Archaea on the move

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Chemotaxis, the ability to sense and respond to environmental stimuli, allows microorganisms to navigate chemical and physical gradients in natural systems. Chemical stimuli that can be sensed by microorganisms include variations in pH and osmolarity as well as concentrations of toxins and oxygen, whereas physical stimuli sensed by microorganisms include the intensity and wavelength of light (Wadhams and Armitage, 2004). More recently, hydrogenotrophic microorganisms have been shown to be able to sense the concentration of hydrogen (Brileya *et al.*, 2013). The ability to sense the environment is made possible by simple one-component (Ulrich *et al.*, 2005) and more complex two-component signal transduction systems (Stock *et al.*, 2000). A key difference between one- and two-component signal transduction systems is the location of the signals that are detected. One-component systems are thought to function primarily in detecting cytoplasmic signals, whereas two-component systems are thought to detect extracellular signals (Wuichet and Zhulin, 2010). One-component systems consist of a single protein that typically comprises a sensory and a regulatory domain, whereas two-component systems comprise two conserved proteins: a sensor and a response regulator.

Chemotaxis relies on a type of two-component signal transduction to both sense and bias movement in response to environmental stimuli. In *Escherichia coli*, chemosensing and taxis are accomplished by the activities of a receptor complex and a flagellar motor complex (Bren and Eisenbach, 2000). The receptor complex is a special case of a two-component system that in *E. coli* consists of seven different proteins including histidine kinase (CheA), a response regulator (CheY), as well as a methyltransferase (CheR) and methylesterase (CheB) (Wadhams and Armitage, 2004). CheA is connected to an array of transmembrane methyl group-accepting chemoreceptors through the docking protein CheW (Fig. 1). Activation of this signalling complex by stimuli induces the autophosphorylation of a histidine residue on CheA, and this phosphoryl group is then transferred to CheY or CheB, which 'compete' for phosphorylation.

Phosphorylated CheB has increased demethylation activ-ity of membrane receptors rendering them less effective at inducing CheA autophosphorylation. Transfer of the phosphoryl group to CheY results in its dissociation from CheA, allowing it to bind to a switch at the base of the flagellar motor, causing the flagellum to change the direction of rotation from counterclockwise (CCW) to clockwise (CW), which induces a change from 'run' to 'tumble' motion (Eisenbach, 1996). This results in an abrupt turning motion allowing the cell to change directions (Eisenbach, 1990). Finally the phosphatase CheZ catalyses the dephosphorylation of CheY allowing for signal termination and a return to CCW flagellar rotation (McEvoy *et al.*, 1999).

Homologues of the core chemotaxis machinery, as described above, have been identified in most bacterial genomes, but exhibit a patchy distribution among archaea and have yet to be discovered in eukarya. Evolutionary analyses of the core components of the chemotactic machinery reveal that it likely evolved from a simpler two-component system that was involved in regulating transcription (Wuichet and Zhulin, 2010). Moreover, it was found that while the core chemotaxis machinery is con-served (chemoreceptors, CheA, CheW), auxiliary func-tions appear to be routinely lost or substituted during evolution. This has led to a wide diversity in the configu-ration and function of chemotactic systems, which likely played a key role in allowing microorganisms to diversify into new ecological niches. Importantly, 'refinement' of the chemotaxis machinery through gene recruitment, loss and duplication events is far from unprecedented in biology. For example, our group has shown that the evo-lution of a number of protein systems including the Hg detoxification machinery mercuric reductase (Boyd and Barkay, 2012), the most primitive of the iron–sulfur biosynthesis pathways termed the sulfur formation pathway (Boyd *et al.*, 2014), and nitrogenase (Boyd *et al.*, 2015) have been adapted and refined from simpler systems. Adaptation and refinement of these complex protein systems from their more primitive precursors took place at a time that postdates the divergence of *Bacteria* and *Archaea* from their last universal common ancestor.
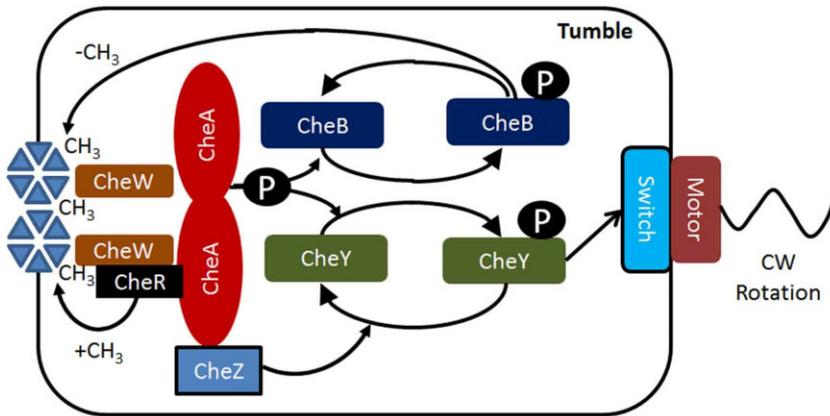
On page •• of this issue, Briegel and colleagues (2015) employ electron cryotomography (ECT) to characterize the structures of the membrane-bound and cytoplasmic chemoreceptor machinery that sense environmental stimuli and illicit taxis in four taxonomically diverse archaea. ECT images reveal chemoreceptors of remarkable resolution, which allowed for the order and packing of membrane-bound arrays to be compared with bacterial systems. Structural comparison of the membrane-bound and cytoplasmic chemoreceptor arrays revealed strong similarities between those from *Bacteria* and *Archaea*, implying that they share a common ancestor. Moreover, robust phylogenetic analysis of a concatenation of CheABR shows that this configuration of the chemotactic machinery was unlikely to be present in the last universal ancestor of *Archaea*, but rather was acquired via an early lateral gene transfer at a time that predates the divergence of the bacterial phyla *Firmicutes*, *Thermotogales* and *Synergistetes* (Briegel *et al*., 2015). By extension, this also suggests that these chemoreceptor arrays and chemotactic machinery were not a property of the last universal common ancestor of *Bacteria* and *Archaea*. These observations imply that the ability to sense and respond to environmental stimuli is a physiological trait that has been recently evolved when compared with numerous other physiological functions. In particular, the relatively recent acquisition of chemotactic machinery in *Archaea* makes it difficult to imagine how early *Archaea*, which lacked chemotactic ability, could have successfully competed with their chemotactic bacterial counterparts for available nutrients and niche space. Perhaps this is one explanation for why *Archaea* have been suggested to be restricted to ecological niches that impose chronic energy stress (Valentine, 2007). In such a scenario, the ability of

chemotactic *Bacteria* to outcompete *Archaea* for niche space with ample energy and nutrient sources relegated *Archaea* to adapt to niches with lower available energy or which impose higher maintenance energy (e.g. acid, saline or high-temperature environments).

Among the *Archaea*, chemotaxis systems were found to be present in euryarchaeotes (118 of the 178 available genomes) and thaumarchaeotes (2 of the 9 available genomes), but are absent from crenarchaeotes (51 genomes), korarchaeotes (1 genome) and nanoarchaeotes (1 genome). Phylogenetic data from Briegel and colleagues (2015) indicate that substantial diversification of *Archaea* had taken place prior to successful acquisition of chemotactic machinery in *Euryarchaeota*, with a second lateral gene transfer of the machinery from a euryarchaeote to a thaumarchaeote. Could the ability to sense and respond to environmental stimuli in *Euryarchaeota* be one reason for the substantially greater phylogenetic (and presumably ecological) diversity associated with this lineage when compared with the *Crenarchaeota*? Perhaps an answer to this question comes from a recent phylogenomics analysis of 1847 bacterial and 134 archaeal genomes, which indicates that the major radiations (phylum level) among *Archaea* were driven by gene acquisitions from *Bacteria* (Nelson-Sathi *et al*., 2015). Chemotactic machinery was not a focal point of the aforementioned study, but almost assuredly pro-moted the ecological expanse of *Euryarchaeota* and thus the successful evolutionary diversification of this lineage.

The ever-expanding genomic databases are now allowing researchers to ask broader questions regarding the taxonomic distribution and evolutionary history of target processes. In this regard, the work by Briegel and colleagues (2015) is no exception. One logical next step

would be to focus on the evolutionary history of chemoreceptors and to further develop understanding of the phylogenetic markers that demarcate classes of chemotaxis systems and to relate these to the types of stimuli that they sense (Wuichet and Zhulin, 2010). An expanded database of phylogenetic markers, when applied to metagenomics sequences that span environmental gradients, could provide intriguing new insights into the role of geochemical variation in shaping the evolutionary history of the ability of microorganisms to sense their environment. For example, one would not expect the chemosensors that respond to oxygen to have evolved prior to *Cyanobacteria*. Such receptors therefore may be useful in calibrating molecular phylogenies of chemoreceptors and for understanding the interplay between a changing environment, adaptations that allow organisms to sense particular components of their environment and the diversification of microbial life.

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