



Review

Electron transfer process in microbial electrochemical technologies: The role of cell-surface exposed conductive proteins

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ABSTRACT

Electroactive microorganisms have attracted significant interest for the development of novel biotechnological systems of low ecological footprint. These can be used for the sustainable production of energy, bioremediation of metal-contaminated environments and production of added-value products. Currently, almost 100 microorganisms from the Bacterial and Archaeal domains are considered electroactive, given their ability to efficiently interact with electrodes in microbial electrochemical technologies. Cell-surface exposed conductive proteins are key players in the electron transfer between cells and electrodes. Interestingly, it seems that among the electroactive organisms identified so far, these cell-surface proteins fall into one of four groups. In this review, the different types of cell-surface conductive proteins found in electroactive organisms will be overviewed, focusing on their structural and functional properties.

1. Introduction

Microbial electrochemical technologies (METs) have become the focus of intense fundamental and applied research to harness the vast metabolic versatility of microorganisms towards sustainable industrial processes (Logan and Rabaey, 2012). The versatility of the concept has spawned a veritable zoo of device designs among which microbial fuel cells (MFC) and microbial electrosynthesis (MES) are the most prominent examples (Wang and Ren, 2013). Microorganisms in MFCs are used as biocatalysts to produce bioenergy from organic matter, while in MES electroactive microorganisms collect electrons from the electrode to generate useful chemical compounds. In both cases, the microorganisms have to perform extracellular electron transfer (EET), i.e. transfer electrons across the cell envelope and establish an electrical contact with the electrode, or vice versa. The study of EET has been mainly focused on two model organisms, *Shewanella oneidensis* MR-1 and *Geobacter sulfurreducens* PCA, both Gram-negative mesophilic bacteria that are able to transfer electrons to extracellular substrates during respiration. However, electroactivity is not limited to organisms with an outer-membrane since the ability to transfer electrons to electrode surfaces was also observed for some Gram-positive bacteria, Archaea, microalgae and even fungi (Koch and Harnisch, 2016; Logan, 2009;

Salar-García et al., 2016). Indeed, recently it was shown that the hyperthermophile iron-reducing archaea *Ferroglobus placidus* and *Geoglobus ahangari* present electroactive behavior in single-chamber microbial electrolysis cells (Yilmazel et al., 2018). Moreover, thermophilic Gram-positive bacteria that belong to *Thermincola* genus were identified as the dominant organisms in the anode of microbial fuel cells operating at high temperature (Mathis et al., 2008; Wrighton et al., 2008).

From the extensive studies on *S. oneidensis* MR-1 and *G. sulfurreducens* PCA, it is now established that the general mechanism for EET involves multiheme c-type cytochromes (MHC) that are responsible for linking the cellular metabolism to the electrode, or vice versa (Breuer et al., 2015b; Santos et al., 2015; Shi et al., 2012).

Two general mechanisms for EET are now recognized: *direct electron transfer* (DET) and *indirect electron transfer* (IET) (Gralnick and Newman, 2007). In DET microorganisms establish direct contact with the insoluble electron acceptor (e.g. electrode or insoluble substrates) via proteins that decorate the cell surface (Richardson et al., 2012a,b), or through cellular appendages such as pili or nanowires (Gorby et al., 2006). In several organisms these appendages are also covered with c-type cytochromes (Leang et al., 2010; Pirdadian et al., 2014). On the other hand, IET relies on the ability of microorganisms to use soluble redox active compounds as electron shuttles to mediate the electron

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Table 1
Cell-surface exposed cytochromes identified in electroactive organisms.

Microorganism	Locus tag	Protein name	Heme bind. motif ^a	Number of aminoacids	Reference
<i>Acidithiobacillus ferrooxidans</i> ATCC 23270	AFE_3153	Cyc2	1	485	(Yarzabal et al., 2002)
<i>Aeromonas hydrophila</i> ATCC 7966	AHA_2764		10	743	(Shi et al., 2012)
<i>Desulfuromonas acetoxidans</i> DSM 684	Dace_0364	OmcB	13	762	(Alves et al., 2011)
<i>Ferroglobus placidus</i>	Ferp_0670		35	1732	(Smith et al., 2015)
	Ferp_0672		31	1639	
<i>Geobacter sulfurreducens</i> PCA	GSU2737	OmcB	12	744	(Kim et al., 2005; Leang et al., 2010; Liu et al., 2014; Richter et al., 2009)
	GSU2731	OmcC	12	768	
	GSU0618	OmcE	4	232	
	GSU2432	OmcF	1	104	
	GSU2076	OmcS	6	432	
	GSU2432	OmcZ	8	473	
<i>Rhodospirillum rubrum</i> T118	Rfer_0244		4	261	(Liu et al., 2014; Risso et al., 2009)
	Rfer_4079		10	885	
	Rfer_4080		10	936	
	Rfer_4083	MtrC	10	826	
<i>Rhodopseudomonas palustris</i> TIE-1	Rpal_0817	PioA	10	540	(Jiao and Newman, 2007)
<i>Shewanella oneidensis</i> MR1	SO_1778	MtrC	10	671	(Beliaev et al., 2001; Hartshorne et al., 2007; Myers and Myers, 1997)
	SO_1780	MtrF	10	639	
	SO_1779	OmcA	10	735	
	Slit_2497	MtoA	10	355	
<i>Sideroxydans lithotrophicus</i> ES-1	TherJR_2595		9	525	(Shi et al., 2012)
<i>Thermincola potens</i> JR					(Carlson et al., 2012)

^a The heme binding motif is identified by the sequence CXXCH, where X is any aminoacid.

transfer between cell-surface exposed conductive proteins and insoluble electron acceptors, such as electrodes in METs (Brutinel and Gralnick, 2012).

Cell-surface exposed cytochromes are among the most prevalent proteins in EET pathways of electroactive organisms being responsible for both DET and IET (Beliaev et al., 2001; Coursolle et al., 2010; Leang et al., 2010; Liu et al., 2014; Myers and Myers, 1997; Richter and Ludwig, 2009). Due to their cellular position and functional role, these proteins form one of the most important classes of proteins to be targeted for genetic manipulation (Teravest and Ajo-Franklin, 2015). This review focusses on the insights gained over the years on the role of surface exposed proteins, mainly MHC in mediating EET in METs (Table 1).

2. Cell-surface exposed conductive proteins of electroactive organisms

Besides the cytoplasmic membrane, which is the primary barrier to the external environment, the microbial cell envelope often includes other structural features, such as the peptidoglycan, the outer-membrane and the S-layer. Microorganisms have evolved specialized cellular components to overcome this physical barrier for EET reactions. So far, four types of proteins have been identified to be responsible for the transfer of electrons across the cell-surface of electroactive bacteria (Scheme 1):

(i) *Porin-cytochrome complexes*, typically composed by one porin protein and one or more redox proteins, mainly MHC;

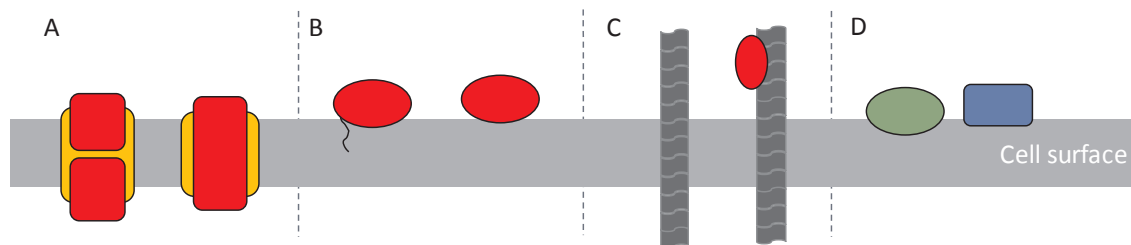
(ii) *Cell-surface exposed cytochromes*, which can be lipoproteins or cytochromes loosely bound to the cell surface;

(iii) *Conductive nanowires*, typically pili composed by protein filaments anchored to the cell;

(iv) *Other redox proteins*, including copper and iron-sulfur proteins.

2.1. Porin-cytochrome complexes

Up to date, porin-cytochrome complexes were only found in Gram-negative bacteria (Shi et al., 2014), where a β -barrel protein is long and wide enough (White et al., 2013) to cross the outer-membrane and incorporate redox proteins, most commonly MHC. These complexes are responsible for conducting electrons across the outer-membrane for the reduction of extracellular electron acceptors outside of the cell (Richardson et al., 2012a,b). One of the most intensely studied, and also the most understood porin-cytochrome complex is MtrCAB from *S. oneidensis* MR-1 (Hartshorne et al., 2009; Ross et al., 2007). This complex is composed of the outer-membrane decaheme cytochrome MtrC, the periplasmic decaheme cytochrome MtrA, and the β -barrel MtrB where the cytochromes are embedded (Hartshorne et al., 2009; Ross et al., 2007). The arrangement of these proteins in the complex MtrCAB that spans the ~ 40 Å of the outer-membrane of *Shewanella*, enables the transfer of electrons from one side of the lipid bilayer to the other through a chain of 20 hemes that is formed between the two cytochromes (Richardson et al., 2012a,b). *S. oneidensis* MR-1 contains a series of paralogs of these porin-cytochrome complexes: the MtrDEF, highly homologous to the MtrCAB complex; the DmsEFABGH responsible for DMSO reduction (Gralnick et al., 2006) and the SO4362-



Scheme 1. Representation of the four types of cell-surface exposed conductive proteins from electroactive organisms: (A) porin-cytochrome protein complexes; (B) cell-surface exposed cytochromes, which can be lipoproteins or cytochromes loosely bound to the cell surface; (C) conductive nanowires and (D) other redox proteins. The proteins are colored for type of protein: red are *c*-type cytochromes, yellow are porins, grey are pilin, blue and green are iron-sulfur and copper proteins, respectively.

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