How bacteria swim

Bacteria are the smallest free-living (self-replicating) organisms. Most swim in aqueous media by rotating flagella, long thin filaments driven at their base by rotary motors. In most cases, the filaments are helical and extend out into the external medium; in some cases, as in spirochetes, they remain inside the cell (under the outer membrane). Motors are embedded in a multi-layered cell wall, with the rotor turning a drive shaft connected to the filament via a flexible coupling (called the hook) and the stator connected to a rigid layer of the cell wall (called peptidoglycan). The motors are driven by the passage of ions, usually protons, sometimes sodium ions, from the outside to the inside of a cell down an electrochemical gradient.

Long ago (1972) we determined, by tracking individual cells in three dimensions, the strategy used by the best-understood bacterium, \textit{Escherichia coli} (\textit{E. coli}, for short), to swim up gradients of chemicals (mostly nutrients) if the cell liked their taste. Swim in a direction chosen at random and ask whether the concentration of the chemical goes up or down. If it does not go up (or it goes down) try another direction at random. If it goes up, postpone that choice. Thus, the bacterium plays this game via a biased random walk. The bias is positive (favorable runs get longer). If life is getting better, enjoy it more; if it is getting worse, don’t worry about it. \textit{E. coli} is an optimist. The smooth segments of travel are called runs, and the periods during which the cells change direction are called tumbles. Runs occur when all of the several flagella on a cell (typically four) turn counterclockwise (viewed from the outside of the cell), and tumbles occur when one or more of the flagella switch to clockwise, which leads to changes in filament shape. When all of the flagella turn counterclockwise, the filaments form a coherent bundle behind the cell that pushes the cell steadily forward; when one or more flagella turn clockwise, the bundle comes apart and the cell moves erratically in place (tumbles).

Later (2000) we learned how to label flagellar filaments with fluorescent dyes, enabling us to see what they were doing from base to tip. In our recent work, Turner, L. et al. (2016) Visualizing flagella while tracking bacteria. Biophys. J. 111, 630-639, we combined tracking with fluorescence labeling to get a more complete perspective about what happens as cells swim. The earlier results were confirmed, but one interesting new result was that filaments sometimes change their direction of rotation and their shape but remain within the bundle, in which case deflections in run direction are small.

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