





## Unsteady and inertial dynamics of a small active particle in a fluid

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It is well known that the reversibility of Stokes flow makes it difficult for small microorganisms to swim. Inertial effects break this reversibility, allowing new mechanisms of propulsion and feeding. Therefore it is important to understand the effects of unsteady and fluid inertia on the dynamics of microorganisms in flow. In this work, we show how to translate known inertial effects for nonmotile organisms to motile ones, from passive to active particles. The method relies on a principle used earlier by Legendre and Magnaudet (1997) to deduce inertial corrections to the lift force on a bubble from the inertial drag on a solid sphere, using the fact that small inertial effects are determined by the far field of the disturbance flow. The method allows us, for example, to compute the inertial effect of unsteady fluid accelerations on motile organisms, and the inertial forces such organisms experience in steady shear flow. We explain why the method fails to describe the effect of convective fluid inertia.

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### I. INTRODUCTION

Active-matter research asks, among other questions, how small active particles such as motile microorganisms move in a fluid, how they interact via hydrodynamic interactions, and how their motion is affected by obstacles, such as the walls that contain the fluid. It is usually assumed that the particles are so small that their dynamics is overdamped. In this steady creeping flow or Stokes limit, fluid accelerations caused by the moving particle can be neglected, and it is well known that the reversibility of Stokes flow makes it difficult for small microorganisms to swim [1]. How does the particle dynamics change when the particles become larger, so that inertial effects begin to matter? When fluid inertia is weak, one can compute the inertial dynamics by perturbation theory around the creeping-flow limit [2–13]. Singular perturbation theory and asymptotic-matching methods have been used to investigate the effect of fluid inertia upon the motion of small passive particles. For example, convective fluid inertia enhances the drag in homogeneous [14] and stratified [15] flows, and it causes a torque on nonspherical particles moving in a spatially uniform flow [16–19]. Fluid accelerations due to shear result in lift forces [13,20,21]. They modify the angular velocity of small particles in shear flow [22,23], and in turbulence [24]. Even weak inertial forces can have a substantial effect on the dynamics, for example, if the unperturbed motion is marginally

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stable [7,25–27]. The results mentioned above apply in the steady limit. Unsteady fluid inertia gives rise to the BBO history force [28–30] and added-mass effects [31–33].

For active particles less is known. The rich biodiversity of phytoplankton and zooplankton results in a substantial diversity of propulsion strategies. The associated inertial parameters span a wide range of values. Fluid inertia matters more for larger organisms, and for those with vigorous swimming gaits. Inertial effects break the time reversibility of Stokes flow, and may thus provide new mechanisms of propulsion. Hamel *et al.* [34], for example, showed that the ciliate *paramecium* makes use of inertial effects to escape predators. The clam *clione antartica* exploits unsteady fluid inertia for propulsion [35]. Most of our present understanding of such fluid-inertia effects relies on *ab initio* computer simulations, and upon perturbation theory in the relevant inertia parameter. Lauga [36] calculated how much inertia is needed to allow for significant motion with reciprocal strokes. Khair and Chisholm [37] and Wang and Ardekani [38] computed the effect of convective inertia on a small spherical swimmer by perturbation theory in the particle Reynolds number. The *ab initio* simulations of Chisholm *et al.* [39] confirm these results, and demonstrate how the theory fails for larger particle Reynolds numbers. Ishimoto [40,41] studied how unsteady inertial effects on the dynamics of a microswimmer depend upon its swimming stroke. Convective fluid inertia also affects the amount of fluid an active particle moves around [42]. Finally, feeding strategies of many marine organisms rely on unsteady inertial effects [43,44]. Last but not least, artificial swimmers are usually larger than millimeters, because it is challenging to construct reliable and controllable propulsion mechanisms for very small robotic swimmers. As a consequence, fluid inertia tends to matter for such self-propelled robots [45,46].

The motion of *copepods*, in particular, illustrates the importance of fluid inertia for the swimming of marine microorganisms. During their life cycle, these organisms grow and change their gait. The steady creeping-flow approximation may hold for early life stages [47], but not necessarily for grown organisms [48–50], and certainly not for the large accelerations generated when these organisms escape predators by jumping [49,51], as mentioned above. For such jumps, the unsteady term  $\partial \mathbf{w} / \partial t$  in the Navier-Stokes equations matters ( $\mathbf{w}$  is the velocity of the disturbance flow created by the particle). In the simplest case, the inertial effect of this unsteady acceleration is described by the unsteady time-dependent Stokes equation, resulting in the above-mentioned history force. For time-dependent but spatially homogeneous flows, it is understood how weak convective fluid inertia changes the history force for passive particles [3,4,10]. But it is not known in general how the different inertial effects compete to determine the unsteady motion of microswimmers.

Wang and Ardekani [52] solved the time-dependent Stokes equation to describe how history effects delay the decay of the velocity of a *copepod* after a jump. The authors found that the history force is essentially that of a passive particle, with a kernel that decays as  $t^{-1/2}$  (a consequence of the diffusion of vorticity). Fitting the parameters of their theory, the authors found agreement with earlier measurements by Jiang *et al.* [51], despite the fact that the Reynolds number for jumping *copepods* is not small. The agreement is surprising because one might expect convective inertia to cause the kernel to decay more rapidly, as it does for passive particles [3,4,10].

The results of Wang and Ardekani [52] raise further questions. First, is there a principle dictating that the history force for an active particle is essentially that of a passive one? Second, how does the history force depend on the shape of the swimming particle? After all, not all motile microorganisms are spherical. Third, since natural environments are rarely perfectly quiescent, how do fluid-velocity gradients affect the inertial dynamics? Does a small swimmer in a shear flow experience a lift force, analogous to Saffman’s lift force on a passive particle in shear? Can we predict the motion of an active particle in a rotating or in a stratified fluid, mirroring what a passive particle experiences? Does fluid inertia give rise to drag reduction for a swimmer in an elongational flow? More generally, how important are unsteady effects for swimmers in time-dependent, spatially inhomogeneous flow?

The point of the present paper is to show that certain results regarding the inertial dynamics of active particles can be directly inferred from the corresponding results for passive particles, making use of a fundamental principle employed by Legendre and Magnaudet to determine the inertial lift on a small bubble in shear flow [53]. This allows us to answer at least some of the above questions.

The remainder of this paper is organized as follows. In Sec. II we briefly summarize the standard squirmer model, an idealized model for a motile microorganism. Section III recapitulates how small inertial effects can be treated in perturbation theory. In Sec. IV we describe the fundamental principle that allows us to translate known results on the inertial dynamics of passive particles to active ones. Section V describes an example, and answers some of the questions raised above. We also discuss that the principle fails under certain circumstances, and speculate about the possible reasons for this failure. We summarize our results in the conclusions, Sec. VI.

## II. SQUIRMERS: MODELS FOR SWIMMING AT LOW REYNOLDS NUMBERS

Swimming at low Reynolds numbers is commonly studied using the squirmer model originally developed by Lighthill [54] and Blake [55]. In the simplest version of this idealized model, the effect of beating cilia is represented in terms of a boundary condition, in the form tangential flow components on the surface of a spherical swimmer [38,39,49,56,57]

$$v_s(\theta) = B_1 \sin \theta + B_2 \sin \theta \cos \theta. \quad (1)$$

The dynamics is usually discussed in terms of the parameter  $\beta = B_2/B_1$ , where  $B_1$  is defined to be positive. One distinguishes pullers ( $\beta > 0$ ) from pushers ( $\beta < 0$ ), reflecting the form of the fluid disturbance caused by the swimmer. The first term in Eq. (1) has dipole symmetry, the second term is a stresslet with quadrupolar symmetry. Higher-order contributions are neglected in Eq. (1), but may matter for artificial swimmers, for instance, for Janus particles [58–60].

Blake’s solution for the disturbance flow assumes a steady swimming velocity  $\dot{\mathbf{x}}$  (the dot stands for the time derivative) and makes use of the fact that the total force on the particle vanishes because drag must equal thrust for a steady swimmer [39]. In other words, to compute the steady swimming velocity  $\dot{\mathbf{x}}$ , one solves the steady Stokes equation for arbitrary  $\dot{\mathbf{x}}$  to find the hydrodynamic force [54,55]

$$\mathbf{f}_h^{(0)} = 6\pi\mu a \left( \frac{2}{3} B_1 \mathbf{n} - \dot{\mathbf{x}} \right). \quad (2)$$

Here the superscript “<sup>(0)</sup>” denotes the leading-order steady Stokes contribution. Furthermore,  $\mathbf{n}$  is the swimming direction of the spherical swimmer. Its radius is denoted by  $a$ , and  $\mu$  is the dynamic viscosity of the fluid. The first term in Eq. (2) is the active force produced by the beating cilia, and  $6\pi\mu a$  is the resistance coefficient of the spherical particle. For a passive particle,  $B_1 = 0$ , Eq. (2) reduces to force on a passive sphere. Setting  $\mathbf{f}_h^{(0)} = \mathbf{0}$  in Eq. (2) yields the swimming velocity

$$\dot{\mathbf{x}} = \frac{2}{3} B_1 \mathbf{n} \quad (3)$$

in the steady Stokes limit. This expression is independent of  $\beta$  or any higher multipole corrections to Eq. (1).

Oseen corrections to Eq. (3) describe how steady convective fluid inertia affects the steady swimming speed. Khair *et al.* [37] found that

$$\dot{\mathbf{x}} = \frac{2}{3} B_1 \mathbf{n} \left( 1 - \frac{3\beta}{20} \text{Re}_p \right). \quad (4)$$

Here  $\text{Re}_p$  is the particle Reynolds number, measuring the effect of steady convective fluid inertia (see Sec. III for the nondimensional parameters of the problem). Equation (4) corrects an earlier result of Wang and Ardekani [38] who obtained the value 0.11 for the numerical coefficient in front of  $\text{Re}_p$ , instead of 3/20. Khair *et al.* [37] also computed the  $\text{Re}_p^2$  correction. Their results are in good agreement with those of numerical simulations [39].

Strictly speaking, beating cilia cause time-dependent perturbations, resulting in time-dependent coefficients  $B_l(t)$  in Eq. (1) and thus a time-dependent swimming speed  $\dot{\mathbf{x}}(t)$ . To take into account such time-dependent boundary conditions, Wang and Ardekani [52] solved the time-dependent Stokes equation for a spherical squirmer, neglecting the effect of convective fluid inertia. They

showed that the unsteady acceleration in the time-dependent Stokes equation gives rise to a history force, much like the history force [28–30] experienced by a passive sphere in a quiescent fluid.

### III. SINGULAR PERTURBATIONS AND THEIR NONDIMENSIONAL PARAMETERS

The swimmer accelerates the surrounding fluid as it moves, and this causes the fluid-inertia correction in Eq. (4), as well as the history force mentioned above. When such inertial corrections are small, one can use perturbation theory to analyze their effects. To determine the relevant nondimensional parameters, one expresses the Navier-Stokes equations for the disturbance velocity in nondimensional form. It is customary to nondimensionalize lengths by the size of the swimmer (its radius  $a$ , say); time by a characteristic time  $\tau_c$  over which the slip velocity varies over surface of the swimmer; velocities by a characteristic slip velocity  $u_c$ ; and fluid-velocity gradients by a characteristic strain rate  $s_c$ . This leads to three independent nondimensional parameters

$$\text{Re}_p = \frac{au_c}{\nu}, \quad \text{Re}_s = \frac{a^2 s_c}{\nu}, \quad \text{Sl} = \frac{a}{u_c \tau_c}. \quad (5)$$

Here  $\nu = \mu/\rho$  is the kinematic viscosity of the fluid with mass density  $\rho$ . First, the particle Reynolds number  $\text{Re}_p$  describes how convective terms based on the slip velocity affect the dynamics of the fluid disturbance. This is the Oseen problem. Convection can make a qualitative difference because it can carry the disturbance away from the swimmer more rapidly than diffusion alone. Second, for swimmers in spatially inhomogeneous flows, the shear Reynolds number  $\text{Re}_s$  quantifies how the imposed fluid-velocity gradients affect the disturbance caused by the swimmer (Saffman problem). Third, the magnitude of unsteady effects is determined by the product  $\text{Re}_p \text{Sl} = a^2/(\nu \tau_c)$  where  $\text{Sl}$  is the Strouhal number. Unsteady fluid accelerations are described by the time-dependent Stokes equation. Nevertheless, they are essentially an inertial effect, describing how the hydrodynamic forcing decays after a perturbation.

From now on we use the nondimensional variables described above, and expand the hydrodynamic force in a small parameter  $\varepsilon$ :

$$\mathbf{f}_h = \mathbf{f}_h^{(0)} + \varepsilon \mathbf{f}_h^{(1)} + \dots \quad (6)$$

When convective effects dominate the inertial correction, the perturbation parameter is  $\varepsilon = \text{Re}_p$ . When fluid-velocity gradients are more important, the parameter is instead  $\varepsilon = \sqrt{\text{Re}_s}$ . When unsteady effects matter most,  $\varepsilon = \sqrt{\text{Sl} \text{Re}_p}$  is the natural parameter. In general it is challenging to compute the first inertial correction,  $\varepsilon \mathbf{f}_h^{(1)}$ , in Eq. (6). Regular perturbation theory fails when perturbations, which are small close to the particle dominate far from it. In this case, singular perturbation theory is required. Masoud and Stone [61] used the reciprocal theorem to compute such inertial corrections (a particular example is given in the Appendix of Ref. [37]). This approach relies upon the fact that the disturbance flow decays as  $r^{-2}$  far from the swimmer, faster than the Stokeslet, which decays as  $r^{-1}$ . This follows from the fact that the lowest-order dynamics is obtained by setting  $\mathbf{f}_h^{(0)}$  to zero, and it allows us to apply the reciprocal theorem in its simplest form.

Here we use the method of matched asymptotic expansions instead, a standard scheme to compute small fluid-inertia effects on the dynamics of passive particles in a fluid. For a passive sphere in uniform flow, for example, Proudman and Pearson [2] computed the correction  $\mathbf{f}_h^{(1)}$  due to convective fluid inertia, obtaining the Oseen correction [62] to Stokes force, with  $\varepsilon = \text{Re}_p$ . Childress [5] computed the hydrodynamic force on a light sphere rising in a solid-body rotating fluid, to order  $\varepsilon$ . Saffman [7] derived the lift force on a passive sphere in shear flow to order  $\varepsilon = \sqrt{\text{Re}_s}$ . Note that the time-dependent term  $\partial \mathbf{w} / \partial t$  in the time-dependent Stokes equation is an inertial perturbation to the steady Stokes equation. This term gives rise to the BBO history force at order  $\varepsilon = \sqrt{\text{Re}_p \text{Sl}}$ . So the history force is essentially an inertial effect, just like the inertial Oseen and Saffman corrections to the hydrodynamic force. The advantage of matched asymptotic expansions is that it allows us to translate much of what is known for passive particles to active swimmers, as we show below.

#### IV. A FUNDAMENTAL PRINCIPLE OF ASYMPTOTIC MATCHING

The method of matched asymptotic expansions can be used when the disturbance flow  $w$  produced by the swimmer is given by Stokes equation plus inertial corrections that are small near the particle. In this inner region, the disturbance velocity can simply be expanded in the small parameter  $\varepsilon$ . Far from the particle, in the outer region, the perturbation may be substantial. In this case regular perturbation theory fails. To obtain the outer solution, far from the particle, the boundary conditions on the particle surface are approximated by a source term in the form of Dirac  $\delta$  function [63]. As a consequence, the outer problem can be solved in closed form by Fourier transform. Inner and outer solutions are matched in the matching region, at  $r \sim \varepsilon^{-1}$  [7]. In practice this means that one needs to solve the inner problem with an  $\varepsilon$ -dependent boundary condition in the matching region [23], determined by the  $\varepsilon$ -dependent outer solution. Note that this solution may depend on time if the boundary conditions on the surface of the particle are time dependent, such as the time-dependent coefficients  $B_l(t)$  mentioned in Sec. II.

The calculations are greatly simplified because the boundary condition for the inner solution far from the particle is just a uniform flow [7]. In order to illustrate how this uniform flow may arise, we disregard the details and consider only the schematic form of an outer solution, namely

$$w(r, t) = \frac{\exp[-\varepsilon \mathcal{U}(t)r]}{r}. \quad (7)$$

Here  $r$  is the distance from the particle, and  $\mathcal{U}(t)$  is a time-dependent velocity. Recall that Eq. (7) is written in nondimensional form (Sec. III). For small values of  $\varepsilon$ , Eq. (7) can be expanded as

$$w(r, t) = \frac{1}{r} - \varepsilon \mathcal{U} + \mathcal{O}(\varepsilon^2 r) + \dots \quad (8)$$

In this expansion, the first term  $r^{-1}$  corresponds to the Stokeslet, decaying as  $r^{-1}$  far from the particle. The presence of this slowly decreasing term makes the perturbation problem singular. The next term, of order  $\varepsilon$ , is the uniform flow mentioned above, a uniform velocity that does not depend on the spatial coordinate  $r$ . This term becomes an outer boundary condition for the inner problem that must be solved to obtain the  $\varepsilon$  correction to the hydrodynamic force. Note that all terms in Eq. (8) are of the same order in the matching region, for  $r \sim \varepsilon^{-1}$ , which reveals that the problem is singular.

An important feature of the uniform boundary condition at order  $\varepsilon$  is that it depends on the shape of the swimmer in a simple way. The shape of the swimmer is encoded in the amplitude of this  $\delta$  function mentioned above, in terms of the Stokes resistance tensor  $\mathbb{R}$  of the swimmer [13], and through the known propulsive force produced by the particle in Stokes limit, the first term in Eq. (2). As a consequence, only the resistance tensor  $\mathbb{R}$  and the propulsion force are needed to determine the leading-order inertial correction to the hydrodynamic force. This elegant trick appears to be due to Legendre and Magnaudet [53] who used it to determine the lift force on a bubble in shear flow. In short, the resistance tensor of a solid sphere is  $\mathbb{R} = 6\pi \mathbb{I}$ , with identity tensor  $\mathbb{I}$ , whereas the resistance tensor for a bubble is smaller by a factor of  $\frac{2}{3}$ . This implies that the amplitude of the uniform flow far from the bubble equals  $\frac{2}{3}$  that of a solid sphere. This uniform flow in turn generates an inertial correction of the same form as the Saffman lift force on a solid sphere, but scaled by a factor of  $\frac{2}{3}$ . Taken together this means that the inertial lift force on a bubble equals that for a solid sphere multiplied by a factor  $\frac{4}{9}$ , to order  $\varepsilon$ . Harper and Chang [8] used related considerations to determine the lift force on a dumbbell in a shear flow. More recently, the same principle was employed by Candelier, Mehlig, and Magnaudet [13] to determine inertia effects on a passive particle of arbitrary shape in steady linear flow.

## V. INERTIAL CORRECTIONS TO THE HYDRODYNAMIC FORCE ON AN ACTIVE PARTICLE

The main point of the present paper is to note that the principle outlined in the previous section can be applied to active particles. This allows us to infer inertial corrections to the hydrodynamic force and torque on an active particle moving through a fluid. As we will show, the principle applies provided that the equations for the disturbance flow close to the swimmer are essentially Stokes equations, perturbed by small terms that scale as  $\varepsilon^n$  with  $n > 1$ . More precisely, consider an inertial problem of the form

$$-\nabla p + \Delta \mathbf{w} = \mathcal{L}(\mathbf{w}, \varepsilon), \quad (9)$$

a Stokes problem for the disturbance velocity  $\mathbf{w}$ , perturbed by an inertial correction  $\mathcal{L}(\mathbf{w}, \varepsilon)$  with perturbation parameter  $\varepsilon$ . An example is the Saffman problem, describing a particle moving with a steady velocity in a time-independent linear undisturbed flow with fluid-velocity gradients  $\mathbb{A}$ . In this case,  $\mathcal{L}(\mathbf{w}, \varepsilon) = \varepsilon^2(\mathbb{A} \cdot \mathbf{w} + (\mathbb{A} \cdot \mathbf{r}) \cdot \nabla \mathbf{w})$ , and the perturbation parameter is given by  $\varepsilon = \sqrt{\text{Re}_s}$ . A second example is the unsteady Stokes equation, where  $\mathcal{L}(\mathbf{w}, \varepsilon) = \varepsilon^2 \partial \mathbf{w} / \partial t$  with  $\varepsilon = \sqrt{\text{Sire}_p}$ . Now, if the perturbation is of the order

$$\mathcal{L} \sim \varepsilon^n \quad \text{with } n > 1, \quad (10)$$

then the two first terms of the inner expansion—the first two terms in the expansion of Eq. (9) in the parameter  $\varepsilon$ —are both solutions of the steady Stokes equation. This is the key fact that allows us to apply the principle.

As an example, consider the second case, the unsteady inertial perturbation. Since the perturbation parameter is  $\varepsilon^2$ , one might expect that only terms even in  $\varepsilon$  occur in the perturbation expansion for the disturbance velocity. For singular perturbation problems, however, other terms may appear: in the present case terms that are odd in  $\varepsilon$ , in other cases even terms that contain  $\log \varepsilon$  [64]. This is well known, and such additional terms are sometimes called switchback terms. Our point here is that the leading switchback term, of order  $\varepsilon$ , has a very simple form.

In order to flesh out these arguments, consider first the expansion of the disturbance velocity close to the particle

$$\mathbf{w}_{\text{in}} = \mathbf{w}_{\text{in}}^{(0)} + \varepsilon \mathbf{w}_{\text{in}}^{(1)} + \dots \quad (11)$$

Here  $\mathbf{w}_{\text{in}}^{(0)}$  obeys Stokes equation with boundary condition  $\mathbf{w}_{\text{in}}^{(0)} = \dot{\mathbf{x}} + v_s \mathbf{n}$  on the surface of the swimmer. Under condition (10), the first-order correction  $\mathbf{w}_{\text{in}}^{(1)}$  too obeys Stokes equation, but now with boundary condition  $\mathbf{w}_{\text{in}}^{(1)} = \mathbf{0}$  on the swimmer surface. To solve these two Stokes problems, boundary conditions far from the swimmer are needed. They are obtained by matching the inner solution to an outer solution for the disturbance velocity, evaluated in the matching region. This outer solution,  $\mathbf{w}_{\text{out}}(\mathbf{r}, t)$ , is obtained by solving the full inertial problem (9), including the perturbation  $\mathcal{L}$ . This becomes possible if one replaces the boundary condition on the surface of the swimmer by a source term that represents the presence of the swimmer. This source term is of the form  $\mathbf{D}(t) \delta$ , where  $\delta$  is the Dirac  $\delta$  function, and the amplitude  $\mathbf{D}$  remains to be determined. To this end,  $\mathbf{w}_{\text{out}}$  is expanded as

$$\mathbf{w}_{\text{out}}(\mathbf{r}, t) = \mathcal{T}^{(0)}(\mathbf{r}, t) + \varepsilon \mathcal{T}^{(1)}(t) + \dots \quad (12)$$

To lowest order, the outer solution is [23]

$$\mathcal{T}^{(0)}(\mathbf{r}, t) = \mathbb{G}(\mathbf{r}) \mathbf{D}(t) \quad \text{with} \quad [\mathbb{G}]_{ij} = \frac{1}{8\pi} \left( \frac{\delta_{ij}}{r} + \frac{r_i r_j}{r^3} \right). \quad (13)$$

When condition (10) holds, the first order is given by [23]

$$\mathcal{T}^{(1)}(t) = - \int_0^t d\tau \mathbb{K}(t - \tau) \frac{d\mathbf{D}(\tau)}{d\tau} \equiv \mathcal{U}(t), \quad (14)$$

where it is assumed that  $\mathbf{D}(0) = \mathbf{0}$  [13], otherwise the lower bound of the integral extends to  $-\infty$ . It is important to note that  $\mathcal{T}^{(1)}(t)$  is a uniform flow,  $\mathbf{U}(t)$ , just like the second term in Eq. (8). The nature of the inertial perturbation,  $\mathcal{L}$ , is encoded in the temporal behavior of the kernel  $\mathbb{K}(t)$ , which does not depend on particle shape. The kernel is known for the Saffman problem (see Ref. [13] and references cited therein), when the undisturbed problem is a shear, solid-body rotation, or a two-dimensional elongational flow. For the unsteady problem,  $\mathbb{K}(t)$  is just the BBO kernel  $\mathbb{I}/[6\pi\sqrt{\pi t}]$  [28–30].

Equations (13) and (14) provide the desired boundary conditions for  $\mathbf{w}_{\text{in}}^{(j)}$ , namely  $\mathbf{w}_{\text{in}}^{(j)} = \mathcal{T}^{(j)}$  at  $r \sim \varepsilon^{-1}$  for  $j = 0$  and 1. Consider first the Stokes problem at order  $\varepsilon^0$ . Since  $\mathbf{w}_{\text{in}}^{(0)}$  is the Stokes disturbance velocity, we infer that  $\mathbf{D}$  must equal the Stokes force exerted by the swimmer upon the fluid:

$$\mathbf{D}(t) = -\mathbf{f}_{\text{h}}^{(0)}(t) = -[\mathbf{f}_{\text{a}}(t) - \mathbb{R}(t)\dot{\mathbf{x}}(t)]. \quad (15)$$

Equation (15) reflects the fact that the velocity over the surface of the organism can be written as a sum of two terms. The first one is the active contribution [65], written in terms of the active force produced by the swimmer,  $\mathbf{f}_{\text{a}}(t)$ . The second term is the passive part of the disturbance force. It depends upon the instantaneous shape of the particle encoded in the resistance tensor  $\mathbb{R}(t)$ .

Since  $\mathbf{U}(t)$  is a uniform flow, the order- $\varepsilon$  Stokes problem for  $\mathbf{w}_{\text{in}}^{(1)}$  is just the Stokes problem for a frozen particle (a particle kept at fixed position and orientation in the uniform flow  $\mathbf{U}(t)$  at infinity). The desired inertial correction  $\varepsilon \mathbf{f}_{\text{h}}^{(1)}(t)$  is thus simply given by the hydrodynamic force such a particle experiences,

$$\mathbf{f}_{\text{h}}^{(1)}(t) = \mathbb{R}(t)\mathbf{U}(t). \quad (16)$$

Taking Eqs. (14), (15), and (16) together we find the following expression for the inertial correction to the hydrodynamic force for an active particle:

$$\mathbf{f}_{\text{h}}^{(1)}(t) = \mathbb{R}(t) \int_0^t d\tau \mathbb{K}(t - \tau) \frac{d}{d\tau} [\mathbf{f}_{\text{a}}(\tau) - \mathbb{R}(\tau)\dot{\mathbf{x}}(\tau)]. \quad (17)$$

This is the main result of the present paper. Note that the active part  $\mathbf{f}_{\text{a}}(t)$  in  $\mathbf{f}_{\text{h}}^{(0)}(t)$  contributes linearly to the inertial correction at order  $\varepsilon$ , whereas the resistive part appears in the form of two possibly time-dependent factors  $\mathbb{R}(t)$ , one inside the integral, and one outside.

As an example, consider how to obtain the history force upon a spherical squirmer moving with velocity  $\dot{\mathbf{x}}(t)$  in direction  $\mathbf{n}(t)$  in a fluid at rest [52]. Assuming that convective and shear inertia are negligible, Stokes equations are perturbed only by the unsteady term. In this case, the small parameter is  $\varepsilon = \sqrt{a^2/(\nu\tau_c)}$  and the uniform flow is given by

$$\mathbf{U}(t) = \frac{1}{6\pi} \int_0^t d\tau \frac{1}{\sqrt{\pi(t-\tau)}} \frac{d\mathbf{f}_{\text{h}}^{(0)}(\tau)}{d\tau}. \quad (18)$$

The  $t^{-1/2}$  decay of the kernel describes how disturbance-velocity gradients relax due to viscous diffusion [28–30]. The resistance tensor is simply that of a sphere,  $6\pi\mathbb{I}$ , and the active force is  $\mathbf{f}_{\text{a}}(t) = 6\pi\frac{2}{3}B_1(t)\mathbf{n}(t)$ . Using Eqs. (6), (17), and (18), immediately gives

$$\mathbf{f}_{\text{h}}(t) = -6\pi(\dot{\mathbf{x}}(t) - \frac{2}{3}B_1(t)\mathbf{n}(t)) - 6\pi\varepsilon \int_0^t d\tau \frac{1}{\sqrt{\pi(t-\tau)}} \frac{d}{d\tau} \left[ \dot{\mathbf{x}}(\tau) - \frac{2}{3}B_1(\tau)\mathbf{n}(\tau) \right] \quad (19)$$

for the unsteady hydrodynamic force on a squirmer (the added-mass term is a higher-order contribution to the force of order  $\varepsilon^2$ ). In the special case where  $\mathbf{n}$  is a constant vector, Eq. (19) reduces to a result obtained earlier by Wang and Ardekani [52] using the method of Laplace transforms. This expression was first derived by Morrison [66], describing the electrophoretic force upon a dielectric sphere in a transient electric field.

Equation (17) explains why the hydrodynamic force on an unsteady spherical squirmer must be of the form (19), and it demonstrates how to generalize the result to arbitrary shapes. Since motile

aquatic microorganisms exhibit a rich variety of shapes and swimming gaits [67,68], it is useful that Eq. (17) separates the contributions to the hydrodynamic force due to particle shape, through the tensor  $\mathbb{R}$ , from those due to the time dependence of the fluid disturbance, through the kernel  $\mathbb{K}$ .

Equation (17) implies that the inertial correction vanishes in the steady limit, for example for a steady squirmer with  $\dot{\mathbf{x}} = \frac{2}{3}B_1\mathbf{n}$ . In this case  $\mathbf{f}_h^{(0)}$  vanishes, so that there is no inertia-induced force at order  $\varepsilon$  (see, for example, Refs. [69,70]). As a consequence, the disturbance flow produced by the swimmer is a stresslet. For transient dynamics, on the other hand,  $\mathbf{f}_h^{(0)}(t)$  is nonzero, resulting in transient inertial corrections. Such corrections arise for sudden starts or stops, and also when  $B_1(t)$  is a smooth but rapidly varying time-dependent function, so that a difference between  $\dot{\mathbf{x}}(t)$  and  $\frac{2}{3}B_1(t)\mathbf{n}(t)$  is maintained.

The above example concerns unsteady inertia effects, and answers two questions raised in Sec. I, namely why is the history force the same for active and passive particles? How does it depend on the shape of the swimmer? There are several other situations where Eq. (17) may help to determine the influence of fluid inertia on the dynamics of active particles, for example active particles in shear flows. The amoeba *Naegleria Fowleri*, for example, thrives in water-discharge flows from industrial plants, which can have shear rates as high as  $85000 \text{ s}^{-1}$  [71]. For a  $\mu\text{m}$ -sized organism this results in a shear-Reynolds number of the order of  $\text{Re}_s \sim 0.1$ , so that  $\varepsilon \sim 0.3$ , which means that fluid inertia should matter. The equation of motion for a spherical squirmer in a shear flow follows directly from Eq. (17). In nondimensional form it reads:

$$R\frac{4\pi}{3}\varepsilon^2\ddot{\mathbf{x}}(t) = -6\pi\left[\dot{\mathbf{x}}(t) - \mathbf{U}^\infty(\mathbf{x}) - \frac{2}{3}B_1(t)\mathbf{n}(t)\right] - 6\pi\varepsilon\int_0^t\mathbb{K}(t-\tau)\frac{d}{d\tau}\left[\dot{\mathbf{x}}(\tau) - \mathbf{U}^\infty(\mathbf{x}) - \frac{2}{3}B_1(t)\mathbf{n}(\tau)\right]d\tau + \mathbf{F}_{\text{ext}}. \quad (20)$$

Here  $R$  is the particle-to-fluid density ratio,  $\mathbf{U}^\infty(\mathbf{x})$  is the undisturbed shear flow at distance  $\mathbf{x}$  from the particle center [13], and  $\mathbf{F}_{\text{ext}}$  is an external force. In the steady limit, when  $B_1\mathbf{n}$  tends to a steady vector, the velocity of the particle approaches

$$\dot{\mathbf{x}} = \mathbf{U}^\infty(\mathbf{x}) + \frac{2}{3}B_1\mathbf{n} + \frac{1}{6\pi}\mathbf{F}_{\text{ext}} - \varepsilon\frac{1}{6\pi}\bar{\mathbb{K}} \cdot \mathbf{F}_{\text{ext}}. \quad (21)$$

Here  $\bar{\mathbb{K}}$  is the steady-state limit of the kernel. In this limit, the  $\varepsilon$ -inertia correction induced is the same as for a passive particle. However, the time required to reach the steady state is usually very long (typically much larger than the inverse shear rate). During this transient, the inertial effects on passive and active particles differ. The last term of Eq. (21) shows that an active particle moving with a steady velocity in a shear flow may experience a lift force, but only if there is an external force. Also note that if  $B_1(t)\mathbf{n}(t)$  varies rapidly, then  $\mathbb{K}$  simplifies to the BBO kernel. In this limit, convective inertia effects induced by shear do not matter.

Finally, Eq. (17) can be used to describe active particles in density-stratified fluids, provided that convective inertia does not matter. Equation (17) shows that there may be important inertial corrections even for  $\text{Re}_p = 0$ , when the particle density exceeds the fluid reference density, resulting in an external force  $\mathbf{F}_{\text{ext}}$  due to gravity. In Refs. [72,73], by contrast, inertial effects due to convective fluid inertia were considered. As explained below, the principle does not apply in this case.

Last but not least let us discuss when and how the principle may fail. We encountered one example where the principle does not work, an active particle moving with a large enough slip velocity so that convective inertia cannot be neglected. This is the Oseen problem mentioned in Sec. V. In this case, the perturbation in the perturbed Stokes problem (9) takes the form  $\mathcal{L} = -\varepsilon\dot{\mathbf{x}} \cdot \nabla\mathbf{w}$  in a quiescent fluid, with  $\varepsilon = \text{Re}_p$ . This perturbation is of order  $\varepsilon$ , so the above condition needed to justify the principle is not fulfilled. As a consequence, the inner solution is no longer governed by a Stokes equation, as assumed above, but by an inhomogeneous differential equation including terms arising from the solution at leading order in  $\varepsilon$ . This explains why the inertial  $\text{Re}_p$  corrections to the force acting on a spherical squirmer described in Refs. [38,39] are not entirely recovered by



the principle. Returning to the results of Legendre and Magnaudet [53], note that the principle does give the correct Oseen correction to the drag force on a bubble: setting  $\mathbf{f}_a = \mathbf{0}$  in Eq. (17), and inserting the resistance tensor of a spherical bubble,  $\mathbb{R} = 4\pi\mathbb{I}$ , gives the correct result, namely that convective-inertial correction to the drag force on a bubble is  $\frac{4}{9}$  times that for a solid sphere. We speculate that the result is correct for a spherical bubble because the additional terms mentioned above vanish due to spherical symmetry.

## VI. CONCLUSIONS

We described a fundamental principle that allows us to infer the effect of fluid inertia on the dynamics of motile microorganisms moving in a fluid. In its original form, the principle was used by Legendre and Magnaudet [53] to infer the lift force on a bubble in shear flow from Saffman's result for a solid particle. Here we showed how the principle works for active particles. We demonstrated how it allows us to infer the leading-order inertial corrections to the hydrodynamic force experienced by the particle, as it swims through the fluid. Our results explain why the history force has essentially the same form for active and passive particles. We show that particle shape affects the inertial correction to the hydrodynamic force in a very simple way, making it possible to investigate the effect of particle shape on the hydrodynamic force in a straightforward manner. As an example we considered the effect of unsteady inertia on the hydrodynamic force. We also discussed other situations where the principle applies, namely shear flows and density-stratified fluids.

Naturally, the method has limitations. As presented here, certain conditions must be fulfilled for the principle to work (Sec. V). These conditions are met for unsteady and Saffman problems, but not for the Oseen problem (convective fluid inertia). Therefore it remains an open problem how to compute convective inertial corrections to the history force on an active swimmer, even for a time-dependent homogeneous flow. One question is how the convective corrections to the history force differ from those obtained by Lovalenti and Brady [4] for a passive particle. At any rate, such convective effects must be considered to describe the disturbance velocities generated by jumping *copepods*, where unsteady and convective fluid inertia are likely to be equally important.

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