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Abstract. The swimming of a pair of spherical bladders that change their volumes and mutual distance is superior to other models of artificial swimmers at low Reynolds numbers. The swimming resembles the wriggling motion known as *metaboly* of certain protozoa.

Contents

1. Introduction and statement of results

Swimming at low Reynolds numbers can be remote from common intuition because of the absence of inertia [1]. In fact, even the direction of swimming may be hard to foretell [2]. At the same time, and not unrelated to this, it does not require elaborate designs: any stroke that is not self-retracing will, generically, leads to some swimming [3]. A simple model that illustrates these features is the three linked spheres [4], (figure 1, right), that swim by a periodic contraction (in quadrature) of the distances $\ell_{1,2}$ between neighbouring spheres. The swimming stroke is a closed, area enclosing, path in the $\ell_1 - \ell_2$ plane. Another mechanical model, Purcell's two hinge model [5], has actually been built recently and can be viewed on the website [6].

Swimming efficiently is an issue for artificial micro-swimmers [7]. As we have been cautioned by Purcell not to trust common intuition at low Reynolds numbers [2], one may worry that efficient swimming may involve unusual and non-intuitive swimming styles. The aim

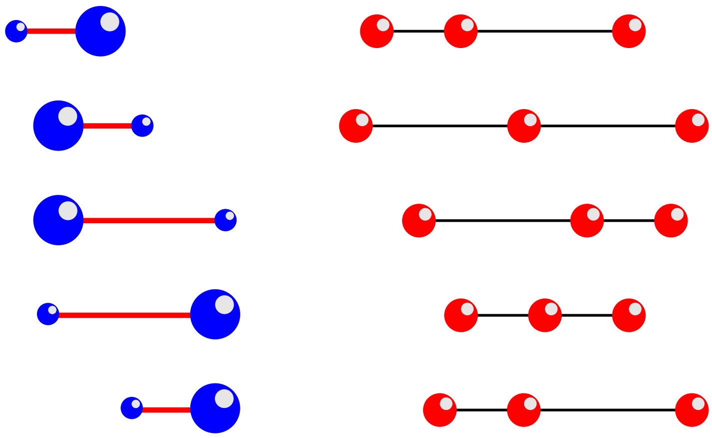

Figure 1. Five snapshots of the pushmepullyou swimming stroke (left) and the corresponding strokes of the three linked spheres (right). Both figures are schematic. After a full cycle, the swimmers resume their original shape but are displaced to the right. Pushmepullyou is both more intuitive and more efficient than the three linked spheres. See the accompanying movie.

of this paper is to give an example of an elementary and fairly intuitive swimmer that is also remarkably efficient provided it is allowed to make large strokes.

The swimmer is made of two spherical bladders that exchange volumes in each stroke, figure 1(left). For the sake of simplicity and concreteness we assume that the total volume, v_0, is conserved. The bladders are elastic bodies that impose no-slip boundary conditions. The swimming stroke is a closed path in the $v - \ell$ plane, where v is the volume of, say, the left sphere and ℓ the distance between them. For reasons that shall become clear below, we call the swimmer pushmepullyou.

Like the three linked spheres, pushmepullyou is mathematically elementary only in the limit where the distance between the spheres is large, i.e. when $\varepsilon_i = a_i/\ell \ll 1$ (a_i stands for the radii of the two spheres and ℓ for the distances between the spheres). In this limit, one can construct a solution to a collection of spheres from the known solution to a single sphere using the linearity of the Stokes equations for low Reynolds number $R = \rho a v/\mu \ll 1$ (see the appendix). We further assume that the distance ℓ is not too large, i.e. $\ell v \ll \mu/\rho$. This last assumption is not essential and is made for simplicity only. (To treat large ℓ one needs to replace the Stokes solution, equation (A.1), by the more complicated, but still elementary, Oseen–Lamb solution [8].)

Pushmepullyou is simpler than the three linked spheres: it involves two spheres rather than three; it is more intuitive physically and is easier to solve mathematically. It also swims a larger distance per stroke and is considerably more efficient.[1] If large strokes are allowed, it can outperform conventional models of biological swimmers that swim by beating a flagellum [9]. If only small strokes are allowed then pushmepullyou, like all squirmers [7], becomes rather inefficient.

[1] A competetion between the three linked spheres and pushmepullyou can be viewed at http://physics.technion.ac.il/ãvron. The competition is made with the following rules: the spheres have the same (average) radii and the same (average) ℓ. Furthermore, the strokes are similar rectangles in shape space with identical periods. Pushmepullyou is then both faster and spends considerably less energy.

The swimming velocity is defined, geometrically, by $\dot{X} = (U_1 + U_2)/2$ where U_i are the velocities of the centres of the two spheres. Our sign convention is, as usual, that velocity to the right is considered positive. To solve a swimming problem, one needs to find the (linear) relation between the (differential) displacement $đX$ and the (differential) controls $(\mathrm{d}\ell, \mathrm{d}v)$. This relation, as we show in the appendix of this paper, takes the form:

$$2đX = \frac{a_1 - a_2}{a_1 + a_2}\mathrm{d}\ell + \frac{1}{2\pi\ell^2}\mathrm{d}v, \tag{1.1}$$

where a_1 and a_2 are the radii of the left and right spheres respectively, v is the volume of the left bladder and $đX > 0$ represents an infinitesimal displacement to the right. The bar in $đX$ stresses that the differential displacement does not integrate to a function $X(\ell, v)$. Rather, the displacement $X(\gamma) \equiv \int_\gamma đX$ depends on the path in the space of controls, represented by a curve in the $\ell - v$ plane. A stroke is a closed path γ in the space of controls and swimming means that $X(\gamma) \neq 0$.

The first term in equation (1.1) says that increasing ℓ leads to swimming in the direction of the small sphere. It can be interpreted physically as the statement that the larger sphere acts as an anchor while the smaller sphere does most of the motion when the 'piston' ℓ is extended. The second term says that when ℓ is held fixed, the swimming is in the direction of the contracting sphere: the expanding sphere acts as a source pushing away the shrinking sphere which acts as a sink to pull the expanding sphere. This is why the swimmer is dubbed pushmepullyou.

Using Stokes' theorem of elementary calculus and equation (1.1), one readily sees that the swimming distance δX associated to an infinitesimal closed loop is

$$\delta X = \tfrac{1}{2}\left[\partial_v\left(\frac{a_1 - a_2}{a_1 + a_2}\right) - \partial_\ell\left(\frac{1}{2\pi\ell^2}\right)\right]\mathrm{d}v \wedge \mathrm{d}\ell, \tag{1.2}$$

where $\mathrm{d}v \wedge \mathrm{d}\ell$ denotes the signed area enclosed by the loop (the sign reflects the sense of traversal of the loop: clockwise or anticlockwise).

To gain insight into what formula (1.2) implies, consider the special case of small strokes near equal bi-spheres. Dropping sub-leading terms in $\varepsilon_i = a_i/\ell$, one finds:

$$\delta X = \tfrac{1}{6}\mathrm{d}(\log\, v) \wedge \mathrm{d}\ell. \tag{1.3}$$

The distance covered in one stroke scales like the area in the $(\log v) - \ell$ plane. Remarkably, the swimming distance is independent of the distance between the two spheres, even though the two may be far apart and ε is small. This is in contrast with the three linked spheres where the swimming distance of one stroke is proportional to ε. For a small cycle in the $\ell_1 - \ell_2$ plane, Najafi and Golestanian found for a symmetric swimmer (equation (11) in [4]):

$$\delta X = 0.7\varepsilon\, \mathrm{d}(\log \ell_2) \wedge \mathrm{d}\ell_1, \tag{1.4}$$

which scales to zero linearly with ε.

Consider now a large stroke associated with the closed rectangular path enclosing the box $\ell_s \leqslant \ell \leqslant \ell_L,\ v_s \leqslant v_1, v_2 \leqslant v_L \equiv v_0 - v_s$, where $v_1 = v$ and v_2 are, respectively, the volumes of the left and right bladders. If $a_s \ll a_L$ then from equation (1.1), $X(\gamma)$ is essentially $\ell_L - \ell_s$:

$$X(\gamma) = \left(\frac{a_L - a_s}{a_L + a_s}\right)(\ell_L - \ell_s)[1 + O(\varepsilon^3)]. \tag{1.5}$$

This implies that the distance covered in one stroke is of the order of the change of the distance between the balls.

Certain protozoa and species of *Euglena* perform a wriggling motion known as *metaboly* [10] which resembles the swimming stroke of pushmepullyou. Metaboly is, at present, not well understood and while some suggest that it plays a role in feeding others argue that it is relevant to locomotion [11]. The pushmepullyou model shows that at least as far as fluid dynamics is concerned, metaboly is a viable method of locomotion. In any case, pushmepullyou is an oversimplification of the biological swimmer. Euglena resemble a deformed pear more than it resembles two disconnected spheres. However, there is no known solution to the flow equations for deformed pears. Equation (1.5) can be expected to be qualitatively, but not necessarily quantitatively, right. Racing tests made by Triemer [12] show that Euglenoids swim 1–1.5 their body length per stroke. This is in qualitative agreement with equation (1.5) for reasonable choices of stroke parameters.

The second step in solving a swimming problem is to compute the power P needed to propel the swimmer. At this point, we shall make the further simplifying assumption that the viscosity of the fluid contained in the bladders is negligible compared with the viscosity of the ambient fluid. This makes the model soluble. By general principles, P is a quadratic form in the velocities in the control space and is proportional to the (ambient) viscosity μ. The problem is to find this quadratic form explicitly. If the viscosity of the fluid inside the bladders is negligible, one finds that in order to drive the controls ℓ and v, pushmepullyou needs to invest the power

$$\frac{P}{6\pi\mu} = \left(\frac{1}{a_1} + \frac{1}{a_2}\right)^{-1} \dot{\ell}^2 + \frac{2}{9\pi}\left(\frac{1}{v_1} + \frac{1}{v_2}\right)\dot{v}^2. \tag{1.6}$$

In the appendix, we derive this expression from first principles. Note that the dissipation associated with $\dot{\ell}$, is dictated by the *small* sphere and decreases as the radius of the small sphere shrinks. (The radius cannot get arbitrarily small and must remain much larger than the atomic scale for the macroscopic Stokes equations to hold.) The moral of this is that pushing the small sphere is frugal. The dissipation associated with $\dot{v}$ is also dictated by the small sphere. However, in this case, dilating a small sphere is expensive.

In artificial realizations of pushmepullyou, the bladders could be filled with low-viscosity gases and equation (1.6) would then apply. This is not the case for Euglena, where the viscosity of the fluid inside is comparable to the viscosity of the fluid outside. Metaboly involves significant dissipation inside the organism and equation (1.6) does not apply. If one attempts to take the inside flow into account then the model becomes intractable and there is no closed form solution to the metric. An intermediate approach is to try and estimate roughly the inside dissipation: in a tube of length ℓ and radius a, which transports flux $\dot{v}$ of fluid with viscosity μ_{in}, the dissipation is of the order of $\mu_{in}\ell\dot{v}^2/a^4$. This term is similar to the second term in equation (1.6) but is larger by a factor $1/\varepsilon$. In any case, it is clear that the inside flow, dissipative or not, cannot affect the swimming equation (1.1), which is wholly determined by the outside flow.

The drag coefficient is a natural measure to compare different swimmers. It measures the energy dissipated in swimming a fixed distance at a fixed speed. (One can always decrease the dissipation by swimming more slowly.) Let τ denote the stroke period. The drag is formally defined by [9, 13]:

$$\delta(\gamma) = \frac{\tau\int_0^\tau P\,\mathrm{d}t}{6\pi\mu X^2(\gamma)}, \tag{1.7}$$

where $X(\gamma)$ is the swimming distance of the stroke γ. The smaller the δ the more efficient is the swimmer. δ has the dimension of length (in three dimensions) and is normalized so that dragging of a sphere of radius a by an external force has $\delta = a$.

We shall now compute the dissipation associated with the rectangular path of equation (1.5) for an ideal pushmepullyou. To do so we need to choose rates for traversing the path. The optimal rates are constant on each leg provided the coordinates are chosen as $\left(\ell, \arcsin\sqrt{\frac{v}{v_0}}\right)$. This can be seen from the fact that if we define $x = \arcsin\sqrt{\frac{v}{v_0}}$, then $4v_0\dot{x}^2 = \left(\frac{1}{v_1} + \frac{1}{v_2}\right)\dot{v}^2$ and the Lagrangian associated with equation (1.6) is quadratic in $(\dot{\ell}, \dot{x})$ with constant coefficients, like the ordinary kinetic Lagrangian of non-relativistic mechanics. It is a common fact that the optimal path of such a Lagrangian has constant speed.

From equation (1.6) we find, provided also $\ell_L^2 \gg \ell_s^2,\ \ell_L \gg \sqrt{v_0/a_s}$

$$\frac{1}{6\pi\mu}\int P\,\mathrm{d}t \approx \frac{2a_s\ell_L^2}{T_\ell}\left(1 + O\left(\varepsilon^2\frac{v_L}{v_s}\frac{T_\ell}{T_v}\right)\right), \qquad T_\ell + T_v = \tau/2, \tag{1.8}$$

where T_ℓ (T_v) is the time for traversing the horizontal (vertical) leg. (Here, ε^2 is actually $(a_s/\ell_L)^2$ rather than the much larger $(a_L/\ell_s)^2$. Also note that the second term in equation (1.6) contributed $O(v_L/T_\ell)$ rather than $O(v_L^2/(v_sT_\ell))$, as one may have expected from equation (1.6) which is dominated by the small volume.) The optimal strategy, in this range of parameters, is to spend most of the stroke's time on extending ℓ. By equations (1.7), (1.5) and (1.8), this gives the drag

$$\delta \approx 4a_s, \tag{1.9}$$

where a_s is the radius of the small bladder. *This allows for the transport of a large sphere with the drag determined by the small sphere.*

Equation (1.9) says that in principle at least, the drag can be made arbitrarily small by letting a_s get smaller. Small drag involves large strokes ($\ell_L \geqslant O(\sqrt{v_0/a_s})$ by the condition preceding equation (1.8)). The fact that one can make the drag arbitrarily small is a feature of the ideal pushmepullyou where the inside fluid is inviscid. Small a_s and large ℓ_L are penalized when the fluid inside pushmepullyou is viscous. The inner viscosity would add to equation (1.9), a term of order $\frac{\mu_{in}}{\mu_{out}}a_L^6\ell^{-1}a_s^{-4}$ which would mean that the drag can be optimized, but cannot be made arbitrarily small.

It is instructive to compare the ideal pushmepullyou with the swimming efficiency of models of (spherical) microorganisms that swim by beating flagella. These have been extensively studied by the school of Lighthill and Taylor [9, 14] where one finds $\delta \geqslant 100\,a$. This is much worse than dragging. (We could not find estimates for the efficiency δ for swimming by ciliary motion [15], but we expect that they are rather poor, as for other squirmers [7].) For models of bacteria that swim by propagating longitudinal waves along their surfaces Stone and Samuel [13] established the (theoretical) lower bound $\delta \geqslant \frac{4}{3}a$. (Actual models of squirmers do much worse than the bound.) If the pushmepullyou swimmer is allowed to make large strokes, it can beat the efficiency of all of the above.

It is likely that some artificial micro-swimmers will be constrained to make only small (relative) strokes. Small strokes necessarily lead to large drag [7], but it is still interesting to see how large. Suppose $\delta \log\, \ell \sim \delta \log\, v$, then $a_1 \sim a_2$. The dissipation in one stroke is then

$$\frac{\int P\,\mathrm{d}t}{6\pi\mu} = (\delta\ell)^2 \left(\frac{a}{T_\ell}\right)\left[1 + O\left(\varepsilon^2 \frac{T_\ell}{T_v}\right)\right]. \tag{1.10}$$

From equation (1.3) and noting that $T_\ell = \frac{1}{2}\tau$, one finds

$$\delta \approx \frac{72}{(\delta \log v)^2} a. \tag{1.11}$$

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Appendix. Derivation of the key formulas

We shall now outline how the key results, equations (1.1) and (1.6), are derived. The flow around a pair of spheres is a classical problem in fluid dynamics which has been extensively studied [16, 17]. We could have borrowed from the general results, e.g. in [16], and adapt them to the case at hand. However, it is both simpler and more instructive to start from scratch: the classical Stokes solution [8] describing the flow around a single sphere of radius a dragged by a force f and, in addition, dilated at rate $\dot{v}$

$$\pi\vec{u}(\vec{x};a,\, f, \dot{v}) = \frac{1}{6\mu|x|}\left[\left(3 + \frac{a^2}{x^2}\right)\vec{f} + \left(1 - \frac{a^2}{x^2}\right)3(\vec{f}\cdot\hat{x})\hat{x}\right] + \frac{\dot{v}}{x^2}\hat{x}, \tag{A.1}$$

where $\vec{u}(\vec{x};\, a,\, f, \dot{v})$ is the velocity field at a position $\vec{x}$ from the centre of the sphere. The left term is the known Stokes solution. (A Stokeslet, [8], is defined as the Stokes solution for $a = 0$.) The term on the right is a source term.

Since Stokes' equations are linear, a superposition of the solutions for two dilating spheres is a solution of the differential equations. However, it does not quite satisfy the no-slip boundary condition on the two spheres: there is an error of order ε. The superposition is therefore an approximate solution provided the two spheres are far apart.

The (approximate) solution determines the velocities U_i of the centres of the two spheres:

$$U_i = \vec{u}[a_i\hat{f};\, a_i,\, (-)^j f, 0] + \vec{u}[(-)^i \ell\hat{f};\, a_j,\, (-)^i f, (-)^i \dot{v}], \qquad i \neq j \in \{1, 2\}. \tag{A.2}$$

The first term on the right describes how each sphere moves relative to the fluid according to Stokes' law as a result of the force $\vec{f}$ acting on it. The second term (which is typically smaller) describes the velocity of the fluid surrounding the sphere (at distances $\gg a$ but $\ll \ell$) as a result of the movement of the other sphere. By symmetry, the net velocities of the two spheres and the net forces on them are parallel to the axis connecting the centres of the two spheres, and can be taken as scalars. To leading order in ε, equation (A.2) reduces to

$$2\pi U_i = (-)^j \frac{1}{3a_i}\frac{f}{\mu} + \frac{\dot{v}}{2\ell^2}. \tag{A.3}$$

Using $\dot{\ell} = -U_1 + U_2$ gives the force in the rod

$$f = -6\pi\mu\left(\frac{1}{a_1} + \frac{1}{a_2}\right)^{-1}\dot{\ell}. \tag{A.4}$$

Using the last two expressions, we get equation (1.1) for $2\dot{X} = U_1 + U_2$.

We now turn to equation (1.6). Consider first the case $\dot{v} = 0$. The power supplied by the rod is $-f(U_2 - U_1) = -f\dot{\ell}$ which gives the first term. Now consider the case $\dot{\ell} = 0$. The stress on the surface of the expanding sphere is given by

$$\sigma = -\frac{2\mu\dot{v}}{4\pi}\left(\frac{1}{x^2}\right)' = \frac{\mu\dot{v}}{\pi a^3}. \tag{A.5}$$

The power requisite to expand one sphere is then

$$4\pi\, a^2\sigma\dot{a} = \sigma\dot{v} = \frac{4\mu}{3v}(\dot{v})^2. \tag{A.6}$$

Since there are two spheres, this give the second term in equation (1.6). Finally, we note that there are no mixed terms in the dissipation proportional to $\dot{\ell}\dot{v}$. This is because the velocity field and the field of force on the surface of each sphere generated by $\dot{\ell}$ are constants (parallel to $\hat{f}$), while the components generated by $\dot{v}$ are radial. The two cannot be coupled to give a scalar.

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