

Continuum Model for Polymorphism in Bacterial Flagella

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Model for Polymorphic Transitions in Bacterial Flagella

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Escherichia coli cells uses rotating, helical flagella to swim through water. The molecular motors which drive the individual helical filaments that make up the flagella can turn both clockwise and counterclockwise. It is known that when the motors turn counterclockwise, the filaments are left-handed and wrap into a bundle that pushes the cell along. When a motor reverses, the corresponding filament unwinds from the bundle and undergoes a “polymorphic” transformation to a right-handed helical shape, which causes the cell to tumble and change direction. This primitive (though familiar to some drivers) method of searching is how *E. coli* can hunt for food. Not surprisingly, changes in solvent pH and temperature can also cause polymorphic transformations.

When the nature of the structure of the flagellar filament began to emerge in the late 1960s, the origin of the helical shape was a puzzle. The flagellar filament consists of identical protein subunits (“flagellin”) arranged in eleven protofilaments wrapping around the core of a filament. How can identical subunits lead to a helical shape? To resolve this puzzle, Asakura [1] proposed that the subunits making up the protofilaments could take on two slightly inequivalent conformations. If all the protofilaments were short or all were long, then the filament would be straight. However, if some protofilaments are short and some are long, the filament is helical. This picture was borne about by experiments showing there are two straight filaments, one consisting of only short protofilaments, one consisting of only long ones.

However, a puzzle remained. The bent shape of the helical filament requires a variation in the length of protofilaments – some will be short, some will be long, and some will be in between. It would seem that this state costs more energy than one in which all protofilaments are the same length. To address this issue, Srigiriraju and Powers have developed a new coarse-grained continuum theory for polymorphism. Motivated by experiments that show that a filament missing its inner core is straight, the authors propose a lattice mismatch between the preferred spacing of subunits in the inner and outer core of the filament. Much as a bimetallic strip is bent in its ground state, the proposed mismatch can cause the energy of the helical shape to be smaller than that of a straight state. Another key aspect of their theory is a cooperative interaction between neighboring subunits on the same protofilament, giving an energy penalty when these subunits are in different conformations. This interaction ensures that the elastic twist of the filament is precisely equal to the geometrical torsion, and indeed is mathematically required to get unique helical ground states. Thus, the observation that all the subunits in a protofilament are in the same state is a natural consequence of the new theory. Unlike previous theories [2], which predict a discrete set of possible filament shapes, the theory of Srigiriraju and Powers predicts continuous as well as discontinuous variation in shape as a function

of material parameters. What is more, the authors compute the static response of the filament to an external torque, and find that the filament twist and curvature should both jump at the same critical torque. These predictions can and should be tested with new micromanipulation experiments.

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- [1] S. Asakura, *Advan. in Biophys.* **1** (1970) 99
 - [2] C.R. Calladine, *Nature* **255** (1975) 121