0.1 g/L yeast extract, 2 mL/L ferric quinate solution ($FeCl_3 \cdot 6H_2O$ 4.5 g/L, quinic acid 1.9 g/L), and 5 ml/L Wolfe's mineral solution (DSMZ recipe No. 141). The media was purged with N_2 and pH was adjusted to 6.75 prior to autoclavation at 121 °C for 20 min.

For the growth experiments, the medium described above was used, and cultures were inoculated from fresh overnight cultures. Growth was quantified by measuring optical density at 600 nm. Cultures were grown in sealed serum bottles containing a 25 mL growth medium with a 35 mL headspace. Oxygen was added to a final concentration of 1% through a sterile filter to establish an oxygen gradient (Le Nagard et al., 2018).

2.2 MFC design and operation

The electroactive potential of the two *Magnetospirillum* strains was tested in sterile H-shaped MFCs. Each MFC reactor was assembled by using two 250 mL glass bottles as two half-cells. The half-cells were separated by a cation exchange membrane. Carbon brushes (The Mill-Rose Company, Ohio, US) were pretreated at 450 °C for 30 min and used as anodes (Lanas and Logan, 2013). The surface area of the anodes were 1204 cm^2 (Lanas and Logan, 2013). The cathode was a 4 cm by 4 cm titanium mesh connected to a titanium wire. The anode and cathode were placed in the center of each half-cell. The assembled MFCs without anolyte and catholyte were sterilized by autoclavation at 121 °C for 20 min. The anode chambers of the MFCs were filled with a sterile growth medium with $NaNO_3$ omitted. The catholyte was a solution of 50 mmol/L phosphate buffer (pH 7) containing 50 mmol/L $K_3[Fe(CN)_6]$. The anode chamber was closed with a gas-tight butyl rubber stopper, while the cathode was left open for aeration. The anolyte was purged with N_2 through a 0.22 µm filter to ensure anoxic conditions. The MFC reactors were inoculated with MTB in the exponential growth phase and operated at 30 °C in batch mode. The cells were concentrated by centrifugation, and the cell suspension was diluted to an OD_{600} of 3.2. 1 mL of cell suspension was used as inoculum. The cathode and anode were connected with a 1000 Ω resistor. The voltage was recorded automatically every 30 min. No mediators were added to the medium in the MFCs. Duplicate reactors were run in parallel.

2.3 Iron reduction and electron mediators

To test the ability of the two *Magnetospirillum* strains to reduce iron oxides as terminal electron acceptors in serum bottle cultures, $NaNO_3$ and O_2 in the media were replaced by either 25 mg/L amorphous iron oxyhydroxide (FeOOH) or 25 mg/L hematite (Fe_2O_3, Sigma-Aldrich, nanopowder, < 50 nm particle size). Amorphous iron oxyhydroxide (FeOOH) was prepared as described previously by neutralizing a $FeCl_3$ solution with NaOH until the pH reached 7 (Lovley and Phillips, 1986). The solution was washed several times before being added to the medium. In experiments with electron mediators (AQDS, humic acid, neutral red, and resazurin), they were added to a final concentration of 5 µmol/L. The cultures were incubated for ~30 d in the dark at 25 °C. For analysis of iron reduction, 200 µL samples were taken from the serum bottles at regular intervals. The samples were added directly into 200 µL of 1 mol/L HCl. The samples were incubated in the dark at 25 °C for 24 h and Fe^{2+} concentrations were measured. For Fe_2O_3, 400 µL culture was mixed with 800 µL 5 mol/L HCl. Tubes were rotated for 2 d to dissolve Fe_2O_3 prior to quantification of Fe^{2+}. The Fe^{2+} concentrations were determined by colorimetry using Ferrozine (Stookey, 1970). Briefly, 10 µL sample was mixed with 75 µL Ferrozine solution (2 g/L Ferrozine, 5 mL/L 5 mol/L HCl) and 75 µL acetate buffer (285 g/L sodium acetate, 116 mL/L acetic acid) in a 96-well plate, followed by measuring absorbance at 562 nm with a plate reader (BioTek Synergy Mx).

2.4 Statistical testing

Statistical significance was determined by comparing to the given control cultures with a one-tailed *t*-test assuming unequal variance. The threshold for significance was a *p*-value below 0.05.

3 Results and discussion

3.1 Current generation in MFCs

Both *M. magneticum* AMB-1 and its purified magnetosomes can convert mechanical energy to electrical energy by applying Faraday's law of electromagnetic induction (Smit et al., 2018). This discovery led us to explore the ability of *M. magneticum* AMB-1 to convert chemical energy to electrical energy in the search for new EAM. In our MFC setup, *M. magneticum* was grown in the anode chamber, where the only available electron acceptor was the carbon electrode. Therefore, *M. magneticum* could only proliferate in these reactors by exporting electrons generated during cell metabolism over the cell membrane to the electrode. In the reactors, *M. magneticum* generated current immediately upon inoculation (Fig. 1A). The current continued to increase until it peaked after approximately 30 d at 27 µW/m^2. *Magnetospirillum gryphiswaldense* MSR-1 was also able to generate current in the MFCs, even though the current was slightly lower

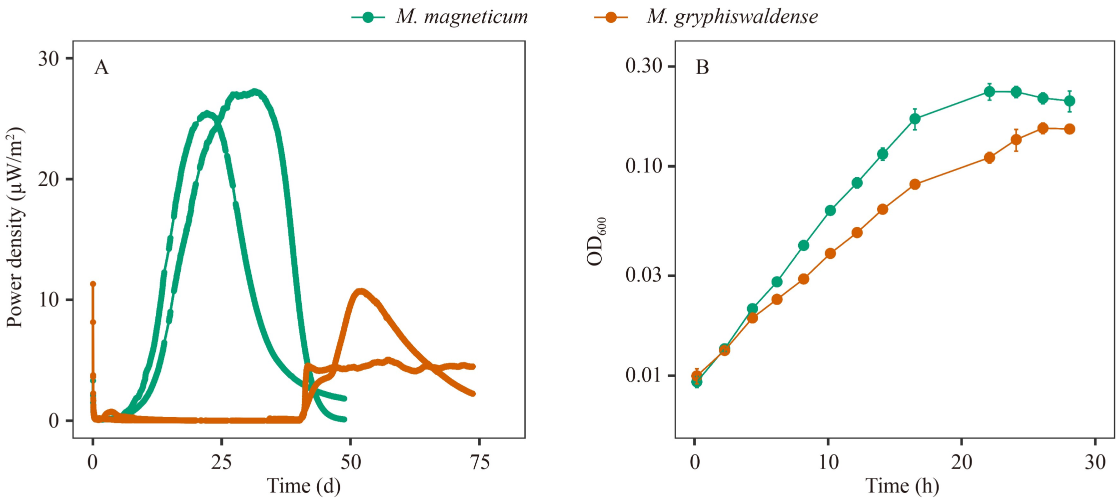

Fig. 1 Power density of *M. magneticum* and *M. gryphiswaldense* in MFCs (A, $n = 2$), and growth in serum bottles with $NaNO_3$ and 1% O_2 (B, $n = 4$). Error bars show standard deviation.

and the acclimatization period was substantially longer (Fig. 1A). *M. gryphiswaldense* might not be as strong of an electroactive as *M. magneticum*, as seen by the lower and slower current output. Also, part of the explanation for the observed difference in power density may be due to the fact that *M. gryphiswaldense* in general has a higher doubling time and did not reach the same cell density as *M. magneticum*, as seen by the growth in MTB medium with $NaNO_3$ as the electron acceptor (Fig. 1B). Under these conditions the doubling times for *M. magneticum* and *M. gryphiswaldense* were 3.97 h (± 0.14, $n = 4$) and 5.67 h (± 0.18, $n = 4$), respectively. Nevertheless, both *Magnetospirillum* species showed electroactive properties, suggesting that electroactivity might be common for MTB within *Magnetospirillum* genus. However, additional studies of more species from the *Magnetospirillum* genera are required to support this.

The maximum power densities reached by *M. magneticum* and *M. gryphiswaldense* were 27 and 11 μW/m^2, respectively, which compared to other electroactive species in pure and mixed culture is quite low (Logan et al., 2019). However, it is important to note that the purpose of the study presented here was to identify electroactive bacteria within the group of MTB, and further optimization of the MFCs is needed to reach the highest possible power density. This makes the comparision with other electroactive species that have been extensively studied difficult (Logan et al., 2019). In the future, to reach the full electroactive potential of the studied MTB, medium composition, cell density, and electrode material must be examined. For instance, a higher current output might be achieved by taking advantage of the unique property of MTB by using magnetic electrodes. Furthermore, the extracellular electron transfer mechanisms (e.g., through direct contact or shuttles) of the two bacteria could be an essential topic that is definitely something we would like to investigate in the future.

3.2 Reduction of iron oxides

Having established that both MTB strains were electroactive in MFCs, it was important to determine if the extracellular electron transfer to other electron acceptors than electrodes was possible. The interaction of the two MTB strains with the solid electron acceptor, Fe_2O_3 (hematite) failed to happen, as none of the two MTB were able to reduce Fe_2O_3 (Fig. 2A). Although Fe_2O_3 is one of the most abundant iron oxides in natural environments (Jiang et al., 2016), it has a relatively low reduction potential (Straub et al., 2001), meaning adequate electron export mechanisms are required to sustain microbial growth. On the other hand, FeOOH is less abundant in nature but more suitable for microbial reduction due to its higher reduction potential (Levar et al., 2017). *M. magneticum* was able to reduce FeOOH (Fig. 2A). The Fe^{2+} concentration in the incubation with *M. magneticum* continued to increase until 26 days after inoculation, after which Fe^{2+} concentrations remained stable. After Day 26, Fe^{2+} concentration reached 22 mg/L, which was significant different than 14 mg/L in the uninoculated control ($p < 0.05$, Day 52). Minimal iron(III) reduction was observed in the *M. gryphiswaldense* cultures with FeOOH (Fig. 2B) ($p < 0.05$, Day 52). This is consistent with the observations from the MFCs, which indicated only weak electroactive properties of *M. gryphiswaldense* (Fig. 1A). Therefore, it is not surprising that iron(III) reduction rates observed here are in the lower range compared to the reported values by other Fe(III) reducing bacteria, such as *Geobacter sulfurreducens* (Levar et al., 2017; Fessler et al., 2023). MTB incorporate high amounts of dissolved

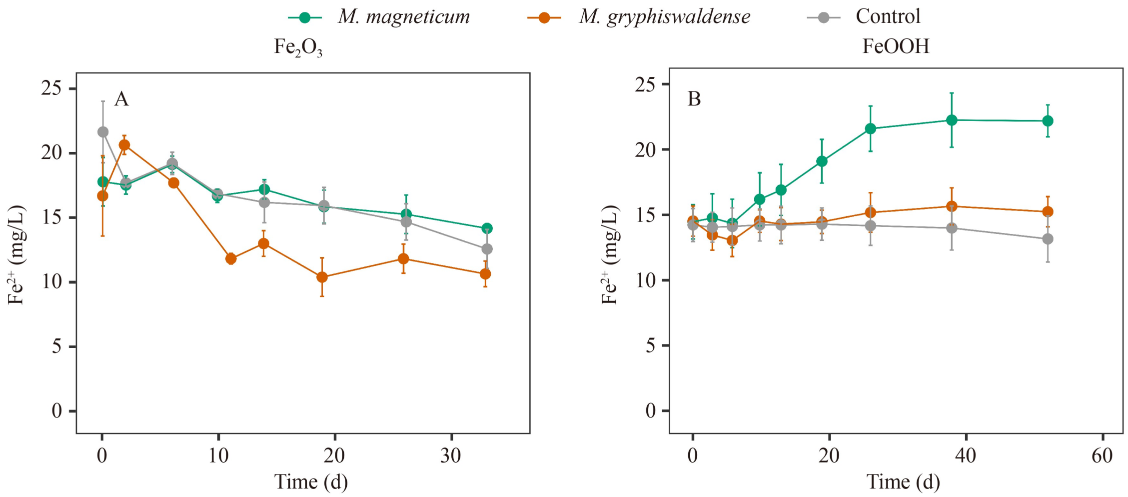

Fig. 2 Reduction of Fe_2O_3 (A, $n = 3$) and FeOOH (B, $n = 3$) by *M. magneticum* and *M. gryphiswaldense*. Error bars show standard deviation and the controls are uninoculated medium.

iron from the environment for the synthesis of magnetite or greigite nanoparticles produced in magnetosomes, which leads to the hypothesis that MTB could contribute significantly to the biogeochemical iron cycle (Amor et al., 2020). Our results suggest that some MTB can actively reduce iron oxides to Fe^{2+}, which could be assimilated and used in the formation of iron nanoparticles. The question remains if MTB can actively grow by dissimilatory iron reduction.

3.3 Fe_2O_3 reduction mediated by electron shuttles

In natural environments, it is common for microbes to produce electron shuttles to mediate extracellular electron transfer (Glasser et al., 2017). Electron shuttles can transfer electrons between the bacterial cells and extracellular electron acceptor, allowing for an alternative electron pathway that does not require direct contact with the extracellular acceptor. To test the effect of various electron shuttles on iron(III) reduction by *M. magneticum* and *M. gryphiswaldense*, the bacteria were grown with Fe_2O_3 and four different electron shuttles (Fig. 3) (Voordeckers et al., 2010; Fathey et al., 2016; Li et al., 2022). Increased iron(III) reduction by both MTB strains was observed in incubations with added resazurin, while the effect of humic acid, neutral red, and AQDS was negligible (Fig. 3). This is consistent with previous findings by Li and coworkers, where the shuttles with proton-associated characteristics (i.e., riboflavin and AQDS) cannot enhance EET in *Shewanella* (Li et al., 2019). The difference between the shuttles and the iron reduction might be due to the shuttles' molecular size or the different enzymes required for using various electron shuttles. Further research is necessary to unveil the mechanisms behind it. The concentration of Fe^{2+} increased to 25 mg/L in the beginning of the incubation with *M. gryphiswaldense* and added resazurin, while Fe^{2+} levels stayed relatively constant after Day 6 (Fig. 3A). On the other hand, the Fe^{2+} concentration in the *M. magneticum* culture increased continuously throughout the experiment, ending at 40 mg/L after 33 d. At the end of the experiment, both MTB cultures with resazurin were significantly different from the control cultures ($p < 0.05$, for both species on Day 33). Even though iron(III) reduction is still rather limited compared to stronger EAM such as *Geobacter* spp. and *Shewanella* spp. (Fessler et al., 2023), the results indicate that MTB are able to reduce Fe_2O_3 given that appropriate electron shuttles are present.

3.4 Environmental relevance and future perspectives

Our results show that MTB possess electroactive properties. Of the two species tested, *M. magneticum* displayed the strongest ability to reduce extracellular electron acceptors and produce current in MFCs. However, their electricity production was relatively low compared to other bacteria, such as *Bacillus subtilis and Escherichia coli* (Logan et al., 2019). To proper assess the electroactivity of *M. magneticum* in relation to other EAMs, it is necessary to optimize MFC cultivation conditions. The cell density under more favorable growth conditions than the MFCs was fairly low (Fig. 1B), and therefore, the full potential of the large surface area of the anode is most likely not utilized in our MFC setup, which may make the two MTB seem weaker when it comes to electroactivity. For instance, higher cell densities could be achieved in reactors with continuous flow medium.

To the best of our knowledge, MTB have not been identified in mixed species MFC biofilms (Fessler et al., 2022). Even though the power densities of the two MTB stains are insufficient for these species to dominate in

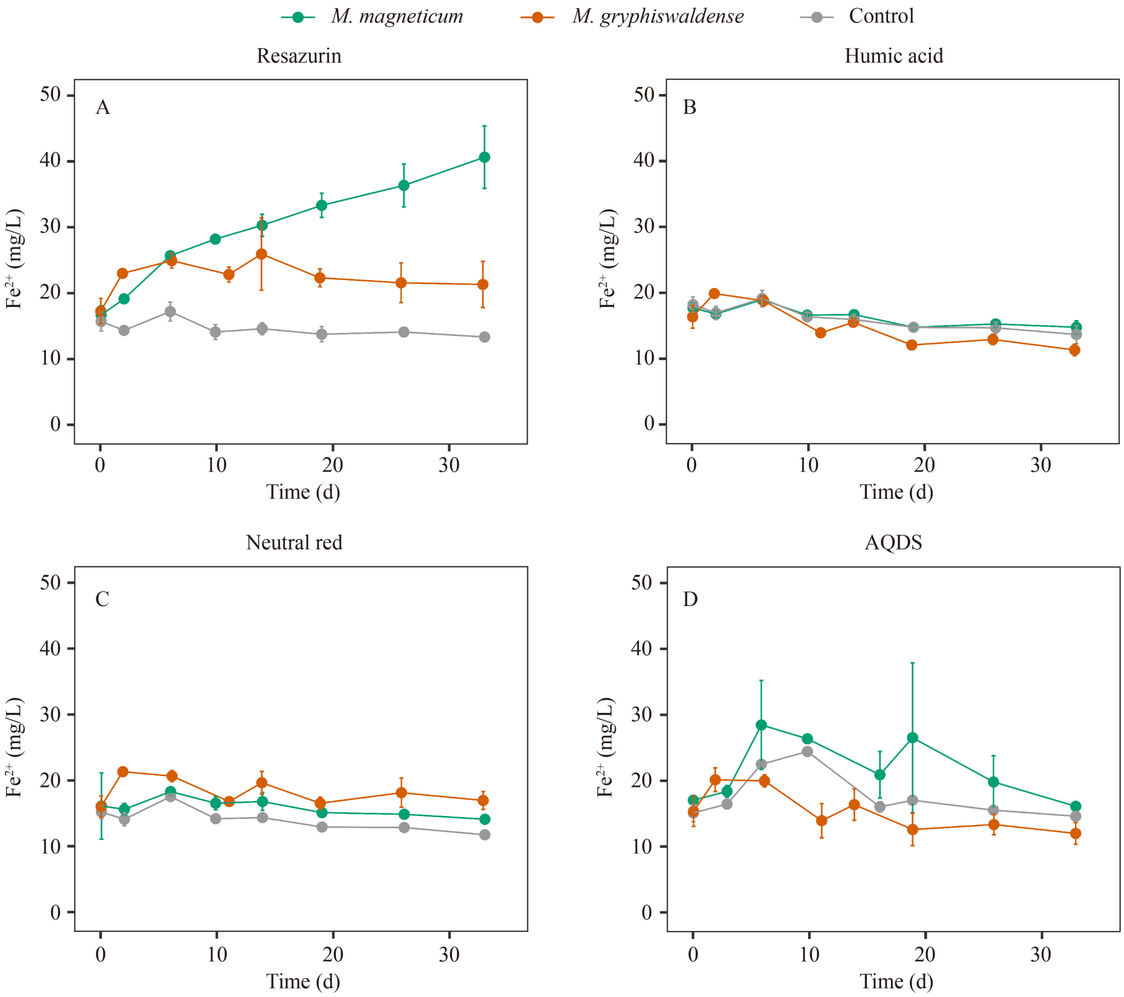

Fig. 3 Fe_2O_3 reduction by *M. magneticum* and *M. gryphiswaldense* in cultures with resazurin (A, *n* = 3), humic acid (B, *n* = 3), neutral red (C, *n* = 3), and AQDS (D, *n* = 3). Error bars show standard deviation and the controls are uninoculated medium.

mixed-species reactors, other qualities such as the microaerophilic nature of MTB may be of advantage. The availability of oxygen is not uniform across microbial biofilms. Offen, an oxygen gradient builds up between the oxic outer layers and the inner anoxic layers of the biofilm (Wessel et al., 2014). Opposite to *Geobacter*, both spp., *M. magneticum* and *M. gryphiswaldense* are able to grow in the presence of oxygen, and can potentially inhabit different parts of the biofilm than anaerobic EAM. In other words, thriving in an electrode-respiring biofilm does not simply depend on the relative strength of electroactivity, as external factors such as oxygen concentration also contribute to shaping the bacterial community, which can allow the proliferation of weaker EAM. Magnetotactic bacteria mostly live and sequester diverse elements at oxic-anoxic boundaries of aquatic habitats, and thus, exploring their electroactivity is important. In future studies, it is important to clarify whether *M. magneticum* and *M. gryphiswaldense* can sustain their presence in mixed-species microbial electrochemical reactors.

In *M. magneticum* there are 33 annotated cytochromes and 30 annotated ferredoxins (Matsunaga et al., 2005) and none of these are predicted to be localized in the outer membrane based on sequence (Yu et al., 2011). As it was not possible to predict the localization of all the proteins, and many of the predictions have not yet been verified experimentally, there might still be cytochromes or ferredoxins in the outer membrane of of *M. magneticum*, potentially mediating EET. Genes coding for electron export pathways in numerous EAM, including *Geobacter sulfurreducens* and *Shewanella oneidensis* have been identified (Zou et al., 2021). Identifying the genes responsible for EET in MTB will add to the existing knowledge within the field, and indicate how well the different electron export pathways are represented in nature. Despite the ability of purified magnetosomes and *M. magneticum* to convert mechanical energy to electricity (Smit et al., 2018), it is not known at this point whether the magnetosomes are involved in EET. As current profiles and ability to reduce iron(III) varied for the two investigated MTB strains, mangetosome involvement seems less likely. However, further examination of the EET mechanism of MTB is needed.

MTB and their magnetosomes have been applied for a variety of biotechnological applications, including removal of inorganic and organic pollutants (e.g., pesticides, phosphate, selenium), heavy metals, and radionuclides from wastewater (Wang et al., 2020b). Since some MTB are electroactive, it may bepossible to use the electrode potential to manipulate their metabolism, thereby controlling the processes of these applications (Hirose et al., 2018). Furthermore, with bacteria that are both magnetotactic and electroactive, we might be able to promote growth of electroactive biofilms using magnetic electrodes. Therefore, magnetotactic microorganisms possessing electroactive properties will allow the development of applications that are not feasible with organisms that only possess one of these two properties. A recent study by Su et al. (2023) showed that *M. magneticum* strain AMB-1 can store huge amounts of intracellular Polyhydroxyalkanoates (PHAs), which are a family of biodegradable polymers with promising applications (Su et al., 2023). Wastewater-driven MFCs where MTB convert the organic material in wastewater into electricity, combined PHA recovery from wastewater, also by the MTB, should be investigated in future studies.

4 Conclusions

In conclusion, the two magnetotactic bacteria, *M. magneticum* and *M. gryphiswaldense,* were shown to be electroactive, as these two strains produce could both produce current in MFCs and reduce insoluble iron oxides. Electroactivity has, to the best of our knowledge, not previously been demonstrated in MTB. This ability makes MTB even more unique. Optimization of reactor design and performance, and elucidation of the electron export pathway will increase our understanding of both magnetotactic and electroactive bacteria. The next step from here is to deepen the understanding of electroactive MTB, which may lead to development of specialized technological and environmental applications.

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Conflict of Interests Yifeng Zhang is a guest editor of Frontiers of Environmental Science & Engineering. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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