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Synchronization of Eukaryotic Flagella and the Evolution of Multicellularity[1]

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Flagella, among the most highly conserved structures in eukaryotes, are responsible for such tasks as fluid transport, motility and phototaxis, establishment of embryonic left-right asymmetry, and intercellular communication, and are thought to have played a key role in the development of multicellularity. These tasks are usually performed by the coordinated action of groups of flagella (from pairs to thousands), which display various types of spatio-temporal organization. The origin and quantitative characterization of flagellar synchronization has remained an important open problem, involving interplay between intracellular biochemistry and interflagellar mechanical/hydrodynamic coupling. The Volvocine green algae serve as useful model organisms for the study of these phenomena, as they form a lineage spanning from unicellular *Chlamydomonas* to germ-soma differentiated *Volvox*, having as many as 50,000 biflagellated surface somatic cells. In this talk I will describe extensive studies [1], using micromanipulation and high-speed imaging, of the flagellar synchronization of two key species - *Chlamydomonas reinhardtii* and *Volvox carteri* - over tens of thousands of cycles. With *Chlamydomonas* we find that the flagellar dynamics moves back and forth between a stochastic synchronized state consistent with a simple model of hydrodynamically coupled noisy oscillators, and a deterministic one driven by a large interflagellar frequency difference. These results reconcile previously contradictory studies, based on short observations, showing only one or the other of these two states, and, more importantly, show that the flagellar beat frequencies themselves are regulated by the cell. Moreover, high-resolution three-dimensional tracking of swimming cells provides strong evidence that these dynamical states are related to reorientation events in the trajectories, yielding a eukaryotic equivalent of the "run and tumble" motion of peritrichously flagellated bacteria. The degree of synchronization is found to depend upon the presence of external fluid flow, an important aspect of the dynamics in the context of evolutionary transitions to multicellularity. Comparison is made with dynamics of somatic cells of *Volvox*, which we have found can display metachronal waves, not previously reported in this organism. Implications of these findings for phototactic steering are also discussed.

[1] M.Polin, I. Tuval, K. Drescher, J.P. Gollub, and R.E. Goldstein, submitted (2009).

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