

The locomotion of microorganism plays important roles in many biological processes including reproduction. Many microorganisms propel themselves by propagating traveling waves along their flagella. Depending on the species, propagation of planar waves (e.g. *Ceratium* and helical waves (e.g. *Trichomonas*) were observed in eukaryotic flagellar motion, and hydrodynamic models for both were proposed in the past. However, the motility of insect spermatozoa remains largely unexplored. An interesting morphological feature of such cells, first observed in *Tenebrio molitor* and *Bacillus rossius*, is the double helical deformation pattern along the flagella, which is characterized by the presence of two superimposed helical flagellar waves (one with a large amplitude and low frequency, and the other with a small amplitude and high frequency). Here we present the first hydrodynamic investigation of the locomotion of insect spermatozoa. Resolving hydrodynamic interactions with a non-local slender body theory, we predict the swimming dynamics of these superhelical swimmers based on experimentally collected geometric and kinematic data. We then compare our theoretical predictions with experimental measurements, and explore the dependence of the swimming performance on the geometric and dynamical parameters. Counter-intuitive results are revealed, particularly for the case when the minor and major helical structures are of opposing chirality.

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Effect of Reprogramming on Primary Cilia Mechanics

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The advent of human induced pluripotent stem cell (hiPSC) reprogramming has revolutionized the field of developmental biology. To realize the full potential of this promising technology, it is imperative to understand mechanical and chemical signaling pathways that coordinate the process of reprogramming. Primary cilia have been shown to play a critical role in mechano-chemical signaling across a wide spectrum of cell types, with major implications in maintaining homeostasis. Their functions in hiPSCs and their characteristic changes during the reprogramming process remain largely vague. This work focused on understanding how reprogramming affects the mechanical characteristics of primary cilia. Using immunofluorescence imaging assays and electron microscopy studies, we established for the first time the presence of primary cilia on fibroblasts derived hiPSCs. Using quantitative PCR assays, we identified changes of expression levels of pluripotency markers *Nanog* and *Cripto* as well as primary cilia signaling partners *Hh*, *Ptch1*, *Gli1*, *Gli2*, and *Gli3*. Furthermore, morphometric analysis revealed that reprogramming resulted in an increase in curvature of primary cilia from $\sim 0.16 \mu^{-1}$ to $\sim 0.78 \mu^{-1}$ ($p < 0.02$), indicating a significant change in Young's modulus ratio of at least 5-fold, and a decrease in the length of primary cilia from $\sim 2.64 \mu$ to $\sim 0.7 \mu$ ($p < 1.76 \times 10^{-13}$). Taken together, this was the first systematic study showing the presence of primary cilia on human reprogrammed cells and demonstrating significant effects of the reprogramming process on primary cilia mechanics.

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Twitching Flow Taxis Upstream Motility of Surface Attached Bacteria

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Twitching motility is a mechanism in which bacteria move about solid surfaces by repeatedly extending and retracting long extracellular filamentous structures known as pili. We investigated the effects of flow on *P. aeruginosa* cells and found that surface shear stress causes surface-attached *P. aeruginosa* cells to migrate against the flow direction while pivoting in a zig-zag motion. Because this directed motility depends on polar type IV pili and results from the effects of flow on the polar attachment of bacterial cells, we describe it as twitching flow-taxis. Finally, we examined the function of two molecular motors responsible for this motion and characterized their individual functions. Our results suggest a model in which there are two distinct modes of twitching motility.

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Microscopic Analysis of Bacterial Motility at High Pressure

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The bacterial flagellar motor is a molecular machine that converts ion flux to the rotation of a helical flagellar filament [1]. Its counterclockwise rotation allows several filaments to join in a bundle and propel the cell forward in solution. Loss of motility can be caused by environmental factors, such as temperature, pH and solvation. Hydrostatic pressure is also a physical inhibitor

of bacterial motility, but the detailed mechanism is still unknown. Here, we developed a novel assay that monitored the motility of *Escherichia coli* cells under various hydrostatic pressure conditions [2]. The fraction and speed of swimming cells decreased with increased pressure. At 80 MPa, all cells stopped swimming, and diffused in solution. After the release of pressure, most cells immediately recovered their initial motility. A rotating tethered cell assay demonstrated that single flagellar motors at 80 MPa rotated with $\sim 60\%$ of their initial speed, meaning that the motor still generates the torque at high pressure. The discrepancy between free swimming cells and tethered cells could be explained by that applied pressure inhibited the rapid motor rotation and/or change the helical structure of flagella.

[1] Sowa *et al.*, *Nature*. **437**: 916-919 (2005).

[2] Nishiyama *et al.*, *Biophys. J.* **96**: 1142-1150 (2009).

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Integrated Global and Local Field Sensing in *Magnetospirillum Magnetotacticum*

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The ability for organisms to evolve specialized functions is often correlated to unique intracellular structures, non-obvious to typical biological systems. One example is the biosynthesis of magnetic particles. Biology has evolved important magnetic sensing structures in a range of organisms from radula teeth in the chiton, algae, honeybees homing pigeons and humans. Unicellular organisms also have this ability in the case of magnetotactic bacteria, but here we show an even more intriguing finding, which is that *Magnetospirillum Magnetotacticum* strain AMB-1 have both a global sensing system for magnetic fields as well as a localize sensing that has intensity sensitivity. To investigate this global and local intensity based magnetic field response, permalloy microfabricated structures and a pair of Helmholtz coils were custom-built to induce localized control of the magnetotactic bacteria. In the global sense, at low fields these bacteria have the choice to follow the magnetic field lines or to meander around without following the magnetic field lines until about 11 Oe when about 90% of the bacteria seem to align with the field and thus begin to act as actuators rather than as biological sensors. When they were exposed to localize magnetic fields, these 2-3 micrometer organisms would deflect their motility paths to sense very small magnetic fields as well. Furthermore, when the AMB-1 sense local gradients, interestingly there is a bifurcation in response. Faster moving bacteria will deflect their direction based upon sensing local magnetic field gradients, but slower moving bacteria will either reverse their directions or perform multiple oscillations around specific sharp gradients and then continue swimming in the original direction. We believe that these results have implications ranging from synthetic biology to biologically inspired nanostructures to evolutionary biology.

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Synchronization of Swimming Microorganisms

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Some microorganisms, such as spermatozoa, have been observed to synchronize their flagella when swimming in close proximity. Using a two-dimensional model we show that phase-locking can arise from hydrodynamic forces alone. In a Newtonian fluid, as a consequence of the kinematic reversibility of the field equations, there must exist front-back asymmetry in the geometry of their flagellar waveform. The time-evolution of the phase difference between co-swimming cells depends only on the nature of this geometrical asymmetry, and microorganisms can phase-lock into conformations which minimize or maximize energy dissipation. In a viscoelastic fluid the presence of polymeric stresses removes the geometrical asymmetry constraint, and therefore even symmetric swimmers synchronize. Such synchronization occurs on asymptotically faster time scales than in a Newtonian fluid, and the swimmers evolve into a stable in-phase conformation minimizing the energy dissipated in the surrounding fluid. Furthermore, we show that if we consider flexible sheets, with internal symmetric forcing instead of prescribed kinematics, they deform when interacting with each other through the fluid in such a way as to systematically break the overall waveform symmetry, thereby always evolving to an in-phase conformation where energy dissipation is minimized. These dynamics are shown to be mathematically equivalent to those obtained for prescribed waveforms in viscoelastic fluids, emphasizing the crucial role of flexibility in symmetry-breaking and synchronization - be it that of the fluid, or the swimmers themselves.