HYDRODYNAMIC INTERACTIONS OF MICROSWIMMERS WITH NEARBY SURFACES

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Contents

1. Overview of our research

We are addressing a very basic yet significant problem in the area of hydrodynamic interaction of microswimmers. We are studying how microswimmers, locomoting in an incompressible fluid with Re ≈ 0 (Stokes regime), hydrodynamically interact with nearby surfaces. Till now, we have understood how a microswimmer interacts with a nearby surface of zero curvature (assuming that no other such surface is present in its proximity), i.e a flat wall, and how two identical microswimmers interact in an infinite fluid, i.e. a fluid with no solid boundaries. In this article, we explicitly address these two cases. Our next motive is to combine these results to understand how two microswimmers interact near a flat surface and thereby generalise this problem to more complex scenarios with three or more interacting swimmers. Some more interesting directions that we plan to explore are to replace the flat surface with a surface having some curvature, as is the case with all rough surfaces, or replace it with a microchannel, or more generally with an arbitrary confinement having dimensions comparable to the intrinsic size of the swimmer.

2. Far-Field Description of a Swimmer

In this section, we introduce the mathematical framework necessary to answer our questions, i.e. to quantify the swimming hydrodynamics in the far-field. This concept is useful for cases in which the flow field in close proximity of a swimmer is not of interest but the far-field behaviour is, for example, to determine the influence of a nearby boundary, or of another swimmer nearby, cases which are ubiquitous to the analysis of our problems. Physically, it is equivalent to zooming out and observing the swimmer over length scales much larger than its intrinsic length. Under this approximation, the geometrical details of the swimmer are therefore unimportant and some generic features of low-Reynolds number swimming may thus be obtained.

2.1. **Stokeslet.** To formulate such a perspective, we place a point force $f\mathbf{e}\delta(\mathbf{x})$ at the origin ($\mathbf{x}=\mathbf{0}$) in an otherwise quiescent infinite fluid (fluid with no solid boundaries), where $\delta(\mathbf{x})$ is the Dirac delta function centred at $\mathbf{x}=\mathbf{0}$, i.e.

$$\delta(\mathbf{x}) = \begin{cases} 1, & \mathbf{x}=\mathbf{0}, \\ 0, & \mathbf{x}\neq\mathbf{0}, \end{cases}$$

$\mathbf{e}$ a unit vector represents the direction of the point force, and f the magnitude of the force. Hence, the forced Stokes equations are given by

$$\nabla p = \mu\nabla^2\mathbf{v} + f\mathbf{e}\delta,$$

$$\nabla\cdot\mathbf{v} = 0,$$

where p and $\mathbf{v}$ are, respectively, the pressure and velocity fields, and μ is the dynamic viscosity of the fluid. The solution $\mathbf{v}(\mathbf{x})$ can be obtained by a variety of methods, such as Fourier transformation and superposition of vector harmonic functions, and is given by

$$\mathbf{v}(\mathbf{x}) = f\mathbf{G}(\mathbf{x};\mathbf{e}) = \frac{f}{8\pi\mu}\left[\frac{\mathbf{e}}{r} + \frac{(\mathbf{e}\cdot\mathbf{x})\mathbf{x}}{r^3}\right],$$

where $r=|\mathbf{x}|$ is the distance from the origin (or the singularity), and

$$\mathbf{G}(\mathbf{x};\mathbf{e}) = \frac{1}{8\pi\mu}\left[\frac{\mathbf{e}}{r} + \frac{(\mathbf{e}\cdot\mathbf{x})\mathbf{x}}{r^3}\right]$$

is the Green's function for the Stokes equations. This fundamental singular solution in viscous flows is called a Stokeslet. It decays as $1/r$ and is therefore long-ranged.

It is interesting to observe that the flow field of a Stokeslet is the one given by a translating sphere (as shown in Fig. 1**a**) in the far-field as in both cases a net force is exerted on the fluid. Physically, as we increasingly zoom-out from a translating sphere, it becomes sufficiently small that it can be regarded as a point acted on by a force, and thus a Stokeslet may be physically understood as the far-field approximation of a translating sphere.

It is important to note that a Stokeslet cannot be considered as an approximation of a swimmer, since a swimmer does not exert a net force on the surrounding fluid but a Stokeslet does. But, still, we will see now how the concept of a Stokeslet is relevant to the approximation of a swimmer.

2.2. **Stokes dipole.** Now let us understand what a Stokes dipole is and how it serves as the far-field approximation of a microswimmer.

The first derivative of an $\mathbf{e}$-directed Stokeslet of strength f along the $\mathbf{d}$ direction is known as a Stokes dipole, and is given by

$$\begin{aligned}\mathbf{d}\cdot\nabla\mathbf{v}(\mathbf{x}) &= \mathbf{d}\cdot\nabla f\mathbf{G}(\mathbf{x};\mathbf{e}) = f\mathbf{d}\cdot\nabla\mathbf{G}(\mathbf{x};\mathbf{e}) = f\mathbf{G}_D(\mathbf{x};\mathbf{d},\mathbf{e}) \\ &= \frac{f}{8\pi\mu}\left\{\frac{(\mathbf{d}\times\mathbf{e})\times\mathbf{x}}{r^3} + \left[-\frac{(\mathbf{e}\cdot\mathbf{d})\mathbf{x}}{r^3} + 3\frac{(\mathbf{e}\cdot\mathbf{x})(\mathbf{d}\cdot\mathbf{x})\mathbf{x}}{r^5}\right]\right\}.\end{aligned}$$

Since the Stokes equations are linear, a derivative of any order of a Stokeslet is also a solution, forming higher-order singular solutions, and hence a Stokes dipole is also a solution. In fact, as we will see now, it is the most useful singular solution in the study of swimming microorganisms. The flow due to the symmetric part of the Stokes dipole is termed a stresslet,

$$f\mathbf{S}(\mathbf{x};\mathbf{d},\mathbf{e}) = \frac{f}{8\pi\mu}\left[-\frac{(\mathbf{e}\cdot\mathbf{d})\mathbf{x}}{r^3} + 3\frac{(\mathbf{e}\cdot\mathbf{x})(\mathbf{d}\cdot\mathbf{x})\mathbf{x}}{r^5}\right],$$

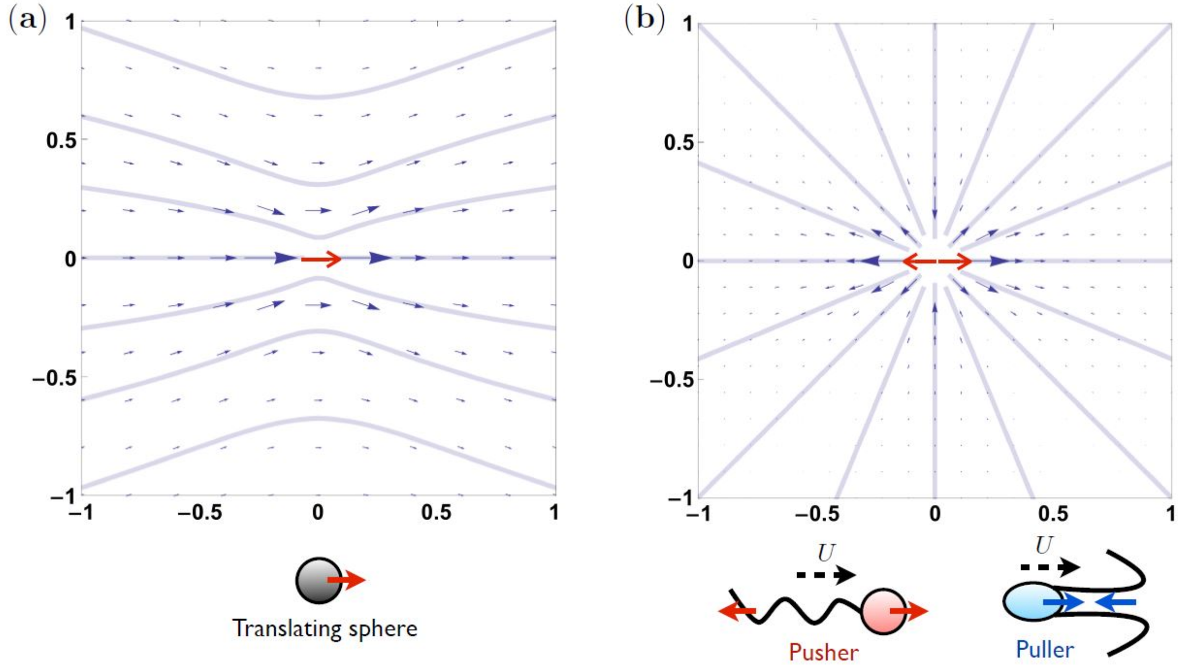

FIGURE 1. (**a**) Velocity field due to a Stokeslet at the origin, the fundamental singular solution in Stokes flows due to a point force, and a model for the far-field approximation of a translating sphere. (**b**) Velocity field due to a positive Stokes dipole at the origin. The vectors represent local fluid velocity and the lines represent streamlines. The flow field of a negative Stokes dipole (two point forces acting towards each other) has the same streamline pattern with the sign of the velocity field reversed. A positive (resp. negative) Stokes dipole is the far-field approximation of a pusher (resp. puller). The arrows on the swimmers indicate local forces exerted on the fluid.

physically representing straining motion of the fluid, whereas the flow due to the antisymmetric part is termed a rotlet,

$$f\mathbf{R}(\mathbf{x};\mathbf{d},\mathbf{e}) = \frac{f(\mathbf{d}\times\mathbf{e})\times\mathbf{x}}{8\pi\mu r^3},$$

physically representing the flow due to a point torque. So,

$$\mathbf{G}_D(\mathbf{x};\mathbf{d},\mathbf{e}) = \mathbf{S}(\mathbf{x};\mathbf{d},\mathbf{e}) + \mathbf{R}(\mathbf{x};\mathbf{d},\mathbf{e}).$$

A Stokes dipole decays as $1/r^2$, one order of magnitude faster than a Stokeslet.

Physically, a Stokes dipole can be understood as the limit when the distance between two Stokeslets of equal magnitudes but opposite directions becomes vanishingly small and the strength-/magnitude is adjusted to give a finite flow field. We will see how. Consider a Stokeslet, $\mathbf{v}^+(\mathbf{x})$, of strength $f\mathbf{e}$ acting at a small distance $d/2$ from the origin along the direction $\mathbf{d}$. Using Green's function and Taylor's expansion about the origin, we can express the Stokeslet as

$$\mathbf{v}^+(\mathbf{x}) = f\mathbf{G}\left(\mathbf{x} - \frac{d}{2}\mathbf{d};\mathbf{e}\right) = f\left[\mathbf{G}(\mathbf{x};\mathbf{e}) - \frac{d}{2}\mathbf{d}\cdot\nabla\mathbf{G}(\mathbf{x};\mathbf{e}) + \cdots\right].$$

Consider another Stokeslet, $\mathbf{v}^-(\mathbf{x})$, of opposite strength $-f\mathbf{e}$ acting at an opposite position of $-\frac{d}{2}\mathbf{d}$ from the origin. Again by using Green's function and Taylor's expansion about the origin, this

Stokeslet is expressed as

$$\mathbf{v}^{-}(\mathbf{x}) = f\mathbf{G}\left(\mathbf{x} + \frac{d}{2}\mathbf{d}; -\mathbf{e}\right) = f\left[\mathbf{G}(\mathbf{x}; -\mathbf{e}) + \frac{d}{2}\mathbf{d} \cdot \nabla\mathbf{G}(\mathbf{x}; -\mathbf{e}) + \cdots\right]$$
$$= f\left[-\mathbf{G}(\mathbf{x}; \mathbf{e}) - \frac{d}{2}\mathbf{d} \cdot \nabla\mathbf{G}(\mathbf{x}; \mathbf{e}) - \cdots\right].$$

Superposing the two Stokeslets gives an overall flow field

$$\mathbf{v}(\mathbf{x}) = \mathbf{v}^{+}(\mathbf{x}) + \mathbf{v}^{-}(\mathbf{x}) = -df\mathbf{d} \cdot \nabla\mathbf{G}(\mathbf{x}; \mathbf{e}) + \cdots ,$$

where the leading-order contribution $-df\mathbf{d} \cdot \nabla\mathbf{G}(\mathbf{x}; \mathbf{e})$ is a Stokes dipole (first derivative of a $-\mathbf{e}$-directed Stokeslet of strength df along the $\mathbf{d}$ direction). The distance d and strength f of the Stokeslets can be adjusted so that higher-order terms vanish upon taking the limit, leaving only the flow field due to a Stokes dipole. Physically, we can thus understand a Stokes dipole as the leading-order contribution of the overall flow field due to two point forces of strength f acting at a fixed and sufficiently small separation distance d.

Consider a special case where the two point forces in a Stokes dipole are aligned in the same direction as the one along which derivatives are taken, i.e. $\mathbf{e} = \pm\mathbf{d}$. This implies that $\mathbf{d} \times \mathbf{e} = \mathbf{0}$, which in turn implies that $\mathbf{R}(\mathbf{x}; \mathbf{d}, \mathbf{e}) = \mathbf{0}$. Hence, it is the case where the rotlet component of the Stokes dipole vanishes as there is no net torque on the swimmer, leaving only the symmetric stresslet component. Setting $\alpha = d\mathbf{d} \cdot f\mathbf{e}$, the flow field due to the Stokes dipole is given by

$$\mathbf{v}(\mathbf{x}) \approx -df\mathbf{G}_D(\mathbf{x}; \mathbf{d}, \mathbf{e}) = -df\mathbf{S}(\mathbf{x}; \mathbf{d}, \mathbf{e}) = \frac{\alpha}{8\pi\mu}\left[\frac{\mathbf{x}}{r^3} - 3\frac{(\mathbf{e} \cdot \mathbf{x})^2\mathbf{x}}{r^5}\right].$$

Here $\alpha = \pm df$ represents the two different opposite configurations:

(1) $\alpha > 0$ (which is exactly when $\mathbf{e} = \mathbf{d}$) represents the configuration where the two point forces act away from each other (positive Stokes dipole), pushing fluid away along the direction of the dipole and drawing fluid towards the dipole from the side.
(2) $\alpha < 0$ (which is exactly when $\mathbf{e} = -\mathbf{d}$) represents the configuration where the two point forces act towards each other (negative Stokes dipole), drawing fluid along the direction of the dipole and repelling fluid to the side.

We call α the strength of the Stokes dipole.

With this concept in mind, we can now analyze the motion of self-propelled microorganisms from a sufficiently large distance that the geometrical details of the swimmer may be ignored. They can be broadly classified into two categories when observed from far-field:

- **Pusher:** In such a swimmer, one can identify two parts, namely the cell body and the flagellum. As the cell moves through a viscous fluid (from left to right, as shown in Fig. 1**b**, pusher), the cell body experiences a viscous drag acting to the left. Since a self-propelled swimmer is force-free, the fluid has to exert (due to the action of the flagellum) a force of equal magnitude acting to the right to balance the drag force on the cell body, forming a pair of force acting towards each other on the cell. By Newton's third law, the swimmer exerts therefore on the fluid a pair of forces acting away from each other (indicated by red arrows in Fig. 1**b**, pusher). Hence, they generate a positive stokes dipole with $\alpha > 0$. A spermatozoon or an *E. coli* cell are examples of pushers.

- **Puller:** Such a swimmer obtain their thrust from the front part of the body and hence exerts a pair of force towards each other on the fluid (Fig. 1**b**, puller), generating a negative Stokes dipole with $\alpha < 0$. This is, for example, the case for the algae *Chlamydomonas* which uses two flagella.

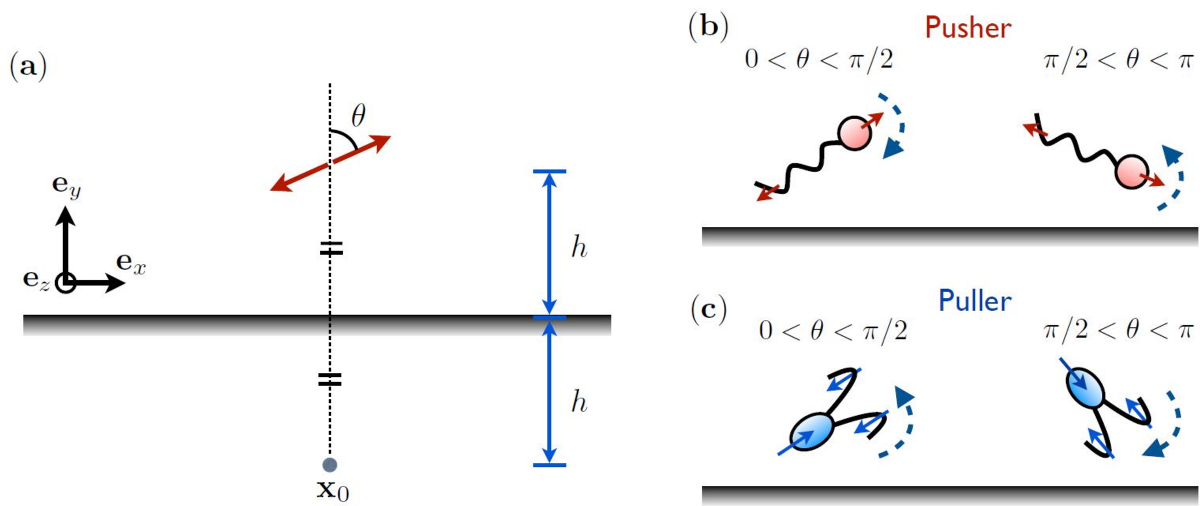

FIGURE 2. (**a**) Geometrical setup for the image system of a Stokes dipole (here as a model swimmer). Hydrodynamic reorientation near a surface of a (**b**) pusher and a (**c**) puller.

It is noteworthy that the flow fields around a pusher and puller with the same absolute strength differ only by a sign and hence have the same streamline pattern.

3. Hydrodynamic Interactions

In the previous section we introduced the theoretical model of far-field description of an isolated swimming microorganism in an unbound fluid. In this section, we will use this model to analyse the hydrodynamic interactions between cells and boundaries.

3.1. **Swimming near a boundary.** We have already shown that swimming microorganisms can be described as Stokes dipoles in an unbounded fluid under far-field approximations. However, the presence of rigid boundaries requiring that the no-slip and no-penetration boundary conditions be enforced modifies the flow around the singularity, and has an impact on the swimmer motion (unlike the case of the motion of a swimmer in an unbound fluid). Let us see how.

Consider a swimmer (or Stokes dipole) of strength α, oriented at an arbitrary angle θ and located at an arbitrary distance h from a wall with zero curvature in the proximity of the swimmer, and also assume that no other such walls are present in its proximity, as illustrated in Fig. 2**a**. Without loss of generality, we assume that the dipole lies on the $x - y$ plane. Further, let us consider the swimmer to be of the shape of a prolate spheroid with major and minor axis lengths given by a and b respectively, and a body aspect ratio defined as $\gamma = a/b$. Using image system of a Stokes dipole and Faxen's law, the (wall-induced) translational velocity, $\mathbf{U}$, and rotational velocity, $\mathbf{\Omega}$, of the swimmer due to an arbitrary (wall-induced) ambient flow is given by

$$\mathbf{U} = \frac{\alpha}{8\pi\mu}\left[\frac{3\sin(2\theta)}{8h^2}\mathbf{e}_x - \frac{3(1-3\cos^2\theta)}{8h^2}\mathbf{e}_y\right],$$

$$\mathbf{\Omega} = \frac{\alpha}{8\pi\mu}\left\{-\frac{3\sin(2\theta)}{16h^3}\left[1 + \frac{\gamma^2-1}{2(\gamma^2+1)}(1+\cos^2\theta)\right]\right\}\mathbf{e}_z.$$

Hence, we have

$$U_x(\theta,h)=\frac{3\alpha\sin(2\theta)}{64\pi\mu h^2},\ U_y(\theta,h)=-\frac{3\alpha}{64\pi\mu h^2}(1-3\cos^2\theta),\ U_z(\theta,h)=0,$$

and

$$\Omega(\theta,h)=-\frac{3\alpha\sin(2\theta)}{128\pi\mu h^3}\left[1+\frac{\gamma^2-1}{2(\gamma^2+1)}(1+\cos^2\theta)\right].$$

Consider any arbitrary swimmer with strength α, body aspect ratio γ, swimming at a distance h from the wall, and oriented at an arbitrary angle θ. If $\alpha>0$,

$$U_x(\theta,h)\begin{cases}=0, & \theta=0,\\ >0, & 0<\theta<\pi/2,\\ =0, & \theta=\pi/2,\\ <0, & \pi/2<\theta<\pi.\end{cases}$$

Due to the linearity of the wall-induced flow with α, the opposite inequalities hold for a puller ($\alpha<0$). But, in any case, we see that there is no motion in the x direction when the swimmer is oriented parallel or perpendicular to the wall.

Again if $\alpha>0$, it is easy to see that

$$U_y(\theta,h)\begin{cases}>0, & 0\le\theta<\sin^{-1}\sqrt{\frac{2}{3}},\\ =0, & \theta=\sin^{-1}\sqrt{\frac{2}{3}},\\ <0, & \sin^{-1}\sqrt{\frac{2}{3}}<\theta<\pi-\sin^{-1}\sqrt{\frac{2}{3}},\\ =0, & \theta=\pi-\sin^{-1}\sqrt{\frac{2}{3}},\\ >0, & \pi-\sin^{-1}\sqrt{\frac{2}{3}}<\theta<\pi.\end{cases}$$

So, we now know for which values of θ the wall attract or repel a pusher. For example, if the swimmer is swimming parallel to the wall ($\theta=\pi/2$), we see that $U_y<0$, meaning that it is attracted towards the wall. Again, due to the linearity of the wall-induced flow with α, the opposite inequalities hold for a puller ($\alpha<0$) and in that case swimming parallel to the wall leads to a repulsion.

In addition to inducing attraction or repulsion, the wall also hydrodynamically re-orients the swimmer, as can be analysed from the expression of Ω_z. For any swimmer, $\gamma>1$, implies that

$$1+\frac{\gamma^2-1}{2(\gamma^2+1)}(1+\cos^2\theta)>1>0,$$

which in turn implies that the direction of the induced rotational velocity $\mathbf{\Omega}$ is independent of the shape of the swimmer γ, and therefore has the same sign as that of $-\alpha\sin(2\theta)$. Hence, it is easy to see that if $\alpha>0$,

$$\Omega(\theta,h)\begin{cases}=0, & \theta=0,\\ <0, & 0<\theta<\pi/2,\\ =0, & \theta=\pi/2,\\ >0, & \pi/2<\theta<\pi.\end{cases}$$

This means that the hydrodynamic interactions (due to the wall) are expected to re-orient a pusher parallel to the wall (Fig. 2**b**). On the other hand, they are expected to re-orient a puller in the direction perpendicular to the surface (Fig. 2**c**).

With the above analysis in mind, we now move on to set up the framework for numerically finding out the trajectory of various swimmers hydrodynamically interacting with a nearby boundary.

Consider a swimmer of strength α and body aspect ratio γ, initially (at time $t = 0$) located at the point $\mathbf{x} = (x_0, y_0, 0)$ and oriented at an angle θ_0, where $0 \leq \theta_0 < \pi$. Writing U_x, U_y, U_z and Ω in the form of derivatives, we have the following system of ODEs:

$$U_x = \frac{dx}{dt} = \frac{3\alpha \sin(2\theta)}{64\pi\mu h^2} = \frac{\kappa \sin(2\theta)}{y^2},$$

$$U_y = \frac{dy}{dt} = -\frac{3\alpha}{64\pi\mu h^2}(1 - 3\cos^2\theta) = \frac{\kappa}{y^2}(3\cos^2\theta - 1),\ U_z = \frac{dz}{dt} = 0,$$

$$\Omega = -\frac{d\theta}{dt} = -\frac{3\alpha\sin(2\theta)}{128\pi\mu h^3}\left[1 + \frac{\gamma^2 - 1}{2(\gamma^2+1)}(1 + \cos^2\theta)\right]$$

$$\implies \frac{d\theta}{dt} = \frac{\kappa \sin(2\theta)}{2|y|^3}\left[1 + \beta(1 + \cos^2\theta)\right],$$

where $\kappa = \frac{3\alpha}{64\pi\mu}$ and $\beta = \frac{\gamma^2-1}{2(\gamma^2+1)}$ and they are subject to the initial conditions: $x(t = 0) = x_0$, $y(t = 0) = y_0$, $z(t = 0) = 0$ and $\theta(t = 0) = \theta_0$. So, $z(t) \equiv 0$ and the remaining system can be solved using various numerical methods of integration such as Euler's method or Runge-Kutta method. Fig. 3 shows the trajectory of swimmers, swimming in a fluid of dynamic viscosity $\mu = 10^{-3}$ Pa.s, with body-aspect ratio $\gamma = 3$, strength $\alpha = \pm1, \pm2, \ldots, \pm7$, initially located at $\mathbf{x}_0 = (0\mu\text{m}, 100\mu\text{m}, 0\mu\text{m})$ and initially oriented at angles $\theta_0 = \pi/6$ (3**a** and 3**b**), $2\pi/3$ (3**c** and 3**d**) and $5\pi/6$ (3**e** and 3**f**).

It is important to point out that these trajectories are based on the system of ODEs developed using far-field approximations of microswimmers near a boundary in which the flow field in close proximity of the swimmer is not taken into account; only the far-field behaviour is considered. Hence, our system of ODEs is not very accurate when the swimmer is very close to the wall and hence each trajectory in 3 might deviate from the original trajectory when the swimmer is very close to the surface ($y = 0$). We are currently working on to modify our system of ODEs to fix this inaccuracy to the maximum extent possible.

3.2. **Interaction between swimmers.** We can use similar calculations to draw conclusions on the hydrodynamic interactions between two identical swimmers swimming in an infinite fluid. Consider swimmer A and its mirror-image swimmer B, separated by a distance $2h$ (Fig. 4). By symmetry, the effect of swimmer A on swimmer B is identical to that from B on A. The translational and rotational velocities induced on swimmer A by the (ambient) flow created by swimmer B are found using Faxen's law applied to the flow generated by swimmer B, which is simply the mirror image of a Stokes dipole, leading to

$$\mathbf{U} = -\frac{\alpha}{32\pi\mu h^2}(1 - 3\cos^2\theta)\mathbf{e}_y,$$

$$\boldsymbol{\Omega} = -\frac{3\alpha\sin(2\theta)}{512\pi\mu h^3}\left(1 + \frac{\gamma^2-1}{\gamma^2+1}\cos^2\theta\right)\mathbf{e}_z.$$

Rewriting these in terms of κ and β, we have

$$\mathbf{U} = -\frac{2\kappa}{3h^2}(1 - 3\cos^2\theta)\mathbf{e}_y,$$

$$\boldsymbol{\Omega} = -\frac{\kappa\sin(2\theta)}{8h^3}(1 + 2\beta\cos^2\theta)\mathbf{e}_z.$$

Suppose that A and B are pushers with strength $\alpha > 0$. Then it is easy to see that

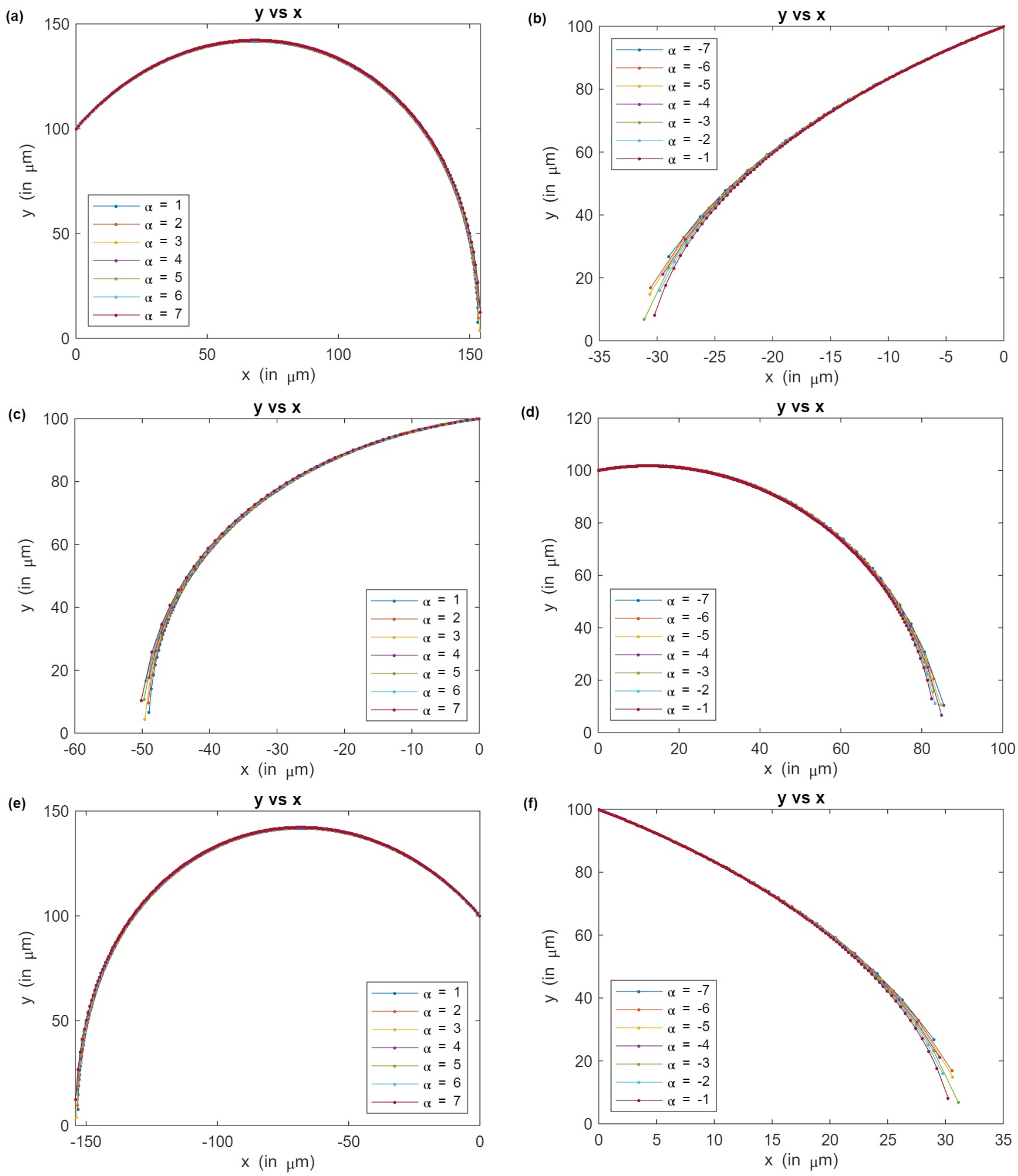

FIGURE 3. Trajectory of swimmers, swimming in a fluid of dynamic viscosity $\mu = 10^{-3}$ Pa.s, with body-aspect ratio $\gamma = 3$, strength $\alpha = \pm 1, \pm 2, \ldots, \pm 7$, initially located at $\mathbf{x}_0 = (0\mu\text{m}, 100\mu\text{m}, 0\mu\text{m})$ and initially oriented at angles $\theta_0 = \pi/6$ (**a** and **b**), $2\pi/3$ (**c** and **d**) and $5\pi/6$ (**e** and **f**).

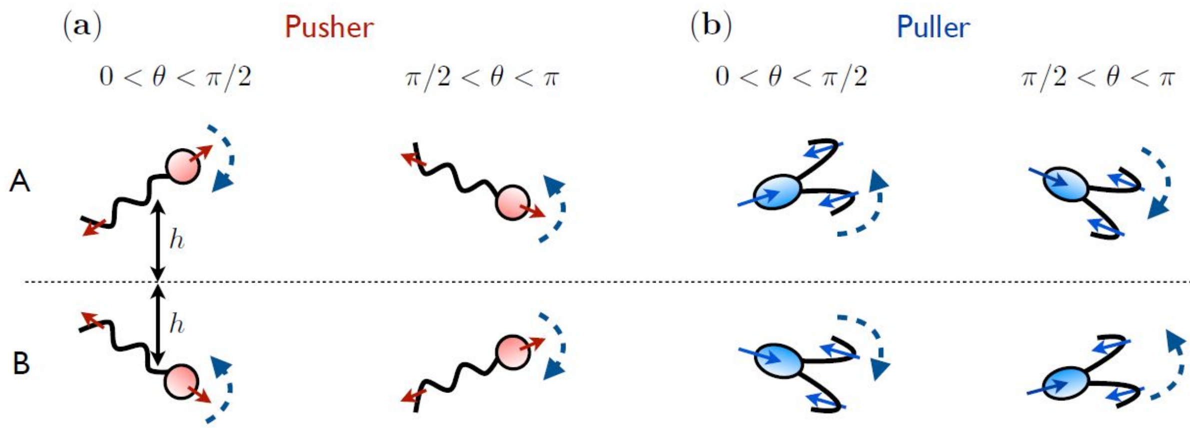

FIGURE 4. Hydrodynamic interactions between two identical swimmers oriented side-by-side. (**a**): Pushers are reoriented to be perpendicular to their line of centers. (**b**): In contrast pullers are reoriented to be parallel to their line of centers.

$$U_y(\theta, h) \begin{cases} > 0, & 0 \leq \theta < \sin^{-1}\sqrt{\frac{2}{3}}, \\ = 0, & \theta = \sin^{-1}\sqrt{\frac{2}{3}}, \\ < 0, & \sin^{-1}\sqrt{\frac{2}{3}} < \theta < \pi - \sin^{-1}\sqrt{\frac{2}{3}}, \\ = 0, & \theta = \pi - \sin^{-1}\sqrt{\frac{2}{3}}, \\ > 0, & \pi - \sin^{-1}\sqrt{\frac{2}{3}} < \theta < \pi. \end{cases}$$

i.e. we obtain effects qualitatively similar to the case of swimming near a solid boundary. For example, when A and B swim side-by-side ($\theta = \pi/2$), $U_y < 0$, meaning that hydrodynamic interactions act to attract A and B. The opposite holds for the case where two cells swim head on ($\theta = 0$), as $U_y > 0$. Due to the linearity of the induced migration velocity with α, the opposite inequalities hold when A and B are pullers ($\alpha < 0$) and hence opposite conclusions can be made.

The body aspect ratio of A and B, $\gamma > 1$, which implies that $1 + 2\beta\cos^2\theta \geq 1 > 0$. This means that the direction of the induced rotational velocity $\mathbf{\Omega}$ is independent of the shape of the swimmer, and if A and B are pushers, we have

$$\Omega(\theta, h) \begin{cases} = 0, & \theta = 0, \\ < 0, & 0 < \theta < \pi/2, \\ = 0, & \theta = \pi/2, \\ > 0, & \pi/2 < \theta < \pi. \end{cases}$$

This means that two pushers are reoriented to be perpendicular to their line of centers, and thus end up swimming parallel to each other (Fig. 4**a**). On the other hand, two pullers are reoriented so as to be parallel to their line of centers (Fig. 4**b**). As a final remark, we note that the configuration in Fig. 4 is physically equivalent to swimmer A swimming at a distance h from a flat stress-free surface, since in that case the image singularity required to satisfy the surface condition is simply the mirror image of the Stokes dipole.

So, we have the following governing system of ODEs:

$$\frac{dy}{dt} = \frac{2\kappa}{3y^2}(3\cos^2\theta - 1), \;\; \frac{d\theta}{dt} = -\frac{\kappa\sin(2\theta)}{8|y|^3}(1 + 2\beta\cos^2\theta),$$

which can be numerically solved subject to given appropriate initial conditions.

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