

Swimmer-tracer scattering at low Reynolds number

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Understanding the stochastic dynamics of tracer particles in active fluids is important for identifying the physical properties of flow generating objects such as colloids, bacteria or algae. Here, we study both analytically and numerically the scattering of a tracer particle in different types of time-dependent, hydrodynamic flow fields. Specifically, we compare the tracer motion induced by an externally driven colloid with the one generated by various self-motile, multi-sphere swimmers. Our results suggest that force-free swimmers generically induce loop-shaped tracer trajectories. The specific topological structure of these loops is determined by the hydrodynamic properties of the microswimmer. Quantitative estimates for typical experimental conditions imply that the loops survive on average even if Brownian motion effects are taken into account.

I. Introduction

Scattering processes are ubiquitous in Nature, ranging from elementary particle collisions at subatomic scales to gravitational encounters in galactic clusters. Traditionally, scattering experiments have played an important role in elucidating the interactions between ‘non-living’ physical objects. Nowadays, modern experimental techniques allow us to track the motion of individual microorganisms,^{1–4} as beautifully illustrated by recent high-speed microscopy observations of *Volvox*⁵ and *Chlamydomonas reinhardtii*.^{6,7} These and similar experiments on colloidal systems⁸ suggest that it should be possible in the near future to systematically study the effective hydrodynamic interaction forces generated by algae, bacteria or artificial microswimmers^{9,10} through suitably designed biophysical scattering experiments.

Additional motivation for studying swimmer-tracer scattering comes from recent experiments by Leptos *et al.*,⁶ who observed that a passive tracer particle exhibits non-Gaussian diffusion when surrounded by a dilute suspension of self-motile *Chlamydomonas reinhardtii* algae. Qualitatively, the anomalous diffusive behavior arises because the algae modify the velocity field of the fluid, thereby occasionally accelerating the tracer particle to relatively large velocities. A satisfactory quantitative explanation for this phenomenon is still missing, and a better understanding of the underlying elementary scattering processes is a key step en route to deriving the corresponding generalized diffusion equation.

The present paper aims to identify generic features that should be observable when a small colloidal tracer particle is scattered by an artificial or natural microswimmer. Specifically, we address the following problems: How does the tracer dynamics differ depending on whether a swimmer’s motion is externally forced or internally generated? Is it sufficient to consider an effective time-averaged description in order to correctly predict the tracer trajectories – or is it necessary to use a time-resolved model that

captures the details of the swimming stroke? How does Brownian motion, which plays a non-negligible role for (sub-)micron-sized colloidal particles, affect the tracer dynamics? To answer these questions, we will compare both analytically and numerically the dynamics of a tracer in the presence of various simplified model swimmers.

The first part of our discussion focusses on deterministic scattering processes. In order to clarify how the effective interaction range determines the asymptotic state of the tracer, we shall consider a simplified power-law interaction model and, as a more realistic example, tracer displacement due to an externally driven colloid. The main part of the paper is dedicated to the scattering of a tracer by 2-sphere and 3-sphere swimmers that generate predominantly dipolar and quadrupolar flow fields, respectively. We show that, asymptotically, the tracer motion in the presence of a self-motile, force-free swimmer converges to a closed loop. The shape and direction of the loops is a signature of the specific properties of a given swimmer. For experimentally accessible parameters, Brownian motion effects may dominate the trajectories of an individual tracer particle. In the last part of the paper, we will demonstrate that, after averaging over a few hundred to thousand samples, the mean tracer trajectories look very similar to those obtained in the deterministic limit.

II. Mathematical model

We consider the motion $\mathbf{x}(t)$ of a passive, colloidal tracer particle in a fluid due to the presence of an active object (‘swimmer’). The latter, which may be an externally forced colloid, an artificial microswimmer or a microorganism (*e.g.*, an alga or a bacterium), is described by a phase space coordinate vector $\Gamma(t)$. For example, for a spherical colloid with position vector $\mathbf{X}(t)$ and velocity $\dot{\mathbf{X}}(t) = d\mathbf{X}(t)/dt$, $\Gamma(t)$ is simply given by $\Gamma(t) = (\mathbf{X}(t), \dot{\mathbf{X}}(t))$. For more complex objects, such as multi-sphere swimmers,^{11–13} Γ comprises all the coordinates necessary to uniquely specify the motion of the swimmer. Throughout, we shall assume that, in good approximation, the tracer particle does not affect the swimmer motion, *i.e.*, $\Gamma(t)$ is taken to be independent of $\mathbf{x}(t)$.

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A. Langevin dynamics of the tracer

In principle, when studying the scattering of a tracer particle by a self-swimming object, one can distinguish (at least) two different approaches:

(i) analyzing the approximate mean motion of the tracer particle in the time-averaged (or stroke-averaged) effective flow field of the swimmer.

(ii) computing the exact, time-resolved motion of the tracer particle in the full oscillatory flow field of the swimmer.

Below we will compare results from both methods for multi-sphere swimmer models.^{12,13} We will start from the time-averaged description (i) which is less accurate, but allows us to obtain analytical estimates. When adopting this coarse-grained approach, the swimmer state is approximated by $\Gamma(t) = (\mathbf{X}(t), \dot{\mathbf{X}}(t))$, and the swimmer is assumed to move at constant velocity $\dot{\mathbf{X}}(t) \equiv \mathbf{V}$ along the straight line

$$\mathbf{X}(t) = \mathbf{X}_0 + t\mathbf{V}. \quad (1)$$

The effective stroke-averaged swimmer velocity \mathbf{V} results from the microscopic swimmer dynamics.

Let us assume we know the velocity field $\mathbf{v}(\mathbf{x}|\Gamma(t))$ that is generated by a given swimmer configuration $\Gamma(t)$. In this case, we can model the motion of a micron-sized tracer particle by the overdamped Langevin equation

$$\dot{\mathbf{x}}(t) = \mathbf{v}(\mathbf{x}(t)|\Gamma(t)) + (2D_0)^{1/2}\zeta(t). \quad (2a)$$

This equation is valid in the Stokes (zero Reynolds number) regime, which is realized to good approximation under typical experimental conditions.⁵⁻⁷ The second contribution on the rhs of eqn (2a) is Gaussian white noise $\zeta(t) = (\zeta_i(t))$, which describes thermal fluctuations in the fluid and is characterized by

$$\langle \zeta_i(t) \rangle = 0, \quad \langle \zeta_i(t)\zeta_j(s) \rangle = \delta_{ij}\delta(t-s). \quad (2b)$$

For a spherical tracer particle of radius a_0 , the thermal diffusion constant D_0 is given by the Stokes formula

$$D_0 = kT/\gamma_0 = kT/(6\pi\eta a_0) \quad (2c)$$

where a_0 is the tracer radius and γ_0 the Stokes friction coefficient. For example, considering $a_0 = 1\mu\text{m}$ and water at room temperature $T = 25^\circ\text{C}$ with viscosity $\eta = 10^{-3}\text{kg m}^{-1}\text{s}^{-1}$ and $kT = 4.11 \times 10^{-21}\text{kg m}^2\text{s}^{-2}$, we have $D_0 = 0.22\mu\text{m}^2\text{s}^{-1}$.

B. Initial conditions

We intend to analyze swimmer-tracer scattering processes for well-defined, reproducible initial conditions. For this purpose, we choose the coordinate system such that the spherical tracer particle is initially located at the origin, $\mathbf{x}(0) = \mathbf{0}$. The swimmer (characteristic length scale A) starts at $\mathbf{X}_0 = (X_0, Y_0, 0)$ with $|Y_0| > a_0 + A$ and moves in the ($z=0$)-plane with an average velocity $\mathbf{V} = (V, 0, 0)$ parallel to the x -axis, see Fig. 1.

III. Tracer scattering in time-dependent flow fields

Our main objective is to understand the motion of the tracer in the velocity field $\mathbf{v}(\mathbf{x}|\Gamma(t))$ of an externally driven or self-motile

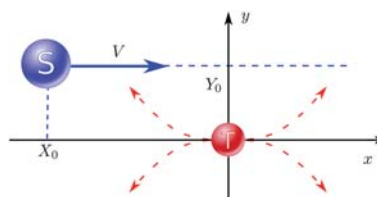


Fig. 1 Swimmer-tracer scattering. The swimmer (S) starts at $\mathbf{X}_0 = (X_0, Y_0, 0)$ and moves with velocity $\mathbf{V} = (V, 0, 0)$ parallel to the x -axis. The trajectory of the tracer (T), initially located at $\mathbf{x}(0) = (0, 0, 0)$, depends on the flow field generated by the swimmer.

object. In order to simplify the notation, it is convenient to define the distance vector between tracer and swimmer by

$$\mathbf{r}(t) = \mathbf{x}(t) - \mathbf{X}(t) \quad (3a)$$

and to introduce two unit vectors

$$\hat{\mathbf{r}}(t) = \frac{\mathbf{r}(t)}{|\mathbf{r}(t)|}, \quad \hat{\mathbf{n}} = \frac{\mathbf{V}}{|\mathbf{V}|} \quad (3b)$$

with $\hat{\mathbf{n}}(t)$ characterizing the orientation of the swimmer motion. In the examples considered below, the effective hydrodynamic interaction between swimmer and tracer is mediated by non-diagonal tensors $\mathbf{H} = \mathbf{H}(|\mathbf{r}|, \hat{\mathbf{r}}, \hat{\mathbf{n}}) = (H_{ij})$, which relate the fluid velocity at the position $\mathbf{x}(t)$ to the velocity \mathbf{V} of the swimmer through

$$\mathbf{v} = \mathbf{H}\mathbf{V}. \quad (4)$$

The exact structure of \mathbf{H} encodes the details of the propulsion mechanism. For example, consider an externally forced colloid of radius A that is pulled at constant velocity \mathbf{V} . If the colloid passes the tracer particle at a sufficiently large distance $|\mathbf{r}(t)| = |\mathbf{x}(t) - \mathbf{X}(t)| \gg A + a_0$, then \mathbf{H} is given by the Oseen tensor

$$H_{ij} = \frac{3A}{4|\mathbf{r}|}(\delta_{ij} + \hat{r}_i\hat{r}_j) \quad (5)$$

By contrast, the effective velocity field generated by a self-swimming microorganism usually decays more rapidly as $|\mathbf{r}|^{-\alpha}$, $\alpha \geq 2$. In Sections IIIB, IIIC and IIID we shall compare the scattering of tracers by externally forced colloids and multi-sphere swimmers. However, in order to demonstrate how the effective interaction range α affects the scattering process, it is instructive to analyze a simplified power law interaction model first.

A. Simplified power law interaction (α -model)

Let us assume that a hypothetical 'swimmer' of radius A generates a fluid velocity field of the simple power law form

$$\mathbf{v}(\mathbf{x}|\mathbf{X}(t), \mathbf{V}) = \kappa\mathbf{V} \left[\frac{A}{|\mathbf{r}(t)|} \right]^\alpha \quad (6)$$

The dimensionless parameter κ quantifies the interaction strength. In order to understand the basic dynamics of a tracer in this field, we will focus on the deterministic limit $D_0 = 0$ in the Langevin eqn (2a). Brownian motion effects (corresponding $D_0 > 0$) will be discussed later for more realistic flow fields.

Adopting the initial conditions $\mathbf{V} = (V, 0, 0)$, $\mathbf{X}(0) = (X_0, Y_0, 0)$, and $\mathbf{x}(0) = \mathbf{0}$ as depicted in Fig. 1, the swimmer moves in the x -direction and its x -position at time t is given by $X(t) = X_0 + tV$. The isotropic power law model (6) corresponds to the diagonal tensor $H_{ij} = \kappa (A/|r|)^\alpha \delta_{ij}$, which implies that the tracer particle also moves along the x -axis, *i.e.*, $\mathbf{x}(t) = (x(t), 0, 0)$ where

$$\dot{x}(t) = \kappa V \left(\frac{A}{\left\{ [X(t) - x(t)]^2 + Y_0^2 \right\}^{1/2}} \right)^\alpha \quad (7)$$

It is possible to find exact, implicit solutions of eqn (7) for $\alpha = 1, 2, \dots$ by transforming to the comoving swimmer frame. For example, for long-range interactions with $\alpha = 1$, we obtain, in the original coordinate system,

$$\begin{aligned} x(t) = \kappa A \left\{ \log \left(\frac{X(t) - x(t) + \sqrt{[X(t) - x(t)]^2 + Y_0^2}}{X_0 + \sqrt{X_0^2 + Y_0^2}} \right) \right. \\ - \frac{\kappa A}{\sqrt{Y_0^2 - \kappa^2 A^2}} \left[\arctan \left(\frac{\kappa A X_0}{\sqrt{X_0^2 + Y_0^2} \sqrt{Y_0^2 - \kappa^2 A^2}} \right) \right. \\ - \arctan \left(\frac{\kappa A [X(t) - x(t)]}{\sqrt{[X(t) - x(t)]^2 + Y_0^2} \sqrt{Y_0^2 - \kappa^2 A^2}} \right) \\ \left. \left. + \arctan \left(\frac{X_0}{\sqrt{Y_0^2 - \kappa^2 A^2}} \right) - \arctan \left(\frac{X(t) - x(t)}{\sqrt{Y_0^2 - \kappa^2 A^2}} \right) \right] \right\} \quad (8a) \end{aligned}$$

whereas for shorter range interactions with $\alpha = 2$

$$\begin{aligned} x(t) = \frac{\kappa A^2}{\sqrt{Y_0^2 - \kappa A^2}} \left[\arctan \left(\frac{X(t) - x(t)}{\sqrt{Y_0^2 - \kappa A^2}} \right) \right. \\ \left. - \arctan \left(\frac{X_0}{\sqrt{Y_0^2 - \kappa A^2}} \right) \right] \quad (8b) \end{aligned}$$

The exact results (8) are transcendental equations for $x(t)$ which can be numerically inverted for a given value $t > 0$ to give the trajectory of the tracer particle. In particular, these equations cover both the near- and far-field scattering behavior. However, to gain additional analytic insights, it is useful to consider in more detail the far-field scattering, corresponding to

$|x(t)| \ll \max\{|Y_0|, |X(t)|\}$ and $\kappa^{3-\alpha} A^2 \ll Y_0^2$. In this limit one obtains, for $\alpha = 1$, the approximate result

$$x(t) \approx \kappa A \log \left[\frac{X(t) + \sqrt{X(t)^2 + Y_0^2}}{X_0 + \sqrt{X_0^2 + Y_0^2}} \right]. \quad (9a)$$

Inserting $X(t) = X_0 + tV$, we see that asymptotically (for $t \rightarrow \infty$)

$$x(t) \approx \kappa A \log \left[\frac{2tV}{X_0 + \sqrt{X_0^2 + Y_0^2}} \right]. \quad (9b)$$

Thus, for $\mathbf{v} \propto |\mathbf{r}|^{-1}$ the solution is logarithmically divergent in time, implying that the tracer particle is slowly dragged away to infinity. Defining the asymptotic displacement as a function of α by

$$(\Delta x)_\alpha^\infty := \lim_{t \rightarrow \infty} [x(t) - x(0)], \quad (10)$$

the divergence implies $(\Delta x)^\infty_1 = \infty$. Performing a similar analysis for $\alpha = 2$ yields

$$x(t) \approx \kappa A \left(\frac{A}{|Y_0|} \right) \left[\arctan \left(\frac{X(t)}{|Y_0|} \right) - \arctan \left(\frac{X_0}{|Y_0|} \right) \right], \quad (11a)$$

and thus, in the limit $t \rightarrow \infty$,

$$(\Delta x)_2^\infty = \kappa A \left(\frac{A}{|Y_0|} \right) \left[\frac{\pi}{2} - \arctan \left(\frac{X_0}{|Y_0|} \right) \right] \quad (11b)$$

i.e., for $\alpha = 2$ the tracer particle comes to rest after a finite distance $(\Delta x)^\infty_2$. Analogous results can be obtained for arbitrary values $\alpha \geq 2$. For example, for $\alpha = 3$

$$x(t) \approx \kappa A \left(\frac{A}{|Y_0|} \right)^2 \left[\frac{X(t)}{\sqrt{X(t)^2 + Y_0^2}} - \frac{X_0}{\sqrt{X_0^2 + Y_0^2}} \right], \quad (12a)$$

yielding the maximal displacement

$$(\Delta x)_3^\infty = \kappa A \left(\frac{A}{|Y_0|} \right)^2 \left(1 - \frac{X_0}{\sqrt{X_0^2 + Y_0^2}} \right). \quad (12b)$$

To briefly summarize, for long-range hydrodynamic interactions with $\mathbf{v} \propto |\mathbf{r}|^{-1}$ the tracer experiences an infinite displacement, whereas for shorter range interactions with $\mathbf{v} \propto |\mathbf{r}|^{-\alpha}$, $\alpha \geq 2$

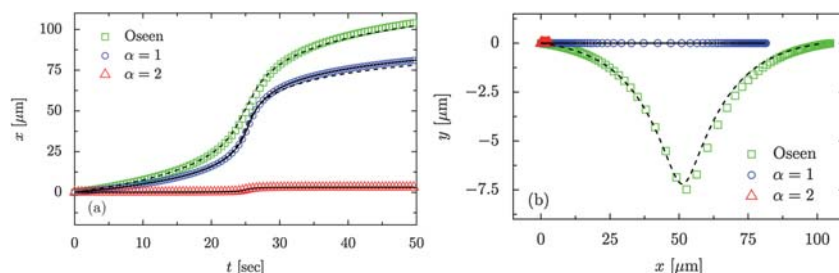


Fig. 2 Deterministic tracer trajectories for three different model interactions. (a) Tracer displacement in the direction of the swimmer's motion as a function of time t for the simplified α -model with $\kappa = 1$ and the Oseen interaction. (b) Tracer trajectories in the (x, y) -plane. For colloidal-type long-range interactions that scale with distance as $|\mathbf{r}|^{-1}$ the tracer is dragged to infinity - the divergence is logarithmic in time. By contrast, for shorter range interactions with $|\mathbf{r}|^{-\alpha}$, $\alpha \geq 2$ the maximal tracer displacement remains finite, see red curve/triangles. Solid lines correspond to the exact result (8), and dashed lines to the approximate far-field result (9). The symbols were obtained by numerically integrating the deterministic equations of motion (2a) with $D_0 = 0$ using a simulation time step $\Delta t = 2.2 \times 10^{-7}$ s. Parameters: swimmer velocity $V = 100 \mu\text{s}$, swimmer radius $A = 10 \mu\text{m}$, tracer radius $a = 1 \mu\text{m}$, impact parameter $Y_0 = 10A$, initial swimmer position $X_0 = -25A$.

the displacement is finite. These results are illustrated graphically in Fig. 2.

The simple power law model (6) is useful for illustrating how the range of the effective hydrodynamic interactions affects the asymptotic state of the tracer particle. However, this truncated model neglects fluid velocity components that act perpendicular to the swimmer's direction of motion. In the remainder, we will focus on more physical models that account for these effects. As the first example, we consider the scattering of a tracer by a driven colloid.

b Externally forced colloid

Consider a spherical colloid (radius A) dragged at constant velocity V past a smaller tracer particle (e.g., by a movable laser trap). If the distance between tracer and colloid is sufficiently large, $|r(t)| \gg A + a_0$, the velocity field components $v_i = H_{ij}V_j$ experienced by the tracer are determined by the Oseen tensor (5) and we can approximate $r(t) \approx X(t)$. Considering the deterministic limit $D_0 = 0$ and the same initial conditions as before, we then find that the trajectory of the tracer particle in the ($z = 0$)-plane is determined by the differential equation

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \kappa V \frac{A}{\sqrt{X(t)^2 + Y_0^2}} \left[\begin{pmatrix} 1 \\ 0 \end{pmatrix} + \frac{X(t)}{X(t)^2 + Y_0^2} \begin{pmatrix} X(t) \\ Y_0 \end{pmatrix} \right] \quad (13)$$

Owing to the non-vanishing off-diagonal components of the Oseen tensor, the tracer experiences a transverse force (velocity field) component in the y -direction. Eqn (13) can be directly integrated, yielding

$$x(t) = \kappa A \left\{ 2 \log \left[\frac{X(t) + \sqrt{X(t)^2 + Y_0^2}}{X_0 + \sqrt{X_0^2 + Y_0^2}} \right] + \frac{X_0}{\sqrt{X_0^2 + Y_0^2}} - \frac{X(t)}{\sqrt{X(t)^2 + Y_0^2}} \right\} \quad (14a)$$

$$y(t) = \kappa A \left[\frac{Y_0}{\sqrt{X_0^2 + Y_0^2}} - \frac{Y_0}{\sqrt{X(t)^2 + Y_0^2}} \right] \quad (14b)$$

where $X(t) = X_0 + tV$. Letting $t \rightarrow \infty$, we find that asymptotically

$$x(t) \approx 2\kappa A \log \left[\frac{2tV}{X_0 + \sqrt{X_0^2 + Y_0^2}} \right] \quad (15a)$$

$$y(t) \rightarrow \kappa A \left[\frac{Y_0}{\sqrt{X_0^2 + Y_0^2}} \right] \quad (15b)$$

Note that the logarithmic divergence predicted by eqn (15a) is in agreement with the earlier result (11a), i.e. the tracer particle slowly follows the colloid to infinity.

The deterministic result (14) can be expected to correctly describe a single tracer trajectory only if Brownian fluctuations are negligible corresponding to the low-temperature, high-viscosity regime. For a micron-sized tracer particle in water at

room temperature, Brownian motion effects can become relevant if the speed V of the 'swimmer' colloid is too low and/or the distance between tracer and swimmer colloid becomes too large. In this case, eqn (14) provides an approximate description of the ensemble mean when the scattering experiment is repeated using identical (i.e., deterministic) initial conditions. The statistical fluctuations around the mean trajectory (14) can be estimated by $\sqrt{2D_0t}$, where $D_0 \approx 0.22 \mu\text{m}^2/\text{s}$ for a micron-sized tracer. This suggests that for the parameters and initial conditions used in Fig. 2, the characteristic features of the solution (14) should remain observable even for a single tracer trajectory.

Having discussed the scattering of a tracer by an externally driven colloid, we shall focus on self-motile swimmers in the remainder of the paper.¹⁴⁻¹⁷ In particular, we would like to identify characteristic features of the tracer trajectories that provide a signature of truly self-swimming objects, which do not generate a net force during a swimming stroke. Specifically, we are interested in understanding how the tracer trajectories differ depending on

(i) whether a force-free swimmer is extensile ('pusher') or contractile ('puller');

(ii) whether a force-free swimmer generates a dipolar or a quadrupolar flow field.

For this purpose, we will study simple multi-sphere swimmers that are analytically tractable and can be easily tuned from extensile to contractile. An additional advantage of the simplified models is that the underlying microscopic swimming mechanisms can be implemented numerically using the methods described in ref. [16,17]. This allows us to compare analytic estimates, which are based on a time-averaged description, with numerical results for the exact time-resolved dynamics.

C. Dipolar two-sphere swimmer

As the first example of tracer scattering by a self-motile object, we consider a slender 2-sphere swimmer consisting of two beads (radii $A_{1,2}$) at positions $X_{1,2}(t)$ that are connected by an oscillating leg of length

$$L(t) = \ell + \xi \sin(\omega t + \theta), \quad \ell \gg \xi > 0 \quad (16)$$

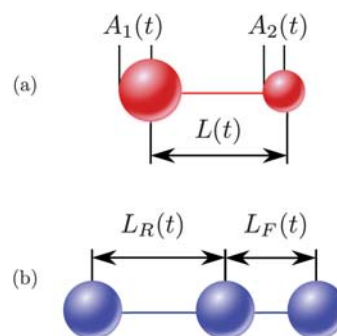


Fig. 3 Simple multi-sphere swimmer models. (a) The 2-sphere swimmer with variable radius spheres generates a dipolar net flow field that can be either extensile or contractile with respect to the swimmer axis, see Fig. 4. (b) The 3-sphere swimmer¹² generates a flow field that is essentially quadrupolar,¹³ see Fig. 7. Consequently, the trajectories of tracer particles are qualitatively different when scattered by the two swimmers.

see Fig. 3 (a). The orientation vector of the swimmer is defined by

$$\hat{\mathbf{n}}(t) := \frac{\mathbf{X}_2(t) - \mathbf{X}_1(t)}{|\mathbf{X}_2(t) - \mathbf{X}_1(t)|} \quad (17)$$

If the sphere radii A_1 and A_2 are constant then this 2-sphere swimmer reduces to an oscillating dumbbell,^{14,15,17} which is prevented from swimming by the scallop theorem.^{15,18} A simple, self-motile 2-sphere swimmer can be obtained if the size of the spheres changes periodically in time according to

$$\begin{aligned} A_1(t) &= A + \lambda \sin(\omega t + \phi_1), \\ A_2(t) &= A + \lambda \sin(\omega t + \phi_2), \quad A \gg \lambda > 0 \end{aligned} \quad (18)$$

For simplicity, we neglect secondary flow contributions produced by the expansion and shrinkage of the spheres by assuming that (to good approximation) they merely change their hydrodynamic resistance in a manner consistent with a changed radius. Considering the limit $\lambda, \xi \ll A, \ell$ and averaging over a stroke-period $[t, t + 2\pi/\omega]$, one can show that the 2-swimmer moves at an average velocity $\mathbf{V} = V\hat{\mathbf{n}}$, where

$$V = \frac{1}{4} \omega \lambda \left(\frac{\xi}{A} \right) \left(1 - \frac{3A}{2\ell} \right)^{-1} \sin(\Delta\phi) \cos(\Delta\theta) \quad (19a)$$

and

$$\Delta\phi := \frac{1}{2}(\phi_1 - \phi_2), \quad \Delta\theta := \frac{1}{2}(\phi_1 + \phi_2) - \theta \quad (19b)$$

The derivation of eqn (19) is analogous to those for other multi-sphere swimmers.^{13,19} By choosing the phase parameters ϕ_1, ϕ_2 , and θ such that $\Delta\phi \in (0, \pi)$ and $\Delta\theta \in (-\pi/2, \pi/2)$, we have $V > 0$, *i.e.*, the swimmer moves in the direction of positive $\hat{\mathbf{n}}$.

The stroke-averaged velocity field generated by the swimmer at large distances is obtained by summing the Stokeslets of the two spheres, performing a far-field Taylor (multipole) expansion and averaging the leading far-field contributions over a swimming stroke (13). By means of this procedure, one finds that the averaged far-field fluid flow generated by the swimmer is *dipolar*,

$$\mathbf{v}(\mathbf{x}(t)|\mathbf{X}(t), \mathbf{V}) = \kappa_2 V \left(\frac{A}{|\mathbf{r}(t)|} \right)^2 \left[3(\hat{\mathbf{n}}\hat{\mathbf{r}})^2 - 1 \right] \hat{\mathbf{r}} \quad (20a)$$

with unit vectors $\hat{\mathbf{n}}$ and $\hat{\mathbf{r}}$ as defined in eqn (3b) and

$$\kappa_2 = \frac{3}{4} \left(\frac{\ell}{A} \right) \left(1 - \frac{3A}{2\ell} \right)^{-1} \frac{\tan(\Delta\theta)}{\tan(\Delta\phi)} \quad (20b)$$

Note that, depending on the choice of $\Delta\phi$ and $\Delta\theta$, the coefficient κ_2 can be either negative or positive for a swimmer with $V > 0$. Swimmers with $\kappa_2 > 0$ are extensile ‘pushers’, whereas negative values $\kappa_2 < 0$ correspond to contractile ‘pullers’. In our simulations, we used $\theta = 0$, $\Delta\phi = \Delta\theta = \pi/4$ to realize an extensile swimmer and $\theta = 0$, $\Delta\phi = 3\pi/4$, $\Delta\theta = \pi/4$ in the contractile case. The structure of the dipolar flow fields (20) for these parameter values is illustrated in Fig. 4. The arrows show the normalized velocity field $\hat{\mathbf{v}} := \mathbf{v}/|\mathbf{v}|$. The color shading indicates the projection ($\hat{\mathbf{r}}\hat{\mathbf{v}}$), *i.e.*, dark (bright) areas correspond to regions where the mean flow points towards (away from) the swimmer.

Tracer motion in the deterministic limit.—Based on eqn (20), it is possible to obtain an analytic estimate for the mean tracer trajectory in the deterministic, far-field limit. To this end, we

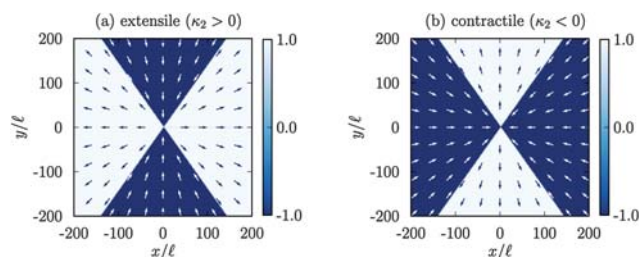


Fig. 4 Dipolar fluid flows generated by 2-sphere swimmer. – The diagrams show the stroke-averaged fluid velocity field (20) for two different swimmer setups: (a) extensile pusher with $\kappa_2 > 0$ and (b) contractile puller with $\kappa_2 < 0$. In both cases the swimmer is located at the origin, points along the x -axis, and swims in the positive x -direction. Swimmer parameters: $\ell = 20\mu\text{m}$, $\xi = A = 0.1\ell$, $\lambda = 0.1A$, $\omega = 5 \times 10^2 \text{s}^{-1}$ with $\Delta\phi = \Delta\theta = \pi/4$ for extensile swimmers and $\Delta\phi = 3\pi/4$, $\Delta\theta = \pi/4$ in the contractile case, yielding $V \approx 14.7\mu\text{m/s}$ and $\kappa_2 = \pm 8.8$. The flow fields are rotationally invariant about the x -axis. Arrows indicate the local direction $\hat{\mathbf{v}} := \mathbf{v}/|\mathbf{v}|$ of the stroke-averaged flow (20). Dark (bright) areas show the projection ($\hat{\mathbf{r}}\hat{\mathbf{v}}$), corresponding to regions where the mean flow points towards (away from) the swimmer.

consider initial conditions with $\hat{\mathbf{n}} = (1, 0, 0)$ as depicted in Fig. 1 and approximate

$$\mathbf{r}(t) \approx \mathbf{X}(t), \quad \hat{\mathbf{n}}\hat{\mathbf{r}} \approx \frac{X(t)}{\sqrt{X(t)^2 + Y_0^2}} \quad (21)$$

with $X(t) = X_0 + tV$ denoting the swimmer’s x -coordinate. The approximations (21) hold in the far-field scattering limit where eqn (20) is valid. Integrating the equations of motion (2a) for $D_0 = 0$ yields the trajectory $\mathbf{x}(t) = (x(t), y(t), 0)$ of the tracer particle in the ($z = 0$)-plane

$$x(t) \approx -\kappa_2 A \left\{ \frac{A(2X_0^2 + Y_0^2)}{(X_0^2 + Y_0^2)^{3/2}} - \frac{A[2X(t)^2 + Y_0^2]}{[X(t)^2 + Y_0^2]^{3/2}} \right\} \quad (22a)$$

$$y(t) \approx -\kappa_2 A \left\{ \frac{AX_0 Y_0}{(X_0^2 + Y_0^2)^{3/2}} - \frac{AX(t) Y_0}{[X(t)^2 + Y_0^2]^{3/2}} \right\} \quad (22a)$$

Letting $t \rightarrow \infty$, we see that asymptotically

$$x(t) \rightarrow -\kappa_2 A \left[\frac{A(2X_0^2 + Y_0^2)}{(X_0^2 + Y_0^2)^{3/2}} \right] \quad (23a)$$

$$y(t) \rightarrow -\kappa_2 A \left[\frac{AX_0 Y_0}{(X_0^2 + Y_0^2)^{3/2}} \right] \quad (23b)$$

According to eqn (23), the tracer particle is displaced by a finite distance reflecting the fact that the effective interaction is short-range $\alpha \geq 2$. Furthermore, eqn (23) predicts that, if the swimmer starts very far away, corresponding to the limit $X_0 \rightarrow -\infty$, the tracer returns to its initial condition $\mathbf{x}(0) = \mathbf{0}$, thus forming a closed loop in the ($z = 0$)-plane.

This is illustrated in Fig. 5, which shows tracer trajectories in the (x, y)-plane. The dotted lines in both diagrams indicate the

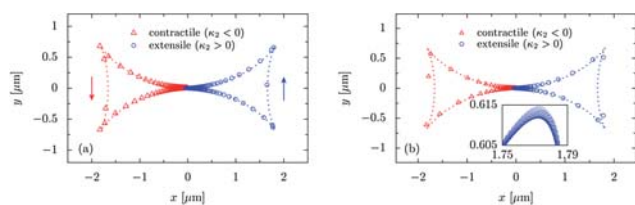


Fig. 5 *Deterministic tracer scattering by a dipolar 2-sphere swimmer.* In the limit $D_0 = 0$ the tracer trajectories converge to closed loops if the force-free 2-sphere swimmer starts sufficiently far away from the tracer (arrows indicate how the loop is traversed). The dotted lines in either diagram indicate the analytic estimate from eqn (22). (a) Results for the stroke-averaged dynamics. Symbols were obtained by numerically integrating eqn (2a) for $D_0 = 0$ for the dipolar flow field (20) using the same parameters as in Fig. 4. (b) Results for the time-resolved dynamics. Symbols were obtained from numerical simulations of the tracer trajectories as described in Sec. IV. The inset shows the details of the oscillatory motion of the tracer particle near the turning point at the top-right corner of the extensile (right hand) path. The plots are based on initial conditions $X_0 = -350A$, $Y_0 = 10A$ for the swimmer and $x(0) = 0$ for the tracer. The tracer trajectories are depicted for the time interval $[0, 100s]$. The swimmer parameters are the same as those in Fig. 4. Tracer radius: $a_0 = 1\mu\text{m}$. Simulation time step: $\Delta t = 2.2 \times 10^{-7}s$. A comparison of the two diagrams implies that the stroke-averaged description is able to capture the main features of the mean particle trajectory.

analytic estimates from eqn (22). Symbols in Fig. 5 (a) were obtained by numerically integrating eqn (2a) for $D_0 = 0$ for the time-averaged dipolar velocity field (20) using the same swimmer parameters as in Fig. 4. For comparison, we also plot in Fig. 5 (b) the result from simulations that resolve the microscopic dynamics of the swimmer (details of the numerical implementation are given in Sec. 4). In the latter case, one finds that the tracer particle performs a small oscillator motion around its mean trajectory. Hence, by comparing Fig. 5 (a) and (b), one readily observes that the stroke-averaged description is able to capture the main features of the mean particle trajectory.

Brownian motion effects.— As exemplified by eqn (20), the effective hydrodynamic flow fields of self-swimming objects decay more rapidly with distance than those of externally forced colloids. Hence, the hydrodynamic displacement of a tracer particle in the far-field flow of a force-free swimmer will, in general, be smaller, so that thermal Brownian motion of the tracer becomes more relevant. This raises the question as to whether loop-like structures could actually be observed under typical experimental conditions, *e.g.*, similar to those considered by Leptos *et al.*⁶ who tracked the motions of algae in water at room temperature. In order to estimate how Brownian effects may affect the loop-like structures, we numerically integrated the stochastic equations of motions (2a) for both the time-averaged flow field (20) and the time-resolved swimmer dynamics, using a diffusion constant $D_0 = 0.22\mu\text{m}^2/s$ corresponding to a tracer particle of radius $a_0 = 1\mu\text{m}$ and water at room temperature.

Fig. 6 (a) depicts the mean tracer trajectories obtained numerically for the time-averaged model for an extensile (red triangles) and a contractile swimmer (blue circles). Fig. 6 (b) shows the corresponding results for the time-resolved swimmer dynamics. The numerical data points (filled symbols) in Fig. 6

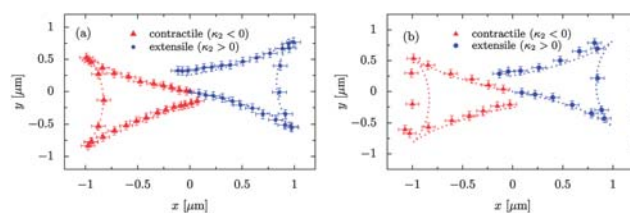


Fig. 6 *Brownian tracer scattering by a dipolar 2-sphere swimmer.* For $D_0 > 0$ loop-like scattering patterns can be recovered by averaging over many sample trajectories with identical initial conditions $x(0) = 0$. (a) Results for the stroke-averaged dynamics obtained by numerically integrating eqn (2a) with $D_0 = 0.22\mu\text{m}^2/s$. (b) Results from the corresponding time-resolved simulations. The filled symbols in both figures were obtained by averaging over 1000 sample trajectories and dotted lines represent the analytic estimate from eqn (22). Statistical error bars correspond to the sample standard deviation, divided by $10 \times \sqrt{t}$ for better visibility. Prior to rescaling the length of the error bars agreed with the theoretically expected value $\sqrt{2D_0t}$. Compared to Fig. 5, we used the same swimmer parameters but the swimmer was started nearer to the tracer at $X_0 = -10A$ and sample trajectories were recorded for the shorter interval $t \in [0, 10s]$. This explains why the loops are not fully closed.

were obtained by averaging over 1000 sample trajectories with identical initial conditions. In both cases, we used the same swimmer parameters as in Fig. 5, but the swimmer was started closer to the tracer at $X_0 = -35A$. The simulation time per run was limited to 10s. For comparison, isolated *Chlamydomonas* algae typically swim on an almost straight line for about 5–10s before changing their directions due to tumbling and rotational Brownian motion.⁷ The statistical error bars in Fig. 6 correspond to the sample standard deviation and were divided by $10 \times \sqrt{t}$ for better visibility. Prior to this rescaling the length of the error bars agrees well with the theoretically expected value $\sqrt{2D_0t}$.

To summarize, the diagrams in Fig. 6 suggest that after averaging over a sufficiently large sample size the loop-like patterns can be recovered. Individual trajectories may however look very different due to Brownian motion.

D. (Quasi-)quadrupolar three-sphere swimmer

As the final example, we consider the scattering of a tracer by a linear 3-sphere swimmer,^{12,13} as illustrated in Fig. 3 (b). The main difference when compared to the 2-sphere swimmer occurs because the flow field of this swimmer is essentially quadrupolar, see Fig. 7. The lengths of the rear leg (R) and the front leg (F) of the 3-sphere swimmer vary in time as

$$L_{F,R}(t) = \ell + \xi_{F,R} \sin(\omega t + \phi_{F,R}), \quad \ell \gg \xi_{R,F} > 0, \quad \ell \gg A > 0 \quad (24)$$

where ℓ is the mean leg length and $\xi_{R,F}$ denotes the oscillation amplitude. If the initial phases $\phi_{R,F}$ are chosen such that

$$\Delta\phi := \phi_R - \phi_F > 0 \quad (25)$$

then the swimmer moves with stroke-averaged speed

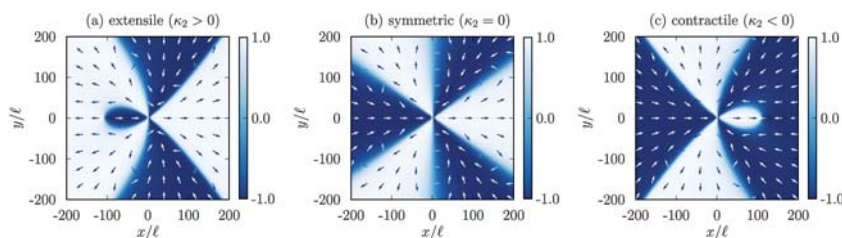


Fig. 7 Quasi-quadrupolar fluid flows generated by 3-sphere swimmers. Structure of the stroke-averaged flow field (27) for three different parameter sets: (a) extensile pusher with $0.2\ell = \xi_R > \xi_F = 0.1\ell$, (b) symmetric swimmer with $\xi_R = \xi_F = \sqrt{0.02}\ell$, and (c) contractile puller with $0.1\ell = \xi_R < \xi_F = 0.2\ell$. In all three cases, the swimmer is located at the origin, points along the x -axis, and swims in the positive x -direction. The flow fields are rotationally invariant about the x -axis. Arrows indicate the local direction $\hat{v} := \mathbf{v}/|\mathbf{v}|$ of the stroke-averaged flow field (27). Dark (bright) areas show the projection $(\hat{r}\hat{v})$, corresponding to regions where the mean flow points towards (away from) the swimmer. Note that in all three cases the quadrupolar contribution dominates at intermediate distances. Swimmer parameters: $\ell = 10\mu\text{m}$, $A = 0.2\ell$, $\omega = 10^3\text{s}^{-1}$, $\Delta\phi = \pi/2$, corresponding to $V \approx 12\mu\text{m/s}$.

$$V = \frac{7}{24}A\omega \sin(\Delta\phi) \left(\frac{\xi_F \xi_R}{\ell^2} \right) \quad (26)$$

in the direction of the front leg. The time averaged flow field at distances far away from the 3-sphere swimmer is¹³

$$\mathbf{v}(\mathbf{x}(t)|\mathbf{X}(t), V) = \kappa_2 V \left(\frac{A}{|\mathbf{r}(t)|} \right)^2 [3(\hat{\mathbf{n}}\hat{\mathbf{r}})^2 - 1]\hat{\mathbf{r}} + \quad (27)$$

$$\kappa_3 V \left(\frac{A}{|\mathbf{r}(t)|} \right)^3 \left\{ [15(\hat{\mathbf{n}}\hat{\mathbf{r}})^3 - 9(\hat{\mathbf{n}}\hat{\mathbf{r}})]\hat{\mathbf{r}} - [3(\hat{\mathbf{n}}\hat{\mathbf{r}})^2 - 1]\hat{\mathbf{n}} \right\}$$

with unit vectors $\hat{\mathbf{n}}$ and $\hat{\mathbf{r}}$ as defined in eqn (3b). The constants $\kappa_{2,3}$ are determined by the swimmer's geometry and read

$$\kappa_2 = \frac{9}{32} \frac{\xi_R^2 - \xi_F^2}{A\ell}, \quad \kappa_3 = \frac{51}{56} \left(\frac{\ell}{A} \right)^2 \quad (28)$$

The quadrupole coefficient is always positive, $\kappa_3 > 0$, but we can have either $\kappa_2 > 0$ (extensile ‘pusher’), $\kappa_2 = 0$ (symmetric quadrupolar swimmer) or $\kappa_2 < 0$ (contractile ‘puller’), depending on the choice of the oscillation amplitudes $\xi_{R,F}$. It is important to note, however, that the geometric restriction $\ell > 2A + \xi_R + \xi_F$ implies that $\kappa_2 \ll \kappa_3$. Consequently, the quadrupolar κ_3 -term effectively dominates the flow field (27) unless one considers unreasonably large distances.¹³ This is illustrated in Fig. 7 which shows the normalized flow field $\hat{v} := \mathbf{v}/|\mathbf{v}|$ from eqn (27) and also its projection onto the unit vector $\hat{r}(t)$ for $\kappa_2 > 0$, $\kappa_2 = 0$, and $\kappa_2 < 0$, respectively.

Tracer motion in the deterministic limit. – Based on eqn (27) it is again possible to derive an analytic estimate for the mean tracer trajectory. To this end, we consider initial conditions with $\hat{\mathbf{n}} = (1, 0, 0)$ as depicted in Fig. 1 and make use of the approximation (21), which holds in the far-field scattering limit where eqn (27) is valid. Integrating the equations of motion (2a) for $D_0 = 0$, we find that the trajectory of the tracer particle in the ($z = 0$)-plane is given by $\mathbf{x}(t) = (x(t), y(t), 0)$, where

$$x(t) \approx -\kappa_2 A \left\{ \frac{A(2X_0^2 + Y_0^2)}{(X_0^2 + Y_0^2)^{3/2}} - \frac{A[2X(t)^2 + Y_0^2]}{[X(t)^2 + Y_0^2]^{3/2}} \right\} + \kappa_3 A \left\{ \frac{A^2 X_0(2X_0^2 - Y_0^2)}{(X_0^2 + Y_0^2)^{5/2}} - \frac{A^2 X(t)[2X(t)^2 - Y_0^2]}{[X(t)^2 + Y_0^2]^{5/2}} \right\} \quad (29a)$$

$$y(t) \approx -\kappa_2 A \left\{ \frac{AX_0 Y_0}{(X_0^2 + Y_0^2)^{3/2}} - \frac{AX(t) Y_0}{[X(t)^2 + Y_0^2]^{3/2}} \right\} + \kappa_3 A \left\{ \frac{A^2(2X_0^2 - Y_0^2) Y_0}{(X_0^2 + Y_0^2)^{5/2}} - \frac{A^2[2X(t)^2 - Y_0^2] Y_0}{[X(t)^2 + Y_0^2]^{5/2}} \right\} \quad (29b)$$

Note that the dipolar κ_2 -contributions are formally equivalent to the result (22) for the 2-sphere swimmer, but with V and κ_2 now determined by the geometry of the 3-sphere swimmer. Letting $t \rightarrow \infty$ we find that asymptotically

$$x(t) \rightarrow -\kappa_2 A \left[\frac{A(2X_0^2 + Y_0^2)}{(X_0^2 + Y_0^2)^{3/2}} \right] + \kappa_3 A \left[\frac{A^2 X_0(2X_0^2 - Y_0^2)}{(X_0^2 + Y_0^2)^{5/2}} \right], \quad (30a)$$

$$y(t) \rightarrow -\kappa_2 A \left[\frac{AX_0 Y_0}{(X_0^2 + Y_0^2)^{3/2}} \right] + \kappa_3 A \left[\frac{A^2(2X_0^2 - Y_0^2) Y_0}{(X_0^2 + Y_0^2)^{5/2}} \right] \quad (30b)$$

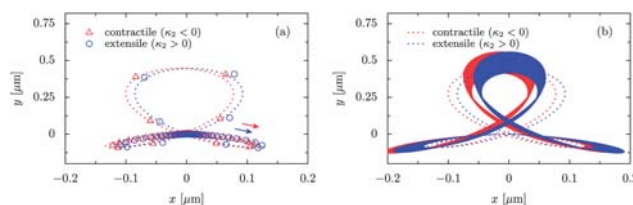


Fig. 8 Deterministic tracer scattering by a (quasi)-quadrupolar 3-sphere swimmer. In the deterministic limit $D_0 = 0$, the tracer trajectories converge to closed loops if the force-free 3-sphere swimmer starts sufficiently far away from the tracer, $X_0 \rightarrow -\infty$. The dotted lines in either diagram represent the analytical estimate from eqn (29). (a) Results from the stroke-averaged dynamics for the time interval $[0, 55\text{s}]$. The tracer particle starts at $\mathbf{x}(0) = \mathbf{0}$ and the swimmer at $X_0 = -150A$, $Y_0 = 10A$. Symbols were obtained by numerically integrating eqn (2a) for $D_0 = 0$ using the averaged flow field (27). (b) Results from the corresponding time-resolved simulation for the same time interval and same initial conditions for the geometric center of the swimmer. The tracer oscillates due to the periodicity of the swimming stroke. Swimmer parameters: $\ell = 10\mu\text{m}$, $A = 0.2\ell$, $\omega = 10^3\text{s}^{-1}$, $\Delta\phi = \pi/2$, which results in $V \approx 12\mu\text{m/s}$, $\kappa_2 \approx \pm 0.04$, $\kappa_3 \approx 22$. Tracer radius: $a_0 = 1\mu\text{m}$. Simulation time step: $\Delta t = 2.2 \times 10^{-7}\text{s}$.

which implies that the tracer particle is displaced by a finite distance due to the effective short-range interaction with $\alpha \geq 2$. Eqn (30) predict that, if the swimmer starts very far away, corresponding to the limit $X_0 \rightarrow -\infty$, the tracer returns to its initial condition $\mathbf{x}(0) = \mathbf{0}$, thus forming a closed loop in the ($z = 0$)-plane. This is similar to our previous result (23) for the 2-sphere dipolar swimmer. However, comparing with Fig. 5 (a), the shape of the loop in Fig. 8 (a) differs significantly, because the flow field (27) of the 3-sphere swimmer is dominated by the quadrupolar κ_3 -contribution (for the initial conditions considered).

The analytical estimate (29) is based on the stroke-averaged field and it is interesting to compare with simulations for the corresponding time-resolved swimmer. The results for the latter case are depicted in Fig. 8 (b). Due to the oscillations of the swimmer's legs, the tracer particle performs an oscillatory motion around its mean trajectory. The relative magnitude of the oscillations is bigger than in the dipolar 2-sphere swimmer case, since the effective quadrupolar flow field of the 3-sphere swimmer decays more rapidly, resulting in a smaller absolute loop-size at similar initial conditions and swimmer speeds. As evident from Fig. 8, the stroke-averaged result (29) captures the main features of the mean tracer motion in the time-resolved flow field but there is a quantitative difference of about 20 to 30 percent. However, we observe that, asymptotically, the time-resolved tracer trajectory approximately returns to its initial position, if the swimmer starts sufficiently far from the tracer particle.

Brownian motion effects.— When Brownian motion is taken into account, corresponding to $D_0 > 0$ in eqn (2a), individual tracer trajectories may differ strongly from each other. As for the 2-sphere dipolar swimmer, loop-shaped scattering patterns can be reconstructed by averaging over a tracer ensemble with identical initial conditions. Fig. 9 (a) and (b) show mean tracer trajectories obtained by averaging over 1000 sample trajectories. We used the same swimmer parameters as in Fig. 8, but the swimmer was started closer to the tracer at $X_0 = -10A$. The

simulation time per run was limited to 11s, as this corresponds roughly to the time scale during which an isolated alga performs a quasilinear motion.⁷ The statistical error bars in Fig. 9 illustrate the sample standard deviation and were divided by $10 \times \sqrt{t}$ for better visibility. Prior to this rescaling the length of the error bars agreed well with the value $\sqrt{2D_0 t}$ expected theoretically. In both Fig. 9 (a) and (b), we notice a small, systematic drift of the mean Brownian trajectories compared to the corresponding deterministic trajectories (unfilled symbols) and the analytic estimate (dotted lines). The shift occurs in the direction of the swimmer motion and is probably caused by a noise-induced Stokes drift²⁰ and an additional, noise-induced bias due to the gradients of the flow field.

IV. Numerical methods

One of our objectives was to compare the tracer dynamics in the stroke-averaged and explicitly time-dependent flow fields of dipolar and quadrupolar model swimmers. For this purpose, we focussed on multi-sphere swimmer models that can be implemented numerically in Brownian dynamics simulations.^{16,17,21,22}

The time-resolved, 'microscopic' dynamics of the 2-sphere swimmer was computed numerically by using a spring-based model.¹⁷ Within this approach, the two spheres are linked by a harmonic spring (stiffness k_0) with periodically varying equilibrium length $L(t)$ determined by eqn (16). Compared to the implementation in ref. [17], the only technical difference arises because our dipolar 2-sphere swimmer is characterized by an oscillating sphere radius, leading to time-dependent Stokes friction coefficients $\gamma_i(t) = 6\pi\eta A_i(t)$, $i = 1, 2$. If the stiffness parameter k_0 of the spring model is chosen large enough, the swimmer essentially behaves like a shape-driven swimmer (in our simulations we fixed $k_0 = 0.001 \text{ kg/s}^2$).

The time-resolved microscopic dynamics of the linear 3-sphere swimmer can be implemented in a similar manner.¹⁶ Analogous to the 2-sphere swimmer case, two neighboring spheres (constant radius A) are connected by a time-dependent harmonic spring (the 'leg') with the same value of the stiffness parameter k_0 as above. Each spring has an oscillating equilibrium length given by eqn (24). The velocity field acting on the tracer and the hydrodynamic interactions between the spheres were calculated using the Rotne-Prager-Yamakawa-Mazur tensor.^{23–27}

Upon adopting the same swimmer parameters for both the microscopic and the averaged model, one finds that the average swimmer speed measured in the microscopic simulations agrees well with the analytical estimates from eqn (19) and (26), respectively. We also compared the Lagrangian net fluid flow, which was obtained from the time-resolved simulations by tracking a grid of non-interacting tracer particles over a stroke period $[t, t + 2\pi/\omega]$. The dipolar and quadrupolar flow field structures obtained by this method were found to be identical to those from eqn (20) and (27) depicted in Fig. 4 and 7.

The equations of motion for both swimmer and tracer were numerically integrated with a two-step Heun integrator using Nvidia's CUDA toolkit. The simulations for the time-resolved model were performed on a consumer-level GTX 275 GPU embedded in an Intel i860 PC running Gentoo Linux. The GPU-based parallel computation of sample trajectories in the case of Brownian tracer particles leads to a considerable speed-up (up to

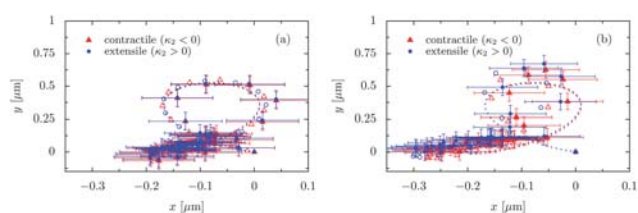


Fig. 9 Brownian tracer scattering by a (quasi-)quadrupolar 3-sphere swimmer. For $D_0 > 0$ loop-like scattering patterns can be recovered by averaging over many sample trajectories with identical initial conditions $\mathbf{x}(0) = \mathbf{0}$. (a) Results for the stroke-averaged dynamics obtained by numerically integrating eqn (2a) with $D_0 = 0.22 \mu\text{m}^2/\text{s}$. (b) Results from the corresponding time-resolved simulations. The filled symbols in both figures were obtained by averaging over 1000 sample trajectories, unfilled symbols show the results of simulations with $D_0 = 0$, and dotted lines represent the analytic estimate from eqn (29). Statistical error bars correspond to the sample standard deviation, divided by $10 \times \sqrt{t}$ for better visibility. Prior to rescaling the length of the error bars agreed with the theoretically expected value $\sqrt{2D_0 t}$. Compared to Fig. 8, we used the same swimmer parameters but the swimmer was started nearer to the tracer at $X_0 = -10A$ and sample trajectories were recorded for the shorter interval $t \in [0, 11\text{s}]$. This explains why the loops are not fully closed.

a factor of a few hundreds) compared with a conventional un-parallelized CPU-based implementation.²⁸

V. Summary & discussion

We have studied the hydrodynamic scattering of a tracer particle by different types of model swimmers. We showed, both analytically and numerically, that scattering by a force-free swimmer may lead to quasi-closed, loop-shaped tracer trajectories. The shapes and orientations of the loops are a signature of the properties of the stroke-averaged flow field. A detailed comparison with the time-resolved scattering dynamics implies that a time-averaged description is sufficient to capture the main features of swimmer-tracer scattering. Our analysis has focussed on two specific 2-sphere and 3-sphere swimmer models that are analytically tractable and can be implemented numerically. However, the result (29) is generic; it holds for the large class of low Reynolds number swimmers that generate a dipolar or quadrupolar flow as given in eqn (27).

We have also compared the scattering due to swimmers to that resulting when a colloid is pulled past a tracer. This allowed us to demonstrate the role played by the range of the interactions between the scatterer and the tracer. For interactions decaying as $\sim |r|^{-\alpha}$, the tracer is slowly dragged to infinity by the particle for the colloidal case $\alpha = 1$ (within the zero Reynolds number approximation), whereas its displacement remains finite for scattering by a force-free swimmer with $\alpha \geq 2$.

We conclude the paper by addressing potential experimental realizations and by commenting on generalizations. The 3-sphere swimmer considered in the last part of the paper could possibly be realized in practice by adapting the experimental setup of Leoni *et al.*,⁸ who constructed a colloidal linear 3-sphere pump using optical tweezers, to mimic a self-motile, force-free swimmer. With regard to hydrodynamic scattering experiments, an advantage of artificially created colloidal microswimmers lies in the fact that one could tune the fluid viscosity to suppress Brownian motion effects in the tracer dynamics. In the case of a colloidal 3-sphere swimmer one should expect to observe loops that are shaped similar to those in Fig. 8.

In general, Brownian motion can obscure individual tracer trajectories, but our analysis shows that averaging over many trajectories may allow one to reconstruct the loops even from noisy data. This suggests that such patterns could also be studied in biophysical experiments similar to those of Leptos *et al.*⁶ These authors investigated how the diffusion of (an ensemble of) tracer particles in water is affected by the presence of self-motile unicellular *Chlamydomonas reinhardtii* algae. Indeed loop-shaped tracer trajectories (or, at least, segments thereof) have already been observed in their experiments, see inset of Fig. 1(c) in ref. [6]. By systematically analyzing the trajectories of individual tracer particles in a sufficiently large, dilute suspension of algae, one could achieve the required sample size to reconstruct the exact structure of the loops and thus infer details about the fluid flow generated by the microorganisms.

Lastly it is plausible to assume that an improved understanding of the underlying, elementary swimmer-tracer scattering processes may eventually help to model quantitatively the

anomalous diffusive behavior of tracer particles in dilute, active suspensions.⁶ The aim would be to derive an analytic expression for the time-dependent position probability density function of a tracer particle by averaging a representative trajectory, resulting from a superposition of the flow field contributions from many algae, over a set of suitably chosen random initial configurations. However, the averaging procedure is both mathematically and computationally demanding; we hope to tackle this problem in future work.

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References

- 1 H. C. Berg, *Phys. Today*, 2000, **53**, 24–29.
- 2 A. Sokolov, I. S. Aranson, J. O. Kessler and R. E. Goldstein, *Phys. Rev. Lett.*, 2007, **98**, 158102.
- 3 M. F. Copeland and D. B. Weibel, *Soft Matter*, 2009, **5**, 1174–1187.
- 4 Z. Gitai, *Curr. Opin. Microbiol.*, 2009, **12**, 341–346.
- 5 K. Drescher, K. C. Leptos, I. Tuval, T. Ishikawa, T. J. Pedley and R. E. Goldstein, *Phys. Rev. Lett.*, 2009, **102**, 168101.
- 6 K. C. Leptos, J. S. Guasto, J. P. Gollub, A. I. Pesci and R. E. Goldstein, *Phys. Rev. Lett.*, 2009, **103**, 198103.
- 7 M. Polin, I. Tuval, K. Drescher, J. P. Gollub and R. E. Goldstein, *Science*, 2009, **325**, 487–490.
- 8 M. Leoni, J. Kotar, B. Bassetti, P. Cicuta and M. C. Lagomarsino, *Soft Matter*, 2009, **5**, 472–476.
- 9 R. Dreyfus, J. Baudry, M. L. Roper, M. Fermigier, H. A. Stone and J. Bibette, *Nature*, 2005, **437**, 862–865.
- 10 P. Tierno, R. Golestanian, I. Pagonabarraga and F. Sagues, *J. Phys. Chem. B*, 2008, **112**, 16525–16528.
- 11 C. M. Pooley, G. P. Alexander and J. M. Yeomans, *Phys. Rev. Lett.*, 2007, **99**, 228103.
- 12 R. Golestanian and A. Ajdari, *Phys. Rev. E*, 2008, **77**, 036308.
- 13 G. P. Alexander, C. M. Pooley and J. M. Yeomans, *J. Phys.: Condens. Matter*, 2009, **21**, 204108.
- 14 G. P. Alexander and J. M. Yeomans, *Europhys. Lett.*, 2008, **83**, 34006.
- 15 E. Lauga and D. Bartolo, *Phys. Rev. E*, 2008, **78**, 030901(R).
- 16 J. Dunkel and I. M. Zaid, *Phys. Rev. E*, 2009, **80**, 021903.
- 17 V. B. Putz, J. Dunkel and J. M. Yeomans, *Chem. Phys.*, 2010, DOI: 10.1016/j.chemphys.2010.04.025, in press.
- 18 E. M. Purcell, *Am. J. Phys.*, 1977, **45**, 3–11.
- 19 A. Najafi and R. Golestanian, *Phys. Rev. E*, 2004, **69**, 062901.
- 20 K. M. Jansons and G. D. Lythe, *Phys. Rev. Lett.*, 1998, **81**, 3136–3139.
- 21 S. van Teeffelen, U. Zimmermann and H. Löwen, *Soft Matter*, 2009, **5**, 4510–4519.
- 22 J. Brady and G. Bossis, *Annu. Rev. Fluid Mech.*, 1988, **20**, 111–157.
- 23 J. Rotne and S. Prager, *J. Chem. Phys.*, 1969, **50**, 4831–4837.
- 24 H. Yamakawa, *J. Chem. Phys.*, 1970, **53**, 436–443.
- 25 C. W. Oseen, *Neuere Methoden und Ergebnisse in der Hydrodynamik*, Akademischer Verlag, Leipzig, 1927.
- 26 J. Happel and H. Brenner, *Low Reynolds Number Hydrodynamics*, Prentice-Hall, Inc., Englewood Cliffs, N.J., 1965.
- 27 P. Mazur, *Physica*, 1982, **110A**, 128–146.
- 28 M. Januszewski and M. Kostur, *Comput. Phys. Commun.*, 2010, **181**, 183–188.