BACTERIAL PHYSIOLOGY

Exporting electrons

> a previously unknown flavin-based electron-transfer pathway that is relevant across diverse environments

In anaerobic environments, microorganisms can use metal ions within minerals as terminal electron acceptors for respiration. However, as the microbial cell envelope is not permeable to minerals, microorganisms exchange electrons with extracellular minerals in a process termed microbial extracellular electron transfer (EET), which involves the transfer of electrons from the cytoplasmic membrane to minerals outside the cell via redox proteins.

For example, in metal-reducing microorganisms, such as the Gram-negative bacterium *Shewanella oneidensis*, the EET pathway involves the transfer of an electron from NADH to a quinone molecule via an inner membrane-associated NADH dehydrogenase, and subsequent transfer of the electron to protein-associated haem groups to cross the periplasm and outer membrane, and, ultimately to extracellular minerals that contain Fe^{3+}. Previously, it was reported that the Gram-positive bacterium *Listeria monocytogenes* possesses the ability to reduce extracellular Fe^{3+}; however, the existence and mechanism of such an EET system remained unknown. In this study, Light et al. identify a novel and simple electron transport chain in *L. monocytogenes*, whereby electrons are transported from intracellular NADH to quinone and subsequently via an extracellular flavoprotein to a terminal electron acceptor.

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The authors used a forward genetic screen to identify *L. monocytogenes* mutants with reduced Fe^{3+} reductase and electrochemical activity, which revealed a previously uncharacterized genetic locus associated with EET activity. One of the genes in this locus encodes a novel NADH dehydrogenase, termed Ndh2, which catalyses the electron transfer from NADH to a membrane-localized demethylmenaquinone derivative. During aerobic respiration, *L. monocytogenes* uses Ndh1 to transfer electrons to a menaquinone derivative, and the authors suggest that NADH dehydrogenases might channel electrons to distinct quinone derivatives to promote either EET or aerobic respiration. Next, the authors investigated the downstream electron-transfer pathway from the quinone pool to extracellular electron acceptors. They showed that FmnB, which posesses flavin mononucleotide (FMN) transferase activity (also encoded in the EET locus), post-transcriptionally modifies the extracellular-surface-associated PplA protein. On the basis of their findings the authors propose that electrons are transferred from a quinone derivative to the flavoprotein PplA or free flavin shuttles, possibly via uncharacterized membrane proteins encoded in the EET locus. The terminal electron acceptor remains to be determined, although the authors show that ferric iron is sufficient. Thus, in contrast to mineral-respiring Gram-negative bacteria, which use intricate haem-based electron transfer mechanisms, electron transport in *L. monocytogenes* is characterized by fewer electron transfer steps, which might be owing to their single-membrane architecture.

The authors went on to show that colonization of the mouse gut by mutant strains that were deficient in EET was decreased compared to wild-type strains, which suggests that EET supports anaerobic growth and confers a competitive advantage in this niche.

Finally, the authors identified orthologues of the genes responsible for EET across the Firmicutes phylum, including pathogens and commensal members of the intestinal microbiota, which suggest that this mode of electron transport is widespread in bacteria that occupy various ecological niches.

In summary, this study describes a previously unknown flavin-based electron-transfer pathway that is relevant across diverse environments.

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ORIGINAL ARTICLE Light, S. H. et al. A flavin-based extracellular electron transfer mechanism in diverse Gram-positive bacteria. *Nature* https://doi.org/10.1038/s41586-018-0498-z (2018)

FURTHER READING Shi, L. et al. Extracellular electron transfer mechanisms between micro-organisms and minerals. *Nat. Rev. Microbiol.* **14**, 651–662 (2016)