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Hydrodynamics of linked sphere model swimmers

G P Alexander, C M Pooley and J M Yeomans

Rudolf Peierls Centre for Theoretical Physics, 1 Keble Road, Oxford OX1 3NP, UK

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Abstract
We describe in detail the hydrodynamics of a simple model of linked sphere swimmers. We calculate the asymptotic form of both the time averaged flow field generated by a single swimmer and the interactions between swimmers in a dilute suspension, showing how each depends on the parameters describing the swimmer and its swimming stroke. We emphasize the importance of time reversal symmetry in determining the far field flow around a swimmer and show that the interactions between swimmers are highly dependent on the relative phase of their swimming strokes.

(Some figures in this article are in colour only in the electronic version)

1. Introduction

Tiny organisms, such as bacteria, produce fluid flows characterized by very low Reynolds numbers, typically 10^{-4} or smaller, so that their motion is dominated by the action of viscous stresses rather than inertia. The topic of swimmer hydrodynamics has developed into a flourishing field since Taylor's seminal work in the early 1950s [1, 2], with considerable interest both in the locomotion of individuals [3–6] and in the interactions between swimmers and their collective hydrodynamics [7–14].

Considerable insight into swimmer hydrodynamics has been gained by the analysis of simple models that capture the essence of swimming whilst remaining analytically tractable, following the examples laid down by Taylor [2] and Purcell [4]. This has included both a more detailed analysis of the models proposed by Taylor and Purcell [15, 16] and the proposal of new models based on a small number of linked spheres [17–21] or phoretic effects generated by chemical reactions at the swimmer's surface [22, 23]. Initial experiments are beginning to show the viability of some of these simple models as the basis for artificial microswimmers that may be developed for drug delivery or manipulating payloads in microchannels [24–28].

However, whilst our understanding of the motility of single organisms has developed significantly, rather less is known about the detailed hydrodynamics of swimmers; the time averaged flow fields that they generate, the interactions that occur between individuals and the collective behaviour that results. These interactions may be expected to be substantial because of the long range $1/r$ nature of the fluid flow generated by point forces at low Reynolds number. Indeed, they have been shown to be important in the gyrotactic focusing of bottom heavy algal cells [7], band formation in magnetotactic bacteria [29] and in many aspects of bacterial behaviour near surfaces [30–33]. Hydrodynamic interactions have also recently been shown to provide a novel mechanism for cooperative motility in groups of reciprocal swimmers, which otherwise would not swim [34–36].

The flow field generated by a swimmer is often described as being dipolar at large distances [8, 14, 37]. This is because a swimmer is self-motile and locomotion is produced by distorting its shape with the forward motion determined precisely by the requirement that it experiences zero resultant force [2, 3]. A multipole description of the flow produced by a swimmer will then have as its most slowly decaying part a dipolar term, varying with distance as $1/r^2$. However, it is noteworthy that a detailed discussion by Lighthill of the flow field produced by a helical filament found that in many cases the flow decayed much more rapidly than $1/r^2$ and that in the particular case of *Spirochaetes* the flow falls off exponentially with no algebraic terms in the far field [38]. More generally, even when the far field flow is dipolar it is unclear exactly how far from the swimmer one needs to be before this dipolar character is evidenced. Nor is it apparent how this distance depends on the type of swimmer, or the detailed properties of its swimming stroke. A naive expectation might be that the magnitude of the far field flow should scale with the slenderness of the swimmer and the amplitude of the swimming stroke in the same way as the swimming speed, which is in general linearly and quadratically, respectively [1, 5], and that this should apply to all terms in a multipole expansion. The transition between near and far field fluid flow would then occur at a distance determined by purely numerical factors, which might even be generic across many different types of swimmer. However, as we shall describe, these naive expectations are not borne out for a particular model of linked sphere swimmers.

Hydrodynamic interactions between swimmers and collective behaviour have been studied using a variety of theoretical models. Continuum descriptions have been developed on the basis that each individual swimmer acts like a point dipole and have established the inherent instability of a fully aligned state where all organisms swim in the same direction [13, 14, 39]. Another common approach is to resolve individual swimmers, but only in an effective sense, imagined as a 'body' and a 'thruster' [37, 40–42]. More detailed descriptions have also been adopted, some of the earliest of which made use of flagella driven micromachines [9, 10] and looked at the propulsive advantage, or disadvantage, of side-by-side and tandem swimming. The interactions between two fixed, parallel, rotating helices were investigated [43], revealing that they do not phase synchronize when driven at constant torque. Ishikawa and co-workers [44–46] have studied in detail a simple 'squirmer' model, matching far field asymptotics onto near field lubrication theory and recently applied their results to the description of collective behaviour in small groups of up to two hundred individuals [47].

Nonetheless there remains a sizeable gap in our understanding of how the specific properties of a given swimmer and its swimming stroke influence the hydrodynamic interactions between them. Even many simple questions remain largely unanswered, such as how the interactions scale with the separation between the swimmers, how sensitive are the interactions to the particular details of the swimming stroke, how important is the relative phase of the swimmers, or even at what stage does the zero Reynolds number approximation begin to break down. Therefore, in this paper, we develop a description of the hydrodynamics of a simple model of linked sphere swimmers, first introduced by Najafi and Golestanian [17]. Working within an Oseen tensor approximation, we consider the locomotion of individual swimmers, the flow field they generate, and the hydrodynamic interactions between swimmers pointing out, in particular, the importance of the symmetry of the swimming stroke.

We first, in section 2, describe the Najafi–Golestanian swimmer and then define the concept of T-duality which describes the symmetry of a swimmer under time reversal. In section 3 we calculate the flow field around the swimmer and show that although the leading term is, in general, dipolar [8] there are important limits when this ceases to be the case. We then, in section 4, consider the hydrodynamic interactions between two swimmers and calculate their relative rotation and translation to leading order in a perturbative expansion. We find that the relative phase of the swimmers is key to determining the way in which they interact.

2. The Najafi–Golestanian swimmer

Linked sphere model swimmers provide a useful framework with which to address many aspects of low Reynolds number hydrodynamics and swimmer–swimmer interactions [19, 48–52]. Their utility arises primarily because the simplicity of the model allows for detailed analytic and numerical analysis. As a result, the form and origin of the hydrodynamics as well as the role of model parameters can be fully determined, permitting considerable insight into swimmer motility and interactions.

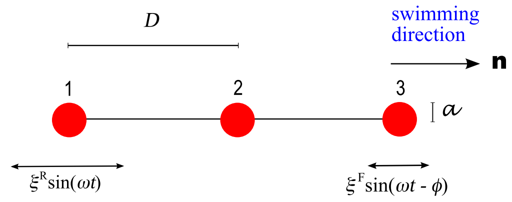

Figure 1. Schematic diagram of the variant of the three linked sphere swimmer first introduced by Najafi and Golestanian [17] that we employ here.

Perhaps the simplest of these models, first introduced by Najafi and Golestanian [17], consists of three spheres of radius a arranged colinearly and connected by rigid, thin rods of 'natural' length D. The rods are made to extend and contract, e.g., by the imagined action of an internal motor, in a periodic and non-reciprocal manner, allowing the organism to swim in the direction of its long axis. The swimming direction breaks the symmetry of this axis so that the spheres can be labelled unambiguously 1, 2 and 3, as indicated in figure 1, increasing in the direction $\mathbf{n}$ in which it swims.

Numerous variants of this model exist, for example allowing for different sized spheres [51] or for a bend between the two rods, enabling the swimmer to rotate [19]. Here we confine our attention to a simple version of the swimmer in which the lengths of the rear and front rods are prescribed to vary sinusoidally as

$$D + \xi^{\mathrm{R}} \sin(\omega t) \qquad \text{and} \qquad D + \xi^{\mathrm{F}} \sin(\omega t - \phi), \qquad (1)$$

respectively. Throughout this paper we will employ a shorthand notation $\tilde{\xi}^{\mathrm{R}} := \xi^{\mathrm{R}} \sin(\omega t)$ and $\tilde{\xi}^{\mathrm{F}} := \xi^{\mathrm{F}} \sin(\omega t - \phi)$ to reduce the length of our formulae.

Before embarking on a detailed analysis of this model, we first describe some simple, but important, features that can be elucidated purely from symmetry considerations and the kinematic reversibility of Stokes flows. It has long been appreciated that kinematic reversibility excludes net motility in organisms that employ reciprocal swimming strokes, such as a waving rudder or a single-hinged scallop [4, 53, 54]. This is because such reciprocal motions look identical whether viewed forwards or backwards in time. However, if instead we view the motion of an organism that actually does swim backwards in time, then kinematic reversibility allows us to interpret this as a different organism swimming forwards in time. Clearly these two swimmers are not really distinct, but merely time reversed versions of each other, and for this reason we refer to them as T-dual. In the case of the Najafi–Golestanian swimmer the T-dual simply corresponds to an interchange of the two amplitudes, $\xi^{\mathrm{R}} \leftrightarrow \xi^{\mathrm{F}}$. From this we see an important limiting case that if the two amplitudes are equal, $\xi^R = \xi^F$, the swimmer and its dual in fact perform the same swimming stroke, and we thus refer to it as self-T-dual. To be more precise, and avoid any potential confusion with reciprocal swimming strokes, we should say that a swimmer is self-T-dual if its swimming stroke is time reversal covariant. By contrast, reciprocal swimming strokes are time reversal invariant. Although this seems like a highly specialized type of swimmer, many of the simple models that have been suggested in the literature belong to this class. For example, the rotating anchor ring described by Taylor [2], Purcell's three link swimmer [4], the 'pushmepullyou' swimmer [18], a sinusoidally waving sheet [1] and a rigidly rotating helical filament [3] are all self-T-dual. As we shall now describe, many of the general features of the hydrodynamics of the Najafi–Golestanian swimmer may be best understood and interpreted in terms of these symmetries arising from kinematic reversibility.

We begin our analysis of the hydrodynamics of the Najafi–Golestanian swimmer with a brief review of the motion of a single swimmer [17, 19, 51] to establish our notational conventions and obtain a number of results that we shall use in subsequent sections. The linearity of the Stokes equations allows the velocity field generated by any low Reynolds number flow to be written as a linear combination of the forces acting on the fluid

$$\mathbf{u}(\mathbf{x}) = \sum_r \mathbf{G}^r(\mathbf{x})\mathbf{f}^r, \tag{2}$$

where $\mathbf{f}^r$ is the force acting on sphere r of the swimmer and $\mathbf{G}^r(\mathbf{x})$ is the appropriate Green function for the fluid domain under consideration. Here we restrict our analysis to the case where the separation between spheres is large compared to their radius and hence replace a distribution of forces over the sphere surface with a single force applied at its centre. Part of the difficulty in applying equation (2) is that when many spheres are present neither the forces, nor the Green function are, in general, known exactly so that some form of approximation is needed. A common approximation, relevant to a dilute suspension of spherical objects in an otherwise unbounded fluid, is to take the Green function to reduce to the Oseen tensor far from the sphere and to reproduce the familiar Stokes drag at the sphere [55, 56]

$$\mathbf{G}^r(\mathbf{x}) = \begin{cases} \dfrac{1}{6\pi\mu a}\mathbf{I} & \text{if } |\mathbf{x}-\mathbf{x}^r| = a, \\ \dfrac{1}{8\pi\mu}\dfrac{1}{|\mathbf{x}-\mathbf{x}^r|}\left(\mathbf{I} + \dfrac{(\mathbf{x}-\mathbf{x}^r)\otimes(\mathbf{x}-\mathbf{x}^r)}{|\mathbf{x}-\mathbf{x}^r|^2}\right) & \text{if } |\mathbf{x}-\mathbf{x}^r| \gg a, \end{cases} \tag{3}$$

where μ is the fluid viscosity and a is the sphere radius. Within this framework the fluid motion is then entirely determined by a knowledge of the forces $\mathbf{f}^r$ with which the swimmer acts on the fluid as a result of its changing shape. These are determined by the combined requirements that each swimmer generates no net force, $\sum_r \mathbf{f}^r = \mathbf{0}$, and that the flow field produced is consistent with the shape changes that it undergoes during its swimming stroke

$$\mathbf{u}(\mathbf{x}^2) - \mathbf{u}(\mathbf{x}^1) =: \mathbf{b}^R = (\partial_t\xi^R)\mathbf{n}, \tag{4}$$

$$\mathbf{u}(\mathbf{x}^3) - \mathbf{u}(\mathbf{x}^2) =: \mathbf{b}^F = (\partial_t\xi^F)\mathbf{n}. \tag{5}$$

Inserting equation (2) for the fluid flow converts these consistency requirements into a relationship between the changing shape of the swimmer and the forces with which it acts on the fluid

$$\left\{\frac{1}{6\pi\mu a}\mathbf{I}\begin{pmatrix}-2 & -1\\ 1 & 2\end{pmatrix} + \mathbf{G}^1(\mathbf{x}^2)\begin{pmatrix}2 & 1\\ -1 & 0\end{pmatrix} + \mathbf{G}^2(\mathbf{x}^3)\begin{pmatrix}0 & 1\\ -1 & -2\end{pmatrix} + \mathbf{G}^1(\mathbf{x}^3)\begin{pmatrix}0 & -1\\ 1 & 0\end{pmatrix}\right\}\begin{pmatrix}\mathbf{f}^1\\ \mathbf{f}^3\end{pmatrix} = \begin{pmatrix}\mathbf{b}^R\\ \mathbf{b}^F\end{pmatrix}, \tag{6}$$

where we have eliminated $\mathbf{f}^2$ using the force-free constraint. In our approach the shape of the swimmer is specified as a function of time and the forces are the unknowns, which are determined by inverting equation (6). The simple linear geometry of the Najafi–Golestanian swimmer allows this inverse to be calculated exactly, however, in anticipation of our subsequent calculations we will not pursue this, and instead give a perturbative inversion, using a/D as a small parameter

$$\begin{pmatrix}\mathbf{f}^1\\ \mathbf{f}^3\end{pmatrix} = 2\pi\mu a\left\{\mathbf{b}^R\begin{pmatrix}-2\\ 1\end{pmatrix} + \mathbf{b}^F\begin{pmatrix}-1\\ 2\end{pmatrix} - 2\pi\mu a\left[\mathbf{G}^1(\mathbf{x}^2)\left\{\mathbf{b}^R\begin{pmatrix}4\\ 1\end{pmatrix} + \mathbf{b}^F\begin{pmatrix}-1\\ 2\end{pmatrix}\right\} + \mathbf{G}^2(\mathbf{x}^3)\left\{\mathbf{b}^R\begin{pmatrix}-2\\ 1\end{pmatrix} + \mathbf{b}^F\begin{pmatrix}-1\\ -4\end{pmatrix}\right\} + \mathbf{G}^1(\mathbf{x}^3)\left\{\mathbf{b}^R\begin{pmatrix}4\\ -5\end{pmatrix} + \mathbf{b}^F\begin{pmatrix}5\\ -4\end{pmatrix}\right\}\right] + \mathrm{o}([a/D]^2)\right\}. \tag{7}$$

To determine the translational motion of the swimmer during any given swimming stroke it suffices to track the position of any one of the three spheres, since from this and the prescribed shape of the swimmers the positions of the other spheres automatically follow. We choose to track the position of the centre sphere, although this choice is somewhat arbitrary and any other choice would be just as good. In the zero Reynolds number limit the velocity of each sphere is required to match instantaneously the local velocity of the fluid surrounding it, so that the position of the sphere evolves according to

$$\frac{\mathrm{d}\mathbf{x}^2}{\mathrm{d}t} = \mathbf{u}(\mathbf{x}^2), \tag{8}$$

$$= \frac{1}{3}(\mathbf{b}^R - \mathbf{b}^F) + \frac{2\pi\mu a}{3}\{\mathbf{G}^2(\mathbf{x}^3)[2\mathbf{b}^R + \mathbf{b}^F] - \mathbf{G}^1(\mathbf{x}^2)[\mathbf{b}^R + 2\mathbf{b}^F] + \mathbf{G}^1(\mathbf{x}^3)[\mathbf{b}^F - \mathbf{b}^R]\} + \mathrm{o}([a/D]^2). \tag{9}$$

Integrating this expression gives the displacement of the centre sphere from its initial position as

$$\delta\mathbf{x}^2(t) = \mathbf{n}\int_0^t \mathrm{d}t'\left\{\tfrac{1}{3}\partial_{t'}(\tilde{\xi}^R - \tilde{\xi}^F) + \frac{a}{6}\left[\frac{1}{D+\tilde{\xi}^F}\partial_{t'}(2\tilde{\xi}^R + \tilde{\xi}^F) - \frac{1}{D+\tilde{\xi}^R}\partial_{t'}(\tilde{\xi}^R + 2\tilde{\xi}^F) + \frac{1}{2D+\tilde{\xi}^R+\tilde{\xi}^F}\partial_{t'}(\tilde{\xi}^F - \tilde{\xi}^R)\right] + \mathrm{o}([a/D]^2)\right\}. \tag{10}$$

The first term describes an o(ξ) oscillation about its initial position that integrates to zero over a complete swimming stroke. This is precisely the motion the sphere would undergo if the swimmer was in vacuum and corresponds to the centre of mass remaining fixed. However, since the swimmer is in a fluid medium this is not the only contribution to its motion. The additional terms at o(a/D), and higher, arise due to hydrodynamic interactions and describe swimming, since they do not integrate to zero over a complete swimming stroke. Performing the integration we find that to leading order the total distance moved after each stroke is

$$\mathcal{T} = \frac{2\pi a}{3}\frac{\xi^R\xi^F\sin(\phi)}{D^2}\{(D/\xi^R)^2[(1-(\xi^R/D)^2)^{-1/2}-1] + (D/\xi^F)^2[(1-(\xi^F/D)^2)^{-1/2}-1] - \tfrac{1}{4}(2D/\Xi)^2[(1-(\Xi/2D)^2)^{-1/2}-1]\} + \mathrm{o}([a/D]^2), \tag{11}$$

where we have defined

$$\Xi = ((\xi^R)^2 + 2\xi^R\xi^F\cos(\phi) + (\xi^F)^2)^{1/2}. \tag{12}$$

3. Time averaged flow field

In propelling itself through the fluid, the swimmer generates a net time averaged flow field, whose nature we now investigate. The naive expectation is that the far field form of this flow will be accurately described as dipolar, since this is the most slowly decaying term in a multipole expansion, the monopole term vanishing on account of there being no net force acting on the swimmer [8, 14, 37].

The time averaged flow field produced by a Najafi–Golestanian swimmer is given by

$$\bar{\mathbf{u}}(\mathbf{x}) := \frac{1}{T}\int_0^T \mathrm{d}t\,\mathbf{u}(\mathbf{x}) = \frac{1}{T}\int_0^T \mathrm{d}t\,\sum_r \mathbf{G}^r(\mathbf{x})\mathbf{f}^r. \tag{13}$$

Part of the difficulty in evaluating this average flow is that the position of the swimmer changes with time, so that the distance $|\mathbf{x}-\mathbf{x}^r|$ is not a constant. Although the positions of each of the spheres, $\mathbf{x}^r(t)$, are in principle known from equation (10), the use of this directly does not lead to any simple, or convenient expressions for the average flow. However, in the far field, at distances large compared to the size of the swimmer, the magnitude of the oscillations in $\mathbf{x}^r(t)$ will be small compared to the distance to the point of observation. With this in mind we write

$$\mathbf{x}-\mathbf{x}^r = (\mathbf{x}-\mathbf{y}) + (\mathbf{y}-\mathbf{x}^r) =: \mathbf{r} - \delta\mathbf{x}^r, \tag{14}$$

where $\mathbf{y}$ is a fixed point used to represent the (average) position of the swimmer, and make use of a multipole expansion of the stokeslet. In principle the choice of the point $\mathbf{y}$ is somewhat arbitrary, however, for convenience we shall take it to be the position of the centre sphere at a reference time, $t = 0$, corresponding to the start of the swimming stroke; $\mathbf{y} = \mathbf{x}^2(t = 0)$. The stokeslet is then expanded as a formal power series in $1/r$

$$\mathbf{G}^r(\mathbf{x}) =: \frac{1}{8\pi\mu}\sum_{j=0}^{\infty}[\mathbf{S}^{(j)}(\mathbf{r})](\delta\mathbf{x}^r)^{\otimes j}, \tag{15}$$

leading to a multipole expansion for the far field time averaged flow

$$\bar{u}_\alpha(\mathbf{x}) = \sum_{j=0}^{\infty} S^{(j)}_{\alpha\beta\sigma\cdots\tau}(\mathbf{r})n_\beta n_\sigma\cdots n_\tau \times \int_0^T \frac{\mathrm{d}t}{T}\sum_r(\delta x^r)^j\,\frac{1}{8\pi\mu}f^r, \tag{16}$$

where we have made use of the fact that both the forces $\mathbf{f}^r$ and the displacements $\delta\mathbf{x}^r$ are parallel to the swimming direction $\mathbf{n}$. Equation (16) is composed of two factors; the tensorial term $\mathbf{S}^{(j)}\mathbf{n}^{\otimes(j+1)}$ which describes how the flow depends on position relative to the swimmer and how it decays with distance, and an integral which captures how the details of the swimming stroke determine the coefficient of each term in the multipole expansion. We can see immediately that the leading $j = 0$ term vanishes on account of the total force generated by the swimmer being zero. For the Najafi–Golestanian swimmer both of the next two terms, the $j = 1$ dipolar and $j = 2$ quadrupolar terms, provide important contributions to the time averaged far field flow and we shall address them both in turn.

3.1. Dipolar flow

The most slowly decaying term in the multipole expansion, equation (16), is the $1/r^2$ dipolar contribution, so that at sufficiently large distances we can expect this to provide an accurate description of the average flow field generated by most swimmers. To calculate the integral in equation (16) we make use of the useful relations

$$\delta x^1 = \delta x^2 - (D+\tilde{\xi}^R), \qquad \text{and} \qquad \delta x^3 = \delta x^2 + (D+\tilde{\xi}^F), \tag{17}$$

which allow us to write

$$\sum_r(\delta x^r)f^r = (D+\tilde{\xi}^F)f^3 - (D+\tilde{\xi}^R)f^1, = \tfrac{1}{2}(2D+\tilde{\xi}^R+\tilde{\xi}^F)(f^3-f^1) + \tfrac{1}{2}(\tilde{\xi}^F-\tilde{\xi}^R)(f^3+f^1). \tag{18}$$

Inserting equation (7) for the forces we find that the relevant integral for the dipolar flow field is

$$\frac{a}{8T}\int_0^T \mathrm{d}t\,\Bigg\{3\left(2D+\tilde{\xi}^R+\tilde{\xi}^F+\frac{3a}{2}\right)\partial_t(\tilde{\xi}^R+\tilde{\xi}^F) + (\tilde{\xi}^R-\tilde{\xi}^F)\partial_t(\tilde{\xi}^R-\tilde{\xi}^F) + \frac{a}{2}(\tilde{\xi}^R-\tilde{\xi}^F)\Bigg[\frac{1}{D+\tilde{\xi}^R}\partial_t(2\tilde{\xi}^R+4\tilde{\xi}^F) - \frac{1}{D+\tilde{\xi}^F}\partial_t(4\tilde{\xi}^R+2\tilde{\xi}^F) - \frac{1}{2D+\tilde{\xi}^R+\tilde{\xi}^F}\partial_t(\tilde{\xi}^R-\tilde{\xi}^F)\Bigg]\Bigg\}. \tag{19}$$

The first line is a total derivative and thus does not contribute to the final result. The remaining integrals can be done using standard techniques to give

$$\frac{\omega a^2 \sin(\phi)}{8D}\Bigg\{2\xi^{\mathrm{F}}(\xi^{\mathrm{R}}-\xi^{\mathrm{F}}\cos(\phi))\left(\frac{D}{\xi^{\mathrm{R}}}\right)^2 \times\left[\left(1-\left(\frac{\xi^{\mathrm{R}}}{D}\right)^2\right)^{-1/2}-1\right] + \xi^{\mathrm{F}}(\xi^{\mathrm{R}}+2\xi^{\mathrm{F}}\cos(\phi))\left(\frac{D}{\xi^{\mathrm{R}}}\right)^2\left[1-\left(1-\left(\frac{\xi^{\mathrm{R}}}{D}\right)^2\right)^{1/2}\right] - 2\xi^{\mathrm{R}}(\xi^{\mathrm{F}}-\xi^{\mathrm{R}}\cos(\phi))\left(\frac{D}{\xi^{\mathrm{F}}}\right)^2\left[\left(1-\left(\frac{\xi^{\mathrm{F}}}{D}\right)^2\right)^{-1/2}-1\right] - \xi^{\mathrm{R}}(\xi^{\mathrm{F}}+2\xi^{\mathrm{R}}\cos(\phi))\left(\frac{D}{\xi^{\mathrm{F}}}\right)^2\left[1-\left(1-\left(\frac{\xi^{\mathrm{F}}}{D}\right)^2\right)^{1/2}\right] - \frac{\xi^{\mathrm{R}}\xi^{\mathrm{F}}(\xi^{\mathrm{R}}+\xi^{\mathrm{F}})(\xi^{\mathrm{R}}-\xi^{\mathrm{F}})}{8D^2}\left(\frac{2D}{\Xi}\right)^4 \times\left[2-\left(1-\left(\frac{\Xi}{2D}\right)^2\right)^{1/2}-\left(1-\left(\frac{\Xi}{2D}\right)^2\right)^{-1/2}\right]\Bigg\}, \tag{20}$$

where Ξ is again given by equation (12). Although this expression is quite lengthy and complicated its most important feature is readily apparent: namely it vanishes identically if $\xi^{\mathrm{R}} = \xi^{\mathrm{F}}$. This is a direct consequence of kinematic reversibility and is a generic feature of self-T-dual swimming strokes. Such strokes are time reversal covariant, however dipolar flow fields are not: reversing the direction of time converts a dipolar flow in which the fluid flows away from the swimmer along its direction of motion, known as extensile, into one in which the fluid flows towards the swimmer along the same direction, known as contractile. Dipolar flows are thus incompatible with self-T-dual swimming strokes and must therefore be absent for such swimmers, an observation first made by Pooley [48].

3.2. Quadrupolar flow

For both self-T-dual and more general Najafi–Golestanian swimmers, the quadrupolar term ($j = 2$) also makes an important contribution to the time averaged far field flow. It decays more rapidly than the dipolar term, varying with distance as $1/r^3$, however its amplitude turns out to be substantially larger so that over a considerable range of intermediate distances from the swimmer, the time averaged flow field may be well approximated as quadrupolar.

To evaluate the integral in equation (16) we again make use of the relations in equation (17) to write

$$\sum_r (\delta x^r)^2 f^r = (f^3+f^1)[\delta x^2(\tilde{\xi}^{\mathrm{F}}-\tilde{\xi}^{\mathrm{R}}) + (D+\tfrac{1}{2}(\tilde{\xi}^{\mathrm{F}}+\tilde{\xi}^{\mathrm{R}}))^2+\tfrac{1}{4}(\tilde{\xi}^{\mathrm{F}}-\tilde{\xi}^{\mathrm{R}})^2] + (f^3-f^1)(D+\tfrac{1}{2}(\tilde{\xi}^{\mathrm{F}}+\tilde{\xi}^{\mathrm{R}}))(2\delta x^2+\tilde{\xi}^{\mathrm{F}}-\tilde{\xi}^{\mathrm{R}}). \tag{21}$$

Inserting the expressions for the forces from equation (7) and retaining only terms of quadratic order in ξ, the integral in equation (16) becomes

$$\frac{aD}{4T}\int_0^T \mathrm{d}t\,\Bigg\{\left[1+\frac{19a}{8D}\right](\tilde{\xi}^{\mathrm{F}}+\tilde{\xi}^{\mathrm{R}})\partial_t(\tilde{\xi}^{\mathrm{F}}-\tilde{\xi}^{\mathrm{R}}) + 3\left[1+\frac{3a}{4D}\right](2\delta x^2+\tilde{\xi}^{\mathrm{F}}-\tilde{\xi}^{\mathrm{R}})\partial_t(\tilde{\xi}^{\mathrm{F}}+\tilde{\xi}^{\mathrm{R}})\Bigg\}. \tag{22}$$

We integrate the second term by parts and use equation (10) to substitute for $\partial_t \delta x^2$ to find that equation (22) reduces to

$$\frac{17a^2}{32T}\int_0^T \mathrm{d}t\,(\tilde{\xi}^{\mathrm{F}}+\tilde{\xi}^{\mathrm{R}})\partial_t(\tilde{\xi}^{\mathrm{F}}-\tilde{\xi}^{\mathrm{R}}) = \frac{17\omega a^2\xi^{\mathrm{R}}\xi^{\mathrm{F}}\sin(\phi)}{32}. \tag{23}$$

3.3. Far field flow

These two contributions, the dipolar and quadrupolar terms, provide a good description of the far field properties of the time averaged flow generated by the swimmer

$$\bar{\mathbf{u}}(\mathbf{x}) = \frac{21\omega a^2\xi^{\mathrm{R}}\xi^{\mathrm{F}}((\xi^{\mathrm{R}})^2-(\xi^{\mathrm{F}})^2)\sin(\phi)}{256D^3r^2}\{[3(\mathbf{n}\cdot\hat{\mathbf{r}})^2-1]\hat{\mathbf{r}}\} + \frac{17\omega a^2\xi^{\mathrm{R}}\xi^{\mathrm{F}}\sin(\phi)}{64r^3}\{3(\mathbf{n}\cdot\hat{\mathbf{r}})[5(\mathbf{n}\cdot\hat{\mathbf{r}})^2-3]\hat{\mathbf{r}} - [3(\mathbf{n}\cdot\hat{\mathbf{r}})^2-1]\mathbf{n}\} + \mathrm{o}(1/r^4), \tag{24}$$

where we have used the lowest order term in a series expansion in ξ/D for the amplitude of the dipolar term. A comparison of the amplitudes of these two contributions depends on the direction to the observation point relative to the swimming direction, i.e., on $\mathbf{n}\cdot\hat{\mathbf{r}}$. A natural direction in which to make this comparison is along the swimming direction, $\mathbf{n}\cdot\hat{\mathbf{r}} = 1$, whereupon we find that the flow field only becomes dipolar for distances

$$\frac{r}{D} \gtrsim \frac{136D^2}{21(\xi^{\mathrm{R}}+\xi^{\mathrm{F}})|\xi^{\mathrm{R}}-\xi^{\mathrm{F}}|}. \tag{25}$$

This is a remarkable result, which shows that it is only appropriate to view the Najafi–Golestanian swimmer as a simple force dipole at distances of several tens of body lengths from the swimmer. At closer distances the quadrupolar flow is more significant. However, it should be cautioned that this result is in a sense a worst case scenario. The amplitude of the dipolar term is required to vanish if either $\xi^{\mathrm{R}} = 0$ or $\xi^{\mathrm{F}} = 0$, since then the swimming stroke is reciprocal, and also when $\xi^{\mathrm{R}} = \xi^{\mathrm{F}}$ and the swimmer is self-T-dual. This means that the amplitude of the dipolar term must include a factor $\xi^{\mathrm{R}}\xi^{\mathrm{F}}(\xi^{\mathrm{R}}-\xi^{\mathrm{F}})$. For sinusoidal strokes with a single frequency, terms of cubic order in the oscillations all integrate to zero, leading to the dipolar flow field scaling as ξ^4, as in equation (24). However, this is not true for other swimming strokes: in particular, for the original, four-stage swimming stroke [17] we have found that the amplitude of the dipolar flow scales as ξ^3, and that this dominates the far field time averaged flow for distances [48]

$$\frac{r}{D} \gtrsim \frac{68D}{29|\xi^{\mathrm{R}}-\xi^{\mathrm{F}}|}, \tag{26}$$

a rather more conservative result than equation (25).

4. Swimmer–swimmer interactions

We now turn our attention to the hydrodynamics of more than one swimmer. That is, we wish to ask what will be the influence on one swimmer of the presence of other swimmers nearby in the fluid. Our approach to calculating the hydrodynamics of a group of swimmers parallels our analysis of a single swimmer. In particular, the starting point is again the statement that linearity of the Stokes equations allows the fluid flow to be written as a linear combination of the forces acting on the fluid

$$\mathbf{u}(\mathbf{x}) = \sum_A \sum_r \mathbf{G}^r_A(\mathbf{x})\mathbf{f}^r_A. \tag{27}$$

Here the subscript A labels the individual swimmers and the other notation is the same as in equation (2). As for the single swimmer, we will consider that this expression provides a complete solution if the forces $\mathbf{f}^r_A$ can be determined in terms of the prescribed swimming stroke. The constraint that each swimmer is force-free still applies, $\sum_r \mathbf{f}^r_A = \mathbf{0}\ \forall\ A$, however the consistency relations for the fluid flow need to be modified to read (for each swimmer)

$$\mathbf{u}(\mathbf{x}^2_A) - \mathbf{u}(\mathbf{x}^1_A) =: \mathbf{b}^{\mathrm{R}}_A = (\partial_t \xi^{\mathrm{R}}_A)\mathbf{n}^A + [\Omega^A, (D+\xi^{\mathrm{R}}_A)\mathbf{n}^A], \tag{28}$$

$$\mathbf{u}(\mathbf{x}^3_A) - \mathbf{u}(\mathbf{x}^2_A) =: \mathbf{b}^{\mathrm{F}}_A = (\partial_t \xi^{\mathrm{F}}_A)\mathbf{n}^A + [\Omega^A, (D+\xi^{\mathrm{F}}_A)\mathbf{n}^A], \tag{29}$$

in order to account for the rotational motion of the swimmer. Here we employ an unconventional bracket notation, [,], to denote the vector cross product. The additional unknown of the angular velocity Ω^A of each swimmer is determined by imposing the further constraint that its motion impart no net torque to the fluid

$$\sum_r [\mathbf{x}^r_A - \mathbf{y}, \mathbf{f}^r_A] = 0. \tag{30}$$

The point $\mathbf{y}$ about which the torque is measured is completely arbitrary because of the force-free constraint.

As for the motion of a single swimmer, we use equations (27)–(29) to set up a system of linear equations relating the independent forces ($\mathbf{f}^2_A$ being eliminated via the force-free constraint) to the specified changing shape of the swimmer. Schematically, these may be written as a matrix equation

$$\sum_B \mathcal{G}_{AB}\mathcal{F}_B = \mathcal{B}_A, \tag{31}$$

where the vectors $\mathcal{B}_A$, $\mathcal{F}_A$ and the matrix $\mathcal{G}_{AB}$ are themselves vector and matrix valued

$$\mathcal{B}_A := \begin{pmatrix} \mathbf{b}^1_A \\ \mathbf{b}^2_A \end{pmatrix}, \qquad \mathcal{F}_A := \begin{pmatrix} \mathbf{f}^1_A \\ \mathbf{f}^3_A \end{pmatrix}, \tag{32}$$

$$\mathcal{G}_{AB} := \begin{pmatrix} [\mathbf{G}^{12}_B(\mathbf{x}^2_A) - \mathbf{G}^{12}_B(\mathbf{x}^1_A)] & [\mathbf{G}^{32}_B(\mathbf{x}^2_A) - \mathbf{G}^{32}_B(\mathbf{x}^1_A)] \\ [\mathbf{G}^{12}_B(\mathbf{x}^3_A) - \mathbf{G}^{12}_B(\mathbf{x}^2_A)] & [\mathbf{G}^{32}_B(\mathbf{x}^3_A) - \mathbf{G}^{32}_B(\mathbf{x}^2_A)] \end{pmatrix}, \tag{33}$$

and $\mathbf{G}^{rs}_B(\mathbf{x}) = \mathbf{G}^r_B(\mathbf{x}) - \mathbf{G}^s_B(\mathbf{x})$. The forces will be known if the matrix $\mathcal{G}_{AB}$ can be inverted. To perform the inversion we make use of the fact that the swimmers are in a dilute suspension so that the interactions are all in the weak, far field regime. Consequently the elements $\mathcal{G}_{AA}$ are much larger than $\mathcal{G}_{AB}$, $A \neq B$, which may be exploited in writing

$$\mathcal{F}_A = \mathcal{G}^{-1}_{AA}\mathcal{B}_A - \sum_{B\neq A} \mathcal{G}^{-1}_{AA}\mathcal{G}_{AB}\mathcal{F}_B, \tag{34}$$

with the final solution subsequently obtained by iteration. The first term represents the forces associated with the swimming of a single isolated organism and are given as before by equation (7). The second term gives the contribution to the forces due to interactions with all the other swimmers.

In treating the interactions between swimmers we need to consider objects of the form $\mathbf{G}^r_B(\mathbf{x}^s_A)$, stokeslets associated with spheres comprising swimmer B evaluated at the location of the spheres of swimmer A. In the case of a dilute assembly of swimmers considered here it may be assumed that the separation between swimmers is large compared to the size of any given individual organism. Then, generalizing equation (14), we introduce the decomposition

$$\begin{aligned} \mathbf{x}^r_B - \mathbf{x}^s_A &= (\mathbf{x}^2_B(0) - \mathbf{x}^2_A(0)) + (\mathbf{x}^r_B - \mathbf{x}^2_B(0)) - (\mathbf{x}^s_A - \mathbf{x}^2_A(0)), \\ &=: \mathbf{r}_{BA} + \delta\mathbf{x}^r_B - \delta\mathbf{x}^s_A, \end{aligned} \tag{35}$$

and perform a multipole expansion of the stokeslets

$$\mathbf{G}^r_B(\mathbf{x}^s_A) =: \frac{1}{8\pi\mu}\sum_{j=0}^{\infty}\sum_{k=0}^{j}[\mathbf{S}^{(j,k)}(\mathbf{r}_{BA})](\delta\mathbf{x}^s_A)^{\otimes k}(\delta\mathbf{x}^r_B)^{\otimes(j-k)}. \tag{36}$$

This decomposition affords a convenient splitting of the interaction into an essentially geometric piece, $\mathbf{S}^{(j,k)}(\mathbf{r}_{BA})$, dependent only on the relative position of the swimmers, and terms dependent on the details of the swimming motions. The expansion coefficients $\mathbf{S}^{(j,k)}$ are formally defined by equation (36) from which it may be shown that they are given by

$$S^{(j,k)}_{\alpha\beta\ \sigma\cdots\tau}(\mathbf{r}) = \frac{(-)^k}{k!(j-k)!}\partial_\sigma\cdots\partial_\tau\left\{\frac{1}{r}(\delta_{\alpha\beta} + \hat{r}_\alpha\hat{r}_\beta)\right\}. \tag{37}$$

These tensors are fully symmetric in the j indices $\sigma\cdots\tau$ as well as being symmetric in the indices α, β. They scale with the separation between swimmers as $r^{-(j+1)}$ so that the terms with the lowest values of j are expected to dominate the far field interactions. With this expansion of the stokeslets the contribution to the forces coming from interactions is found to be

$$\begin{aligned} \begin{pmatrix} (f^{\mathrm{INT}})^1_A \\ (f^{\mathrm{INT}})^3_A \end{pmatrix}_\alpha &= \frac{a}{4}\sum_{B\neq A}\sum_{j=2}^{\infty}\sum_{k=1}^{j-1} S^{(j,k)}_{\alpha\beta\ \sigma\cdots\tau\ \nu\cdots\rho}(\mathbf{r}_{BA}) \\ &\times \begin{pmatrix} -2(\delta x^1_A)^{\otimes k}_{\sigma\cdots\tau} + (\delta x^2_A)^{\otimes k}_{\sigma\cdots\tau} + (\delta x^3_A)^{\otimes k}_{\sigma\cdots\tau} \\ (\delta x^1_A)^{\otimes k}_{\sigma\cdots\tau} + (\delta x^2_A)^{\otimes k}_{\sigma\cdots\tau} - 2(\delta x^3_A)^{\otimes k}_{\sigma\cdots\tau} \end{pmatrix} \\ &\times \sum_r (\delta x^r_B)^{\otimes(j-k)}_{\nu\cdots\rho}(f^r_B)_\beta. \end{aligned} \tag{38}$$

4.1. Swimmer rotation

Equations (7) and (38) provide the forces generated by the swimmer in performing its swimming stroke so that the sole remaining unknown is its angular velocity, Ω^A. This is obtained by the requirement that the swimmer's motion through the fluid is such that no net torque acts on it, equation (30), which we write as

$$\begin{aligned} \mathbf{0} &= \sum_r [(\mathbf{x}^r_A - \mathbf{y}), \mathbf{f}^r_A], \\ &= [(\mathbf{x}^3_A - \mathbf{x}^2_A), \mathbf{f}^3_A] - [(\mathbf{x}^2_A - \mathbf{x}^1_A), \mathbf{f}^1_A], \\ &= (D + \tfrac{1}{2}(\xi^{\mathrm{R}}_A + \xi^{\mathrm{F}}_A))[\mathbf{n}^A, (\mathbf{f}^3_A - \mathbf{f}^1_A)] \\ &\quad + \tfrac{1}{2}(\xi^{\mathrm{F}}_A - \xi^{\mathrm{R}}_A)[\mathbf{n}^A, (\mathbf{f}^3_A + \mathbf{f}^1_A)]. \end{aligned} \tag{39}$$

In manipulating equation (39) it only proves necessary to balance the o(1) part of the single swimmer forces, equation (7), against the contribution due to interactions, equation (38). There is no fundamental obstacle to retaining the higher order terms from equation (7), however, since these lead to a substantial increase in the length of formulae and play no essential role, they will be omitted in what follows. After some straightforward manipulations the torque balance equation becomes

$$\epsilon_{\alpha\beta\gamma}\Bigg\{Pn_\beta^A n_\delta^A[\Omega^A,]_{\gamma\delta} - \frac{a}{4}\sum_{B\neq A}\sum_{j=2}^{\infty}\sum_{k=1}^{j-1} S^{(j,k)}_{\gamma\lambda\,\sigma\cdots\tau\,\nu\cdots\rho} \times (\mathbf{r}_{BA})\, n_\beta^A A^k_{\sigma\cdots\tau} C^{j-k}_{\lambda\,\nu\cdots\rho}\Bigg\} = 0, \quad (40)$$

where we have defined

$$P := 6(D + \tfrac{1}{2}(\tilde{\xi}_A^{\rm R} + \tilde{\xi}_A^{\rm F}))^2 + \tfrac{1}{2}(\tilde{\xi}_A^{\rm R} - \tilde{\xi}_A^{\rm F})^2, \quad (41)$$

$$A^k_{\sigma\cdots\tau} := 3D((\delta x_A^3)^{\otimes k}_{\sigma\cdots\tau} - (\delta x_A^1)^{\otimes k}_{\sigma\cdots\tau}) + \tilde{\xi}_A^{\rm R}(-2(\delta x_A^1)^{\otimes k}_{\sigma\cdots\tau} + (\delta x_A^2)^{\otimes k}_{\sigma\cdots\tau} + (\delta x_A^3)^{\otimes k}_{\sigma\cdots\tau}) + \tilde{\xi}_A^{\rm F}(-(\delta x_A^1)^{\otimes k}_{\sigma\cdots\tau} - (\delta x_A^2)^{\otimes k}_{\sigma\cdots\tau} + 2(\delta x_A^3)^{\otimes k}_{\sigma\cdots\tau}), \quad (42)$$

$$C^{j-k}_{\lambda\,\nu\cdots\rho} := (b_B^1)_\lambda[-2(\delta x_B^1)^{\otimes(j-k)}_{\nu\cdots\rho} + (\delta x_B^2)^{\otimes(j-k)}_{\nu\cdots\rho} + (\delta x_B^3)^{\otimes(j-k)}_{\nu\cdots\rho}] + (b_B^2)_\lambda[-(\delta x_B^1)^{\otimes(j-k)}_{\nu\cdots\rho} - (\delta x_B^2)^{\otimes(j-k)}_{\nu\cdots\rho} + 2(\delta x_B^3)^{\otimes(j-k)}_{\nu\cdots\rho}]. \quad (43)$$

This equation is easily solved to give the angular velocity of each swimmer as

$$[\Omega^A,]_{\alpha\beta} = \frac{a}{4}\sum_{B\neq A}\sum_{j=2}^{\infty}\sum_{k=1}^{j-1}(\delta_{\alpha\gamma}n_\beta^A - \delta_{\beta\gamma}n_\alpha^A) \times [S^{(j,k)}_{\gamma\lambda\,\sigma\cdots\tau\,\nu\cdots\rho}(\mathbf{r}_{BA})](P^{-1}A^k_{\sigma\cdots\tau})C^{j-k}_{\lambda\,\nu\cdots\rho}. \quad (44)$$

Our main interest is in the net effect that the interactions have over one complete swimming stroke. Now, the orientation of each swimmer evolves according to the equation

$$\frac{{\rm d}n_\alpha^A}{{\rm d}t} = [\Omega^A, \mathbf{n}^A]_\alpha. \quad (45)$$

Technically, this is a set of $N_{\rm swimmer}$ coupled, non-linear, ordinary differential equations. We make no attempt to solve it exactly, being satisfied with a perturbative approach. First we solve for the motion of a single swimmer, which we then substitute into the right-hand side of equation (45). This means the right-hand side may be considered as simply a function of t and integrated directly. In this case a single swimmer does not rotate, so that where $\mathbf{n}$ appears on the right-hand side it may be considered just a constant vector. The net change in orientation over a complete swimming stroke is thus

$$n_\alpha^A(T) - n_\alpha^A = \frac{a}{4}\sum_{B\neq A}\sum_{j=2}^{\infty}\sum_{k=1}^{j-1}(\delta_{\alpha\beta} - n_\alpha^A n_\beta^A) \times [S^{(j,k)}_{\beta\gamma\,\sigma\cdots\tau\,\nu\cdots\rho}(\mathbf{r}_{BA})]n_\gamma^B n_\sigma^A\cdots n_\tau^A n_\nu^B\cdots n_\rho^B(\mathcal{I}^{(j,k)}), \quad (46)$$

where

$$\mathcal{I}^{(j,k)} := \int_0^T {\rm d}t\; P^{-1}A^k C^{j-k}. \quad (47)$$

Again we emphasize that this expression decomposes the effect of the interactions into two parts: the tensorial part involving $\mathbf{S}^{(j,k)}$ which captures how the relative positions and orientations of the swimmers influence their interactions, and the integral $\mathcal{I}^{(j,k)}$ which captures the details of the swimming stroke. In fact, the form of these integrals offers an important insight into the nature of hydrodynamic interactions between swimmers. A short calculation reveals that $A^1 = P$ so that all terms with $k = 1$ in equation (46) are independent of the swimming motion of swimmer A. We refer to these as passive interactions. They correspond to the rotation that would be experienced by an inanimate object, or dead swimmer, drifting passively in the flow field generated by the other swimmers. By contrast, the terms with $k \geqslant 2$ depend on the swimming motion of both swimmers. We call these active interactions. They represent the additional rotation experienced by the swimmers because they are trying to swim simultaneously and encode all of the information about the relative phase of the swimmers and the collective nature of the interactions. As we shall show, it is these active terms that provide the dominant contribution to the interactions between swimmers.

The most slowly decaying active term in the far field is the contribution with $j = 3, k = 2$, which we now determine. A straightforward calculation gives

$$A^2 = P[2\delta x_A^2 + \tfrac{7}{6}(\tilde{\xi}_A^{\rm F} - \tilde{\xi}_A^{\rm R})] - \tfrac{1}{3}(\tilde{\xi}_A^{\rm F} - \tilde{\xi}_A^{\rm R})^3, \quad (48)$$

$$C^1 = 3D\,\partial_t(\tilde{\xi}_B^{\rm F} + \tilde{\xi}_B^{\rm R}) + \partial_t((\tilde{\xi}_B^{\rm F})^2 + \tilde{\xi}_B^{\rm F}\tilde{\xi}_B^{\rm R} + (\tilde{\xi}_B^{\rm R})^2) + {\rm o}(a/D), \quad (49)$$

so that the integral $\mathcal{I}^{(3,2)}$ is given by

$$\mathcal{I}^{(3,2)} = \frac{3\pi D}{2}\{\xi_A^{\rm R}[\xi_B^{\rm R}\sin(\eta_{BA}) + \xi_B^{\rm F}\sin(\eta_{BA} - \phi_B)] - \xi_A^{\rm F}[\xi_B^{\rm R}\sin(\eta_{BA} + \phi_A) + \xi_B^{\rm F}\sin(\eta_{BA} + \phi_A - \phi_B)]\} + {\rm o}(\xi^4). \quad (50)$$

Here, η_{BA} is the phase of swimmer B relative to swimmer A, i.e., if $\tilde{\xi}_A^{\rm R} = \xi_A^{\rm R}\sin(\omega t)$ then $\tilde{\xi}_B^{\rm R} = \xi_B^{\rm R}\sin(\omega t + \eta_{BA})$ and similarly for the front amplitudes. We remark in passing that this amplitude does not vanish for $\phi_A = \phi_B = 0$ when the two swimmers are reciprocal. Instead we find $\mathcal{I}^{(3,2)} = (3\pi D/2)(\xi_A^{\rm R}\xi_B^{\rm R} - \xi_A^{\rm F}\xi_B^{\rm F})\sin(\eta_{BA})$, so that, provided the swimmers are not in phase or exactly out of phase, they can still interact hydrodynamically, despite each individually performing a reciprocal motion, an insight that has recently been applied to the collective locomotion of reciprocal oscillating dumb-bells [35, 36].

Combining equations (46) and (50), we find that the active contributions to the interactions lead to a rotation of the swimmers that in the far field has the asymptotic form

$$\Delta\mathbf{n}^A_{\rm active} \sim \sum_{B\neq A}\frac{-3a\mathcal{I}^{(3,2)}}{8r_{BA}^4}[1 + 2(\mathbf{n}^A\cdot\mathbf{n}^B)^2 - 5(\mathbf{n}^A\cdot\hat{\mathbf{r}}_{BA})^2 - 5(\mathbf{n}^B\cdot\hat{\mathbf{r}}_{BA})^2 - 20(\mathbf{n}^A\cdot\mathbf{n}^B)(\mathbf{n}^A\cdot\hat{\mathbf{r}}_{BA})(\mathbf{n}^B\cdot\hat{\mathbf{r}}_{BA}) + 35(\mathbf{n}^A\cdot\hat{\mathbf{r}}_{BA})^2(\mathbf{n}^B\cdot\hat{\mathbf{r}}_{BA})^2]\{\hat{\mathbf{r}}_{BA} - (\mathbf{n}^A\cdot\hat{\mathbf{r}}_{BA})\mathbf{n}^A\}. \quad (51)$$

For the passive interactions, the rotation can be determined from the $k = 1$ terms or, without need to repeat the integrations, using the time averaged flow field, equation (24), from which we obtain

$$\begin{aligned}\Delta\mathbf{n}^A_{\text{passive}} \sim \sum_{B\neq A} \frac{63\pi a^2 \xi^{\text{R}}_B \xi^{\text{F}}_B ((\xi^{\text{R}}_B)^2 - (\xi^{\text{F}}_B)^2)\sin(\phi_B)}{128 D^3 r^3_{BA}} \\ \times [(\mathbf{n}^A \cdot \hat{\mathbf{r}}_{BA}) + 2(\mathbf{n}^A \cdot \mathbf{n}^B)(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA}) \\ - 5(\mathbf{n}^A \cdot \hat{\mathbf{r}}_{BA})(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA})^2]\{\hat{\mathbf{r}}_{BA} - (\mathbf{n}^A \cdot \hat{\mathbf{r}}_{BA})\mathbf{n}^A\} \\ + \sum_{B\neq A} \frac{51\pi a^2 \xi^{\text{R}}_B \xi^{\text{F}}_B \sin(\phi_B)}{32 r^4_{BA}} \{[3(\mathbf{n}^A \cdot \mathbf{n}^B) \\ - 15(\mathbf{n}^A \cdot \hat{\mathbf{r}}_{BA})(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA}) \\ - 15(\mathbf{n}^A \cdot \mathbf{n}^B)(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA})^2 \\ + 35(\mathbf{n}^A \cdot \hat{\mathbf{r}}_{BA})(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA})^3]\{\hat{\mathbf{r}}_{BA} - (\mathbf{n}^A \cdot \hat{\mathbf{r}}_{BA})\mathbf{n}^A\} \\ + [(\mathbf{n}^A \cdot \hat{\mathbf{r}}_{BA}) + 2(\mathbf{n}^A \cdot \mathbf{n}^B)(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA}) \\ - 5(\mathbf{n}^A \cdot \hat{\mathbf{r}}_{BA})(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA})^2] \\ \times \{\mathbf{n}^B - (\mathbf{n}^A \cdot \mathbf{n}^B)\mathbf{n}^A\}\}. \qquad (52)\end{aligned}$$

The most significant implication of this result is that the rotation generated by the active interactions is substantially larger than that of the passive interactions for all reasonable separations. The passive terms scale as $(a/D)^2$, while the active terms scale as a/D. Thus the former are suppressed by an additional factor of the slenderness of the swimmer, which is always a small number for the Najafi–Golestanian swimmer. The important consequence of this is that the relative phase, which enters only into the active terms, plays a significant role in the hydrodynamic interactions of microswimmers.

4.2. Swimmer advection

In addition to a rotation of their direction of motion, the interactions also give rise to an advection of each swimmer in the flow field produced by the others. This advection enters into the determination of the translational motion of each swimmer described in section 2. Equation (8) still applies, although with the fluid velocity given by equation (27)

$$\frac{\mathrm{d}\mathbf{x}^2_A}{\mathrm{d}t} = \mathbf{u}(\mathbf{x}^2_A) = \sum_s \mathbf{G}^s_A(\mathbf{x}^2_A)\mathbf{f}^s_A + \sum_{B\neq A}\sum_r \mathbf{G}^r_B(\mathbf{x}^2_A)\mathbf{f}^r_B. \quad (53)$$

The advection arises both directly, through the second $\sum_{B\neq A}$ term in equation (53), and indirectly, from the fact that the forces $\mathbf{f}^s_A$ differ from their values for a single isolated swimmer on account of the interactions. When these are combined we find that the advective contribution to $\mathbf{u}(\mathbf{x}^2_A)$ is, to leading order, given by

$$\begin{aligned}\frac{a}{12}\sum_{B\neq A}\sum_{j=1}^{\infty}\sum_{k=0}^{j-1}[\mathbf{S}^{(j,k)}(\mathbf{r}_{BA})]((\delta\mathbf{x}^1_A)^{\otimes k} + (\delta\mathbf{x}^2_A)^{\otimes k} \\ + (\delta\mathbf{x}^3_A)^{\otimes k})\mathbf{C}^{j-k}. \qquad (54)\end{aligned}$$

The equation for the translational motion, equation (53), is also a set of coupled, non-linear, ordinary differential equations and hence we employ the same perturbative approach as for the rotation, obtaining

$$\begin{aligned}[x^2_A]_\alpha(T) - [x^2_A]_\alpha = \mathcal{T} n^A_\alpha \\ + \frac{a}{12}\sum_{B\neq A}\sum_{j=1}^{\infty}\sum_{k=0}^{j-1}[S^{(j,k)}_{\alpha\beta\,\sigma\cdots\tau\;\nu\cdots\rho}(\mathbf{r}_{BA})] \\ \times n^B_\beta n^A_\sigma \cdots n^A_\tau n^B_\nu \cdots n^B_\rho (\mathcal{J}^{(j,k)}), \qquad (55)\end{aligned}$$

where $\mathcal{T}$ is the single swimmer translational motion given by equation (11) and

$$\mathcal{J}^{(j,k)} := \int_0^T \mathrm{d}t\, ((\delta x^1_A)^k + (\delta x^2_A)^k + (\delta x^3_A)^k)\, C^{j-k}. \quad (56)$$

Again a distinction can be made between passive ($k = 0$) terms and active ($k \geqslant 1$) terms. As for the rotational interaction, the passive advection results from the same calculation that gives the time averaged flow field, equation (24), and yields the result

$$\begin{aligned}\Delta\mathbf{x}^2_{A\,\text{passive}} \sim \sum_{B\neq A}\frac{21\pi a^2 \xi^{\text{R}}_B \xi^{\text{F}}_B ((\xi^{\text{R}}_B)^2 - (\xi^{\text{F}}_B)^2)\sin(\phi_B)}{128 D^3 r^2_{BA}} \\ \times [1 - 3(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA})^2]\hat{\mathbf{r}}_{BA} \\ + \sum_{B\neq A}\frac{17\pi a^2 \xi^{\text{R}}_B \xi^{\text{F}}_B \sin(\phi_B)}{32 r^3_{BA}}\{3(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA}) \\ \times [5(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA})^2 - 3]\hat{\mathbf{r}}_{BA} - [3(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA})^2 - 1]\mathbf{n}^B\}. \quad (57)\end{aligned}$$

In addition to this passive advection there will be an active contribution, which we expect to have a substantially larger amplitude, scaling as a/D instead of $(a/D)^2$. However, unlike the rotational interaction, this does not come from the first non-trivial term, i.e., $j = 2, k = 1$. This is because the sum of displacements $\delta x^1_A + \delta x^2_A + \delta x^3_A$ is itself $o(a/D)$, since, as discussed following equation (10), this quantity represents the centre of mass motion of the swimmer, which is only non-zero because of hydrodynamic interactions between the spheres. The same is true of all terms with $k = 1$ so that the leading active contribution comes solely from the term with $j = 3, k = 2$, for which we find

$$\begin{aligned}\mathcal{J}^{(3,2)} = -6\pi D^2\{\xi^{\text{R}}_A[\xi^{\text{R}}_B \sin(\eta_{BA}) + \xi^{\text{F}}_B \sin(\eta_{BA} - \phi_B)] \\ + \xi^{\text{F}}_A[\xi^{\text{R}}_B \sin(\eta_{BA} + \phi_A) + \xi^{\text{F}}_B \sin(\eta_{BA} + \phi_A - \phi_B)]\}, \quad (58)\end{aligned}$$

and the active advection is then given by

$$\begin{aligned}\Delta\mathbf{x}^2_{A\,\text{active}} \sim \sum_{B\neq A}\frac{-a\mathcal{J}^{(3,2)}}{8 r^4_{BA}}\{[1 + 2(\mathbf{n}^A \cdot \mathbf{n}^B)^2 \\ - 5(\mathbf{n}^A \cdot \hat{\mathbf{r}}_{BA})^2 - 5(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA})^2 \\ - 20(\mathbf{n}^A \cdot \mathbf{n}^B)(\mathbf{n}^A \cdot \hat{\mathbf{r}}_{BA})(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA}) \\ + 35(\mathbf{n}^A \cdot \hat{\mathbf{r}}_{BA})^2(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA})^2]\hat{\mathbf{r}}_{BA} \\ + 2[(\mathbf{n}^A \cdot \hat{\mathbf{r}}_{BA}) + 2(\mathbf{n}^A \cdot \mathbf{n}^B)(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA}) \\ - 5(\mathbf{n}^A \cdot \hat{\mathbf{r}}_{BA})(\mathbf{n}^B \cdot \hat{\mathbf{r}}_{BA})^2]\mathbf{n}^A\}. \qquad (59)\end{aligned}$$

Again, although this is higher order in $1/r$ than either of the passive contributions given in equation (57) its prefactor is substantially larger, so that it will dominate the advection for all moderate separations (up to ∼30 times the swimmer length).

4.3. An improved near field calculation

A drawback of the approach we have just described is that it is based on a far field analysis, where the separation between swimmers is large compared to the size of an individual, $D/r \ll 1$. Since the Oseen tensor approach allows us to determine the hydrodynamic interactions between two spheres of the same swimmer when they are a distance D apart (for the determination of the single swimmer motion), it should also allow us to determine the interactions between two spheres of different swimmers when the separation between them is also $o(D)$. Clearly this cannot be done on the basis of a multipole expansion in powers of D/r, since for $r = o(D)$ this will be, at best, very slowly convergent. At these close separations we can replace equation (35) for the relative position of the two spheres with

$$\mathbf{x}_B^r - \mathbf{x}_A^s = (\mathbf{x}_B^r(0) - \mathbf{x}_A^s(0)) + (\mathbf{x}_B^r - \mathbf{x}_B^r(0)) - (\mathbf{x}_A^s - \mathbf{x}_A^s(0)), \\ =: \mathbf{r}_{BA}^{(r,s)} + \delta\mathbf{x}_B^r - \delta\mathbf{x}_A^s. \quad (60)$$

If we consider that the deviation of each sphere from its 'mean' position is small compared to the separation between them, $\xi/D \ll 1$, then we can still make use of an expansion of stokeslets to determine the interactions in the same way as before. The price that we pay for this is that the tensors $\mathbf{S}^{(j,k)}$ appearing in equation (36) are no longer independent of the pair of spheres (r, s), so that each pair needs to be considered individually. This leads to a substantial increase in the length of our formulae. For example, equation (44) becomes

$$[\Omega^A,]_{\alpha\beta} = \frac{a}{4} P^{-1}(\delta_{\alpha\gamma} n_\beta^A - \delta_{\beta\gamma} n_\alpha^A) \\ \times \sum_{B \neq A} \sum_{j=0}^{\infty} \sum_{k=0}^{j} n_\lambda^B n_\sigma^A \cdots n_\tau^A n_\nu^B \cdots n_\rho^B \\ \times \sum_{r,s} [S_{\gamma\lambda\,\sigma\cdots\tau\,\nu\cdots\rho}^{(j,k)}(\mathbf{r}_{BA}^{(r,s)})] \\ \times (\delta x_A^s)^k (\delta x_B^r)^{j-k} [\zeta_A^s\, \partial_t \zeta_B^r], \quad (61)$$

where $\zeta^1 = 3D + 2\tilde{\xi}^{\mathrm{R}} + \tilde{\xi}^{\mathrm{F}}$, $\zeta^2 = \tilde{\xi}^{\mathrm{F}} - \tilde{\xi}^{\mathrm{R}}$ and $\zeta^3 = -(3D + \tilde{\xi}^{\mathrm{R}} + 2\tilde{\xi}^{\mathrm{F}})$. The leading order contribution to the active interaction comes from the $j = 0, k = 0$ and $j = 1, k = 1$ terms and thus can be thought of as a collection of stokeslets, $\mathbf{S}^{(0,0)}$, and stokes doublets, $\mathbf{S}^{(1,1)}$ [57]. The integrals over a complete swimming stroke of these terms are straightforward, but the number of them makes their evaluation tedious and we shall not quote the results here. The advection can be treated in a similar fashion, but again the results will not be quoted explicitly due to the length of the final expressions.

A comparison of the results of the near and far field calculations is presented in figure 2 for two parallel, coplanar swimmers. The swimmers are initially aligned along the x-direction, $\mathbf{n} = (1, 0, 0)$, with swimmer A at the origin and swimmer B at the point $\mathbf{r}_{BA} = r(\cos(\theta), \sin(\theta), 0)$. Both swimmers are identical with parameter values $a = 0.05D$, $\phi_A = \phi_B = \pi/2$ and $\xi^{\mathrm{R}} = \xi^{\mathrm{F}} = 0.2D$.

First, in figure 2(a) we show how the rotation, n_y, depends on the separation, r, between the swimmers at a fixed relative angle of $\theta = 60°$ in the near field calculation. When the swimmers are in phase (solid line), this is found to asymptote onto the predicted far field scaling of r_{BA}^{-4} for distances of greater than about $10D$. At these large separations n_y is negative indicating a tendency for the swimmers to repel each other, however for separations of less than $\sim 3D$ it changes sign revealing a short distance attraction. Since the interactions are dominated by the active term, changing the relative phase can yield qualitative and quantitative changes in the rotation. As a particular example, when the relative phase is $\eta_{BA} = \pi/2$ the amplitude of the active rotation, equation (50), vanishes so that in the far field it decays as r_{BA}^{-5} instead of the expected r_{BA}^{-4}. In

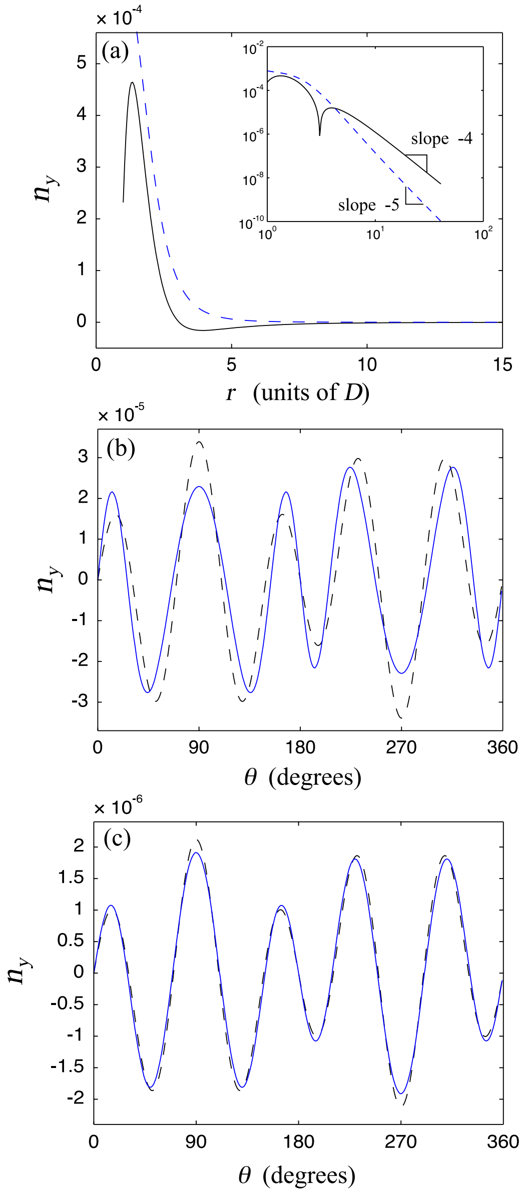

Figure 2. Comparison of the near and far field calculations of the interactions between two swimmers. (a) Dependence of the rotational interaction with distance between the two swimmers when the relative phase is $\eta_{BA} = 0$ (solid line) and $\eta_{BA} = \pi/2$ (dashed line) and the angle between them is $\theta = 60°$. The inset shows the same data with logarithmic axes to illustrate the scaling with r. (b) and (c) Variation of the rotation angle with θ at a fixed separation of (b) $r = 5D$ and (c) $r = 10D$ for two swimmers that are in phase. In both cases the solid blue line represents the near field calculation and the dashed black line the far field calculation.

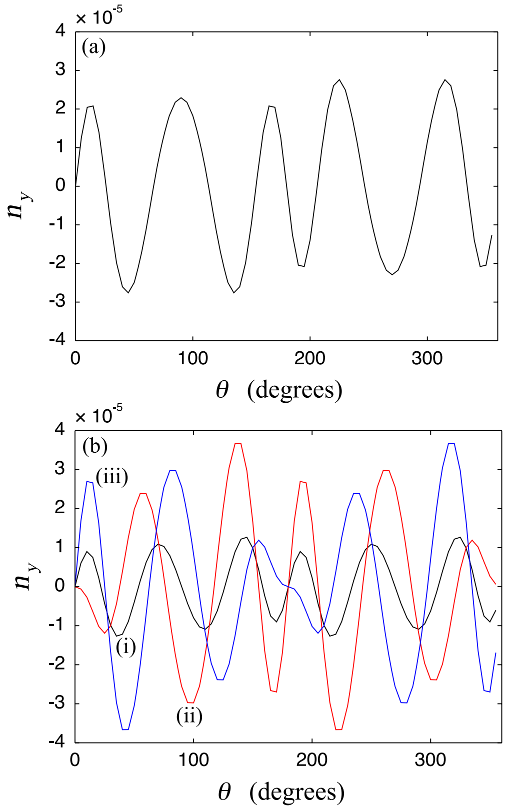

Figure 3. Dependence of the rotation angle n_y on θ at a fixed separation of $r = 5D$ when the arm amplitudes are different. (a) When the swimmers are in phase there is no sensitivity to the arm amplitudes. (b) For a relative phase of $\eta_{BA} = \pi/2$, n_y is strongly dependent on the relative magnitude of ξ^{R} and ξ^{F}: (i) $\xi^{\mathrm{R}} = \xi^{\mathrm{F}} = 0.2D$, (ii) $\xi^{\mathrm{R}} = 0.3D, \xi^{\mathrm{F}} = 0.133D$ and (iii) $\xi^{\mathrm{R}} = 0.133D, \xi^{\mathrm{F}} = 0.3D$.

figures 2(b) and (c) we show how n_y varies as one swimmer is moved in a circle around the other, keeping a fixed separation between them. At a separation of $r = 5D$ (figure 2(b)) there are noticeable differences between the near and far field calculations, although the qualitative features are the same. These discrepancies are substantially reduced when the separation is increased to $r = 10D$ (figure 2(c)), indicating that the far field description is sufficient. In both these cases the relative phase was $\eta_{BA} = 0$.

In figure 3 we illustrate how the form of the rotational interaction changes when the relative magnitude of the arm amplitudes, ξ^{R} and ξ^{F}, are varied. In varying the arm amplitudes we change the difference $\xi^{\mathrm{R}} - \xi^{\mathrm{F}}$ while holding the product $\xi^{\mathrm{R}}\xi^{\mathrm{F}}$ fixed so as to maintain an approximately constant swimming speed. In particular we compare the three cases; $\xi^{\mathrm{R}} = \xi^{\mathrm{F}} = 0.2D$ corresponding to self-T-dual swimmers, $\xi^{\mathrm{R}} = 0.3D, \xi^{\mathrm{F}} = 0.133D$ corresponding to extensile swimmers and $\xi^{\mathrm{R}} = 0.133D, \xi^{\mathrm{F}} = 0.3D$ corresponding to contractile swimmers. In all cases, the other model parameters were $a = 0.05D$ and $\phi_A = \phi_B = \pi/2$.

Intriguingly the relative phase plays an important role with there being no difference between the three cases if the relative phase is either $\eta_{BA} = 0$ or π, figure 3(a). An indication of why this might be so can be found in the amplitude $\mathcal{I}^{(3,2)}$ of the far field calculation of the interactions, which when the swimmers are identical and $\phi = \pi/2$ simplifies to

$$\mathcal{I}^{(3,2)} = (\xi^{\mathrm{R}}+\xi^{\mathrm{F}})(\xi^{\mathrm{R}}-\xi^{\mathrm{F}})\sin(\eta_{BA}) - 2\xi^{\mathrm{R}}\xi^{\mathrm{F}}\cos(\eta_{BA}), \quad (62)$$

showing that varying the amplitudes as we have described does not change the asymptotic form of the active rotation if the swimmers are exactly in phase or exactly out of phase. Since the active terms dominate the interactions this leads to the unexpected consequence that the collective hydrodynamics is insensitive to the relative magnitude of the two arm amplitudes ξ^{R}, ξ^{F} and hence to whether the swimmer is extensile, contractile or self-T-dual. In contrast, when the relative phase is $\eta_{BA} = \pi/2$ the interactions are sensitive to the magnitude of the arm amplitudes, figure 3(b). However, the behaviour does not follow very precisely the asymptotic form described by equation (62), showing again the shortcomings of a simple far field description of the interactions at separations of only a small number of body lengths.

5. Conclusion

In this paper we have described in detail the hydrodynamics of a simple model of linked sphere swimmers, focusing on the time averaged flow field and swimmer–swimmer interactions. The results reveal features that are unexpected from the simple scaling arguments that suggest swimmers behave like force dipoles in the far field limit [8, 13]. For self-T-dual swimmers, such as the Najafi–Golestanian model with equal amplitudes of the two arms, time reversal symmetry forbids the dipolar term, leading to a flow field which scales as $1/r^3$. Moreover, a second swimmer does not behave as a passive scalar, just moving with the flow field generated by the first. Rather, the swimmer–swimmer interaction is dominated by terms that depend on the relative phase of the two swimmers. For the Najafi–Golestanian model this remains true until the swimmer separation exceeds about thirty times the length of an individual, after which the interactions finally become dipolar.

The techniques we have presented here for the analysis of the hydrodynamics of linked sphere swimmers are based on perturbative expansions for swimmers made up of spheres that are small and widely separated. As such, it allows us only to extract the lowest order contributions to the interactions and does not provide a robust framework for the determination of all the higher order corrections that become important when the sphere separations are comparable to their radius. Such a programme could be fruitfully developed by employing the existing techniques for colloidal hydrodynamics [58, 59]. Nonetheless, our analysis is able to shed considerable light on the nature of the far field interactions between swimmers, highlighting an important interplay between active and passive contributions. In particular, the combination of symmetry suppressing the dipolar terms and a substantially larger prefactor for the active terms results in the interactions assuming a higher order $(D/r)^4$ dependence on separation, out to distances of ∼30 swimmer lengths, and in them being sensitive to the relative phase of the swimmers.

There remain many avenues for further research. In particular it is important to understand more fully which of our results are generic. A natural progression is to consider further variants of the linked sphere swimmers utilizing transverse rather than longitudinal swimming strokes. The role of surfaces and external forcing and making connections to continuum models of swimmers are also areas where linked sphere models of swimmers are likely to prove useful.

References

[1] Taylor G I 1951 *Proc. R. Soc.* A **209** 447
[2] Taylor G I 1952 *Proc. R. Soc.* A **211** 225
[3] Lighthill J 1976 *SIAM Rev.* **18** 161
[4] Purcell E M 1977 *Am. J. Phys.* **45** 3
[5] Shapere A and Wilczek F 1989 *J. Fluid Mech.* **198** 557
[6] Stone H A and Samuel A D T 1996 *Phys. Rev. Lett.* **77** 4102
[7] Kessler J O 1985 *Nature* **313** 218
[8] Pedley T J and Kessler J O 1992 *Annu. Rev. Fluid Mech.* **24** 313
[9] Ramia M, Tullock D L and Phan-Thien N 1993 *Biophys. J.* **65** 755
[10] Nasseri S and Phan-Thien N 1997 *Comput. Mech.* **20** 551
[11] Wu X-L and Libchaber A 2000 *Phys. Rev. Lett.* **84** 3017
[12] Dombrowski C, Cisneros L, Chatkaew S, Goldstein R E and Kessler J O 2004 *Phys. Rev. Lett.* **93** 098103
[13] Simha R A and Ramaswamy S 2002 *Phys. Rev. Lett.* **89** 058101
[14] Hatwalne Y, Ramaswamy S, Rao M and Simha R A 2004 *Phys. Rev. Lett.* **92** 118101
[15] Becker L E, Kochler S A and Stone H A 2005 *J. Fluid Mech.* **490** 15
[16] Kulic I M, Thaokar R and Schiessel H 2005 *Europhys. Lett.* **72** 527
[17] Najafi A and Golestanian R 2004 *Phys. Rev.* E **69** 062901
[18] Avron J E, Kenneth O and Oaknin D H 2005 *New J. Phys.* **7** 234
[19] Earl D J, Pooley C M, Ryder J F, Bredburg I and Yeomans J M 2007 *J. Chem. Phys.* **126** 064703
[20] Felderhof B U 2006 *Phys. Fluids* **18** 063101
[21] Tam D and Hosoi A E 2007 *Phys. Rev. Lett.* **98** 060105
[22] Golestanian R, Liverpool T B and Ajdari A 2005 *Phys. Rev. Lett.* **94** 220801
[23] Golestanian R, Liverpool T B and Ajdari A 2007 *New J. Phys.* **9** 126
[24] Dreyfus R *et al* 2005 *Nature* **437** 862
[25] Howse J R *et al* 2007 *Phys. Rev. Lett.* **99** 048102
[26] Keaveny E E and Maxey M R 2008 *J. Fluid Mech.* **598** 293
[27] Keaveny E E and Maxey M R 2008 *Phys. Rev.* E **77** 041910
[28] Gauger E and Stark H 2006 *Phys. Rev.* E **74** 021907
[29] Guell D C, Brenner H, Frankell R B and Hartman H 1988 *J. Theor. Biol.* **135** 525
[30] Riedel I H, Kruse K and Howard J 2005 *Science* **309** 300
[31] DiLuzio W R *et al* 2005 *Nature* **435** 1271
[32] Lauga E, DiLuzio W R, Whitesides G M and Stone H A 2006 *Biophys. J.* **90** 400
[33] Hill J, Kalkanci O, McMurry J L and Koser H 2007 *Phys. Rev. Lett.* **98** 068101
[34] Koiller J, Ehlers K and Montgomery R 1996 *J. Nonlinear Sci.* **6** 507
[35] Alexander G P and Yeomans J M 2008 *Europhys. Lett.* **83** 34006
[36] Lauga E and Bartolo D 2008 *Phys. Rev.* E **78** 030901
[37] Hernandez-Ortiz J P, Stoltz C G and Graham M D 2005 *Phys. Rev. Lett.* **95** 204501
[38] Lighthill J 1996 *J. Eng. Math.* **30** 35
[39] Ramaswamy S and Simha R A 2006 *Solid State Commun.* **139** 617
[40] Llopis I and Pagonabarraga I 2006 *Europhys. Lett.* **75** 999
[41] Cisneros L H, Cortez R, Dombrowski C, Goldstein R E and Kessler J O 2007 *Exp. Fluids* **43** 737
[42] Saintillan D and Shelley M J 2007 *Phys. Rev. Lett.* **99** 058102
[43] Kim M and Powers T R 2004 *Phys. Rev.* E **69** 061910
[44] Ishikawa T, Simmonds M P and Pedley T J 2006 *J. Fluid Mech.* **568** 119
[45] Ishikawa T and Hota M 2006 *J. Exp. Biol.* **209** 4452
[46] Ishikawa T, Sekiya G, Imai Y and Yamaguchi T 2007 *Biophys. J.* **93** 2217
[47] Ishikawa T and Pedley T J 2008 *Phys. Rev. Lett.* **100** 088103
[48] Pooley C M, Alexander G P and Yeomans J M 2007 *Phys. Rev. Lett.* **99** 228103
[49] Golestanian R and Adjari A 2008 *Phys. Rev. Lett.* **100** 038101
[50] Golestanian R 2008 *Eur. Phys. J.* E **25** 1
[51] Golestanian R and Adjari A 2008 *Phys. Rev.* E **77** 036308
[52] Alexander G P, Pooley C M and Yeomans J M 2008 *Phys. Rev.* E **78** 045302(R)
[53] Taylor G I 1967 *Low Reynolds Number Flows* Encyclopaedia Britannica Educational Corp., Chicago, Video No. 21617
[54] Lauga E 2007 *Phys. Fluids* **19** 061703
[55] Happel J and Brenner H 1965 *Low Reynolds Number Hydrodynamics* (Englewood Cliffs, NJ: Prentice-Hall)
[56] Kim S and Karrila S 1991 *Microhydrodynamics* (Boston, MA: Butterworth–Heinemann)
[57] Blake J R and Chwang A T 1974 *J. Eng. Math.* **8** 23
[58] Cichocki B, Felderhof B U and Hinsen K 1993 *J. Chem. Phys.* **100** 3780
[59] Knudsen H A, Werth J H and Wolf D E 2008 *Eur. Phys. J.* E **27** 161