

SURPRISING HYDRODYNAMICS OF BACTERIA NEAR SURFACES

Debasish Das* and Eric Lauga

Department of Applied Mathematics and Theoretical Physics, Centre for Mathematical Sciences,
University of Cambridge, Wilberforce Road, Cambridge CB3 0WA, UK.

Summary Recent experiments [1] have shown that a sulfide-oxidizing bacterium named *T.majus* can transition from swimming in circles to a surface-bound state where it stops swimming while remaining free to move laterally along the surface. In this bound state, the cell rotates perpendicular to the surface with its flagella pointing away from it. Using simulations and theory, we demonstrate the existence of a fluid-structure interaction instability that causes cells with relatively short flagella to become surface bound [2]. In both the bound and dynamic states, we find that bacterium gets attracted to the wall consistent with far-field force dipole assumption [3]. However, on simply changing the shape of the cell body from a sphere *T.majus* to a prolate spheroid, relevant for cells such as *E.coli*, we find that the cell swims in circular trajectories but at a certain height above the surface.

INTRODUCTION

Bacteria are one of the most important life-forms on Earth. Being one of the first organisms to have appeared on the planet, they have evolved to thrive in a variety of environments. Peritrichous (multi-flagellated) bacteria, such as *T. majus* or *E. coli*, self-propel in fluids by using specialized rotary motors to rotate multiple helical filaments, enabling swimming of the whole cell. In the present work, we focus on the surface interactions mechanisms of bacteria such as *T. majus* that have a large spherical cell body compared to their flagellar length, in contrast with *E. coli* that have a relatively smaller but elongated prolate-spheroidal cell body.

In recent experiments, the swimming behavior of *T. majus* cells was studied near surfaces [1]. Quite surprisingly, it was found that instead of swimming along the surface in circles (as well established for many species), many freely swimming cells became dynamically surface-bound. In this bound state, cells remained free to move laterally along the surface and their bodies continuously rotated around their center in the direction perpendicular to the surface while their flagellar filaments pointed away from the surface, rotating in the opposite direction. The bound state is in stark contrast to the classical situation of bacteria swimming in circular paths near surfaces [4]. The question therefore arises regarding the mechanism at the origin of this transition to a bound state.

Mathematically, we define the cell to be in the surface-bound state when the flagellum axis is perpendicular to the surface, i.e. $\theta = \pi/2$ (Fig. 1), and consequently, the radius of circular trajectory is $R = 0$. In the bound state, a small perturbation in the tilt angle of the flagellum is expected to destabilize the cell

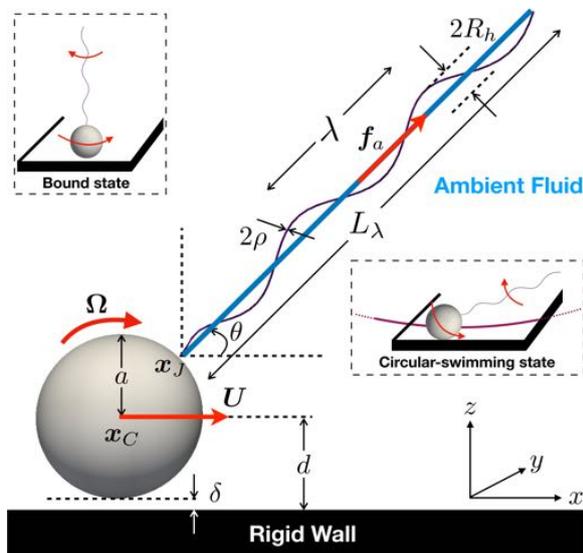


Figure 1: Schematic diagram of a flagellated bacterium swimming near a plane surface. The cell body is modeled as a rigid sphere (case of *T. majus* bacteria) or a prolate spheroid (*E. coli*) and the flagellar filament as a rigid right-handed (*T. majus*) or a left-handed (*E. coli*) helix rotating along its axis for the numerical simulations. The cell body undergoes rigid body translation and rotation at velocities \vec{U} and $\vec{\Omega}$, respectively. The flagellum tilt angle is denoted by θ . The two possible final steady states of a bacterium near a surface are shown as insets: surface-bound (top left) and circular swimming (bottom right).

and cause it to swim parallel to the surface in circles. What exactly makes this state stable? Using a combination of theory and simulations, we show that the transition from swimming to a bound state can be rationalized as an instability due to fluid-structure interaction. We then focus on the question: how does changing the shape of the cell body from a sphere to a prolate spheroid change these swimming dynamics near surfaces?

BIOMECHANICAL MODELING

The fluid dynamics of bacteria are described by the incompressible Stokes equations solved using a combination of slender body theory [5, 6] and boundary element method [7]. *T. majus* cells rotate in a counterclockwise direction when viewed from the posterior side, which motivates us to model the fraction of flagella on the cell-surface that cause propulsion bundled together as a single right-handed clockwise rotating helix in the numerics, or as a rigid active pushing rod for the theory (details of the theory can be found in Ref. [2]). This assumption holds particularly well for *E. coli* as their flagella are known to be in a bundled configuration when swimming. The cell body of *T. majus* is assumed to be a sphere of radius a , also chosen as the relevant length scale for the problem. For *E. coli* cells, we have an additional dimension for body width, $b = \alpha a$, where α is the cell body aspect ratio. The cell body is centered at x_C while the

*Corresponding author. E-mail: dd496@cam.ac.uk.

flagellum is attached to the cell body surface at the junction point, x_J (Fig. 1). The minimum distance between the cell-body surface and the plane rigid wall is δ and the distance between the center of the cell-body and the wall is $d = a + \delta$. The tilt angle of the flagellum measured with respect to the horizontal direction is denoted by θ , so that $\theta = \pi/2$ and $\theta \neq \pi/2$ correspond to surface-bound and circular-swimming state, respectively.

RESULTS AND CONCLUSIONS

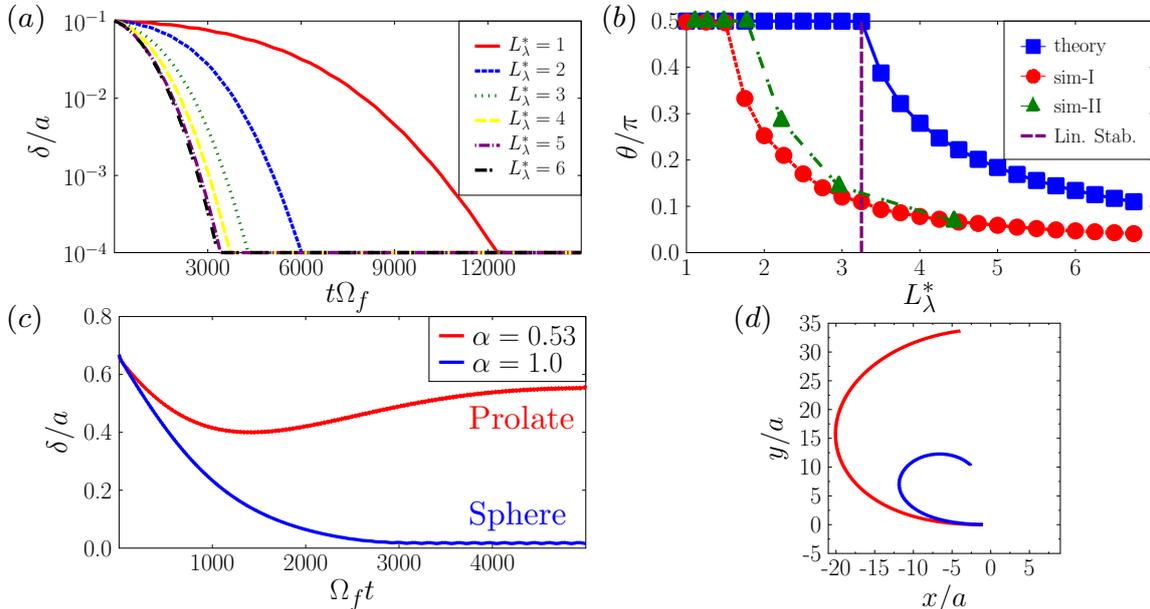


Figure 2: (a) Temporal evolution plot of δ/a for various flagellar lengths L_λ^* ; (b) Pitchfork bifurcation of the tilt angle, θ/π , plotted against the flagellum axial length, L_λ^* ; (c) temporal evolution of δ/a for a swimming bacterium with spherical and prolate-spheroidal cell body; (d) trajectories in the $x - y$ plane corresponding to (c).

In the numerical simulations, the cell body is placed at a distance $\delta^* = 0.1$ from the wall with its flagellar filament initially parallel to the wall ($\theta = 0$). The geometrical parameters of the flagellar filament are assumed to be similar to that of *E. coli*. In the first set of simulations (sim-I), the axial length of the filament is varied from $L_\lambda = 1.0 \mu\text{m}$ to $6.75 \mu\text{m}$ while the cell body radius is fixed at $a = 1 \mu\text{m}$. In the second set of simulations (sim-II), we fix the number of turns at $N = 2$ and axial length at $L_\lambda = 4.44 \mu\text{m}$ while the cell body radius is varied from $a = 1 \mu\text{m}$ to $4 \mu\text{m}$. We plot in Fig. 1a the dynamics of $\delta(t)$ for six values of the flagellum length, L_λ^* , for sim-I. In each case, the cell gets attracted to the wall regardless of the flagellar filament length. As the cell gets closer to the wall, the coupling between translation and rotation becomes stronger which causes the filament to tilt away from the wall, see Fig. 1b. This tendency to tilt away from the wall due to cell body-wall interaction is resisted by the viscous torque experienced by the translating flagella as well as an attractive torque that tends to align the helix parallel to the wall arising from helix-wall hydrodynamic interactions. As a result, the tilt angle reaches a dynamical steady state whose value depends on L_λ^* . Hence, a large ratio of cell body size to flagellar length can cause a transition from circular swimming along the surface to a bound state.

The results in Fig. 2a & b are obtained using a semi-analytical approach [2], while those in Fig. 2c & d are obtained using a full boundary element method. Here, we show next that on simply changing the shape of the cell body from a sphere (relevant for *T. majus*) to a prolate spheroid (relevant for *E. coli*), the cells swimming parallel to the surface in circular trajectories do so at a finite height above the surface of magnitude similar to the width of the body (Fig. 2(c)). The trajectories viewed from above the surface are shown in Fig. 2(d). This is a rather surprising result as bacteria are force-free organisms and, as force-dipoles swimming in a fluid medium, they should always be attracted towards no-slip surfaces [8]. Similar observations were made in a previous work [9] but only for $\alpha < 0.7$. The development of a simple mathematical model to explain these curious findings is under progress.

References

- [1] A. P. Petroff, X.-L. Wu, and A. Libchaber, Phys. Rev. Lett. **114**, 158102 (2015).
- [2] D. Das and E. Lauga, Phys. Rev. E **110**, 043117 (2019).
- [3] S. E. Spagnolie, E. Lauga, J. Fluid Mech. **700**, 105–147 (2012).
- [4] E. Lauga, W. R. DiLuzio, G. M. Whitesides, and H. A. Stone, Biophys. J. **90**, 400 (2006).
- [5] J. Dauparas, D. Das, and E. Lauga, Biomicrofluidics **12**, 014108 (2018).
- [6] E. E. Riley, D. Das, and E. Lauga, Sci. Rep. **8**, 10728 (2018).
- [7] D. Das and E. Lauga, Soft Matter **14**, 5955 (2018).
- [8] A. P. Berke, L. Turner, H. C. Berg and E. Lauga, Phys. Rev. Lett. **101**, 038102 (2008).
- [9] D. Giacche, T. Ishikawa and T. Yamaguchi, Phys. Rev. E **82**, 82, 056309 (2010).