Evaluation of proposed mechanisms for ciliary beating of eukaryotic cells

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The present study aims at understanding the beating mechanism of a cilium — a slender cylindrical appendage that propels eukaryotic cells. The core structure of the cilium, known as the axoneme, consists of nine microtubules doublet surrounding a central pair of microtubules. The dynein motors on the doublets generate active shear forces that are responsible for relative sliding and bending of doublets. Several theories have been put forward over the last several decades to explain the self-organizing beating nature of axoneme, i.e., how the axoneme can spontaneously generate a steady beat without any biochemical control. These theories differ in their predictions of the relation between the forces generated by the motors and the relative sliding of the microtubules. To test these theories we have determined both the forces generated by the motors and the rate of sliding of doublets. A slender body theory together with the experimental data on beating was used to first determine the distribution of the hydrodynamic force acting along the length of a cilium. This force distribution was then combined with the moments balance equation for active filaments to determine the forces generated by the motors. The shape of the beats also allowed us to determine the relative sliding of the doublets. Several different beat patterns were analyzed and the findings were compared with various theories. None of the existing theories appear to be satisfactory. A need for additional measurements will be discussed.

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