Published in final edited form as:

Trends Microbiol. 2015 May ; 23(5): 244–246. doi:10.1016/j.tim.2015.03.001.

A fantastic voyage for sliding bacteria

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Abstract

A recent study showed that *Salmonella enterica* serovar Typhimurium exhibits sliding motility under magnesium-limited conditions. Overall, bacteria that exhibit this passive surface movement described as sliding share few common traits. This discovery provides an opportunity to revisit and better characterize appendage-independent bacterial motility.

Keywords

sliding; gliding; swarming; motility; *Salmonella*

In 1972, Jørgen Henrichsen set definitions for several modes of bacterial surface translocation [1]. Five of the original six terms (swarming, swimming, gliding, twitching, and sliding) are still used widely today. (Darting is not commonly used to describe bacterial motility.)

Three of these motility modes, swimming, twitching, and swarming, require functional appendages. Swimming bacteria traverse liquid environments using their flagella, and twitching bacteria use their type IV pili as extension-retraction appendages to attach to points ahead and pull cells forward. Swarming bacteria move as groups of cells using their flagella through a thin liquid layer on semisolid surfaces. In fact, the cells of many swarming species elongate and/or hyperflagellate in some fashion. (Some have argued that flagellar-dependent surface motile bacteria that do not differentiate their cells are not truly ‘swarming’.) Nonetheless, the original Henrichsen definitions are routinely applied to describe these appendage-dependent motility modes.

Gliding and sliding motility are appendage independent. Figure 1 details some examples of appendage-independent bacterial motility. Certainly one aspect of the bacterial motility field that can be confusing is the evolving discussion of which behaviors and phenotypes are homologous with others. How much novelty is required to label a behavior as different when most of the research is conducted using *in vitro* laboratory assays with agar plates? Should we just default to calculate percent homology in regulatory genes to decide which motility

behaviors are, in fact, similar? Communicating research and ideas on gliding and sliding bacteria can be difficult because homology between systems is rare.

At present, bacterial gliding is best described in three bacterial clusters: the order Myxococcales, the phylum Bacteroidetes, and the genus *Mycoplasma* [2–4]. The hallmark gliding organisms of these three clusters are *Myxococcus xanthus*, *Flavobacterium johnsoniae*, and *Mycoplasma mobile*, respectively. These gliding bacteria do not utilize machinery that the field currently perceives as appendages. Unlike the strong homology that has been determined for flagellar or type IV pili components of swimming, swarming, and twitching bacteria, the motility machineries used by gliding bacteria all appear to be quite distinct. The regulatory elements and biochemistry that have been discerned for *M. xanthus*, *F. johnsoniae*, *M. mobile*, and otherwise, share no common homology outside of their respective clusters.

Besides a shared phenotype, the similarities of sliding bacteria are also unclear at present. However, a recent study by Park and colleagues, indicates that *Salmonella enterica* serovar Typhimurium should be included in the sliding bacteria discussion [5]. They show that *S. Typhimurium* exhibits a phenotype consistent with sliding when growing under low magnesium conditions on 0.2%–0.4% agar. Low magnesium induces PhoP/PhoQ, leading to production of the surface protein PagM, which was required for this sliding behavior. Indeed this behavior is notably distinct from flagellar swarming described for *S. Typhimurium* as PhoP represses expression of *S. Typhimurium* flagella. Additionally, this PagM-dependent motility of *S. Typhimurium* was achieved in the absence of glucose, a known requirement for traditional flagellar-dependent *Salmonella* swarming, and this sliding behavior was recapitulated in several mutants devoid of functional flagella. As this PagM-dependent behavior appears to create “special surface properties of the cells resulting in reduced friction between cell and substrate” [1] and occurs without any appendage, this seems to fit the Henrichsen definition of sliding. But are all sliding bacteria doing the same thing?

Escherichia coli and species of *Bacillus*, *Legionella*, *Mycobacterium*, *Pseudomonas*, *Sinorhizobium*, *Staphylococcus*, and *Vibrio* have all been characterized as exhibiting sliding motility. Some of these bacteria have motile appendages (or have the genes predicted to be needed) while others do not. It may be possible to discern the behavior of single cells and if a specific energy source is utilized during sliding for *S. Typhimurium* and these other sliding bacteria. This will be useful to determine those bacteria that are truly passive sliders versus those that may have (novel) active motility machinery. Perhaps some of these sliding bacteria should really be classified as gliding bacteria. For example, a mutation in the gene *cglF* can be complemented exogenously to restore gliding motility in *M. xanthus* [6] – this bears a resemblance to restoration of *S. Typhimurium* sliding in a *pagM* mutant with a *pagM*-expression strain [5].

At present, the ubiquity of this newly described PagM-dependent behavior is unclear; it may be highly specific to serovars of *Typhimurium* as other serovars are not known to possess the *pagM* gene. However, it will be interesting to determine if PagM is the endpoint, acting as a surfactant or osmolyte to improve spreading or perhaps even as a component of an

unknown active motor. It would be very useful to determine if *S. Typhimurium* or some of these other 'passive' sliding bacterial are, in fact, actively moving by a different mechanism.

Lastly, the environmental dependence of this new behavior of *S. Typhimurium* upon magnesium serves as a reminder that many bacterial behaviors are driven by a response to their environment. Several seminal papers on bacterial motility similarly began by detailing an environmental response [1]. These environmental cues are likely the input signal for many c-di-GMP intracellular signaling cascades that have recently been identified in numerous bacteria to suppress bacterial motility. Few of the external triggering molecules important for c-di-GMP signaling are known [7,8]. It is indeed quite interesting to determine what promotes these bacteria to embark on their fantastic voyages. There may be more similarities than we currently appreciate.

Acknowledgments

Many thanks to Lotte Sogaard-Andersen for helpful discussion. J.D.S. is supported by NIH grant 1R21AI109417-01A1.

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Figure 1.

Examples of appendage-independent motility and their known requirements. **(A)** Gliding bacteria: *Flavobacterium johnsoniae* (adapted from [2], with permission, from *Nat. Rev. Microbiol.*), *Mycobacterium mobile* (adapted from [4], with permission, from *Trends Microbiol.*), and *Myxococcus xanthus*. **(B)** Sliding bacteria: *Bacillus subtilis*, *Legionella pneumophila*, *Mycobacterium smegmatis*, *Salmonella enterica* serovar Typhimurium, *Sinorhizobium meliloti*, *Pseudomonas aeruginosa*, and *Vibrio cholerae*.