Abstract

Dramatic changes in electricity generation, use and storage are needed to keep pace with increasing demand while reducing carbon dioxide emissions. There is great potential for application of bioengineering in this area. We have the tools to re-engineer biological molecules and systems, and a significant amount of research and development is being carried out on technologies such as biophotovoltaics, biocapacitors, microbial fuel cells, biobatteries. However, there does not seem to be a satisfactory overarching term to describe this area, and I propose a new word—‘electrosynbionics’. This is to be defined as: the creation of engineered devices that use components derived from or inspired by biology to perform a useful electrical function. Here, the phrase ‘electrical function’ is taken to mean the generation, use and storage of electricity, where the primary charge carriers may be either electrons or ions. ‘Electrosynbionics’ is distinct from ‘bioelectronics’, which normally relates to applications in sensing, computing or electroceuticals. Electrosynbionic devices have the potential to solve challenges in electricity generation, use and storage by exploiting or mimicking some of the desirable attributes of biological systems, including high efficiency, benign operating conditions and intricate molecular structures.

1. Challenges in electricity generation and storage

Globally, the amount of electricity generated has increased dramatically over recent decades. Although the use of renewables has been increasing, further progress is needed in order to reduce carbon dioxide emissions sufficiently to avoid catastrophic effects due to climate change while keeping pace with increasing electricity consumption.

In 2017, in total 25 606 TWh of electricity was generated globally, over four times the amount produced in 1973 [1]. Despite significant increases in the use of renewable sources such as photovoltaics, the percentage of global electricity generated by the burning of coal was approximately the same in 1973 and 2017, at 38.3%–38.5% [1]. Through burning of fossil fuels and other activities, we pumped an estimated 2040 billion tonnes of CO₂ into the atmosphere between 1750 and 2011 [2]. About 40% of this remained in the air, and consequently the atmospheric concentration of CO₂ in the air increased over the same period from a little over 280 ppm to nearly 400 ppm, based on measurements from ice cores and atmospheric air [2]. As CO₂ absorbs strongly in the infrared part of the spectrum, it contributes strongly to the retention of heat that would otherwise be re-radiated into space. Between 1880 and 2012, the average global surface temperature increased by 0.85 °C, and even with mitigation measures (i.e. reduction of CO₂ emissions) the average global surface temperature in 2100 is likely to be over 1.5 °C higher than in 1880, which could cause significant loss of life and decrease in living standards due to increased frequency and severity of extreme weather events, changes to ecosystems leading to reduced food production, and geopolitical or social issues arising from increases in sea level and migration [2].

The agreement [3] reached in Paris in 2015 set the objective of keeping the global temperature rise this century to well below 2 °C and pursuing efforts to limit the rise to 1.5 °C. To address this, countries are starting to set goals of reducing carbon dioxide emissions to net zero in the coming decades. As electricity and heat production accounts for approximately 25% of greenhouse gas emissions and transport accounts for 14% [2], further expansion of renewable electricity generation and use of electric vehicles will be required in order to meet such commitments. Use of intermittent
The transformation of electrosynbionics from an emerging area to a thriving branch of mainstream science will be driven by the need for new electricity generation and storage techniques, but for electrosynbionics to be commercially viable they must demonstrate a competitive advantage over established techniques. It is therefore essential to view electrosynbionics in the context of the existing landscape of electricity generation and energy storage. To that end, I will proceed to review conventional technologies before describing the biological phenomena that could be used in their biological or bio-inspired counterparts, and then summarizing some of the innovations that I suggest should be rebranded as ‘electrosynbionics’.

I will conclude by arguing that electrosynbionics technologies have great potential but much further work and investment are required to make them competitive, and this will need to be supported by a more systematic approach to the testing of devices/systems and statements of their specifications.

This perspective is intended to be accessible to researchers in disciplines ranging from physical sciences and engineering to the biological sciences. Consequently I assume very little prior knowledge, and parts of sections 2 and 3 present material that could be regarded by specialists as elementary but will not be familiar to all readers.

2. Conventional technologies for electricity generation and storage

Here, ‘conventional’ should be taken to mean ‘without biological parts’. In this discussion, I will focus solely on the technologies that could have electrosynbionics equivalents. Hence, the only electricity generation techniques to be mentioned will be photovoltaics and fuel cells.

2.1. Photovoltaics

In biological and non-biological systems, there are three key steps in light harvesting and energy conversion, namely photoexcitation, charge separation and charge transport. Typical solar cells are based on semiconductors. In the absence of any excitation, electrons in a semiconductor normally occupy a set of filled energy states known as the valence band. For charge to flow, electrons must be excited to the conduction band, which is at a higher energy than the valence band. Conduction and valence band are separated by a set of forbidden states known as the band gap. An electron can only be excited to the conduction band if it is given sufficient energy to overcome the band gap. Photoexcitation (figure 1(a)) can therefore only occur if the energy of the incident photon exceeds the band gap energy. In this case, an electron is elevated to the conduction band and a ‘hole’ is left behind in the valence band. The semiconductor of choice is often silicon. Conventional silicon photovoltaics are either
A conventional solar cell [6] consists of a \( p-n \)-junction, comprising two layers of semiconductor material, doped with different types of impurities (figure 1(b)). The \( p \)-type material is doped with impurities such as boron that tend to accept electrons, creating ‘holes’ in the valence band, and the \( n \)-type material is doped with impurities such as phosphorus that tend to donate electrons to the conduction band. Joining the \( n \) and \( p \) type materials together results in the diffusion of mobile charge carriers across the boundary, leading to the creation of a depletion zone where there is a strong electric field, which helps to separate photoexcited electron–hole pairs. Once the electrons and holes are transported to opposite electrodes, a current can flow in the external circuit. Recombination of electrons and holes prior to separation/transport tends to degrade the performance of the solar cell, as the absorbed photon energy is wasted. The efficiency of a solar cell is usually defined as the quantity of electrical energy extracted divided by the total solar energy incident on the device. The maximum efficiency achievable is fundamentally limited by thermodynamics and is referred to as the Shockley–Queisser limit after those who first calculated it [7]. For a single-junction silicon device Shockley and Queisser originally computed the limit to be approximately 30%. Later calculations incorporating additional physics and utilizing a more accurate solar spectrum produced very similar values [8]. The limit depends on the material used and the value of the band gap.

Multi-junction solar cells consist of several \( p-n \)-junctions based on materials with different band gaps. Multi-junction solar cells can absorb a higher percentage of the solar spectrum and therefore have the potential to display greater efficiency. The Shockley–Queisser limit for a solar cell with an infinite number of junctions has been calculated to be 68% [9]. Some research groups are seeking to circumvent the Shockley–Queisser limit by exploiting physics that was not accounted for in the original models [10].

Thin-film solar cells [11] are made by growing layers of material on a substrate (as opposed to slicing up a large ingot). The layer is less than a few microns thick. Thin-film devices use very little material and are consequently very lightweight, but they only have a small share of the overall photovoltaic market.

In the 1990s, a completely new approach was proposed: the dye-sensitized solar cell [12]. This consists of the following components: a dye, an electron-transporting porous material such as a colloidal film of TiO\(_2\) nanoparticles, an electrolyte and two transparent conducting electrodes (figure 1(c)). The dye acts like the chromophore in photosynthetic reaction centres (see below), absorbing light and producing a photoexcited electron. The electron is transported through the porous material and into one of the transparent electrodes. The electrolyte completes the circuit and contains additives that allow regeneration of the dye after photoexcitation. The efficiency of DSSCs is typically quite low, reaching values of 12% at best [13].
Over the last decade, a new technology has emerged, in the form of perovskites, materials with the chemical formula ABX₃, where A and B are cations (A larger than B) and X is an anion. Perovskites may be used as light absorbers in DSSCs or as the basis of thin-film style devices [14]. These devices have been developed rapidly and the efficiencies achieved have increased dramatically over the last 10 years, although some issues remain about potential environmental issues associated with perovskite-based cells as some of them contain elements such as lead. Perovskite cells can be referred to as one of the ‘emerging PV’ technologies. This category also includes DSSCs and systems based on organic semiconductors, quantum dots etc.

The National Renewable Energy Laboratory (NREL) in the USA provides a much-used chart to show the highest confirmed conversion efficiencies for the different technologies as they develop over time (in a research context—rather than commercial application) [15]. Tables published every six months in the journal Progress in Photovoltaics also show the best confirmed efficiencies in each category [13], some of which are shown graphically in figure 1(d), together with the thermodynamic performance limits for single-junction silicon cells and multi-junction cells. It is essential to note that results are only included in the reference tables and graphs if they have been ‘independently measured by a recognized test centre’ [13] and measurements are made in accordance with international standards. International standards have been developed to define a reference solar spectrum and the procedure for measuring photovoltaic efficiency using artificial solar simulators. The journal Progress in Photovoltaics refers to the standard IEC60904-3, from the International Electrotechnical Commission. Similar standards are also provided by ASTM International (ASTM E-927 and G-173) [16, 17], and the spectra are nearly identical. As shown in the G-173 standard [17], the solar irradiance is greatest at wavelengths of 450–550 nm, dropping steeply at lower wavelengths and more gradually at higher wavelengths. The spectrum is not smooth due to atmospheric absorption at particular wavelengths, and the irradiance drops to zero in two bands centred on approximately 1380 and 1875 nm. The tail of the spectrum falls away to nearly zero in the vicinity of 2500 nm.

Of course, efficiency is not the only important factor in the success of a photovoltaic technology. Economic considerations are particularly important, and the economic competitiveness of electricity generating technologies is often assessed using the levelized cost of electricity (LCOE). This includes all the costs of building and operating the technology over its lifetime, including all the infrastructure [18]. The expected service life of the systems is therefore critical, but so too is the manufacture cost, and high volume mass production methods are essential. It is also vital to consider the costs of the systems required to connect the photovoltaic modules to the grid. Other important aspects include the appearance of the cells, their material content and end-of-life disposal considerations.

2.2. Batteries, capacitors and fuel cells

2.2.1. Batteries

The first battery [19] was demonstrated by Alessandro Volta in 1800, and consisted of a pile of pairs of dissimilar metal discs, separated by brine-saturated cloth. So-called ‘primary’ batteries like Volta’s are single-use devices, whereas ‘secondary’ batteries can be recharged. Inside a typical battery there are two electrodes, an electrolyte and a separator (figure 2(a)). The electrolyte is a substance through which ions can move but which is impermeable to electrons. The function of the separator is simply to prevent the two electrodes from coming into contact. In the example of the lead-acid battery, when current is drawn the following reactions occur:

Positive electrode:

\[ \text{PbO}_2 + \text{HSO}_4^- + 3\text{H}^+ + 2e^- \rightarrow \text{PbSO}_4 + 2\text{H}_2\text{O}. \]

Negative electrode:

\[ \text{Pb} + \text{HSO}_4^- \rightarrow \text{PbSO}_4 + \text{H}^+ + 2e^-. \]
For each reaction a standard electrode potential can be quoted. This is usually given as the potential difference that would be observed between the given electrode system and a so-called standard hydrogen electrode, under standard conditions. The standard voltage for the battery is the difference between the two electrode potentials.

The Nobel Prize in Chemistry 2019 was awarded for the development of lithium-ion batteries [20], a revolutionary technology that has had a dramatic impact in a number of areas. In these batteries, the electrodes consist of materials in which lithium ions intercalate in the crystal structure. During discharge, lithium ions disentangle themselves from the structure of the negative electrode, electrons are produced and pushed into the external circuit. The ions move through the electrolyte to the other electrode, and as they intercalate in the structure an electron is pulled in from the external circuit.

There are many other possible battery chemistries.

2.2.2. Capacitors
The traditional capacitor [21] consists of a dielectric sandwiched between two metal plates (figure 2(b)). When a voltage is applied across the capacitor, charge builds up on the metal plates, giving rise to an electric field in which energy is stored. A variety of capacitors exist, some of which differ in design from the ‘classic’ variety.

Particularly high values of capacitance are achieved in supercapacitors, also known as ultracapacitors or electrochemical capacitors. Supercapacitors [22] fall into two categories: ‘pseudocapacitors’, in which charge is stored via redox reactions at the electrodes, or ‘electrochemical double layer capacitors’. In the latter, two electrodes are immersed in an electrolyte with a separator in between. When an external voltage is applied, the electrodes become charged as a result of the flow of electrons. The mobile ions in the solution move towards the oppositely charged electrodes, and a layer of ions forms at the electrode-electrolyte interface. The so-called double layer [23] consists of the layer of ions in the electrode and the layer of counterions in the electrolyte (Figure 2c). It is extremely thin, which means that the charge is being stored in a very narrow volume, leading to high capacitance.

2.2.3. Fuel cells
Fuel cells [23] produce electricity as a result of electrochemical reactions between reagents that are fed into the cell. Unlike battery electrodes, fuel cell electrodes are inert; they essentially catalyse the reaction. Fuel cells are generally classified by electrolyte, and some systems run at very high temperatures (a few hundred degrees C). The energy conversion can be very efficient because these systems are not subject to the thermodynamic limit for heat engines. Fuels include hydrogen and hydrocarbons, and oxygen/air is usually required.

2.2.4. Overview
The energy storage devices described here are suited to different applications. In general, fuel cells are high-energy systems, and supercapacitors are high-power systems, while batteries are intermediate in both domains.

Key performance indicators for energy storage devices include energy density (either volumetric or gravimetric i.e. by mass), power density, lifetime (and number of charge-recharge cycles), efficiency, and safety.

3. Inspiration from biology

3.1. Ions as biological charge carriers
Many biological processes take place in an aqueous environment, in the presence of various ions such as sodium, potassium and chlorine. The fundamental building block of biology is the cell, which is bounded by a membrane consisting of a phospholipid bilayer (figure 3(a)). Various biological molecules are embedded in the bilayer, including larger molecules such as proteins. The membrane itself is insulating but there are several mechanisms by which substances can be transported from the exterior of a cell to the interior or vice versa. For instance, ions can move through ion channels, protein pores embedded in the membrane.

The conditions inside and outside the cell may differ, in terms of electrical potential (i.e. voltage) and the concentration of ions. For a given type of ion, the tendency of an ion to cross the membrane (outwards) through an open ion channel is quantified by the ion-motive force, which has units of volts. This is given by:

\[ IMF = V_m - \frac{RT}{zF} \ln \left( \frac{[\text{ion}]_{\text{outside}}}{[\text{ion}]_{\text{inside}}} \right), \]

where \( R \) is the molar gas constant, \( z \) is the charge on the ion in multiples of the electronic charge \( e \), and \( F \) is the Faraday constant [24].

The first term in the IMF equation is the membrane voltage, where a negative sign for this quantity indicates that the inside is negative with respect to the outside. The second term in the IMF equation is the chemical potential, where the square brackets denote the concentration of the indicated species. In the case of \( \text{H}^+ \) ions, the term ‘proton motive force’ is used for the IMF.

If only one ionic species is relevant in a particular situation, and the ion is in equilibrium, the ion motive force is zero and the membrane voltage is equal to the chemical potential. In this case, the IMF expression reduces to the form known as the Nernst equation, which defines the membrane voltage at equilibrium. Where multiple ionic species are involved, the more complex Goldman–Hodgkin–Katz (GHK) equations can be used. The GHK voltage equation applies in equilibrium but the GHK current equation applies out of equilibrium.
If the motive force on an ionic species is non-zero, the ions can cross the membrane through ion channels. Such channels can be gated, such that they only open in the presence of a stimulus, in the form of a transmembrane potential, chemical ligand, or a mechanical force. Ion pumps transport ions against the prevailing ion motive force and require a source of energy to operate. Ion channels and pumps are often highly specific to particular types of ion, because they possess a structural feature known as a selectivity filter, in which the amino acids of the protein structure are arranged such that only an ion of the correct size and charge can pass through. In humans, malfunctions of ion channels are associated with a range of diseases known as channelopathies, including a number of neurological, cardiovascular and autoimmune diseases.

The operation of ion channels underpins the transmission of nerve impulses along neurons [25]. When a neuron is resting and there is no impulse, the membrane potential is approximately $-60$ mV. When an action potential is initiated, sodium ion channels begin to open and sodium ions flood into the cell, increasing the membrane potential (figure 3(b)). This causes the opening of additional sodium ion channels that are voltage-gated. The voltage becomes positive, and when it reaches a critical value, the sodium ion channels close, and potassium ion channels open. Potassium ions flow out of the cell, causing the membrane potential to decrease. The original configuration is restored by ion pumps. The action potential propagates along the cell because depolarization of one area of the membrane triggers opening of sodium channels in the next section of the membrane.
The classic mathematical model for nerve impulse transmission was derived by Hodgkin and Huxley in 1952, and they were awarded the Nobel Prize in Physiology and Medicine in 1963, together with Eccles. Hodgkin and Huxley modelled the neuron membrane as a capacitor, the ion channels as a set of resistors in parallel, and the ion motive force as a battery-like entity [26].

The mechanism by which an electric eel generates electricity (figure 3(c)) is similar to that of the action potential propagation. The cells responsible for generating the eel’s shock are known as electrocytes, and they are arranged in columns along the eel. At rest, the transmembrane potential of an electrocyte is around −85 mV [27]. When an electric shock is triggered, sodium ion channels open on one side of the electrocyte, and the potassium channels in the same area close. The membrane on that side of the electrocyte depolarizes, creating a potential difference between one side of the electrocyte and the other. The total voltage of all the stacked electrocytes can be as much as 600 V [28].

Ion channels also underpin the mechanism of sight. In the eye, light is absorbed by the molecule retinal, which is bound to the opsin protein, forming the structure ‘rhodopsin’. Rhodopsin is embedded in the membrane that bounds sub-cellular disks in rod cells in the eye. The absorption spectrum of retinal depends on the structure of the opsin to which it is bound [29]. Light absorption triggers a conformational change in retinal (‘photoisomerization’), which causes the protein to change shape. This transformation initiates a cascade of events that ultimately leads to the transmission of a nerve impulse to the brain. So-called channelrhodopsins, found in organisms such as algae, are light-driven ion pumps, which have been exploited in applications such as optogenetics, the science of controlling gene expression using light.

Bacteriorhodopsin (figure 3(d)) is a specific example of a light-driven ion pump, and it is found in the purple membranes of halobacteria, an extremely halophilic type of Archaea (not actually Bacteria, despite the name) [30]. The purple membrane can be isolated and is approximately 25% lipid and 75% protein by weight. Bacteriorhodopsin itself is a membrane-spanning trimeric protein, and each monomer consists of 7 transmembrane helices surrounding a central pore. As with the rhodopsin protein in the human eye, the chromophore is retinal. Photoisomerization of retinal disrupts a water molecule that is situated in a critical position, and a series of conformational changes ensues, resulting in the transfer of protons between various amino acid residues in the protein. Ultimately, the net result is the transfer of a proton across the membrane, and the protein returns to the ground state. The timescales for the key processes have been measured spectroscopically. Bacteriorhodopsin has potential applications in a range of devices, including photovoltaics (to be discussed below), and can even be acquired commercially. It can form lattices on surfaces, which can be imaged by AFM [31].

3.2. Bioelectrochemistry

In solid state devices current is usually carried by electrons and holes moving through conductive materials, but in biology we usually think of electrons in the context of electrochemistry and electron transport chains. Here, electrons are passed between different types of molecule. This is captured in the classic concepts of reduction (gain of electrons) and oxidation (loss of electrons), collectively referred to as ‘redox’ reactions. The reduction/oxidation potential quantifies the energy required for a species to gain/lose electrons.

3.2.1. Photosynthesis

Oxygenic photosynthesis is the process by which green plants, algae and cyanobacteria extract energy from sunlight. The net result of photosynthesis is the production of a sugar and oxygen from carbon dioxide and water. The details of the biomolecular mechanisms of photosynthesis depend on the type of organism, and the description that follows refers to oxygenic photosynthesis in plants.

Photosynthesis [25] involves light reactions and dark reactions. Both reactions take place in chloroplasts, which contain a number of stacked membrane structures called thylakoids, in which photosystems are embedded. Each photosystem consists of antennae (also known as light harvesting complexes) and reaction centres. In the light reactions, photons are captured by the pigments comprising the antennae, arrays of chromophores in a protein structure. The antennae funnel the photons’ energy to the reaction centre, which is a complex comprising proteins, a chromophore (a chlorophyll) and other components (figure 3(e)). Photoexcitation occurs, elevating an electron to a higher energy state. Charge separation occurs rapidly, and the electron passes along a transport chain, losing energy as it does so. The transport chain consists of a series of molecules that can accept or donate electrons, changing oxidation state as they do so. The energy of the electron is used to pump protons that then drive ATP synthesis. The electron is then transferred to another photosystem, and it is photoexcited again. It moves on once more, and is ultimately used to produce NADPH. The ATP and NADPH can donate electrons for the dark reactions, which take place in the stroma, the medium surrounding the thylakoids, and produce a sugar (glucose). The holes created in the first photoexcitation step are used to split water, which means that water acts as the original source of electrons.

3.2.2. Electromicrobiology

Various microbes have evolved the ability to transport electrons, along distances ranging from nm to cm. This
enables them to use materials in their environment (e.g. iron-based minerals) as electron donors or acceptors, to supply or remove electrons for metabolic reactions [32].

The term exoelectrogen has been applied to organisms that transfer electrons in and out of the cell. There are three main mechanisms for electron transfer in electrically active microbes (figure 3(f)): the use of soluble electron ‘shuttle’ molecules that are produced by the cell, short range electron transfer from molecules embedded on the outer surface of the microbe, and long range transfer through extended structures. Although these mechanisms have been studied intensively, many questions still remain.

Examples of electron shuttles include the flavins produced by *Shewanella ondensis*, which are secreted into the extracellular matrix. When in an appropriate state, flavins can reduce insoluble Fe (III) [32].

Short range direct electron transfer to electrodes or substrates usually involves cytochromes. These are proteins that contain heme complexes, small structures consisting of ring-like molecules with iron at the centre. *Shewanella* requires certain cytochromes in addition to flavins. Pump-probe spectroscopy has been used to measure the rate of charge transfer between heme groups in cytochromes [33].

In the electrically active species *Geobacter sulfurreducens*, long-range electron transfer occurs through nanowire-like structures called pili, which extend from the cells into the surroundings. Experiments have demonstrated that each pilus is conductive, and when the gene for the pilus protein PilA is knocked out the cells can attach to Fe(III) oxide surfaces but are unable to grow [34]. Site-specific modification of amino acids in PilA can increase the conductivity of the pilus dramatically and reduce its diameter [35]. *Shewanella* also possesses external nanowires, but some of these structures appear to differ significantly from the pili of *Geobacter*. For instance, some *Shewanella* nanowires are significantly less conductive than those of *Geobacter*, and it is believed that this is because the conduction mechanism in *Geobacter* is almost metal-like, whereas in *Shewanella* electrons are thought to move in a stepwise manner along a chain of redox-active molecules [32].

Extremely long range transfer has been seen in ‘cable bacteria’ [36]. These remarkable filamentous microbes grow in marine sediments, forming centimetre-scale chains that contain unbranched chains of as many as 10,000 cells or even more [37]. At the bottom of the filament, there is no oxygen but there is a source of sulphide. At the top of the filament there is oxygen but limited sulphide. Bacteria in different positions in the filament therefore perform different redox reactions. At the top of the filament oxygen is reduced to form water, using electrons generated at the bottom of the filament by oxidation of the sulphide source. The outer membranes of the individual cells merge, to cover the complete filament, and electrons are transported through the space between the outer membrane and the inner membranes. nA-scale currents have been measured directly in filaments of intact cells, and similar size currents were seen from the isolated fibre sheath (the part of the filament outside the inner membranes) [38]. Although the mechanism of electron transport is not yet fully known, a recent study suggested that a protein known for forming pili-type structures was the most abundant protein in one particular species of cable bacteria [39], and Raman spectroscopy results reported in another study indicated a lack of cytochromes in the isolated fibre sheath [38]. One hypothesis is that the electrons are transported through an assembly of pili-type proteins located in the periplasm (between the two membranes).

## 4. Electrosbionics: technologies

The phenomena described above can be used as the basis for a wide variety of technologies, some of which I will describe here. Technologies that use chemical sources of energy will be discussed alongside closely related technologies that harvest energy from sunlight.

### 4.1. Biobatteries, enzymatic fuel cells, biosupercapacitors and sub-cellular biophotovoltaics

The principle of enzymatic fuel cells and biobatteries is simply that enzymes catalyse reactions that release electrons, which can be harvested and used to drive a current in an external circuit. The enzymes may be in solution, immobilized on a surface or trapped in a gel. Electron transfer from enzymes to electrodes may be either direct or facilitated by a mediator. Mediators must be chosen such that their redox properties match the process to be mediated. One possible application for an enzymatic fuel cell or biobattery [40] is as an implantable power source for a device such as a pacemaker. Key factors to consider in the assessment of the technologies include stability, power density and costs. Enzymes can potentially be made comparatively cheaply at large scales in a fermenter [40].

Technically, the term fuel cell implies that the fuel is supplied from a source external to the device, whereas the term battery implies an internal fuel source, but in practice some papers use the terms interchangeably, in part because some devices can be used in either way. However, it is important to draw a distinction between enzymatic and microbial fuel cells. Enzymatic fuel cells use subcellular components in the form of enzymes extracted from cells or made synthetically, whereas microbial fuel cells are based on living cells and will be discussed below.

For one biobattery, a synthetic reaction pathway involving 13 enzymes was designed *de novo* [41]. In the anode compartment, maltodextrin was broken down and electrons were transferred to the electrode. The reaction pathway was cyclic, meaning that the enzymes were regenerated. In the cathode compartment, oxygen was consumed and water was produced. The
maximum power seen was 0.8 mW cm\(^{-2}\) at 50 °C but the enzyme activity decreased after a few days.

When enzymes are immobilized on the surface of electrodes (figure 4(a)) it is common to use high surface area electrodes, with some degree of micro- or nano-structuring, in order to achieve efficient electron transfer [42] and, for immobilized enzymes, a high level of enzyme loading. For example, enzymes such as laccase can be chemically conjugated to structures such as carbon nanotubes [43]. The carbon nanotube aggregate known as buckypaper can also be used to make electrodes for biobatteries [44]. In systems based on immobilized enzymes, the orientation of the enzyme must be optimized for effective electron transfer, as must the behaviour of the redox mediators. It has been shown that orientation and mediation can be controlled using a synthetic molecule that performs multiple functions, anchoring itself to the electrode, binding to the enzyme in an appropriate way and also acting as a good mediator [45].

Some architectures have extended lifetimes, such as the ‘enzymatic nanomembrane’ system, in which nanomembranes of titanium were rolled up and the enzymes were trapped between the leaves of the roll [46]. In this device the enzymes used were bilirubin oxidase (on the cathode), glucose dehydrogenase and diaphorase (on the anode). The biobattery discharged over 452 h. The operational lifetime of biobatteries/enzymatic fuel cells can be limited by availability of fuel, in addition to enzyme degradation, and this can be addressed by the use of flow-through systems, in which fuel is continually replenished [47].

Energy is stored in biobatteries and biofuel cells in the form of chemical fuel that is then metabolized. However, a new dimension can be introduced in the form of capacitive storage. It has been shown that cytochromes are responsible for the enhanced capacitance seen in Geobacter biofilms [48] and this has inspired the construction of synthetic biosupercapacitors, including one device based on biophylized graphene oxide and myoglobin [49]. Myoglobin stores charge by means of protonation or deprotonation of charged residues, but the mechanism appears to persist even if the secondary structure of the protein is disrupted.

In self-charging biosupercapacitors (also known as supercapacitor/biofuel cell hybrids), enzyme reactions charge the inbuilt capacitance. As in conventional supercapacitors, the charge can be stored either through electrochemical double layer capacitance or pseudocapacitance, created by redox reactions in the vicinity of the electrode surface. In one example, the electrodes consisted of enzymes integrated with carbon nanotubes [50], and after the system discharged itself it was observed to recharge. It performed numerous charge/discharge cycles but when the glucose fuel was removed the open circuit voltage fell sharply because the enzyme substrate was no longer present. In a later case, graphite electrodes were coated with an osmium-based redox polymer to create a charge storage layer. This was then over-coated with a layer of enzymes trapped in the same polymer. The bioanode was based on a glucose dehydrogenase, while the biocathode was based on bilirubin oxidase. During operation, the action of the enzymes changed the redox state of the polymers, leading to capacitive charge storage. This system was referred to as a Nernstian biosupercapacitor [51] because the same polymer was used for both electrodes and the Nernst equation governed the open circuit voltage of the complete device. It has been shown that supercapacitor/biofuel cell hybrid devices can be used to generate pulses similar to those needed for the operation of a pacemaker [52]. Devices can be made from flexible materials, such that the power output was not changed significantly when the cell was bent, even by an angle of 60° [53]. The biobattery, biosupercapacitor and enzymatic fuel cell systems described so far all charge biochemically, i.e. through metabolism of a fuel. However, in biology many organisms harness solar energy through photosynthesis, and the machinery they use for this can be isolated and incorporated into sub-cellular biophotovoltaics. This term refers to devices in which electricity is generated from sunlight using components such as chloroplasts and thylakoids that have been extracted from cells, in contrast to the systems I call ‘living photovoltaics’, which are based on living cells and will be discussed below.

An early example of a ‘photoelectrochemical cell’ (i.e. a sub-cellular biophotovoltaic system) employed thylakoid membranes extracted from spinach [54]. Photocurrents of several µA were observed, and this effect was suppressed by the addition of particular herbicides, which were known to inhibit photosynthesis. Current could be increased to tens of µA by the addition of artificial electron acceptors and the immobilization of thylakoids in a matrix. In general, in enzymatic fuel cells, biosupercapacitors and biophotovoltaics, immobilization can either enhance or detract from performance, depending on the details of the device under test.

In a more recent study [55], the anode comprised spinach thylakoid membranes chemically tethered to a matrix of multi-wall carbon nanotubes deposited on a gold electrode. The cathode was similar, apart from the use of the enzyme laccase in place of thylakoids (figure 4(b)). The purpose of the laccase was to regenerate water from oxygen. The maximum power observed was 5.3 µW cm\(^{-2}\), the system being characterized under a lamp. Another setup [56] was also based on thylakoid membranes, but utilized the enzyme bilirubin oxidase and electrodes made of ITO glass—the same material that is standard in dye-sensitized solar cells. At peak power output, 0.6 µW cm\(^{-2}\) was delivered. This system was characterized in ambient natural light and was referred to as a solar biosupercapacitor.
In sub-cellular bioPV systems, it is not necessary to use intact thylakoid membranes, and it is possible to build solar cells using isolated photosystems or reaction centres. In one study, an architecture similar to that of a dye-sensitized solar cell was used [57], with photosystem-1 from thylakoid membranes of cyanobacteria as the ‘dye’. The natural redox mediators were replaced with an electrolyte and a nanostructured metal oxide, in the form of TiO2 paste or ZnO nanowires attached to a conducting glass electrode. The system was tested with AM1.5 standard simulated sunlight, and a power of 81 µW cm\(^{-2}\) was achieved, with an external efficiency of 0.08%. In this study, the photosystems were stabilized using designer peptides, which have been shown to protect proteins like this from structural degradation for an extended period [58].

Interestingly, in DSSC-style devices based on photosystems, performance can be improved by incorporation of an artificial light-harvesting antenna—a molecule that absorbs photons and passes their energy to the photosystem. In a recent study, this yielded a power conversion efficiency of 0.13%, measured with a standard solar simulator (AM1.5) [39].

In an alternative approach, the entire Z-scheme of photosynthesis was mimicked using an anode based on photosystem 2 and a cathode based on photosystem 1 [60]. In the anode compartment, water acted as the electron donor, while methyl viologen acted as the electron acceptor. Methyl viologen was ultimately re-oxidized by molecular oxygen. In this case, the photosystems were attached to the electrodes via a redox hydrogel, which acted as a bridge for the electrons that flowed through the external circuit during illumination. The power obtained was 23 nW cm\(^{-2}\) but this was increased subsequently to almost 2 µW cm\(^{-2}\), with corresponding efficiency of 0.0045%, by changing the redox hydrogel used for the anode [61]. However, these power figures are not exactly comparable as illumination conditions were not identical—although LEDs were used in both cases, the stated light intensity was different.

Photocurrent can be generated from isolated Rho
dobacter sphaeroides reaction centres adsorbed on
silver electrodes with cytochrome c [62]. When the electrodes were nanostructured using electrochemical roughening, the number of reaction centres loaded on the surface increased. The rate of electron transfer per reaction centre also increased, and this was attributed to plasmon-enhanced light-harvesting. In another experiment, prior to drop-casting of reaction centres and cytochromes, electrodes were coated with self-assembled monolayers (SAMs) of 11-mercaptoundecanol or 11-mercaptoundecanecanoic acid, to facilitate measurements of electrical properties of the proteins [63]. For the cytochromes to act as an effective bridge between the electrode and the reaction centres, it was found necessary for them to have some mobility; when they were chemically immobilized the photocurrent decreased dramatically.

One major issue with the use of subcellular parts of the photosynthetic machinery in vitro is their limited lifetime. It has been noted that isolated photosystems will only survive for 30–40 min of illumination in vitro, with whole chloroplasts being able to last a little longer (normally a few hours at most) [64]. This may be acceptable for some niche applications [65], but it will not be suitable for mainstream scenarios, where electrical infrastructure is expected to last for years. As mentioned above, additives such as designer peptides may stabilize the structure of photosynthetic proteins to some extent [57, 58], but it is not clear whether this will be sufficient to prevent long-term functional deterioration under continuous illumination. As an alternative, regeneration may be possible. For instance, in one study it was demonstrated that a photosystem I-loaded gold electrode could be replenished with fresh photosystem from solution [66]. In this case, the other electrode was made from eutectic gallium-indium, which is flexible. When illuminated under standard AM1.5 conditions, the response was too small to be measured, but a photocurrent was observed under laser illumination. The efficiency was 0.0025%.

4.2. Microbial fuel cells and living photovoltaics
An obvious way to circumvent the instability of isolated biological parts is to avoid extracting them in the first place, and work with living systems that can refresh proteins as they wear out. These systems include microbial fuel cells (MFCs) and living photovoltaics. MFCs produce electricity by exploiting the metabolic processes of micro-organisms and require a chemical fuel to operate. Some living photovoltaics are described as photoMFCs, and may or may not require additional chemical fuel. As will be seen, there is some overlap between the categories. Terminology is not applied in the same way by all researchers.

4.2.1. MFCs (non-photosynthetic)
In an MFC, microbes oxidize a substrate and pass electrons to an anode [67]. The electrons then flow through an external load to the cathode. The substrate will ultimately be used up and must be replenished. The typical design consists of two chambers separated by a cation exchange membrane such as Nafion. Each chamber contains an electrode. The anode must be conductive, biocompatible and stable, and carbon is often chosen. Cathode materials depend on the application.

For large MFCs, the high internal resistance can limit the power density [68]. In any case, the power output is usually quite low, which means that stacks of MFCs may be needed to generate sufficient power (depending on the application). Some of the components can be expensive, so lower cost options would be useful.

An emerging trend in the area of microbial fuel cells is the use of this technology to simultaneously generate electricity and remove contaminants from wastewater at treatment plants, and pilot projects have taken place [68]. For practical application of this technique it is necessary to operate microbial fuel cells at scale, using large volume reaction chambers. When scaling up from laboratory scale, it may be necessary to introduce design modifications to achieve the necessary performance. For instance, in a 1.5 l-scale system, it was shown that increasing the number of electrodes (both anode and cathode) improved performance significantly [69]. For much bigger systems, at a scale of tens of litres, recirculation of the wastewater can increase the maximum power density by up to 17%, but this depends on the recirculation time and flow path [70].

In one example of a study of large-scale microbial fuel cells for simultaneous electricity production and wastewater treatment, 48 fuel cell modules were connected in a series stack, the total volume of the anode compartments being around 100 l [71]. For power extraction, a commercial energy harvesting system was used, with the capacity for ‘maximum power point tracking’, a means of optimizing output by matching the load impedance in real time. The power output from the system was 84–130 mW and it removed over 75% of the organic matter as well as 80% of the solid content. It was noted that if one weaker source was connected in series with stronger sources, the overall performance could be degraded. Wastewater-based MFCs can function for extended periods of time, but their behaviour is not very reproducible [72].

At the opposite end of the size scale, microbial fuel cells could potentially be used to provide long-term power for autonomous sensors that form part of a network. In order for this to be practical, it is necessary for the technology to be miniaturized. One early example of a miniature MFC consisted of two chambers made from non-conducting plastic, each having a volume of only 1.2 cm³ and housing a carbon-based electrode [73]. The two chambers were separated by a Nafion proton exchange membrane. The microbe used was Shewanella oneidensis, metabolising lactate. Measurements were made over a period of 7 d, with the
addition of lactate where necessary. The maximum output power obtained was 0.3 mW cm$^{-2}$.

Subsequently, even smaller MFCs were developed, reaching microlitre-scale. For one device, based on a single chamber with a volume of 25 µl, gold anodes were fabricated on glass using standard photolithography techniques [74], and a biofilm was formed on the gold surface. The reaction chamber was made from PMMA, and this was placed between the glass and a proton exchange membrane. This device was also based on *Shewanella oneidensis* and produced a maximum power of 2.9 µW cm$^{-2}$ (power per geometric area of electrode).

In standard lab-on-chip microfluidic fabrication, it is common to use PDMS instead of PMMA, but PDMS can cause problems in MFCs because it allows oxygen to enter the reaction chamber. It has been shown that coating PDMS with parylene C significantly reduces the oxygen permeability and this was used in a miniature MFC based on *Geobacteraceae*, in a microfluidic system with a channel 55 µm deep. The peak power density observed was approximately 72 µW cm$^{-2}$, where this was achieved when micropillars had been made on the electrode [75]. It has been shown that electrodes made from conducting nanofibres of the polymer PEDOT worked effectively in a microscale MFC based on *Shewanella oneidensis* [76], a device which produced a peak power density of around 2.25 µW cm$^{-2}$, with an anode chamber volume of 12 µl. Electrodes with micro- or nano-structuring can produce performance enhancements due to the increased area for electron transfer and biofilm formation, but the surface must be well-suited for biofilm growth.

At an intermediate size scale, microbial fuel cells can be used to generate power in marine environments. An anode buried in sediment under seawater is colonized by microbes, and if connected to a cathode immersed in the water above through a resistive load, power is generated [77] (figure 4(c)). Such a device can run for an extended period, and in 2001 was observed to give an average power of 2.8 µW cm$^{-2}$ at an output of 0.27 V over four and a half months. Later, similar systems were used to power a meteorological buoy, and it has been noted that they can operate for long periods without maintenance, potentially for years [78]. Recently a patent was filed for a device of this type that could be deployed remotely [79].

Microbial fuel cells utilize micro-organisms to generate electricity using a chemical fuel source. It is also possible to use microbes to generate chemical fuel using electricity, and the use of bioelectrochemical systems for electrosynthesis has been attracting increasing attention [80].

**4.2.2. Living photovoltaics**

Living photovoltaics contain cells (such as cyanobacteria) that harvest energy from sunlight and export electrons, generating a voltage/current. As these devices possess the ability to renew damaged components, they should be more durable than those counterparts based on isolated subcellular parts. As an example of a living photovoltaic system, when cyanobacteria are grown on the anode of a microbial fuel cell, the electrode acts as an extracellular electron acceptor, and a rapid increase in voltage is seen when the cell is exposed to light [4]. The voltage decreases dramatically when the light is switched off. The response to light of different wavelengths is consistent with the known properties of cyanobacterial light harvesting systems. A photovoltage is also seen from a naturally occurring consortium of organisms. Non-photosynthetic bacteria do produce a voltage in such an MFC, but the voltage produced is independent of illumination. It is important to note that various species of photosynthetic micro-organisms can be used in living photovoltaics including types of algae [81].

It was recently shown that the use of a flow cell could enhance the performance of cyanobacteria-based living photovoltaics [82]. Here, the cyanobacteria were exposed to light in one chamber and the electron transfer occurred in a second chamber. Careful design of the second chamber and the flow parameters also enabled elimination of the membrane that is usually used as a separator between the electrodes. This simplified fabrication and avoided one of the causes of biofouling.

It has also been demonstrated that it is possible to ‘print’ living photovoltaic systems using a modified HP inkjet printer, where cyanobacteria were incorporated into a ‘bioink’ and electrodes were printed using a conductive ink [83]. The solar cell was able to power small electronic devices, namely an LED or a simple digital clock. It also produced some current in the dark due to usage of internal reserves produced in the light. The combination of energy storage and electricity generation in the same device has the potential to reduce cost and complexity in comparison with systems based on a photovoltaic panel connected to a battery.

Despite considerable efforts by a number of groups, the efficiency and power output realized experimentally for living photovoltaics is thought to be considerably below the theoretical maximum [64, 84]. Results obtained up to 2015 were summarized in a review of that year [64], in a form not dissimilar to that of tables for conventional solar cells. The caveat here is that measurement conditions (e.g. illumination) for living photovoltaics differ between studies, whereas measurement techniques are standardized for non-biological technologies. A major challenge in the development of living photovoltaics is that the organisms typically being used have not evolved efficient mechanisms for extracellular electron transfer [64, 84]. Effort is being made accordingly to use synthetic biology to genetically re-engineer some of these organisms, for example by expressing elements of the *Shewanella* electron transport system in other organisms such as *E. coli* and cyanobacteria [84].
In an alternative approach, a system was recently presented in which two engineered micro-organisms worked together to harvest light and produce current [85]. The cyanobacterium *Synechococcus elongatus* used solar energy to produce D-lactate, which was used as a metabolite by *Shewanella oneidensis*, the organism responsible for exporting electrons. When lactate production and electron export were separated both spatially and temporally, it was possible to obtain power for tens of days at levels up to about 20 µW cm$^{-2}$.

4.2.3. Plant microbial fuel cells

Electrical power can also be extracted from plant microbial fuel cells (figure 4(d)). Green plants undergo photosynthesis as described in section 3.2.1, and ultimately use energy from light to produce carbon-containing compounds such as glucose from carbon dioxide and water. A significant quantity of carbon is released by the plants into the medium in which they grow, as a result of secretion, cell death and other phenomena. This carbon can be metabolized by bacteria, which can export electrons that can be used to produce current in an external circuit. In one such plant microbial fuel cell, rice plants grew in a matrix in which anodes had been embedded [86]. The cathode was placed in the water layer above the growth matrix. The matrix had been inoculated with bacteria, and the reactors were kept for a period of months in a greenhouse, under lamps that provided a 16 hour day and an 8 hour night. The temperature was variable. Different growth matrices were tested. The power extracted was a factor of 7 higher in the plant-MFCs than in systems without plants. After an incubation period of 3–4 months, the plant-MFCs started to produce current. During the period of current generation, the average power produced over representative stable periods was 3.3 µW cm$^{-2}$ (anode geometric area).

Another plant MFC was based on *Spartina anglica* [87], which grows in salt marshes. In this case, the anode consisted of a bed of biofilm-covered graphite granules, in which the plant grew. The cathode was made from graphite felt and light was provided for 14 hours per day at a fixed illumination level. Duplicate plant-MFCs were tested, alongside blanks (control systems without plants). After an incubation period of 3–4 months, the plant-MFCs started to produce current. During the period of current generation, the average power was about 1–2 µW cm$^{-2}$ while no significant current was generated from the blanks. Power increased when ferricyanide was added. When the bacteria in a plant-MFC based on *Spartina anglica* were analysed, it was found that the most abundant types were *Proteobacteria* [88]. It is important to note that the use of a salt marsh plant in a plant-MFC would enable deployment of the technology on land that is not cultivated for agricultural purposes [87].

The term ‘vascular plant bio-voltaics’ has also been applied to the plant-MFC technology [89]. Different plants give different results; for instance, when plant-MFCs were made using either the rice species *Oryza sativa* or the weed *Echinochloa glabrescens*, which commonly invades rice paddies, it was found that the rice-based system produced around ten times the power of the weed-based version [89]. In this case, the plant-MFCs were not inoculated with bacteria, and relied on self-forming communities.

For practical use of plant microbial fuel cells outside the laboratory, it will be necessary to ensure long-term operation, and the ability to withstand changing weather conditions. In one study a plant-MFC was deployed on a roof, but the plants did not survive the winter [90]. Indoor plants can also be used [91]. As a demonstration of how a plant-MFC could be used, a concept design was produced for a table incorporating such a system based on moss (the ‘Moss Table’) [92]. Although the lamp in the table was not in fact powered by electricity generated biologically, the Moss Table was intended to demonstrate how technology like this could be used in the future.

As an aside, in connection with the use of plants in electrosynbionic devices, it is interesting to note that conductive materials have been synthesized in living plants, to make wires and capacitors [93].

4.3. The artificial leaf

As an alternative to the direct use of biological organisms and sub-cellular components for harvesting solar energy, it is possible to adopt a biomimetic approach, using entirely inorganic solid state materials. This led to the creation of the ‘artificial leaf’, a device based on a silicon photovoltaic cell coated with catalysts that evolve hydrogen or oxygen [94, 95]. This system produces hydrogen and oxygen by using solar energy to split water. It can use water from a variety of sources, does not require wires, and operates under benign conditions. It has been suggested that this type of system could be particularly advantageous in the developing world.

4.4. Borrowing bacteriorhodopsin

Bacteriorhodopsin and its relatives have attracted considerable interest for the purpose of novel photovoltaics and other optoelectronic systems. Bacteriorhodopsin is usually described as very stable i.e. more stable than chloroplasts. If this is correct, using such a molecule could provide a way to use a biological light harvesting agent without introducing the complexities of a living system and with fewer difficulties with long-term stability than for isolated chloroplasts, thylakoids and photosystems. Bacteriorhodopsin can be reconstituted in a lipid membrane for photoelectric measurements, and a photocurrent is seen [96]. Fragments of bacteriorhodopsin-loaded purple membrane can also be embedded in synthetic materials, for which the photovoltaic properties can be measured. In an early study (in the 1980s), it was stated that the efficiency of energy conversion from one such membrane was approximately 0.5% but this could be improved by
the use of better techniques for ensuring the correct orientation of bacteriorhodopsin [97].

In 2009, a patent application was filed for ‘protein-based photovoltaics and methods of use’ [98]. In this invention, one or more oriented layers of bacteriorhodopsin molecules pump protons from the vicinity of one electrode to the vicinity of the other, creating a gradient (figure 4(e)). Hydrogen is generated at the electrode that has a surplus of protons, drawing electrons through the external circuit from the other electrode, where oxygen is generated. The hydrogen and oxygen can be used to produce electricity. The patent also covers variants based on other types of rhodopsin, including mutants that pump chloride ions instead of protons, and notes that it is possible to prepare mutants with an enhanced ability to bind to substrates. The patent was granted in 2015.

As a variant on this theme, some groups have developed a bacteriorhodopsin-based version of the dye-sensitized solar cell described above, where bacteriorhodopsin replaces the dye [99].

4.5. Electric eel batteries

Studies of electric eels/rays and other examples of physiological electricity provided inspiration for the development of the earliest batteries [100]. It was in 1775 that Henry Cavendish gave to the Royal Society ‘An Account of Some Attempts to imitate the Effects of the Torpedo [electric ray] by Electricity’ [101]. Electric fish have continued to inspire us into the twenty-first century. For example, it has been suggested that a biobattery could be made using synthetic cells that act somewhat like electrolytes, consisting of self-assembled structures enclosed by phospholipid bilayers or equivalent, with embedded ion channels [102].

Recently, a hydrogel-based analogue of an electric organ was constructed [27], in which gel droplets were used to mimic electrolytes (figure 4(f)). The gels were modified chemically to make them selective for different types of ion. In the initial configuration, the droplets were isolated and the concentration of salt varied between droplets. When the droplets were placed in contact, ions could move between them, down the concentration gradient, moderated by the selectivity of the gels. A potential difference was established between the terminal gels, which was then measured as the open-circuit voltage.

5. Discussion

As described above, there are many instances of biological molecules and systems being re-engineered to form the basis of new technologies with electrical applications, or biological phenomena being used as inspiration for new devices. However no overarching term has previously been suggested to cover these endeavours, the term bioelectronics normally being reserved for biosensors etc. I propose that the community should rebrand the technologies described in section 4 (and similar ones yet to be developed) as ‘electrosynbionics’. This term captures the key elements of this emerging area, and the synthetic nature of the devices is central.

In addition to rebranding, a more systematic approach may be needed, with the adoption of testing and measurement methods similar to those developed in engineering and physics laboratories for conventional devices. For example, electrosynbionic solar cells should be tested using solar simulators, using controlled conditions, as is standard for non-biological devices. While this approach has been adopted in some papers, it is far from universal. Properties of electrosynbionic devices should be measured and specified in a manner that enables reliable comparison to existing technologies, to enable competitiveness to be determined.

At present the comparison is likely to be unfavourable to electrosynbionic technologies, which are mostly at low technology readiness levels. At the moment, most devices have short lifetimes and low energy output, and major unanswered questions remain over their long-term competitiveness. However, further investment would be likely to lead to major developments in the field, and could even drive a paradigm shift as the full potential of semi-biological and bio-inspired systems is realized, particularly as they offer the opportunity to generate and store electricity in the same device, with the advantages of cost and simplicity.

The critical challenges to be addressed are the efficiency of generating or storing electricity, and the lifetime or stability of biological components. The first of these two challenges could be addressed by systematic design and exhaustive experimentation, while the latter is likely to be more difficult to overcome. For some technologies the answer may lie in living systems that self-renew, replacing elements that wear out. However, in other cases, this will introduce more difficulties than it solves, and it will be necessary to replace some biological components with solid state analogues, to produce hybrid devices and capture the best of both worlds. There will be significant questions to be answered about how to construct the interface between the biological and the non-biological parts, and insights in this domain may also advance areas other than electrosynbionics [54].

If the challenges can be addressed successfully, it will be possible to exploit the unique advantages of biological and bio-inspired systems. Many biological processes are characterized by excellent energy efficiency, operating near to the limits set by thermodynamics, and where there is scope for improvement this can be addressed by exploiting the capabilities of synthetic biology and genetic engineering, potentially making electrosynbionic technologies more competitive [84, 103]. The functionality of biosystems is usually underpinned by intricate molecular structures, which can be utilized to organize functional groups at the nanoscale. The specificity of biomolecular interactions allows precise targeting mechanisms to be designed, while the function of biological parts can be altered
by deliberate changes to their structure. The operating and storage conditions for biological systems are usually benign, which facilitates handling. In contrast, the process of cleaning silicon wafers involves the use of some of the most dangerous chemicals ever used in laboratories, such as hydrofluoric acid.

There are great opportunities in the energy sector as new and better technologies are sought to make electricity generation and storage cleaner and cheaper. The market for electricity generation, storage and supply is huge [1] and it is possible that in the future electroosymbionic systems will be part of the energy landscape, but a great deal of work remains before these approaches will be commercially viable.

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