Bacterial Extracellular Electron Transfer

Components are Spin Selective

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ABSTRACT Metal-reducing bacteria have adapted the ability to respire extracellular solid surfaces instead of soluble oxidants. This process requires an electron transport pathway that spans from the inner membrane, across the periplasm, through the outer membrane, and to an external surface. Multiheme cytochromes are the primary machinery for moving electrons through this pathway. Recent studies show that the chiral induced spin selectivity (CISS) effect is observable in some of these proteins extracted from the model metal-reducing bacteria, Shewanella oneidensis MR-1. It was hypothesized that the CISS effect facilitates efficient electron transport in these proteins by coupling electron velocity to spin, therefore reducing the probability of backscattering. However, these studies focused exclusively on the cell surface electron conduits, and thus CISS has not been investigated in upstream electron transfer components such as the membrane-associated MtrA, or periplasmic proteins such as STC. Using conductive probe atomic force microscopy (AFM) measurements of protein monolayers adsorbed onto ferromagnetic substrates, we show that electron transport is spin selective in both MtrA and STC. Moreover, we have determined the spin polarization of MtrA to be ~75% and STC to be ~35%. This disparity in spin polarizations could indicate that spin selectivity is length dependent in heme proteins, given that MtrA is approximately 2 times longer than STC. Most significantly, our study indicates that spin-dependent interactions affect the entire extracellular electron transport pathway.
All biological energy generation strategies, including photosynthesis and respiration, require electron flow. In respiration, cells route electron flow from low potential electron donors to higher potential electron acceptors, scavenging free energy in the process. While oxygen is an energetically favorable and soluble electron acceptor that can diffuse inside cells to interact with intracellular electron transfer (ET) components, many microorganisms have adapted to thrive in anaerobic environments by using alternative electron acceptors for respiration, including insoluble redox-active minerals outside the cells. Metal-reducing bacteria transport electrons across the cell envelope, a strategy called extracellular electron transfer (EET), to gain energy from the respiration of abiotic metal-oxide minerals.

In the model metal-reducing bacterium *Shewanella oneidensis*, EET is achieved through a series of iron-containing proteins called multiheme cytochromes (Figure 1A), which localize to the inner membrane, periplasm, outer membrane, and along bacterial nanowires, collectively forming an EET pathway from the interior of cells to extracellular surfaces.

![Figure 1. Schematic representation of extracellular electron transfer and spin polarization measurements. (a) Shows a cartoon of a *Shewanella oneidensis* cell, with emphasis placed on the relative locations of key cytochromes. IM is inner membrane and OM is outer membrane. Full](image)

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**Figure 1.** Schematic representation of extracellular electron transfer and spin polarization measurements. (a) Shows a cartoon of a *Shewanella oneidensis* cell, with emphasis placed on the relative locations of key cytochromes. IM is inner membrane and OM is outer membrane. Full
structures of the MtrA and STC, with length scale bars, are provided for reference. (b) Schematic of the experimental setup of the magnetic conductive atomic force microscopy (AFM) measurements.

EET was initially observed and studied in the context of reducing environmental minerals, but it has since been shown that EET-capable microorganisms can use electrodes as terminal electron acceptors\textsuperscript{7}. As such, these electrochemically-active microorganisms present a unique model system for investigating the biotic-abiotic interface, and for developing hybrid ‘living electronics’ that combine the properties of cells and biomolecules with solid-state electronics\textsuperscript{5} Studies exploring the applications of EET have led to the extensive development of technologies such as microbial fuel cells\textsuperscript{8-10}, bioelectrochemical wastewater treatment\textsuperscript{11}, bioelectronic sensors\textsuperscript{12,13}, and microbial electrosynthesis\textsuperscript{14-16}, while newer research indicates that biological systems have unique properties\textsuperscript{17} which could facilitate the development of bio-spintronic devices\textsuperscript{18}.

A recent study of MtrF and OmcA, two \textit{S. oneidensis} cell surface decaheme cytochromes which function as outermost conduits for EET to surfaces, demonstrated that electron transport in both these molecules is spin selective\textsuperscript{19}. These results are attributed to the chiral induced spin selectivity (CISS) effect\textsuperscript{20,21}, where electron transport through chiral molecules, including proteins, has shown a correlation between the electrons' linear momentum and spin, resulting in preferential transport of certain spin. The CISS effect has been demonstrated experimentally for many types of molecules ranging from single amino acids\textsuperscript{22} to polypeptides\textsuperscript{23}, long alpha-helix proteins and DNA\textsuperscript{24}, and protein complexes used for electron transport such as Photosystem I\textsuperscript{25}. The natural abundance of chiral biological structures gives rise to the possibility of an important role of the CISS effect in biological systems. For example, CISS could improve the efficiency of electron
transport in non-conductive organic structures. However, by demonstrating CISS in biomolecular electron conduits that evolved to naturally interface with abiotic surfaces, the MtrF and OmcA results raise the intriguing possibility that spin filtering plays a role in extracellular respiration and may be exploited at biotic-abiotic interfaces.

Spin polarization induced by the CISS effect has been shown to be length dependent\textsuperscript{26,27}. Spin polarization increases approximately linearly with distance, while total charge flow decreases\textsuperscript{27}. MtrF and OmcA transport charge along similar length scales, but were observed to have different spin selectivities: 63\% in OmcA vs. 37\% in MtrF\textsuperscript{19}. This difference led to a hypothesis that the secondary structure helical content (percentage of residues in $\alpha$-helices within the protein) affects the net spin polarization through the protein.

The relationship between CISS and EET in \textit{S. oneidensis} has just begun to be elucidated. MtrF and OmcA are both responsible for the terminal step in an extended EET chain that starts in the inner membrane. The Mtr-Omc pathway is a subset of cytochromes in \textit{S. oneidensis} responsible for taking electrons from the periplasm, transporting them across and along the outer membrane, and to the terminal electron acceptor\textsuperscript{6}. MtrA (Figure 1A) is a periplasmic and membrane-spanning protein that sits inside of the MtrB porin thereby transporting electrons across the outer membrane to the cell surface conduits\textsuperscript{28}. Collectively, the cytochromes of the Mtr-Omc pathway constitute a heme wire where electrons are driven along the wire via a redox-driven hopping mechanism across the cell envelope\textsuperscript{29}. The small tetraheme cytochrome (STC or CctA, Figure 1A) is thought to act as an electron shuttle between the inner membrane and Mtr-Omc pathway\textsuperscript{30}. If these upstream proteins also exhibit spin selectivity, it could have broader implications for the role of CISS in the EET chain. Additionally, MtrA and STC have significantly different lengths and secondary structures from MtrF and OmcA, providing the opportunity to examine the effects of length and
secondary structure on CISS in these systems. Previous studies have looked at conduction measurements and modeling in STC\textsuperscript{31}, but these investigations focused purely on conductivity and did not attempt to probe spin filtering behaviors. To our knowledge, no similar work has been done in MtrA.

Here, we investigated the CISS effect in two key components of the EET pathway in \textit{S. oneidensis}: the periplasmic 4 nm long tetraheme cytochrome STC and the membrane-spanning 8 nm long decaheme cytochrome MtrA (measured as shown in Figure 1A), which transmits electrons to the previously investigated Mtr/Omc proteins. The measurements show higher spin selectivity in MtrA than STC, and demonstrate that, beyond the terminal cell surface reductases, spin filtering is exhibited by multiple EET proteins that span the cell envelope.

\textbf{Results and Discussion}
Figure 2. Protein adsorption test using AFM, showing the MtrA (A&C) and STC (B&D) monolayers created by the final selected adsorption conditions. (A&B) Show tapping AFM topography images collected immediately after high-force contact scanning. Forces were selected to be sufficient to remove the protein from the surface, but small enough to prevent scratching the gold substrate. (C&D) Show averaged cross sections of the scratched regions, indicating that the depth of the wells left behind (~6 nm for MtrA and ~3 nm for STC) are as expected for a monolayer of these molecules (8 nm for MtrA and 4 nm for STC).

Monolayer deposition orientation and uniformity of both MtrA and STC were examined by AFM scratching experiments of the film deposited on clean gold-covered glass (see Materials and Methods). The tapping topography of the scratched areas (Figure 2A and 2B) showed a 1x1 μm area pit reaching the gold layer. Analyzing the cross section (Figure 2C and 2D) yielded the monolayer height of ~6 nm and ~3 nm for MtrA and STC respectively. These heights correlate with the known length scales of the MtrA and STC (3x4x8 nm and 2x3x4 nm, respectively)\(^{31}\), providing evidence for the deposition of a monolayer of proteins. Protein coverage of gold surfaces with STC was also verified with polarization modulation infrared reflection absorption spectroscopy (PMIRRAS, Figure S1). The proteins were further characterized with protein film electrochemistry, which showed the proteins remained redox active with similar midpoint potentials to their unmodified counterparts (Figure S2)\(^{32}\) despite the modification of adding a gold binding motif.

The spin selectivity of the conduction through MtrA and STC was measured by comparing the currents through the proteins deposited on the ferromagnetic substrate (Figure 1B) when magnetized in the North pole facing up versus down directions.
Figure 3. Spin dependent conduction of MtrA and STC by conductive AFM IV-spectroscopy for protein adsorbed onto magnetizable substrates. Insets show mean as solid lines and standard deviation as shaded error bars with the same axes range as the full plot. (A) IV curves collected for the sample with MtrA. Data was collected at 270 different positions for each magnet orientation. (B) IV curves collected for the sample with STC. Data was collected at 100 positions for each magnet orientation.

Figure 3A shows all data collected from 270 different points on the sample with MtrA proteins and Figure 3B shows the same for 100 points on a sample with STC. Insets in Figure 3 show the mean current vs. voltage of all curves as solid lines and the standard deviation as shaded error bars. It is apparent that the currents going through the proteins when the substrate is magnetized in the up direction are larger than when the substrate is magnetized in the down direction for both MtrA and STC. However, the difference is much more significant for the MtrA proteins. This becomes even clearer when calculating the spin polarization of the current, calculated as \[ \left( \frac{I_{up} - I_{down}}{I_{up} + I_{down}} \right) \times 100, \] and plotting it as a function of applied voltage (Figure 4). To calculate a
figure of merit of the spin polarization, the mean polarization value for the voltage range between 0.5 to 1.5 V was calculated. This voltage range was chosen because it had relatively constant value and it is not in high voltages where the current probe tends to saturate for both directions. The negative voltages were omitted due to the effect of the high voltage of the positive sweep on the integrity of the proteins. The calculated values are 75 ± 2% for the MtrA whereas for the STC it is 35 ± 18%. Due to the lower spin polarization and higher noise measured in STC using this method, additional spin polarization characterization methods were used to corroborate these results. Scanning tunneling microscopy IV-spectroscopy measurements yielded lower noise results, while presenting a spin polarization of 35 ± 6%, similar to the AFM result (Figure S3). Furthermore, 2D electron gas gated Hall device measurements\textsuperscript{19} in liquid also confirmed the presence of spin selectivity in STC, showing it is not limited to dry conditions (Figure S4).

The presented results show that spin polarization of charge is not unique for the cell surface cytochromes (MtrF and OmcA)\textsuperscript{19}, but is prominent in both the membrane-spanning MtrA and the periplasmic STC. Therefore, it seems that components throughout the entire EET chain across the cell envelope of \textit{S. oneidensis} are spin selective. Moreover, all the molecules that have been measured exhibit the same spin-momentum coupling preference. This fact raises the intriguing possibility that the spin polarization from the CISS effect persists across multiple molecules in the extracellular electron transport chain. It has been recently proposed that spin selectivity promotes efficient ET in biomolecules, due to reduced backscattering caused by the fact that a change in the charge direction of motion (momentum) must correspond with a spin flip\textsuperscript{33}. It is possible that in multi-molecule electron transport systems, cooperative CISS (with the same spin preference) facilitates hopping from one molecule to another by suppressing backscattering between molecules.
In the previous work comparing MtrF and OmcA, a significant difference in spin selectivity was observed between the two proteins, in spite of them being similar in size, length and heme arrangement. Differences in helical secondary structure content (18% for OmcA vs. 11% for MtrF) were hypothesized to be the cause of the significant difference between the spin polarizations. This hypothesis holds when comparing these two molecules to MtrA, which has a 28% helical secondary structure and higher spin polarization than either molecule. However, our results show a much lower spin polarization through STC despite having a high concentration (~44%) of helical secondary structure compared to MtrA.\textsuperscript{34,35}

Unlike the comparison between MtrF and OmcA, STC and MtrA differ dramatically in length and structure. It has been shown that the spin polarization driven by the CISS effect is directly proportional to the length of DNA and oligopeptides.\textsuperscript{27} Therefore, due to the difference in length, it is impossible to compare the effects of helical secondary structure between these two systems. Length seems to have a larger effect on spin polarization than helical secondary structure content, creating small spin polarization through the highly helical STC as compared to the longer but less helical MtrA. But a true study of the effect of secondary structure would require comparing pairs of molecules where secondary structure is the primary difference. The key benefit to comparing STC and MtrA is that it allows investigation of the effects of length dependence on CISS in cytochromes for the first time. We find that MtrA, which is approximately 2 times as long as STC, exhibits approximately 2 times larger spin polarization. The strong dependence of charge transport on spin direction in the longer MtrA suggests that coupling the electron’s velocity to its spin enacts a significant penalty on backscattering of electrons of the preferred spin. Thus, CISS may enhance the efficiency of EET through cytochromes.
Figure 4. Percentage of spin polarization \([\frac{(I_{up} - I_{down})}{(I_{up} + I_{down})}] \times 100\) of (A) MtrA and (B) STC. Here, \(I_{up}\) and \(I_{down}\) are the mean currents with the substrate magnetized in the north pole up and down, respectively.

Conclusion

Presented results show that the periplasmic STC and the membrane-spanning MtrA both possess spin polarization properties due to the CISS effect. MtrA exhibits much higher spin selectivity at \(\sim 75\%\) when compared to STC at \(\sim 35\%\). We attribute this result to the difference in length scale (2 times larger for MtrA), rather than the difference in protein secondary structure as was suggested previously by comparing the cell surface cytochromes MtrF and OmcA. This is the first time length dependence effects on CISS are reported for electron transfer proteins such as multiheme cytochromes, and the relationship seems similar to what has previously been reported for length dependence in DNA and polypeptides.

Another important consequence from presented results is that spin selectivity has now been measured for extracellular, membrane-associated, and periplasmic cytochromes. The results
indicate that CISS is present through all parts of the EET pathway and therefore might possess an important role in the efficiency of the process.

Materials and Methods

Protein Purification

pBAD202/D-TOPO vector containing a gene encoding recombinant MtrA was introduced into *E. coli* BL21(DE3) as described previously along with the pEC86 vector for cytochrome *c* maturation. The recombinant MtrA contained a 4xCys/V5/6xHis tag (DDDDKAACCPCGCCKGKIPQPLLGLDSTRTGHMMMBB) at its C-terminus for purification and covalent binding to Au surfaces. Cells were grown in lysogeny broth to an OD*₆₀₀* of 0.6 before induction with 1mM L-arabinose for another 5 h at 25 °C. Cells were harvested at 6000 g for 15 min at 4 °C. Lysis was completed in Buffer A (20 mM Tris-HCl, pH 8.5, 1 mM TCEP, 10% glycerol, 500 mM NaCl, 1 mg/mL lysozyme, 2 µL/10 mL benzonase, 2 mM MgCl₂, protease inhibitor) and passed through the French press three times at 8000 lb/in². The lysate was spun at 15,000 g for 30 min at 4 °C. The supernatant containing tetra-cysteine MtrA was loaded onto a HisTrap column, equilibrated with Buffer B (20 mM Tris-HCl, pH 8.5, 1 mM TCEP, 10% glycerol, 500 mM NaCl, protease inhibitor) and 20 mM imidazole. The protein was washed and eluted with Buffer B with an imidazole gradient (0-500 mM). Fractions containing tetra-cysteine-tagged MtrA were pooled and concentrated to ~1 mL using a 10 kDa molecular weight cut-off (MWCO) Amicon centrifugal filter. This sample was loaded onto a HiLoad 16/600 Superdex 200 pg size exclusion column twice for removal of contaminating proteins. For both times, the column was washed with 20 mM Tris-HCl, pH 8.5, 10% glycerol, 1 mM TCEP, and 150 mM NaCl. After testing by SDS-PAGE, fractions containing pure MtrA (13.2 µM) were pooled and
concentrated using a 5 kDa MWCO Amicon centrifugal filter. Concentrated samples were distributed into 50 µL aliquots and stored at -80 °C.

The pD431-MR vector containing a gene encoding recombinant small tetraheme cytochrome (STC) from *Shewanella oneidensis* with an S87C point exchange and a twin strep tag (AWSHPQFEKAWSHPQFEK) on the C-terminus together with a kanamycin resistance gene was produced by DNA 2.0 and transformed with a pEC86 vector containing a sequence encoding the Ccm pathway (Cytochrome c maturation together with chloramphenicol resistance gene), into *E. coli* using the heat shock method. Cells were grown aerobically with shaking (250 rpm, 24 h, 37 °C) in Luria Bertani media with kanamycin and chloramphenicol added to final concentrations of 50 mg mL⁻¹ and 35 mg mL⁻¹, respectively. Cells were induced at an optical density (OD600) of 0.6 by addition of isopropyl β-D-1-thiogalactopyranoside (IPTG) to a final concentration of 0.2 mM. After growing approximately 18 h, the medium changes color from yellow to brown. Cells were then harvested by centrifugation at 4 °C, 16,128 x g for 1 h. Periplasmic extracts were obtained by adding lysozyme to a final concentration of 28 μM in 20 mM PBS buffer at pH 7.2 (phosphate buffered saline) with 100 mM EDTA, 0.0002 U/µL DNase I (Thermo Fisher Scientific), and 2 tablets of Pierce protease inhibitor and gently stirring for 90 min at 4 °C. The resulting extract was cleared by centrifugation (16,128 x g) for 1 h. The supernatant was kept in 20 mM PBS at pH 7.2 at 4 °C for overnight dialysis and then applied to a 40 mL diethylaminoethyl cellulose (DEAE) column in the same buffer. The column was washed with increasingly concentrated PBS (50 mM, 100 mM, 150 mM, 200 mM, 250 mM, 300 mM, 350 mM and 400 mM) with 5 column volumes of each concentration at pH 7.2. The STC eluted at 400 mM PBS. Brownish-red fractions containing STC were pooled and concentrated with amicon ultra-centrifugal filters (2 kDa molecular weight cut-off) before applying to a 30 ml Strep-Tactin column.
equilibrated with 20 mM PBS at pH 7.2 at room temperature and eluting with 5 mM desthiobiotin. Fractions containing STC were pooled, buffer-exchanged and concentrated with amicon ultra-centrifugal filters (2 kDa molecular weight cut-off) before use. Homogeneity of purified STC was confirmed via SDS-PAGE (Fig. 1) and UV-vis spectroscopy (Fig. 2).^40

**Protein Monolayer Formation**

To form a monolayer of MtrA, undiluted prepared protein was drop-cast on the substrate of choice. The device was then incubated for one hour at 4 °C in a humid environment, rinsed with buffer solution and then DI water, and dried overnight.

To prepare a monolayer of STC, the prepared protein was diluted by a factor of 100X and drop-cast on the substrate of choice. The device was then incubated for four hours at 4 °C in a humid environment, rinsed with first buffer solution and then DI water, and dried overnight.

**Protein Monolayer Characterization by AFM**

Protein attachment to gold was studied for both proteins using commercially available polycrystalline 100 nm Au on aluminosilicate glass substrates (Sigma-Aldrich 643246-5EA) on a Cypher ES AFM (Oxford Instruments). Substrates were cleaned by sonication for 15 min each in acetone, isopropanol, and deionized water (in order). Substrates were immediately dried and fixed to AFM pucks.

High resolution imaging and scratching experiments were performed on each of the following conditions to determine optimal conditions for protein monolayer formation: bare gold, buffer incubated overnight, undiluted MtrA incubated for 1 h, undiluted MtrA incubated for 16 h, 10X diluted STC for 4 h, 100X STC diluted for 4 h, and 1000X STC diluted for 4 h. Scratching
experiments were performed by quickly scanning a 1x1 µm square with a tip force large enough to scratch away the protein, but insufficient to scratch the gold surface. Then, the AFM was switched to tapping mode and a 3x3 µm image was collected (Figure S5, 2A, and 2B). The topographic image was background corrected with a linear plane-fit and the cross-sections were taken as an average of 50 scan lines from the scratched sample area (Figure 2C and 2D).

*Magnetic Heterostructure Fabrication*

Magnetic substrates were fabricated by an epitaxial nanostructure growth procedure by using the Molecular Beam Epitaxy (MBE PREVAC) system at the Institute of Physics of the Polish Academy of Sciences in Warsaw.

The sample configuration is: Al2O3(0001)/Pt 5 nm/Au 20 nm/Co 1.5 nm/Au 5 nm, the magnetization easy axis direction of the samples is out-of-plane, exhibiting perpendicular anisotropy with a coercive field of ~160 G, as shown by polar magneto-optic Kerr effect (P-MOKE) measurement (Figure S6). The fully rectangular shape of the hysteresis loop indicates that all cobalt spins are aligned in one direction perpendicular to the film surface. The top gold layer acts both as a capping layer to prevent oxidation of the Co layer and as a surface for covalent bonding of the Cysteine tags of the protein complexes.

Substrates were washed in acetone, isopropanol and ethanol and then dried with high-pressure Nitrogen gas flow and fixed to an AFM puck prior to the protein adsorption process.

*Magnetic Conductive AFM Experiment*
AFM measurements were performed on a Cypher ES Environmental System AFM (Oxford Instruments) using conductive AFM tips (MicroMasch HQ:NSC18/Pt). Bias was applied to the sample while the AFM tip was kept grounded. The substrate was placed in a ~1000 G magnetic field with north oriented in the down direction (applied magnetic field is much higher than the ~160 G coercive field of the substrate—Figure S4), then carefully removed from the field and placed in the AFM. For each condition tested, a 10x10 µm tapping scan was performed to image protein coverage. After scanning, IV spectra were collected at 270 locations for the MtrA with an engage force of 45 nN and at 100 locations for the STC with an engage force of 17 nN. The sample was then removed from the AFM, placed in a magnetic field oriented in the opposite direction, and returned to the AFM for an identical set of images and IV curves.

ASSOCIATED CONTENT

Supporting Information.

The following files are available free of charge.

One supporting information file (PDF), including six supplemental figures and associated materials and methods. Fig. S1: electrochemical characterizations of modified STC and MtrA, Fig. S2: PMIRRAS characterization of STC monolayer, Fig. S3: STM magnetic dependent IV curves of STC, and Fig. S4: Hall effect polarization data of STC, Fig. S5: AFM characterization of STC monolayer, Fig. S6: P-MOKE characterization of magnetic heterostructure substrates.

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‡These authors contributed equally. The manuscript was written through contributions of all authors. All authors have given approval to the final version of the manuscript.

Notes

The authors declare no competing financial interest

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ABBREVIATIONS

CISS, chiral induced spin selectivity; EET, extracellular electron transfer; AFM, atomic force microscopy; STC, small tetraheme cytochromes; PMIRRAS, polarization modulation infrared reflection absorption spectroscopy; MBE, molecular beam epitaxy; MWCO, molecular weight cut-off; P-MOKE, polar magneto-optic Kerr effect

REFERENCES


ToC- Current through multiheme cytochromes is spin dependent.