

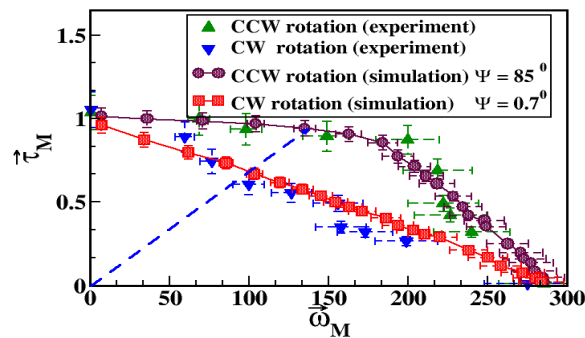
## Regulatory role of a flagellum in bacterial locomotion at low Reynold number

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A multi-flagellated bacterium such as *E. coli* performs its locomotion at low Reynold number through swimming or 'run' motion and idle or 'tumble' motion just by altering the orientation of its locomotive organ, flagellum. A flagellum is an assembly of a reversible rotary nano-motor called bacterial flagellar motor (BFM), a hook and a filament. In run motion, a flagellum rotates in the counter-clockwise (CCW) direction, while the hook bends and becomes flexible due to elasto-hydrodynamic instability. Consequently, flagella bundle together and a bacterium performs a directional swimming. In tumble motion, flagellum changes its rotational direction and its hook becomes straight and rigid; subsequently, flagella fly apart from each other to randomize the bacterial orientation. Basically, BFM is responsible for the rotation of a flagellum. Utilizing  $H^+/Na^+$  ions as fuel, a BFM rotates in both rotational modes due to the motor-torque generated for the stator-rotor interaction. The motor-torque is transmitted from BFM to filament through hook so that the flagellum rotates in the same rotational direction as that of a BFM. Experimentally, motor-torque and speed are measured by the bead-assay technique to understand how much torque is produced by a BFM to rotate a flagellum during locomotion. In experiment, torque versus angular speed (TS) relationships is established for various viscous loads for the CCW and CW rotational modes of a BFM. Following structural studies, it was expected that torque-speed relationships should be symmetric in both rotational modes, but these relationships are non-symmetrical with each other. The inherent reason of this asymmetry along with its role in the bacterial locomotion is unclear and has not been explored yet.

Proposing a detailed mechanistic model based on the bead-assay experiment, we resolve this contradiction and show that this asymmetry is a consequence of the coupling between the motor rotational dynamics and the conformational/stiffness changes of the hook due to rotational switching. Torque analysis illustrates that the bent hook generates revolution and spinning motions of the filament and bead. In CCW rotational mode, when the hook remains bent and flexible, the revolution motion predominates, whereas, in CW mode, the spinning motion dominates as the hook becomes straight and rigid. In both modes, the restoring torque for the dominated motions decides the shape of the TS relationships; and the hydrodynamic drag acting on the filament and bead induces these restoring torques. Our study reveals that a bacterium exhibits the precession motion of its flagellum during its locomotion instead of the previously considered spinning motion. The study also infers that a BFM exhibits more power output in CCW mode compared to its CW rotation, which may be due to the exhibition of the swimming capability of a bacterium in run motion. A previously unnoticed role of the hook *i.e.*, its behaviour as a clutch to modulate the transmission of the motor torque to the load, is also explored in this work. Our study illuminates the role of a BFM in bacterial locomotion and paves the way for further experimental exploration of the structural origin of such asymmetry.



Ref: B. Das, J. Xing, A. K. Sharma, and H. Ge, The asymmetric torque-speed relationships reveal that the universal hook functions as a clutch for a bacterial flagellar motor, under review in *Proc. Natl. Acad. Sci. (USA)*.