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ABSTRACT
The perception of hydrodynamic signals by self-propelled objects is a problem of paramount importance ranging from the field of biomedical engineering to bio-inspired intelligent navigation. By means of a state-of-the-art fully resolved immersed boundary method, we propose different models for fully coupled self-propelled objects (swimmers, in short), behaving either as “pusher” or as “puller.” The proposed models have been tested against known analytical results in the limit of Stokes flow, finding excellent agreement. Once tested, our more realistic model has been exploited in a chaotic flow field up to a flow Reynolds number of 10, a swimming number ranging between zero (i.e., the swimmer is freely moving under the action of the underlying flow in the absence of propulsion) and one (i.e., the swimmer has a relative velocity with respect to the underlying flow velocity of the same order of magnitude as the underlying flow), and different swimmer inertia measured in terms of a suitable definition of the swimmer Stokes number. Our results show the following: (i) pusher and puller reach different swimming velocities for the same, given, propulsive force: while for pusher swimmers, an effective slender body theory captures the relationship between swimming velocity and propulsive force, this is not for puller swimmers. (ii) While swimming, pusher and puller swimmers possess a different distribution of the vorticity within the wake. (iii) For a wide range of flow/swimmer Reynolds numbers, both pusher and puller swimmers are able to sense hydrodynamic signals with good accuracy.

I. INTRODUCTION
Motility of swimming animals and micro-organisms is an issue attracting a great deal of attention in different fields of research, covering aspects that range from feeding, reproduction, and prey-predator interactions to biological-inspired intelligent navigation.\textsuperscript{2-4}

The individual swimming strategies have been the subject of several investigations carried out by means of experimental,\textsuperscript{5-9} theoretical, and numerical strategies.\textsuperscript{10-13} A series of contributions analyzed the dynamics of a population of swimming organisms, e.g., in relation to encounter rates and other collective behaviors.\textsuperscript{14-17} Some of them focus on the mutual interactions of micro-organisms with the fluid flow environment\textsuperscript{18-20} and others on active matter clustering induced by non-homogeneous flows or turbulence.\textsuperscript{21,22} Moreover, scientific evidence clearly shows that swimming organisms are able to react to hydrodynamic cues both in laminar and turbulent conditions in order to take different actions.\textsuperscript{23-26}

The perception of hydrodynamic signals is an important issue for researchers oriented to the development of bio-inspired mechanosensitive receptors to promote the advancement of multifunctional sensors in the fields of bio-medical engineering, robotics, and artificial intelligence.\textsuperscript{27} Moreover, the combination of the navigation system and biologically inspired approaches has attracted considerable attention, thus becoming an important research area in the field of intelligent robotic system.\textsuperscript{28} Since the emergence of trend of bio-metric underwater robots, as an alternative to traditional propeller-driven underwater vehicles, the capability of recognizing and characterizing flow properties through hydrodynamic sensing makes it possible to take advantage of the flow,\textsuperscript{29} e.g., by increasing the propulsion efficiency and stability of an underwater robot.\textsuperscript{30} In recent years, efforts have been made for the development of behavioral schemes and bio-inspired sensor for hydrodynamic detection,\textsuperscript{7,31-33} which turns out to be useful in many everyday applications, environmental monitoring, and industrial affairs.

From the point of view of fluid dynamics, self-propelled objects can be classified based on how they set the surrounding fluid during motion. If the induced flow field describes a fluid pushed away along the propulsion axis and dragged in from the sides, the swimmer is named “pusher.” In contrast, when the fluid is pulled inwards toward

the swimmer along the propulsion axis and ejected to the sides, it is classified as a "puller."

Let us now focus on the main concern of the present paper, i.e., whether the self-propelled object (i.e., a solid object which may possess inertia and internal elastic degree of freedom) may detect some features of the unperturbed flow field despite its perturbing presence. Such an issue is highly not trivial: even a rigid rod in a fluid flow modifies the unperturbed flow because of the no-slip condition. Pre-existing flow velocity gradients along the rod axis are flattened out owing to the rigidity condition of the rod structure. The perturbation will be even stronger if the rod is self-propelled. Are there features of the flow field very close to the swimmer which remain unperturbed (e.g., as they would be in the absence of the swimming object)? Answering this question is the main concern of the present paper, with potential interesting applications also in the field of flow measuring techniques via non-intrusive Lagrangian techniques (see, e.g., Ref. 34 for the recently proposed "fiber tracking velocimetry").

To answer our question, following the idea of Lushi and Peskin, we build a model for a slender self-propelled object able to accurately reproduce the flow disturbance generated by a pusher or puller swimmer, with the goal of identifying flow properties which remain essentially unchanged despite the invasive presence of the swimmer.

The rest of the paper is structured as follows: Sec. II presents the strategy used to build our swimmer model, in terms of a state-of-the-art immersed boundary (IB) method. A careful validation of the flow field generated by our swimmer model will be also presented. Section III is devoted to characterize the swimmer inertia and analyze differences in locomotion between pushers and pullers. Finally, results on hydrodynamics sensing by slender swimmers will be presented. Section IV will draw some relevant conclusions.

II. METHODS

A. Governing equations

We consider an inertial, elastic, one-dimensional, and self-propelled slender object, characterized by non-dimensional length $l$, diameter $d \ll l$, linear density $\rho$ (denoting the density difference between the slender object and the surrounding fluid), and bending stiffness $\gamma$. We refer to Huang et al. for the list of relevant dimensionless parameters. Given a point material belonging to the slender body $X = X(s,t)$, as a function of the curvilinear coordinate $s$ and time $t$, its dynamics is governed by the Euler–Bernoulli beam equation

$$\rho \ddot{X} = \partial_t (T \partial_t (X)) - \gamma \partial_s^2 (X) - F - F_T. \quad (1)$$

In Eq. (1), $F$ is the forcing (per unit length) caused by the fluid-structure coupling enforcing the no-slip condition and $F_T$ is a unit-length forcing, mimicking the propulsion mechanism causing a net motion along the swimmer axis. In plain terms,

$$F_T = k \dot{p}, \quad (2)$$

where $k$ is kept constant and controls the propulsion magnitude, and $\dot{p}$ is the unit vector indicating the swimmer’s orientation. In the present paper, we focus on a rigid self-propelled slender body; to this end, throughout the work, we select sufficiently large $\gamma$, for which we have an essentially rigid behavior of the slender body, i.e., we checked a posteriori that the relative swimmer deformation is always smaller than $\mathcal{O}(10^{-6})$. $T$ is the tension field necessary to enforce the inextensibility condition

$$\partial_t (X) \cdot \partial_s (X) = 1. \quad (3)$$

Such condition leads to a Poisson equation for the tension field $T(s, t)$ which is solved efficiently as described in Ref. 36. The swimmer boundary conditions at its ends are

$$\partial_s X|_{s=0,c} = \partial_s X|_{s=0,c} = 0; \quad T|_{s=0,c} = 0. \quad (4)$$

The slender body is discretized along $s$ into segments with spatial resolution $\Delta s = c/(N_l - 1)$, where $N_l$ is the number of Lagrangian points.

The fluid-structure interaction is modeled in terms of a two-way coupling approach, following the immersed boundary (IB) method proposed by Huang et al. for anchored filaments in laminar flows. In a cubic tri-periodic domain, of size $L$, we solve numerically the incompressible Navier–Stokes equations for a Newtonian fluid, which in dimensionless form (see Ref. 36) are

$$\partial_t u + u \cdot \nabla u = -\nabla p + \frac{1}{Re} \partial_s^2 u + f^V + f, \quad (6)$$

$$\partial_s \cdot u = 0, \quad (7)$$

where $u$ is the fluid velocity, $p$ is the pressure, and $Re$ is the Reynolds number. The volume forcing $f^V$ is used to generate the desired flow field whose characteristic velocity/length scales are used to define the Reynolds number, $Re$. $f$ represents the effect of the immersed boundary, mimicking the presence of the slender body by means of the no-slip enforcement at the Lagrangian points. Accordingly, in the IB method, the Lagrangian forcing $F$ in Eq. (1) is first evaluated on the Lagrangian grid in order to enforce the no-slip condition $X = U(X(s,t), t)$. Namely,

$$F(s,t) = \beta (X - U), \quad (8)$$

where $\beta$ is a problem-dependent large negative constant, and

$$U(X(s,t), t) = \int u(x,t) \delta (X - X(s,t)) dx \quad (9)$$

is the interpolated fluid velocity on the Lagrangian points. A spreading operation is finally performed around the surrounding Eulerian points, yielding the volume forcing acting on the flow

$$f(x,t) = \int F(s,t) \delta (X - X(s,t)) ds. \quad (10)$$

Both the interpolation and spreading are performed in terms of a suitable regularized Dirac $\delta$. The one proposed by Roma et al. has been used in the present work.

The above strategy has been implemented and extensively validated to study fiber dynamics in both laminar and turbulent flows. We will use this numerical framework to build an idealized swimmer model able to reproduce the main features of aquatic swimmer organisms.

Direct numerical simulations (DNS) are performed in a cubic domain of side $L = 4\pi$ and $8\pi$, which is discretized in terms of a uniformly spaced Cartesian grid, using $N = 128$ and 256 cells per side,
respectively. The number of Lagrangian points describing the slender motile object is chosen in such a way that the Lagrangian spacing Δs is very close to that of the Eulerian grid Δx (Δs ≈ Δx). Doubling the resolution, of both the Eulerian and Lagrangian grid, gave no substantial variation of the results we are going to show. The same sensitivity analysis has been carried out also for the time step. The numerical solutions we are going to show have been obtained after a convergence study, ensuring that halving the time step causes relative variations of the resulting flow field smaller than a few percent.

As far as the unperturbed flow is concerned, we will consider the time-dependent ABC (Arnold–Beltrami–Childress) flow, with Reynolds numbers up to Re = 10.

The solution is obtained by using a finite difference, fractional step method on a staggered grid with fully explicit space discretization and third-order Runge–Kutta scheme for advancement in time. Finally, the resulting Poisson equation enforcing incompressibility is solved using a fast Fourier transform. More details can be found in Refs. 36, 39, 40, and 43.

B. Our swimmer models

1. An IB realization of the “di-Stokeslet” model

Let us start by presenting the simplest swimmer model based on the IB strategy mimicking swimming micro-organisms generating dipolar flow fields which is characterized by the well-known r⁻² decay in space of the flow disturbance triggered by the swimmer motion. Depending on the characteristics of the propulsion mechanism, one can have rear-actuated swimmers, i.e., pushers (such as bacteria *E. coli* or *Spermatozoon*), or front-actuated swimmers, i.e., pullers (such as *rotifer Brachionus plicatilis*). For pusher/puller swimmers, we describe the locomotion in terms of two oppositely directed point forces of equal magnitude, but acting in different points on the Lagrangian grid, a configuration used to mimic the so-called stresslet (or di-Stokeslet). Focusing for the sake of example on a pusher swimmer, one force (blue arrow in Fig. 1) acts on the last point of the Lagrangian grid, where both the no-slip condition and the propulsion force are imposed, and it is associated with the swimmer body. The second force (red arrow in Fig. 1) acts on the fluid (by spreading a point force applied to the first Lagrangian point of the grid). The no-slip condition is not applied on this point and the same is for all remaining points of the Lagrangian grid. While the first point force mimics the propulsion caused by, e.g., the flagella, the second mimics its pushing effect on the fluid. Although Fig. 1 refers to a pusher, the description for a puller proceeds in a very similar way. It will be discussed in Sec. II B 2 for a slender swimmer.

The main limitation of the present model is that it condensates all details of a swimming object only in a point (blue dot in Fig. 1). In Sec. II B 2, we will discuss a generalization allowing us to overcome such a limitation.

2. A slender swimmer model

We now focus our attention on a less idealized swimmer model able to describe a more elongated organism, which at level of minimal model can be thought as a slender swimmer. By taking inspiration from Lushi and Peskin, we build a model for a slender swimmer by imposing the no-slip condition and the propulsion force on the same half length, ℓ = c/2, of the slender motile object, the spreading of the pushing/pulling forcing acting on the fluid being imposed on the other half. One obtains a pusher by imposing the pushing force on the first half edge of the Lagrangian grid, starting from the trailing edge. The second half part of the slender body corresponds to the region where the propulsion is acting on the fluid, as shown in Fig. 2 top. A puller is obtained in a similar way but the pulling force is applied on the second half of the Lagrangian grid, as depicted in Fig. 2 bottom.

C. Validation of the swimmer models based on the IB method

1. di-Stokeslet model

We start to validate the flow field generated by the IB method sketched in Fig. 1. In a still fluid, we let the swimmer to evolve from rest until it reaches its terminal velocity, *u*ₚ, with a resulting swimmer Reynolds number, *Re* = ∞. After a transient time, also the flow field reaches a steady-state regime characterized by a constant kinetic energy. In what follow, the comparison between the results from our numerical simulations and theory is presented for time instants

**FIG. 1.** Sketch of the realization based on the IB method of a di-Stokeslet, modeling a pusher swimmer, such as *Spermatozoon*. The blue arrow indicates the propulsive force on the swimmer (acting along its axis), *F*ₚ, used in Eq. (1), coinciding with the direction of the motion. The red arrow represents the force exerted by the swimmer flagella to the fluid. The dashed line indicates the separation distance, ℓ = nΔs, with *n* being the number of intervals Δs between the two point forces. The gray dots represent the Lagrangian grid points. The no-slip condition and the propulsion force are imposed only on the blue grid point. The inextensibility constraint makes the propulsion force to propagate on the rest of the rigid slender body, causing the latter to swim. By using Eq. (10), the spreading of −*F*ₚ is imposed on the red dot. Finally, it denotes the force acting on the fluid due to the friction between the fluid and the immersed body. Note that in the Stokes regime forces acting on the swimmer and on the fluid are both balanced.

**FIG. 2.** Top: sketch of a slender pusher swimmer. The spreading of the pushing force on the fluid is applied to the lower half, the no-slip condition is applied to the upper half. Bottom: sketch of a slender puller swimmer. The spreading of the pulling force is applied to the upper half; the no-slip condition is applied to the lower half. The red dots identify the end-to-end swimmer distance.
corresponding to the steady state. Different snapshots taken at different times are identical provided that a translation of the reference system (moving with the swimming velocity \( u_s \)) is considered. Here, \( \text{Re}_s = u_s/\nu \) is based on the separation distance, \( l \), between the two point forces of Fig. 1. To check the resulting flow field, we use as basic ingredient the well-known solution of the Stokes flow past a sphere for \( \text{Re}_s \ll 1 \). Written in polar coordinates, its expression reads

\[
\frac{u_r}{u_s} = \left[ 1 - \frac{3 \, R}{2 \, r} + \frac{1}{2} \left( \frac{R}{r} \right)^3 \right] \cos \theta, \tag{11a}
\]

\[
\frac{u_\theta}{u_s} = \left[ -1 + \frac{3 \, R}{4 \, r} + \frac{1}{4} \left( \frac{R}{r} \right)^3 \right] \sin \theta, \tag{11b}
\]

where \( u_r \) and \( u_\theta \) are the radial and the transversal velocity components, respectively. \( R \approx \delta x \) is the radius associated with the sphere, according to the regularized Dirac \( \delta \)-function. To mimic the di-Stokeslet, we combine Eq. (11) with a similar solution for another sphere, separated from the former by a distance \( l \) (here \( l = 0.6 \)). The two spheres are associated with two unperturbed flows having opposite directions but possessing the same magnitude \( u_s \). The resulting flow configuration is considered in a periodic domain to match the periodic boundary conditions of the simulations based on the IB strategy.

The comparison between the analytical flow solution and the one obtained from the IB strategy shows an excellent agreement (see Fig. 3) while capturing both the near field and the far field fluid flow. Figure 3 shows the decay of the flow field velocity magnitude, \( u_{rt} \), both along the swimming direction [Fig. 3(a)] and along its normal [Fig. 3(b)]. A pusher swimmer is considered in the figure.

Note that a clear \( r^{-2} \) scaling, the fingerprint of a dipolar flow, is very well reproduced by the numerical simulations, despite the use of the periodic boundary conditions. The latter cause a degradation of the power law behavior which is however limited to the region close to the side of the periodicity box.

As shown in Fig. 3, the effect of the periodicity can be moved away from the swimmer by simply increasing the size of the periodicity box. Its effect on the near-field behavior turns out to be negligible with a box size of \( 4 \pi \), where a clear \( r^{-2} \) decay (see Fig. 3) can be detected. Accordingly, we will fix to \( 4 \pi \) the size of the periodicity box for the analysis reported in the following.

2. Slender swimmer model

Let us now to pass to validate our model for a slender swimmer.

Also in this case we let the swimmer, starting from rest, to reach its terminal velocity \( u_s \). In this case, \( \text{Re}_s = u_s/\nu \) is based on the length of the slender swimmer, \( L \) (here \( L = 0.4 \)). The resulting flow field is compared with the solution for an extended stresslet, where the velocity field in a point \( r \) is reconstructed by superimposing several (here 5) di-Stokeslet solutions. Namely,

\[
u(r) = \frac{|F_r|}{8 \pi l} \sum_{p=1}^{\infty} \left( S \left( r - \frac{i \Delta s}{2} p \right) - S \left( r + \frac{i \Delta s}{2} p \right) \right) \hat{p} + \cdots, \tag{12}
\]

where dots stay for contributions coming from all other boxes when the effect of periodicity is explicitly accounted for. In Eq. (12), \( \mu \) is the dynamic viscosity, \( F_r \) is the propulsive force (per unit length) used in the IB method, and

\[
S(r) = \frac{1}{r}(I + \hat{r} \otimes \hat{r}) \tag{13}
\]

is the bulk Stokeslet, with \( I \) the identity matrix, \( \hat{r} \equiv |r| \), \( \hat{r} \equiv r/|r| \), and \( \otimes \) the tensorial product.
In Fig. 4, the flow behavior due to slender pusher/puller swimmer is reported along the motion direction and along the direction perpendicular to it. Both pushers and pullers accurately capture the decay of the flow velocity with respect to $r$. Moreover, we have also verified that the model captures the fluid flow generated by a swimmer from a more qualitative point of view. In Fig. 5, a pusher and a puller swimmer, together with the flow field they generate due to their locomotion, are shown. Our model accurately captures the flow field that a swimmer generates by its locomotion, as also observed in experiments.

### III. RESULTS

#### A. Rotational Stokes time

As the first step, we characterize the swimmer inertia, a property we will use in Sec. III C. To this end, we considered the steady two-dimensional Beltrami–Childress (BC) cellular flow,\textsuperscript{46,47,49} described by

\begin{align}
  u &= \cos y, \\
  v &= \cos x,
\end{align}

\[(14)\]

To obtain the BC flow as a stable solution of the Navier–Stokes equations, we apply a volume force $f = (1/Re)u$ for $Re$ up to 10 (see Ref. 47). To evaluate the Stokes time, we have placed the slender swimmer, without propulsion (i.e., $F_T = 0$), initially at rest, at the center of one cell in the BC flow. Under the action of the flow, the swimmer starts to rotate (fully coupled to the flow) around its center of mass. We measure the time it takes for the swimmer peripheral velocity, $V(t)$, to adapt to the corresponding flow velocity $V_0$. This procedure has been done in terms of exponential fits

\begin{equation}
  V(t) = V_0(1 - e^{-t/\tau_s}),
\end{equation}

from which the Stokes time, $\tau_s$, has been extracted. In the inset of Fig. 6, an example of this procedure is provided. The resulting behavior of $\tau_s$ as a function of $\rho$, is reported in Fig. 6. The linear fit of $\tau_s$ vs $\rho$ gives $\tau_s = a\rho$, with $a \approx 1$ for $Re = 1$. Since we are also interested in investigating the swimming behavior for larger $Re$, we performed the same analysis in a fluid with $Re = 10$. Also in this case we found that a linear relationship between $\tau_s$ and $\rho$ holds, with $a \approx 10$ (not shown). The increase in $a$ by a factor 10 is reasonable because of the expected inverse proportionality between the Stokes time and the viscosity we reduced to obtain the desired Reynolds number.

Our numerical experiments are performed in the chaotic ABC time-dependent flow.\textsuperscript{48} In this case, we define $St = \tau_s/\lambda$, where $\lambda$ is the
maximum Lyapunov exponent of the flow (see Ref. 48 for the computation of $\lambda$ for this flow configuration). Throughout this work, we fix two Stokes numbers, $St = 0.04$ and 0.1. More details are given in Sec. III C.

B. Swimming velocity of pushers and pullers

We now assess the swimming velocity reached by pushers and pullers, starting from rest, given the propulsion $F_T$. When $Re_s/C^2 < 1$, the swimming terminal velocity is given by the balance between the propulsive force and the Stokes drag exerted by the surrounding flow, as we have shown in Sec. II C. Here we study the resulting swimming velocity for the pusher and puller swimmers for different values of $Re_s$ and $F_T$.

The behavior of $F_T$ vs the swimming velocity, $u_s$, and the corresponding Reynolds number, $Re_s$, for pushers and pullers, are shown in Fig. 7; $u_s$ is normalized with the maximum swimming velocity investigated, while $F_T$ with the expression from the slender body theory, $F_{sl} = u_s^4 pl h g$, where $h = l/2$ is the half length of the slender object, and $\eta = 1/\ln x$, with $x = h/R$ being the aspect ratio. Velocities reached by pusher and puller swimmers in a fluid initially at rest with $Re = 1$, for $0.04 \leq Re_s \leq 0.4$, are shown in Fig. 7(a). Figure 7(b) reports the same quantities for $Re = 10$ (and $0.4 \leq Re_s \leq 4$).

Considering fluids with different $Re$ allows us to investigate differences in locomotion of pushers and pullers when inertia becomes important. When $Re_s \ll 1$, for a given $F_T$, pushers and pullers reach exactly the same $u_s$. As $Re_s \leq C/11$, we find that for a given $F_T$, pusher and puller swimmers reach different swimming velocities. Pushers show a constant ratio $F_T/F_{sl}$ as $u_s$ increases, indicating a linear relationship between $u_s$ and $F_T$ up to $Re_s = 4$. With a pre-factor on the order of unity, the external force acting on a pusher swimmer can be reasonably described by a slender body theory [see Fig. 7(a)]. This is not the case for pullers: a non-linear relationship between $u_s$ and $F_T$ indeed holds in the range $0.04 \leq Re_s \leq 4$. Moreover, pullers are less efficient
since they need a greater propulsive force to reach the same swimming velocity of pushers. The origin of this finding can be detected in Fig. 7(c) where we show the ratio between the maximum vorticity generated by pushers and pullers, $\omega_{\text{max}}^*/\omega_{\text{max}}^*$, in the range $0.4 \leq Re \leq 4$. The ratio passes from being $0.1(1)$ at small $Re$, to about $0.5$ at $Re = 2$, almost monotonically.

Our findings are consistent with the results in Ref. 53 where the self-propulsion of pusher and puller squirmers has been investigated for Reynolds numbers between 0.01 and 1000. Authors found that pushers have efficient convection of vorticity past their surface, leading to a steady axisymmetric flow that remains stable up to large Reynolds numbers. In contrast, pullers trap vorticity within their wake, which leads to flow instabilities, causing a decrease in the swimming velocity for Reynolds numbers between 0.01 and 1000. Authors found that self-propulsion of pusher and puller squirmers has been investigated in terms of the flow Lyapunov exponent, the absence of the swimmer (i.e., excluding the swimmer self-motion).

We are now ready to investigate the capability of a slender swimmer to measure flow properties in terms of swimmer position and velocity of the swimmer end points (red dots in Fig. 2).

To do that, we consider a time-dependent version of the three-dimensional ABC (Arnold–Beltrami–Childress) flow

\[ u = \sin (z + \varepsilon \sin (\Omega t)) + \cos (y + \varepsilon \sin (\Omega t)), \]
\[ v = \sin (x + \varepsilon \sin (\Omega t)) + \cos (z + \varepsilon \sin (\Omega t)), \]
\[ w = \sin (y + \varepsilon \sin (\Omega t)) + \cos (x + \varepsilon \sin (\Omega t)), \]

(16)

where $\varepsilon = 1$ is the cell oscillation amplitude, and $\Omega = 1.5$ is the cell oscillation frequency. This choice ensures high chaoticity uniformly distributed in space with a maximum Lyapunov exponent $\lambda = 0.8$ (see Ref. 48). In order to obtain the ABC flow as a solution of the Navier–Stokes equations, we apply a volume force, $F_1 = \partial \mathbf{u}/\partial t - (1/Re)\partial^2 \mathbf{u}$, on the right hand side of Eq. (6). For the Reynolds numbers analyzed here, the resulting flow field turns out to be a stable (time-dependent) fixed point of the Navier–Stokes equations which agrees with the analytical expression.

Simulations with $Re = 1$ and 10 have been performed, always checking that the flow remained stable for values of $Re$ at least up to 100. The use of this setting allows us to perform a direct and reliable comparison between the swimmer velocity differences evaluated at its ends and the corresponding underlying (unperturbed) fluid flow velocity. With unperturbed flow velocity, we mean the velocity field in the absence of the swimmer (i.e., excluding the swimmer self-motion). A natural way to quantify the swimmer inertia is done via the Stokes number expressed here in terms of the flow Lyapunov exponent, $St = \lambda \tau$. Moreover, we define the swimming number, $S$, in terms of the ratio between the measured swimming velocity and the fluid root mean square velocity, namely, $S = u_s/\langle \mathbf{u}^2 \rangle^{1/2}$. The parameter $S$, $Re$, and $Re_s$ are the control parameters entering in our numerical experiments.

We consider the velocity difference between the swimmer end points (red dots in Fig. 2), $\delta \mathbf{V}$, and denote by $\delta \mathbf{u}$ the corresponding unperturbed flow velocity difference. Our aim here is to find a relationship among the two even if in general we do not expect $\delta \mathbf{V} \sim \delta \mathbf{u}$.

The easiest way to show this fact is to project $\delta \mathbf{V}$ and $\delta \mathbf{u}$ along the swimmer axis. While the first is trivially zero due to the inextensibility constraint, this is not for the underlying (unperturbed) flow velocity, which may assume any value. Our idea is to assume, as done in Ref. 48, projections of $\delta \mathbf{V}$ and $\delta \mathbf{u}$ on a plane normal to the swimmer axis in a way to minimize the effect of inextensibility constraint.

In terms of the normal unit vector $\mathbf{p}_\perp$, we define the two projections as

\[ \delta V_\perp = \delta V \cdot \mathbf{p}_\perp, \]
\[ \delta u_\perp = \delta u \cdot \mathbf{p}_\perp. \]

In three-dimensions, we have an infinite number of directions belonging to the normal plane to the swimmer orientation. We choose, for the sake of example, $\mathbf{p}_\perp = (0, -p_1, p_2)$, verifying that the results we are going to show do not depend on this particular choice.

It is worth noting that $\delta V_\perp$ and $\delta u_\perp$ are related to the velocity (of the swimmer and of the flow, respectively) derivative along the swimmer orientation projected along the normal direction $\mathbf{p}_\perp$. This is true provided that the swimmer length $\ell$ is sufficiently smaller than the typical flow length scale. Because these velocity derivatives can always be seen as the sum of the strain-rate tensor and the rotation tensor, both kinematic observables contribute to $\delta V_\perp$ and $\delta u_\perp$. The normalized root mean square error (NRMSE), between $\delta V_\perp$ and $\delta u_\perp$, with the corresponding error bars is reported in Fig. 8, for the time-dependent ABC flow. Examples of time series of $\delta V_\perp$ and $\delta u_\perp$ are shown in the insets. We report the measured NRMSE for both pushers and pullers with $St = 0.04$ and 0.1 for $Re = 1$ [Fig. 8(a)] and for $Re = 10$ [Fig. 8(b)], while $\Phi$ is ranging between 0 and 1. For the sake of comparison, we also show the NRMSE for $\Phi = 0$, i.e., the slender body without propulsion.

The NRMSE is defined as

\[ \text{NRMSE} = \left( \frac{1}{t_{\text{max}}} \int_{t=0}^{t_{\text{max}}} (\delta V_\perp - \delta u_\perp)^2 dt \right)^{1/2}, \]

(18)

where $G = \sqrt{\langle \gamma^2 \rangle}$ being the flow strain rate, with $\langle \gamma^2 \rangle = \langle \sigma_{ij}\sigma_{ij} \rangle$, $\epsilon_2 = 1/2 (\partial u_i + \partial u_i)$ is the strain tensor, and $\varepsilon$ is half of the periodicity box size. $t_{\text{max}}$ has been chosen in a way to obtain a statistical convergence of the selected statistical indicator. Error bars represent the residual variability of the mean values at convergence.

Apart from short time intervals where $\delta V_\perp$ and $\delta u_\perp$ are quite different, due to rapid changes of the underlying strain-rate/vorticity, both pusher and puller swimmers are able to “measure” the unperturbed flow transverse velocity difference with satisfactory agreement across the different values of $\Phi$ (see Fig. 8). In particular, when $Re = 1$ and $St = 0.04$, the NRMSE of pushers and pullers is almost the same, with a slight growth by increasing $\Phi$. If $St = 0.1$, larger differences arise between pushers and pullers. NRMSE of puller remains almost constant across the swimming numbers, $\Phi$, while for pushers the NRMSE presents a general increase by increasing $\Phi$, with a maximum NRMSE just over 2% [Fig. 8(a)]. When considering $Re = 10$ and $St = 0.04$, the NRMSE of puller increases more than the NRMSE of pushers. Moving to $St = 0.1$, pullers maintain almost constant the NRMSE up to $\Phi = 1$. For pushers, the NRMSE behaves as that of pushers up to $\Phi = 0.7$; for larger swimming numbers, the NRMSE of pusher starts to increase up to a value around 3% [Fig. 8(b)].
In light of the results discussed above, two different patterns can be identified: first, pushers are more able to measure flow properties when their inertia is low; second, when swimmer inertia is relatively high, the conclusion is opposite: pullers are now more able than pushers to "measure" flow properties. The conclusions drawn above hold for both value of Re we have considered, thus suggesting the robustness of our findings, at least in the range of Reynolds number investigated.

IV. CONCLUSIONS

We have exploited a state-of-the-art fully resolved immersed boundary method to investigate the perception of hydrodynamic signals by slender swimmers commonly classified as pusher or puller type. Two different models have been proposed. In the simplest model, the locomotion of a self-propelled organism is described in terms of two oppositely directed point forces of equal magnitude, but acting on different points of the Lagrangian grid associated with the swimmer. The resulting numerical solution of the flow field generated by the swimmer motion has been compared with the analytical solution corresponding to the so-called di-Stokeslet, obtaining excellent agreement.

As a less idealized model of a swimmer, we have built a model for a slender swimmer by imposing the no-slip condition and the propulsion force on the same half length of the slender motile object, the spreading of the pushing/pulling forcing acting on the fluid being imposed on the other half (the so-slip condition was not applied in that portion of the Lagrangian grid). The resulting flow motion has been successfully compared with the solution for an extended stresslet, where the velocity field in a point of the flow domain is reconstructed by superimposing several (5 in the present study) di-Stokeslet solutions.

Once our models have been validated in the limit of Stokes flows in a fluid initially at rest, our more realistic model has been exploited in a chaotic flow field up to a flow Reynolds number of 10 (i.e., far from the Stokes regime), a swimming number ranging between zero and one, and different swimmer inertia. Our main results can be summarized as follows: (i) Pushers and pullers differently react to an imposed propulsive force. The net result of this observation is that they reach different swimming velocities for the same, given, propulsive force. Interestingly, if one exploit the slender-body theory to relate the imposed propulsion to the resulting swimming velocity, one finds that it reasonably works for pushers, while this is not for pullers. The reason we invoked to understand this finding is the different vorticity generated by the motion of the two swimmer types. (ii) For a wide range of flow/swimmer Reynolds numbers, both pusher and puller swimmers are able to sense hydrodynamic signals with good accuracy, net of swimmer self-motion. This means that, despite the perturbation caused by the swimmer motion, there exist hydrodynamics observable practically unaffected by the swimmer motion. Among them, we identified the swimmer velocity differences evaluated at the swimmer ends, projected along a direction on a plane normal to the swimmer orientation.

For sufficiently short (but slender) swimmers, such a kinematic observable reduces to the flow derivative along the swimmer orientation projected along the normal (to the swimmer) direction. This finding opens to unconventional non-intrusive techniques to measure two-point flow properties (e.g., gradients) by following artificial self-propelled slender objects, thus generalizing the founding idea at the origin of the recently proposed "fiber tracking velocimetry."

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DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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