

Chapter 3

Extracellular Electron Transfer in Bioelectrochemically Active Microorganisms



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3.1 Introduction

Electrochemically active microorganisms capable of transferring electrons to/from electrodes play essential roles in bioelectrochemical systems, such as microbial fuel cells and microbial electrosynthesis (MES). Electrochemical and molecular biological studies have demonstrated the detailed mechanisms of extracellular electron transfer (EET) between microorganisms and electrodes. Extensive studies in the last two decades revealed that various microorganisms can transfer electrons to/from electrodes. Detailed mechanisms of electron transfer from microorganisms to electrodes have been intensively studied on two model microorganisms, *Geobacter sulfurreducens* and *Shewanella oneidensis*. These microorganisms are also capable of receiving electrons from electrodes, and the mechanisms of electron uptake have been also studied.

3.2 Extracellular Electron Transfer from Microorganisms to Electrodes

In the bioelectrochemical systems, such as microbial fuel cells, electrons are transferred from electrochemically active microorganisms to the electrodes (Fig. 3.1a). Electrons from cytoplasm are transferred across the cell membranes composed of lipid bilayers via proteins possessing redox-active cofactors, such as *c*-type cytochromes and iron-sulfur proteins and electrically conductive nanowires (Fig. 3.2).

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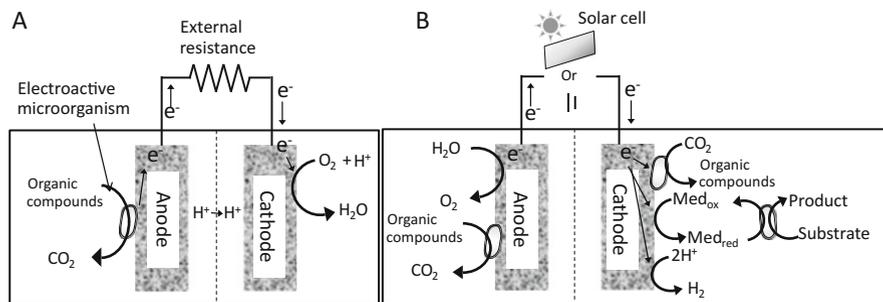


Fig. 3.1 Schematics of a microbial fuel cell (a) and a microbial electrosynthesis (microbial electrolysis cell) (b)

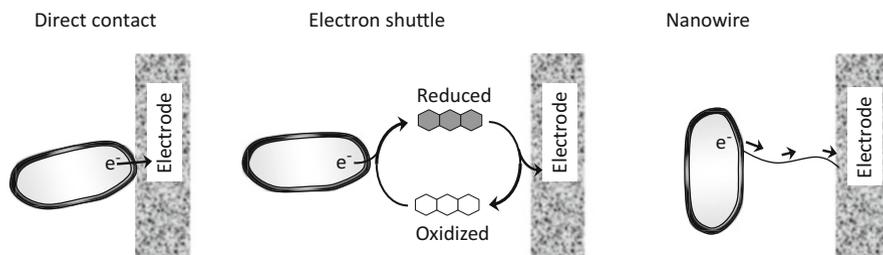


Fig. 3.2 Proposed mechanisms for electron transfer from electroactive microorganisms to the anode

Electron acceptors outside the cells are reduced by primary three different mechanisms, direct contact, electron conductive nanowires, and electron shuttles. The electron transfer mechanisms from the cell surface to the electrode mentioned here are not independently in typical cases but cooperatively, e.g., direct contact and nanowires for *G. sulfurreducens* and direct contact, nanowires, and electron shuttles for *S. oneidensis* (Fig. 3.3).

3.2.1 Direct Contact

In order to transfer electrons from inside the cell to an electrode outside the cell, the electrons must be passed through cell membranes which have insulator property. Electron carrier proteins, *c*-type cytochrome and/or iron-sulfur protein, localized near the cell membrane play essential roles for electron transfer from the cells to the outside in both well-studied microorganisms, *G. sulfurreducens* and *S. oneidensis* (Fig. 3.3). NADH produced in the process of respiration produces quinol by transferring electrons to quinone by NADH dehydrogenase. The electrons of NADH are transferred from inner membrane proteins to the redox-active proteins

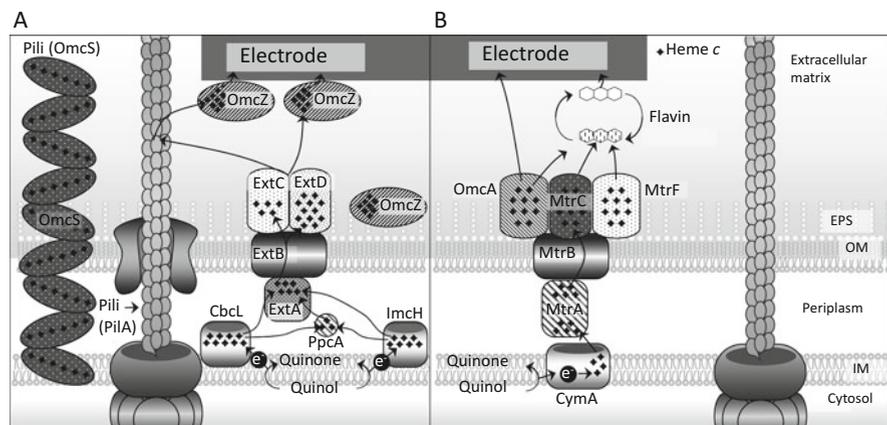


Fig. 3.3 Model for electron transfer from the inner membrane quinone pool to outside the cells in *Geobacter sulfurreducens* (a) and *Shewanella oneidensis* (b)

in periplasm, which subsequently transfer electrons to also redox-active outer membrane proteins.

In *G. sulfurreducens*, primary *c*-type cytochromes play essential roles in EET by direct contact (Fig. 3.3a). Inner membrane cytochromes, ImcH and CbcL, play important roles in transferring electrons to periplasm. EET via ImcH and CbcL is proposed to be in a redox potential-dependent manner. CbcL and ImcH are required for electron transfer to low (< -0.1 V [vs. SHE]) and high redox potential ($> +0.24$ V [vs. SHE]) electrodes, respectively (Levar et al. 2014; Zacharoff et al. 2016).

In the periplasm, triheme *c*-type cytochromes (most abundant and well-studied PpcA and its homologues PpcB, PpcC, PpcD, and PpcE) are thought to transfer electrons to other redox-active proteins in the outer membrane (Fig. 3.3a) (Lloyd et al. 2003). Among the well-studied outer membrane cytochromes, OmcB is an essential outer membrane cytochrome in the EET from the cells to ferric iron oxide, whereas the deletion of *omcB* gene showed no significant impact on current production (Leang et al. 2003). Electron conduits composed of ExtABCD (ExtA, a periplasmic *c*-type cytochrome; ExtB, an outer membrane integral protein with transmembrane domains; ExtC and ExtD, outer membrane lipoprotein *c*-type cytochromes) are proposed to be involved in electron transfer from periplasm to outer-surface or outer-surface redox-active proteins (Otero et al. 2018). Another essential protein for EET is an octaheme outer membrane cytochrome, OmcZ. OmcZ has a wide redox range (-420 to -60 mV [versus standard hydrogen electrode]) for OmcZ and specifically localized on the surface of the electrode (Inoue et al. 2010; Inoue et al. 2011). It has been also suggested that the wide redox range and multiple hemes contribute to the electron-storage capacity of the biofilms (Malvankar et al. 2012).

In *S. oneidensis*, also *c*-type cytochromes play important roles in EET (Fig. 3.3b). Electrons from intracellular quinol are transferred to *c*-type cytochrome CymA in the intracellular membrane (Myers and Myers 2000). In the periplasm, Fcc₃ (flavocytochrome c₃) and STC (small tetraheme cytochrome *c*) are thought to transfer electrons to the outer membrane complex composed of MtrA, MtrB, and MtrC, in the outer membrane (Ross et al. 2007; Fonseca et al. 2012; McMillan et al. 2013). MtrF, a homologue of MtrC and OmcA, is also responsible for electron transfer to the extracellular electron acceptor (Coursolle and Gralnick 2010). These proteins, except for MtrB (integral outer membrane β -barrel protein), are also multi-heme cytochromes. *omcA* gene-disrupted strain had less power generation capability in microbial fuel cells, and *mtrA*, *mtrB*, and *mtrC* gene-disrupted strains and *omcA* and *mtrC* double mutants almost lost power generation capabilities (Coursolle et al. 2010).

EET via direct contact by *S. loihica* (Newton et al. 2009), *Aeromonas hydrophilia* (Pham et al. 2003), *Rhodoferrax ferrireducens* (Chaudhuri and Lovley 2003), and *Desulfobulbus propionicus* (Holmes et al. 2004) has been reported other than *G. sulfurreducens* and *S. oneidensis*.

3.2.2 Electrically Conductive Nanowire

G. sulfurreducens and *S. oneidensis* are known to produce electrically conductive nanowires. Microscopic and electrochemical analyses of pili produced by *G. sulfurreducens* using atomic force microscope equipped with a conductive tip revealed that the nanowire was electrically conductive (Reguera et al. 2005). Purified nanowire had temperature-dependent electrical conductivity similar to metals (Malvankar et al. 2011). *G. sulfurreducens* produces two kinds of electrically conductive nanowires composed of PilA and OmcS.

Deletion mutant of a proposed pilin domain protein, *pilA*, could not reduce insoluble Fe(III) oxide (Reguera et al. 2005), and, also, the *pilA* disruption showed severe inhibition of current production (Reguera et al. 2006). A recent biochemical study demonstrated that PilA was stabilized by electrostatic interaction with Spc (short pilin chaperone) encoded by the gene immediately downstream of *pilA* (Liu et al. 2019). Localization analysis by electron microscopy and immunogold labeling suggests that OmcS is localized along the nanowires (Leang et al. 2010). A recent study using cryoelectron microscopy of purified nanowire extracted from *G. sulfurreducens* cells revealed that the nanowires were composed of a *c*-type cytochrome OmcS (Filman et al. 2019; Wang et al. 2019). According to the three-dimensional structure, the nanowire had 46.7–47.5 Å filament repeat, and each subunit contained six hemes corresponding to the heme numbers of OmcS molecule.

S. oneidensis is also thought to produce electrically conductive nanowires (Gorby et al. 2006). The nanowires produced by the OmcA-disrupted mutant and the MtrC-disrupted mutant do not exhibit electrical conductivity, and these *c*-type cytochromes contribute to the electrical conductivity of the nanowire. A recent study

by electron cryotomography revealed that the nanowires were dynamic chains of interconnected outer membrane vesicles (Subramanian et al. 2018). *Synechocystis* and *Pelotomaculum thermopropionicum* also produced electrically conductive nanowires other than iron-reducing bacteria (Gorby et al. 2006).

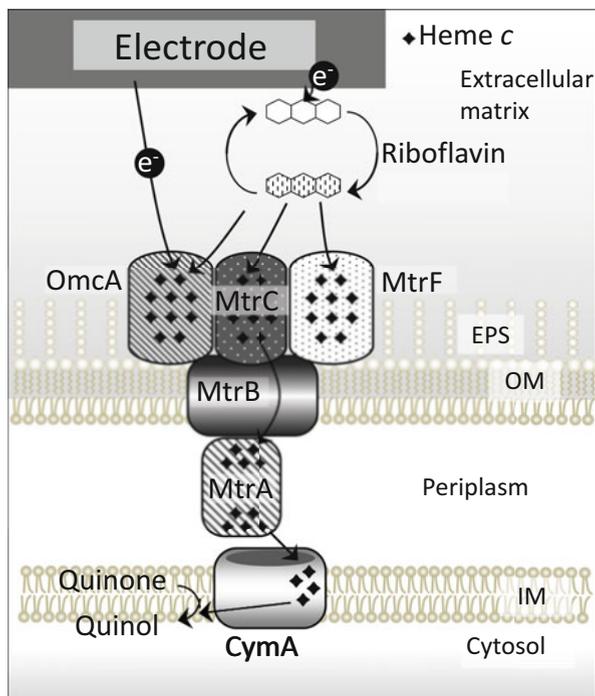
3.2.3 Electron Shuttle

Electron shuttle is a soluble electron mediator, also called as mediator. The electron shuttles are reduced by receiving electrons from microorganisms and are oxidized by transferring electrons to an extracellular electron acceptor located far from the cells (Watanabe et al. 2009). Oxidized electron shuttles receive electrons again from the microorganism and reduce the electron acceptors. This process is repeated to transfer electrons between the microorganism and the electrode. There are known examples where natural substances, such as humic acid and sulfur, are used for iron reduction (Thygesen et al. 2009; Straub and Schink 2004). Some microorganisms can produce electron shuttles, such as flavin (*S. oneidensis* [Marsili et al. 2008] and other *Shewanella* species [Canstein et al. 2008]), riboflavin (*Geothrix fermentans* [Mehta-Kolte and Bond 2012]), phenazine (*Pseudomonas chlororaphis* [Hernandez et al. 2004], *P. aeruginosa* [Rabaey et al. 2005], *Pseudomonas* sp. [Pham et al. 2008]), quinone (*S. putrefaciens* [Newman and Kolter 2000], *Lactococcus lactis* [Freguia et al. 2009]), and melanin (*S. algae* [Turick et al. 2002]), by themselves. The advantage of electron transfer by the electronic shuttles is that they can transfer electrons to the electrode even if the electrode is physically distant.

3.3 Extracellular Electron Transfer from Electrodes to Microorganisms

In the microbial electrosynthesis (MES), also called electro-fermentation, electrons are transferred from cathodes to electrochemically active microorganisms (Fig. 3.1b). *G. metallireducens* and *G. sulfurreducens* were firstly reported to convert nitrate to nitrite and fumarate to succinate, respectively, by directly accepting electrons from cathodes (Gregory et al. 2004). The “microbial electron uptake” has been observed in various microorganisms, such as *Sporomusa ovata* (Nevin et al. 2010), *Sporomusa sphaeroides*, *Sporomusa silvacetica*, *Clostridium ljungdahlii*, *C. aceticum*, *Moorella thermoacetica* (also known as *C. thermoacetica*) (Nevin et al. 2011), *G. lovleyi* (Strycharz et al. 2008), *Anaeromyxobacter dehalogenans* (Strycharz et al. 2010), *Rhodopseudomonas palustris* (Bose et al. 2014), *Prosthecochloris aestaurii* (Ha et al. 2017), *Acidithiobacillus ferrooxidans* (Nakasono et al. 1997), and *Methanobacterium palustre* (Cheng et al. 2009),

Fig. 3.4 Model for electron transfer from the cathode to *Shewanella oneidensis* cell



whereas very little is known about the molecular mechanisms of accepting electrons from electrodes in these microorganisms.

The mechanisms of the electron uptake from electrodes in *G. sulfurreducens* (Gregory et al. 2004; Dumas et al. 2008) and *S. oneidensis* (Ross et al. 2011) have been studied as well as EET from microorganisms to electrodes. In a *G. sulfurreducens* cell, PccH (GSU3274), a monoheme *c*-type cytochrome proposed to be localized at periplasm, plays an important role in electron uptake process (Strycharz et al. 2011). Deletion mutant of *pccH* did not accept electrons from electrodes, whereas the deletion of *c*-type cytochromes required for EET, such as OmcZ, OmcS, OmcB, and OmcE, did not show significant impact on electron uptake. Biochemical analysis demonstrated that PccH has unusually low redox potential (-24 mV versus standard hydrogen electrode) (Dantas et al. 2013). In *G. sulfurreducens*, the predicted electron pathway from electrodes to the cells is different from EET from cells to the electrodes. In contrast, in *S. oneidensis*, electrons from electrodes were proposed to be transferred via Mtr/CymA pathway by which electrons from cells are transferred to the electrodes (Ross et al. 2011; Okamoto et al. 2014) (Fig. 3.4). In *S. oneidensis*, MtrDEF was suggested to complement the function of MtrCAB significant partially, and riboflavin could be used as an electron shuttle as well as EET from microorganisms to the electrodes. There are only limited knowledge about the molecular mechanisms of microbial

electrosynthesis, and, thus, it requires further investigations for practical applications for producing various compounds.

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