

# Dynamics of the bacterial flagellar motor with multiple stators

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**Short Abstract** — The bacterial flagellar motor drives the rotation of flagellar filaments and enables many species of bacteria to swim. A recent experiments [2] show that at near-zero load the speed of the motor is independent of the number of torque generating units. Here [1], we introduce a mathematical model of the motor dynamics that explains for this behavior. The model provides the microscopic explanation for the existence of two characteristic regimes in the torque-speed curves observed experimentally. It also predicts that the speed fluctuation for a single motor is determined by the number of steps per revolution at low load and is controlled by external noise for high load.

**Keywords** — torque–speed relationship, model, rotary, stepping statistics, speed fluctuation.

## I PURPOSE

THE swimming motion of bacterium *Escherichia coli* is propelled by the concerted rotational motion of its flagellar filaments (3,4). Each filament ( $\approx 10\mu\text{m}$  long) is driven by a rotatory motor embedded in the cell wall, with an angular speed of the order of 100Hz. The motor has one rotor and multiple stators in a circular ring-like structure of roughly 45nm in diameter. Torque is generated by interaction of stator units, anchored to the peptidoglycan cell wall, with the rotor. The motor can generate torques of more than  $10^3\text{pNnm}$  ( $250k_B T$ ). Each filament can be driven up to the speed of 300Hz, at energy consumption of only around  $10^{-16}\text{W}$ , with an estimated efficiency near 1. These high performances make this self-assembled nanomachine far better than the most sophisticated man-made motors.

The molecular details of the flagellar motor has been the subject of intense research (4) and its microscopic step-like motion was recently demonstrated by direct observation (5), but a general understanding of the stepping dynamics of a single flagellar motor is still lacking. The torque generate by the motor as function of the rotational speed of the flagella is the key characteristic of the motor. The measured torque-speed curve for bacterial flagellar motor shows two distinctive regimes. From its maximum value  $\tau_{\text{max}}$  at stall (zero angular velocity), the torque first falls slowly (by  $\approx 10\%$ ) as angular velocity increases at up to a large fraction ( $\approx 60\%$ ) of the maximum velocity, forming a plateau in the

torque speed curve. Then the torque starts to decrease quickly with increasing angular velocity, eventually approaching zero at the maximum velocity. Moreover, a recent experiment (2) shows that near-zero load the velocity of the motor is independent of the number of stators. Here, we aim at understanding both the torque-speed relationship and the individual motor dynamics by using a simple model describing the rotor’s mechanical motion and the stator’s stepping probability.

## II RESULTS

Our model of the motor dynamics explains the observed behavior based on a general assumption that the stepping rate of a stator depends on the torque exerted by the stator on the rotor, in analogy to the Huxley model for Myosin (6). We find that the motor dynamics can be characterized by two timescales: the moving-time interval for the mechanical rotation of the rotor and the waiting time interval determined by the chemical transitions of the stators. We show that these two timescales depend differently on the load, and that their cross-over provides the microscopic explanation for the existence of two regimes in the torque-speed curves observed experimentally. The fluctuation of the motor rotation is also studied in our model. We show that the sources of the motor speed fluctuation are totally different in the high- and low-load regimes and that the number of steps per revolution can only be extracted from the analysis of motor speed fluctuation in the low-load limit. Finally, this theoretical description can be generalized to study other molecular motor systems with multiple power-generating units, as for example kinesin-1 motor (7).

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