Microbial Energizers: Fuel Cells That Keep on Going

Microbes that produce electricity by oxidizing organic compounds in biomass may someday power useful electronic devices

Derek R. Lovley

Has this happened to you? You have a layover between flights, would like to use your computer and cell phone, but both sets of batteries are drained and the nearby electrical outlets are being used. What if you could instead recharge your electronic devices with a little sugar from the nearby coffee stand? With help from electricity-producing microorganisms, known as electricigens, some day you might have new options for ignoring the current “grid” by generating electricity in an alternative, environmentally friendly manner.

Electricigens are recently discovered microorganisms with the ability to oxidize organic compounds to carbon dioxide while transferring electrons to electrodes with extraordinarily high efficiencies. Electricigens make it possible to convert renewable biomass and organic wastes directly into electricity without combusting the fuel, which wastes substantial amounts of energy as heat. Efforts to eliminate the inefficiencies of combustion are behind the recent interest in hydrogen fuel cells, which oxidize hydrogen and reduce oxygen to water while producing electricity in a controlled chemical reaction.

With electricigens, however, it becomes possible to make microbial fuel cells, which offer potential advantages over hydrogen fuel cells. For example, hydrogen fuel cells require a very pure source of a highly explosive gas that is difficult to store and distribute. Furthermore, hydrogen is derived mainly from fossil fuel rather than renewable sources. In contrast, the energy sources for microbial fuel cells are renewable organisms, including some that are dirt cheap.

**Summary**

- Electricigenic microorganisms such as *Geobacter* and *Rhodoferax* efficiently oxidize organic compounds to carbon dioxide while directly transferring electrons to electrodes.
- Electricigen-based microbial fuel cells mark a paradigm shift because these cells completely oxidize organic fuels while directly transferring electrons to electrodes without mediators.
- Although microbial fuel cells are unlikely to produce enough electricity to contribute to the national power grid in the short-term, the cells may prove feasible in some specific instances such as covering the local energy needs for processing food wastes.
- Optimizing microbial fuel cells will entail developing a better understanding of how electron transfers occur along the outer surfaces of electricigens; key challenges include increasing anode surface areas and increasing electricigen respiration rates.

**Geobacteraceae Producing Electricity in Mud**

Several years ago, Leonard Tender of the Naval Research Laboratories in Washington, D.C., and Clare Reimers of Oregon State University in Corvallis developed systems in which electricigens produce electricity from mud! When a slab of graphite (the anode) is buried in anaerobic marine sediments and then connected to another piece of graphite (the cathode) that is suspended in the overlying aerobic water, electricity...
flows between them (Fig. 1). Although this arrangement typically produces meager electrical currents, they are adequate for running analytic monitoring devices similar to those that investigators place in remote locations such as the ocean bottom.

How do such sediment fuel cells produce electricity? The simple answer is, with microbes. Dawn Holmes, working with Daniel Bond in my laboratory, scraped the anode surface with a razor blade, extracted DNA from those scrapings, and determined what species were present based on their 16S rRNA genes. The surprising result is that such anodes are highly enriched with microorganisms in the family Geobacteraceae. When similar pieces of graphite are incubated in sediments but not connected to a cathode in overlying water, there is no such enrichment.

Which Geobacteraceae prove to be prevalent in such samples depends on the specific environment being tested. For example, if electrodes are placed in marine sediments, Desulfuromonas species predominate, whereas if the electrodes are placed in freshwater sediments, Geobacter species predominate. Although Geobacter and Desulfuromonas species have similar physiologies, Desulfuromonas prefer marine salinity, while Geobacter favor freshwater.

A hallmark of Geobacteraceae is their ability to transfer electrons onto extracellular electron acceptors. For example, Geobacter and Desulfuromonas species support growth by coupling the oxidation of organic compounds to the reduction of Fe(III) or Mn(IV) oxides. Furthermore, these microorganisms can transfer electrons to other metals and to the quinone moieties of humic substances, which are so large
that they must be reduced outside bacterial cells. Reducing Fe(III) oxides is an important means for degrading organic matter in aquatic sediments, submerged soils, and subsurface environments. Molecular analyses of such environments reveal that, in general, Geobacteraceae are the predominant Fe(III)-reducing microorganisms in zones in which Fe(III) reduction is important.

Holmes and Bond found that Geobacteraceae can also use electrodes as extracellular electron acceptors. Both Desulfuromonas and Geobacter species can grow by oxidizing organic compounds to carbon dioxide, with electrodes serving as the sole electron acceptor. Moreover, more than 95% of the electrons derived from oxidizing such organic matter can be recovered as electricity. In sediment fuel cells, Geobacteraceae oxidize organic compounds but, instead of transferring electrons to Fe(III) or Mn(IV), their natural electron acceptors, they transfer electrons onto electrodes (Fig. 1). The electrons flow through the electrical circuit to the cathode, where they react with oxygen to form water.

**Self-Perpetuating, Highly Efficient, Geobacter-Based Microbial Fuel Cells**

The sediment fuel cell can be recreated with pure cultures of Geobacter (Fig. 2). The anaerobic anode chamber contains organic fuel and a graphite electrode. The cathode chamber has a similar electrode and is aerobic. Geobacter transfers electrons released from oxidized organic matter onto the anode. The electrons flow from the anode to the cathode. The two chambers are separated by a cation-selective membrane that permits the protons that are released from oxidized organic matter to migrate to the cathode side, where they combine with electrons and oxygen to form water.

The cation-selective membrane limits oxygen diffusion to the anode chamber, preventing Geobacter from oxidizing the organic fuels with the direct reduction of oxygen. By inserting an electrical circuit within the flow of electrons to oxygen, energy can be harvested that otherwise would go to the electricigenic microbe via aerobic respiration. However, the electricigens still recover some energy from electron transfer to the electrode. This energy recovery is very important because the energy that the electricigens conserve allows them to maintain viability and to produce electricity as long as fuel is provided.

Nearly a century ago, M. C. Potter at the University of Durham in England measured electrical currents when electrodes were placed in microbial cultures. In this and other studies carried out throughout much of the 20th century, microbes generated electricity by producing soluble, reduced compounds that could react abiotically with electrode surfaces. In initial studies these were natural reduced end products of fermentation or anaerobic respiration such as hydrogen, sulfide, alcohols, or ammonia. However, many of these reduced products react only slowly with electrodes, and other end products, such as organic acids, do not appreciably react with electrodes at all. Adding soluble electron acceptors, known as electron shuttles or mediators, enhances current production in such sys-
tems. These electron shuttles enter cells in the oxidized form, accept electrons from respiratory components within the cell, exit in reduced form, and donate electrons to an electrode, which recycles them into the oxidized form. However, there are drawbacks to using such mediators—they add expense to electricity production, and many of them are toxic to humans and/or unstable. Mediators are especially unsuitable for electricity-generating strategies in open environments. Furthermore, the microbes used in these systems typically were fermentative and thus most of the electrons available in the organic fuel remained in organic products instead of being transferred to the electrodes.

More recently, studies in the laboratory of Byung Hong Kim at the Korea Institute of Science and Technology demonstrated that fuel cells containing Shewanella species could produce electricity from lactate without the addition of electron shuttles. However, the efficiency of electron transfer was low in part because Shewanella species only incompletely oxidize lactate to acetate.

**Geobacter-Based Fuel Cells Mark a Paradigm Shift**

Although a few years ago fuel cell experts thought that direct electrochemical contact between microorganisms and electrodes was virtually impossible, this mechanism appears to be how Geobacteraceae carry out electron transfer to electrodes. Thus, the use of Geobacteraceae in microbially based fuel cells marks a paradigm shift. They completely oxidize organic fuels to carbon dioxide while directly transferring electrons to electrodes without mediators.

There has been no known evolutionary pressure on microorganisms to produce electricity. Therefore, it is hypothesized that Geobacter cells transfer electrons to electrodes via the same mechanisms that they use when reducing extracellular, insoluble electron acceptors, such as Fe(III) oxides, that they encounter in natural environments.

Evidence for direct electron transfer from Geobacteraceae to electrodes comes from a variety of studies. For instance, Kelly Nevin at UMASS-Amherst demonstrated that G. metallireducens has to directly contact Fe(III) oxides to reduce them. Daniel Bond found that the cells of closely related G. sulfurreducens that attach to electrode surfaces (Fig. 3), rather than planktonic cells, are responsible for producing power in microbial fuel cells. Electrochemically active proteins on the outer surface of G. sulfurreducens could serve as electrical contact points between the microbes and electrode surfaces.

If the electrode is adjusted to a low enough potential, it can act as an electron donor for Geobacter species, rather than an electron acceptor, according to Kelvin Gregory in my lab. Laboratory studies have suggested that this process might be used to provide Geobacter with electrons to remove contaminants, such as uranium, from polluted water via reductive precipitation.

**Electricigens Other than Geobacteraceae**

Microorganisms outside the Geobacteraceae family can also oxidize organic compounds to carbon dioxide, with electrodes serving as the sole electron acceptor. For example, Swades Chaudhuri from my lab found that Rhodoferax
*ferrireducens* can completely oxidize sugars with electron transfer to electrodes.

Sugars are important constituents of many wastes and renewable biomass. Although *Geobacter* species oxidize a variety of organic acids and aromatic compounds as well as hydrogen, none appears to oxidize sugars. Therefore, producing electricity from sugars with *Geobacter* species also requires fermentative microorganisms to convert those sugars to organic acids and hydrogen. *Rhodoferax* offers the possibility of directly converting these sugars to electricity with a single organism.

In sediment fuel cells that we tested in freshwater sediments, we detected 16S rRNA gene sequences on the anodes that appear closely related to *Geothrix fermentans*, although at much lower levels than *Geobacter* sequences. *G. fermentans* is an acetate-oxidizing Fe(III) reducer, and Daniel Bond found that *G. fermentans* can also oxidize acetate with the production of electricity. The *G. fermentans* cells appear to be enmeshed in an extracellular matrix on the electrode, in contrast with *Geobacter*-covered electrodes, which carry little, if any, extracellular material. We speculate that *Geothrix* produces this material to limit losses of an electron shuttling compound it releases and that the high energetic cost of producing a shuttle limits the ability of *Geothrix* to compete with *Geobacter* species on electrodes.

In marine sediments with high concentrations of sulfide, electrodes may also be colonized by microorganisms in the family *Desulfobulbaceae*, according to my colleague Dawn Holmes. Sulfide can react directly with electrodes, where it is oxidized to elemental sulfur. *Desulfobulbus propionicus*, a Fe(III)-reducing representative of the *Desulfobulbaceae*, can oxidize elemental sulfur to sulfate with an electrode as the electron acceptor. Thus, when sulfate reducers are actively involved in degrading organic matter in marine sediments, sulfate might serve as an electron carrier that can be generated at a distance from the electrode surface—providing electrons for electricity from both abiotic and biotic reactions.

It seems likely that many other types of microorganisms can directly transfer electrons to electrodes, and some of them may have properties with practical significance. Furthermore, if the capacity for direct electron transfer to electrodes is a general characteristic of microorganisms capable of reducing Fe(III), it may be possible to produce electricity under extreme conditions. Most notably, the capacity for reducing Fe(III) is highly conserved among hyperthermophilic bacteria and archaea.

**Potential Practical Applications for Fuel Cells**

The primary near-term practical application of fuel cells powered by electricigens is likely to be sediment fuel cells designed to power electronic monitoring equipment in remote locations. However, electricigens can extract electricity from a wide range of other sources of microbially degradable organic wastes or renewable biomass. Although oxidizing these organic fuels yields carbon dioxide, this process returns only recently fixed carbon to the atmosphere and thus is not a net contributor to atmospheric carbon levels. Furthermore, oxidizing these materials in fuel cells would produce none of the pollutants usually associated with combustion. When wastes are the energy source, potential environmental contaminants are consumed while producing electricity.

Kelvin Gregory in my lab showed that microbial fuel cells can convert swine wastes to electricity, avoiding the usual waste-handling process that releases methane and odor-causing organic acids. In his studies, *Geobacteraceae* accounted for more than 70% of the microbes living on the surface of anodes that were immersed in the swine waste.

Meanwhile, Willy Verstraete at Ghent University in Ghent, Belgium, and Bruce Logan at Pennsylvania State University in University Park, among others, are designing reactors for efficiently converting high volumes of animal wastes and human sewage into electricity. Which microorganisms are producing electricity in these systems is not well understood, but organisms other than *Geobacteraceae* typically predominate.

Microbial fuel cells that produce enough electricity from organic wastes are unlikely to substantially contribute to the national power grid in the short term. Not only would such a system be an engineering marvel but, even if optimized, it would be difficult to compete with other sources of relatively cheap electricity, such as fossil fuels and nuclear fission. Nonetheless, microbial fuel cells may prove practical sooner for...
some relatively high-energy liquid wastes, such as those from processing food or milk, where electricity generation could help to cover treatment costs.

Another short-term practical application could be the powering of electronic devices without connecting them to the grid—especially, say, in developing countries where microorganisms are widely used to convert domestic waste to methane gas that is used locally for cooking. Converting such wastes to electricity instead of methane would provide greater versatility. Another possibility is to develop aquatic or terrestrial "gastrobots," robots that consume organic matter to power their locomotion and sensing and computational needs.

Meanwhile, Bruce Rittman at Arizona State University and his collaborators are evaluating whether microbial fuel cells can be designed to use astronaut wastes as an electric energy source during space travel. More down to earth, other engineers are considering whether microbial fuel cells could provide energy for mobile electronic devices or automobiles.

Fuel Cells Need Optimizing before Applications Become Common

Why are some of these applications not yet in place? For one thing, electricigens were discovered only recently. For another, they produce power slowly, suitable for low-energy devices such as simple calculators (Fig. 4) or as trickle-charging devices for traditional batteries (see www.geobacter.org). In order for microbial fuel cells to power a wider assortment of electronic devices, the cells will need to oxidize fuels more rapidly than they now can.

A key design challenge is to increase anode surface areas because of the direct relationship between anode surface area and power output. Other electrochemical considerations include ensuring that internal resistances and oxygen reduction rates at the cathode do not restrict electron flow.

Optimizing microbial fuel cells will also entail developing a better understanding of how electricigens transfer electrons from their outer surface onto anodes. As we learn more about the electrical contacts between microbes and electrodes, we can begin to develop materials for electrodes that better interact with the electron transfer proteins of the electricigens. Moreover, we can perhaps genetically engineer these microbes to produce more or better contacts with electrodes.

We are evaluating several outer-membrane proteins that might serve as electrical contact points between *G. sulfurreducens* and fuel-cell electrodes. One candidate is a highly abundant c-type cytochrome, OmCS, that is displayed on the outside of the cell. Teena Mehta in my lab demonstrated that OmCS is required for extracellular electron transfer onto Fe(III) oxides. Another candidate is pili, according to Gemma Reguerra in my lab and Kevin McCarthy and Mark Tuominen in the University of Massachusetts-Amherst Physics Department. They demonstrated that *G. sulfurreducens* pili are electrically conductive and function as microbial nanowires (Fig. 5). Genetic studies and the physical location of the pili suggest that they can serve as the final conduit for electron transfer between the cell and the Fe(III) oxides.
Another path to increasing the electricity output of microbial fuel cells may be to increase *Geobacter's* respiration rate. Mounir Izallalen from my laboratory and Radhakrishnan Mahadevan at Genomatica, Inc., in San Diego, Calif., used a genome-based model of *G. sulfurreducens* to formulate a strategy for increasing its respiration rate. They then used genetic engineering to produce cells that respired faster.

These efforts to understand how *Geobacter* and other electricigens produce electricity come when market forces encourage development of smaller, more efficient electronic devices as well as alternative sources for increasingly costly fossil fuels. Hence, further study of electricigens not only will provide valuable insights into the elegance of extracellular electron transfer but could also lead to novel engineering concepts that bring practical benefits to consumers.

**SUGGESTED READING**


**FIGURE 5**

Transmission electron micrograph of the abundant electrically conductive pili of *Geobacter sulfurreducens*. (Photo courtesy of Gemma Reguera, University of Massachusetts-Amherst.)