Surfing of bacterial droplets: *Bacillus subtilis* sliding revisited

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Hennes et al. (1) report on the collective slipping of *Bacillus subtilis* colonies across the agar surface, termed "colony surfing." We read this article with great interest. However, we understand that specific points require a more detailed discussion. We would like to highlight complementary biological observations on this area previously published by us and others but omitted by Hennes et al. (1) with the aim of bringing about a common terminology that facilitates understanding between the biophysics and the microbiology communities.

Bacterial movement on surfaces can be powered by various active appendages, such as flagella, pili, or interaction of cytoskeletal and focal membrane complexes, but can also be driven by passive factors (2–4). Hennes et al. (1) report that *B. subtilis* droplets surf down agar surfaces independently of the presence of flagella, by recruiting water from the environment to these moving colonies, lowering surface tension, and enhancing substrate wettability. Importantly, this process is demonstrated to be dependent on surfactin production.

Regarding the flagellum-independent movement of *B. subtilis*, we noticed that the biological aspects were poorly covered by Hennes et al. (1), despite the wealth of available experimental examples and scientific literature. *B. subtilis* engages in an already-known form of flagellum-independent, surface movement called "sliding." This has been analyzed over more than a decade and many publications are available in PubMed. Sliding is defined in microbiology as the passive surface translocation of bacteria driven by the growth of bacteria (commonly associated with the production of surfactant) and occurs in a wide range of species such as *B. subtilis* and *Mycobacterium smegmatis* (3, 4). Sliding of *B. subtilis* is dependent on surfactin and exopolysaccharide (EPS) in addition to hydrophobin protein (5–7). Confusingly, the terms droplet/colony surfing and sliding are intermingled by Hennes et al. (1), not following the previously established microbiology criteria (2).

In addition, Hennes et al. (1) highlight the presence of EPSs in the bacterial drop. EPSs are known to facilitate both colony biofilm expansion (8) and sliding by generating osmotic pressure in the extracellular space (6); however, these previous works are not mentioned.

Notably, movement is enabled when cell density in the bacterial droplets on sloped surfaces is lower than in sliding colonies. It seems likely that the effect of gravity pulling the droplets down distinguishes the seemingly simpler mechanism of contact line depinning in droplets from the complex cell–cell interactions present in sliding expansions.

In view of the available literature, and overlapping components, we therefore propose considering the finding of Hennes et al. (1) as a novel example of sliding motility (surfactant/EPS-dependent and flagella-independent mechanism of surface translocation) of low-density *B. subtilis* cells on a sloped surface. The Hennes et al. (1) paper is an interesting demonstration of the physical forces that need to be overcome for groups of bacteria to be able to move.

We hope that these additional observations will help to reduce confusion between the different fields and contribute to a clearer definition of the fascinating modes of bacterial movement.

1 Hennes M, Tailleur J, Charron G, Daerr A (2017) Active depinning of bacterial droplets: The collective surfing of *Bacillus subtilis*. *Proc Natl Acad Sci USA* 114:5958–5963.
2 Henrichsen J (1972) Bacterial surface translocation: A survey and a classification. *Bacteriol Rev* 36:478–503.
3 Kearns DB (2010) A field guide to bacterial swarming motility. *Nat Rev Microbiol* 8:634–644.
4 Hölscher T, Kovács ÁT (2017) Sliding on the surface: Bacterial spreading without an active motor. *Environ Microbiol* 19:2537–2545.
5 Kinsinger RF, Shirk MC, Fall R (2003) Rapid surface motility in *Bacillus subtilis* is dependent on extracellular surfactin and potassium ion. *J Bacteriol* 185:5627–5631.
6 Grau RR, et al. (2015) A duo of potassium-responsive histidine kinases govern the multicellular destiny of *Bacillus subtilis*. *MBio* 6:e00581.
7 van Gestel J, Vlamakis H, Kolter R (2015) From cell differentiation to cell collectives: *Bacillus subtilis* uses division of labor to migrate. *PLoS Biol* 13:e1002141.
8 Seminara A, et al. (2012) Osmotic spreading of *Bacillus subtilis* biofilms driven by an extracellular matrix. *Proc Natl Acad Sci USA* 109:1116–1121.

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