Cilia and flagella are found throughout nature. These slender cellular appendages—which range from a few micrometres to many millimetres in length—perform a wide range of roles in many different types of cells. They propel single-celled sperm and multi-celled algae through fluids, they direct chemicals called morphogens that are important for development in the growing embryo, and they pump mucus out of human lungs (Gray, 1928; Fliegauf et al., 2007). Many of these tasks involve a beating motion, which is driven by dynein motors inside the cilium or flagellum.

Cilia and flagella beat at a range of frequencies between once per second and 100 times per second. Two cilia never have exactly the same intrinsic beating frequency. Moreover, these frequencies randomly fluctuate during beating—this is known as noise. Nevertheless, thousands of cilia that are closely spaced on a surface can beat in synchrony to collectively perform a task, although this process is only partially understood.

Perhaps an obvious way cilia and flagella may be synchronised is through a central pacemaker inside the cells that controls the beating of several cilia on the same cell or tissue. However, this has been ruled out as even unconnected cells can synchronise their beating; for example, sperm cells can synchronise their flagella when swimming close together (Gray and Hancock, 1955; Riedel et al., 2005). Alternative sources of synchronisation control—including mechanical, chemical, or electrical signals—have been suggested, but the roles of each are still unknown. Now, in eLife, Raymond Goldstein and colleagues at the University of Cambridge—including Douglas Brumley as first author—report an elegant experiment that elucidates a physical mechanism that keeps cilia and flagella beating in time with each other (Brumley et al., 2014).

Previous experiments in which sperm were held in vibrating micro-needles showed that external physical forces can influence the intrinsic beating frequency of a single flagellum (Okuno and Hiramoto, 1976). The relationship between force and frequency has also been measured in green algal cells that were free to swim around normally (Geyer et al., 2013). Measuring how flagella respond to loads can provide insight on how the thousands of dynein motors inside the flagellum—each sensitive to external forces—work together to shape the beat.

Brumley et al. isolated two cells from the alga Volvox, with each cell containing (effectively) a single beating flagellum. Each cell was attached onto a separate micropipette. This prevented the cells from communicating with each other in any way other than through the fluid flows created by the beating flagella. It also allowed the researchers to experimentally vary the relative distance and orientation of both flagella. Provided this distance was small, the two beating flagella settled into a common rhythm. When the distance between the cells was increased, the synchronisation became imperfect—for example, one flagellum would sometimes add an extra
beat—and eventually synchronisation broke down completely.

So how do multiple flagella synchronise? As each flagellum beats, it disturbs the liquid around it, generating a periodically varying fluid flow that exerts friction forces on other nearby flagella. This mechanically couples the flagella to each other. If this hydrodynamic coupling is strong enough to overcome both noise and the mismatch in the natural beating frequencies, then the flagella synchronise in a purely self-organised fashion.

Importantly, Brumley et al. determined exactly how the hydrodynamic coupling depends on the distance between flagella. The hydrodynamic phenomena experienced by beating flagella inside water are rather different to those experienced by a human swimming through water: indeed, they are akin to what a human would experience if they tried to swim through honey (Purcell, 1977). Theory predicts that the strength of the flow field around a beating flagellum is inversely proportional to the distance from the flagellum (Lauga and Powers, 2009). This is exactly what Brumley et al. measured, both when looking at an isolated flagellum, and also when examining how two flagella synchronise. Hence, the further apart two flagella are, the less force they apply on each other, eventually leading to a breakdown of synchrony. (Note, for freely moving cells, like swimming sperm cells, the flow field is instead inversely proportional to the square of the distance between flagella.)

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