Micro-swimmers with hydrodynamic interactions

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A B S T R A C T

The low-Reynolds-number motions of Purcell’s three-link swimmer, and of a closely related two-paddle swimmer, are investigated and compared using slender-body theory and resistive-force theory. The results are compared (in the case of the three-link swimmer) with the resistive-force calculations of Becker, Koehler and Stone (BKS). In particular, we examine the effect of hydrodynamic interaction and slenderness on the displacement and efficiency of the swimmers. The BKS analysis is, for the most part, confirmed and extended. However, deviations of up to 43% are found in cases where the swimmer propels itself with large stroke angles. Finally, we discuss recent experimental data in light of our numerical results.

1. Introduction

The self-propulsion of microorganisms is a topic of considerable biological significance [1–5]. As a topic in low-Reynolds-number hydrodynamics (Re ≪ 1), the physics is characterized by the overwhelming dominance of viscous forces over inertial forces. As a result, dynamics at low Reynolds number has special and unique characteristics, and the locomotion mechanisms of microorganisms at low Reynolds number are essentially different from that of larger creatures (such as cephalopods, fish and marine mammals), which obtain propulsive momentum from the reaction force of surroundings objects or fluid, and rely largely on the inertia of the surrounding medium. In addition to understanding existing patterns of micro-biological movements and flows, studies of low-Reynolds-number locomotion are fundamental to the design and control of self-propelled micro-mechanical robots and swimmers [6].

E.M. Purcell introduced the concept of a three-link swimmer in his famous article “Life at low Reynolds number”, published in 1977, but transcribed from a lecture given a couple years earlier at a symposium in honor of the physicist Victor Weisskopf [7]. The three-link swimmer is sometimes referred to as Purcell’s swimmer. Purcell’s swimmer was originally proposed as a hypothetical construct that could (in principle) propel itself at low Reynolds numbers. However, it was reported recently that the bacterium Spiroplasma propels itself in a similar way [8–10]. In fact, the analogy is more suggestive than exact, and subsequent analysis and modeling [11,12] has revealed the kink–pair kinematics of spiroplasmic swimming. Purcell’s swimmer can also be viewed as a planar, piecewise-linear flagellum—a highly simplified picture of eukaryotic flagella and cilia [13,14]. As a useful prototype for exploring the fundamental mechanisms of self-propulsion at low Reynolds number, Purcell’s swimmer has been investigated extensively in recent years [13,15–19]. In addition to the three-link...
swimmer, Purcell introduced a singly hinged “scallop” whose reciprocal motion resulted in no net translation or rotation. This “scallop theorem” for reciprocal motions follows from the kinematic reversibility of the Stokes equations.

In this paper, we introduce a two-paddled variation on Purcell’s three-link swimmer. While this swimmer at first appears even more hypothetical than Purcell’s, we shall give an example of a recent experimental realization (for a rendering of the two-paddle swimmer and its attached motors, see Fig. 1) [20]. A schematic view of Purcell’s original swimmer is shown in Fig. 2(a): three slender rods are articulated at two hinges, with the front and rear links rotating alternately around their respective shafts. The cyclic stroking strategy is shown in the configuration space of linkage angles \( \theta_1 \) and \( \theta_2 \) (see Fig. 2(c) and (d)), where \( \theta_1 \) and \( \theta_2 \) are the angles between the rods and the x axis of the coordinate system. The two-paddle swimmer (see Figs. 1 and 2(b)) is similar to Purcell’s swimmer, but lacks a middle rod. The two paddles (each of length \( a \)) are attached on shafts separated by a fixed distance \( b \) and rotate according to the same strategy as Purcell’s swimmer, except that, in the case of Purcell’s swimmer, the stroke angles cannot be greater than 360° (to avoid self-interaction). The paddle swimmer has no such angle restrictions. The paddle swimmer has applications in the design of a mechanical robot for granular media, and as a model system for studying the locomotion of creatures swimming in sand [20,21].

Here we focus on comparing resistive-force theory (RFT) with slender-body theory (SBT). Becker et al. [13] have conducted a comprehensive study of Purcell’s swimmer using resistive-force theory; however, the simulation results have not been tested by experimental data. Furthermore, details of the velocity field, as well as the hydrodynamic interaction induced by the swimmer, cannot be provided under the restrictions of resistive-force theory. Even though RFT is widely applied in investigations of the locomotion of microorganisms due to the advantage of its simplicity, it cannot account for the hydromechanical interactions [22]. More accurate predictions of self-propulsion can be made with slender-body theory by means of the fundamental singularities of Stokes flow. There are only a few works that study Purcell’s swimmer with the hydrodynamic interactions included [17–19], and none (as far as we know) that have studied the hydrodynamics of the two-paddle swimmer. Here, our aim is to examine the effect of hydrodynamic interactions on the motility of both swimmers.
Fig. 1. Drawing of a robotic two-paddle sand swimmer. It consists of two servo-motors mounted to a skid and attached to rotating paddles. The latter are immersed about 5 cm into the granular medium, while the skid rides on the surface.

Fig. 2. Schematic illustration of (a) Purcell’s swimmer, (b) Paddle swimmer (dashed line is for illustration only), (c) Stroking strategy in configuration space (• is the initial state), and (d) Stroking sequence in four steps.

The paper is organized as following: The RFT and SBT are reviewed in Section 2, as well as the finite-element method used to implement these theories numerically. Section 3 reviews a relevant experiment, and the numerical simulation results are presented and discussed in Section 4.

2. Self-propulsion models

The inertial parts of the Navier–Stokes equations are negligible for microorganisms swimming at low Reynolds number due to the dominant viscous forces. The governing equations can be simplified to the Stokes equations:

\[ \nabla \cdot \mathbf{u} = 0 \]
\[ \mu \nabla^2 \mathbf{u} = \nabla p \]

where \( \mathbf{u} \) is the velocity, \( p \) is the pressure field, and \( \mu \) is the (dynamic) viscosity. Most importantly, the Stokes equations are linear in \( \mathbf{u} \). Two theories available for solving problems of low-Reynolds-number flow, resistive-force theory [23,24] and slender-body theory [25,26], are introduced in the following sections.

2.1. Resistive-force theory

For microorganisms swimming at low Reynolds number, the propelling forces are balanced by the resistance forces exerted by the surrounding fluid, which can be approximated by resistive-force theory. Accordingly, the relationship between the velocity of the object and the frictional force can be represented as a resistance matrix, i.e., \( \mathbf{R} \mathbf{u} = \mathbf{F} \) (where \( \mathbf{R} \) is the resistance matrix, \( \mathbf{F} \) is the force, and \( \mathbf{u} \) is velocity). More specifically, it can be written as following [27]:

\[ \int_{\Gamma(s)} \mathbf{n} \cdot \mathbf{a} d\Gamma = -\left[ \frac{2\pi \mu}{\ln(2/\varepsilon)} \right] (2\mathbf{I} - \mathbf{\tau} \mathbf{\tau}) \cdot \mathbf{u}(s) + \mathcal{O} \left[ \ln^{-2}(2/\varepsilon) \right] \]

where \( s \) is the arc-length along the centerline, \( \Gamma \) is the perimeter of the slender body cross-section, \( \varepsilon \) is the slenderness ratio of diameter to length, \( \mathbf{\tau} \) is the tangential vector, and \( \mathbf{u} \) is the local velocity. (For \( \varepsilon \) we follow the slightly misleading terminology in [13]—it is actually a “fatness ratio”, since larger values mean a fatter body.) Thus, the force distribution along the particle can be obtained by solving the resulting system of equations with boundary conditions on the particle surface.
2.2. Slender-body theory

In slender-body theory, the rigid body is replaced with fundamental singularities, such as stokeslet, doublet, or higher-derivative type functions, which are solutions of the Stokes equation. The singular solutions can be superposed due to the linearity of the Stokes equation. The stokeslet represents the velocity distribution induced by a point force applied to the fluid, and the doublet represents the limiting velocity field as a source approaches a sink infinitesimally [28]. The singularity distributions can be obtained by enforcing the boundary conditions on the slender-body surface. The velocity and pressure fields caused by a stokeslet and a doublet located at the origin of a Cartesian coordinate system are, respectively, stokeslet:

\[
\begin{align*}
    u &= \frac{F}{8\pi\mu} \left( \frac{x^2 + \frac{\ell^2}{3}}{\ell^3}, \frac{xy}{\ell^3}, \frac{xz}{\ell^3} \right), \\
p &= \frac{Fx}{4\pi\ell^3}
\end{align*}
\]

doublet:

\[
\begin{align*}
    u &= \frac{Fr^2}{16\pi\mu} \left( \frac{1}{\ell^3} - \frac{3x^2}{\ell^5}, -\frac{3xy}{\ell^5}, -\frac{3xz}{\ell^5} \right), \\
p &= 0
\end{align*}
\]

where \((x, y, z)\) are the coordinates of a field point, \(F\) is the point force at the origin, \(\ell\) is the distance from the origin to the field point, \(\mu\) is the fluid viscosity, and \(r\) is the radius of the slender body.

2.3. Numerical implementation

A finite-element method is used to implement the RFT and SBT numerically. The swimmers are discretized into elements consisting of line segments, and for each element the force distribution is assumed to be constant. For SBT, the choice of element size (segment length) is largely by rule of thumb. If the element size is too large, the solution will not be sufficiently resolved. However, if the element size is too small, the element will have a high effective \(\varepsilon\) ratio and it will not be slender any more. In this study, the element size was chosen by running some test cases, and we found that \(N \simeq 10\) elements (per length \(a\)) achieved the optimal trade-off between resolution and convergence. The velocity field is obtained by integrating over the entire geometry, and the velocity on the slender-body surface has to satisfy the no-slip boundary condition. The singularity distribution is solved from the resulting system of linear equations based on the boundary conditions, as well as the kinematic conditions, i.e., force-free, torque-free, and constant applied torque difference between the two linkages rotating around one of the hinges. The kinematic conditions can be stated as following:

\[
\begin{align*}
    \sum F &= 0 \\
    \sum M &= 0 \\
    M_1 - M_2 &= \text{const.}
\end{align*}
\]

Physically speaking, the propulsion is driven by the finite applied torque difference in the third equation. The resulting linear-equation system can be written generally as \(Ax = b\), where \(A\) is the matrix of coefficients and \(x\) is the unknown vector of velocity, angular velocity, and force distributions along the slender body.

3. Experimental studies

To probe the physics of locomotion in granular media, Bzdega et al. [20] constructed a two-paddled robotic sand-swimmer especially designed for granular beds. The two-paddle swimmer was chosen because Purcell’s three-link design proved unsuitable—the tendency of granular material to jam in tight spaces prohibited the addition of a middle link. The driving mechanism consisted of two computer-controlled stepper motors mounted on a plate suspended above the surface of the granular medium. Each motor independently controlled the slow rotation (approximately 10 rpm) of a rectangular paddle, and only the paddles and shafts were inside the granular bed, which consisted of 5 mm diameter glass beads. Murray’s group at Caltech, in their study of low-Reynolds-number swimming near a planar wall, has recently built two- and three-sphere swimmers driven in a similar manner [29,30]. Different stroking sequences of the paddles could be programmed, and the displacement of the robot’s center-point could be measured after many stroking iterations. Despite major differences in the fluid-like behavior of granular media and simple fluids, these experiments reveal surprising agreement between swimming in granular beds and swimming in viscous fluids, as will be discussed in the next section.

4. Results and discussion

For the two types of swimmer considered in this paper, Purcell’s swimmer and the paddle swimmer (see Fig. 2(a) and (b)), RFT and SBT are each applied to simulate the locomotion induced by different stroking strategies. Based on the simulation, the effects of the stroking angle, slenderness ratio and hydrodynamic interaction on the displacement and efficiency of the swimmers are determined.

Fig. 3 presents the paddle swimmer’s displacement per stroking cycle in the \(x\) direction as a function of stroking angle \(\Delta \theta\) with different slenderness ratios \(\varepsilon\). The net displacement in the \(y\) direction per stroking cycle should be zero, so only the
displacement in the $x$ direction, $\Delta_x$, is considered herein, and that displacement is de-dimensionalized by dividing by the characteristic length scale $a$. The displacement as a function of stroking angle obtained by RFT is shown by the solid line, and the displacements as a function of stroking angle for the paddle swimmer with different slenderness ratios obtained by SBT are indicated by the dotted line ($\varepsilon = 0.02$), dashed line ($\varepsilon = 0.06$), and dotted–dashed line ($\varepsilon = 0.1$). The experimental data of Bzdegia et al. are shown by the solid line with circle symbols. The cross-section of the swimmer used in the experiment is rectangular ($3 \times 25$ mm) rather than circular; it is therefore assumed that the rectangular bar is equivalent to a circular rod having the same cross-sectional area. The resulting effective diameter $d^*$ for the bar is then used to compare the numerics with the experimental data. The effective slenderness ratio $\varepsilon^* = d^*/a$ corresponding to the experiment’s swimmer is 0.17 according to the aforementioned calculation. The results show that the displacement per cycle changes direction periodically with the stroking angle, and that the amplitude of the displacement per cycle is higher for larger stroking angle. Additionally, the displacement is largely overestimated by resistive-force theory compared with the experimental data. By contrast, the predictions of slender-body theory approach the data as the slenderness ratio is increased toward the experimental value.

One of the convenient features of resistive-force theory is that it knows nothing about the finite diameter of the paddle. Despite the $\varepsilon$-dependent drag coefficient in Eq. (3), any constant multiplier can be factored out of Eqs. (6) and (7). In this approximation, the displacement per cycle is merely a function of stroking angle, and it has nothing to do with the slenderness ratio. (Strictly speaking, it corresponds to $\varepsilon = 0$.) For the case of our swimmers, the comparison to the slender-body simulations shows the inadequacy of the resistive-force approach. From the slender-body theory results, the displacement per cycle is not only a function of the stroking angle, but also of the slenderness ratio. However, it is precisely in this regard that SBT presents its own limitations, since it becomes less and less valid as the width-to-length ratio becomes larger and larger. The breakdown of the numerical scheme is signalled by a lack of convergence, and is due to the inability of the stokeslet and doublet source terms, which have different long-range dependences on distance, to satisfy the uniform boundary conditions. These boundary conditions cannot be realized by discretized elements having effective slenderness values ($\varepsilon_{\text{eff}} = N\varepsilon$) greater than $\sim \mathcal{O}(1)$. In other words, the maximum practical slenderness ratio is given by $\varepsilon \sim \mathcal{O}(1/N)$. Therefore, the largest slenderness ratio simulated in this present work is $\varepsilon = 0.1$, which still does not reach the value in the experiment. Despite these limitations, the numerical results obtained from slender-body theory at aspect ratio $\varepsilon = 0.1$ are much closer to the experimental results than the resistive-force numerics, and capture all the major experimental trends. It is remarkable that zero displacement per cycle is found consistently at certain particular stroking angles, at approximately $200^\circ$, $380^\circ$, $540^\circ$, $740^\circ$ and $960^\circ$ (numerical error bars are of order $\pm 3^\circ$ in each case), no matter which theoretical approach is used for simulation. A plot of these zero-displacement stroking angles versus their index $k$ gives a best-fit linear relation of $\Delta \theta = 186k$ (see Fig. 4). The actual slope is $186 \pm 4^\circ$, which is close to $180^\circ$, but the deviation is measurable and systematic variations with a period of $720^\circ$ may be present. The question is raised of whether there is an invariance which obtains only at multiples of a certain angle. First, following the BKS analysis as applied to the general two-paddle case, the $x$ displacements over quarter cycles are identical. Second, let us consider separately the cases of even and odd multiples $k$ of $180^\circ$. For the case of a $360^\circ$ stroke angle, the key to showing a Purcell-type scallop theorem is to divide each quarter cycle into two halves and apply kinematic reversibility to show that a displacement of $+\Delta_x$ over the first $1/8$ cycle implies a displacement of $-\Delta_x$ over the second $1/8$ cycle. The first stroke angle (half stroke) for which the $1/8$-cycle geometrical symmetry holds is $180^\circ$, meaning that zero net displacement should appear at strokes equal to even multiples of $180^\circ$. For the case of an approximately $180^\circ$ stroke angle (and odd multiples thereof), during the first one-eighth stroke, the central axis of the swimmer is pushed (positive $x$ displacement), and during the second one-eighth stroke, it is pulled (negative $x$ displacement). This combination can and will result in zero net $x$ displacement over the quarter cycle, if the push and the pull exactly cancel. However, it is difficult to use symmetry arguments to see where the resultant is exactly zero. This is because, on the first one-eighth cycle, the displacement is lessened by the far paddle which, at approximately $90^\circ$ to the central axis, is in the “least aligned” position; however, on the second one-eighth cycle, the progressively more-aligned far
paddle restrains the motion less (the midpoint motion over the two one-eighth cycles is denoted by 1 and 2 in Fig. 5). That these arguments cannot precisely identify the angles seen in our numerics is due to our focus (over a one-eighth cycle) on just one paddle at a time. The zeros of net displacement appearing in Fig. 9 of the BKSpaper [13] are qualitatively consistent with a deviation from exact multiples: a first (nontrivial) zero at ~218° and a second zero at ~378° (extrapolated).

The displacement per cycle as a function of slenderness ratio for various stroking angles is illustrated in Fig. 6. The dimensionless displacement is plotted in log scale, and the stroking angles considered here (300°, 460°, 630°, 880°) are those values at which maximum displacement is achieved. The results indicate that the displacement per cycle at fixed stroking angle decreases exponentially with slenderness ratio, and that the rate of decay (in ε) correlates with the direction of net motion. In other words, the ε decay rates for positive displacements are the same even at different stroking angles (460° and 880°), and likewise for the negative displacements (300° and 630°). Furthermore, the ε decay rate for positive displacements is faster than that for negative displacements. As the ε becomes smaller and smaller, the results obtained
The velocity field and the stream-function isolines at snapshots during the locomotion of the paddle swimmer are presented in Fig. 7. Time \( t \) is made dimensionless by the characteristic time scale (stroking cycle \( t_{\text{cyc}} \)) as the dimensionless time \( t^* = t/t_{\text{cyc}} \), so that the total time \( t^* \) of a stroking cycle is one. The profiles shown in Fig. 7 start at the beginning (see Fig. 2(d)) and divide each stroking cycle into the four steps corresponding to the four straight lines in the phase-space loop (see Fig. 2(c)). The small circles mark the shafts that the rods rotate around. At time \( t^* = 0 \), the left arm rotates counterclockwise and the right arm has no rotation. At the next step, \( t^* = 0.25 \), the right arm is rotating clockwise and the left arm has no rotation. The left and right arms alternately rotate around the shaft on each step. The velocity fields show that the fluid velocity close to the rod is much larger than far from the rod, and that only the fluid within a small region surrounding the swimmer is disturbed by the swimming stroke. The interesting thing is that there is a hyperbolic fixed point located between the two arms, as is evident from the stream-function isolines. Also, the velocity fields at the instants \( t^* = 0 \) and \( t^* = 0.25 \) and \( t^* = 0.5 \) and \( t^* = 0.75 \), are related to each other by mirror symmetry, as one expects from the phase-space cycle (Fig. 2(c)). The degree to which this is obtained in Fig. 7 can be used to verify whether the program is properly implemented.

Fig. 8 indicates the effect of hydrodynamic interaction on the net displacement of swimmers with different geometries, comparing Purcell’s swimmer and the paddle swimmer. The displacement per cycle as a function of stroking angle obtained from RFT is illustrated by the dashed lines with triangular symbols, while the solid lines with circular symbols are the results from SBT. The results show how hydrodynamic interaction can have a large effect on the dynamics of Purcell’s swimmer; for instance, even the displacement direction is reversed for the stroking angles from 220° to 240°. For Purcell’s swimmer, the zero-displacement stroke angles are no longer interchangeable between RFT and SBT. However, as far as the paddle swimmer is concerned, the results obtained by the two methods are still qualitatively consistent—the direction of motion and zero-displacement stroke angles are the same; just the magnitude of the displacement is smaller from slender-body theory.

The efficiency of the paddle swimmer as a function of stroke angle at various slenderness ratios is shown in Fig. 9, where the solid line is the efficiency corresponding to the RFT simulation, and various dashed lines correspond to SBT with different slenderness ratios. As conventionally defined, the swimming efficiency \( E \) is the power needed to pull the straightened swimmer along its axis with average velocity relative to the mechanical energy input to achieve that velocity [31,13], i.e.

\[
E = \frac{(2a + b)\xi u_k^2}{\langle \Phi \rangle}
\]

where the drag coefficient is \( \xi = 2\pi \mu / \ln(2/\varepsilon) \), \( u_k \) is the projected average velocity of the swimmer, and \( \langle \Phi \rangle = \int_0^{t^*} \Phi \, dt / t \) is the time average of the input mechanical energy \( \Phi = M \omega \) (where \( M \) is torque, and \( \omega \) is angular velocity). The results show that the efficiency varies with the stroking angle in a periodic fashion, going to zero at those special angles corresponding to zero displacement. The efficiency of the paddle swimmer reaches a global maximum at a stroking angle around 300°. In addition, the efficiency decreases monotonically as \( \varepsilon \) increases; i.e., the fatter the swimmer, the less efficient it is. Note that the maximum efficiency is smaller than 1%, which is consistent with the values reported in the literature [7].

5. Conclusions

A comprehensive numerical study of the comparative locomotion of Purcell’s swimmer and a two-paddled variation, using both resistive-force theory and slender-body theory, is presented in this paper. The simulations employing RFT largely
overestimate the performance of both swimmers compared with SBT, and where experimental results are available, SBT provides consistently converging results for finite slenderness ratio. As the paddle’s width-to-length ratio increases, both the swimmer’s displacement per cycle and efficiency decrease. Certain special stroke angles correspond to most efficient swimming, and others are spectacularly inefficient, as these correspond to no net displacement at all. The approximate symmetries responsible for these special stroke angles are related to the geometry of the strokes over one eighth of the swimming cycle.

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References