Global synchronisation in microswimmer suspensions

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We study synchronisation in bulk suspensions of spherical microswimmers with chiral trajectories using large scale numerics. The model is generic. It corresponds to the lowest order solution of a general model for self-propulsion at low Reynolds numbers, consisting of a non-axisymmetric rotating source dipole. We show that both purely circular and helical swimmers can spontaneously synchronise their rotation. The synchronised state corresponds to a high orientational order in the polar and azimuthal directions. Finally, we consider a racemic mixture of helical swimmers where intra-species synchronisation is observed while the system remains as a spatially uniform fluid. Our results demonstrate how hydrodynamic synchronisation can arise as an emergent collective phenomenon of chiral microswimmers.

Introduction. Microswimmers are a subset of active matter systems and correspond to microscopic elements self-propelling within a fluid environment. Natural microswimmers consist of biological microorganisms [1–3] and their collective dynamics has gained a lot of interest of late [4,12]. This has inspired research on synthetic microswimmers, typically based on phoretic Janus particles [13–15]. The interest for developing artificial swimmers has been fuelled by the various promising possibilities for applications such as micro-cargo transportation [16–19], targeted drug delivery [19–22], artificial insemination [19,23] and microsurgery [19,20,24–26].

Most theoretical studies of microswimmer suspensions have concentrated on particles that swim in straight lines, with simulations predicting the spontaneous formation of collective swimming along a common direction – uniform polar order [27–33]. However, microorganisms typically have intrinsic chirality and tend to swim along helical paths [34–44]. Similarly, any asymmetry due to imperfections in the shape of the colloids or in their catalytic coating would also lead to chiral motion for artificial swimmers [13,45,48].

Continuum descriptions based on the long-range hydrodynamics produced by flow singularities [49–52] have been extensively used in the past, with some works including chiral flows [53–55]. However, these models fail to capture near-field hydrodynamic effects, which are believed to be crucial for the formation of polar order [29,30].

Most of the current theoretical work of active particles moving along chiral paths relies on dry microscopic descriptions such as active Brownian particle (ABP) models [56–61]. These effectively account for excluded volume effects, but neglect hydrodynamic interactions. Simulations of rotational ABPs have predicted synchronisation, when a Kuramoto-type alignment term is included [57]. Very recently, work on chiral swimmers has started to emerge, but has so far been limited to single and two particle systems [65,69].

Explicitly incorporating chirality in models used to study microswimmer suspensions could have an important effect regarding the emergence of collective states, such as large-scale collective oscillations [70,71], polar order [27,33] or hydrodynamic synchronisation [72–78]. While synchronisation arising from active flows has been predicted for linear trimers [72] and for rotors on a 2-dimensional lattice [76], the ability of microswimmers to spontaneously synchronise (or not) in freely moving bulk suspensions, remains an open question.

Here, we show that swimmers with chiral trajectories can synchronise their rotation in a fully three-dimensional suspension. We consider finite sized swimmers with a surface slip-flow arising from the general solution for self-propulsion at low Reynolds numbers [79] and corresponding to a rotating source dipole flow inclined at an angle ψ with respect to the particle polar direction. A synchronised state, corresponds to the alignment of these dipoles. We study three distinct cases: circular swimmers, helical swimmers, and a racemic mixture of left-handed and right-handed helical swimmers. In all cases, the spontaneous formation of synchronised states is observed.

Model for rotational squirmer.- To model the microswimmers, we consider spherical particles of radius a, and extend the standard squirmer model [80,81] to include rotational slip-flows. Based on Lamb’s general solution, the tangential slip-flow at the particle surface, is given in spherical coordinates by an infinite series of modes for the polar and azimuthal components eφ and eθ [79]. The lowest order modes correspond to self-propulsion (source dipoles and rotlets), while the higher order terms correspond to fluid mixing. We choose [79,82]

\[
\begin{align*}
  u_\theta|_{r=a} &= B_1 \sin \theta + \tilde{B}_{11} \cos \theta \sin \phi \\
  u_\phi|_{r=a} &= C_1 \sin \theta + \tilde{B}_{11} \cos \phi.
\end{align*}
\]  

The B1 mode corresponds to the source dipole in the standard squirmer model (top right panel in Fig. [1]). C1 leads to a rotation of the particle around its polar axis with a frequency ω = C1/a (bottom left panel in Fig. [1]). \( \tilde{B}_{11} \) is a source dipole along y (bottom right
FIG. 1. Model for rotational squirmers. (a) The surface slip-flows corresponding to the different modes: $B_1$, $C_1$ and $B_{11}$ in the particle frame. The magnitude of the normalised surface velocity (slip flow) for each mode is represented by a colour-code and the streamlines are coloured black. (b) The particle trajectories corresponding to circular (left) and helical (right) swimming. The unit vectors $\mathbf{m}$ and $\mathbf{s}$ correspond to the particle polar and azimuthal axes respectively. (c) Flow field of the swimmers obtained from the simulations, corresponding to a source dipole (neutral squirmer). The magnitude of the fluid velocity is coloured using a logarithmic scale and overlaid by black streamlines.

The swimmer flow field corresponds to a single source dipole which rotates around the polar axis $m$ at an inclination $\psi = |\tan^{-1}(B_{11}/B_1)|$ (Fig. 1)). When $\psi = 90^\circ$ ($B_1 = 0$) the swimmers have circular trajectories in a plane perpendicular to their polar axis (left in Fig. 1b). The radius of the trajectory is given by $r = v_0/a/C_1 = 2B_{11}a/(3C_1)$ and the period by $T_0 = 2\pi/\omega_0 = 2\pi a/C_1$. For $\psi \neq 90^\circ$ and $\psi \neq 0^\circ$ the trajectories become helical (right in Fig. 1b).

We use the lattice Boltzmann method to simulate the system composed of the fluid and the suspended active particles \[2\]. The typical particle Reynolds number is $Re \sim 0.01$ and a simulation time $\sim 100s$. (see supplementary material \[2\] for details of simulations and mapping to SI units).

To quantify the amount of alignment in a system composed of $N$ swimmers, we define azimuthal $P_s(t)$ and polar $P_m(t)$ order parameters: $P_{s/m}(t) = \sum_N \mathbf{s}_i[h_{s/m}]$. Where $P_{s/m} = 1$ corresponds to complete orientational order, and $0$ to an isotropic state.

Synchronisation of circular swimmers.- Starting from isotropic initial conditions, we find that the circular swimmers spontaneously synchronise their rotation when $\phi \sim 1 \ldots 10\%$ and $r_t \sim a$ (Fig. 2). The synchronisation corresponds to the growth of both azimuthal and polar order, where typically $P_s \approx P_m \gtrsim 0.8$ at long times (Fig. 2). In the steady state, the system shows both frequency and phase locking (Fig. 3a and d). The angular velocity $\omega$ distribution has a peak at the single particle value $\omega_0$ and its width corresponds to the fluctuations arising from the hydrodynamic coupling between the particles. These are reduced in the synchronised state (Fig. 3a).

The phase locking is apparent from the distribution of the lag angle $\alpha = \alpha_{1,2}^{g,c}$ calculated from all the particle pairs, considering the $s$ vectors of two different rotors in the plane perpendicular to the global polar director, $P_m = \sum_i \mathbf{s}_i$. The distribution of $\alpha$ changes from uniform at $t \sim 0$ to a normal distribution with a peak at $\alpha \approx 0$ in the globally synchronised state (Fig. 3h).

In this state, the particle trajectories are circular and aligned perpendicularly to $P_m$ (bottom row in Fig. 2). The particle positions remain isotropic (top row in Fig. 3e) and the pair-correlation function $g(r)$ shows liquid like structure (Fig. 3b).

The likelihood of the synchronisation depends on the volume fraction $\phi$ and the trajectory radius $r_t$ (Fig. 2). At low $\phi$ the particles do not interact, and the system remains in an isotropic state with the circular trajectories randomly oriented and distributed.

The lower-$\phi$ limit for synchronisation, is well fitted with a random close packing of discotic cylinders with an aspect-ratio $a/r_t$ and $\phi = \pi r_t a^2 \sim 75\%$ \[33,34\] (white line in Fig. 2). Below this line, the swimmers can be randomly oriented with no, or very few collisions.

Moving above this line, the particles will have, on average, at least one collision during their rotation time $T_0$ in the isotropic state. This renders particle trajectories non-circular at early times (bottom left in Fig. 3d).
FIG. 3. (a) Circular swimmers: Example of a typical time evolution of the azimuthal $P_s$ (red) and polar $P_m$ (black) order parameters. (b) Radial distribution function $g(r)$ of the system. Probability distribution of the (c) angular velocities $\omega$ and (d) phase lag angle $\alpha$ between all particle pairs, at the start and end of the simulation. (e) Snapshots of the system at the beginning (left) and end (right). (Top row) The $N = 286$ particles are coloured according to the orientation of their $s$ vector along the lab frame $y$-axis. (Bottom row) 25 selected particles rotating clockwise as seen from the readers perspective, with their trajectories over one period coloured according to the orientation of their $m$ vector along the lab frame $x$-axis. (The data corresponds to $\phi = 0.15$ and $r_t = 3.33$).

At long times, the trajectories align and synchronisation is observed (right in Fig. 3). This suggests that the near-field hydrodynamics are crucial for synchronisation, similar to the case of neutral linear squirmers [29, 30].

We define $t_{\text{sync}}$ as the total time elapsed from the beginning of the simulation until the system is synchronised (both $P_s$ and $P_m$ reach a plateau). For a given $r_t$, if $\phi$ is too large no synchronisation is observed. This implies the existence of a dynamic bottleneck where the particles have multiple collisions during their rotation time $T_0$, hindering the growth of global alignment. For simulations towards the high-$\phi$ end of the synchronisation region the $t_{\text{sync}}$ is increased (Fig. 2), and the order parameters fluctuate close to zero before the growth of the order begins. We plan to study these systems in more detail in the future.

Helical swimmers.- Helical trajectories arise when $B_1 \neq 0$ (Fig. 1b), and synchronisation is observed at lower $\phi$ than in the case of pure rotors (Fig. 2). The alignment of the source dipoles, is first led by the formation of polar order before eventual azimuthal alignment. This tendency is amplified for increasing $B_1/\tilde{B}_{11}$ (see e.g. Fig. 5a and b, for $\psi \approx 50^\circ$ and $\psi \approx 31^\circ$, respectively). Both the frequency matching and the phase locking show comparable behaviour with the circular swimmers (Fig. 5c and d). In the synchronised state, the particles swim along a common axis, with their helical trajectories aligned (Fig. 5e).

When $r_t = 0$, the swimmers correspond to achiral neutral squirmers and the formation of pure polar order ($P_m > 0; P_s \sim 0$) is observed (blue diamonds in Fig. 4) in agreement with [27-33]. Interestingly, we also find cases with $r_t \neq 0$ where polar order is present in the absence absence of azimuthal order ($P_m > 0; P_s \approx 0$) (yellow diamonds in Fig. 4).

Racemic mixture.- Finally, we construct a racemic mixture composed of right-handed and left-handed helical swimmers by choosing $C_1 = \pm 0.001$ (Fig. 6). Start-
FIG. 5. Helical swimmers: Time-evolution of the order parameters $P_s$ and $P_m$ for (a) $\phi = 0.083$, $r_t = 4$, $\psi \approx 50^\circ$ and (b) $\phi = 0.125$, $r_t = 1.33$, $\psi \approx 31^\circ$. The distributions of (c) the spinning frequency $\omega$ and (d) the phase-angle difference $\alpha$ showing frequency and phase-locking, respectively. (e) Snapshot of the system in the stable synchronised state with the 286 helical swimmers and their trajectories over 4 periods coloured according to the orientation of the $m$ vector of each particle along the lab frame $x$-axis (left). 8 selected microswimmers with their trajectories coloured as a function of time (right). The particles are coloured according to the orientation of their $s$ vector along the lab frame $y$-axis. (The data in c, d and e correspond to $\phi = 0.15$, $r_t = 3.33a$ and $\psi = 45^\circ$).

FIG. 6. Racemic mixture: Distributions of the (a) spinning frequency $\omega$ and (b) the phase-angle difference $\alpha$ calculated for all swimmer pairs. (c) The distribution of $\alpha$ for all the particles (black), for clockwise (blue) and counter-clockwise (blue) rotating populations, as well as for the cross population (orange). (e) Snapshot of the unwrapped trajectories at the steady state during $20T_0$. (f) Schematic showing the parallel ($\alpha = 0$) and anti-parallel ($\alpha = \pm \pi$) configurations of a pair of rotors with opposite chirality in the plane perpendicular to the average global polar director $P_M$. The data correspond to $\phi = 0.1$, $r_t = 3.33a$ and $\psi = 45^\circ$.

From an isotropic state, the system develops polar order $P_m \sim 0.83$ (Fig. 5c) and shows both frequency and phase locking (Fig. 5a and b) in the steady state. On average, the system does not have a stable azimuthal order, due to the opposite spinning of the swimmers, but the phase-lag angle $\alpha$ calculated for each population, shows a strong synchronisation within the same species (Fig. 5c). We observe no spatial separation of the swimmers — the fluid-like pair-correlation function calculated within species and cross-species matches with the $g(r)$ for all the particles (Fig. 5d).

The cross-population distribution of $\alpha$, is not completely flat, but shows a slight preference for $\alpha = \pm \pi$ (orange curve in Fig. 5c) corresponding to the alignment of the source dipoles (right panel in Fig. 5f), which is expected to be favourable, from the prediction of stable polar order in neutral squirmer suspensions [27,83].

Conclusions. — In summary, using computer simulations we have investigated suspensions of microswimmers with chiral trajectories at the limit of zero thermal noise. Our model is generic and it is based on the general solution of self-propulsion at low $Re$ [79]. Our predictions should be applicable to a wide variety of artificial and microbial microswimmer systems; especially for the collective dynamics of spherical ciliates, where rotational surface flows occur naturally [86].

Our work represents the first finding of hydrodynamic synchronisation as an emergent collective phenomenon in a bulk suspension of microswimmers. The observation of the intra-species synchronisation in the racemic mixture, provides a surprising example of two synchronised, in-
terpenetrating fluids. Further, it demonstrates that the hydrodynamic fluctuations from the source-dipole $1/r^3$ far-fields do not lead to the destruction of synchronisation nor spatial separation of the oppositely rotating swimmers.

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