Hydrodynamic synchronization of nonlinear oscillators at low Reynolds number

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Hydrodynamic synchronisation of non-linear oscillators at low Reynolds number.

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We introduce a generic model of weakly non-linear self-sustained oscillator as a simplified tool to study synchronisation in a fluid at low Reynolds number. By averaging over the fast degrees of freedom, we examine the effect of hydrodynamic interactions on the slow dynamics of two oscillators and show that they can lead to synchronisation. Furthermore, we find that synchronisation is strongly enhanced when the oscillators are non-isochronous, which on the limit cycle means the oscillations have an amplitude-dependent frequency. Non-isochronity is determined by a nonlinear coupling α being non-zero. We find that its (α) sign determines if they synchronise in- or anti-phase. We then study an infinite array of oscillators in the long wavelength limit, in presence of noise. For $\alpha > 0$, hydrodynamic interactions can lead to a homogeneous synchronised state. Numerical simulations for a finite number of oscillators confirm this and, when $\alpha < 0$, show the propagation of waves, reminiscent of metachronal coordination.

Collections of cilia and flagella are examples of systems that display synchronisation [1]. They are microscopic active filaments attached to the membrane of pro- and eukaryote cells [2] whose synchronisation is thought to aid the efficiency of transport at the cellular scale. Typically arrays of cilia generate fluid flows along tissues but can also be used, like flagella, for the self-propulsion of swimming cells. Due to their tiny size, the Reynolds number associated with these flows is negligible. The coordinated beating of cilia is also thought to have important developmental implications, such as the left-right symmetry breaking in the arrangement of the internal organs in the early embryo [3]. A precise understanding of the role hydrodynamics plays in their synchronised motion, is still missing.

Both cilium and flagellum are made of complex subunits, microtubules driven by molecular motors, and their modelling can be done at many levels. As synchronisation takes place on length-scales larger than the individual filaments, to a first approximation the fine details of their internal structure can be ignored. This coarse-grained approach has led to model studies of self-sustained oscillators [4], rotating beads [5–7]; beating filaments [8], as well as rigid rotating helices, [9, 10]. More recent work has focused on the conditions for hydrodynamic synchronisations for two oscillators [11] and the phase dynamics of oscillators with long range interactions [12]. Related experiments investigating the dynamics of micro-systems have been performed in vivo on algae, [13, 14] and on simple model systems [15], and even a macroscopic scale model of rotating paddles [16]. All these studies suggest that simple forms of active forces, e.g. as prescribed functions of time, are not enough to guarantee synchronisation. Rather, a complex, nonlinear relation between forces and velocities is necessary. Important questions therefore are what aspects of hydrodynamic interactions aid synchronisation and what features of oscillators make them good hydrodynamic synchronizers.

The dynamics of a system close to an oscillatory instability can be conveniently described by weakly nonlinear oscillators whose averaged equations are universal [1]. This implies that the long time behaviour of many systems with *simple* spontaneous oscillations can be captured by a generic model with a few parameters. Using this insight, in this paper we introduce a minimal model of an oscillator at low Reynolds number. To simplify our presentation, we study our model in one-dimension. At a coarse grained level, this degree of freedom can be interpreted as the centre of a filament beating in a plane [17].

The slow dynamics of the oscillator is naturally characterised using of two variables: the amplitude and the phase. Under arbitrary initial conditions, the trajectories of an isolated oscillator on long timescales converge to a closed curve, the limit cycle [18]. While the amplitude is tightly constrained to the limit cycle curve, the phase can vary more freely. Hence many model studies of synchronisation have focused only on the phase dynamics [5–7, 11, 12]. Our goal in this paper is to analyse the role played by both the *amplitude* and *phase* dynamics on *phase* synchronisation mediated by hydrodynamics. We first study a pair of well separated deterministic oscillators and find that hydrodynamic interactions strongly enhance phase locking, if the oscillations are non-isochronous, which on the limit cycle means that the frequency of oscillations depends on the amplitude. We then consider an array of many oscillators, still well separated, in the presence of fluctuations. On long wavelengths their slow dynamics can be naturally represented in terms of a broken symmetry (phase) variable, which is a non-equilibrium analogue of a Goldstone mode [19]. Denoting by $\alpha \neq 0$ the parameter responsible for the non-isochronity of the oscillations, we find that when $\alpha > 0$, hydrodynamic interactions can lead to in-phase synchronisation of the array. These results are confirmed by numerical simulations, which show also that conversely, for $\alpha < 0$, the synchronisation is more subtle and leads to the propagation of waves.

a. The model oscillator A universal model for stable spontaneous oscillations is provided by the normal form of a dynamical system close to a supercritical Hopf bifurcation [18]. To be concrete, we represent the oscillator in a low Reynolds number fluid as a sphere of radius a subject to a time-varying force f. The equation of motion for the sphere, with x its deviation from its equilibrium position, is

$$\dot{x} = \frac{f}{\gamma} \tag{1}$$

where $\gamma = 6\pi\eta a$ is the Stokes drag. The dynamics is encoded in the evolution equation for the force f :

$$\dot{f} = \Psi(f, x) := -\frac{k}{\tau}x + \mu\frac{f}{\gamma}\left(1 - \sigma x^2\right) + \alpha x^3. \tag{2}$$

Here, all the parameters, except α are positive quantities, The 1st and 3rd term of eq (2) give rise to respectively, a linear and a non-linear *passive* oscillator, while the 2nd term is responsible for active, self-sustained oscillations. We emphasize that all the terms in eq (2) would emerge naturally from coarse-graining any friction-dominated microscopic model oscillator [4, 10, 17]. Eqs (1), (2) can be conveniently non-dimensionalised as $\dot{x} = f$; and $\dot{f} = -x + \epsilon_\mu f(1 - x^2) + \epsilon_\alpha x^3$, choosing units where $\tau = \frac{\gamma}{k}$. They correspond to a weakly non-linear Van der Pol-Duffing oscillator [18]. The parameters $\epsilon_\mu := \frac{\mu}{k}$ and $\epsilon_\alpha := \frac{\alpha\tau}{k\sigma}$ are small quantities. We restrict ourselves here mainly to cases where $\epsilon_\alpha/\epsilon_\mu = O(1)$.

b. Two oscillators coupled hydrodynamically The oscillators are arranged along the x-axis. The forces f_i acting on the spheres, for $i = 1, 2$, are directed along the same axis and cause sphere 1 to oscillate around the origin and sphere 2 around position d. We denote by x_i the deviations from these equilibrium positions, see fig 1. Their equations of motion are

$$\begin{cases} \dot{x}_1 = \frac{1}{\gamma}\left(f_1 + H(r)f_2\right); \\ \\ \dot{x}_2 = \frac{1}{\gamma}\left(f_2 + H(r)f_1\right), \end{cases} \tag{3}$$

where $H(r)$ is a scalar, representing the hydrodynamic interactions, and $r := d + x_2 - x_1$ is the separation between the sphere centres. We shall consider the limit of large separation r compared to the sphere radius a. Then, for an unbounded three-dimensional fluid, interactions are described by the Oseen tensor [20] as $H(r) = \frac{3a}{2r}$. For a rigid surface with a non-slip boundary condition, placed at distance h from the oscillators, one obtains effective interactions scaling as $H(r) \sim \frac{ah^2}{r^3}$ [21]. For an assembly of oscillators arranged on a regular lattice, d can be thought of as the lattice spacing, see fig 1. We assume that it is large compared to the amplitude of the oscillations, $d > x_2 - x_1$, and that the ratio $\epsilon_d := a/d$, characterising the hydrodynamic coupling, satisfies $\epsilon_d \ll \epsilon_\mu, \epsilon_\alpha$. The time evolution of forces is given by $\dot{f}_i = \Psi(f_i, x_i)$, with $\Psi(f_i, x_i)$ defined in eq (2), and is entirely local [4]. The long-range hydrodynamic coupling links the coordinates x_i via eq (3). In the following we denote the nonlinear parts of $\Psi(f_i, x_i)$ by $\mathcal{F}_i(x_i, f_i) := \frac{\mu}{\gamma}f_i\left(1 - \sigma x_i^2\right) + \alpha x_i^3$.

To proceed, we take the time derivative of both sides of eq (3) and use, on the rhs, the evolution equation for

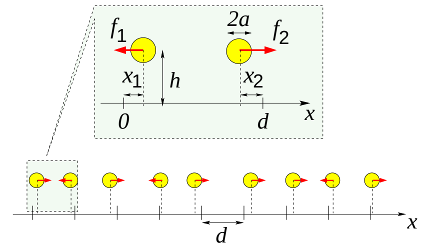

FIG. 1: (color online) One dimensional lattice of oscillators. The inset illustrates the dynamic variables of a pair.

the forces and the expression of forces as functions of velocities $\dot{x}_i$ obtained by inverting eq (3) as an expansion in a/r. Thus, to leading order, we obtain equations for oscillators with reactive couplings [1] (given by $\frac{\mathfrak{D}}{\gamma}$) as $\ddot{x}_1 + \omega_0^2 x_1 = \frac{1}{\gamma}\mathcal{F}_1(x_1, \gamma\dot{x}_1) + \frac{\mathfrak{D}}{\gamma}x_2$ and $\ddot{x}_2 + \omega_0^2 x_2 = \frac{1}{\gamma}\mathcal{F}_2(x_2, \gamma\dot{x}_2) + \frac{\mathfrak{D}}{\gamma}x_1$, where $\mathfrak{D} := -H(d)\frac{k}{\tau}$. ω_0 represents the natural frequency of the linear oscillators, defined by $\omega_0^2 = \frac{k}{\gamma\tau}$. Note terms like $\frac{H(r)}{\gamma}\mathcal{F}_i(x_i, \gamma\dot{x}_i)$, of order $\mathcal{O}(\epsilon_d\epsilon_\mu)$ and $\frac{dH}{dr}\dot{r}f_i$, of order $\mathcal{O}(\epsilon_d^2)$ have been neglected.

We now derive the equations governing the slow dynamics of the oscillators [1]. This is done naturally using a complex amplitude A_k and its complex conjugate A_k^* related to position and velocities by $x_k = \frac{1}{2}(A_k e^{i\omega t} + A_k^* e^{-i\omega t})$ and $\dot{x}_k = \frac{i\omega}{2}(A_k e^{i\omega t} - A_k^* e^{-i\omega t})$ for $k = 1, 2$. This requires of course that $\dot{A}_k^* = -\dot{A}_k e^{2i\omega t}$. Here ω is the (unknown) frequency of the non-linear oscillators, determining the period, $T = \frac{2\pi}{\omega}$ of the (fast) oscillations. The (slow) complex amplitudes, on the other hand, hardly change on this timescale. Writing eq (3) and the dynamic equations for the forces in terms of A_k and A_k^* and averaging over the period T one obtains

$$\dot{A}_1 = -i\Delta A_1 + \lambda A_1 - (\beta + i\chi)A_1|A_1|^2 + i\delta A_2$$

$$\dot{A}_2 = -i\Delta A_2 + \lambda A_2 - (\beta + i\chi)A_2|A_2|^2 + i\delta A_1. \tag{4}$$

The parameters are defined as $\Delta := \frac{\omega^2 - \omega_0^2}{2\omega}$, $\lambda := \frac{\mu}{2\gamma}$, $\beta := \frac{\mu\sigma}{8\gamma}$, $\chi := \frac{3}{8}\frac{\alpha}{\gamma\omega}$, and $\delta(d) := \frac{H(d)}{2\gamma\omega}\frac{k}{\tau}$.

Writing the complex amplitudes A_k in polar form, $A_k = R_k e^{i\phi_k}$, eqs (4) become a coupled system for the amplitudes R_k and the phases ϕ_k. Finally, this system can be reduced to a single equation for the phase difference [1]. This can be achieved perturbatively, when the parameter δ, parametrising the hydrodynamic interactions, is small compared to the other terms. If interactions are neglected, R_k have fixed points given by $R_k = \sqrt{\frac{\lambda}{\beta}}$. The dynamics of small deviations from these fixed points can be studied by writing $R_k = \sqrt{\frac{\lambda}{\beta}}(1 + s_k)$, for $s_k \ll 1$. One finds that the deviations s_k relax quickly to zero. Setting $\dot{s}_k = 0$ we obtain s_k as functions of the phase difference $\psi := \phi_2 - \phi_1$. The resulting expressions are then substituted in the equations for the phases.

From them one obtains an Adler equation [1] for ψ,

$$\dot{\psi} = \tilde{\nu} - 2\frac{\delta\chi}{\beta}\sin\psi. \quad (5)$$

Hence, eq (5) illustrates that phase locking is determined by the hydrodynamic coupling, via δ, provided the oscillator is nonisochronous, i.e. $\alpha \neq 0$. Note that $\frac{\delta\chi}{\beta}$ scales as $\sim \frac{1}{\tau}\frac{\epsilon_\alpha}{\epsilon_\mu}\epsilon_d$ and $\tilde{\nu}$ is related to the difference of the natural frequencies of the oscillators. We choose them to be identical, so we can set $\tilde{\nu} = 0$. While for $\tilde{\nu} \neq 0$ varying the ratio of $\tilde{\nu}$ and $\frac{\delta\chi}{\beta}$ controls the saddle-node bifurcation of cycles [18], for $\tilde{\nu} = 0$ eq (5) has a stable fixed point given by one of the zeros of $\sin(\psi)$ for $\psi \in [0, 2\pi]$. The position of the stable point is determined by the sign of $-\frac{\delta\chi}{\beta}$, which in turn is determined solely by the sign of the non-isochronism parameter α: when $\alpha < 0$, then the equation has a stable fixed point at $\psi = \pi$, i.e. the oscillators lock in anti-phase; vice-versa, if $\alpha > 0$ then the equation has a stable fixed point at $\psi = 0$ and the oscillators lock in-phase. A numerical solution, using the Euler method, of eq (3) confirms this.

It is also interesting to note that the two flagella of the microscopic algae *C. Reinhardtii* are found to alternate between periods of synchronised (with small phase difference) and non-synchronized beating [13, 14]. This is well described by a stochastic Adler equation, of the same form as eq (5) but with an additional fluctuating term [14]. The estimates of the parameters presented in [14], for the flagellar synchronisation, indicate positive values for α and $\tilde{\nu}$ of our model.

When $\alpha = 0$, we need to include higher order corrections in deriving eq (5). Upon doing this we find to leading order $\dot{\psi} \approx -3\epsilon_d\epsilon_\mu[1+\frac{3}{4}\frac{\epsilon_d}{\epsilon_\mu^2}\cos\psi]\sin\psi$. When $\epsilon_d < \frac{4}{3}\epsilon_\mu^2$ the synchronisation is in-phase. Otherwise, both in- and anti-phase states are possible and synchronization depends on details such as initial conditions (confirmed numerically). These higher order terms also indicate that the transition from in-phase to anti-phase in general occurs at some $\alpha_c \neq 0$. Unsurprisingly when $\alpha = 0$, synchronisation occurs more slowly (a higher order effect).

c. Many oscillators coupled hydrodynamically As we have discussed above, the amplitudes of the oscillators are tightly constrained to the limit cycle and the long time behaviour can be reduced to an effective (amplitude dependent) dynamics of the phases. For a large number N of oscillators, in the dilute regime, this is done by introducing the one-particle probability $c(\varphi, y, t) = \langle \frac{1}{N}\sum_{k=1}^{N}\delta(\varphi - \phi_k(t))\,\delta(y - y_k(t))\rangle$ of having an oscillator with slow phase φ, at site y at time t, where the brackets $\langle\rangle$ indicate the average over noise. The probability satisfies a Smoluchowski equation

$$\partial_t c = D\partial^2_{\varphi\varphi}c - \partial_\varphi([\omega_1 + \Omega]c). \quad (6)$$

D is the diffusion coefficient resulting from both thermal and active fluctuations, ω_1 the deterministic contribution of an isolated oscillator with $\omega_1 = -\Delta - \frac{\chi\lambda}{\beta}$ and Ω the deterministic effect of the hydrodynamic interactions,

$$\Omega(y, \varphi, t) := \int dy_2 d\varphi_2 c(\varphi_2, y_2, t)\dot{\phi}^{int}(y_2 - y, \varphi, \varphi_2). \quad (7)$$

$\dot{\phi}^{int} = \frac{\chi\delta'}{\beta}\sin(\varphi_2 - \varphi) + \delta'\cos(\varphi_2 - \varphi)$ is obtained from the dynamics of two oscillators, (see eq (5)). It describes the effect of the interactions on the phase of one oscillator due to the presence of the another. Here, $\delta' := \delta(|y_2 - y|)$.

The 1-particle probability can be expressed as an expansion in its moments:

$$c(\varphi, y, t) = \frac{1}{2\pi}\left[\rho(y, t) + \left(e^{-i\varphi}\Phi(y, t) + \text{c.c.}\right) + \ldots\right] \quad (8)$$

To study synchronization we only need the first two :

$$\rho(y, t) := \int_0^{2\pi} d\varphi c(\varphi, y, t)\ ; \quad \text{(density)}$$
$$\Phi(y, t) := \int_0^{2\pi} d\varphi e^{i\varphi}c(\varphi, y, t)\ ; \quad \text{(1st harmonic)}\ . \quad (9)$$

The emergence (or not) of a globally synchronized state is obtained from the homogeneous probability $c^0(\varphi, t)$, with associated moments $\rho^0(t)$, $\Phi^0(t)$ representing spatially homogeneous dynamical states. The corresponding expression for Ω^0 is obtained by evaluating the space integral in eq (7) with $c \equiv c^0$. For hydrodynamic interactions scaling as $H(r) \sim \frac{a}{r}$ the leading term from the integral depends both on the lattice spacing d, and the total length L of the array. Hence, $\Omega^0(t) = \frac{3ak}{4\omega\tau\gamma}\ln(L/d)[-i\frac{\chi}{\beta} + 1]e^{-i\varphi_1}\Phi^0(t) + \text{c.c.}$ For interactions scaling as $H(r) \sim \frac{ah^2}{r^3}$, the leading term in the integral depends only on the lattice spacing d. Consequently, the term $a\ln(L/d)$ is replaced by one $\sim \frac{ah^2}{d^2}$. Dynamic equations for the homogeneous moments are derived by taking the time derivative of both sides of eq (9), inserting eq (6) and using eq (8) to close the system. Since ρ is a conserved variable, $\partial_t\rho^0 = 0$, while Φ^0 satisfies

$$\partial_t\Phi^0 = \Gamma\Phi^0. \quad (10)$$

It is worth noting that in the absence of noise $c^0(\varphi, t) = \frac{1}{N}\sum_{k=1}^{N}\delta(\varphi - \varphi_k(t))$ and $\Phi^0(t)$ reduces to the order parameter introduced by Kuramoto, $\Phi^0(t) = \frac{1}{N}\sum_{k=1}^{N}e^{i\varphi_k(t)}$, representing the (mean field) average over a population of oscillators [1, 12, 22].

It is useful to express $\Phi^0(t) = P^0(t)e^{iQ^0(t)}$ in polar form (reflecting the $U(1)$ symmetry). We obtain equations for its amplitude and phase as $\partial_t P^0 = Re[\Gamma]P^0$ and $\partial_t Q^0 = Im[\Gamma]$. $Re(\Gamma) = -(D - \frac{\chi}{\beta}\frac{3ak}{4\omega\tau\gamma}\ln(L/d)\rho^0)$ is the real part of Γ. Here, the first term is due to noise, whereas the second term encodes the effect of two body interactions. The imaginary part is $Im(\Gamma) = [\omega_1 + \frac{3ak}{4\omega\tau\gamma}\ln(L/d)\rho^0]$.

As in the Kuramoto model [1, 22], order (synchronisation) is determined by a non-zero, constant value of P^0. Here, the dynamic equation for P^0 shows that the onset

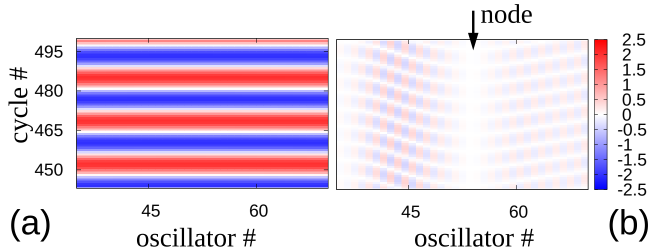

FIG. 2: (color online) Space-time plots of the positions for $N = 100$ deterministic oscillators, ($D = 0$). (a), (b) describe respectively the case for $\alpha > 0$ and $\alpha < 0$, after long time. The initial conditions of the oscillators are the same for both values of α: identical amplitudes, close to the maximum value, and random, Gaussian distributed, phases. The parameters of the model are $\gamma = 10^{-3} Pa \;\; s \;\; \mu m$; $\frac{k}{\tau} = 1 \frac{pN}{\mu m \;\, s}$; $\mu = 0.05 \frac{pN}{\mu m}$; $\sigma = 1 (\mu m)^{-2}$; $|\alpha| = 0.05 \frac{pN}{(\mu m)^3 s}$ and $a/d \approx 0.005$.

of order is controlled by the sign of $Re[\Gamma]$. If $Re[\Gamma] < 0$, order is suppressed. On the contrary, when $Re[\Gamma] > 0$, order is enhanced. A stabilising term of the type $\sim \Phi^0 |\Phi^0|^2$ in eq (10) is needed for P^0 to stop unbounded growth and attain a finite value at long times. Such a term could be generated for instance by taking into account three-body interactions. Finally, the condition $Re[\Gamma] = 0$ defines a transition line in the space of parameters [19]. Crucially, from these considerations, homogeneous synchronization is possible only when $\alpha > 0$: (i) in presence of noise ($D \neq 0$) and by keeping all the parameters fixed, synchronisation occurs only above a particular value of density; (ii) neglecting noise ($D = 0$), instead, synchronisation occurs for any (finite) value of the density. On the contrary, when $\alpha < 0$ both terms in $Re(\Gamma)$ are negative and homogeneous order is prohibited. This behaviour suggests a spin analogy, where $\alpha > 0$ (ferromagnet) promotes alignment of neighbouring oscillator phase (spins) while $\alpha < 0$ (antiferromagnet) promotes anti-alignment.

We compared these results with numerical simulation for a large but finite number of deterministic oscillators ($D = 0$). In fig 2 we show typical space-time plots for the positions of $N = 100$ oscillators and compare the effects of different signs of α. For $\alpha > 0$, see fig 2(a), the system displays spatially homogeneous order, i.e. in-phase synchronised state. Interestingly, when $\alpha < 0$, although homogeneous order is lacking, fig 2(b) still shows a coherent motion of the oscillators, with propagating waves. As suggested by the antiferromagnetic analogy, the oscillators self-organise into a dynamical state which is close to the anti-phase synchronised state, but deviates from it at long wavelengths.

In conclusion, we have presented a simple, one-dimensional model (that can be generalised to higher dimensions [23]) to investigate analytically the role of hydrodynamic interactions on the synchronisation dynamics of oscillators at low Reynolds number. We studied the case of two oscillators and found that synchronisation, either in- or anti-phase, was determined to leading order by both hydrodynamic interactions and non-isochronism of the oscillations ($\alpha \neq 0$). We then derived a coarse grained description for an infinite array of oscillators and found that spatially homogeneous order, corresponding to the in-phase synchronisation of the array, can occur only for $\alpha > 0$. Systems of cilia are known to display metachronal waves [24]. Our analysis suggests that these could be obtained in two different ways: either as slow hydrodynamic (phase) modes, like spin waves, when $\alpha > 0$; or alternatively, for $\alpha < 0$, as a spatially inhomogeneous, approximately anti-phase synchronised state, as indicated by the numerics. A more extensive investigation of these issues is left for the future.

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