

Synchronization and metachronal waves of elastic cilia caused by unsteady viscous flow

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Hydrodynamic coordination of cilia is ubiquitous in biology. It is commonly modeled using the steady Stokes equations. The flow around ciliated cells, however, exhibits finite-time vorticity diffusion, requiring a dynamical description. We present a model of elastic cilia coupled by unsteady viscous flow in the bulk fluid. Therein, vorticity diffusion impacts cilia coordination qualitatively and quantitatively. In particular, pairs of cilia synchronize in antiphase for long diffusion times. Moreover, metachronal waves occur in cilia chains larger than the viscous penetration depth, whereas global synchronization occurs in Stokes flow.

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Introduction. In eukaryotic life forms, hair-like cell extensions called cilia or flagella fulfill a wide variety of biological functions [1–4], ranging from swimming of microorganisms [5–7] to physiological flows in animals [8–10] and feeding of marine life [11,12]. Their cyclic motions are often strikingly coordinated, showing perfectly synchronized beating on small scales [13] and traveling waves in the beating phase, called metachronal waves, on large scales [14–16]. Inspired by the ubiquity of cilia in nature, there has been considerable effort in microengineering to replicate biological principles in artificial cilia [17–19]. The emergence of coordinated motions is often attributed to hydrodynamic interactions [20–22], described by low Reynolds number fluid dynamics [23]. In the limit of zero Reynolds number, the viscous flow is governed by the Stokes equations [24], whose fundamental solutions can be readily used to model hydrodynamic coordination [25–27]. Indeed, measurements of average flow fields around flagellated cells can be fitted by Stokes flow [28]. Thus, most models of cilia coordination use this approximation to describe hydrodynamic interactions between cilia [29–65]. For coordinated motions to arise, the kinematic reversibility of Stokes flow must be broken [66], which is most notably achieved by the elasticity of cilia [32,36,67] or by specific variations in the forces driving their motion [37].

However, recent highly temporally resolved measurements with flagellated algae indicate that the flow surrounding microorganisms fundamentally differs from Stokes flow [68]. In particular, the oscillatory flow velocity measured at a distance from the algae is phase-shifted with respect to the flagella

beating phase, and the spatial decay of the oscillatory flow velocity is faster than predicted for Stokes flow. Here, we address these observations through modeling a viscous flow by the time-dependent equations [69,70]

$$\rho \frac{\partial \mathbf{v}}{\partial t} = -\nabla p + \rho \nu \Delta \mathbf{v} + \mathbf{f}, \quad \nabla \cdot \mathbf{v} = 0, \quad (1)$$

where $\mathbf{v}$ is the velocity field, p the pressure field, ρ the fluid density, ν the kinematic viscosity, and $\mathbf{f}$ a body force density. An oscillatory forcing with period T causes an oscillatory flow that extends over the viscous penetration depth $d_v = \sqrt{\nu T}$ [71]. The unsteady flow spreads by vorticity diffusion, requiring the time $t_v = d^2/\nu$ to diffuse a distance d from the forcing [69]. Using Eq. (1) to model the microscopic flow gives good agreement between theory and experiment [72]. If the acceleration in Eq. (1) is neglected, the Stokes equations follow. This term, however, breaks the kinematic reversibility of Stokes flow, which causes synchronization independent of an external symmetry breaking [73]. The importance of the acceleration term for ciliary fluid dynamics has been noted in previous work [74,75]. In particular, its involvement in metachronal coordination has been conjectured [72].

In this Letter, we study dynamics of interacting cilia beyond the limit of zero Reynolds number, taking into account the effect of vorticity diffusion. Our model consists of small spheres rotating elastically bound on a circular orbit in the bulk fluid [elastic rotors, Fig. 1(a)], coupled to each other by unsteady viscous flows caused by their motion. We show that vorticity diffusion qualitatively and quantitatively influences synchronization and metachronal waves. Contrary to the findings in Stokes flow [36], pairs of rotors with the same chirality switch to antiphase synchronization [Fig. 1(b)] when the vorticity diffusion time and the rotation period are similar, i.e., when the reduced frequency $\tau_v = d^2/(\nu T)$ is of order one. The finite diffusion time reveals itself as a phase-delayed coupling, as we will demonstrate by reducing the rotor dynamics to coupled phase oscillators. We will use the resulting phase-oscillator model to study metachronal coordination in

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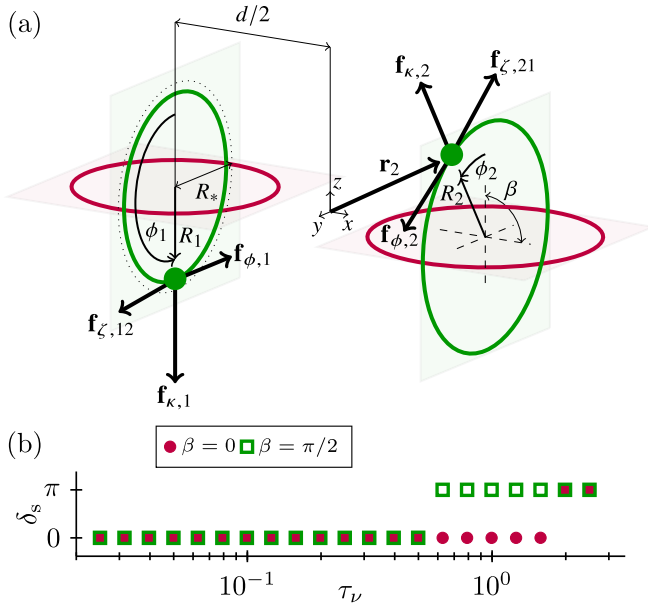


FIG. 1. (a) Geometry of elastic rotors, whose orbits are either in the same plane ($\beta = 0$, purple), or in parallel planes ($\beta = \pi/2$, green). The forces exerted on the rotors and other symbols are explained in the main text. (b) Stationary phase difference $\delta_s = \lim_{t \rightarrow \infty} \phi_1(t) - \phi_2(t)$, according to Eq. (3), as a function of the reduced frequency $\tau_v = d^2/(\nu T)$, which is the ratio of vorticity diffusion time and period of rotor motion.

chains of rotors with periodic as well as open-ended boundaries. Through simulations and linear stability analysis we show that unsteady flow affects coordination in rotor chains by increasing the wave numbers of metachronal waves. Compared to elastic rotors in Stokes flow, the collective dynamics is fundamentally different in rotor chains whose length L is much larger than the viscous penetration depth $d_v = \sqrt{\nu T}$.

Rotor model. We consider spherical rotors of radius a , as depicted in Fig. 1(a). Their positions are written as

$$\mathbf{r}_i(t) = \mathbf{r}_{c,i} + \mathbf{R}_\beta \cdot [R_i \cos \phi_i, R_i \sin \phi_i, 0], \quad (2)$$

where $i \in \{1, 2\}$, $\mathbf{r}_{c,i} = (-1)^i d/2 \mathbf{e}_x$, d is the center distance, $\mathbf{e}_x$ the unit vector in x -direction, $R_i(t)$, $\phi_i(t)$ are radius and phase in polar coordinates, respectively, and the rotation matrix $\mathbf{R}_\beta$ (Supplemental Material [76]) orients the orbits either in the same plane (purple) or in parallel planes (green). The rotors are driven by a constant tangential force $\mathbf{f}_{\phi,i} = F \mathbf{e}_{\phi,i}$ of magnitude F , where $\mathbf{e}_{\phi,i} = \mathbf{R}_\beta \cdot [-\sin \phi_i, \cos \phi_i, 0]$. A harmonic restoring force $\mathbf{f}_{\kappa,i} = \kappa(R_* - R_i) \mathbf{e}_{R,i}$ with spring constant κ , reference radius R_* , and $\mathbf{e}_{R,i} = \mathbf{R}_\beta \cdot [\cos \phi_i, \sin \phi_i, 0]$ allows deviations from a pure circular motion. The fluid exerts a viscous drag force $\mathbf{f}_{\zeta,ij} = \zeta[\mathbf{v}_j(t, \mathbf{r}_i) - d\mathbf{r}_i/dt]$, where $\zeta = 6\pi\rho\nu a$ and the background velocity field $\mathbf{v}_j$ is generated by the neighboring rotor. These forces put isolated rotors in circular motion with a period $T = 2\pi\zeta R_*/F$, while perturbations in radial direction relax on a timescale $t_\kappa = \zeta/\kappa$.

The dynamics of a small sphere in unsteady viscous flow is described by the Basset-Boussinesq-Oseen equation [77–80], which reduces to Stokes drag law if $a \ll \sqrt{\nu T}$ [76]. In this case, the rotors obey the force balance $\mathbf{f}_{\phi,i} + \mathbf{f}_{\kappa,i} + \mathbf{f}_{\zeta,ij} = 0$,

which gives the dynamics of the i th rotor as

$$\frac{d\mathbf{r}_i}{d\tau} = 2\pi \mathbf{e}_{\phi,i}(\phi_i) + \frac{1 - \bar{R}_i}{\tau_\kappa} \mathbf{e}_{R,i}(\phi_i) + \bar{\mathbf{v}}_j(\tau, \bar{\mathbf{r}}_i) \quad (3)$$

in terms of the dimensionless quantities $\tau = t/T$, $\tau_\kappa = t_\kappa/T$, $\bar{\mathbf{r}}_i = \mathbf{r}_i/R_*$, $\bar{R}_i = R_i/R_*$, and $\bar{\mathbf{v}}_j = \mathbf{v}_j T/R_*$. To describe the hydrodynamic interactions, we neglect the finite size of the orbits ($R/d \ll 1$) and retain only the leading order in the interaction strength ($a/d \ll 1$). Then, the velocity at the i th rotor, which is caused by the j th rotor, reads [76]

$$\bar{\mathbf{v}}_j(\tau, \bar{\mathbf{r}}_i) \approx 2\pi \int_0^\tau \bar{\mathbf{G}}(\tau - \tau'; \gamma, \tau_v) \cdot \mathbf{e}_{\phi,j}[\phi_j(\tau')] d\tau' \quad (4)$$

with $\bar{\mathbf{G}}(\tau; \gamma, \tau_v) = 6\pi\gamma/\tau_v [\bar{\mathbf{M}}_1(\tau) \mathbf{I} - \bar{\mathbf{M}}_3(\tau) \mathbf{e}_x \mathbf{e}_x]$, where $\gamma = a/d$, $\mathbf{I}$ is the identity matrix, and the memory kernels read $\bar{M}_\alpha(\tau) = (1 + 2\alpha\tau/\tau_v)[\tau_v/(4\pi\tau)]^{3/2} \exp[-\tau_v/(4\tau)] - \alpha \text{erf}[\sqrt{\tau_v/(4\tau)}]/(4\pi)$ [73]. Thus, the rotor dynamics (3) is parametrized by the reduced frequencies τ_κ and τ_v , which indicate the softness of the rotor orbits and the vorticity diffusion time, respectively. The time-independent fundamental solution of the Stokes equations is called the Stokeslet. We call elastic rotors coupled by the Stokes equations the Stokeslet model.

We simulate the rotor dynamics (3) with the Euler method and calculate the velocity functional (4) in each time step with the trapezoidal rule [76]. Figure 1(b) shows that the rotors synchronize either inphase ($\delta_s = 0$) or antiphase ($\delta_s = \pi$), depending on τ_v , while in the Stokeslet model ($\tau_v \rightarrow 0$) only in-phase synchronization occurs.

Figure 2(a) shows the diffusion of a vortex, emanated by an oscillating point force. The finite diffusion time causes a phase delay between the oscillatory flow velocity and the forcing [Fig. 2(b)]. We will see shortly that this phase delay causes the transition to antiphase synchronization. The phase delay grows with distance [Fig. 2(c)] as the diffusion over a larger distance takes a longer time. The growth of the phase delay is larger perpendicular to the forcing, which motivates studying rotors either in the same or in parallel planes.

Phase-oscillator model. The rotor dynamics (3) involve three inherent timescales: the period of rotor motion T , the elastic restoring time t_κ , and the vorticity diffusion time t_v . From the hydrodynamic coupling another timescale emerges: the synchronization time $t_s = O(d/a)$. In the far field, the interaction is weak ($a/d \ll 1$). Thus, synchronization is slow ($t_s \gg T, t_\kappa, t_v$). Hydrodynamic changes in the history of phases $\phi_i(\tau) = \phi_i(0) + 2\pi\tau + O(a/d)$ cause contributions of order $O[(a/d)^2]$ in the velocity (4). By neglecting these corrections and by assuming slow synchronization, we are able to derive an effective phase-oscillator model, which reflects the hydrodynamic coupling of rotors on the synchronization timescale [76]. For the phases of the two rotors we obtain the dynamics

$$\frac{d\phi_i}{d\tau} = 2\pi + A[\cos(\phi_i - \phi_j + \psi) - 2\pi\tau_\kappa \sin(\phi_i - \phi_j + \psi)] \quad (5)$$

with amplitude $A(\gamma, \tau_v) = (12\pi^2\gamma/\tau_v)\sqrt{\mathcal{X}^2 + \mathcal{Y}^2}$ and phase delay $\psi(\tau_v) = \arctan(\mathcal{Y}/\mathcal{X})$. The effect of vorticity diffusion

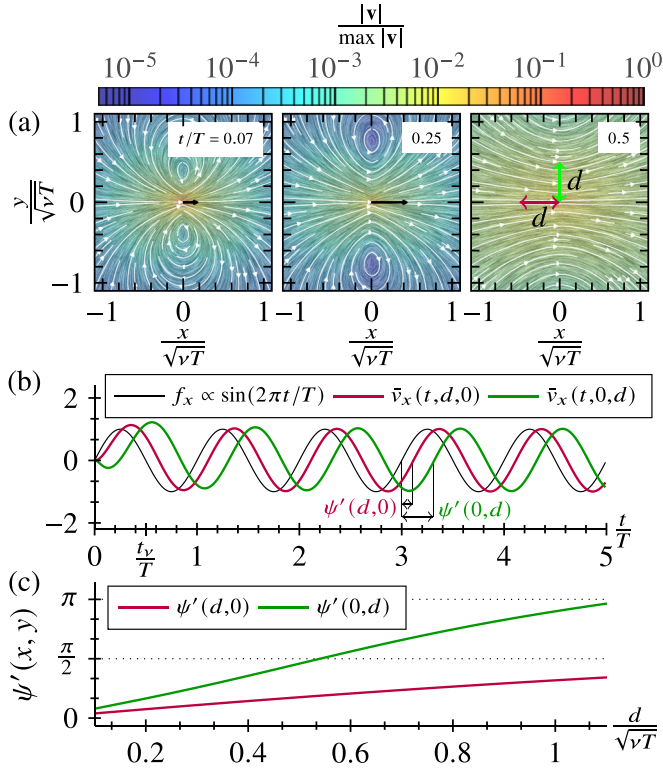


FIG. 2. (a) Bulk fluid solution of Eq. (1) for a horizontal point force $f_x \propto \sin(2\pi t/T)$, with period T . (b) Normalized velocity $\bar{v}_x(t, x, y)$ initiated by f_x at a distance $d = (\nu T/2)^{1/2}$, in vertical (green) and horizontal (purple) directions, corresponding to a vorticity diffusion time $\tau_v = T/2$. (c) Phase shift ψ' between velocity and forcing in both directions.

enters through the history integrals

$$\begin{bmatrix} \mathcal{X} \\ \mathcal{Y} \end{bmatrix} = \int_0^\infty \left(\bar{M}_1(\tau) - \frac{\bar{M}_3(\tau)}{2} \cos^2 \beta \right) \begin{bmatrix} \cos 2\pi\tau \\ \sin 2\pi\tau \end{bmatrix} d\tau, \quad (6)$$

which, in general, we solve numerically [76].

Figure 3(a) shows the memory kernel that weights the history of rotor motion [colored arrows in Fig. 3(b)] to generate the hydrodynamic coupling in the rotor model (3) and (4). The effective phase-oscillator model (5) replaces this history dependence by an effective force $\mathbf{f}_{e,j} \propto \mathbf{e}_{\phi,j}[\phi_j(\tau) - \psi]$ that acts on the fluid with a constant phase delay [black arrow

in Fig. 3(b)]. This delay reflects the finite vorticity diffusion time. Furthermore, a reduced coupling amplitude relative to the Stokeslet model [compare solid and dotted lines in Fig. 3(b)] reflects cancellation of opposing directions in the history of rotor motion. On the timescale of synchronization, phase delay ψ and amplitude A can be calculated using the long-time behavior of the coupling functionals [76], which is represented by Eq. (6).

The collective phenomena of the rotor pair are encoded in the dynamics of the phase difference $\delta(\tau) = \phi_1(\tau) - \phi_2(\tau)$ and the phase sum $\sigma(\tau) = \phi_1(\tau) + \phi_2(\tau)$. From the dynamics of phases (5) we derive

$$\frac{d\delta}{d\tau} = -\tau_s^{-1} \sin \delta, \quad (7)$$

$$\frac{d\sigma}{d\tau} = 4\pi + \omega_s \cos \delta. \quad (8)$$

Here, $\tau_s^{-1} = 2A(\gamma, \tau_v)[\sin \psi(\tau_v) + 2\pi\tau_k \cos \psi(\tau_v)]$ and $\omega_s = 2A(\gamma, \tau_v)[\cos \psi(\tau_v) - 2\pi\tau_k \sin \psi(\tau_v)]$ denote the synchronization rate and the frequency gain, respectively. Note that the phase difference obeys the well-known Adler equation [81].

In the Stokeslet model, $\psi = 0$ so that τ_s^{-1} and ω_s are strictly positive, corresponding to in-phase synchronization and a cooperative increase in rotational frequency, respectively. The crucial difference in unsteady flow is that vorticity diffusion causes a finite phase delay $\psi \neq 0$. Thus, τ_s^{-1} and ω_s can be negative, which causes antiphase synchronization and a cooperative decrease in frequency, respectively. In particular, for soft rotors with $2\pi\tau_k \gg 1$, the transition to antiphase synchronization occurs at $\psi \approx \pi/2$; for stiff rotors with $2\pi\tau_k \ll 1$, it occurs at $\psi \approx \pi$. For small phase delay $\psi \ll 1$, we obtain $\tau_s^{-1} \approx 3\pi^2\gamma\tau_k/2(5 + \cos 2\beta) + 4\pi^{3/2}\gamma\sqrt{\tau_v}(1 - 2\pi\tau_k)$. The leading order behavior of ω_s is given in the Supplemental Material [76]. Note that in the Stokeslet model ($\tau_v \rightarrow 0$), no synchronization occurs for rigid rotors ($\tau_k \rightarrow 0$), while a phase-delayed coupling can synchronize rigid rotors with a rate $\tau_s^{-1} \propto \sqrt{\tau_v}$ [73].

In general, vorticity diffusion delays the coupling of the rotors by the phase shown in Fig. 4(a), as a function of τ_v . At the phase delays indicated by the dashed lines, τ_s^{-1} changes sign, as implied by the divergences in Fig. 4(c). As a result, the synchronization mode changes from inphase to antiphase and vice versa. Note that the dependence of phase delay $\psi(\tau_v)$ on the reduced frequency $\tau_v \propto d^2$ can cause the

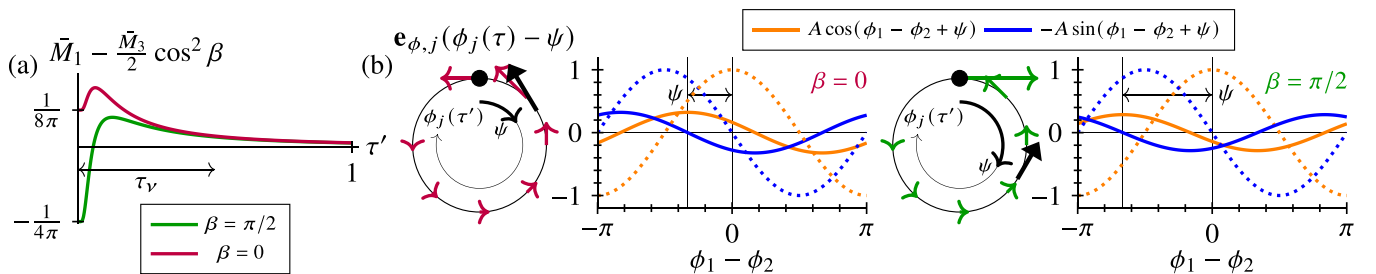


FIG. 3. (a) Memory kernel of hydrodynamic coupling. (b) In the rotor model (3) and (4), the hydrodynamic coupling depends on the history of rotor motion weighted by the memory kernel (colored arrows). In the effective phase-oscillator model (5), the coupling is caused by an instantaneous force with phase delay ψ (black arrow). The resulting coupling functions (solid lines) are shifted and have a reduced amplitude compared to the Stokeslet model with $\psi = 0$ (dotted lines).

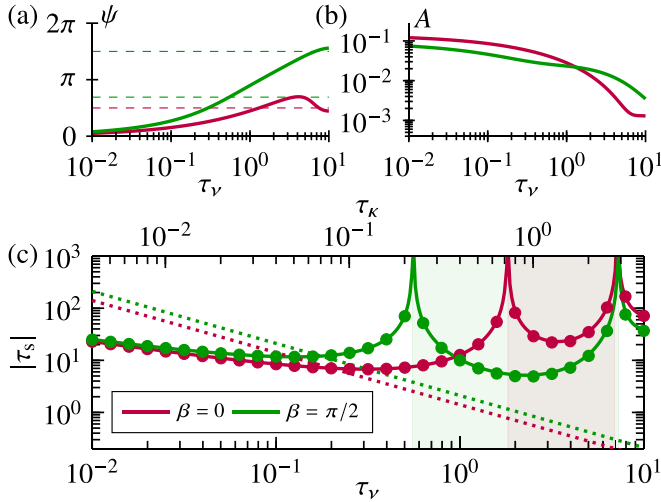


FIG. 4. (a) Phase delay, (b) coupling amplitude, and (c) synchronization time as functions of reduced frequency τ_v and τ_k . Purple and green solid lines and symbols denote data of the phase-oscillator model (5) and of the rotor model (3) and (4), respectively. The dashed lines in (a) indicate the delays corresponding to the divergences in (c). The colored regions in (c) correspond to antiphase synchronization. Dotted lines in (c) indicate the Stokeslet model, which always favors in-phase synchronization. Data are generated with $\tau_v/\tau_k = 2.5$ and $\gamma = 1/50$.

switching of synchronization mode with increasing distance. The Stokeslet model predicts that the rotors synchronize in a time inversely proportional to τ_k [dotted lines in Fig. 4(c)]. This is counteracted by vorticity diffusion, which reduces the coupling amplitude at high frequency [Fig. 4(b)], leading to optimal synchronization at a finite frequency, either inphase ($\beta = 0$) or antiphase ($\beta = \pi/2$).

Next, we use the phase-oscillator model (5) to investigate metachronal coordination in a chain of N rotors, with lattice constant ℓ (Fig. 5). The pair interactions in the chain are calculated by solving the history integrals (6) with $d_{ij} = \ell|i - j|$, where $i, j \in \{0, \dots, N - 1\}$ and $j \neq i$. This defines the coupling amplitudes $A_{ij} = A[a/d_{ij}, (d_{ij})^2/(vT)]$ and phase delays $\psi_{ij} = \psi[(d_{ij})^2/(vT)]$. From Eq. (5) we obtain the dynamic equations of the phase angles

$$\frac{d\phi_i}{d\tau} = 2\pi + \frac{1}{2} \sum_{j \neq i} [\omega_{s,ij} \cos(\phi_i - \phi_j) - \tau_{s,ij}^{-1} \sin(\phi_i - \phi_j)], \quad (9)$$

where $\tau_{s,ij}^{-1} = 2A_{ij}(\sin \psi_{ij} + 2\pi\tau_k \cos \psi_{ij})$ and $\omega_{s,ij} = 2A_{ij}(\cos \psi_{ij} - 2\pi\tau_k \sin \psi_{ij})$. We solve Eq. (9) numerically by the classical Runge-Kutta method with time step $\Delta\tau = 0.01$. We consider a periodic chain as well as a chain with open-ended boundaries. For the periodic boundaries we impose a cutoff radius of half the system size.

Metachronal waves in a periodic chain. Metachronal waves are frequency-locked solutions of Eq. (9). In the periodic chain, the metachronal waves with wave number k are generated by uniform phase shifts $\phi_i - \phi_{i+1} = \ell k$ with $|k| = 2\pi K/N$, where K is an integer. We perform a linear stability analysis of such a wave [76] and obtain the growth rates of

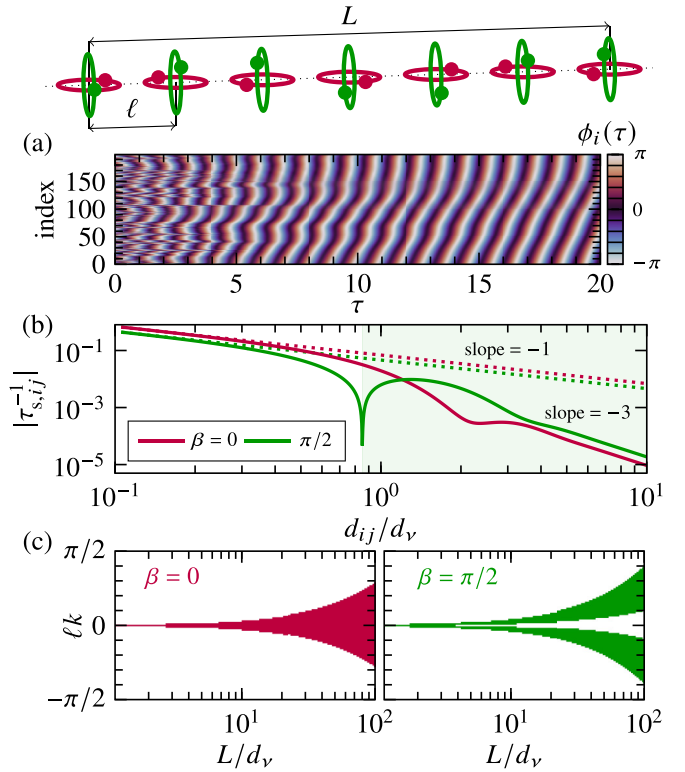


FIG. 5. Metachronal waves in a periodic chain with $N = 200$ and $\tau_k = 0.2$. (a) Formation of a metachronal wave from random initial conditions in a simulation of Eq. (9) with $\beta = \pi/2$, $a/\ell = 1/20$, and $L/d_v = 10$. (b) Synchronization rate as a function of distance. The colored region indicates $\tau_s^{-1} < 0$ for $\beta = \pi/2$ and the dotted lines show data of the Stokeslet model. (c) Range of wave numbers k for which metachronal waves are stable (colored regions) as a function of L/d_v .

perturbations $\text{Re } \lambda_n(k) = -\sum_{j=1}^m 1/\tau_{s,0j} \cos(j\ell k) + \sum_{j=1}^m 1/\tau_{s,0j} \cos(j\ell k) \cos(2\pi jn/N)$, where $n \in \{0, \dots, N - 1\}$, $m = (N - 1)/2$ for odd N , and $m = N/2 - 1$ for even N . A wave with wave number k is linearly stable if $\text{Re } \lambda_n < 0$ for all n . We discard $\text{Re } \lambda_0$, which reflects the symmetry of Eq. (9) with respect to a global phase shift.

In the Stokeslet model, the synchronization rate decays slowly as $\tau_{s,ij}^{-1} \propto d_{ij}^{-1}$ and metachronal waves are never stable [38,45]. In our model, however, stable waves emerge from random initial conditions [Fig. 5(a)], because vorticity diffusion crucially affects the spatial decay of synchronization rate [Fig. 5(b)]. Beyond the penetration depth $d_v = \sqrt{vT}$, the decay crosses over to $\tau_{s,ij}^{-1} \propto d_{ij}^{-3}$, which stabilizes metachronal waves. In Stokes flow, a similar effect occurs at surfaces [38,45]. Furthermore, in our model the synchronization rate can become negative, as indicated by the divergence for $\beta = \pi/2$ in Fig. 5(b). Here, rotor pairs separated by a distance $d_{ij} \gtrsim d_v$ synchronize in antiphase. This renders the globally synchronized collective state unstable. Thus, the infinite wavelengths $\ell k = 0$, which are exclusively stable in the Stokeslet model, are unstable [$\beta = \pi/2$ in Fig. 5(c)].

Whether vorticity diffusion causes metachronal waves depends on the ratio of chain length $L = N\ell$ and penetration depth d_v , as seen in Fig. 5(c). Here, bands of stable wave numbers [colored regions in Fig. 5(c)] emerge from $\ell k = 0$

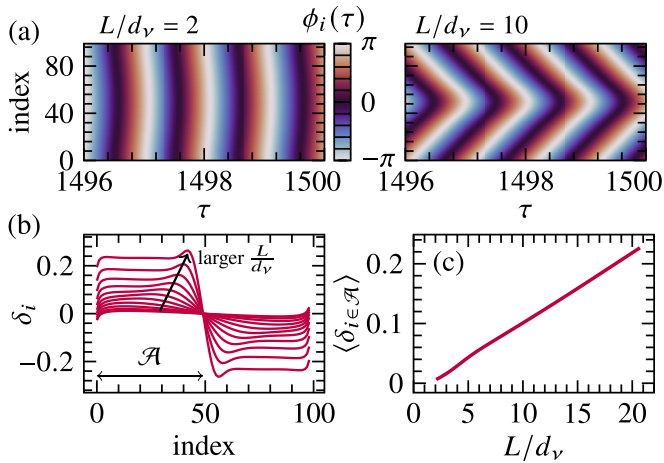


FIG. 6. Simulation of an open-ended chain with $\beta = 0$, $a/\ell = 10^{-2}$, $N = 100$, and $\tau_k = 1$. (a) Emergent phases $\phi_i(\tau)$ for various L/d_v . (b) Steady-state phase shifts $\delta_i = \phi_i - \phi_{i+1}$ for $L/d_v \in [2, 20]$. (c) Half chain average of phase shifts $\bar{\delta} = \langle \delta_{i \in \mathcal{A}} \rangle$ as function of L/d_v , where $\mathcal{A} = \{0, 1, \dots, N/2 - 1\}$.

as L/d_v increases. Notably, long wavelengths (small ℓk) can either be stable ($\beta = 0$) or unstable ($\beta = \pi/2$).

Metachronal coordination in an open-ended chain. In the periodic chain, unidirectional metachronal waves [Fig. 5(a)] emerge from random initial conditions with various wave numbers from the linearly stable band. In a chain with open boundaries, the symmetry between left and right neighbors is broken at the chain ends. Figure 6 shows an example for the collective motion in this geometry. Here, the phases $\phi_i(\tau)$ attain a pattern comprised of two oppositely directed metachronal waves, which is akin to a chevron pattern [Fig. 6(a)]. The two waves are characterized by non-uniform steady-state phase shifts $\delta_i = \phi_i - \phi_{i+1}$, which have opposite sign in the left and right half of the chain, respectively [Fig. 6(b)]. We use the half chain average of phase shifts $\bar{\delta}$ to associate a wave number $\ell \bar{k} = \bar{\delta}$ to the chevron pattern. The dependence of this wave number on the viscous penetration depth reveals once more the importance of vorticity diffusion. Namely, the unsteady flow increases the wave number $\ell \bar{k}$ [Fig. 6(c)]. While the phases for large penetration depth are almost globally synchronized [$L/d_v = 2$ in Fig. 6(a)], vorticity diffusion generates wave propagation in chains with short penetration depth [$L/d_v = 10$ in Fig. 6(a)].

Discussion. In living matter, the linear extensions of ciliated systems range over several orders of magnitude, while the beating frequency is typically of the order of 10 Hz [1]. The two flagella of the algae *Chlamydomonas reinhardtii* are separated by a few micrometers [6]. Unicellular organisms, such as *Paramecium*, have densely ciliated surfaces, extending over some hundred micrometers [5]. Large ciliated tissues, such as in brain ventricles [9], extend up to the centimeter scale. Whether finite-time vorticity diffusion qualitatively impacts cilia coordination can be estimated as follows. For pair coordination, antiphase synchronization requires at least a phase delay $\psi(\tau_v) \approx \pi/2$, which corresponds to a reduced frequency $\tau_v = d^2 f / \nu \approx 0.3$ [Fig. 4(a)]. Thus,

in water at body temperature with $\nu \approx 0.7 \text{ mm}^2/\text{s}$, rotors with a frequency $f \approx 50 \text{ Hz}$ would synchronize in antiphase when separated by a distance $d \approx 65 \mu\text{m}$. In tissue, the typical separation between cilia bundles can be comparable [82]. Furthermore, the properties of metachronal waves in cilia chains are strongly affected by vorticity diffusion if $L/d_v \gtrsim 10$ [Figs. 5(c) and 6(c)]. With f and ν as before, the penetration depth is $d_v = \sqrt{\nu/f} \approx 140 \mu\text{m}$. Thus, vorticity diffusion becomes significant on a length scale $L \gtrsim 1.4 \text{ mm}$. However, in ciliated systems smaller than the penetration depth, no qualitative impact on the wave dynamics is expected. Nevertheless, vorticity diffusion has an effect on small length scales. Namely, the rate of synchronization of rotor pairs contains an $O(\tau_k)$ term reflecting orbit compliance, as well as an $O(\sqrt{\tau_v})$ term reflecting vorticity diffusion. For nodal cilia, the elastic relaxation time $t_k = \zeta/\kappa$ is estimated between $2 \times 10^{-4} \text{ s}$ and $2 \times 10^{-5} \text{ s}$ [36]. Using our analytical expression for τ_s^{-1} with $f = 10 \text{ Hz}$, $d = 10 \mu\text{m}$, $\beta = 0$, and ν as before, we get a 5- to 50-fold increase in synchronization rate compared to the simple Stokeslet model, whose exclusive contribution to synchronization is through orbit compliance.

The phase delay and the spatial decay of coupling amplitude in our phase-oscillator model are in line with measurements on flows around flagellated cells [68,70]. There, the oscillatory flow at large distances decays as $1/d^3$ in contrast to what is expected for Stokes flow ($1/d$). Moreover, the flow is phase-shifted relative to the flagella beat. This phase shift grows with distance and strongly depends on the direction, along which the phase shift is measured. These characteristics of microscopic flow are reflected in our model by the spatial decay of synchronization rate τ_s^{-1} [Fig. 5(b)] and the phase delay ψ depending on reduced frequency [Fig. 4(a)], respectively.

In biology, cilia are attached to cell surfaces, whose presence influences the flows through which they are coupled considerably. The cilia near a surface generate a directed net flow, which prompts a dependence of wave properties on the direction of this net flow [65]. Steady flow fields near surfaces decay throughout space proportional to $1/d^3$, which facilitates metachronal waves with finite wavelengths in models of elastic cilia [7,65]. Long-range interactions near surfaces nevertheless contribute significantly to the selection of wave numbers [83]. To further unravel the involvement of unsteady flows in hydrodynamic coordination of cilia, our theory could be extended using the unsteady Green's function of Eq. (1) subject to a no-slip condition at a surface [84].

Our model is highly simplified and does not capture several important aspects, such as complicated filament motion [58], variable driving forces during power and recovery stroke [37,38], surface effects [7,55,65], and near-field hydrodynamics [63,85]. However, our work gives a first account of the generic phenomena expected for elastic rotors interacting through unsteady flows and provides estimates for the scales at which they occur. Importantly, we have shown that the effects of unsteady flow on synchronization and wave dynamics can be captured by a simple phase-oscillator model. This provides a convenient platform for more realistic modeling of hydrodynamic coordination in biological and artificial cilia. The predictions of our theory are suitable for experimental tests with optical-tweezer experiments [27,86,87].

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