Chapter 5
Bacterial Nanowires: An Invigorating Tale for Future

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5.1 Introduction: Bacterial Nanowires – Nanostructures, More Than We Thought

Bacteria are well known to produce nanomachinery like pili, flagella, and periplasmic outgrowth. All are proteinaceous and made up of amino acid monomers (Reardon and Mueller 2013). Bacterial nanowires are an extracellular protein which is electrically conductive in nature. Electrogens are the microorganisms which can transfer electrons from cell to extracellular substances through their nanowires. Such organisms were employed in different areas like microbial fuel cell (MFC) to produce green energy (Das and Mangwani 2010), other fuel production (Du et al. 2007), and bioremediation (Du et al. 2007).

For the past decades, the world has been looking for different fields of energy generation. All our major energy generation sectors are almost entirely dependent on nonrenewable energy source, which is a major concern of the present scenario. MFC plays an important role in renewable energy production as it converts the chemical energy into electrical energy (He et al. 2005; Siegert et al. 2019; Shah et al. 2019). Various substrates can be used in MFCs to produce green energy (Pant et al. 2010) (Fig. 5.1). Bacterial nanowires serve as a bridging material between the electrogens and the anode of MFC (Ntarlagiannis et al. 2007). Bacterial nanowires also help the biofilm formation on anode which enhances the electron transport in MFC (Malvankar and Lovley 2014). In addition to the application in MFC, bacterial nanowires are also employed in bioelectronics and biosensor production, among other areas. In this chapter, we take an effort to discuss all the scientific potential of bacterial nanowire research with special emphasis on its structural diversity, molecular manipulation, bioenergy production, bioremediation, and bioelectronics.

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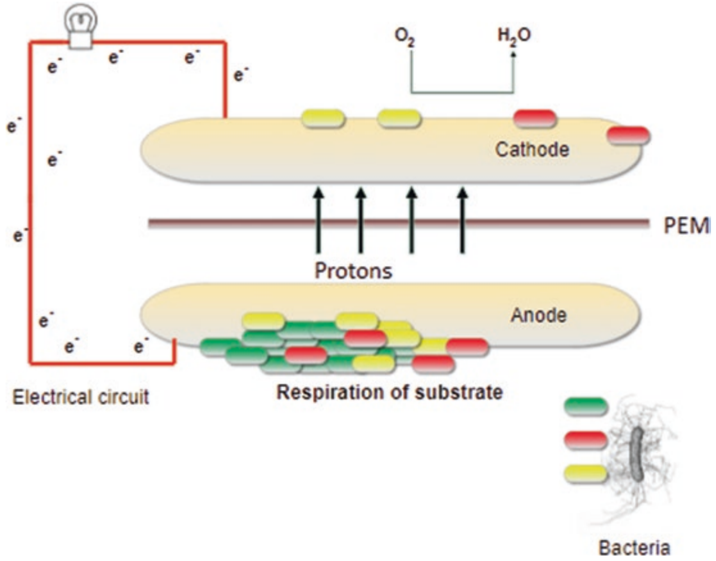

Fig. 5.1 Schematic representation of MFC: Green energy production using MFC

5.2 Milestones in Bacterial Nanowire Research

Some bacteria can transfer electrons from cell to outer environmental extracellular electron carrier during anaerobic respiration. Such energy-extracting process is known as extracellular respiration (Sure et al. 2016a). Metal-reducing bacteria like *Geobactor sulfurreducens* and *Shewanella oneidensis* are good examples of microorganisms which can perform extracellular electron transfer. Exoelectrogen is the common term used to describe such microorganisms that have the ability to transport electrons extracellularly, utilizing three common strategies: (i) exoelectrogens transfer electrons directly to electron acceptor through outer membrane proteins; (ii) some mediators like metal chelators, dyes, and pigments act like a puppet master to transfer electrons from cell to outer electron carrier; and (iii) the bacterial nanowires can act as a circuit through which the energy is transferred from the living system to outer electron acceptor (Fig. 5.2).

The conductive nature and direct role in extracellular electron transfer of conductive proteins were not revealed in early times of research. Even extracellular pili-like structures (PLSs) of various exoelectrogens like *Shewanella* and *Geobacter* were also believed as nonconductive (Sure et al. 2016b). But later it was experimentally evidenced that PLSs of some *Shewanella* spp. are electrically conductive (Pirbadian et al. 2014). Detection and identification of the presence and role of bacterial nanowires seemed to be of little difficulty in early times due to several possible reasons. The culture used for cultivation is an important factor. Complex

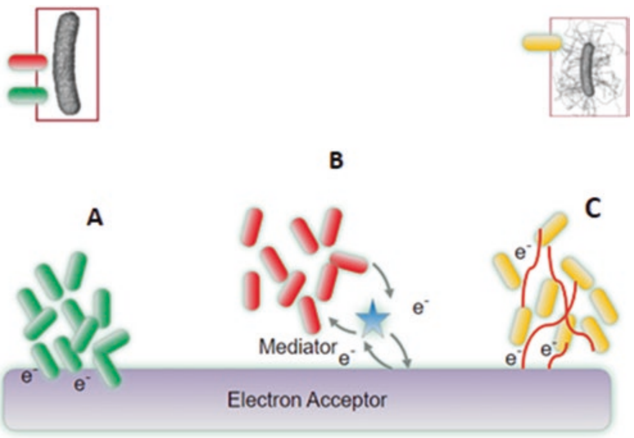

Fig. 5.2 Electron transfer strategies of electrogens: Electrogens can transfer electrons by direct attachment to electron acceptor (**a**) or through mediators (**b**) or can employ bacterial nanowires (**c**)

formulations, such as Luria-Bertani, were used in early studies (Reguera et al. 2005), which limited the extracellular electron transfer. The particular nature of pili and diverse types of PLSs also led to delay the proper identification of the role of bacterial nanowires in electron transfer. Development of research led to the discovery of various exoelectrogens which can oxidize and reduce vivid extracellular substances present in its external environment. With this identification, a novel hypothesis about bacterial nanowires describing its capability to connect cells with extracellular electron donor and acceptor was proposed. Not only exoelectrogen candidates which are mentioned here but also many other candidates were identified as a result of further efforts and research. The presence of bacterial nanowires in exoelectrogens was also confirmed using various techniques in nanotechnology such as different modes of atomic force microscopy, scanning tunneling microscopy, and electrostatic force microscopy (Sure et al. 2016b). The major exoelectrogens which can produce bacterial nanowires are shown in Table 5.1 (Sure et al. 2016b).

5.3 Bacterial Nanowire Diversity

Various types of exoelectrogens which can produce nanowire were identified so far (Table 5.1). Each and every species differ in its structure and composition of nanowires. Based on the available information, bacterial nanowires can be classified as follows.

Table 5.1 The major exoelectrogens which produce bacterial nanowires

Exoelectrogens	Protein component	Physiological Role	Conductivity	References
I. Metal reducing				
G. sulfurreducens	Pilin subunit Pili A	Extracellular electron transfer	Along the length and width	
S. oneidensis MR1	Periplasmic extension with cytochromes	Unknown	Along the length and width	Pirbadian et al. (2014)
D. desulfuricans	Unknown	Unknown	Along the width	Eaktasang et al. (2016)
II. Photosynthetic				
Synechocystis sp. PCC 6803	Pilin subunit Pili A	Unknown	Along the width	Sure et al. (2015)
Mi.aeruginosa	Unnamed protein (GenBank:CAO90693.1)	Unknown	Along the width	Sure et al. (2015)
R. palustris RP2	Unknown	Unknown	Along the length and width	Venkidusamy et al. (2015)
No. punctiforme	Unknown	Unknown	Along the width	Sure et al. (2016b)
III. Chemoautotrophs				
Aci. ferrooxidans	Unknown	Unknown	Along the width	Carmona et al. (2014)

5.3.1 Pili

A pilus is a surface structure found in many bacteria. Common types of pili are conjugate pili, which usually participated in gene exchange between two bacteria and Type IV pili (T4P), which is responsible for the generation of motive force and electrical conductance (Feliciano et al. 2015). T4P is the most widespread type of pili in exoelectrogens. We can undoubtedly consider T4P as a multifunctional extracellular structure because its role in the physiological process is diverse such as cell adhesion, motility, DNA exchange, biofilm formation, and most deliberately the electron transport.

The structural and dimensional properties of pili are varying with different exoelectrogens. Table 5.2 shows a comparison of *Geobacter sulfurreducense* and *Synechocystis* (Malvankar and Lovley 2014; Reardon and Mueller 2013). T4P has bundle formation capacity which alters the width of pili. Sample preparation method and the age of culture can affect the length of pili also. Hence, the length and width of the pili are different under different cultural conditions.

5.3.2 Other Extracellular Proteins

Msh pili and flagella are other extracellular structures in addition to T4P pili in exoelectrogens. Various deletion mutation analysis confirms the role of such extracellular structures in extracellular electron transfer. But its exact role as bacterial nanowires is still unknown (Sure et al. 2016b).

Table 5.2 Structure and function of Pili in *Geobacter sulfurreducense* and Synechocystis

Exo electrogens	Subunit of Bacterial nanowire	Associated protein	Molecular mass of subunit	Dimensions	References
G. sulfurreducense	PiliA	Cytochromes	~10 kDa	Width/length: 3–5 nm/ 10–20 μm	Lovley (2011)
Synechocystis	PiliA1	Unknown	~20 kDa	Width/length: 4.5–7 nm/2–10 μm	Lovley (2011)

Table 5.3 Exoelectrogens producing unknown pili-like nanowires

Exoelectrogens	Descriptions	References
No. punctiforme	Two distinct types of nanowires (a) Short/thin BNWs of size 6–7.5 nm in diameter and 0.5–2 μm in length (b) Long/thick BNWs of size ~20–40 nm in diameter and ~10 μm long	Sure et al. (2016a)
Mi. aeruginosa	Composed of a protein similar to an unnamed protein (GenBank: CAO90693.1)	Sure et al. (2016a)
Pe. thermopropionicum	Produces electrically conductive flagellum-like appendages (10–20 nm in diameter)	Gorby et al. (2006)
G. sulfurreducens	Produce flagella which were found to be nonconductive	

5.3.3 *Mysterious Conductive Structures*

Table 5.3 describes the details of the other unknown pili-like conductive structures, which have been identified in different microbial species. Further functional and structural analysis is required to reveal their mysterious role in electron transport to the outer environment.

5.4 A Bacterial Nanowire, as a Vital Organ

As each and every bacterial nanowire was originated as a physiological requirement of specific bacteria, it is not necessary that they should share a common structural strategy. And hence each specific bacterial nanowire has its own specific structural composition. As mentioned earlier, the complete structural and functional elucidation of bacterial nanowires is still under development. The most commonly discussed functions are as follows.

5.4.1 As a Corridor in Electron Transfer

The most widely accepted hypothesis about the functions of the bacterial nanowire is that it acts as a bridge in electron transfer between a cell and an external substance as well as between two living cells.

5.4.1.1 Between Cell and Outer Electron Acceptor/Donor

Bacterial nanowire acts as a mediator for the bidirectional transfer of electrons. For example, in metal-reducing bacteria, bacterial nanowire helps to transfer the electrons to an extracellular electron acceptor (Sure et al. 2016a), and in a metal-oxidizing organism, it helps to transfer the electrons toward the cell itself (Reguera et al. 2005).

5.4.1.2 Between Two Specific Cells

Without any external intermediate for electron transfer, the microorganism can transfer electrons from one living cell to another as interspecific (between two species of the same genus) electron transfer as well as an intergeneric (between two genera) electron transfer. The various interspecific and intergeneric electron transfers are shown in Table 5.4.

Table 5.4 Electron transfer with bacterial nanowires

Exo electrogens	Descriptions	References
I. Between cell and electron acceptor		
G. sulfurreducens	Direct transfer to metal	Reguera et al. (2005)
Aci. Ferrooxidans	Direct transfer to metal	Carmona et al. (2014)
Synechocystis	Direct transfer to metal	Sure et al. (2016a)
II. Interspecies electron transfer		
G. metallireducens *G. sulfurreducens*	Directly transfer electrons to each other, rather than use hydrogen and formate as intermediate electron carriers	Morita et al. (2011)
III. Inter-generic electron transfer		
Eubacteria and *Archaea*	A part of symbiotic microbial consortium	Wegener et al. (2015)
Cyanobacteria and other microbes	Cyanobacteria transfer electrons to other microbes in the microbial mat	Lea-Smith et al. (2016)

5.4.2 *As an SOS Factor in* Cyanobacteria

Bacterial nanowires stimulate plastoquinone to donate electron during photophosphorylation in cyanobacteria. This stimulation and the extra electron donation of plastoquinone reduce the risk of cell damage due to the poor electron flow during the carbon-limiting condition.

5.5 Bacterial Nanowires as an Electron Shuttling Gadget

Various mechanisms were proposed in order to describe the actual mechanism of electron transfer through conductive proteins. Experimental analysis finally suggests two major mechanisms can be possible for transferring the charged particles through a conductive protein and they are the metallic-like conductive model and the electron-hopping model (Morita and Kimura 2003).

5.5.1 The Metallic-Like Conductive Model of Electron Transport

The experimental analysis in *G. sulfurreducens* revealed that the bacterial nanowires have metallic-like electrical conductivity as in some organic conductors (Bai et al. 2016). But most of the biological system shows electron-hopping mechanism for electron transfer; hence, this metallic-like electrical conductivity model seems to be distinct (Sure et al. 2016a). The following identifications will support the metallic-like conductivity model of electron transfer in bacterial nanowires.

5.5.1.1 Acid-Base-Dependent Electrical Conductivity

pH changes induce the conformational changes in individual amino acids, which may alter the conductive nature of proteins. Experimental studies in *Geobacter* supported the above-mentioned fact as the conductivity of pili increases during low pH due to the conformational change in individual aromatic amino acids (Malvankar et al. 2015).

5.5.1.2 Role of Aromatic Amino Acids in Electrical Conductivity

The overlapping π-π orbitals of the aromatic ring are one of the most contributing factors for electron transfer in synthetic materials. Pilin-like protein also contains aromatic amino acids with overlapping π-π orbitals, and hence in both the case of synthetic organic materials and conductive proteins, electron transfer mechanism seems to be same. Various deletion and substitution mutation analyses were performed to confirm the role of aromatic amino acids in electron transfer. For example, the *Geobacter Aro-5*, a genetically modified bacteria, with five aromatic amino acids in pili A, one of the subunits of pili was replaced with alanine (Sure et al. 2016b). In this study, the electron conductivity was found to be reduced in transformed bacteria when compared to the wild type. It is also clear that the conformational change alters the functional properties of proteins. Hence the removal of aromatic amino acids definitely alters the three-dimensional structure, which may lead to the change in conductivity of pili (Vargas et al. 2013).

In addition to this, molecular tilting and the interplanar distances also have a role in the electron transport. The studies of pili on *Neisseria gonorrhoeae* show that the aromatic amino acids are placed too far (Yan et al. 2015). But the further experiments using techniques like synchrotron X-ray microdiffraction and rocking-curve X-ray diffraction in *Geobacter* pili again proved the role of aromatic amino acids in electron transfer even in long-range distance (Malvankar et al. 2015).

5.5.1.3 In Silico Modeling Analysis

Modeling studies also proved that the metallic-like conductivity model suggests the lowest energy model in *Geobacter.* It suggests that a close-packed central core chain of aromatic monomers facilitated the electron transport along the entire length of the pilus (Xiao et al. 2016). The gene deletion study on *G. sulfurreducens* also reveals the role of the pilus structure in electron transport (Liu et al. 2014). From all the above-observed findings, scientists argue that the electron transfer mechanism in bacterial nanowires is the metallic-like conductivity model (Sure et al. 2016b)

5.5.2 Electron-Hopping Model

Another emerging view on electron transport in exoelectrogens like *Geobacter* and *Shewanella* is the electron-hopping model. Aromatic amino acids are the central attraction factor in electron transport of bacterial nanowires of *Geobacter* (Yan et al. 2015), but in *Shewanella*, it is believed that cytochromes have the central role in electron transport (Gorby et al. 2006). Whatever may be the crucial factor in electron transport, the mechanism followed to transport the charged particle through the conductive bacterial nanowires of any organism is still debatable. It can be by the electron-hopping model or by the previously described metallic-like conductive model.

Various in silico modeling studies strongly supported the electron-hopping model of electron transfer in bacterial nanowires of *Geobacter* (Feliciano et al. 2012; Yan et al. 2015). Another experimental evidence has come in order to substantiate the electron-hopping model of electron transport in *Geobacter*, such that at low voltage cryogenic STM of *Geobacter* pili showed the thermal activation of the differential transversal conductance, which is in accordance with electron-hopping mechanism (Sure et al. 2016a).

5.6 The Potential Suits of Microbial Nanowires

The benefits of an object make it more popular. The applications of bacterial nanowires are widespread in vivid areas. Here we are discussing the major applications of bacterial nanowires which are supposed to be the major boom of the coming era.

5.6.1 Green Energy Production

Microbial fuel cell is a promising technology to generate green energy. In microbial fuel cell, chemical energy is converted to electrical energy, through the action of microorganisms called electrogens. Technically an MFC consists of an anode and a cathode, and sometimes, it needs a membrane (Fig. 5.2). It utilizes a different substrate as fuel to produce green electricity with oxidation-reduction reaction.

Biofilm formation is one of the most critical factors in MFC which enhances the electron flow even between distantly located substrates or electrogens, and thereby it increases the efficiency of power generation (Du et al. 2007). Bacterial nanowires help electrogens to make biofilm (Steidl et al. 2016), and thereby, it increases the power generation efficiency of MFC (Das and Mangwani 2010). Bacterial nanowires also act as a bridge between electrogens and electrode as in *Geobacter sulfurreducens* (Sure et al. 2016b), which facilitate the long-range electron transfer and there by energy production (Steidl et al. 2016).

5.6.2 Fuel Generation

Bacterial nanowires can be employed for the production of hydrogen and methane-like fuels, in MFC with a slight modification. Generally, in a MFC, the proton and electrons were produced in anode, which are then transported to cathode, and from cathode they were combined with oxygen to form water. Thermodynamically the hydrogen production in such ways is not feasible. But in a MFC, the increased cathode potential overcomes the energy barrier which may lead to hydrogen gas production by combining the proton and the electron. The experimental analysis suggests that MFC can probably produce hydrogen as the amount of hydrogen produced in glucose fermentation method (Zhou et al. 2013).

Anaerobic digestion of some wastewater and biomass produces methane as a secondary product in MFC (Wegener et al. 2015). MFC with little modification produces methane in the cathode chamber. Here also the increased cathode potential facilitates to cross the thermodynamic barrier to produce methane in the cathode (Zhou et al. 2013). Bacterial nanowires of exoelectrogens play a crucial role in both hydrogen production and methane production in MFC as an electron shuttle mediator between the bacteria and the anode (Sure et al. 2016a).

5.6.3 Bioremediation

Uses of electrogens and their bacterial nanowires to treat the contaminated water and the biomass were successfully employed in MFC. As the waste waters are rich sources of carbon and other organic substances, it can definitely act as an ideal substrate in MFC. In addition to organic waste, bacterial nanowires are particularly employed to treat the heavy metal contamination like uranium contamination (Cologgi et al. 2011). Gene deletion mutation analysis on *Geobacter* proved that the presence of bacterial nanowires in electrogens increases the efficiency of uranium contamination treatment (Cologgi et al. 2011). Bacterial nanowires help in different ways to treat the heavy metal contaminations, such as it increases the surface area and thereby increases the bioavailability of uranium for absorption (Cologgi et al. 2011) and it increases the cellular tolerance to heavy metal by preventing the cellular accumulation (Cologgi et al. 2011). In addition to uranium, bacterial nanowires also help to precipitate arsenic, chromium like metal and there to facilitate the bioremediation process of heavy metals (Sure et al. 2016b).

5.6.4 Green Electronics

The maximum conductive nature of the bacterial nanowires makes them a delightful substance for the construction of electron transport materials, electronic devices, and sensors for medical or environmental applications. Experimental characterization of bacterial nanowires in *Shewanella oneidensis* shows that it is capable of being used as building blocks for constructing electronic devices (Lovley and Malvankar 2015). Protein engineering or molecular manipulation of bacterial nanowires may alter the conductive nature which ultimately leads to the change in the electric behavior of the organism (Tan et al. 2016). Protein engineering studies have been performed in *Geobacter*, in order to increase its conductivity especially for the usage in the bio-electronics field, such as C-terminal modification of pili A protein (Lovley and Malvankar 2015), which reduces the diameter of pili and their by increases the conductivity.

5.7 Future Directions

From all the findings, it is clear that microbes may develop bacterial nanowires according to their physiological needs. Extensive and elaborate research is required to study the needs and mechanism of development of bacterial nanowires, which may reveal the exact role of nanowires in nature. In order to identify the super candidate among the known electrogens, molecular, biochemical, and mechanical characterization of all bacterial nanowires which are known so far should be done. Extensive researches are also needed in the field of electron transport mechanism, simple ways for the culturing of electrogens and the over production of bacterial nanowires. The most important fact that a few laboratories are involved in bacterial nanowire research till to date. The identical or similar research data on bacterial nanowires from other laboratories definitely increases the authenticity and the scope of bacterial nanowire research. Understanding the knack of nanowire electric work has applications well beyond the discussion. Such structures have the potential to address some of the big questions about the nature of life itself.

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