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Hydrodynamic Interaction between Two Swimmers at Low Reynolds Number

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We investigate the hydrodynamic interactions between micro-organisms swimming at low Reynolds number. By considering simple model swimmers, and combining analytic and numerical approaches, we investigate the time-averaged flow field around a swimmer. At short distances the swimmer behaves like a pump. At large distances the velocity field depends on whether the swimming stroke is invariant under a combined time-reversal and parity transformation. We then consider two swimmers and find that the interaction between them consists of two parts: a *passive* term, independent of the motion of the second swimmer, and an *active* term resulting from the simultaneous swimming action of both swimmers. The swimmer-swimmer interaction is a complicated function of their relative displacement, orientation, and phase, leading to motion that can be attractive, repulsive, or oscillatory.

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Because of their size, the swimming motion of microscopic and mesoscopic organisms, such as bacteria and cells, corresponds to low Reynolds number. As pointed out by Purcell [1], in this regime swimming mechanisms are very different from those operative at human length scales. In particular, any swimming strategy must involve a cyclic and non-time-reversible motion. Examples include the motion of a sperm flagellum [2], the synchronized beating of cilia on ciliated protozoa [3], and the Dreyfus microswimmer [4] where a colloid is driven by a tail of magnetic particles actuated by an oscillating field.

Interesting progress has been made in understanding the propulsion of individual swimmers [2,5] and in developing optimal swimming strategies [6,7]. However, much less is understood about the collective behavior of microswimmers. Experiments include works by Dombrowski *et al.* [8], who observed large-scale coherence in bacterial dynamics in sessile drops, and Wu and Libchaber [9], who found particle superdiffusion in soap films containing bacteria. Numerical simulations have been performed on suspensions of rod shaped motile particles [10,11], which show that at high concentrations collective motion and local ordering can occur, but that long ranged nematic ordering is hydrodynamically unstable. Such behavior has been previously predicted theoretically [12] and appears to be a generic feature of so-called active systems [13].

An important step towards understanding the behavior of many swimmers is to calculate the hydrodynamic interaction between two swimmers. Previous studies have investigated this problem for a number of special cases. For example, Ishikawa and Hota [14] performed experiments to find the interactions between two swimming *Paramecium* cells. Computational modeling of the hydrodynamic interaction between two flagella was reported in [15,16]. Ishikawa *et al.* [17] modeled swimmers as spheres with prescribed tangential velocities (known as squirmers). They calculated the far field interaction between two squirmers and matched the results onto a near field lubrication theory. Because this approach involves taking the time average of the flow field around each swimmer, any interaction arising from the flow generated at time scales shorter than the swimming stroke is neglected. We find that these neglected terms are, in fact, very important for the dynamical behavior of a wide class of swimmers.

The aim of this Letter is to calculate two swimmer interactions, emphasizing the importance of the details of the swimming stroke. We present both analytic and numerical results based on a minimal swimming model, first introduced by Najafi and Golestanian [18]. We first consider the average flow field around a swimmer. At short distances the swimmer behaves like a pump that moves forward by pushing fluid from in front to behind itself. At large distances the average flow field around a swimmer is naively expected to be dipolar ($\sim r^{-2}$). However, we argue that for a wide class of swimmers, which are invariant under a combined time-reversal and parity (TP) transformation, the leading order term vanishes and the far flow field has a r^{-3} dependence. (The parity transformation is $\mathbf{r} \Leftrightarrow -\mathbf{r}$.) Examples of these swimmers include Purcell's three link swimmer [1], the three sphere swimmer of Najafi and Golestanian [18], the snake swimmer, and a helical filament. Indeed, the r^{-3} term in the velocity field will remain important for many swimmers that are close to TP invariant.

We then consider two swimmers, *A* and *B*, say. We find that the effect on *A* of *B*'s swimming consists of two principal components: a *passive* term, which depends only on the average flow field generated by *B* and which takes the expected dipolar form, and an *active* term resulting from the simultaneous swimming motion of both *A* and *B*, which does not. Interestingly, it is the latter that dominates, meaning that interactions become not only a complicated function of relative displacement and orientation, but also of relative phase. We show that trajectories of the two swimmers can be attractive, repulsive, or oscillatory.

Locomotion is initiated by shape changes in the swimmer, which induce forces acting on the surrounding fluid and thus create a flow. The fundamental solution of the Stokes equations describing the response to a point force, **f**, is called a stokeslet and creates a fluid flow

$$u_i(\mathbf{x}) = \frac{f_j}{8\pi\mu}\left\{\frac{\delta_{ij}}{r} + \frac{(\mathbf{x}-\mathbf{y})_i(\mathbf{x}-\mathbf{y})_j}{r^3}\right\}, \tag{1}$$

where **y** is the point of application of the force, $r = |\mathbf{x} - \mathbf{y}|$, and μ is the fluid viscosity. Since the Stokes equations are linear, the fluid motion associated with swimming may be given by a superposition of such stokeslet flows. At large distances these may be expanded in r^{-1} to obtain the asymptotic behavior. Since the total force on the swimmer has to be zero, the leading order term vanishes [2]. The next term, which varies as r^{-2}, is called a force dipole and is generally assumed to dominate the far field behavior [19,20].

Indeed, this is always true of the *instantaneous* fluid velocity. However, an intriguing feature of the *average* flow is that the force dipole term can be absent. To show this, we employ a simple model swimmer consisting of three spheres of radius a joined by thin rods, or “arms.“ It moves by shortening and extending these arms in a periodic and time irreversible manner, as depicted in Fig. 1. A unit vector **n** pointing in the direction of motion, left to right in Fig. 1, defines an orientation for the swimmer. The variable D gives the extended arm length, and ξ^F and ξ^B denote the amplitudes of the strokes performed by the front and back arms, respectively. Najafi and Golestanian [18] obtained an analytic expression for the velocity of the swimmer for $\xi^F = \xi^B$ using the Oseen tensor formulation of hydrodynamics, valid in the limit $a/D \ll 1$.

Using a similar approach, we have calculated the average flow field generated by the swimmer:

$$\begin{aligned}\langle \mathbf{u}\rangle = \frac{a}{T}\Bigg\{&\left[\frac{29a\xi^B\xi^F(\xi^B-\xi^F)}{64D^2}\right](3[\mathbf{n}\cdot\hat{\mathbf{r}}]^2-1)\frac{\hat{\mathbf{r}}}{r^2}\\ &+\left[\frac{17a\xi^B\xi^F}{32}\right]\Bigg((1-3[\mathbf{n}\cdot\hat{\mathbf{r}}]^2)\frac{\mathbf{n}}{r^3}\\ &+(5[\mathbf{n}\cdot\hat{\mathbf{r}}]^2-3)\frac{3[\mathbf{n}\cdot\hat{\mathbf{r}}]\hat{\mathbf{r}}}{r^3}\Bigg)\Bigg\},\end{aligned} \tag{2}$$

where T is the period of the swimming stroke. For $\xi^F = \xi^B$ the swimmer is TP invariant and the dipolar term vanishes.

The reason TP invariant swimmers do not have any dipole contribution can be seen as follows. If a general swimming motion is invariant under simultaneous time reversal and parity transformations, then the average flow field must also have this property. The dipole term, however, changes sign under a TP transformation, and so the coefficient multiplying it must be zero. [This can be verified for the first term in Eq. (2).]

When the front and back arms have different amplitudes, the TP invariance is broken and both r^{-2} and r^{-3} contributions appear in the averaged far field flow in Eq. (2). A comparison of the magnitude of the two contributions shows that the dipolar term only dominates for distances

$$\frac{r}{D} \gtrsim \frac{68}{29}\frac{D}{|\xi^B - \xi^F|}, \tag{3}$$

which diverges when the amplitudes of the two arms become equal, as required by the TP invariance.

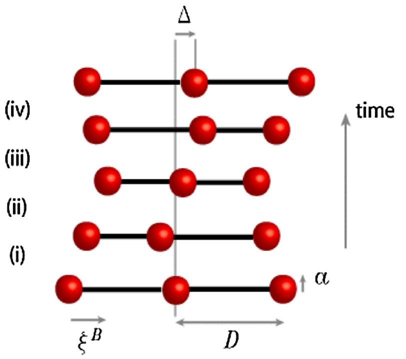

FIG. 1 (color online). The cyclic motion of the linear three sphere swimmer [18]. The swimmer goes through the four steps (i)–(iv) and returns to its original shape, but is displaced by a distance Δ to the right.

The velocity field generated by this swimmer, averaged over a swimming cycle, is shown in Fig. 2. It was obtained using a numerical integration of the Oseen tensor equation, subject to the constraint that the swimmer is force and torque-free. Details of this method are given in [21]. Close to the middle sphere the fluid is clearly seen to move to the left; essentially the swimmer acts like a pump that moves fluid from in front of it to behind it, leading to the swimmer moving to the right. The analytic far field expansion Eq. (2) accurately describes (to within 10%) the numerical flow for distances further than around

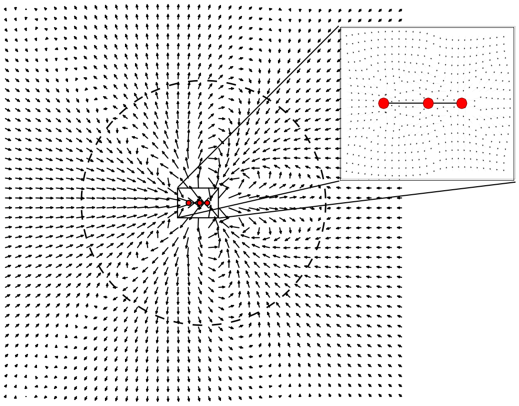

FIG. 2 (color online). The flow field around a swimmer, averaged over one swimming cycle. The direction of swimming is from left to right and the flow is axisymmetric about the swimmer. The magnitude of velocities are plotted on a logarithmic scale to enable both the near sphere and far field behavior to be observed simultaneously. The parameters used were $a = 0.1D$, $\xi^B = 0.2D$, and $\xi^F = 0.4D$.

three swimmer lengths. The dashed circle demarcates the estimated distance, Eq. (3), at which the far field flow crosses over from r^{-3} to r^{-2} dipolar scaling.

We now consider how the trajectory of a second nearby swimmer (A) will be altered by this flow field. The interaction will involve A both being advected by, and rotating in, the flow field generated by B. We find that there are two contributions to the interaction. The first, which we refer to as the *passive* term, is independent of the motion of A. This contribution may be calculated directly using the average flow field for a single swimmer, Eq. (2).

In addition, there is an *active* term that describes the more interesting interaction arising as a consequence of both organisms trying to swim. This term encodes all of the information about how the interactions depend on the relative phase of the swimmers. Using the Oseen tensor to describe the hydrodynamics, we have determined the leading order contribution to the active interaction, finding a net swimming stroke rotation and translation given by

$$\begin{aligned}\boldsymbol{\Delta}\boldsymbol{\theta}_A^{\text{active}} &= \left[\frac{-9aD\xi^B\xi^F}{8}\Phi\right]\left(\frac{\mathbf{n}_A\times\hat{\mathbf{r}}}{r^4}\right)\\ &\quad\times\{1+2[\mathbf{n}_A\cdot\mathbf{n}_B]^2-5[\mathbf{n}_A\cdot\hat{\mathbf{r}}]^2\\ &\quad-5[\mathbf{n}_B\cdot\hat{\mathbf{r}}]^2-20[\mathbf{n}_A\cdot\mathbf{n}_B][\mathbf{n}_A\cdot\hat{\mathbf{r}}][\mathbf{n}_B\cdot\hat{\mathbf{r}}]\\ &\quad+35[\mathbf{n}_A\cdot\hat{\mathbf{r}}]^2[\mathbf{n}_B\cdot\hat{\mathbf{r}}]^2\},\\ \boldsymbol{\Delta}\mathbf{x}_A^{\text{active}} &= \left[\frac{3aD\xi^B\xi^F}{2}\Phi\right]\left(\frac{\hat{\mathbf{r}}-[\mathbf{n}_A\cdot\hat{\mathbf{r}}]\mathbf{n}_A}{r^3}\right)\\ &\quad\times\{[\mathbf{n}_A\cdot\hat{\mathbf{r}}]+2[\mathbf{n}_A\cdot\mathbf{n}_B][\mathbf{n}_B\cdot\hat{\mathbf{r}}]\\ &\quad-5[\mathbf{n}_A\cdot\hat{\mathbf{r}}][\mathbf{n}_B\cdot\hat{\mathbf{r}}]^2\},\end{aligned} \tag{4}$$

where the subscripts A and B label the swimmers, and $\mathbf{r}$ is the position vector of A relative to B. $\boldsymbol{\Delta}\mathbf{x}_A$ represents the translation vector, and $\boldsymbol{\Delta}\boldsymbol{\theta}_A$ the rotation vector (whose magnitude and direction define the rotation angle and axis, respectively), induced in A as a result of the hydrodynamic interaction with B. Although the rotation is higher order in r^{-1}, it should not be considered less important. This is because small changes in angle can give rise to large positional displacements in the long time limit. The relative phase of the swimmers enters through the function Φ, which we illustrate for a selection of parameter values in Fig. 3.

When the two contributions to the interactions are compared, we find that the active contribution dominates for all distances

$$\frac{r}{D} \lesssim \frac{96}{29}\frac{D}{a}\frac{D}{|\xi^F-\xi^B|}\Phi. \tag{5}$$

This behaves similar to the average fluid flow in that it diverges as the swimmer becomes TP invariant. However, there is a crucial difference for non-TP invariant swimmers. The additional factor of D/a is large, and therefore ensures that for all distances over which the interactions are strong enough to be significant, the dominant contribution is from the active term, despite the fact that it is higher order in r^{-1}. Thus, in general, even though the average flow field may be dipolar, the interactions are not.

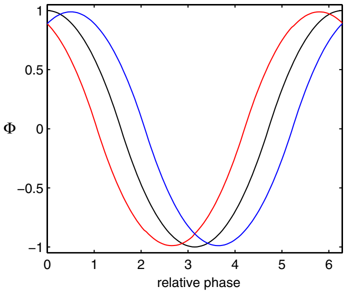

FIG. 3 (color online). The function Φ describing the effect of the relative phase of the swimmers on the interactions. The parameters used were the following: black line $\xi^B=\xi^F=0.3D$, curve to the left of this (red), $\xi^B=0.4D$, $\xi^F=0.2D$, and curve to the right of this (blue), $\xi^B=0.2D$, $\xi^F=0.4D$.

We turn now to an investigation of the long time behavior resulting from these interactions by considering how the trajectories of two identical swimmers depend on their relative position, orientation, and phase. We focus only on the case when the swimmers follow almost parallel trajectories since this allows time for the weak r^{-3} interactions to have an appreciable effect. We consider first symmetric swimmers ($\xi^B=\xi^F$) swimming in phase, before looking at how the behavior changes when these constraints are relaxed. The results are summarized in Fig. 4(a). Swimmer A initially lies at the origin (as shown in the figure) and B is aligned parallel and displaced to the corresponding point in the diagram. The figure is divided into different regions, labeled A, R, O, and P, corresponding to the four different types of long term behavior that were observed: attractive, repulsive, oscillatory, and parallel trajectories.

Typical trajectories for each of these types of behavior are shown in Figs. 4(i), 4(ii), 4(iii), 4(iv), 4(v), and 4(vi). For accuracy, the trajectories were obtained numerically [21], although the results that follow from iterating the analytic formulas, Eqs. (4), are in close agreement. All scales are in units of D, the swimmer arm length. The parameters chosen were $a=0.1D$ and $\xi=0.3D$, giving a displacement per cycle of $\Delta\approx(7/12)a\xi^2/D^2=0.005D$. Thus, since the length scale of the swimming motion is typically $\sim 50D$, the trajectories evolve over time scales 3 or 4 orders of magnitude larger than that of the individual swimming stroke. The lines terminate when the swimmers get too close, as here the Oseen tensor approximation breaks down.

In addition to simple attractive or repulsive behavior, the swimmers also exhibit intriguing oscillatory trajectories that may be either of small amplitude about separated parallel swimming paths, as in region P, or of larger amplitude with the two swimmer's trajectories crossing each other, as in region O. It is notable that these trajectories exhibit a slow drift superimposed onto the oscillations.

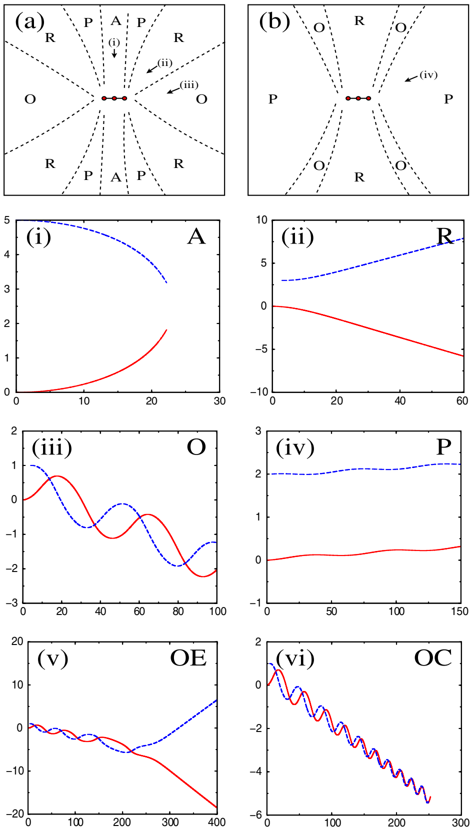

FIG. 4 (color online). Long time behavior of two swimmers, A and B, (a) in phase, and (b) π out of phase. (i)–(vi) illustrate a selection of trajectories representing attractive (A), repulsive (R), oscillatory (O), parallel (P), expanding oscillatory (OE), and contracting oscillatory (OC) behavior, respectively.

The oscillations originate from the rotational part of the active interaction, while the superimposed drift is a consequence of the translational part. This highlights the significance of rotational interactions, despite their being higher order in r^{-1}.

The type of trajectories observed depends on the relative phase of the swimmers. For example, Fig. 4(b) shows the long term behavior of two swimmers that are exactly π out of phase. This change in behavior is well accounted for by Φ changing sign (see Fig. 3) in the far field analytic results of Eqs. (4).

Breaking the TP invariance gives rise to qualitatively new trajectories. In particular, the oscillatory behavior characteristic of region O is no longer stable, with the swimmers diverging for $\xi^F < \xi^B$ [Fig. 4(v)] and converging for $\xi^F > \xi^B$ [Fig. 4(vi)]. This behavior is of particular interest as it suggests that suspensions of swimmers driven in phase might spontaneously start to form chains.

In this Letter, we have considered the collective dynamics arising from hydrodynamic interactions between two model microswimmers. These interactions are not dominated by the leading nonzero term in a far field expansion of stokeslets, but rather by a higher order *active* term describing the simultaneous motion of both swimmers while they swim. Consequently, the long time behavior is sensitive to the relative phase of the two swimmers and may be tuned by making small alterations to the details of the swimming stroke.

Understanding the interaction between two swimmers is only a first step towards interpreting the collective dynamics of larger groups of micro-organisms. Both near field hydrodynamic interactions between cells that approach closely and many body interactions are likely to be important. Moreover, the relative phases of real swimmers will vary unless a locking mechanism is operative, although it will be possible to control the phases of artificial swimmers that are externally actuated.

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