Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Biotechnology

Bacterial chemotaxis to xenobiotic chemicals and naturally-occurring analogs

Rebecca E Parales[1], Rita A Luu[1], Jonathan G Hughes[1] and Jayna L Ditty[2]

The study of chemotaxis to xenobiotic chemicals in soil bacteria has revealed that the core mechanism for transduction of chemotactic signals is conserved. Responses to chemicals degraded by specialized catabolic pathways are often coordinately regulated with degradation genes, and in some cases auxiliary processes such as transport are integrated into the sensory process. In addition, degradation genes and associated chemotaxis genes carried on transmissible plasmids may facilitate the dissemination and evolution of catabolic and sensory systems. However, the strategies and receptors used by bacteria to sense chemicals are difficult to predict solely by bioinformatics, and much work is needed to uncover the range of chemicals detected and the specific functions of the numerous chemoreceptors present in catabolically versatile soil bacteria.

Addresses
[1] Department of Microbiology and Molecular Genetics, College of Biological Sciences, University of California, Davis, CA, United States
[2] Department of Biology, University of St. Thomas, St. Paul, MN, United States

Corresponding author: Parales, Rebecca E (reparales@ucdavis.edu)

Current Opinion in Biotechnology 2015, **33**:318–326

This review comes from a themed issue on **Environmental biotechnology**

Edited by **Spiros N Agathos** and **Nico Boon**

For a complete overview see the Issue and the Editorial

Available online 15th April 2015

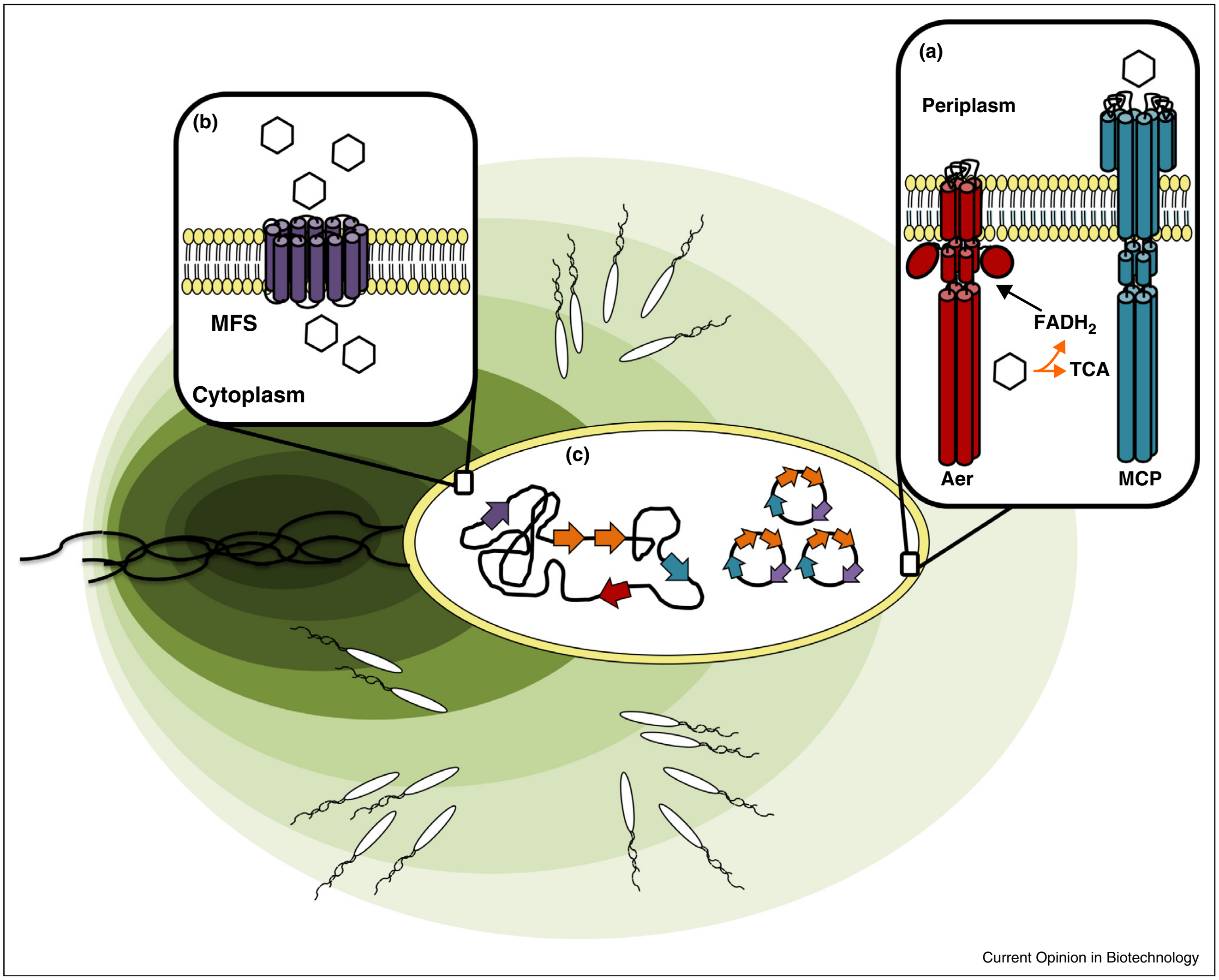
http://dx.doi.org/10.1016/j.copbio.2015.03.017

Introduction

An influx of xenobiotic compounds into the environment has occurred over the last hundred years as a result of industrial and agricultural processes. Xenobiotics are compounds, often of abiotic or manmade origin, that are found at levels higher than would be expected to occur naturally within an ecosystem. Xenobiotic chemicals include synthetic products, such as pesticides, dyes, pharmaceuticals and munitions. Naturally-occurring chemicals that are artificially introduced into an ecosystem, such as components of crude oil or its products, or unusually high levels of biologically-produced chemicals and/or their breakdown products can also be considered xenobiotic. Many bacterial strains that are capable of degrading a wide range of xenobiotic chemicals have been isolated, and many of these microorganisms also exhibit chemotaxis toward the compounds they are capable of utilizing [1–3]. Chemotaxis is the mechanism by which bacteria temporally detect chemical gradients and swim toward higher concentrations of attractants or lower concentrations of repellents. Although there are minor variations, the core mechanism for the transduction of chemotactic signals is conserved throughout the *Bacteria* and *Archaea* [4]. Chemicals are sensed by cytoplasmic membrane-bound receptors that affect the autophosphorylation rate of the CheA/CheY two-component regulatory system, altering the direction of flagellar rotation and modulating swimming behavior [5].

Chemotaxis has been well studied in *Escherichia coli*, but recent work has shown that the *E. coli* chemosensory system reflects only a small fraction of the diversity of bacterial chemotactic responses. Simple sugars and amino acids are the primary attractants for *E. coli*, whereas in soil bacteria, a much wider range of attractants has been documented [1–3]. This diversity of attractants correlates with the greater numbers and diversity of receptors present, and reflects the more omnivorous catabolic capabilities in bacteria such as the pseudomonads, compared to *E. coli* [6–8]. The receptors necessary to sense xenobiotic compounds have likely evolved from existing chemoreceptors that detect structurally similar chemicals [9,10]. Aromatic compounds are commonly produced by plants, and are ubiquitous in soil environments [11,12]. Evidence is beginning to accumulate that bacteria capable of exhibiting chemotaxis to naturally occurring compounds can also recognize similar compounds, such as those that are nitro-substituted or halogen-substituted aromatics [13–15]. What is becoming increasingly clear is that the specific receptors used by bacteria to sense particular chemicals, and whether those chemicals are sensed directly or indirectly, cannot be predicted based on receptor sequences. In addition, some sensory systems are intimately linked with metabolism and transport, and in some cases involve genetic elements outside the main chromosome (Figure 1). Here, we summarize recent work that has focused on identifying and characterizing bacterial responses to xenobiotic compounds and their natural analogs.

Figure 1



Simplified representation of interconnected physiological pathways important for chemotaxis to xenobiotics and natural analogs in a generic gram-negative soil-dwelling bacterial species. Concentric green-shaded circles represent an environmental chemoattractant (or repellent) gradient. **(a)** Types of cytoplasmic membrane-bound chemoreceptors known to play a role in the detection of xenobiotics. Classical methyl-accepting chemotaxis proteins (MCPs) directly detect chemoattractants that enter the periplasm to elicit the behavioral response. Other compounds are indirectly detected via energy taxis receptors such as Aer, which sense the FAD/FADH$_2$ ratio resulting from catabolism. **(b)** A key aspect of metabolism-dependent detection of some chemoattractants is efficient transport of charged substrates across the cytoplasmic membrane. **(c)** Chemotaxis of bacteria to sources of pollutant contamination may increase the possibility of catabolic plasmid transfer. Since genes encoding degradation pathway enzymes, chemoreceptors, and transporters are sometimes carried on catabolic plasmids, horizontal transfer of such plasmids may increase the repertoire of chemicals sensed as chemoattractants as well as the range of chemicals a bacterium is capable of degrading. Evolution has resulted in a variety of chemotaxis pathways for the detection of xenobiotic compounds, involving physiological processes for direct detection, active transport, and metabolism. This diversity emphasizes the importance of environmental sensing in the search for optimal niches under the continuously changing conditions of the soil environment.

Receptor-mediated chemotaxis

Although the chemotaxis signaling pathway is well conserved among motile bacteria, the numbers and types of methyl-accepting chemotaxis proteins (MCPs), which are typically membrane bound proteins responsible for the detection of extracellular signals, varies greatly between bacterial species. The presence of large numbers of MCPs in soil bacteria is thought to reflect their metabolic versatility and their ability to adapt to the complex environment in which they live. For example, *Pseudomonas* species have on average 33 MCPs [7]. Despite the wealth of MCPs found in soil bacteria, only a handful of chemoreceptors have been functionally characterized to bind pollutants or related chemicals (Figure 2).