**Regular Article - Living Systems** 



# Modeling straight and circle swimmers: from single swimmer to collective motion

Francesco Michele Ventrella<sup>1,a</sup>, Guido Boffetta<sup>1</sup>, Massimo Cencini<sup>2,3</sup>, and Filippo De Lillo<sup>1</sup>

<sup>1</sup> Dipartimento di Fisica and INFN, Università degli Studi di Torino, Via P. Giuria 1, 10125 Torino, Italy

 $^2$ Istituto dei Sistemi Complessi, CNR, via dei Taurini 19, 00185 Rome, Italy

<sup>3</sup> INFN, Sezione di Roma 2 Tor Vergata, Rome, Italy

Received 25 July 2024 / Accepted 26 October 2024

© The Author(s), under exclusive licence to EDP Sciences, SIF and Springer-Verlag GmbH Germany, part of Springer Nature 2024

**Abstract** We propose a simple numerical model for the motion of microswimmers based on the immersed boundary method. The swimmer, either pusher or puller, is represented by a distribution of point forces corresponding to the body and the flagellum. We study in particular the minimal model consisting of only three beads (two for the body and one for the flagellum) connected by rigid, inextensible links. When the beads are collinear, standard straight swimming is realized and, in the absence of propulsion, we demonstrate that the model recovers Jeffery's equation for a thin rod. Conversely, by imposing an angle between body and flagellum the swimmer moves on circular orbits. We discuss how two swimmers, in collinear or non-collinear geometry, scatter upon encounter. Finally, we explore the dynamics of a large number of swimmers reacting to one another only via hydrodynamic interactions, and exemplify their complex collective dynamics in both straight and circular swimmers.

# 1 Introduction

The study of motility in swimming animals and microorganisms is a captivating subject in the biological realm, encompassing various aspects, such as feeding, reproduction and prey-predator interactions [1,2] with potential applications to biomedicine [3]. Additionally, it extends to the field of biological-inspired intelligent navigation [4,5]. Moreover, in recent years, a growing amount of research has focused on wet active matter [6]. i.e. dense suspensions of swimmers moving in a viscous fluid where the hydrodynamic disturbances are a key mode of interaction. Consequently, the dynamics of a single swimmer becomes the focal point of numerous experimental [7-10], theoretical [11], and numerical investigations [12–16]. The overarching goal is to model the dynamics of a single swimmer in its environment and understand how the interaction of these organisms influences global behavior and the background flow field, leading to collective organized motion [16-20].

Modeling self-propelled bodies can be broadly categorized based on the streamlines they produce around them as "pushers" or "pullers" [11]. Spermatozoa and some bacteria like *E. coli*, which propel via (single or bundled) flagella pushing the fluid away along the propulsion axis and drawing it in from the sides, are typical examples of pushers. Many biflagellates, such as microalgae like *Chlamydomonas*, which draw the

<sup>a</sup>e-mail: francescomichele.ventrella@unito.it (corresponding author) fluid inwards along the propulsion axis and ejected it to the sides, are pullers. Direct numerical simulations are crucial to understand swimmer-swimmer and swimmer-fluid interactions. Several models, with different degrees of complexity, have been developed, including the boundary integral method for ellipsoidal swimmers [21,22], simple dumbbell models [23–27], Stokesian dynamics of 'squirmers' propelled by a surface slip velocity [19,28–31], immersed boundary (IB) method [32–35], penalty methods [16] and the method of regularized Stokeslets for non-interacting swimmers [36–38].

This paper aims at proposing a swimmer model based on immersed boundary methods. The IB method [39], initially developed to simulate blood flows into the heart, has found applications in various biological fluid dynamics problems [40-44], including animal locomotion [45, 46]. In essence, the method treats the elastic material as part of the fluid: body motion is obtained by interpolating the forces due to fluid stress onto a set of points representing the surface of the immersed body, and the body feedback on the fluid is applied by using the same interpolation method. This allows the straightforward application of Navier–Stokes (NS) solvers to complex flow geometries without the constraint of a boundary-conforming grid, which is valuable especially in the case of biological problems, where non-static walls or bodies are the norm. In our case, the NS equations are solved using a standard pseudospectral solver [47–50] on a regular, triple-periodic grid, while each swimmer is represented by as few as three

Eur. Phys. J. E (2024)47:65

Lagrangian points whose geometry is prescribed by the internal forces. Two kinds of swimmer will be considered: a straight-swimming model in which the beads are in a line and, in a still fluid, move in a straight line with a stationary velocity proportional to a fixed propulsion force, also parallel to the swimmer itself; a model in which the flagellum and the body are at a constant angle, which at stationarity swims in a closed, circular trajectory. We will call the second model a *circle swimmer*, based on previous literature [51–55].

The paper is structured as follows. In Sect. 2, we present the model and its numerical implementation, including a series of preliminary studies needed to set parameters and prove the robustness of the method. Sections 3 and 4 present the numerical results for single swimmers and a pair of swimmers in the straight and circular swimming mode, respectively. In Sect. 5 we present a preliminary exploration of the dynamics of a large number of swimmers and of how their collective organization changes when passing from straight to circular swimmers. The appendices present some more technical material. Appendix A describes the Stokeslets solution used to fit the beads radius from the numerical simulations. Appendix B details the way inextensibility and rigidity are ensured in the model, while Appendix C presents an analytical derivation of the dynamics of the swimmer in the absence of propulsion, demonstrating that it behaves as an infinitely elongated rod.

# 2 The immersed boundary method for a microswimmer

We consider a simple swimmer model consisting in a body and a flagellum. Following [27, 56] both the body and the flagellum are represented via a linear distribution of spherical beads connected by inextensible rods. Flagellum dynamics is not directly modeled and the effects of propulsion are taken into account via localized forces applied to the fluid. The swimmer's body and flagellum are connected by inextensible rods whose configuration is held constant by internal forces, making the swimmer's shape rigid and inextensible. We will consider both the case of straight swimmers, in which the flagellum is parallel to the body, and that of circle swimmers, in which flagellum and body are at a fixed angle, causing the swimmer to move on a curved trajectory. At each bead, a point force acts on the fluid. The nature of the forces acting along the body differs from those along the flagellum [35]. The body is considered as a rigid structure immersed in the fluid, along which no-slip conditions are assumed for the fluid velocity. The no-slip conditions are numerically enforced with a strategy derived from the IB methods, which will be described shortly. As a consequence, the body exchanges momentum with the fluid through viscous interaction, with no further modeling needed. On the contrary, the flagellum beads are not subject to no-slip conditions: they are instead used to apply the propulsive force onto the fluid, while momentum conservation is guaranteed by applying an opposite force on the beads themselves and, thanks to rigidity of the rods, to the whole swimmer.

The simplest bead-based swimmers proposed are made of two beads, i.e. one for the body and one for the flagellum [27]. As discussed above, the flagellum bead is not directly influenced by fluid velocity. It follows that a two-beads swimmer, with only one affected by the flow, is unaffected by velocity gradients along its body and, consequently, cannot behave as a passive rod in limit of vanishing propulsion. The minimal swimmer must therefore have at least two beads with no-slip boundary condition to describe the body. In principle, one bead is sufficient to describe the flagellum. It was shown that, if the same number of beads are used for the body and the flagellum, the velocity field surrounding the swimmer in steady motion is qualitatively similar to that produced by a force doublet [27]. In the following we will consider the simpler threebead swimmer model, in analogy to previous theoretical [25] and numerical works [23, 26], which studied similar models with slightly different approaches. One of the novelties of the present paper is the possibility to have curved trajectories, when the beads are not collinear. In perspective, one can dynamically change the bodyflagellum geometry allowing for controlling the swimming direction. The latter property can be exploited to model the dynamics of microrobots to be employed, eg., in biomedical applications [3, 57] Fig. 1a represents a sketch of the three-sphere model for a pusher. The flagellum bead is labeled as bead 1. The force acting on it is the propulsion force per unit mass  $\mathbf{f}_p$ . This force is considered as fixed in modulus and parallel to the flagellum rod connecting beads 1 and 2. The inextensibility of the connecting rods implies that a similar force is applied to the body beads so that, in an otherwise still fluid, the resulting movement relative to the fluid produces on the body beads two drag forces, denoted as  $\mathbf{f}_{IB}$ in the figure, in the opposite direction. Equal and opposite forces (indicated in gray) are applied to the fluid in the corresponding positions and guarantee momentum conservation. The model for pullers (Fig. 1b) is obtained by reversing  $\mathbf{f}_p$  relative to the body. A generic, non-collinear configuration is shown in Fig. 1c. We will show in Sect. 4 that when the flagellum is at a fixed, nonzero angle with the body, the swimmer moves on a circular trajectory. For this reason we will refer to this case as a circle swimmer [51-55].

#### 2.1 The numerical implementation

As outlined above, the swimmer is described in terms of N spheres with centers at the points  $\mathbf{x}_i$ , with i = 1, ..., N. In what follows we will consider the cases N = 2and N = 3 and assume that the 3D Eulerian problem of the evolution of the velocity field  $\mathbf{u}(\mathbf{x}, t)$  is discretized in space on a uniform grid with grid spacing  $h_x = h_y =$  $h_z = h$  equal along all the axes. If the radius of the particles is comparable with h we can assume that the



**Fig. 1** Schematic view of the model swimmer. **a** Threesphere model for a pusher. The red vector  $\mathbf{f}_p$  is the propulsion force per unit of mass (i.e. acceleration) that allows the motion. The blue vector is the acceleration due to the no-slip condition. The gray arrows are the forces exerted by

3D Navier–Stokes equations take the form

$$\frac{D\mathbf{u}}{Dt} = -\frac{\nabla p}{\rho_0} + \nu \Delta \mathbf{u} + \sum_{i=1}^{N} \frac{\mathbf{F}_i}{\rho_0 h^3} \Phi(\mathbf{x} - \mathbf{x}_i), \quad (1)$$

where  $\rho_0$  is the fluid density,  $\nu$  the kinematic viscosity,  $\mathbf{F}_i$  is the force applied on the fluid by the sphere in  $\mathbf{x}_i$ . As typical with immersed boundary methods, the forces are regularized by spreading their effects on the nearby grid points with the function  $\Phi(\mathbf{x})$ , which has the following properties:  $\Phi(\mathbf{x}) \geq 0$ ;  $\Phi(\mathbf{x}) = 0$  for  $|\mathbf{x}| > nh$ , with n not necessarily integer, i.e. it has support over a finite stencil surrounding the particle; normalization, i.e.  $\sum_{\mathbf{x} \in grid} \Phi(\mathbf{x}) = 1$  (sum over the points  $\mathbf{x}$  of the numerical discretized domain) [41,43]. Following [32] we use

$$\Phi(\mathbf{x}) = \begin{cases} \frac{1+\sqrt{-3|\mathbf{x}|^2+1}}{3}, & \frac{|\mathbf{x}|}{h} < \frac{1}{2} \\ \frac{5-3|\mathbf{x}|-\sqrt{-3(1-|\mathbf{x}|)^2+1}}{6}, & \frac{|\mathbf{x}|}{h} \in \left[\frac{1}{2}, \frac{3}{2}\right] \\ 0, & \text{otherwise.} \end{cases}$$
(2)

The Lagrangian problem associated with the motion of the swimmer requires the knowledge of the fluid velocity  $\mathbf{u}(\mathbf{x}_i)$  at the position of each bead, which is defined as a weighted average of the fluid velocity surrounding the bead

$$\mathbf{u}(\mathbf{x}_i) = \sum_{\mathbf{x} \in grid} \mathbf{u}(\mathbf{x}) \Phi(\mathbf{x} - \mathbf{x}_i).$$
(3)

For what concerns the forces, as discussed above we consider two kinds of beads, for the flagellum and the body, respectively, whose interactions with the fluid are treated differently. A flagellum bead is characterized by a constant propulsion force contributing an acceleration  $\mathbf{f}_p$  applied on the bead along the flagellum. An equal and opposite force is applied on the fluid to guarantee conservation of momentum. A body bead is instead part of a material boundary along which the natural no-slip condition applies. In line with the IB strategy, each body bead is subjected to the acceleration  $\mathbf{f}_{IB} = \beta(\mathbf{u}(\mathbf{x}_i) - \mathbf{v}_i)$ , where  $\mathbf{v}_i$  is the velocity

the pusher on the fluid. **b** Three-sphere model for a puller. Notice that the position of beads 1,3 is exchanged with respect to panel (**a**). In both cases the swimming direction is from left to right. **c** A generic configuration for a pusher with a nonzero angle  $\phi_0$  between the body and the flagellum

of the *i*-th bead and  $\beta$  is a large, positive numerical parameter. Also in this case a force of opposite sign is applied to the fluid. Such IB forces lead to the reciprocal relaxation, with a characteristic time  $\beta^{-1}$  of bead and fluid velocities to the same values, thus enforcing the no-slip condition. Clearly  $\beta$  affects the relative error on the implementation of the no-slip condition. If the swimmer moves with a constant swimming velocity  $v_s$ in a still fluid the IB forces are the equivalent of the viscous drag forces so one must have  $f_{IB} \simeq v_s/\tau_S$ , with  $\tau_S$  an effective Stokes time of a bead which can be estimated from the parameters obtained with the fitting procedure described below. This implies that  $|\mathbf{u}(\mathbf{x}_i) - \mathbf{v}_i|/v_s \simeq (\tau_S \beta)^{-1}$ .

The resulting equations of motion for a 3-bead swimmer are:

$$\begin{cases} \dot{\mathbf{v}}_1 = f_p \mathbf{n}_1 + \lambda_{12} \mathbf{n}_1 + g \mathbf{t}_1 \\ \dot{\mathbf{v}}_2 = -\lambda_{12} \mathbf{n}_1 + \lambda_{23} \mathbf{n}_2 - \beta \left( \mathbf{v}_2 - \mathbf{u}(\mathbf{x}_2) \right) + g \mathbf{t}_2 \\ \dot{\mathbf{v}}_3 = -\lambda_{23} \mathbf{n}_2 - \beta \left( \mathbf{v}_3 - \mathbf{u}(\mathbf{x}_3) \right) + g \mathbf{t}_3 \end{cases}$$

$$\tag{4}$$

In these equations  $\lambda_{ij}$  denotes the Lagrange multiplier associated with the inextensibility of the rod connecting beads *i* and *j*,  $\mathbf{n}_1$  and  $\mathbf{n}_2$  are unit vectors parallel to the rods and  $g\mathbf{t}_i$  are stiff elastic forces acting normal to the rods and implementing the constraint of fixed angle  $\phi_0$  (see Fig. 1). The individual terms are discussed in details in Appendix B. The evolution of the Eulerian velocity field is realized by means of a standard, fully de-aliased, pseudo-spectral code [49,50]. Although both the model and its integration are fully three-dimensional, in the following, for the sake of simplicity in visualizing the results, we will restrict the dynamics to the (x, y) plane by a suitable choice of the initial conditions for the swimmers.

The rhs of both (1) and (4) have the dimension of forces per unit mass. As detailed above, each force  $\mathbf{F}_i$  in the last term of (1) is due to conservation of momentum and is the opposite of forces acting on the beads and causing the propulsion acceleration or the relaxation to fluid velocity. If we denote with  $\mathbf{f}_i$  one of those Lagrangian accelerations in (4), one must have  $\mathbf{F}_i = -m\mathbf{f}_i$  where m is the bead's mass. For a spherical

bead we can write

$$\frac{\mathbf{F}_i}{\rho_0 h^3} = -\mathbf{f}_i \frac{\rho}{\rho_0 h^3} \frac{4}{3} \pi R^3 \equiv -\mathbf{f}_i c, \tag{5}$$

where  $\rho$  and R are the bead's density and radius, respectively, and  $c = \frac{4}{3}\pi \frac{\rho}{\rho_0} \left(\frac{R}{h}\right)^3$  determines the relative intensity of Lagrangian acceleration and feed-back on the fluid. For simplicity, in the following, we consider neutrally buoyant swimmers only ( $\rho = \rho_0$ ).

#### 2.2 Fixing the numerical parameters

At Re  $\ll 1$  an approximate analytical solution for the flow can be easily obtained and used to fix the numerical parameters. We do so by considering the simpler case of a pusher composed by two beads connected by a rigid, inextensible rod (see Fig. 2a). One of those beads represents the flagellum and one the body and this configuration produces two opposite forces on the flow and, therefore, an approximate force dipole field which decays as  $r^{-2}$  in space [7]. Let 1 and 2 be the index of the flagellum and body beads, respectively, in this case the equations of motion (4) simplify to

$$\begin{cases} \dot{\mathbf{v}}_1 = f_p \mathbf{n} + \lambda \mathbf{n} \\ \dot{\mathbf{v}}_2 = -\lambda \mathbf{n} - \beta (\mathbf{v}_2 - \mathbf{u}(\mathbf{x}_2)), \end{cases}$$
(6)

where  $\mathbf{n} = (\mathbf{x}_2 - \mathbf{x}_1)/|\mathbf{x}_2 - \mathbf{x}_1|$  and  $\lambda$  is the Lagrange multiplier associated with inextensibility.

The value of c in (5) can be fixed by using the (approximate) analytical solution of the Stokes flow around the two spheres. Let L represent the distance between the spheres moving at velocity  $v_s$ . We consider the swimmer Reynolds number Re =  $v_s L/\nu = 10^{-2}$ and we compute the longitudinal component of the fluid velocity along the axis of the swimmer. Periodicity of the domain is taken into account by considering the images in the three directions. Figure 2b shows the comparison between the analytical (discussed in Appendix A) and numerical results, which gives the fit  $c \simeq 5.58$ , corresponding to  $R \simeq 1.1h$ . The analytical solution in the regions within the effective radius of the beads (the gray regions in Fig. 2b) is excluded from the comparison since it is singular and unphysical. The numerical solution, on the other hand, is well behaved also in those regions. We have tested the consistency of the definition of c by verifying that it is not affected by the resolution of the grid (up to  $256^3$  points) and it is also independent on Re when  $\text{Re} \lesssim 1$ .

# 3 Numerical results for rectilinear swimmers

Here we focus on the case of rectilinear swimmers composed by three spheres connected by two rods of length L. In Fig. 1 bead 1 represents the flagellum, while beads 2 and 3 define the body. The whole system is considered rigid and inextensible. Inextensibility is enforced via Lagrange multipliers while bending rigidity is guaranteed via a stiff spring, which is sufficient to prevent oscillations. The length of the swimmer is defined as the distance L between the two beads of the body, thus neglecting the presence of the flagellum. Therefore, the Reynolds number is defined as in the case of two-sphere model Re =  $v_s L/\nu$ .

#### 3.1 Single swimmer

In Fig. 3 we show the results of a numerical simulation of a single 3-bead swimmer moving with constant velocity, at  $Re = 10^{-2}$ , in an otherwise quiescent fluid. In Fig. 3a, a 2D section of the 3D domain containing the pusher is shown. At the stationary state, from Eq. (4)one must have  $\mathbf{f}_p = -\beta(\mathbf{v}_2 - \mathbf{u}(\mathbf{x}_2)) - \beta(\mathbf{v}_3 - \mathbf{u}(\mathbf{x}_3))$ . In this case the distribution of forces among the three spheres is less trivial than the completely symmetric case of the 2-sphere model. Figure 3a shows that the velocity produced by propulsion around the flagellum bead is, in agreement with the above relation, larger in magnitude than the disturbance produced by viscous drag around each of the body beads and it is comparable with the sum of the velocity field produced by the others, according to the rigidity condition and to the conservation of momentum. Further details on the implementation of inextensibility and rigidity can be found in Appendix B. While the far field properties of the flow are dominate by the pusher/puller nature of the swimmer, the differences between our three bead model and other models like the dipole swimmers or squirmers are particularly relevant close to the swimmer itself and therefore can affect short-range hydrodynamic interactions [58].

In Fig. 3c-d the puller dynamics is shown. The results are symmetric with respect to the pusher case, as expected in the very low Re regime. In the case of higher Re, the pusher and puller dynamics should present substantial differences. Indeed this is observed in simulations of our model for Re = O(1). Figure 4 shows the velocity fields produced by a pusher and a puller at  $\text{Re} \simeq 1.6$ . In this case the asymmetry between the two configurations is apparent. It should also be noted that the force applied to the pusher attains the same velocity with a force that is smaller (about 0.7 times) than the one applied to the puller. In other words, at finite Re a pusher swims *faster* than a puller with the same propulsion, at least in this regime. This is consistent with results obtained with other models [27, 59]. We stress that the absence of an analytical benchmark for such values of Re does not allow a quantitative validation of our model in this regime

#### 3.2 Non-motile swimmer

As a preliminary test for the dynamics of the model we consider the case of a swimmer without any propulsive force, i.e.  $\mathbf{f}_p = 0$ , immersed in a steady shear flow. As a



(c)

Fig. 2 a Scheme of a two-sphere pusher. The gray arrows are the forces exerted by the pusher on the fluid. **b** *x*-component of the velocity field along the swimming direction produced by the two-sphere pusher with  $\text{Re} = 10^{-2}$ .

The red line represents the analytical Stokes solution, blue points are the numerical values computed with c = 5.58 with resolution  $64^3$ 





Fig. 3 Velocity field surrounding a 3-bead pusher  $(\mathbf{a}, \mathbf{b})$ and puller  $(\mathbf{c}, \mathbf{d})$  at the stationary state for Re = 0.01. Velocities are rescaled with the constant swimming speed. **a** The color map indicates the amplitude of the velocity, while the arrows (not scaled with amplitude) indicate the local velocity direction. The typical *pusher* configuration (outwards streamlines along the swimmer axis, inwards in the normal direction) can be clearly appreciated. The swimmer is moving to the right. The leftmost white bead represents the flagellum, where propulsion is applied. The corresponding reaction force on the fluid produces an intense velocity perturbation (red region). The black arrow on the right indi-

cates the swimming direction. **b** Plot of the x-component of the velocity field along the swimming direction of a 3-beads swimmer. The numerical solution (blue dots) is compared with the approximate analytical solution (continuous line, see text). Note that, as expected, the fluid field on the tail beads (on the left) is comparable with the sum of the velocity field produced by the others, as a consequence of inextensibility and conservation of momentum. **c**, **d** Same as panels (**a**, **b**) but for a puller. Notice the leading (white) flagellum bead. The clear specular symmetry between the two configurations is due to the time-reversal invariance of the equations at low Re



Fig. 4 Velocity field produced by a a pusher and b a puller at  $\text{Re} \simeq 1.6$ . In contrast to Fig. 3 the two configurations show no clear reflection symmetry, due to the breaking of time reversal symmetry at finite Re

model flow we chose, for numerical convenience, a Kolmogorov flow  $\mathbf{u} = (\cos(z), 0, 0)$  [60, 61]. We will therefore consider a non-motile swimmer initially resting in the (x, z) plane and perpendicular to the flow itself at  $z = 3\pi/2$ , i.e. in the flexus of the flow. As detailed in Appendix C, in the absence of propulsion, i.e. when the flagellum does not play any role, the body of the swimmer should behave as an infinitely thin rod and its dynamics is ruled by Jeffery's equation [62]. Indeed, the equation for the swimming direction  $\mathbf{n}$  (C21) can be written as

$$\dot{\mathbf{n}} = \frac{1}{2}\omega \times \mathbf{n} + \Lambda[\mathbb{S}\mathbf{n} - (\mathbf{n}\mathbb{S}\mathbf{n})\mathbf{n}]$$
(7)

where  $\Lambda$  is the shape parameter ( $\Lambda = 0$  for spheres and  $\Lambda = 1$  for infinitely thin rods) and  $\omega = \nabla \times \mathbf{u}$  is the vorticity. In the configuration described, the flow can be approximated as a homogeneous shear with shear rate  $\sigma = du_x/dz$ . Using a 2D reference system in which the swimming angle is measured from the horizontal direction ( $n_x = \cos \theta$ ,  $n_y = \sin \theta$ ), one can write

$$\dot{\theta} = -\frac{\sigma}{2} [1 + \Lambda (1 - 2\cos^2 \theta)], \qquad (8)$$

where, in our case,  $\sigma = 1$ . If  $\Lambda = 1$ ,  $\theta = 0$  is a marginally stable fixed point. The solution for a rod that starts perpendicular to the shear direction is given by

$$\begin{cases} \theta(t) = \operatorname{arccot}(\sigma t) \\ \theta(0) = \pi/2. \end{cases}$$
(9)

We expect Eq. (9) to describe the motion of a threebead swimmer in a linear shear when the propulsion is switched off. We stress that the flagellum bead can be completely disregarded in this regime.

Figure 5 shows the time evolution of the orientation of a non-motile swimmer compared with the analytical solution (9). The numerical solution is obtained by the integration of a three-bead swimmer placed in the inflection point at  $z = 3\pi/2$ . The numerical result in Fig. 5 is compared with the analytical expression (9)valid for an ideal rod-like particle. The deviations can be quantified by observing that the time it takes for the numerical swimmer to reach 0.1rad is only 10% larger than the theoretical prediction. Such a small difference should be irrelevant when time dependent flows are considered. We conclude that for our model swimmer, a linear shear in a creeping flow regime gives rise to a dynamics that can be described by Jeffery's equation (7) with  $\Lambda = 1$ . This suggests that, for an isolated swimmer in flow that varies on a scale sufficiently larger than the swimmer's body, our model could be substituted with a kinematic model obtained from Jeffery's equations for a rod with a superposed swimming velocity. However, when more than one swimmer is considered, hydrodynamic interactions would not be accounted for by such model. Moreover, if many swimmers are considered, the flow itself would be strongly affected by the swimmers, which could be the main forcing in the fluid as in the case of active turbulence.

#### 3.3 Swimmers interaction

We now consider the interaction between two swimmers and the resulting trajectories. We only consider the effects of hydrodynamic interactions without any additional repulsive potential to account for steric interactions. The latter can be anyway added to the model in straightforward ways. We remark that in our model swimmer there are no physical rods connecting the beads. Therefore, in principle, swimmers can overlap with crossing trajectories. Nevertheless, we find that, if the beads are not too far apart, swimmers feel each other as effective *continuous* bodies, thanks to the flow produced in their motion and overlaps are observed only in very special conditions.



Fig. 5 Comparison between the solution (9) of Jeffery's equation for a rod (formally, an ellipsoid with  $\Lambda = 1$ , dashed line) and numerical data from the 3-beads model (blue dots) without propulsion in a Kolmogorov flow. Numerical simulations are done at resolution  $N = 64^3$  grid points in a cube of size  $2\pi$  for a swimmers of length L = 0.5 with initial orientation  $\theta = \pi/2$ . Inset: zoom of the long-time behavior, see text for a discussion

We start by considering the scattering of two identical swimmers, moving at the same speed, with an incident angle  $\theta_i$ . One example is shown in Fig. 6a with  $\theta_i = \pi/4$ . The scattering is a complex process during which the two swimmers orient temporarily in a parallel direction and finally emerge with a different output angle  $\theta_o$ . In the case of pusher swimmers, the velocity field (see Fig. 3a) causes the flagella to come closer together, turning the swimmers and leading first to the alignment of the swimmers and subsequently to a separation of the directions. The above described phenomenology is consistent to what found in [25, 26] starting from parallel swimmers. For a pair of pullers, the kinematics is qualitatively very similar, except that the hydrodynamics which produces it is opposite to that of pushers, see Fig. 3c. The flagella, which in this case are the first to interact, tend to repel each other, leading to the same kinematics of alignment and subsequent divergence of the trajectories. The exit angle is consequently different in the two cases, as evident from comparing Fig. 6a, b. We remark that the model does not exclude the possibility of observing the overlap between swimmers under certain conditions (for example, in the case of high Reynolds numbers or very large collision angle). The most common case is a superposition of the flagella. This event is not per se problematic because in our model the flagella are not affected by hydrodynamic interactions. We stress that with our method (and at variance with other approaches [26] where the particles have a finite volume which behaves as a second fluid with a large viscosity) the beads are effectively represented as regularized point forces whose effective radius is a numerical parameter used to fit the resulting velocity field. The occasional partial overlap of the force stencils can therefore cause numerical stiffness, by introducing large local forces, but is not necessarily physically

inconsistent. The cases in which also the bodies overlap can be avoided with an effective, short-range repulsion potential. Such potential can take different forms essentially corresponding to steric interactions between the beads or between the bodies (through the definition of an effective shape). We consider here only the effects of hydrodynamic interactions and remark that no numerical instability was observed as a result of the overlap of the tails or the bodies in the case of binary collisions.

# 4 Circle swimmer dynamics

The 3-beads model allows to control the swimming direction in a simple and natural way. Indeed, when the three beads are not in a collinear configuration, the drag on the body together with the propulsion from the flagellum produce a torque that rotates the swimmer. In what follows we will present only results about circle pushers, in which the flagellum bead is the trailing one. As discussed above, puller-like circle swimmers can be obtained by reversing the propulsion. The controlling parameter for the swimmer is the equilibrium angle  $\phi_0$  between the flagellum rod and the body rod. The resulting trajectory of a single swimmer is a circle with a radius  $R_c$  depending on  $\phi_0$ . Clearly in the limit  $\phi_0 \rightarrow 0$  one recovers the original collinear model, with  $R_c \to \infty$ . One should note that when circular trajectories are observed in biological microswimmers, these are due to the swimmer's chirality. The latter results in helical swimming in the bulk and circular trajectories when confined to a surface [51]. A model describing a chiral swimmer would in principle require at least four beads, considering such an extension to the model goes beyond the scope of this paper.

Once the bending angle is set, the rigidity of the swimmer is guaranteed by an elastic force that causes the relative position of the two rods to relax to that angle. This elastic force is implemented in the form of internal forces  $\mathbf{g}_i$ , one for each bead (see Appendix B). Referring to (B9), this means that if a perturbation produces deviations from the equilibrium angle  $\phi_0$  these are compensated by the torques due to the internal forces, bringing the system to the wanted configuration. It is worth noting that Eq. (B9) should produce a harmonic oscillation of the angle  $\phi$  around  $\phi_0$ . These oscillations are damped by viscosity through the no-slip condition on the body beads, thus causing a relaxation to the prescribed angle  $\phi_0$ .

#### 4.1 Circular trajectories of isolated swimmers

Figure 7 shows two examples of circular trajectories produced by circle swimmers with different bending angles, together with the dependence of the radius of the trajectory on  $\phi_0$ . Observing that the segments identifying the body and the flagellum are approximately tangent to the circles described by head and middle beads, respectively, one can tentatively estimate the radii of those circles as  $r_{\text{head}} \sim L/\tan(\phi_0)$ 



Fig. 6 Collision of two identical swimmers starting with a relative angle of  $\pi/4$ . The hydrodynamic interaction between by the body's beads allows the swimmers to scatter without touching each other. **a** Pusher dynamics. The subsequent positions of the swimmers are plotted, left to right, at regular time intervals. The solid arrows indicate the inextensible rod connecting the body beads, while the

and  $r_{\rm mid} \sim L/\sin(\phi_0)$ . The actual radii (see Fig. 7c) are smaller than the estimate (dashed lines) except for  $\phi_0 \sim \pi/2$ , in which case the head is almost stationary ( $r_{\rm head} \sim 0$ ) and the flagellum rotates by remaining approximately tangent to the outer circle ( $r_{\rm mid} \sim L$ ). More complex trajectories can be obtained if we allow the angle to change in time, and this can be used to control the swimming trajectory. We leave the dynamics of active steering for future investigations.

#### 4.2 Swimmers interaction

In analogy with the case of straight swimmers, we studied the interaction of two circle swimmers. The bending angle is fixed at  $\pi/4$  as shown in Fig. 7a. Two different behaviors were observed, depending on the relative initial positions of the swimmers. If the initial separation is large enough, as expected, each swimmer tends to swim on its own curvilinear trajectory without interacting, in some cases after a brief transient characterized by a repulsive interaction. Two examples of this behavior are shown in Fig. 8a, corresponding to different initial conditions. If the initial separation is further decreased (Fig. 8b) the interaction changes qualitatively. After a more complex initial transient, the two trajectories intertwine and start revolving around the same center. It is worth noting that the reciprocal positions of the swimmers are not locked along the orbit but change dynamically in a non-trivial way. In the presence of many swimmers, a random initial configuration can lead one swimmer to decouple from one neighbor (as in Fig. 8a) only to be attracted by another one into forming a strongly coupled pair (as in Fig. 8b). This mechanism could lead to an ordered collective behavior as briefly discussed in the next section.



(b)



dashed lines represent the flagella, connecting the rear body beads to the flagellum beads. Only the body segment is considered as a rigid boundary, on which the no-slip condition is applied for the fluid. **b** Pullers dynamics. The same time series of pushers' case is shown. The interaction in this case produces a smaller output angle due to the different hydrodynamic interaction between the swimmers

# 5 Collective behavior

The numerical method proposed in this work can be easily scaled to a large number of swimmers to study their interaction and the emergence of collective motion. In this section, we consider the evolution of the distributions of hundreds of straight (in the next subsection) and circle swimmers (in the following one).

#### 5.1 Rectilinear swimmers

As first example we considered 500 identical straight pushers initially placed at random positions and directions on a (x, y) plane in the 3D domain. In the absence of perturbations in the z direction, the motion remains planar, thus confirming the accuracy of the numerical integration.

One snapshot of the configuration of the swimmers at late time is shown in Fig. 9. We observe that the distribution is not random any more, with local clusters (or schools) swimming in a parallel direction, similarly to the intermediate state observed in Fig. 6. This configuration is highly dynamical, as different clusters appear and dissolve in time in a statistically stationary condition (see Fig. 9b, c, d). Figure 10 shows the correlation function of the swimming angle as a function of the distance between the swimmers [63]. Being s the unit vector in the swimming direction we define for the case of N swimmers:

$$C(r) = \left\langle \frac{\sum_{ij}^{N} \delta \mathbf{s}_{i} \cdot \delta \mathbf{s}_{j} \delta(\mathbf{r} - \mathbf{r}_{ij})}{\sum_{ij}^{N} \delta(\mathbf{r} - \mathbf{r}_{ij})} \right\rangle$$
(10)

where  $\delta \mathbf{s}_i = \mathbf{s}_i - \frac{1}{N} \sum_i \mathbf{s}_i$  is the deviation of the orientation from the mean,  $r_{ij}$  is the distance between two swimmers and  $\langle \cdot \rangle$  is an ensemble average which in our case was exchanged with a time average, assuming

Fig. 7 Trajectories of isolated swimmers with a constant bending angle. a, **b** Two typical trajectories, with  $\phi_0 = \pi/4$  and  $\phi_0 = \pi/6$ , respectively. The red (blue) lines mark the trajectory of the head-bead (mid-bead). c Dependence of the radii of the trajectories of the head and mid beads (solid lines) on the angle  $\phi_0$  between the flagellum and the body. The results obtained with a simple model (dashed lines, see text) are given for comparison

Fig. 8 Interaction between a pair of circle swimmers. a Two configurations are shown in which after a transient the two swimmers settle onto essentially independent trajectories. **b** Dynamics of two swimmers starting initially very close and nearly parallel. In this case the two trajectories are intertwined and revolve around a common center. Note how the relative positions of the swimmers change during their orbits. The position is rescaled with the rod length between two beads and times are rescaled with the period of the isolated circular trajectory



Deringer



Fig. 9 Panels (a-d): collective behavior of 500 straight pushers in a 2D configuration within a 3D fluid domain. In this figure the flagella are not drawn and each swimmer is colored based on its angle with respect to the x axis, so that parallel swimmers have the same color. The fluid is forced into a chaotic flow by the motility of the swimmers. The resulting velocity fluctuations induce relatively large velocity differences between nearby swimmers which occasionally defeat the repulsive effect of hydrodynamic interactions and cause the bodies to overlap more frequently. The formation of clusters of schools of swimmers sharing the same swim-

ergodicity. The correlation is positive over a distance of the order of the length L. For a large enough number of swimmers the correlation length becomes independent on the number of swimmers. In this dense condition confined on a plane, the occurrence of overlapping swimmers is not uncommon. In a realistic application with the full 3D motion, the overlap would be much more occasional as the mean free path of swimmers would be much larger. Remarkably, even in the case of Fig. 9 we find that the swimmer model does not develop numerical instabilities as a consequence of the close encounters. However, when a similar case is studied for pullers (not shown), the ensuing clustering is much stronger than for pushers [64, 65] and rapidly leads to numerical instabilities due to the overlap of a large number of beads, with their relative force stencils. Clearly in this case a steric repulsion force must be implemented. Steric interactions could likely modify also the correlations (10) and other characteristic of the collective motion.

ming direction is highlighted by the coloring scheme. On the left a 2D snapshot of the whole domain at time  $t \simeq 23$ (rescaled with the typical time in which the swimmer covers its length) is shown. (b), (c) and (d): three zoomed snapshots of the dynamics within the dashed square in panel (a). Panel (b) and (d) are taken at a time interval  $\Delta t = 0.30$ before and after the main panel (corresponding to panels (a) and (c)), respectively. It is here evident that the schools persist several swimmer lengths following the surrounding dynamics

#### 5.2 Circle swimmers

The discussion in the previous section, as well as previous literature [53, 55], suggest that circle swimmers can present interesting collective dynamics. Also in this case we show here only results regarding circle pushers, since pullers tend to undergo strong clustering that requires the implementation of steric interactions. We considered the case of 250 circle pushers (Fig. 11). The collective dynamics in this case is characterized by a transient in which swimmers with an initial condition similar to those observed in Fig. 8a tend to move apart until they intersect other trajectories with which to form a collective circular trajectory, as shown in Fig. 8b. An example of the resulting collective motion is shown in the side panels of Fig. 11. Once swimmers achieve this coupled configuration, the dynamics become rather complex because each orbit is traveled at different and nonconstant speeds. Starting from a configuration where all swimmers are closely packed (Fig. 11b), the flow generated by each pusher accelerates the nearby swimmers, causing a fast rotation and a progressive separa-



Fig. 10 Correlation function of swimming directions C(r) between swimmers separated by a distance r (see text), computed for different numbers of swimmers. The angles of neighboring swimmers are correlated over a distance roughly equivalent to the length L, which is consistent with the clusters shown in Fig. 9. As a comparison, the same observable is shown for random configurations

tion (Fig. 11c, d) of the swimmers along their collective orbit. At later times a packed configuration forms again. This behavior repeats and allows the formation of these structures on the scale of the swimmer. Preliminary observations suggest that, once formed, these structures tend to persist and produce a global configuration characterized by many swimmer vortices (Fig. 11a). Such vortices survive for several orbital periods (estimated via the orbital period of an isolated circle swimmer) and are therefore qualitatively robust, as shown in figure Fig. 11b–d. Quantitative assessment of the persistence of the collective structures as well as their statistical correlations is needed, in order to fully characterize this system, and will be the subject of future investigations focused on the collective motion.

# 6 Conclusions

In this paper we have proposed and analyzed a numerical model based on immersed boundary methods of a minimal swimmer, whose body is modeled by two beads and flagellum represented by a single bead. The model can be used for both pushers and pullers, by simply changing the direction of the applied forces. The choice of two beads, with no slip conditions, for the body make the swimmer to feel the gradient of the velocity field allowing it to be rotated by the flow. In particular, we showed that, when the propulsion is switched off, the



Fig. 11 Collective behavior of 250 turning swimmers in a 2D configuration. The dynamics is characterized by the formation of groups of swimmers that, thanks to the hydrodynamic interaction, pair up to form groups of swimmers that evolve along nearly circular, approximately concentric trajectories. These structures are very robust and survive for several orbits. On the left a 2D snapshot of the whole

domain. On the right three zooms of the dynamics of one structure. The central plot (c) shares the same time of the snapshot on the left and is preceded in time by the snapshot (b) at time  $t \simeq -3T_0$  (in units of the period  $T_0$  of a circular trajectory of the single circle swimmer) and followed by the snapshot (d) at time  $t \simeq +3T_0$ 

swimmer moves approximately according to Jeffery's equations for a thin rod.

When the three beads are collinear the model swimmer display straight swimming, while by maintaining an angle between body and flagellum it swims in circles. We analyzed the close encounters between both straight and circle swimmers showing how hydrodynamic interactions mediated by the solvent fluid cause the two swimmers to scatter. Then we scaled up the system by considering many either straight or circle swimmers and showed that the active suspension can give rise to nontrivial collective motions. For straight swimmers, local alignment can be observed in the presence of the sole hydrodynamic interactions leading to dynamic schools of swimmers swimming in the same directions. Remarkably, interactions between co-rotating circle swimmers lead to the formation of approximately ordered vortices of swimmers, moving on approximately circular trajectories.

The preliminary results on the collective motion of swimmers suggest the directions in which the numerical investigation could be pursued more extensively, also in light of previous results on circle swimmers [53, 55]. In particular, it will be interesting to assess whether and to what extent the structures observed with other model swimmers are model-independent and how the collective dynamics changes with steric interactions. Another interesting direction of investigation is to allow the swimmers to change dynamically their geometry, this can be used to control the swimming direction internally so to the swimmer can steer and direct its motion in a desired direction. Eventually, this can be supplemented by artificial intelligence, e.g. via reinforcement learning [66] so to allow the swimmers to accomplish some single (e.g. reach a target or control dispersion [67–69]) or collective goal [70] (e.g. swimming in schools). These features can be useful to microrobots design in biomedical applications, to model animal interactions, etc.

**Acknowledgements** We thank A. Mazzino and M. Cavaiola for enlightening discussions on the IBM. We acknowledge HPC CINECA for computing resources within the INFN-CINECA Grant INFN24-FieldTurb.

# Author contribution statement

FMV and FDL designed the model and the computational framework. FMV carried out the numerical simulations. GB and MC analyzed the data and verified the methods. All authors discussed the results and contributed to the final manuscript.

**Data availability** Data sets generated during the current study are available from the corresponding author on reasonable request.

# Springer

### Appendix A Stokeslets solution

Let's start by considering a single sphere with a constant speed  $\mathbf{v}$ . The velocity field produced, in the very low Re regime, is described by the Stokes equation and leads to the following solution [71]:

$$\mathbf{u} = \frac{3}{4}R\frac{\mathbf{v} + \hat{\mathbf{r}}(\mathbf{v} \cdot \hat{\mathbf{r}})}{r} + \frac{1}{4}R^3\frac{\mathbf{v} - 3\hat{\mathbf{r}}(\mathbf{v} \cdot \hat{\mathbf{r}})}{r^3}$$
(A1)

where  $\hat{\mathbf{r}}$  is a unit vector pointing from the center of the sphere (origin) to a point in space, r is the distance with respect to the origin and R is the radius of the sphere. The previous equation could be rewritten as:

$$u_{\alpha} = \frac{3}{4} \frac{R}{r} [v_{\alpha} + \hat{r}_{\alpha} (v_{\beta} \hat{r}_{\beta})] + \frac{1}{4} \frac{R^3}{r^3} [v_{\alpha} - 3\hat{r}_{\alpha} (v_{\beta} \hat{r}_{\beta})]$$
  
=  $\frac{1}{4} \left( \frac{3R}{r} + \frac{R^3}{r^3} \right) v_{\alpha} + \frac{3}{4} \hat{r}_{\alpha} (v_{\beta} \hat{r}_{\beta}) \left( \frac{R}{r} - \frac{R^3}{r^3} \right)$   
(A2)

where the Greek subscript stands for spatial components. On the surface of the sphere r = R the no slip condition  $u_{\alpha} = v_{\alpha}$  is enforced. The fluid field around a dumbbell swimmer is approximately given by the superposition of two solutions having the same form of (A2). This approximation clearly breaks down on the surface of the beads because it violates the no-slip condition, but this is not relevant to our numerical model because the beads have only an effective radius and their surface is not resolved. Carrying on with this approximation, we denote by  $v_i^*$  the speed of the *i*-th sphere if it were isolated. Taking into account the disturbance induced by the other bead, one gets a linear relation between these speeds and the ones resulting from hydrodynamic interaction, formally

$$\begin{cases} v_1 = v_1^* + v_2^* S\\ v_2 = v_2^* + v_1^* S, \end{cases}$$
(A3)

where 1 and 2 are the indices of the flagellum and body beads, respectively, and S is a geometric factor which can be computed from (A2). S appears in a symmetric way in both equations because the beads are identical. Using  $v_{\alpha}$ known from the numerical computation, equations (A3) can be inverted obtain the unknown velocities  $v^*$ , which can then be plugged into (A2) to compute the disturbance field. Thus this two Stokes solutions are superposed and compared with the numerical velocity field in order to fit the effective radius R of each sphere.

# Appendix B Implementation of inextensibility and rigidity

Here we detail how inextensibility and rigidity are imposed and used to fix the model parameters. Consider the 2-beads model discussed in the introduction. The inextensibility condition is:

$$|\mathbf{x}_2 - \mathbf{x}_1| = \text{const} \quad \Rightarrow \quad \frac{d}{dt} |\mathbf{x}_2 - \mathbf{x}_1|^2 = 0$$
 (B4)

from which expanding the square  $\mathbf{x}_2 - \mathbf{x}_1$  and considering further derivation we obtain a condition on accelerations

$$(\dot{\mathbf{v}}_2 - \dot{\mathbf{v}}_1) \cdot \mathbf{n} = -\frac{|\mathbf{v}_2 - \mathbf{v}_1|^2}{|\mathbf{x}_2 - \mathbf{x}_1|}.$$
 (B5)



Fig. 12 Schematic view of the model swimmer. The internal forces  $\mathbf{g}_1, \mathbf{g}_2$  and  $\mathbf{g}_3$  allow to control the angle or (like in this paper) keep it fixed

In the last equation we have introduced the unit vector  $\mathbf{n} = (\mathbf{x}_2 - \mathbf{x}_1)/|\mathbf{x}_2 - \mathbf{x}_1|$ . Equation (B5) is trivial for the 1D case, where a zero relative acceleration leads to a zero relative velocity difference. From this point on, the simplified notation  $\mathbf{u}_i = \mathbf{u}(\mathbf{x}_i)$  is used to denote the fluid velocity in the position of the i-th bead.

From the (B5) and (6) we get:

$$\lambda = \frac{1}{2} \left[ \frac{|\mathbf{v}_2 - \mathbf{v}_1|^2}{|\mathbf{x}_2 - \mathbf{x}_1|} - f - \beta [\mathbf{v}_2 - \mathbf{u}_2] \cdot \mathbf{n} \right]$$
(B6)

that is the module of the tension. From (6) it is easy to obtain the stationary state  $f\mathbf{n} = \beta(\mathbf{v}_2 - \mathbf{u}_2)$  when  $\dot{\mathbf{v}}_1 = \dot{\mathbf{v}}_2 = 0$ . Numerical simulations of the model here introduced, with the constrain expressed by (B6), were carried out on a dumbbell 0.5*h* long (where *h* is the grid step) in a 2D Kolmogorov flow of period  $2\pi$  with velocity  $\mathbf{u} = (\cos(z), 0, 0)$  and we observed a maximum relative deviation of the length of each rod of order  $10^{-6}$ , which validates the model.

The model can be easily extended to the 3-beads swimmer. We define two unit vectors  $\mathbf{n}_1 \in \mathbf{n}_2$  that point, respectively, from the tail to the central bead and from the central to the head bead. This model introduces a new degree of freedom that is the angle  $\phi$  between the two unit vectors (see Fig. 1c in the main text). To maintain a rigid shape we need this angle to relax to a fixed value  $\phi_0$ . We define the unit vectors  $\mathbf{t}_1$  and  $\mathbf{t}_3$  perpendicular to  $\mathbf{n}_1$  and  $\mathbf{n}_2$ , respectively, such that they lie in the plane defined by the swimmer (Fig. 12), in formulae:

$$\mathbf{t}_1 = \frac{\mathbf{n}_2 - \cos\phi \mathbf{n}_1}{|\mathbf{n}_2 - \cos\phi \mathbf{n}_1|} \tag{B7}$$

$$\mathbf{t}_3 = \frac{-\mathbf{n}_1 + \cos\phi \mathbf{n}_2}{|-\mathbf{n}_1 + \cos\phi \mathbf{n}_2|} \tag{B8}$$

We introduce  $\mathbf{g}_1$  along  $\mathbf{t}_1$ ,  $\mathbf{g}_3$  along  $\mathbf{t}_3$ , and  $\mathbf{g}_2$  such that  $\mathbf{g}_2 = -(\mathbf{g}_1 + \mathbf{g}_3) = -g(\mathbf{t}_1 + \mathbf{t}_3)$ . In the last equality we suppose that  $|\mathbf{g}_1| = |\mathbf{g}_3| = g$ . At each time step t we compute g as

$$g = -a(\phi - \phi_0), \tag{B9}$$

where a is a constant setting the stiffness of the spring which keeps  $\phi$  close to  $\phi_0$ . The equations of the dynamics for a generic angle  $\phi$  are:

$$\begin{cases} \dot{\mathbf{v}}_1 = f\mathbf{n}_1 + \lambda_{12}\mathbf{n}_1 + g\mathbf{t}_1 \\ \dot{\mathbf{v}}_2 = -\lambda_{12}\mathbf{n}_1 + \lambda_{23}\mathbf{n}_2 - \beta(\mathbf{v}_2 - \mathbf{u}_2) + g\mathbf{t}_2 \\ \dot{\mathbf{v}}_3 = -\lambda_{23}\mathbf{n}_2 - \beta(\mathbf{v}_3 - \mathbf{u}_3) + g\mathbf{t}_3 \end{cases}$$
(B10)

where  $\lambda_{12}$  and  $\lambda_{23}$  are the tension forces that guarantee the inextensibility. The condition (B5) is now applied on each rod and we obtain:

-

$$\begin{split} \lambda_{23} &= \left[ -\frac{|\mathbf{v}_2 - \mathbf{v}_1|^2}{|\mathbf{x}_2 - \mathbf{x}_1|} - \frac{2}{\cos\phi} \frac{|\mathbf{v}_3 - \mathbf{v}_2|^2}{|\mathbf{x}_3 - \mathbf{x}_2|} + f - \beta(\mathbf{v}_2 - \mathbf{u}_2) \right. \\ &\left. \cdot \left( \frac{2\mathbf{n}_2}{\cos\phi} - \mathbf{n}_1 \right) + \frac{2\beta}{\cos\phi} (\mathbf{v}_3 - \mathbf{u}_3) \cdot \mathbf{n}_2 - g_2 \mathbf{t}_2 \right. \\ &\left. \cdot \left( \frac{-2\mathbf{n}_2}{\cos\phi} + \mathbf{n}_1 \right) \right] \frac{1}{\cos\phi - \frac{4}{\cos\phi}} \\ \lambda_{12} &= \left[ -\frac{|\mathbf{v}_3 - \mathbf{v}_2|^2}{|\mathbf{x}_3 - \mathbf{x}_2|} - \frac{2}{\cos\phi} \frac{|\mathbf{v}_2 - \mathbf{v}_1|^2}{|\mathbf{x}_2 - \mathbf{x}_1|} + \frac{2f}{\cos\phi} \right. \\ &\left. + \beta(\mathbf{v}_2 - \mathbf{u}_2) \cdot \left( \frac{2\mathbf{n}_1}{\cos\phi} - \mathbf{n}_2 \right) \right. \\ &\left. + \beta(\mathbf{v}_3 - \mathbf{u}_3) \cdot \mathbf{n}_2 - g_2 \mathbf{t}_2 \cdot \left( \frac{2\mathbf{n}_1}{\cos\phi} - \mathbf{n}_2 \right) \right] \\ &\left. \frac{1}{\cos\phi - \frac{4}{\cos\phi}} \right] \end{split}$$

# Appendix C The limit to Jeffery's model of a rod

In this appendix we show that the dynamics of a short dumbbell is well described by Jeffery's equation for an infinitely thin rod, see also the discussion in Sec. III and in particular Fig. 5. Consider a dumbbell with fixed length L and particles  $\mathbf{x}_1$  and  $\mathbf{x}_2$ . Assume the dynamics is Stokesian with relaxation time  $\tau$ . The equations of motion are

$$\begin{cases} \dot{\mathbf{v}}_1 = -\frac{\mathbf{v}_1 - \mathbf{u}_1}{\tau} - \lambda \mathbf{n} \\ \dot{\mathbf{v}}_2 = -\frac{\mathbf{v}_2 - \mathbf{u}_2}{\tau} + \lambda \mathbf{n} \end{cases}$$
(C11)

where  $\mathbf{u}_i = \mathbf{u}(\mathbf{x}_i)$  is the fluid's velocity at the *i*-th particle and  $\mathbf{n} = \mathbf{L}/L$ , with  $\mathbf{L} = \mathbf{x}_2 - \mathbf{x}_1$ . The modulus of the rod's tension  $\lambda$  is obtained by imposing inextensibility  $dL^2/dt =$ 0 (see (B4)). Further derivation to obtain a condition on accelerations gives

$$\ddot{\mathbf{L}} \cdot \mathbf{L} + |\dot{\mathbf{L}}|^2 = 0, \qquad (C12)$$

where  $\dot{\mathbf{L}} = \mathbf{v}_2 - \mathbf{v}_1$  and  $\ddot{\mathbf{L}} = \dot{\mathbf{v}}_2 - \dot{\mathbf{v}}_1$ . Defining  $\mathbf{w}_i = \mathbf{v}_i - \mathbf{u}_i$ , we get from (C11)

$$\ddot{\mathbf{L}} = -\frac{\mathbf{w}_2 - \mathbf{w}_1}{\tau} + 2\lambda \mathbf{n} \tag{C13}$$

and from (C12) and the definition of n

$$\lambda = -\frac{|\dot{\mathbf{L}}|^2}{2L} + \frac{\mathbf{w}_2 - \mathbf{w}_1}{2\tau} \cdot \mathbf{n}.$$
 (C14)

Finally, the equations of motion for the positions of the dumbbell's beads are

$$\begin{cases} \dot{\mathbf{v}}_1 = -\frac{\mathbf{w}_1}{\tau} + \frac{|\mathbf{v}_2 - \mathbf{v}_1|^2}{2L} \mathbf{n} - \frac{\mathbf{w}_2 - \mathbf{w}_1}{2\tau} \cdot \mathbf{n} \otimes \mathbf{n} \\ \dot{\mathbf{v}}_2 = -\frac{\mathbf{w}_2}{\tau} - \frac{|\mathbf{v}_2 - \mathbf{v}_1|^2}{2L} \mathbf{n} + \frac{\mathbf{w}_2 - \mathbf{w}_1}{2\tau} \cdot \mathbf{n} \otimes \mathbf{n}. \end{cases}$$
(C15)

65 Page 14 of 16

The latter equations are essentially the same obtained when imposing no-slip conditions on the two spheres via an immersed boundary method. If we now take the overdamped (or Re = 0) limit  $\tau \to 0$ , we get

$$\begin{cases} 0 = -\mathbf{w}_1 - \frac{\mathbf{w}_2 - \mathbf{w}_1}{2} \cdot \mathbf{n} \otimes \mathbf{n} \\ 0 = -\mathbf{w}_2 + \frac{\mathbf{w}_2 - \mathbf{w}_1}{2} \cdot \mathbf{n} \otimes \mathbf{n}. \end{cases}$$
(C16)

By summing the two equations one gets  $\mathbf{w}_1 = -\mathbf{w}_2$ , and by substituting this relation into each equation

$$(\mathbb{I} - \mathbf{n} \otimes \mathbf{n})\mathbf{w}_{1,2} = 0. \tag{C17}$$

Since  $(\mathbf{v}_2 - \mathbf{v}_1) \cdot \mathbf{n} = 0$  because of inextensibility, we can take the difference of (C17) for  $\mathbf{w}_2$  and  $\mathbf{w}_1$  and get

$$\dot{\mathbf{L}} = (\mathbb{I} - \mathbf{n} \otimes \mathbf{n})(\mathbf{u}_2 - \mathbf{u}_1).$$
(C18)

Now, since  $\dot{\mathbf{n}} = (\mathbb{I} - \mathbf{n} \otimes \mathbf{n})\dot{\mathbf{L}}/L$ , one gets

$$\dot{\mathbf{n}} = \frac{1}{L} (\mathbb{I} - \mathbf{n} \otimes \mathbf{n}) (\mathbb{I} - \mathbf{n} \otimes \mathbf{n}) (\mathbf{u}_2 - \mathbf{u}_1) = \frac{1}{L} (\mathbb{I} - \mathbf{n} \otimes \mathbf{n}) (\mathbf{u}_2 - \mathbf{u}_1)$$
(C19)

with the last equality stemming from the idempotence of the projector. If the dumbbell's length is very small we can write  $\mathbf{u}_2 - \mathbf{u}_1 = \nabla \mathbf{un} L + O(L^2)$ , so we get to first order in L

$$\dot{\mathbf{n}} = (\mathbb{I} - \mathbf{n} \otimes \mathbf{n}) \nabla \mathbf{u} \mathbf{n}. \tag{C20}$$

The latter is Jeffery's equation [62] with elongation parameter  $\Lambda = 1$ . Indeed Jeffery's equation can be written as

$$\dot{\mathbf{n}} = \mathbb{O}\mathbf{n} + \Lambda \mathbb{S}(\mathbb{I} - \mathbf{n} \otimes \mathbf{n})\mathbf{n}$$
(C21)

with  $\mathbb{O}$  and  $\mathbb{S}$  the antisymmetric and symmetric part of the velocity gradient tensor  $\nabla \mathbf{u}$ , respectively. Because of symmetry  $\mathbb{O}\mathbf{n} = (\mathbb{I} - \mathbf{n} \otimes \mathbf{n})\mathbb{O}\mathbf{n}$  so for  $\lambda = 1$  one can reconstruct the gradients and obtain (C20).

## References

- T. Kiørboe, A mechanistic approach to plankton ecology. ASLO Web Lect. 1(2), 1–91 (2009)
- J. Elgeti, R.G. Winkler, G. Gompper, Physics of microswimmers-single particle motion and collective behavior: a review. Rep. Prog. Phys. 78(5), 056601 (2015)
- B. Wang, K. Kostarelos, B.J. Nelson, L. Zhang, Trends in micro-/nanorobotics: materials development, actuation, localization, and system integration for biomedical applications. Adv. Mater. 33(4), 2002047 (2021)
- B. Bonnard, M. Chyba, J. Rouot, D. Takagi, Sub-Riemannian geometry, Hamiltonian dynamics, microswimmers, copepod nauplii and copepod robot. Pac. J. Math. Ind. 10, 1–27 (2018)
- S. Colabrese, K. Gustavsson, A. Celani, L. Biferale, Flow navigation by smart microswimmers via reinforcement learning. Phys. Rev. Lett. 118(15), 158004 (2017)
- M.C. Marchetti, J.-F. Joanny, S. Ramaswamy, T.B. Liverpool, J. Prost, M. Rao, R.A. Simha, Hydrodynamics of soft active matter. Rev. Mod. Phys. 85(3), 1143 (2013)

- K. Drescher, R.E. Goldstein, N. Michel, M. Polin, I. Tuval, Direct measurement of the flow field around swimming microorganisms. Phys. Rev. Lett. 105(16), 168101 (2010)
- K. Drescher, J. Dunkel, L.H. Cisneros, S. Ganguly, R.E. Goldstein, Fluid dynamics and noise in bacterial cell– cell and cell–surface scattering. Proc. Natl. Acad. Sci. 108(27), 10940–10945 (2011)
- R. Di Leonardo, L. Angelani, D. Dell'Arciprete, G. Ruocco, V. Iebba, S. Schippa, M.P. Conte, F. Mecarini, F. De Angelis, E. Di Fabrizio, Bacterial ratchet motors. Proc. Natl. Acad. Sci. 107(21), 9541–9545 (2010)
- M. Carlson, S. Seyler, S. Pressé, Swimming, fast and slow: strategy and survival of bacterial predators in response to chemical cues. BioRxiv, 2020-11 (2020)
- E. Lauga, T.R. Powers, The hydrodynamics of swimming microorganisms. Rep. Prog. Phys. **72**(9), 096601 (2009)
- K. Gustavsson, L. Biferale, A. Celani, S. Colabrese, Finding efficient swimming strategies in a threedimensional chaotic flow by reinforcement learning. Eur. Phys. J. E 40, 1–6 (2017)
- E. Lauga, Bacterial hydrodynamics. Annu. Rev. Fluid Mech. 48, 105–130 (2016)
- M. Seyrich, Z. Alirezaeizanjani, C. Beta, H. Stark, Statistical parameter inference of bacterial swimming strategies. New J. Phys. 20(10), 103033 (2018)
- A. Andersen, N. Wadhwa, T. Kiørboe, Quiet swimming at low Reynolds number. Phys. Rev. E **91**(4), 042712 (2015)
- S. Chibbaro, A. Decoene, S. Martin, F. Vergnet, Irreversibility and chaos in active particle suspensions. Phys. Rev. Fluids 6(1), 013104 (2021)
- C. Datt, G.J. Elfring, Active particles in viscosity gradients. Phys. Rev. Lett. **123**(15), 158006 (2019)
- C. Hoell, H. Löwen, A.M. Menzel, Particle-scale statistical theory for hydrodynamically induced polar ordering in microswimmer suspensions. J. Chem. Phys. 149(14), 144902 (2018)
- A.W. Zantop, H. Stark, Emergent collective dynamics of pusher and puller squirmer rods: swarming, clustering, and turbulence. Soft Matter 18(33), 6179–6191 (2022)
- J. Huang, Z.-G. Shao, Collective motion of chiral particles in complex noise environments. Eur. Phys. J. E 47(2), 11 (2024)
- C. Pozrikidis, Boundary Integral and Singularity Methods for Linearized Viscous Flow (Cambridge University Press, Cambridge, 1992)
- A. Kanevsky, M.J. Shelley, A.-K. Tornberg, Modeling simple locomotors in stokes flow. J. Comput. Phys. 229(4), 958–977 (2010)
- J.P. Hernandez-Ortiz, C.G. Stoltz, M.D. Graham, Transport and collective dynamics in suspensions of confined swimming particles. Phys. Rev. Lett. 95(20), 204501 (2005)
- J.P. Hernandez-Ortiz, P.T. Underhill, M.D. Graham, Dynamics of confined suspensions of swimming particles. J. Phys.: Condens. Matter 21(20), 204107 (2009)
- V. Gyrya, I.S. Aranson, L.V. Berlyand, D. Karpeev, A model of hydrodynamic interaction between swimming bacteria. Bull. Math. Biol. 72, 148–183 (2010)
- A. Furukawa, D. Marenduzzo, M.E. Cates, Activityinduced clustering in model dumbbell swimmers: the role of hydrodynamic interactions. Phys. Rev. E 90(2), 022303 (2014)

- M. Cavaiola, A. Mazzino, Self-propelled slender objects can measure flow signals net of self-motion. Phys. Fluids 33(5), 053603 (2021)
- T. Ishikawa, T. Pedley, Diffusion of swimming model micro-organisms in a semi-dilute suspension. J. Fluid Mech. 588, 437–462 (2007)
- T. Ishikawa, J. Locsei, T. Pedley, Development of coherent structures in concentrated suspensions of swimming model micro-organisms. J. Fluid Mech. 615, 401–431 (2008)
- F. Rühle, A.W. Zantop, H. Stark, Gyrotactic cluster formation of bottom-heavy squirmers. Eur. Phys. J. E 45(3), 26 (2022)
- F. Rühle, H. Stark, Emergent collective dynamics of bottom-heavy squirmers under gravity. Eur. Phys. J. E 43, 1–17 (2020)
- A.M. Roma, C.S. Peskin, M.J. Berger, An adaptive version of the immersed boundary method. J. Comput. Phys. 153(2), 509–534 (1999)
- 33. C.S. Peskin, D.M. McQueen, A general method for the computer simulation of biological systems interacting with fluids, in: Symposia of the Society for Experimental Biology, vol. 49, pp. 265–276 (1995)
- R. Mittal, G. Iaccarino, Immersed boundary methods. Annu. Rev. Fluid Mech. 37, 239–261 (2005)
- E. Lushi, C.S. Peskin, Modeling and simulation of active suspensions containing large numbers of interacting micro-swimmers. Comput. Struct. 122, 239–248 (2013)
- R. Cortez, The method of regularized stokeslets. SIAM J. Sci. Comput. 23(4), 1204–1225 (2001)
- R. Cortez, L. Fauci, A. Medovikov, The method of regularized stokeslets in three dimensions: analysis, validation, and application to helical swimming. Phys. Fluids 17(3), 031504 (2005)
- B. Zhao, E. Lauga, L. Koens, Method of regularized stokeslets: flow analysis and improvement of convergence. Phys. Rev. Fluids 4(8), 084104 (2019)
- C.S. Peskin, The immersed boundary method. Acta Numer. 11, 479–517 (2002)
- C.S. Peskin, Flow patterns around heart valves: a numerical method. J. Comput. Phys. 10(2), 252–271 (1972)
- C.S. Peskin, Numerical analysis of blood flow in the heart. J. Comput. Phys. 25(3), 220–252 (1977)
- C.S. Peskin, D.M. McQueen, Cardiac fluid dynamics, in High-Performance Computing in Biomedical Research, pp. 51–59 (2020)
- C.S. Peskin, D.M. McQueen, Modeling prosthetic heart valves for numerical analysis of blood flow in the heart. J. Comput. Phys. **37**(1), 113–132 (1980)
- 44. C.S. Peskin, D.M. McQueen, A three-dimensional computational method for blood flow in the heart I. Immersed elastic fibers in a viscous incompressible fluid. J. Comput. Phys. 81(2), 372–405 (1989)
- L.J. Fauci, C.S. Peskin, A computational model of aquatic animal locomotion. J. Comput. Phys. 77(1), 85– 108 (1988)
- L.J. Fauci, Interaction of oscillating filaments: a computational study. J. Comput. Phys. 86(2), 294–313 (1990)
- B. Fornberg, D.M. Sloan, A review of pseudospectral methods for solving partial differential equations. Acta Numer. 3, 203–267 (1994)

- D. Gottlieb, S.A. Orszag, Numerical Analysis of Spectral Methods: Theory and Applications (SIAM, Philadelphia, 1977)
- C. Canuto, M.Y. Hussaini, A. Quarteroni, T.A. Zang, Spectral Methods in Fluid Dynamics (Springer, New York, 2012)
- 50. J.P. Boyd, *Chebyshev and Fourier Spectral Methods* (Courier Corporation, Chelmsford, 2001)
- H. Löwen, Chirality in microswimmer motion: from circle swimmers to active turbulence. Eur. Phys. J. Spec. Top. 225, 2319–2331 (2016)
- R. Ledesma-Aguilar, H. Löwen, J.M. Yeomans, A circle swimmer at low Reynolds number. Eur. Phys. J. E 35, 1–9 (2012)
- Y. Yang, F. Qiu, G. Gompper, Self-organized vortices of circling self-propelled particles and curved active flagella. Phys. Rev. E 89(1), 012720 (2014)
- 54. F. Kümmel, B. Ten Hagen, R. Wittkowski, I. Buttinoni, R. Eichhorn, G. Volpe, H. Löwen, C. Bechinger, Circular motion of asymmetric self-propelling particles. Phys. Rev. Lett. **110**(19), 198302 (2013)
- A. Kaiser, H. Löwen, Vortex arrays as emergent collective phenomena for circle swimmers. Phys. Rev. E 87(3), 032712 (2013)
- M. Cavaiola, Swarm of slender pusher and puller swimmers at finite Reynolds numbers. Phys. Fluids 34(2), 027113 (2022)
- 57. J. Li, B. Avila, W. Gao, L. Zhang, J. Wang, Micro/nanorobots for biomedicine: delivery, surgery, sensing, and detoxification. Sci. Robot. 2(4), 6431 (2017)
- T. Ishikawa, M. Simmonds, T.J. Pedley, Hydrodynamic interaction of two swimming model micro-organisms. J. Fluid Mech. 568, 119–160 (2006)
- N.G. Chisholm, D. Legendre, E. Lauga, A.S. Khair, A squirmer across Reynolds numbers. J. Fluid Mech. **796**, 233–256 (2016)
- 60. M. Borgnino, G. Boffetta, M. Cencini, F. De Lillo, K. Gustavsson, Alignment of elongated swimmers in a laminar and turbulent Kolmogorov flow. Phys. Rev. Fluids 7(7), 074603 (2022)
- 61. L. Meshalkin, I.G. Sinai, Investigation of the stability of a stationary solution of a system of equations for the plane movement of an incompressible viscous liquid. J. Appl. Math. Mech. 25(6), 1700–1705 (1961)
- 62. G.B. Jeffery, The motion of ellipsoidal particles immersed in a viscous fluid, in *Proceedings of the Royal Society of London. Series A, Containing papers of a mathematical and physical character* vol. 102(715), pp. 161–179 (1922)
- F. Ginelli, The physics of the vicsek model. Eur. Phys. J. Spec. Top. **225**, 2099–2117 (2016)
- D. Bárdfalvy, V. Škultéty, C. Nardini, A. Morozov, J. Stenhammar, Collective motion in a sheet of microswimmers. Commun. Phys. 7(1), 93 (2024)
- 65. V. Škultéty, D. Bárdfalvy, J. Stenhammar, C. Nardini, A. Morozov, Hydrodynamic instabilities in a twodimensional sheet of microswimmers embedded in a three-dimensional fluid. J. Fluid Mech. **980**, 28 (2024)
- R.S. Sutton, A.G. Barto, *Reinforcement Learning: An Introduction* (MIT Press, Cambridge, 2018)
- 67. F. Borra, L. Biferale, M. Cencini, A. Celani, Reinforcement learning for pursuit and evasion of microswimmers at low Reynolds number. Phys. Rev. Fluids 7(2), 023103 (2022)

- C. Calascibetta, L. Biferale, F. Borra, A. Celani, M. Cencini, Taming Lagrangian chaos with multi-objective reinforcement learning. Eur. Phys. J. E 46(3), 9 (2023)
- 69. M. Putzke, H. Stark, Optimal navigation of a smart active particle: directional and distance sensing. Eur. Phys. J. E 46(6), 48 (2023)
- 70. M. Durve, F. Peruani, A. Celani, Learning to flock through reinforcement. Phys. Rev. E 102(1), 012601 (2020)
- L.D. Landau, E.M. Lifshitz, Fluid Mechanics: Landau and Lifshitz: Course of Theoretical Physics, vol. 6 (Elsevier, Amsterdam, 2013)

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.