Flagellar synchronization independent of hydrodynamic interactions
Phys. Rev. Lett. **109** (2012) 138102.
Benjamin M. Friedrich and Frank Jülicher

Recommended with a commentary by Thomas R. Powers, Brown University

One of the most striking phenomena exhibited by swimming microorganisms is the coordination of their beating cilia. Cilia, sometimes called flagella, are the thin filaments used for propulsion by eukaryotic organisms. Figure 1a shows a sketch of the beating pattern of the two flagella of the green alga *Chlamydomonas*. The flagella tend to beat in synchrony in a mirror-symmetric manner at a frequency of about 50 Hz, with the periods of synchrony interrupted occasionally by random bursts of asynchronous beating [1]. Coordinated beating occurs in a wide variety of geometries and organisms. It can occur among hundreds of cilia on a single organism, as in the case of *Paramecia*, which are covered in cilia that beat together to generate the so-called metachronal waves that sweep along the the surface of the cell and propel it along [2]. Coordinated beating can even occur between flagella on different cells, such as in the case of nearby swimming mammalian spermatazoa [3].

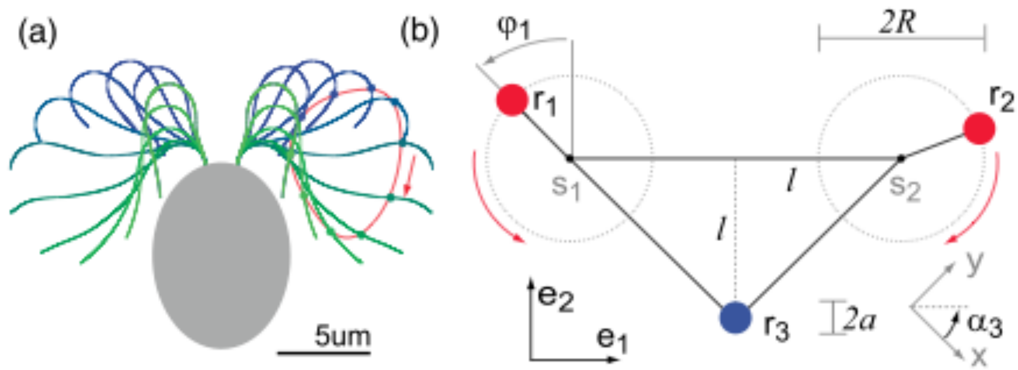

Figure 1: Left panel: a. Right panel: b. Figure adapted from [4].

How does the coordination arise? At the small scale of a cell, inertia is unimportant, and viscous forces dominate. This is the realm of Stokes flow. In Stokes flow, hydrodynamic interactions are long-ranged, falling off like a power law with distance. It has long been suggested that hydrodynamic interactions are the means by which coordination arises. In recent years, the idea of coordinated beating via hydrodynamic interactions has been developed quantitatively using numerics, theory, and experiment with reduced models [5, 6, 7, 8, 9, 10, 11, 12]. Perhaps the simplest theoretical model replaces the flagella with spheres traveling on a circular trajectory, with each sphere driven by a constant force aligned tangentially to its orbit, and hydrodynamic interactions treated using the far-field approximation. Synchronization via hydrodynamic interactions can occur when the orbits are squashed into ellipses and tilted relative to a nearby wall [8], or if the balls are given some flexibility, such as by supposing they are held onto the circular track by a stiff restoring radially force [9]. Much more generally, hydrodynamic interactions can lead to synchronization whenever the phase-dependence of the driving forces satisfies a certain criterion—walls or flexibility are not required [12].

Friedrich and Jülicher have introduced a new mechanism for the phase-locking of beating flagella: synchronization via viscous friction, independent of hydrodynamic interactions [4]. To first order, the viscous friction is simply the drag force experienced by a sphere moving though an infinite fluid with no other objects. The authors model *Chlamydomonas* as three spheres in a triangular arrangement. One sphere corresponds to the body, and the other two represent the beating flagella by rotating along circular tracks in opposite directions (Fig. 1b). When the cell swims forward and the spheres are not in phase, the body rocks back and forth, which in turn causes changes in the viscous friction forces experienced by the spheres. It is these viscous friction forces, arising from the swimming and rocking of the model *Chlamydomonas*, that cause phase-locking of the counter-rotating spheres. Hydrodynamic interactions make only a small contribution. The spheres phase-lock even if hydrodynamic interactions are disregarded in the model. The authors also consider a more realistic model, replacing the rotating spheres with the sequence of flagellar shapes shown in Fig. 1a. Assuming that the hydrodynamic friction forces affect only the rate each flagellum passes through the sequence of shapes, and disregarding the hydrodynamic interaction between the two flagella, the authors calculate realistic swimming motion with phase-locked flagella.

It is important to point out that experimentally, the flagella of *Chlamydomonas* phase-lock even if the cell body is held and prevented from rotating and translating. While the hydrodynamic interactions between the flagella can lead to phase-locking in this situation, the time for the flagella to synchronize by this mechanism is long. Friedrich and Jülicher suggest instead that the elastic connection of the flagella to the cell body provides the rocking required for their mechanism.

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