Order spreads fast from special edges

Nonreciprocal interactions give rise to fast cilium synchronisation in finite systems
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Recommended with a Commentary by Bryan VanSaders [iD] *,*
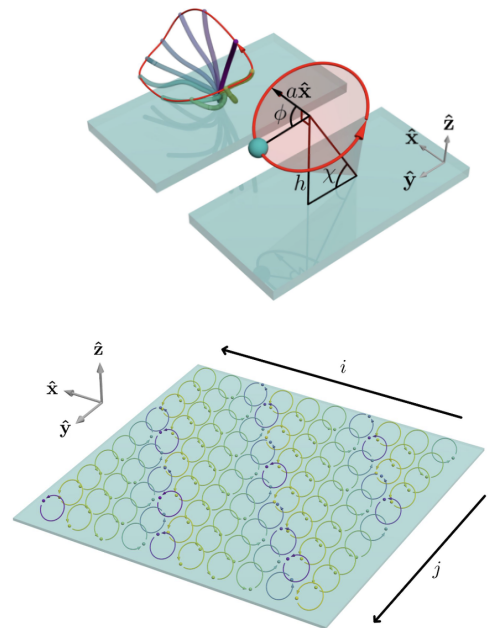*Department of Physics, Drexel University*

Figure 1: *Top* A realistic beat pattern of a cilium, and the simplified bead model used in Hickey et al. *Bottom* A two-dimensional carpet of bead model cilia. Reproduced from [1].

Non-reciprocal interactions have recently garnered much attention in the soft (and active) matter community. A classic example are vision cone-interactions, relevant to many social animals who use sight to coordinate (birds, pedestrians, etc.). Such agents can only react to neighbors in their field of vision, and agents are often not mutually visible to each other. Non-reciprocity opens the door for new kinds of pattern formation transitions [2], but Hickey et al. study its effect in quickening, and stabilizing an existing order transition for coupled oscillators. What is so striking here is the dramatic speed up - for two dimensional systems, reaching global order hastens from $t \propto N^2$ to $\sqrt{N}$. First, a brief introduction to the biological inspiration.

Many eukaryotic cells are coated in cilia - microscopic hairs that beat the fluid around them by cycling through a series of bending configurations. Cilia are a key component of extra-cellular transport systems, often acting as fluid pumps (for low Reynolds number flows, hence the need for considerable shape change in their stroke). Free swimming cells such as members of genus *Paramecium* use many cilia over their surface to self-propel, while our respiratory tracts contain vast quantities of cilia to transport mucus and expel debris. Individual cilium can be thought of (and reasonably modeled) as oscillators with an intrinsic frequency and constant driving power. Their beat cycle is split into two parts, a fast 'power stroke' and slower recovery stroke. Cilia carpets are typically ordered arrays of many cilia, where the

direction of the power stroke for all is fixed by an underlying polarity of the host cell or tissue. Crucially, hydrodynamic coupling between nearby cilia can shift their frequencies and synchronize them into wave states, known as 'metachronal' waves. Metachronal waves are commonly observed, and generally enhance fluid transport. How do these synchronized states emerge?

At first look, cilia carpets should seem to display the basic characteristics of a Kuramoto model in two dimensions. This model admits plane wave solutions, with dominant contribution $k = 0$. Furthermore, the slowest decaying perturbation mode is set by the longest dimension of the system L, and the Lyapunov exponent of this mode can be shown to scale as $\propto L^2$. Therefore, as the system size increases, perturbations will relax ever slower and no synchronization is to be expected in the infinite system [3]. This is an expression of the Hohenberg-Mermin-Wagner theorem that prohibits global order in two-dimensional systems with continuous symmetries and local coupling [4], also responsible for a lack of true long-range order in the classical 2D XY model.
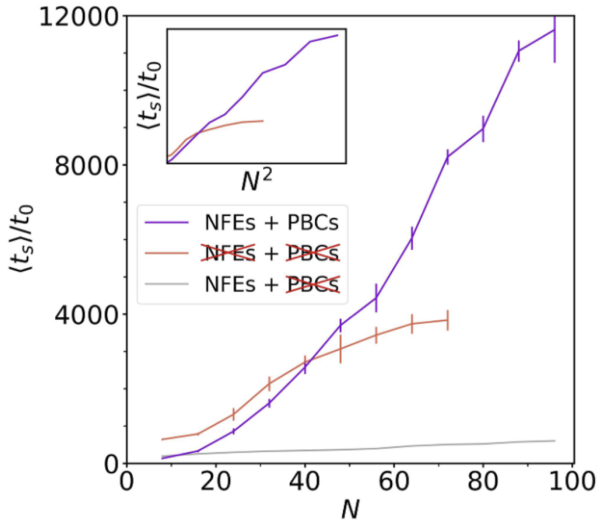

Figure 2: Time to synchronization for a chain of bead model cilia. When near-field effects (NFEs) and periodic boundary conditions are used, synchronization is slow (purple curve). Note that NFE's are responsible for non-reciprocal effects in this model system. Finite systems without NFEs only partially synchronize (orange curve). Finite systems with NFEs globally synchronize rapidly (grey curve). Reproduced from [1].

A combination of non-reciprocal interactions and finite system size dramatically alters this picture. Hickey et al. construct a model of cilia carpets in which near-field (and hence nonlinear) hydrodynamic effects are included. When only far-field flows are considered, coupling interactions between cilia are reciprocal, due to the linear nature of Stokesian dynamics and the Lorentz reciprocal theorem. To more fully model cilia carpets at realistic area densities, coupling due to close-range non-linear flows must be considered, and these effects have pronounced non-reciprocity. Hickey et al. refer to such corrections as 'near field effects' (NFEs).

Non-reciprocal effects (from NFEs) have apparently subtle consequences for the dynamics of synchronization in the bulk. When an ordered patch randomly occurs, it tends to migrate in the direction of greatest non-reciprocity. Much like a tread-milling filament [5] (that returning readers may recall [6]) the ordered patch synchronizes cilia ahead of it, while disorder behind it consumes it at a similar rate. Non-reciprocal coupling is responsible - the ordered patch exerts great influence over disordered cilia ahead of it, and recruits them, but is powerless to synchronize cilia behind. Consequentially, NFEs have little effect on the mean time to synchronization in the absence of boundaries (fig. 2, purple curve). The time to synchronize is dramatically shortened when boundaries and NFEs are present (fig. 2, grey curve). The

reason is beautifully simple - ordered domains that begin near a boundary wall and grow perpendicular to it do not have disordered neighbors behind them, and their 'vulnerable' side is protected by the system boundary. These edge-nucleated domains grow unchecked, and span the system in time proportional to L. Introducing an edge boundary (of the correct orientation!) to a large 2D system of N cilia could therefore reduce expected synchronization time from $\propto N^2$ to a mere $\propto \sqrt{N}$. As Hickey et al. point out, this is relevant to biological systems because fully periodic 2D cilia carpets are quite rare. Domains with edges, or with curvature extreme enough to require lattice defects, are the norm.

Note also that reciprocal models of cilia in finite domains struggle to achieve global order, instead becoming trapped in multi-domain or chimera states. Accordingly, synchronization times appear to saturate for such models as the typical stable domain size is reached (fig. 2 orange curve), but this is just an indication of multi-domain synchronization. When modeled with NFEs, domains rapidly converge to a single, stable metachronal wave solution. Prior studies have shown that even in periodic domains, multiple solutions are stable [3], and open boundaries complicate matters further. This work is another reminder that biological systems are very finely tuned, and our understanding is just catching up. Nature has apparently known about the advantages of non-reciprocal coupling for quite some time.

In summary, Hickey et al. present an interesting turn in our understanding of how cilia carpets synchronize, but perhaps more exciting are extensions to the many other systems that can be mapped to the Kuramoto model. Furthermore, one wonders how effectively localized defects could play the part of domain boundaries here. Interesting to consider that the emergence of order in the form of synchronization could be dramatically helped by a breakdown of positional order.

References

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