



Review

Weak electricigens: A new avenue for bioelectrochemical research

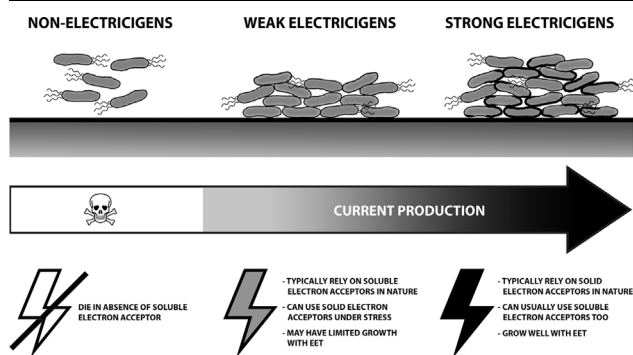
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GRAPHICAL ABSTRACT



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ABSTRACT

Electroactivity appears to be a phylogenetically diverse trait independent of cell wall classification, with both Gram-negative and Gram-positive electricigens reported. While numerous electricigens have been observed, the majority of research focuses on a select group of highly electroactive species. Under favorable conditions, many microorganisms can be considered electroactive, either through their own mechanisms or exogenously-added mediators, producing a weak current. Such microbes should not be dismissed based on their modest electroactivity. Rather, they may be key to understanding what drives extracellular electron transfer in response to transient limitations of electron acceptor or donor, with implications for the study of pathogens and industrial bioprocesses. Due to their low electroactivity, such populations are difficult to grow in bioelectrochemical systems and characterise with electrochemistry. Here, a critical review of recent research on weak electricigens is provided, with a focus on the methodology and the overall relevance to microbial ecology and bioelectrochemical systems.

1. Introduction

Microorganisms capable of electronically interacting with conductive surfaces have been described by various names; electroactive microorganisms, exoelectrogens, electric bacteria and electricigens, as they will be referred here (Koch & Harnisch, 2016; Logan, 2009; Lovley, 2006; Nealson, 2017). Electricigens are defined by their ability to carry

out extracellular electron transfer (EET). As the name hints, EET involves the movement of electrons between the internal cellular environment and a conductive solid beyond the cell boundary, which can act as either an electron acceptor or donor. The conductive solid usually takes the form of either an electrode, as is common in the laboratory, or a metal, which typifies the natural environment that has driven the evolution of this mode of respiration (Lovley, 2008). EET can be viewed

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as a survival strategy employed when soluble electron acceptors or donors are not available at sufficient concentrations, thus enabling biomass synthesis and/or cellular maintenance to proceed (Hernandez & Newman, 2001). EET can occur under both anodic conditions (the electrode/metal is reduced) and cathodic conditions (the electrode/metal is oxidised). Most studies refer to anodic EET, as this mode is common among electricigens and is easily observed in short-term experiments. Conversely, cathodic EET was only reported after the discovery of anodic EET (Gregory et al., 2004), is much less frequent, and is characterised by slow kinetics (Liu et al., 2014).

Both anodic and cathodic EET are facilitated by a number of specific mechanisms (Schroder et al., 2015), with electricigens typically employing one or more at a time. Focusing on the anodic flow of electrons from the interior to the exterior of the cell: direct electron transfer (DET) is the movement of electrons across outer-membrane proteins, typically c-type cytochromes, to a solid external electron acceptor (Okamoto et al., 2011). A related mechanism is the conduction of electrons across pilus-like appendages termed nanowires, which extend from the cell membrane and close the distance between the cell and the external electron acceptor (Reguera et al., 2005; Reguera et al., 2006). The reader is referred to a recent comprehensive review by Lovley (2017) on this topic. Finally, the last described mechanism is mediated electron transfer (MET), whereby the cell secretes soluble redox shuttles that carry electrons to a nearby acceptor and diffuse back to the cell upon oxidation, facilitating a revolving door strategy of electron transport (Marsili et al., 2008; von Canstein et al., 2008; Wang et al., 2010). Recent research shows that the lines distinguishing these three modes of EET are somewhat fuzzy, as intermediate strategies such as adsorption of redox mediators to the cell surface (Okamoto et al., 2013) or immobilisation of mediators in the biofilm matrix (Xiao & Zhao, 2017) are also possible. For example, x-ray crystallography of key outer membrane multiheme cytochromes from *Shewanella* has unveiled not only intramolecular electron transfer pathways, but also the interaction between flavins and the cytochromes (Edwards et al., 2017). While DET, MET and nanowires are the main modes of EET described to date, it is important to note that these findings may not be exhaustive, and could be a consequence of the narrow range of electricigens discovered, with a recent review identifying 94 species described to date (Koch & Harnisch, 2016). Several reports suggest that the electricigens are much more abundant in nature (Cournet et al., 2010) and are present in most ecosystems (Chabert et al., 2015). In spite of this predicted and observed abundance of electricigens, the majority of in-depth bioelectrochemical studies still focus on strong electricigens present in niche environments, with little mechanistic insight available for the majority of alternative electricigens discovered. This trend is likely due to the initially envisioned application of electricigens in microbial fuel cells (MFCs), where strong current producers are highly desirable to maximise power output. However, as researchers have gradually relaxed this criterion, other electricigens have raised interest for their biotechnological and even biomedical applications. In this review, the recent developments in electricigen enrichment and characterisation are summarised, with particular regard to weakly electroactive populations and communities, who may find application in bioprocesses, biosensors and bioremediation; paths related to, but distinct from, the traditional power generation envisioned for strong electricigens.

2. Strong vs. weak electricigens

A previous review (Doyle & Marsili, 2015) identified enrichment conditions as a possible reason for the relative lack of diversity seen in microbes capable of EET. The authors would here like to further build upon that discussion by suggesting that screening protocols may also play a large part in underestimating electricigen abundance in a culture, as strains producing a low current may quickly be ruled out. From an applied perspective, this elitist approach to quantifying electroactivity makes sense; the more efficient the microorganism at

converting organic matter to current, the more interesting it may prove to the researcher or engineer keen to develop MFCs. However, this approach limits observation of what can be termed weak electricigens; microbes engaging in EET on a smaller scale.

There is not yet an agreed definition of weak electricigens. However, viewing electroactivity as existing along a spectrum may be a good starting point. On the extreme end lay non-electricigens, who die in the absence of a soluble electron acceptor. Beyond this are weak electricigens, who typically rely on soluble electron acceptors in their natural environment, but who can avail of solid electron acceptors while under stress, likely with an associated limitation in growth during this mode of respiration. Finally, at the other extreme end lay strong electricigens. These species typically rely on solid electron acceptors in their environment, growing well under such conditions, and can usually avail of soluble acceptors if required. Operatively, a microorganism can be classed as a weak electricigen if it produces a small current or has low coulombic efficiency (CE). Small, in this case, is relative, as even between the strongest electricigens, *Geobacter* and *Shewanella*, a large difference in current production is seen. As *Geobacter* can produce up to 10 times the current of *Shewanella*, the genus can be viewed at the extreme end of the electricigen spectrum. Therefore, *Shewanella* can be taken as a fair reference point, with weak electricigens deemed as delivering a 10-fold smaller comparative current. However, as current production and CE depend on a multitude of parameters, such as electrode size, carbon source and the extent an anaerobic environment is maintained, the authors have opted not to provide specific cut-off numbers which separate the strong from the weak.

This difference in electroactivity between *Geobacter* and *Shewanella* may be indicative of the important physiological conditions that drive EET. *Geobacter* is a strict anaerobe that can use oxidised metals as its sole electron acceptor indefinitely (Caccavo et al., 1994; Lovley et al., 1993). It is likely that the more a species avails of oxygen as its terminal electron acceptor, the less efficient it will be at performing EET. In spite of being conducive to a relatively high level of electroactivity, strict anaerobic conditions are often accompanied by slow growth rates that could pose challenges in real-world applications, e.g., generating sufficient biomass to provide a time-sensitive signal in a biosensor. This may not be a limitation of weak electricigens, who are by definition not as specialised and therefore likely to grow more easily in a range of different environments. As an extension of this, weak electricigens may be able to compensate for a specific metabolic shortcoming of a strong electricigen, enabling a more stable bioprocess in the context of a mixed community.

In contrast, *Shewanella*, a facultative anaerobe with a diverse metabolism (Ong et al., 2014) and easily amenable to genetic manipulation on the lab bench (Coursolle & Gralnick, 2012), is an example of a much less fastidious electricigen. As the deep ocean serves as a common habitat to this genus, psychrophilic (Zhao et al., 2006), thermophilic (Ghosh et al., 2003) and piezophilic (Toffin et al., 2004) strains have been reported, indicating broad metabolic capabilities at the aerobic/anaerobic interface. Nonetheless, weak electricigens likely have an even broader metabolic diversity and, despite their small current output, warrant further investigation in order to develop novel EET-based devices. In pure culture, industrial applications using this niche of weak electricigens may still be challenging due to the inherent inefficiency of their electron transfer. However, in the absence of a strong counterpart, they may prove very useful.

It must be noted that there is always a trade-off by generalists; the weak electricigen may well be a “jack of all trades”, but might not be considered a master of any, and therefore will likely not thrive while forced to carry out EET, with benefits for the cell itself open to discussion (Koch & Harnisch, 2016). Indeed, one possibility worth exploring is that certain weak electricigens engaging in EET may merely be able to survive, and not divide, during these conditions, enabling cell maintenance but not biomass production.

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