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Exploring Microbial Electroactivity: From Skin Microbiota to Cable Bacteria in Microbial Fuel Cells

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Abstract

Bacteria with the remarkable ability to transport electrons both intra and extracellularly for renewable energy production and environmental remediation. Nowadays, some bacteria have applications in the field of environmental sciences as well as physics, involving the production of useful substances and electric current. Prokaryotes have the potential to use charged electrodes to donate and accept electrons. These bacteria use a mechanism namely extracellular electron transport (EET) for multiple purposes; small power sources, pollution remedy, water reclamation, and electrosynthesis. Researchers are currently working on bacteria having EET ability at a basic level and looking forward to remarkable applications in the future. Microbial fuel cells (MFCs) are recognized as the most potent candidate for future alternative energy production. Nanowires such as those produced by Geobacter sulfurreducens and Shewanella oneidensis, facilitate electron transfer over longer distances, enhancing the efficiency of bioelectricity generation. This review briefly explains the components of bacteria involved in the EET mechanisms for the production of electric current and the role of biofilm for electrogenic bacteria. It also highlights the different methods used to promote the EET mechanism and some unusual external electrons used recently in MFC.

Keywords: Electricity-Carrying Bacteria; Electrogenic Bacteria; Proton Motive Force, Extracellular Electron Transport; Biomass Concentration

Abbreviations: EET: Extracellular Electron Transport; MFCs: Microbial Fuel Cells; PMF: Proton Motive Force; DET: Directly Transferring Electron; EPS: Extracellular Polymeric Substances; EAB: Electroactive Bacteria

Introduction

Bacteria capable of transporting electrons from the extracellular environment or through cell membranes are termed electricity-carrying bacteria [1]. Bacteria use both intra as well as extracellular systems linked with the acceptance or donation of electrons [2]. The electrons from organic or inorganic sources, are taken up by NAD brought to the cell wall, and donated to an electron acceptor [3]. Due to the accumulation of protons across the membranes, a proton gradient is generated known as the proton motive force leading to transport across the membrane, ATP production, and flagella movement [4]. Soluble protons are involved in this process which is pumped in and out of the membrane of bacterial cells leading to proton motive force (PMF). This is the reason bacteria are interacting for electricity production now [4].

Both yeast and bacteria were used to produce an electric current in an experiment by Potter in 1911 (Potter, 1911). Bioelectricity production from bacterial cells was first presented by him [5]. A great variety of bacteria is available in nature that is electrically active. *Geobacter sulfurreducens* and *Shewanella oneidensis* for microbial fuel cells (MFCs) first studied [6]. Both these strains of bacteria are studied in detail for being electrically active [7]. *Pseudomonas* and *Clostridium* bacteria are reported as exoelectrogens [8]. *Rhodoferax ferrireducens* are reported as having the potential to transfer electrons to an anode involving nano wires or c type cytochromes [9].

Electricity Production by using bacterial cells as a catalyst is done by the decomposition of biomass such as grass pieces, vegetables, food, fruit wastes, plant leaves, and mud [10]. Bioelectricity is produced by using microbial fuel cells and soil having industrial effluents i.e., brewery wastewater, colored wastewater, sludge, and ocean sediments [11-13]. Biofilm of mixed as well as pure bacterial cultures is used for electricity production via MFC [9].

Bacteria from human sources also can produce electricity, the largest organ of the human body “skin” is covered by many microbes that can transfer electrons efficiently to produce an electric current [14]. *Enterococcus faecalis* and *Listeria monocytogenes* both gram-positive bacteria can produce electric current as well as the mechanism for the transfer of electrons namely the EET pathway [15]. Both bacteria found in the gut of bacteria are now under study due to their ability for electric current production and their role in human health [16].

Electricity sources used by humans for many centuries are fossil fuels. As we know fossil fuels are renewable sources, but they require a lot of time for its formation and now worldwide these sources are depleting very fast due to the needs of the increasing population. Moreover, the production of electricity from these sources adds toxic gases and pollutants to the air to which scientists are looking for pollution-free sources [17]. Other renewable energy sources such as wind, geothermal, tidal, biomass, and solar are of great interest [18]. Still, now other sources of electricity production have not competed with conventional electricity production from fossil fuels but the hybrid system of solar energy with hydrogen fuel and solar energy with the wind will improve efficiency as well as electricity production [19]. These conversions of solar energy into bioelectricity and hydrogen are under study [17]. In this review, we will discuss history, electrochemically active bacteria, and mechanism of electron transfer, and potential applications of electricity-carrying bacteria.

Electricity Carrying Bacteria

Both yeast and bacteria were used to produce an electric current in an experiment by Potter in 1911 (Potter, 1911). Many scientists have worked in the mid-20th century but at that time generation of current was not enough to be used for running any power machine. Two bacteria were reported at the same time in 1988 as having the ability to accept electrons by growing on solid metal oxides (manganese or iron) [20,21]. *Shewanella* facultative bacterium isolated from the Oneida Lake, N.Y was found capable of reducing manganese oxides and was tested in a laboratory where it reduces manganese by accepting its electrons [21]. Another delta proteobacteria namely *Geobacter*, oxygen-sensitive found in the Potomac River, N.Y was isolated and tested that it reduces iron oxides by accepting electrons [4].

Both bacteria are studied for three decades to explain the mechanism now known as extracellular electron transport (EET). This ability of these bacteria is different from all other microbial worlds [20]. All the energy-producing biosystems work on the same principle which is electron flow involving in the conservation of energy in soluble electron acceptor and donor in the biological membranes having minimum chances of losing an electron to the exterior of the cell [4]. In *Shewanella* species, there is a series of proteins having multiheme groups involving in the conduction of electrons [22,23]. This mechanism through these linked proteins involves the movement of electrons across the membrane and outer substrates (Figure 1). In different strains of *Shewanella* extracellular electrons, transport occurs by the different mechanism which includes compounds involved in endogenous electron shuttling, reduction by exogenous, direct reduction and reduction with the help of nanowires along the membranes in the form of cytochromes [24,25] (Figure 1).

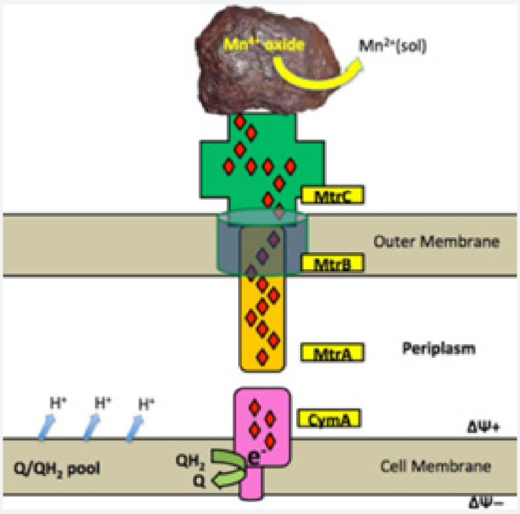

Figure 1: Linked proteins and movement of electrons across the membrane and outer substrates.

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Geobacter species case it is found that there is physically utilization of c-type cytochromes with multiheme groups, but pili are involved in the process of conduction of electrons without any c-type cytochromes [26]. These bacteria have no c-type cytochromes but still, there is extracellular electron transport in them which means that there is another extracellular electron transport (EET) mechanism that needs to be discovered [27]. Both bacteria elaborated above are the first bacteria named “electric bacteria”. Before the experimental study of Dr. Byung-Hong Kim [28] about EET, none of the electrically active bacteria was given attention. In his experiment *S. oneidensis* MR-1 was studied which showed the production of electric current without any electron shuttle system. Many scientists in different laboratories of the world worked on this experiment and lead to the production of current [29,30]. Another experiment has reported that microbes can accept electrons from electrodes for their maintenance and growth. This process also involves the isolation of microbes from different environments with the help of electrodes and c-type multiheme cytochromes [31].

Electrochemically Active Bacteria

The natural environment is enriched by electrically active microbes. Sources of microbes include brewery wastewater, sludge, ocean sediments, dairy manure, and natural ecosystems. Microbial fuel cells can grow under anaerobic conditions, digestive sludge, rumen liquids, granular sludge, and domestic wastewater [13].

α-Proteobacteria

Acidiphilium cryptum from *Rhodospirillales acetobacteraceae* class is a gram-negative bacterium isolated from the drainage of mine water. These bacteria under acidic conditions are the first electrically active bacteria for microbial fuel cells [32]. Another gram-negative bacterium namely *Rhodobacter sphaeroides* from class *Rhodobacteraceae, Rhodobacter* uses different acids as a substrate to produce electric current [33]. *Rhodopseudomonas* belongs to α-proteobacteria is first electrically active from this class [13]. *Gluconobacter oxydans* a gram-negative bacterium reported in 2002, uses carbon dioxide as a substrate to produce electricity and it belongs to group *Acetobacteraceae* and *Gluconobacter* [34].

β-Proteobacteria

R. *ferrireducens* facultative, gram-negative bacterium belongs to class *Comamonadaceae*. It uses Fe (III) as an electron acceptor and fully oxides glucose to carbon dioxide at a temperature ranging from 25-30 ºC. From this class, it is the first bacteria that was reported as having the ability to oxides glucose completely to carbon dioxide and use its energy for electricity generation [13]. *Comamonas denitrificans* belong to denitrifying bacteria having the potential to yield electricity [13,35].

γ-Proteobacteria

Shewanella a facultative, anaerobic gram-negative bacterium belongs to *Shewanell*aceae class. It has been reported as a reference in MFC (microbial fuel cell). Visualization of electron transfer can be seen among the bacteria and electrodes. S. putrefactions IR-1 first electrically active bacterium reported as having the potential to accept electrons from electrodes [36]. *Pseudomonas aeruginosa* gram-negative, an aerobic facultative bacterium from class *Pseudomonadaceae* produces Pyocyanin as an electron acceptor not only for itself rather than for other strains during electricity production. It is the first bacterium that has an electron shuttle system [37]. *Klebisella pneumonia* is a gram-negative bacterium having the ability to oxidize different kinds of organic matter to produce electric current with the help of electrodes as an electron acceptor [38].

δ-Proteobacteria

G. sulfurreducens is an anaerobic gram-negative bacterium that uses Fe (III), Co (III)- EDTA, malic acid, and fumaric acid as an electron acceptor while hydrogen and acetic acid electron donors [39]. Sequencing of the whole genome of this bacterium revealed that it can be used as a reference bacterium to explain the mechanism by which they transfer electron from electrodes [13]. *Geobacter* uses iron as an electron acceptor and can reduce the radioactive pollutants from the environment such as benzene, short-chain fatty acids, ethanol, etc. That is why it is used as an eliminator of environmental pollutants [40]. *Geopsychrobacter electrodiphilus* a gram-negative bacterium has the potential to produce electric current by completely oxidizing citric acid, acetic acid, fumaric acid, and malic acid [41]. *Desulfoblbus propionicus* is also a gram-negative bacterium but with very low current production as compared to other bacteria [42].

ε-Proteobacteria

There is a production of 296mW/liter power by the two strains of genus Arcobacter that can grow in highly enriched acetate-fed MFC [43].

Mechanism of Electricity Production

Extracellular Electron Transfer

Mechanism of extracellular electron transfer (EET) can be explained by the following steps:

1) Directly transferring electron (DET) using nanowire or through direct contact.

2) Linked shuttle that may be endogenous or exogenous.

3) Extracellular polymeric substances (EPS) of biofilms [44] (Figure 2).

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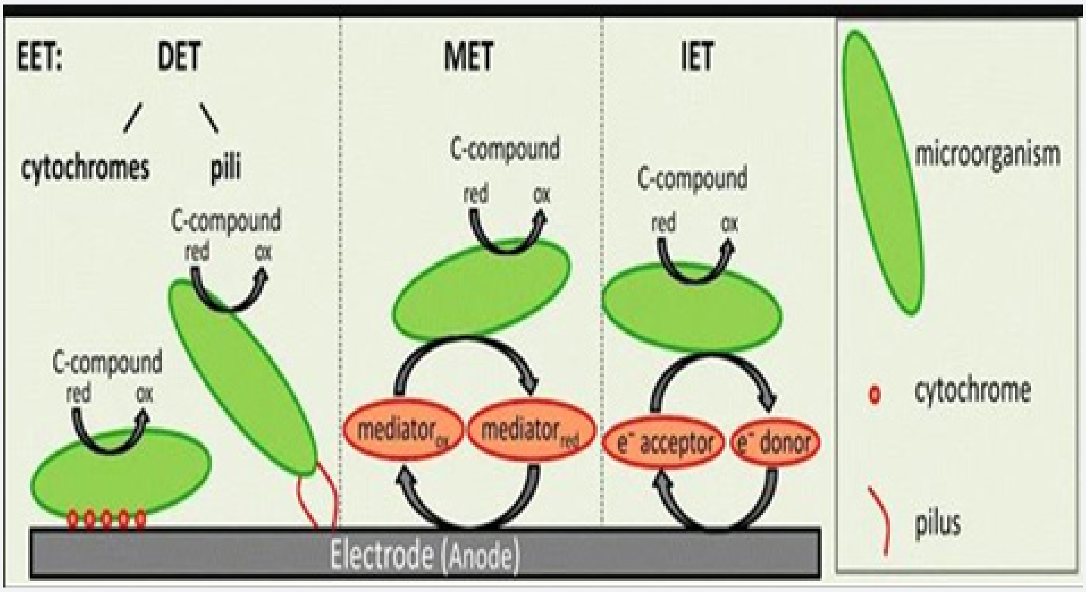

Figure 2: Extracellular Electron Transfer (EET) Mechanisms.

G. sulfurreducens and *S. oneidensis* have ability to transfer electron across the biological membranes with the help of c-type heme-containing cytochromes regarding DET. This cytochrome has multiheme with different redox potentials due to microorganism transfer electron across membranes [45]. In the case of MES mode flow of electrons in a cell is against the concentration gradient from low to high potential while opposite in the case of MFC. Moreover, DET is under experimental study due to hydrogenases and Rusticyanin protein [46,47]. *S. oneidensis* and *G. sulfurreducens* have extracellular appendages namely pili sometimes called nanowires that connect two bacteria due to which they can accept and donate an electron to solid surfaces at greater distances [48].

DET depends on the existence of biofilm to produce electricity and connection in the extracellular environment for the successful transfer of an electron between in and out of the cell [49]. In a biofilm, all the cells work collectively to transfer electrons and its thickness is directly proportional to the current production [48]. Electroactive bacteria (EAB) and formation of biofilm have great importance in the biochemical production of current. Soluble inert shuttle molecules in the MET are involved in the transport of electrons in and out from acceptor to donor with higher tendencies of electron transfer even at higher distances [2].

Mediators also help in the transfer of electrons across membranes. These mediators may be natural or artificial. *S. oneidensis* and *P. aeruginosa* secrete flavins, phenazines respectively which are natural mediators [2]. IET is based on the production of chemicals such as fumaric acid and hydrogen which will serve as an electron acceptor and donor in microbes. Microbes produce metabolic substances which are also involved in the transfer of an electron between microorganisms and the electrode. Irrespective of the mediators in MET there is an irreversible redox process due to electron transfer shuttling compounds. Electrically active bacteria are extended by the IET. Genetic tools are a great source that helps to study the cellular metabolism for the maintenance of efficiently working strains [2]. Genetic tools allow us to do desired modification with the help of which electron transfer across membranes is controlled [2].

Role of Nanostructured Material in EET

MFC and MES technologies were developed as a result of the discovery of bacterial bidirectional EET. However, several intrinsic challenges, such as low biofilm conductivity and weak bonding of bacteria to an electrode, and a lack of knowledge of the two-way EET mechanism, keep these technologies from becoming widely used. Biofilm ability is thought to be a key aspect of the EET process's efficiency [50]. Unfortunately, biofilm conductivity alone is insufficient to efficiently transmit electrons to and from an electrode. To improve the bidirectional EET process, material scientists have recently begun to use recently manufactured nanostructured materials such as nanotubes of carbon, inorganic nanomaterials, semiconductors, conducting polymers, grapheme, and noble metal nanoparticles as bioanodes and biocathodes (Kalathil & Pant).

The use of nanostructured materials, in particular, has resulted in remarkable modifications in two ways EET process. Biofilm formation is a vital step in both MFCs and MES, a previous understanding of the basic mechanism required in bacterial adhesion to metal surfaces. The bacterial adhesion to diverse nanostructured surfaces has been studied in several ways, including theoretical and experimental studies. All of the advantages of employing such nanomaterials to improve electron transfer in BESs, as well as existing problems and future potential, are highlighted (Kalathil & Pant). In the ambient environment, thin-film devices have been built from protein wires extracted from *G. sulfurreducens* bacterium. The current density is approximately 17 microamperes per square centimeter. These devices provide approximately 0.5 volts on a 7-micron thick film [51].

Biofilm, Nanowire, Ion channel and Bio Surfactant Formation Leads to Increased Current

Biofilm Formation

A biofilm is a collection of bacteria encased in a complex, self-produced polymeric matrix that adheres to living or living surfaces [52]. Electroactive biofilms, on the other hand, are those that may respire final electrons released from metabolism on surfaces of the electrode. A single bacterial species can build a biofilm [53] or through multiple biofilms [54]. To generate power more efficiently in MFCs, electroactive biofilms are required. The amount of current production in MFCs is directly linked to biomass concentration in biofilm and the type of surface of the electrode. Electroactive biofilm prefers anode surfaces that are positively charged and hydrophilic [55]. The basic principle of microbial fuel cell creation also influences the performance of fuel cells [55].

Compare to bacteria that can form thin biofilms on the anode, bacteria that can create thick biofilms generate higher current densities e.g. *G. sulfurreducens*, develops a large biofilm with multiple layers (50 mm) is formed, and the gram-positive bacterium *Thermincola ferriaceta* also forms a thick biofilm (38 mm). On the other hand, the potent *Thermincola* and *Clostridium ljungdahlii* form a thin monolayer biofilm, resulting in low current density [27]. However, very thick biofilm deposition also restricts electron flow. As a result, thickness is advantageous for generating high current densities. As previously stated, electro-active biofilm is characterized by its ability to transmit electrons to electrode surfaces or to minimize the concentration of soluble as well as insoluble electron acceptors. These proteins have active redox potential (e.g., c-type cytochromes) [56].

The growth and activity of electroactive biofilms can be influenced by certain ions or minerals. Aside from having similar effects on different microbes, the same ions affect different microorganisms differently. The increased amount of Ca_2 ions in the bio electrochemical system's anolyte, for example, has proven lethal to exoelectrogens (mixed culture from anaerobic sludge) [57]. The study found that increasing the Ca_2 concentration to 5 mM reduced the current output of the system by 72 percent when compared to the control system, which can be attributed to the buildup of non-active bacterial cells in the biofilms [57]. In contrast, adding $CaCl_2$ (concentration of 1400 mM) to a mini MFC inoculated with *S. oneidensis* increases the density of current by about 80% in comparison to reference MFC which was primarily due to biological factors rather than ionic effects [58].

Furthermore, calcium ions encourage *Shewanella xiamenensis* for the production of EPS (extracellular polymeric substances). Furthermore, calcium ions encourage *S. xiamenensis* to produce EPS (extracellular polymeric substances). The structure of flagella and the cell membrane is influenced by the ions which stimulate the generation of EPS even more. At a 2 mM $CaCl_2$ concentration, the EPS yield rose from 0.56 g/L to 1.74 g/L at a 20 mM $CaCl_2$ concentration. The study went on to look at the influence of calcium ions on the production of current in an MFC and discovered that calcium ions had a beneficial impact on MFC performance, producing approximately 20% more current than the reference MFC [59]. What is in the environment that could be a rich source of exoelectrogens? Typically, anaerobic sediment, primary industrial effluent, sludge from industrial wastewater treatment plants, and even the soil contain exoelectrogens that can be extracted as pure or impure culture from the particular sources and used them in MFCs [60].

Effect of Certain Ions and Minerals in Biofilm Formation and Activity

The activity of electrically active biofilms is affected by the minerals as well as ions. It is reported that the same ions may have different effects on different strains of microbes. Higher the level of calcium ions in the anodic electrolyte have proven dangerous for the electrical activity of exoelectrogens. It is reported in an experimental study that only a 5mM concentration of calcium ions leads to a reduction of 72% current production as compared to a controlled system [57]. The addition of 1400mM Calcium chloride solution to the biofilm of *S. oneidensis* also increases the current production by 80% in comparison to controlled MFC [58]. The addition of calcium chloride is also involved in the increased synthesis of extracellular polymeric substances in *S. xiamenensis*, done by affecting the structure of flagella and membranes of the bacterial cell. With the increase of calcium chloride solution's concentration production of extracellular polymeric substances also increases. When studied the effect of calcium on MFC to produce current it is revealed that it increases its production by 20% [59]. Sources for the utilization of MFC include industrial effluents, wastewater treatment, sludge, and soil [60].

Nanowires

Nanowires help in the transfer of electrons along long distances due to the thickness of biofilm [48]. When there is no oxygen or less amount of oxygen in the environment bacteria use it as an end point for electron acceptor [61]. Bacterial electron shuttle, unknown components, and proteins help in the transfer of electrons in making biofilm electrically active [52]. Due to the deficiency of pilA and omcZ in *G. sulfurreducens* bacteria, there is inhibition of biofilm formation as a result of which electric current also reduces [52]. PilA belongs to IV pili, has two segments; long PilA and short PilA [61]. It is reported that the long PilA segment is more important used to attach cells to graphite electrodes to form biofilms as compared to the short PilA [62]. However, short PilA is involved in the conductance of electrons across membranes via c-type cytochromes and OmcZ in the outer membrane [62].

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It is also revealed from another study that pili do not involved in the transfer of electrons in the cells transpiring near to electrode, but it helps in the aggregation of cells that ultimately leads to the formation of biofilm [63]. It also promotes the formation of a thicker layer of biofilm formation by involving a series of a network of cytochromes [63]. When *G. sulfurreducens* grow in the form of biofilm certain genes are reported as compared to single cells [64]. Genetic studies have revealed that there is the involvement of genes that are coding pilus. It also revealed the role of these certain genes in the production of extracellular polymeric substances for biofilm formation and cyclopropane fatty acids [64]. Modification in the structure of biofilm occurs due to the presence of a sugar matrix that alters the receptor site and helps in the attachment of c-cyts [65].

It is reported that the morphology and structure of biofilm is associated with the growth phases of microbes. *G. sulfurreducens* in lag phase has a single layer of cells with less amount of c-Cyts due to which there is low production of current but when there is biofilm formation with three to four-fold more c-Cyts leading to high production of electric current [66]. Level of c-Cyts in *G. sulfurreducens* increases with the lag phase proceeding to log phase due to the increased concentration of c-Cyts [66]. Thicker the biofilm greater the transport of electrons and vice versa [67]. The morphology of biofilm greatly varies with the change of electrode in MFCs. *G. sulfurreducens* form layers of cells with pillars when grown on carbon cloth [64].

The structure of biofilm varies from gram-negative bacterium to gram-positive bacterium, which is based on the working principle of MFC, which may work as an open or closed-circuit system. It is reported that when microbial fuel cells behave as the closed system there is more attraction between bacteria and anode and vice versa in the case of an open system. Similarly, microbial fuel cells on the surface of bacteria are more easily available than the lower ones [1]. Biofilm formation by *S. oneidensis* MR-1 on the surface coated with minerals is experimentally treated with cyclic dinucleotide messenger. A phosphodiesterase namely pdeB has shown a negative effect on the formation of biofilm [68]. Deletion of this factor enhanced the production of biofilm formation under controlled conditions. When studied wild and mutant types of strains it is revealed from the results that the former leads to the formation of biofilm up to 10mm thick while 2nd one leads to two folds increase [68].

S. oneidensis MR-1 is very sensitive to the electron acceptors and becomes motile protein kinase in case of response to electron acceptors [69]. Pilin genes in *Shewanella* spp., are involved in the synthesis of a protein called Mannose-sensitive hemagglutinin which enhances its attachment and biofilm production ability [58]. As we know that biofilm formation in this species is based on c-Cyts which also secretes flavin useful for the acceptance of electrons. These help in the transfer of an electron from the inner surface to the outer side of the cell [69].

Desulfovibrio desulfuricans play an important role in the formation of biofilm in MFC which is termed as nanowires which leads to easy transfer of an electron to the anode. These nanowires are very tightly bound to the electrode leading to thicker electrically active biofilm formation by this bacterium [70]. First, it was found that the block that the exchange of water molecules on the nanowire–to-air interface due to the thickness of the upper interface of the nanowire film is put, the energy, while the removal of these density restores a continuous amount of power, and in the second case, an increase in the rate of exchange of water molecules is due to an increase in the relative humidity, respectively, and increases the amount of electrical energy, which is also reversible [51] (Table 1) [71-79].

Table 1: Proteins, genes and mediators in bacteria working as exoelectrogens.

Proteins/Genes/Mediators	Exoelectrogen	References
Homologs of multiheme cytochromes	*Kuenenia stuttgartiensis*	Shaw et al., [71]
Regulation of cell attachment to the electrode by PilA	*G. sulfurreducens*	Luo et al., [72]
Chemotactic mobility to electron acceptors is facilitated by CheA-3 for	*S. oneidensis*	Kumar et al., [64]
Regulation of fimbriae synthesis and assembly by pilR gene	*G. sulfurreducens*	Parameswaran et al., [53]
Type IV pili	*D. desulfuricans*	Lebedev et al., [66]
Msh (Mannose-sensitive hemagglutinin) structural proteins	*S. oneidensis*	Rollefson et al., [65]
Pilin subunit PilA1	*Synechocystis sp. PCC 6803*	Sure et al., [73]
Type IV pili	*A. ferrooxidans*	Jiang et al., [74]
OMCs system, soluble electron carriers	*Escherichia coli*	Zhang et al., [75]
pilA gene encodes Type IV pili	*G. sulfurreducens*	Xiao & He, [76]
Endogenous redox mediators (pyocyanine and phenazine-1-carboxamide)	*P.aeruginosa*	Fernandes et al., [77]
pilus retraction modeled by pilT-4 gene	*G. sulfurreducens*	Parameswaran et al., [53]
c-Cyts:MtoA, MtoD and CymA MtoB	*Sideroxydans lithotrophicus*	Roden, [78]
Pilus biogenesis regulated by pilC gene	*G. sulfurreducens*	Parameswaran et al., [53]

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OM c-Cyt Z encoded by OmcZ	*G. sulfurreducens*	Xiao & He, [76]
c-Cyts	*Thermincola potens*	Marshall et al., [79]

Ion Channel

The investigation of microbial ion channels had also yielded valuable information related to neuronal signaling structures [80]. Electrical signaling is widely used in biological processes to communicate. Ion channels directly alter the action potential in neurons, which is one of the most well-known examples. For several years, research on microbial ion channels has supplied valuable information into the morphological basis of such neuronal signaling [81]. The prokaryotic K ion channel KcsA, in particular, generated the information related to structure for elasticity and selectivity of ions [80].

Microbes have severally significant classes of ion channels: Na channels, Cl channels, Ca-gated, K channels, and ionotropic glutamate receptors just like neurons [82]. Moreover, the native function of such ion channels in microbes is still unknown. Despite previous efforts to reveal ion channel role in microbes, in acid resistance reaction and regulation of fluid have been recognized, ion-specific channels do not seem so to be entirely associated with these biochemical functions. This is the reason that leads to doubts about another specific role of ion channels in prokaryotes [80].

Bio Surfactant

Surfactants belong to a group of very reactive compounds, they may be synthetic as well as natural leading to affect the efficiency of the MFC by different factors. Rhamnolipids and sophorolipids are the only two biological surfactants that are included [83]. It is reported that these bio-surfactants affects the attachment of biofilm, composition, structure as well as the survival of electrode due to interruption of electron transfer [84]. *Brevibacillus 1* and *Brevibacillus 2* are both species are reported as biosurfactants that can produce an electric current. Production of electric current by these biosurfactant bacteria ranges between 55 to 65 mW cm^{-2} [83].

Electron transfer and power output of MFC have been increased by improving the production of biosurfactants. Rhamnolipids synthesis in *P. aeruginosa* was increased by over expressing the gene rh1A and this leads to enhance the flow of electrons through the electron shuttle. It also enhanced the attachment of bacteria to the anode. This genetically modified strain gave us 2.5 times more production of electric current than that of the original strain [85]. Now after this scientists are working on exogenous surfactants which have proved more effective to produce electricity by MFC. Tween 80, EDTA, and polyethyleneimine are used as surfactants to improve the conduction of MFC and EET in bacteria [86,87]. As chemicals surfactants have side effects as well such as toxic to bacteria cells or leads to death of the bacterial cell [86,88]. That is why the addition of chemical surfactants to MFC needs to be improved to prevent bacterial death. As compared to these chemical surfactants the biosurfactants produced by bacteria are less toxic for MFC. Rhamnolipids and sophorolipid both are good biosurfactants that enhanced the performance of MFC and EET [88,89].

Electricity Production by Gut Bacteria

E. faecalis and *L. monocytogenes* both gram-positive bacteria can produce electric current as well as the mechanism for the transfer of electrons namely the EET pathway [15,90]. Both bacteria found in the gut of bacteria are now under study due to their ability for electric current production and their role in human health [16]. Series of experiments are conducted by scientists to explore the EET mechanism by other gram-positive bacteria [91].

Firmicutes and *Bacteroidetes* phyla both facultative anaerobes are a group of gram-positive and gram-negative bacteria found in the gut of a human. Due to their facultative nature, these bacteria grow in less oxygen but use high amount of nutrients leading to more and more EET processes [92,93]. Gut microbes are of great interest after the discovery of electron transfer pathways in them [94]. Five gut bacteria namely *Lactobacillus rhamnosus, E. faecalis,* Lactobacillus reuteri, *Streptococcus agalactiae*, and *Staphylococcus aureus* are reported as having the ability of EET pathway. *E. faecalis, S. agalactiae,* and *S. aureus* are reported as having the ability to transfer electrons and produce electric current as much as well-known *S. oneidensis* gram-negative bacteria. After this, experiments are conducted to evaluate the genes in *S. aureus* that are involved in electrogenicity [94].

Electricity Production by Skin Bacteria

The largest organ of the human body “skin” is covered by many microbes which can transfer electrons efficiently to produce electric current [14]. *Staphylococcus capitis* and *Staphylococcus epidermidis* found on the skin can produce electric current and that can be compared with the highly electrogenic gram-negative bacteria [95]. It is believed that bacteria produce electrons in the inner side of the membrane having an acceptor on the extracellular environment. Bacteria oxidize substances such as acetate to produce electrons which then transfer to other bacteria or metal ions i.e., manganese ion, ferric ion [96,97]. Above listed gram-positive gut bacteria when studied have revealed that they synthesize a special type of proteins that are involved in the process of EET leading to an increase in the bacterial growth rate [98,99].

Ferrozine assay is used to assess the electrogenic property of *S. epidermidis* skin bacteria. It is reported this bacterium is more electrogenic in the presence of glycerol fermentation and the addition of 5-methyl furfural leads to stop the process

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of fermentation because of which electricity production also diminishes [100]. *S. epidermidis* and *Staphylococcus hominis* when exposed to only 2% glycerol for a period of 20 min, an increase of 3 mV is noticed [100].

Electricity Production by Cable Bacteria

Newly discovered cable bacteria are reported as having the ability to produce electric current and can run it along their whole filamentous body [101]. They produce electric current by oxidizing sulfide in the deep layers of sediments and reducing oxygen at the surface of sediment-water [102,103]. Cable bacteria have been discovered at the anaerobic interface in a variety of aquatic sediment environments, including water bodies, as of their discovery [104,105], freshwater [106], and aquifer [107] ground water. Cable bacteria have a significant impact on the elemental cycling of sulfur, iron, methane, and phosphorus in such environments [108-111].

Furthermore, cable bacteria were discovered connected to the anode of an anoxic planktonic microbial fuel cell. [112] or in connection with oxygen-rich areas around plant roots and insect tubes in water bodies [111,113]. Cable microorganisms are members of the *Desulfobulbaceae* family, which also includes planktonic sulfate-reducing bacteria and sulfur- disproportioning bacteria [114]. The filament of the cable microbe is linear and usually consists of hundreds of cells. Though its cells are differentiated by an inflexible septum, they communicate a cytoplasmic space which includes a system of conductive fibers that operate along the longitudinal direction of the filament. [103,115,116] and are linked among both cells by a cartwheel-shaped framework inside the septum [117,118]. The cell division process in cable microorganisms seems to be very similar to the Gram-negative reference microbe *E. coli* [114] (Figure 3).

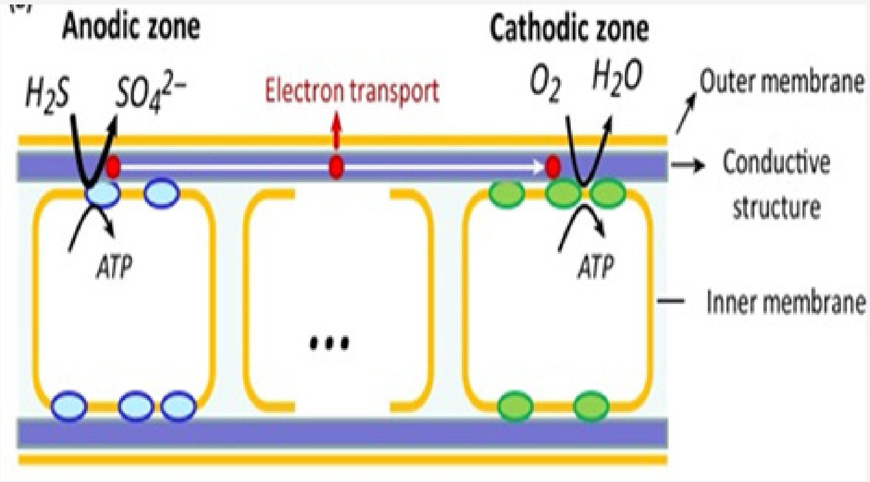

Figure 3: Electron Transport Mechanism in Cable Bacteria.

Long-Distance Electron Transport in Cable Bacteria

Microscopy demonstrates that cable microbes polymerize to form fibers composed of elongated chains of cells extending up to 30-70 mm in length and containing more than 104 cells. These long microbial fibers are naturally slightly bent in the outer surface of water bodies, under which they form dense filament systems [101].

Microbial Fuel Cell

The microbial fuel cell (MFC) is now the most popularly used bacterial EET method, in which bacteria produce electricity by using electrons extracted from the EET [119,120]. MFCs use microbes as an enzyme to metabolize biological molecules such as non-carbon materials like sulfur compounds and plant material including, fruit wastes, food wastes, grass pieces, plant leaves, edible wastes, and muds to generate electricity [121]. As an electron donor for energy production, numerous simple to different substrates has been used. With varying efficiencies, these include ribose and, galactose, acetate, whey, sucrose, xylose, molasses, cellulose, and glucose [122,123]. A few researchers demonstrated that hydrogen can be produced efficiently in MFC, and is used in the mechanism for electricity supply and wastewater treatment. Hydrogen can be used to reduce carbon emissions because it is compatible with both burning and electrochemical processes for electricity production. There are various methodologies for hydrogen production, including water electrolysis and bacterial production [121].

The electricity produced from waste materials, energy production in MFCs can be boosted in several ways. The types of electrodes, electrode dimensions, proton exchange membranes, and other factors all have an impact on electricity production. An appropriate trial on ammonium-treated carbon electrodes was conducted to enhance output power. In this experiment, the anode treated with ammonium is dependent on two distinct factors that influence energy production, like power plant startup, high microbial bond strength, and improved of electron transfer ability to the exterior by microbes. Because of the ammonium treatment, electron transfer has been enhanced [124].

Electricity Production by Using MFC

Components of MFC are the anode, cathode, external wire, and membrane sensitive to protons. Anaerobic a well as aerobic conditions are set at the anode and cathode, respectively. The communicator can be used or not for the working of MFC. Bacteria are also added to aid in the process of oxidation for microbial fuel cells [125]. Suitable substances are given to the bacteria at the anode which anaerobically metabolizes them and releases an electron. These electrons are then transferred to the cathode through an external wire to generate electricity. Electrically active bacteria break down organic substances and covert chemical energy released from bonds into electrical energy. MFCs are of different designs that may be stacked MFC, single or two-chambered MFC [126]. There is a special type of membrane called proton exchange membrane which separates two electrodes and helps in the movement of an electron across cathode for the production of electricity [127] (Figure 4).

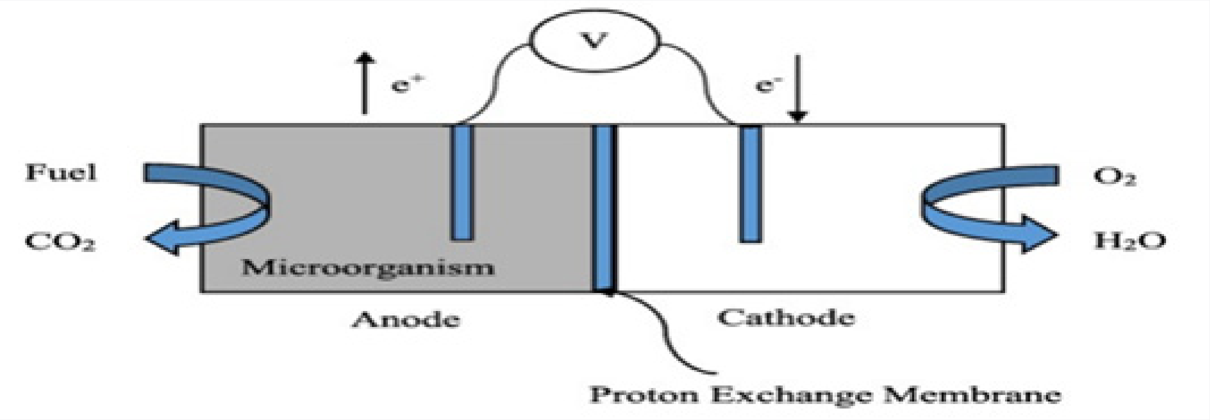

Figure 4: Electricity production by using MFC.

Types of MFCs

Single Chamber MFC

Anode and cathode in MFC with a single chamber may or may not be separated by a membrane. A separating membrane is occasionally linked with a cathode [128]. Electrons produced by the oxidation of carbon compounds at an anode are transferred to the cathode via an external circuit [129]. The presence of cathode is more important in this type of MFC due to its role in oxidation at pH 7 [130]. There is low liquid volume in the case of air cathodes used in this type of MFC while the use of small-sized air cathodes has few drawbacks for output power due to the nature of inoculum, electrode spacing, and nature of PEM [10].

Two-Chamber MFC

Mostly used microbial fuel cells are in the form of this type. In this type, there is the aerated cathode and anaerobic anode. A salt bridge or proton exchange membrane is used to connect these two electrodes. At the anode, formation of biofilm under anaerobic conditions is facilitated by microbes and it is aerobic in the cathode chamber [131]. Positive ions move from the cathode towards the anode leading to a decrease in pH at anode whole increase at the cathode which tends to decrease the electrical potential at the electrode [132]. The performance of MFC is controlled by many parameters like pH, flow rate, nature of electrodes, and external flow [133,134].

MFC and Electricity Carrying Bacteria

R. sphaeroides could grow in aerobic as well as the anaerobic environment. These bacteria when grown in the presence of light under anaerobic conditions they form photosynthetic apparatus in the cytoplasm of the cell to produce electric current [17]. *Rhodobacter capsulate* [135], *Rubrivivax gelatinosus* [136], *Rhodopseudomonas faecalis* [137], *Rhodopseudomonas palustris* are photosynthetic microbes commonly involved in the production of hydrogen [138,139]. *R. sphaeroides* is reported as having electrical activity greatest of all [17]. Klebsiella sp. is a facultative anaerobe that can generate electric current by consuming substrates food wastes, glucose, and sucrose [140-142]. It also can degrade RB19 for the production of electric current. *Klebsiella sp. C* is involved in the synthesis of mediators that help in the production of electric current [143].

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P. aeruginosa is used as a catalyst in the double chamber MFC that uses substrates fructose, sucrose, and glucose to produce an electric current. It uses pentoses and hexoses via anodic respiration to produce power. Bacteria have high affinity in the case of glucose than sucrose and fructose (Ali et al.,). *Mesophilic Aeromonads* grow in water bodies and are facultative anaerobes.

Aeromonas hydrophila bacteria are involved in the breakdown of chitin due to the presence of enzymes Endo-chitinase and b-N-acetylglucosaminidase. These enzymes lead to more degradation of chitin because of which more power is generated [128] (Table 2).

Table 2: Electrically active bacterial species, their anode, cathode, power generation.

Specie	Anode material	Cathode material	Gram +/-	Power	References
P. aeruginosa	Carbon	Carbon	G-	21 mW/m^2	Liu et al., [86]
R. sphaeroides	Platinum	Graphite	G-	408.06 mW/m^2	Cadirci, [17]
Klebsiella sp. C	Graphite	Graphite	G-	84 mW/m^2	Holkar et al., [143]
Tolumonas osonensis	Carbon	Carbon	G-	424 mW/m^2	Luo et al., [72]
A. hydrophila	Carbon	Carbon	G-	6.65 mA/cm^2	Li et al., [129]
S. oneidensis	Graphite	Graphite	G-	0.3–0.6 W/m^2	Dai et al., [144]
G. sulfurreducens	Carbon cloth	Carbon cloth	G-	084 mW/m^2	Inoue et al., [145]
Bacillus licheniformis	Zinc	copper	G+	0.95V	Barua et al., 2018
Bacillus thuringiensis	Hydrate carbon	hydrate carbon	G+	20–35 mW/ m^2	Treesubsuntorn et al., 2019
Comamonas denitrificans	Carbon/ graphite	Pt	G-	35 mW/ m^2	Xing et al., [146]
Anaerolineaceae	Graphite	carbon	G-	105 mA/ m^2	Lu et al., [147]
Corynebacterium sp.MFC03	Carbon	carbon	G+	41 mW/ m^2	Liu et al., [148]
Citrobacter sp SX-1	Carbon	Carbon/ Pt	G-	88 mW/ m^2	Xu and Liu, [149]
C. denitrificans	Graphite	graphite	G-	0.25 W/m^3	Eaktasang et al., 2016
Enterobacter cloacae	Carbon	carbon	G-	42 mW/ m^2	Nimje et al., [150]
Methylosinus trichosposium	Rgo/Ni foam	rGO/Ni foam	G-	205 mW/ m^2	Jawaharraj et al., 2021
Methylococcus capsulatus	Rgo/Ni foam	rGO/Ni foam	G-	110 mW/ m^2	Jawaharraj et al., 2021
Ochrobactrum anthropi YZ-1	Carbon	carbon	G-	89 mW/ m^2	Zhou et al., 2016
E. Coli	Carbon	Pt	G-	0.001 mA	Liu et al., [86]
Kocuria rhizophila	Carbon	carbon	G+	75 mW/ m^2	Luo et al., [147]
Shewanella putrefaciens	Graphite	graphite	G-	3.5 μW	Veerubhotla et al., 2015

S. oneidensis is reported as having electrical activity and is involved in the production of electric current [144-150]. *Bacillus* and *Klebsiella* both strains can produce electric current [151]. Organic carbon content in the soil is also one of the major factors which influence the production of electric current [11].

Conclusion

Shewanella oneidensis and *Geobacter sulfurreducens* demonstrate pioneering electricity-carrying bacteria, showing complex electron transfer mechanisms involving multiheme proteins and unique extracellular electron transport capabilities, respectively. The diverse range of bacteria, from gut microbes like *E. faecalis* and *L. monocytogenes* to skin bacteria like *Staphylococcus capitis* and *Staphylococcus epidermidis*, as well as newly discovered cable bacteria, highlight the potential of microbial electrogenesis across various environments [152-160]. Electricity-carrying bacteria including *Staphylococcus capitis*, *Staphylococcus epidermidis*, and cable bacteria, exhibit diverse mechanisms for bioelectricity production, ranging from skin microbiota to deep sediment environments. Their potential in MFCs highlights a promising avenue for sustainable energy generation from various substrates, underscoring the importance of harnessing microbial electrogenic properties for future energy needs. Electro microbiology is generally an emerging field of biology and microbiology, with a wider range of new developments and ever-growing discoveries. There are many other potential applications currently under study [161-167]. However, we need new methods that can meet our sustainable system requirements. The field of electro microbiology can provide us with some useful and exciting tools for finding a sustainable future. The production of bioelectricity by conversion of organic waste into useful energy through well-organized wastewater treatment is an effective way, which can be used as an alternative energy source to substitute non-renewable energy.

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