Soft Matter

REVIEW

Hydrodynamic synchronization at low Reynolds number†

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After a long gap following the classic work of Taylor, there have recently been several studies dealing with hydrodynamic synchronization. It is now apparent that synchronization driven by hydrodynamic interactions is not only possible, but relevant to the efficiency of pumping by arrays of cilia and to bacterial swimming. Recent work has included experiments demonstrating synchronization, both in model systems and between bacterial flagella. The effect has been demonstrated in model swimmers and pumps, and large scale simulations have been used to investigate synchronization of cilia and of sperm cells. In this review article, we summarize the various experimental and theoretical studies of hydrodynamic synchronization, and put them in a framework which draws parallels between the different systems and suggests useful directions for further research.

I. Introduction

Reynolds number (Re) is defined as the ratio between typical scales of the inertial forces and the viscous forces in the Navier–Stokes equation, which describes the time evolution of fluid flow. For a fluid with mass density ρ and viscosity η that flows with typical velocity v in a region controlled by boundaries of typical length scale ℓ, we have $Re = \rho v \ell / \eta$. In the low Re regime, which could be due to small size and/or high viscosity, hydrodynamics is governed by viscous forces. For microorganisms in water, with typical values $\ell \sim 10\ \mu m$ and $v \sim 10\ \mu m\ s^{-1}$, $Re \sim 10^{-4}$. Therefore, microorganisms live the "life at low Reynolds number".[1]

Towards the end of his distinguished career, which resulted in numerous ground-breaking contributions to solid mechanics and fluid dynamics,[2] G. I. Taylor turned his attention to swimming and hydrodynamic activities of microorganisms.[3] He realized that the absence of inertia means that the conventional knowledge about hydrodynamics of swimming cannot be used to describe how microorganisms propel themselves, and showed,

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† This paper is part of a *Soft Matter* themed issue on Active Soft Matter. Guest editors: Fred MacKintosh and Mike Cates.

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using extensive arguments and explicit calculations, how force-free swimming in a viscous medium is possible. In the same paper, he then went on to propose an original idea, which forms the subject of this review article. Through interactions with the Cambridge zoologist James Gray, Taylor was fascinated to learn of the observations made by several people that when two or more spermatozoa get close to each other their tails tend to beat synchronously.[4] He proposed that hydrodynamic interaction could explain this dynamical phenomenon, and made a calculation that suggested having in-phase synchronized beating minimizes the rate of energy dissipation.[3]

Viscous hydrodynamics is governed by Stokes equation for the fluid velocity field $v_i(\mathbf{r})$ ($i = x,y,z$), which reads

$$-\eta\partial^2 v_i = -\partial_i p + f_i, \tag{1}$$

where $\partial_i \equiv \dfrac{\partial}{\partial r_i}$, $\partial^2 \equiv \partial_i\partial_i$ with summation over repeated indices implicit, p is the hydrostatic pressure, and f_i is the density of the body force exerted on the fluid. The incompressibility of the fluid puts a constraint on the velocity field, $\partial_j v_j = 0$, which can be used to nominally solve for pressure in eqn (1) as $p = \left(\dfrac{1}{\partial^2}\right)\partial_j f_j$. Putting the expression for pressure back in eqn (1), we find the governing equation for viscous hydrodynamics

$$-\eta\partial^2 v_i = \left(\delta_{ij} - \frac{\partial_i\partial_j}{\partial^2}\right)f_j. \tag{2}$$

Eqn (2) shows that the velocity profile in the medium is determined by the distribution of body forces as well as boundary conditions, through a tensorial Poisson equation that suggests an electrostatic analogy. Eqn (2) is reversible, in the sense that for any solution $\mathbf{v}$ corresponding to $\mathbf{f}$, the reverse flow with velocity $-\mathbf{v}$ will be a solution when the force changes to $-\mathbf{f}$. This poses a fundamental difficulty in creating a net directed flow from a periodic activity that involves equal half cycles of $\mathbf{f}$ and $-\mathbf{f}$, such as swimming or pumping strokes. For a point force $\mathbf{F}$ located at the origin, eqn (2) yields a fluid velocity at point $\mathbf{r}$ that reads

$$v_i(\mathbf{r}) = \frac{1}{8\pi\eta r}\left(\delta_{ij} + \frac{r_i r_j}{r^2}\right)F_j, \tag{3}$$

which defines the Green's function for viscous hydrodynamics, eqn (2), called the Oseen tensor.[5] In analogy to electrostatics, the Green's function for point forces near planar[6] or spherical[5] boundaries can also be calculated and understood *via* the method of images.

The long-ranged nature of hydrodynamic interaction apparent from eqn (3) suggests that a collection of active components that dynamically exert forces on the fluid medium they are immersed in could influence each other very strongly, leading to the possibility of novel collective behaviors. This suggests a strong analogy to chemotaxis, where the slowly decaying concentration field near a particle source, $C(r) \sim 1/r$, is used for chemical signalling. It would be interesting to discover what capacities exist for *hydrodynamic signalling*.

Since the original work of Taylor in 1951, active hydrodynamics at low Reynolds number has been the subject of intense investigation in a variety of different contexts. Here, we aim to review a collection of these studies, with an emphasis on the possibility of achieving synchronization, solely *via* hydrodynamic interactions, between active components that undergo independent cyclic motion or deformation.

The rest of the paper is organized as follows. Section II gives a brief overview of the general subject of low Reynolds number hydrodynamics of active particles, such as swimming microorganisms and beating cilia, with emphasis on elements that can lead to hydrodynamic synchronization. Section III is devoted to a comprehensive discussion of the many studies of hydrodynamic synchronization, ranging from detailed simulations of beating elastic filaments to synchronization of swimmers and minimal model systems represented by simple beads, through to experiments. This is followed by discussion of a number of generic features of hydrodynamic synchronization in Sec. IV, and concluding remarks in Sec. V.

II. Active hydrodynamics at low Reynolds number

Before focusing on the specific dynamical phenomenon of synchronization, we first give a brief overview of the subject of active viscous hydrodynamics.[7]

A. Observations, discoveries, and experimental developments

Nature has developed a number of mechanically active components such as cilia and flagella that are capable of moving the neighboring fluid for the purpose of motility, transport (of mucus, for example), feeding (*e.g.* for sponges), or pumping. Bacterial flagella are relatively rigid helical proto-filaments that are attached to highly efficient rotary motors in bacteria such as *E. coli*.[8–10] An *E. coli* could have 6–10 such flagella around its body, and their coordinated action could lead to two distinct types of motion, termed as "run" (when the flagella bundle up and corkscrew together) and "tumble" (when the flagella disorganize and net motility is lost).[11] Cilia (and eukaryotic flagella) are elastic filaments that can cyclically actuate into different conformations.[12] This ability comes from the so-called axonemal structure, which is an assembly of nine microtubule doublet filaments that can slide along one another *via* dynein motor proteins.[13,14] The oscillating beating patterns are believed to be the result of a nonlinear feedback mechanism involving the

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combination of the collective activity of molecular motors and the elasticity of the microtubules.[15–17]

Cilia often appear in the form of arrays that beat with some kind of pattern across the array to generate large scale motion.[4] The beating cycle of an individual cilium is characteristically irreversible: it consists of an *effective stroke* (or *power stroke*) in the first half-cycle when the cilium is sticking out and pushing the fluid to one side, and a *recovery stroke* in the second half-cycle when the cilium is bent (almost folded) and returning to the original conformation.[18] This time irreversibility is a necessity if the beating is to achieve a net movement of the fluid to one side after a full cycle, in light of the reversibility property of the Stokes equation (see above). When positioned in an array, the presumably independent cyclic motion of the cilia is observed to produce large scale patterns[4] called *metachronal waves*. Similar ciliary deformation cycles have been observed to lead to a variety of different forms of metachronism, with varying relative orientations between the direction of the propulsion of water and the direction of the wave propagation,[19] in a way which is sensitive to membrane voltage and calcium levels.[20] The cilia-generated flow is not only used as a means of self-propulsion. There are indications that flow produced by nodal cilia is responsible for the establishment of left and right symmetry breaking in developing embryos.[21]

Cooperativity has been observed in other hydrodynamically active living systems. For example, it has been observed that a group of sperms with dynamically beating tails could self-organize into a vortex above a solid substrate,[22] and that the spherical algae *Volvox* can form a stable hydrodynamic bound-state when they are near a solid surface.[23] A recent experiment by Polin *et al.* probed the dynamics of the two flagella that the algae *Chlamydomonas* use for swimming.[24] It revealed that the beatings of the two flagella occur in two distinct synchronous and asynchronous modes (see Fig. 1), and that the

synchronization and the stochastic transitions between the two modes could result from the hydrodynamic interactions between the flagella.[25]

Suspensions of swimming bacteria have been shown to exhibit enhanced activity, characterized by short time super-diffusive motion of tracer particles with a crossover to diffusive behavior at longer times, with much enhanced effective diffusion coefficient[26–28] and correlated temporal fluctuations.[29] Moreover, sufficiently dense bacterial suspensions develop instabilities and complex large scale flow patterns that are reminiscent of the behavior of turbulent flows.[30] Similarly, bacterial carpets (dense layers of bacteria with their heads adsorbed on substrate and hydrodynamically active tails) cause enhanced diffusion of tracer particles and complex flow patterns with "whirlpools" and "rivers" near the substrate.[31]

Inspired by the hydrodynamic activity of biological organelles and living cells, a number of artificial microswimmers and micro-pumps have been made recently, using magnetic actuation of assemblies of super-paramagnetic colloidal beads[32,33] and manipulation of colloids by optical tweezers.[34] It has also been possible to fabricate artificial cilia driven by magnetic actuation.[40,41] A different class of microswimmers, which takes advantage of nonequilibrium interfacial self-phoretic effects, has also been developed recently,[35–37] and shown to allow a variety of controlled trajectories[38] and to exhibit chemotactic behavior.[39]

B. Theoretical developments

The pioneering works of Taylor[3,42] and a contemporary contribution from Lighthill that introduced the "squirmer" model of microswimming[43] were the starting point for the theoretical studies of active hydrodynamics at low Reynolds number.[44] Initial developments were focused on swimming of microorganisms that use a single elastic tail,[45,46] but they were soon followed by studies of more elaborate phenomena, including the beating patterns of cilia and metachronism.[47–49]

The reversibility of eqn (2) makes it difficult to achieve self-propulsion when there are only a few degrees of freedom available. Purcell showed that a single compact degree of freedom cannot be used for swimming at low Reynolds number and a minimal model swimmer would at least need two such degrees of freedom.[1] His ideas were later used to develop and study simple model microswimmers that undergo prescribed[63–71] and stochastic[72,73] cyclic deformations, which envelope a nonzero enclosed area in the two dimensional configuration space. The cyclic nature of the configuration space trajectory implies the existence of an internal phase for every micro-swimmer, which can strongly affect the interaction between two microswimmers[74,75] and lead to the formation of novel, collective, symmetry-breaking, swimming phases.[76,77] The idea of collective nonlinear oscillations of molecular motors—in analogy to the driving mechanism of the axoneme[16]—has been used to develop a dynamical model for driving of the deformation cycle of a three-sphere microswimmer model.[78] The concept of internal phase can also be introduced for stochastic swimmers in terms of the transition rates for the different conformational changes.[79]

Interaction between hydrodynamically active particles in bulk suspensions and confined geometries (*e.g.* bacterial suspensions
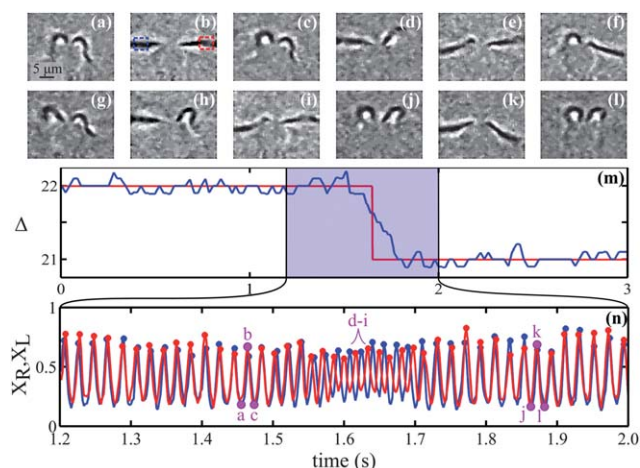

Fig. 1 High-speed imaging probe of the beating patterns of the the flagella of *C. reinhardtii* and the observed phase slip. (a)–(l) snapshots at times indicated in the lower panel (n). (m) Phase difference between the flagellar beating patterns as a function of time. (n) Signals from the indicated areas in panel (b) near the two flagella. Picture reproduced from[25] courtesy of Raymond Goldstein and by permission from the American Physical Society, copyright 2009 (doi:10.1103/Phys-RevLett.103.168103).

and carpets) leads to complex dynamical behaviors[50–52] and fascinating collective effects. Using continuum theories based on phenomenological extensions of the hydrodynamic theory for liquid crystals,[53,54] these active fluids have been studied and found to have instabilities and novel rheological properties,[55–58] which could lead to complex flow patterns as observed in numerical simulations.[59–62]

III. Studies of hydrodynamic synchronization

A. Synchronization: a general perspective

Synchronization is a ubiquitous phenomenon in nature, with a wide variety of examples known in physics, chemistry, biology, engineering, and social sciences.[80] It is defined as the spontaneous uniformity of the phases and/or frequencies of two or many interacting oscillators. Theoretical models of synchronization are often reduced to the phase description, in which the phase $\phi_i = \phi_i(t)$ of the i-th oscillator ($i = 1,2,\ldots,N$) is taken as the dynamical variable. A generic form of the evolution equation is

$$\frac{d\phi_i}{dt} = \omega_i - \sum_{j \neq i} G(\mathbf{r}_i - \mathbf{r}_j) V'(\phi_i - \phi_j), \quad (4)$$

where ω_i is the intrinsic frequency and $\mathbf{r}_i$ is the position of the i-th oscillator, and $G(\mathbf{r})$ is an interaction kernel. The function $V(\phi)$ is a periodic "potential" with a minimum at $\phi = 0$, which drives the system towards the fully synchronized state ($\phi_i = \phi_j$ for any i,j).

In an array of coupled oscillators, collective oscillation may or may not occur depending on the range of the interaction. The phase coherence is characterized by the macroscopic order parameter $S = \frac{1}{N}\left|\sum_i e^{i\phi_i}\right|$, with $S = 1$ in the fully ordered (synchronized) state and $S = 0$ in the disordered (unsynchronized) state. For the mean-field coupling $G(\mathbf{r}) = g_0/N$ ($g_0 = $ const.), collective oscillation with global phase coherence takes place if g_0 exceeds a critical value g_c, which is determined by the distribution of the intrinsic frequencies.[81] The mean-field models exhibit the critical behavior $S = (g_c - g_0)^\beta$ near the transition point, where $\beta = \frac{1}{2}$ or 1 depending on the functional form of $V(\phi)$.[81–83] In contrast, for a short-range (e. g. nearest-neighbor) coupling, global synchronization is not possible.[84] For a long-range coupling $G(\mathbf{r}) \propto 1/r^\alpha$ with $V(\phi) \propto -\cos\phi$, it is shown that global phase coherence is possible if $\alpha < \frac{3}{2}d$.[85] Frequency entrainment without global phase coherence is predicted to be possible for $\frac{3}{2}d < \alpha < \frac{5}{2}d$.[85]

The hydrodynamic interaction is long-ranged with the exponent α being controlled by the geometry of the system. Active elements that exert force monopoles in the bulk interact via the Oseen tensor [see eqn (3)] corresponding to $\alpha = 1$, while force dipoles in the bulk or force monopoles near a surface interact with the dipolar interaction that corresponds to $\alpha = 3$ at large distances. The exponent and the spatial dimension of the array determine whether collective synchronization is possible or not. The anisotropic (tensorial) nature of the hydrodynamic interaction adds a twist to the problem. The anisotropy of the interaction can couple with the structural anisotropy of the oscillators to cause synchronization, as we shall see in more detail below.

B. Models of hydrodynamic synchronization: direct approaches

Synchronization induced by hydrodynamic interactions has been studied with models at various levels of complexity, ranging from direct simulations of elastic filaments/sheets to reduced description by coupled phase oscillator models. In an early work, Gueron and Levit-Gurevich[49] modeled cilia by inextensible elastic filaments with hydrodynamic interaction. They showed that a linear array of cilia exhibit a traveling wave that looks like a metachronal wave. Kim and Netz[86] simulated an array of semiflexible filaments grafted to a surface as shown in Fig. 2, using a Brownian dynamics method. In their study, the filaments were driven at the bottom by a prescribed torque vertical to the substrate. They showed that phase-locking occurs autonomously due to hydrodynamic interactions and enhances the pumping efficiency. The relation between dissipation rate and synchronization was also studied by Elfring and Lauga.[87] In the spirit of Taylor, they considered a model of two elastic sheets with propagating lateral waves with a prescribed waveform. Their analysis shows that front-back asymmetry of the waveform causes either in-phase or anti-phase synchronization, which would minimize or maximize the dissipation rate, respectively. Guirao and Joanny[88] modeled cilia as semiflexible filaments with internal forces described by a two-state model of molecular motors. They showed analytically that spontaneous breaking of the beating symmetry occurs in an array
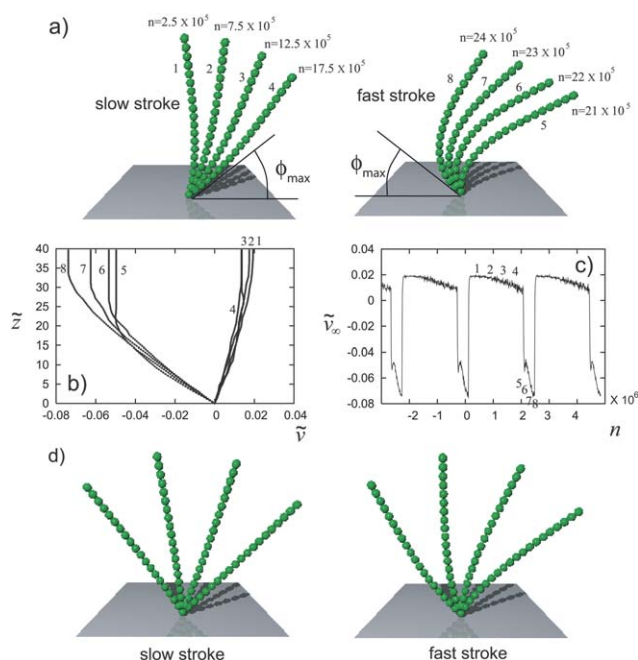

Fig. 2 (a) Snapshots showing the conformation of beating elastic filaments in a Brownian dynamics simulation, with relatively slow (left) and fast (right) strokes. The index n refers to the simulation time. (b) The flow profile as a function of distance from the wall, with the number indices referring to the corresponding conformations in (a). (c) Scale of the bulk fluid pumping velocity as a function of time during the beating cycle. (d) Snapshots of a relatively stiffer elastic filament. Picture reproduced from[86] courtesy of Roland Netz and by permission from the American Physical Society, copyright 2006 (doi:10.1103/PhysRevLett.96.158101).

of cilia, due to macroscopic flow created by synchronization of the beating. These direct approaches have been extremely helpful in elucidating the role of hydrodynamic interactions in realistic situations. However, the complexity of the dynamics of elastic filaments makes it very difficult for such studies to go as far as studying the phase behavior and collective properties of large numbers of hydrodynamically active objects.

C. Hydrodynamic synchronization of swimmers

The original observations of Gray[4] and the more recent experiment on vortex formation of sperms above solid substrates[22] suggest that hydrodynamic synchronization of free low Reynolds number swimmers is a very rich and fascinating—and yet relatively unexplored—subject. Yang et al.[89] modeled swimming sperms as semiflexible filaments with actively bending tails with a prescribed amplitude and frequency. In their 2D simulation, they showed that two sperms attract each other by hydrodynamic interactions, and that the head-head distance decreases with the phase difference. In a multi-sperm system, they obtained swarm behavior with a power-law dependence of the average cluster size on the width of the distribution of the beating frequency. These studies suggest that synchronization of free swimmers is a more complex problem than that of active filaments constrained in fixed positions, as the mutual distances between the swimmers vary with their phases.

Putz and Yeomans[90] extended the definition of a simple linear, three-sphere model swimmer to permit variable stroke periods, hence allowing them to study the phase synchronization of free swimmers. They found that, in general, two swimmers synchronize to a phase difference of 0 or π, depending on their relative positions. For three swimmers the relative phases oscillate, together with a superimposed drift in time, as the swimmer positions vary. The locking is slow, typically taking thousands of swimmer cycles, and becoming slower with increasing separation.

D. Minimal models of hydrodynamic synchronization

The necessary ingredients for hydrodynamic synchronization have been illustrated using a variety of reduced models, in which each active element has a few degrees of freedom, including the phase variable. Kim and Powers[91] showed that two rotating rigid helices with fixed parallel axes do *not* synchronize under constant driving torque. By numerical analysis and symmetry arguments, they proved that hydrodynamic interaction acts to neither enhance nor destroy phase locking. The neutral role of hydrodynamic interaction is well illustrated by a bead model of cilia, due to Ryskin and Lenz.[92] Following them, we consider two rigid spherical beads of radius a, each constrained on a circular trajectory of radius b and suspended at a fixed height h above a substrate. Each bead is driven by a constant torque τ, or equivalently, a tangential force $F = \tau/b$. This corresponds to the case $\delta = \pi/2$ of the model shown in Fig. 3. The centre positions of the trajectories $\mathbf{r}_1$ and $\mathbf{r}_2$ are separated by distance $d \gg b$. The phase $\phi_i = \phi_i(t)$ of the i-th bead ($i = 1,2$) specifies its position as $\mathbf{R}_i = \mathbf{r}_i + b\mathbf{n}(\phi_i)$ and velocity as $\dot{\mathbf{R}}_i = b\dot{\phi}_i\mathbf{t}(\phi_i)$, where $\mathbf{n}(\phi_i) = (\cos\phi_i, \sin\phi_i, 0)$ and $\mathbf{t}(\phi_i) = (-\sin\phi_i, \cos\phi_i, 0)$ are the radial and tangential unit vectors of the trajectories. The equation of motion is obtained by balancing the driving force
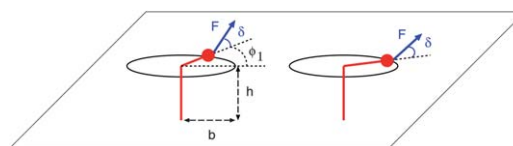

Fig. 3 Spherical beads on circular trajectories exerting constant force F on the surrounding fluid. The beads are supported by L-shaped thin arms of height h from a substrate. The force is parallel to the substrate and makes a finite angle δ from the radial direction. The model reduces to rigid beads driven by constant torque for $\delta = \pi/2$, and the simple cilia model[88] for $\delta = 0$. The δ-dependence of the collective dynamics have been studied in.[100]

$$\mathbf{F}_i = F\mathbf{t}(\phi_i), \qquad (5)$$

$6\pi\eta a$ is the friction coefficient of the bead. The fluid velocity is related to the force via the Oseen-Blake tensor[5,6] $\mathbf{G}(\mathbf{r})$ as $\mathbf{v}(\mathbf{R}_i) \simeq \sum_{j \neq i}\mathbf{G}(\mathbf{r}_i - \mathbf{r}_j) \cdot \mathbf{F}_j$. Then we obtain the phase velocity as

$$b\frac{d\phi_i}{dt} = \frac{\mathbf{t}(\phi_i) \cdot \mathbf{F}_i}{\zeta} + \sum_{j \neq i}\mathbf{t}(\phi_i) \cdot \mathbf{G}(\mathbf{r}_i - \mathbf{r}_j) \cdot \mathbf{F}_j. \qquad (6)$$

From eqn (5) and the symmetry relation $\mathbf{G}(\mathbf{r}) = \mathbf{G}(-\mathbf{r})$, we see that the right hand side of the dynamical equation is invariant with respect to exchanging ϕ_1 and ϕ_2. This means that the phase difference $\Delta\phi = \phi_2 - \phi_1$ is constant and is unaffected by the hydrodynamic interaction.[92]

Thus we have seen that the rigid bead model with constant torque is too simple to produce phase locking solutions. One possible direction of modification is to introduce extra degrees of freedom by adding some flexible elements to the model. Reichert and Stark[94] have shown that two rotating rigid helices can synchronize if they are tethered by harmonic springs so that they can tilt and move parallel to each other. The idea of anchoring rigid rotors by springs has been implemented experimentally by Qian et al.[95] They used two rotating paddles with their shafts anchored by torsional springs which allowed the shafts to tilt slightly. They found that paddles that are asymmetric with respect to the shafts synchronize with the phase difference $\Delta\phi = 0$ (in-phase synchronization), while symmetric paddles are stabilized at $\Delta\phi = \pi/2$, in agreement with their numerical simulation results. Niedermayer et al.[96] modeled cilia by rigid beads that were softly anchored to circular trajectories by harmonic potentials. The additional freedom of radial displacement was shown to be essential to producing a phase-locked state for two cilia and a metachronal traveling wave for a chain of cilia. Guirao and Joanny[88] presented an even simpler description of cilia, where the beating motion in a plane vertical to the surface is averaged over a cycle and is replaced by a constant radial force. This corresponds to the case $\delta = 0$ of the model shown in Fig. 3. It creates a flow field that tends to align the rotors, which is regarded as phase synchronization with zero intrinsic frequency. Under thermal agitation, an array of rotors exhibits a transition from the orientationally disordered (isotropic) state to the ordered (nematic) state.

Cosentino Lagomarsino et al. have studied two related models of metachronal coordination using one dimensional arrays of linear oscillators.[98,99] Using an asymmetric flashing ratchet

model with two distinct modes mimicking the effective stroke and the recovery stroke of cilia, they showed that spontaneous symmetry breaking leading to a unidirectional flow is possible.[98] In a subsequent work, they used a "rower" model for cilia with two internal degrees of freedom (displacement and internal state), and showed that a 1D array of such active oscillators can sustain traveling wave solutions (metachronal waves) under certain conditions.[99] We note that studying synchronization of linear oscillators is more delicate than orbiting particles, as the phase degrees of freedom couple with both the forces and the displacements.[90,99]

Uchida and Golestanian[100] have generalized the model defined in Fig. 3 by assuming the force angle δ to have an arbitrary value between 0 and π/2. They considered the collective dynamics of rotors arrayed on a square lattice with the grid size $d \gg h$. The equation of motion is obtained by using

$$\mathbf{F}_i = F[\sin\delta \cdot \mathbf{t}(\phi_i) + \cos\delta \cdot \mathbf{n}(\phi_i)], \qquad (7)$$

in eqn (6), for $i = 1,2,\ldots,N$. To see that this model contains the necessary elements for synchronization, let us first consider two such oscillators. Using eqn (6) and (7), we can write down the dynamical equation for the phase difference,

$$\Delta\dot{\phi} = -\omega\gamma\cos\delta \sin\Delta\phi, \qquad (8)$$

where $\omega = F/(6\pi\eta ab)$ is the characteristic frequency and $\gamma = 9ah^2/d^3$ is the dimensionless coupling constant. One can readily see that for $\delta \neq \frac{\pi}{2}$, two such rotors can synchronize, as eqn (8) has a stable fixed point at $\Delta\phi = 0$.

Let us now consider a 2D array of active rotors. When γ is small such that $\gamma \ll \sin\delta$, we can regard the deviatoric phase $\Phi_i = \phi_i - (F\sin\delta/\zeta b)t$ as a slow variable, which obeys the dynamical equation

$$\frac{1}{\omega}\frac{d\Phi_i}{dt} = \sin\delta - \gamma\sum_{j\neq i}\frac{d^3}{|\mathbf{r}_i - \mathbf{r}_j|^3}\sin(\Phi_i - \Phi_j - \delta). \qquad (9)$$

In this form, anisotropy of the hydrodynamic interaction is averaged out and the model is mapped onto the standard coupled oscillator description presented in eqn (4). For $\delta = 0$, the authors have numerically reproduced the isotropic-nematic transition predicted by Guirao and Joanny.[88] The nematic phase ordering proceeds via pair annihilation of topological defects characterized by winding numbers +1 and −1. For $\delta = \pi/2$, a fully disordered state is obtained, due to geometric frustration. For intermediate value of δ, the model exhibits turbulent spiral waves as a dynamical steady state, as shown in Fig. 4. The spirals are either clockwise or anticlockwise, depending on the winding number of the defect at the core. The flow field is also turbulent and is highly correlated with the orientational field of the rotors. Such turbulent dynamical patterns may find application in micro-mixing devices. A random distribution of δ (with average $\bar{\delta} = 0$) was also studied,[101] and a synchronized-desynchronized transition was obtained as the randomness was increased. The transition in this case is a smooth crossover, in contrast to the sharp transition in mean-field models.[81–83] However, it is expected that the globally synchronized state in the thermodynamic limit $N \rightarrow \infty$ is fragile, because eqn (9) corresponds to the marginal case $\alpha = 3d/2$ in ref. 85. This might help with the understanding of the local (not global) orientational ordering observed in bacterial carpets.[31] Flagellar tails are often bent and not straight, and this could create a non-radial component of the driving force in a random fashion. A very small randomness in δ could destroy the phase-ordered state.

Another way to produce synchronization by generalizing the basic rigid bead model is to give the driving force some dynamical pattern by allowing it to be a function of the phase, in analogy to the two-mode beating pattern of cilia. Vilfan and Jülicher[97] considered two rigid beads that make tilted elliptic trajectories near a substrate. In their model, the tilt introduces modulation of the intrinsic phase velocity, which is coupled to the anisotropy of the hydrodynamic interaction to cause synchronization. They found in-phase or anti-phase synchronization, depending on the relative orientation of the two trajectories. Ryskin and Lenz[92,93] derived a set of coupled oscillator equations from a generic model of cilia with prescribed beating patterns, and analyzed the linear stability of the collective modes for a linear array of rotors. They also presented specific models of the beating patterns with the power stroke and recovery stroke, which do not stabilize a global synchronized state but allow traveling (metachronal) wave solutions. We can see how the jerkiness of the force can or cannot produce synchronization using the rigid bead model, eqn (6), with the general force profile $\mathbf{F}_i = F(\phi_i)\mathbf{t}(\phi_i)$. It can be shown[102] that two rotors ($i = 1,2$) positioned on the x-axis are synchronized if and only if the Fourier expansion of $\ln F(\phi)$ for $\sin 2\phi$ has a negative sign. For example, the profile $F(\phi) = F_0(1 - \varepsilon\sin 2\phi)$ with $0 < \varepsilon < 1$, contains the second harmonic at $O(\varepsilon)$. The two-mode beating pattern of cilia would be most simply mimicked by the profile $F(\phi) = F_0(1 - \varepsilon\sin\phi)$ with $|\varepsilon| < 1$, which also produces the second harmonic for $\ln F(\phi)$, but only at $O(\varepsilon^2)$ via period doubling. The study suggests that cilia and other active organisms might be exploiting the second-rank tensorial nature of the hydrodynamic interaction kernel to control their coordinated motion.

E. Experimental studies of hydrodynamic synchronization

There are relatively few experimental studies of hydrodynamic synchronization under low Reynolds number conditions. Kim et al.[103] investigated the physics behind bundling of bacterial flagella by studying a macroscopic scale model of the helical filaments in highly viscous silicone oil (such that the low Reynolds number condition was maintained). They observed bundling in their model system, and found that it arises due to an interplay between the hydrodynamic interactions and the geometry of the filaments as well as their bending and twisting elasticity. Other examples that involve living systems, already mentioned above, are the study of synchronization of a group of sperms that form a vortex near a solid substrate,[22] and synchronization and phase-slip in pairs of beating flagella.[24,25] Recently, Kotar et al.[104] studied the synchronization of colloidal linear oscillators using optical tweezers equipped with feedback control. For two oscillating colloidal beads they found that, in the absence of noise, the anti-phase dynamical state is stable, and that the period of oscillation depends on the strength of the hydrodynamic coupling. While these experiments verify that hydrodynamic interaction can lead to synchronization between active objects in a viscous fluid, it would be highly desirable to
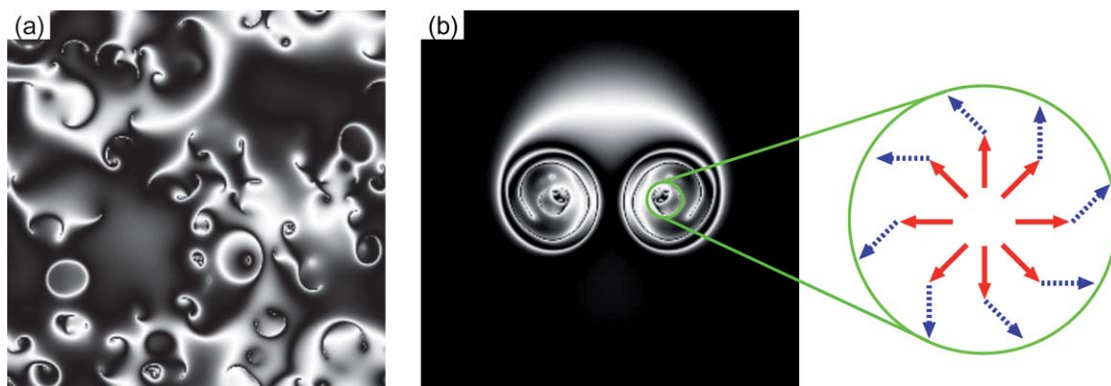
Fig. 4 Snapshots of turbulent spiral waves in a 2D array of hydrodynamically coupled rotors, with the greyscale representing $\cos[\phi(\mathbf{r}) - \bar{\phi}]$.[100] (a) $\delta = \pi/4$. Dynamical steady state. (b) $\delta = \pi/3$. Initial developments of spirals from a pair of topological defects. In the schematic picture of the spiral core (right), the arms of the rotors are shown as solid arrows and the forces they exert on the fluid as dotted arrows.

experimentally demonstrate and explore the full potential of this dynamical phenomenon.

IV. Generic features in hydrodynamic synchronization

a. Exactly which features are relevant for synchronization?

Hydrodynamic synchronization between a pair of oscillators has been studied in a variety of different models, which has led to verdicts about when it is, or it is not, possible. The studies on those models that involve the rotation of beads or rigid filaments on closed trajectories:[91,92,94–97] (where the motion can be described by a scalar dynamical variable that is the corresponding phase) can be summarized very neatly into the following statement[92] if the system is symmetric under the exchange of the two oscillators $(1 \leftrightarrow 2)$, then it cannot synchronize. The statement can be verified using the governing dynamical equations by exchanging the indices $1 \leftrightarrow 2$ everywhere, as discussed in Sec. III D. The condition for synchronization has been studied in more complicated cases where the dynamical variable is vectorial. The study of synchronization of deforming elastic sheets by Elfring and Lauga,[87] revealed a condition of lack of left-right symmetry for the waveform. If we rotate the system of two parallel deforming sheets (that each have a reflection symmetry together with a π phase shift[87]) by 180 degrees, the system will be mapped onto itself with a $1 \leftrightarrow 2$ exchange if the waveform is left-right symmetric. Since the equations of motion should be invariant under such a rotation, we find that the condition of left-right symmetry of the wavefront is equivalent to $1 \leftrightarrow 2$ exchange symmetry. Putz and Yeomans[90] pointed out that swimmers with quadrupolar flow fields (*i.e.* swimmers that are time reversal covariant) do not synchronize. A similar transformation argument could be used for the case of two swimmers, and the condition for their synchronization could also be reinterpreted in terms of lack of the $1 \leftrightarrow 2$ exchange symmetry.

b. Synchronization as a collective behavior

Globally synchronized states or metachronal waves are emergent non-equilibrium steady states of a large collection of mechanical elements with cyclic activity. To understand the phenomena of synchronization and metachronism, a number of issues need to be addressed.[99] First we need to examine whether stationary synchronized states or metachronal wavelike solutions satisfy the governing equations of motion for the model system. The next step is to check whether solutions are (linearly) stable, and which domains of the initial conditions in the phase space will be attracted to each solution. Finally, we need to examine whether this picture persists in the presence of noise, of thermal or other origin, and disorder. The globally synchronized state could be destroyed by arbitrarily weak intrinsic randomness, depending on the dimensionality of the array of oscillators and the geometry, which determine the asymptotic behavior of the interaction.[85]

c. Relation to dissipation

Since the main idea of hydrodynamic synchronization has emerged from observations on the behavior of living systems, it has long been speculated that adopting synchronization or metachrony by the organelles may be driven by a search for a functional dynamical state with the minimum energy consumption rate. A few systematic studies have addressed this issue, and found that the synchronized state can correspond to both the minimum and the maximum energy dissipation rate.[86,87,94,97]

V. Conclusion and outlook

The long-ranged hydrodynamic interaction between objects that undergo cyclic motion or deformation in a viscous fluid is shown to be able to lead to synchronization. Originating from observations in complex living systems, the idea has been examined in a variety of different systems from very complex beating filaments to simple beads on circular trajectories. The more realistic models allow us to study the role of hydrodynamic interactions in the intricate details involved in the biological processes that exhibit synchronization and metachronism. However, the complexities of these systems make them unsuitable for comprehensive studies of the physics behind these emergent phenomena.

There are a number of very interesting open questions concerning the generic features of synchronization that can be addressed using simple, minimal, models of hydrodynamically active objects. For two oscillators, while we know a necessary

condition for synchronization, we have still to address the question of sufficient conditions: what minimal properties should the oscillators have to be able to synchronize? For many oscillators, one would like to know more about the role of different geometries, disorder, and finite size effects, as well as whether or not it is possible to have a phase diagram with more than one type of metachronal phase for a properly constructed minimal model system. It would be interesting to probe the role of dissipation in selecting the dynamical state of the system in models that are sufficiently complex that they can accommodate multiple possible solutions.

Another interesting direction for future work concerns the behavior of bulk suspensions of swimmers, which has been studied using continuum theories that describe the system by a slowly varying density and orientational order parameter.[55–62] In these studies the internal phases of the swimmers have been considered as externally determined parameters. In light of the significant effect of the prescribed internal phase configuration of the swimmers on their collective behavior, it will be interesting to also study the case where the internal phases are treated as dynamical variables, and address issues such as hydrodynamic synchronization in suspensions of model microswimmers (see Sec. III C). We note that the model developed by Günther and Kruse[78] for the driving of the deformation cycle of a three-sphere microswimmer model could be a suitable framework for such a study.

Acknowledgements

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