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How Molecular Motors Shape the Flagellar Beat¹

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Cilia and eukaryotic flagella are slender cellular appendages whose regular beating drives fluid flows across epithelia and propels cells and microorganisms through aqueous media. The beat is an oscillating pattern of propagating bends generated by dynein motor proteins that induce sliding between adjacent axonemal microtubules. A key open question is how the activity of the motors is coordinated in space and time to produce the observed regular oscillatory beat pattern. We have developed a physical description of Flagellar dynamics based on the interplay of collective action of dynein motors and relative sliding of microtubules in two and three dimensions. To elucidate the nature of motor coordination, we have inferred the mechanical properties of the motors by analyzing the shape of beating sperm. Steadily beating bull sperm were imaged at a high frame rate and their shapes were measured with high precision using a Fourier averaging technique. We compared our experimental data with theoretical waveforms and found that the observed flagellar beats were in accordance with a model based on sliding controlled motor activity, but not with curvature controlled motor activity. Furthermore, good agreement between observed and calculated waveforms was obtained only if significant sliding between microtubules occurred at the base. This highlights the role of basal sliding in shaping the flagellar waveform. Thus we conclude, that the flagellar beat patterns are determined by an interplay of the basal properties of the axoneme and the collective behavior of sliding controlled dynein motors that are coordinated mechanically via the sliding of adjacent microtubules.

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