Synchronization in cilia carpets: multiple metachronal waves are stable, but one wave dominates

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Abstract
Carpets of actively bending cilia represent arrays of biological oscillators that can exhibit self-organized metachronal synchronization in the form of traveling waves of cilia phase. This metachronal coordination supposedly enhances fluid transport by cilia carpets. Using a multi-scale model calibrated by an experimental cilia beat pattern, we predict multi-stability of wave modes. Yet, a single mode, corresponding to a dextroplectic wave, has predominant basin-of-attraction. Similar to a ‘dynamic’ Mermin–Wagner theorem, relaxation times diverge with system size, which rules out global order in infinite systems. In finite systems, we characterize a synchronization transition as function of quenched frequency disorder, using generalized Kuramoto order parameters. Our framework termed Lagrangian mechanics of active systems allows to predict the direction and stability of metachronal synchronization for given beat patterns.

Motile cilia are slender cell appendages that bend rhythmically due to the activity of molecular dynein motors inside [1]. Collections of motile cilia can spontaneously synchronize their bending waves, e.g. in carpets of many cilia on airway epithelium [2], as well as on the surface of model organisms, e.g. green alga colonies or unicellular Paramecium [3, 4]. Metachronal coordination manifests itself as a self-organized traveling wave of cilia phase (similar to a Mexican wave in a soccer stadium). Numerical models showed that this synchronization is important for efficient fluid transport [5, 6]. Tissue-scale polarity systems align cilia bases [7], ensuring a common direction of the effective stroke of the cilia beat. In many species, cilia beat patterns are chiral, e.g. with counter-clockwise motion of cilia during their recovery stroke close to the surface [3]. The directions of metachronal waves enclose defined angles relative to the direction of the effective stroke [3, 8], presumably set by the chirality of the cilia beat [9].

Already in 1952, Taylor proposed that hydrodynamic interactions between nearby cilia play a key role for their synchronization [10]. When a beating cilium performs its bending wave, it sets the surrounding fluid in motion, resulting in time-dependent hydrodynamic friction forces that act on nearby cilia. Recent experiments indeed demonstrated synchronization by hydrodynamic coupling in pairs of cilia [11], as well as phase-locking to external oscillatory flows with characteristic Arnold tongues [12, 13]. Recent theoretical work predicts different synchronization modes between pairs of hydrodynamically coupled cilia, depending on their relative positions [14, 15].

Yet, we still do not understand how hydrodynamic interactions and the shape of the cilia beat select the direction of metachronal waves in cilia carpets. Multiple wave directions are possible, yet these may not be stable to small perturbations (local stability) or be unlikely to be selected for random initial conditions (global stability). A key question thus concerns the local and global stability of different metachronal wave modes. The global stability of synchronization states in collections of coupled oscillators, not just interacting cilia, is still a field of active research [16–18].

The periodic sequence of shapes that a cilium assumes during its beat cycle represents a limit cycle in a high-dimensional shape space [19, 20]. This limit cycle can be parameterized by a single phase variable such...
that phase speed is constant in the absence of perturbations and noise [21]. This allows to describe beating cilia as phase oscillators [19, 22]. In the presence of external flows, which change the hydrodynamic load, the phase speed changes, i.e. cilia progress slower or faster along their beat cycle, while deviations from the limit-cycle sequence of shapes remain small for moderate flows [13, 23, 24]. This load-response of cilia (reflected by the load-dependent speed of their phase variable) is a prerequisite for cilia synchronization by hydrodynamic interactions, and is implicit in previous minimal models [9, 13, 25–31].

Previous theory on hydrodynamic synchronization in cilia carpets either employed large-scale numerical simulations [6, 32, 33], or relied on minimal models, where beating cilia are idealized, e.g. as orbiting spheres [9, 13, 25–31].

Here, we harness multi-scale simulations to combine the benefits of detailed hydrodynamic simulations based on experimentally measured cilia beat patterns, and those of minimal models amenable to local and global stability analysis. Our approach, termed \textit{Lagrangian mechanics of active systems} [14], enables us to study global stability in arrays of hydrodynamically coupled cilia.

1. Beating cilia as coupled phase oscillators

We consider a carpet of \( N \) cilia positioned on a regular triangular lattice of base points \( \mathbf{x}_j \) in a rectangular domain with periodic boundary conditions, see figure 1(d). Each cilium is described as a phase oscillator whose phase \( \phi_j \) advances by \( 2\pi \) on each cycle, like a clock. This phase variable \( \phi_j \) parameterizes a periodic sequence of three-dimensional cilia shapes, previously measured for \textit{Paramecium} [3, 34], see figure 1(a).

When the phase \( \phi_j \) increases, i.e. the cilium progresses along its beat cycle, the corresponding shape change of the cilium sets the surrounding fluid in motion, resulting in time-dependent hydrodynamic friction forces that act on the other cilia. For nearby cilia, the resultant hydrodynamic interactions can be computed from the Stokes equation valid at zero Reynolds number [14, 35], see also supplemental material (SM) (https://stacks.iop.org/NJP/24/013015/mmedia). The plane containing the cilia base points is modeled as a non-slip boundary, thus hydrodynamic interactions decay as \( 1/d^3 \) as function of distance \( d \) [14, 36].
We consider the dynamics of \( N \) cilia in a rectangular unit cell with periodic boundary conditions, which is characterized by a \( N \)-component vector \( \Phi = (\phi_1, \ldots, \phi_N) \in \mathbb{R}^N \) of cilia phases. Because the Stokes equation is linear [37], the surface density of hydrodynamic friction forces \( f(x) \) at time \( t \) (defined on the combined surface \( \mathcal{S} \) of all cilia and the boundary surface) is linear in the generalized velocity \( \Phi \). Thus, the power exerted by the moving cilia on the surrounding fluid \( \mathcal{R} = \int_\mathcal{S} \mathrm{d}^2 x f(x) \cdot \dot{x} \) becomes a quadratic form in \( \Phi \) [14]

\[
\mathcal{R} = \dot{\Phi} \cdot \Phi (\Phi) \cdot \Phi
\]

with a symmetric \( N \times N \) matrix of generalized hydrodynamic friction coefficients \( \Gamma = \Gamma(\Phi) \). Here, \( \Gamma_{ii} \) represents self-friction of cilium \( i \), while \( \Gamma_{ij} \) characterizes hydrodynamic interactions between cilia \( i \) and \( j \).

Below, we compute the friction force \( \Phi \) and an active driving force \( P_i \) for a real cilia beat pattern, and calibrate the active driving forces \( \Phi \), hence only depends on \( \phi_{ij} \) and possibly load \( P_i \). We make the simplifying assumption that \( Q_i \) is independent of load. Previous experiments in the green alga Chlamydomonas [24] as well as cilia bundles in external flow [13] showed that this assumption together with equation (3) quantitatively accounts for the load response of cilium [31, 39], i.e. the experimental observation that cilia progress slower/faster along their beat cycle upon increase/decrease of hydrodynamic load. Next, we compute the generalized hydrodynamic friction forces \( P_i = \sum_j \Gamma_{ij} \phi_j \) with friction coefficients \( \Gamma_{ij} \) for a real cilia beat pattern, and calibrate the active driving forces \( Q_i \). Note that previous minimal models of hydrodynamically interacting spheres [25–30] can likewise be written in the form of equation (3), yet with simplified driving and friction forces.

2. Oscillator coupling calibrated from hydrodynamic simulations

Initial simulations showed that the friction coefficient \( \Gamma_{ij}(\Phi) \) is largely independent of the phases of the other cilia, \( \phi_{kl}, k \neq i,j \). This allows us to use an approximation of only pairwise-interactions for \( \Phi(\Phi) \) by averaging out all non-essential variables. In short, we set \( \phi_{kj} = \phi \) for \( k \neq i,j \), and average over \( \phi \) to obtain a function \( \Gamma_{ij}(\phi, \phi) \) of \( \phi_i \) and \( \phi_j \) only, see SM text for details. The active driving force \( Q_i(\phi_i) \) of each cilium is uniquely determined by a reference condition, namely that the phase speed of this cilium should be constant, \( \dot{\phi}_i = \omega_0 \), if the other cilia do not beat. This condition yields

\[
Q_i(\phi_i) = \omega_0 \Gamma_i(\phi_i).
\]

Together, equations (2)–(4) give an equation of motion in implicit form

\[
\dot{\phi}_i = \omega_0 - \sum_{j \neq i} \gamma_{ij} \phi_j \quad \text{with} \quad \gamma_{ij}(\phi_i, \phi_j) = \frac{\Gamma_{ij}(\phi_i, \phi_j)}{\Gamma_{ii}(\phi_i)}.
\]

The normalized hydrodynamic interaction \( \gamma_{ij}(\phi_i, \phi_j) \) between cilium \( i \) and cilium \( j \) characterizes the relative amount by which the motion of cilium \( j \) changes the phase speed of cilium \( i \). Figure 1(c) shows \( \gamma_{ij}(\phi_i, \phi_j) \) as function of the respective phases \( \phi_i \) and \( \phi_j \) of the two cilia. In short, the effective stroke of cilium \( j \) \((\pi \leq \phi_j \leq 2\pi)\) will speed up cilium \( i \) \((\gamma_{ij} < 0)\) and will slow down cilium \( i \) \((\gamma_{ij} > 0)\), but will slow down cilium \( i \) \((\gamma_{ij} > 0, \text{ red colors})\) if cilium \( i \) is in its effective stroke \((0 \leq \phi_j \leq \pi)\). When one of the two cilia transitions from effective stroke to recovery stroke, or vice versa (i.e. \( \phi_i \approx 0, \pi \) or \( \phi_j \approx 0, \pi \)), that cilium moves slowly and the hydrodynamic interaction between the two cilia is weak, \( \gamma_{ij} \approx 0 \). We emphasize that \( \gamma_{ij}(\phi_i, \phi_j) \) is not simply a function of the phase difference \( \phi_i - \phi_j \) as in a classical Kuramoto model, but is much richer.

Numerical computations further show that \( \gamma_{ij} \) is very small except for close neighbors; we therefore set \( \gamma_{ij} = 0 \) except for close neighbors \( i \) and \( j \), see figure 1(d). We can now rewrite the equation of motion equivalently in explicit form as \( \Phi = \Gamma^{-1} \cdot Q \). With pre-computed \( \Gamma_{ij}(\phi_i, \phi_j) \) and \( Q_{\phi}(\phi_i) \) at hand, this explicit ordinary differential equation can be efficiently integrated for ten-thousands of cilia beat cycles.
we first re-visit the classical Kuramoto model with local sinusoidal coupling [40, 41]. Specifically, we consider a Kuramoto model of coupled phase oscillators with phases traveling waves with wave vector $k$, the numerical dispersion relation is well approximated by $\omega_k / \omega_0 \approx 1 + \beta |\sin(\pi |k|/k_{\text{max}})|$ with $\beta \approx 0.04$ and $k_{\text{max}} = 4\pi / (3a)$, inline with analytical results for a slightly more general Kuramoto model [42] with $c_0 = \varepsilon |\sin(\varphi_j - \varphi_i + \delta)|$ involving an additional phase shift $\delta$ in the coupling, see SM text for details.

3. Metachronal wave solutions

We are interested in dynamic steady-state solutions of the equation of motion, equation (5). As a reference, we first re-visit the classical Kuramoto model with local sinusoidal coupling [40, 41]. Specifically, we consider a Kuramoto model of coupled phase oscillators with phases $\varphi_i$ at respective lattice positions $x_i$ and equation of motion $\dot{\varphi}_i(t) = \omega_0 - \sum_{j \neq i} c_{ij} (\varphi_i - \varphi_j)$ with coupling function $c_{ij} = \varepsilon |\sin(\varphi_j - \varphi_i)|$ for all pairs $(i,j)$ of neighbors and $c_{ij} = 0$ else. For this Kuramoto model, the steady-state solution are perfect plane traveling waves with wave vector $k$

$$\Phi_k(t) : \varphi(t) = \omega_k t - k \cdot x_j. \quad (6)$$

Here, $k$ is one of the $N$ reciprocal lattice points in the Brillouin zone of the oscillator lattice (with unit cell of $N$ oscillators and periodic boundary conditions), see also figure 2(a). Note $\omega_k = \omega_0$ for this simple Kuramoto model. In our cilia carpet model, the hydrodynamic interaction coefficients $c_{ij}$ are not perfect sinusoidal functions, but a superposition of many Fourier modes. As a consequence, periodic solutions of cilia carpet dynamics are not perfect plane traveling waves as in equation (6). Nonetheless, we numerically find $N$ periodic wave solutions $\Phi_k(t)$ of cilia carpet dynamics, where each $\Phi_k(t)$ is close to one of the $N$ plane traveling wave $\Phi_0(t)$ of equation (6). We will refer to $\Phi_k(t)$ as metachronal wave solutions. The global frequency $\omega_k$ of these periodic solutions decreases with inverse wavelength $|k|$, see figure 2(a). The numerical dispersion relation is well approximated by $\omega_k / \omega_0 = 1 + \beta |\sin(\pi |k|/k_{\text{max}})| - 1$ with $\beta \approx 0.04$ and $k_{\text{max}} = 4\pi / (3a)$, inline with analytical results for a slightly more general Kuramoto model [42] with $c_0 = \varepsilon |\sin(\varphi_j - \varphi_i + \delta)|$ involving an additional phase shift $\delta$ in the coupling, see SM text for details.

Figure 2. Multi-stability of metachronal waves. (a) Dispersion relation: left: two example metachronal wave solutions: colored dots mark cilia base points, with colors representing cilia phase at a snapshot in time. Middle: metachronal wave solutions can be classified as symplectic, antiplectic, laeoplectic, and analyze the stroboscopic dynamics of the cilia carpet given by $\Phi_k(t)$ with $\tau_{\text{relax}} / T_0$ as function of inverse wavelength $|k|$ large, approaching anti-phase synchronization (as compared to metachronal coordination with short wavelength ($|k|$ small, approaching in-phase synchronization). The wave frequencies approximately follow an analytical result $\Delta \omega_k \sim \cos(\pi |k|/k_{\text{max}})$ for a classical Kuramoto model (black line). Different colors indicate the direction of $k$, see inset. Traditionally, wave directions are classified as symplectic, antiplectic, laeoplectic, and depending on the direction of $k$ relative to the direction $e_0$ of the cilia effective stroke [8]. (b) Linear stability: linear stability analysis for each $k$ reveals that multiple solutions are linearly stable (green colors: stable metachronal wave solution, color represents relaxation time $\tau_{\text{relax}}$ of the slowest decaying perturbation mode, normalized by beat period $T_0 = 2\pi / \omega_0$ of single cilium; red: unstable). For the computation, we define a global phase $\varphi$ and analyze the stroboscopic dynamics of the cilia carpet given by $\varphi = 0$ modulo $2\pi$; fixed points $\Phi_0$ of this Poincaré map correspond to metachronal wave solutions, see left inset. (c) The relaxation time of the slowest-decaying perturbation for the dominant wave solution increases with system length as $L^2$, resembling a dynamic Mermin–Wagner theorem for cilia carpets, which rules out global order in infinite systems. Lattice of $16 \times 16$ cilia; other parameters as in figure 1.
5. Global stability: one wave dominates

Although many metachronal wave solutions with different wave vectors $\mathbf{k}$ are simultaneously stable to small perturbations, we find that trajectories with uniformly sampled random initial conditions will predominantly converge to just one wave solution. The fraction of trajectories converging to $\Phi_k$ equals the volume fraction of the basin-of-attraction of $\Phi_k$, which yields 86% for the dominant wave solution with wave vector $\mathbf{k}_I$, see figure 3(a).
6. Slice-visualization of basins-of-attraction

To visualize basins-of-attraction of metachronal wave solutions, we additionally considered a specific set of initial conditions of the form \( \phi_j = -m \cdot x_j \) with ‘off-lattice’ wave vectors \( m \); these initial conditions correspond to a two-dimensional slice through the \( N \)-dimensional phase space, see figure 3(b). As expected, the majority of initial conditions converged to the dominant wave mode \( k_1 \), while initial conditions \( m \approx k \) in a small neighborhood of other stable modes \( k \) converged to the respective \( \Phi_k \). A magnification shows that the boundaries between basins-of-attraction are rough (and possibly fractal). Finally, a small number of initial conditions did not converge to any \( \Phi_k \) within the simulation time [gray squares in figure 3(b)], but presumably converged to more exotic states, e.g. chimeras states consisting of multiple ordered domains [44], see SM text for examples.

7. Diverging relaxation time

We investigated cilia carpets of different size, and consistently found that the local stability patterns of metachronal waves remain similar to figure 2(b), see SM text. Similarly, we observe a single dominant wave solution for all system sizes tested, with corresponding wave vectors close to \( k_1 \) throughout. Nonetheless, in larger systems, perturbation modes with longer wavelengths and longer relaxation times appear. The relaxation time \( \tau_{\text{relax}} = \max_i \tau_i \) of the slowest-decaying perturbation mode for the respective dominant wave solution increases with system length \( L = \max(L_x, L_y) \) of the \( L_x \times L_y \)-simulation domain approximately as

\[
\tau_{\text{relax}} \sim L^2,
\]

see figure 2(c). While we demonstrate this power law only numerically for cilia carpets, one can in fact prove this power law analytically for a minimal Kuramoto model with local sinusoidal coupling, see SM text. This dynamic behavior parallels the Mermin–Wagner theorem from statistical mechanics for two-dimensional equilibrium systems with continuous symmetries [45]. For example, in the classical XY model of interacting spins in the plane with short-range interactions, so-called Goldstone modes appear; the energy-per-area of these long-wavelength perturbation modes scales as \( 1/L^2 \) if we impose over-damped dynamics. In this sense, one may interpret equation (8) as a dynamic Mermin–Wagner theorem of a non-equilibrium system [46]. The analogy between synchronization and the XY model can be made more explicit for the classical Kuramoto model with local sinusoidal coupling [40].

8. Synchronization in presence of quenched frequency disorder

In real cilia carpets, the intrinsic beat frequencies of individual cilia will slightly differ. In a Kuramoto model with all-to-all coupling, a second-order phase transition occurs as a function of a frequency disorder parameter, whereas in Kuramoto models with local coupling a synchronization transition can only be observed in finite systems [49, 50].

We now investigate a cilia carpet, where each cilium has a slightly different intrinsic beat frequency \( \omega_i \), with the equation of motion given by equation (5), but with \( \omega_0 \) replaced by \( \omega_i \) for cilium \( i \), i.e. \( \dot{\phi}_i = \omega_i - \sum_j g_{ij} \phi_j \). Cilia beat frequencies are drawn from a normal distribution with mean \( \omega_0 \) and standard deviation \( \Delta \omega > 0 \). [As a technical point, we rejected frequency sets whose sample standard deviation differed by more than 1% from \( \Delta \omega \).] We are interested in the synchronization behavior of the cilia carpet as function of \( \Delta \omega \), averaged over different frequency sets and initial conditions, see SM for details.

To characterize steady-state solutions, we introduce a generalized Kuramoto order parameter, see also [51]

\[
r_k(\Phi) = N^{-1} \left| \sum_j \exp i(\phi_j + k \cdot x_j) \right|.
\]

This order parameter \( r_k \) is close to one, whenever the cilia phases approximately form a plane traveling wave \( \Phi_k(t) \) with wave vector \( k \), i.e. \( \phi_j \approx \phi_0 - k \cdot x_j \). The inequality \( r_k(\Phi) > \frac{1}{2} \) defines mutually disjoint neighborhoods for each \( k \) (each of which occupies only a tiny fraction \(< 10^{-10} \) of the whole phase space).

Figure 3(c) shows the fraction of trajectories \( \Phi(t) \) as function of \( \Delta \omega \) that both (i) converge to the neighborhood of a metachronal wave solution \( \Phi_k(t) \) with \( r_k(\Phi(t)) > 2^{-1/2} \), and (ii) exhibit global frequency synchronization, i.e. phase differences between different cilia remain bounded. This definition for global
metachronal coordination generalizes a previous definition for the case $k = 0$, which required both ‘phase cohesiveness’ and ‘frequency synchronization’ [41]. We find that the fraction of synchronized trajectories sharply decreases near a characteristic value of frequency disorder, $\Delta \omega c / \omega_0 \approx 2.5 \times 10^{-3}$. This value likely depends on system size, as suggested by previous work on two-dimensional Kuramoto models with local coupling [49, 50]. For intermediate values of $\Delta \omega$ close to the transition point, $\Delta \omega \approx \Delta \omega_m$, we observe a fraction of trajectories that exhibit partial synchronization, i.e. trajectories satisfy condition (i) [large Kuramoto order parameter], but not condition (ii) [frequency synchronization], apparently because a few cilia did not synchronize and displayed phase drift instead.

9. Discussion

We analyzed global stability of metachronal synchronization in cilia carpets using a multi-scale model, and found that a single dominant wave solution has a basin-of-attraction that spans almost the entire phase space of initial conditions (generalizing early observations for oscillator rings [16]). The wave direction of this dominant metachronal wave solution encloses an angle of $\approx 60^\circ$ with the direction of the effective stroke of the cilia beat, which is close to the experimentally observed value $\approx 90^\circ$, corresponding to a so-called dixolectic wave [3]. The experimentally observed wavelength $\approx 11 \mu m$ is smaller than the wavelength of the dominant wave mode $2\pi / |k| \approx 34 \mu m$ predicted here; this discrepancy may simply be a consequence of the cilia density used in our model, which does not yet allow us to study smaller wavelengths.

Linear stability analysis showed that long-wavelength perturbations of the dominant synchronized state relax only slowly with relaxation time-scales that increase quadratically with system size. This dynamic behavior in a non-equilibrium system parallels the Mermin–Wagner theorem for two-dimensional equilibrium systems with continuous symmetries (such as the XY models of interacting spins in a plane) [45]. In these systems, long-wavelength perturbations known as Goldstone modes appear in large systems, whose energy-per-area becomes arbitrarily small and hence their relaxation times diverge if we impose over-damped dynamics. Noise excites these Goldstone modes, which rules out global order in infinite systems. Based on the observed divergence of relaxation times, we expect a similar behavior for metachronal synchronization in cilia carpets in the presence of noise [52]. The non-equilibrium dynamics in cilia carpets is thus different from other non-equilibrium dynamical models such as the Toner–Tu model of flocking birds [53]; in that two-dimensional model, global order is possible, because the active motion of agents results in a continuous exchange of neighbors. In contrast, the set of neighbors remains fixed in the cilia carpet model.

Our analysis became possible by a multi-scale simulation approach that describes beating cilia as phase oscillators [14, 30, 54]. We describe the cilia carpet as an array of phase oscillators, similar to a Kuramoto model with local coupling [41], yet where direction-dependent coupling functions are calibrated from detailed hydrodynamic simulations using a measured cilia beat pattern from Paramecium [3, 34]. Our approach tries to combine the mathematical elegance of popular minimal models that idealize beating cilia as orbiting spheres [9, 13, 25–31], and the quantitative predictive power of full-scale numerical simulations that are computationally expensive [6, 32, 33].

For technical reasons, cilia spacing in our model ($a = 18 \mu m$) is larger than in real cilia carpets ($2 \mu m$ [3]), similar to the dilute limit considered in most theoretical studies. Therefore, we underestimate hydrodynamic interactions, which are expected to scale as inverse cubed distance of cilia distance in the far field [14, 36]. In dense cilia carpets, near-field hydrodynamic interactions can change though and even steric repulsion can become important. As a consequence, we likely underestimate the characteristic value of disorder of intrinsic beat frequencies at which synchronization is lost.

Our model could be extended to systems consisting of separated cilia bundles found in airway epithelia [13]. Future refined models may include internal friction of cilia beating [13, 24, 35], and cilia waveform compliance [27, 56], which are expected to reduce and increase synchronization strength, respectively. A putative role of basal coupling of cilia contributing to synchronization [12, 56, 57] remains open for cilia carpets, and has therefore not been included here. Real cilia carpets are characterized also by quenched disorder of cilia position, and non-perfect alignment of cilia [7], which should reduce the regularity of emergent metachronal waves. Intriguingly, some disorder of metachronal coordination might actually be beneficial for transport of suspended particles, e.g. virus clearance from ciliated airways [58].
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Data availability

The data that support the findings of this study are available upon reasonable request from the authors. Python code is publically available in git repositories [59]. This publication is accompanied by supplemental material, which cites references [60–65].

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