Pushmepullyou: An efficient micro-swimmer

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Abstract

The swimming of a pair of spherical bladders that can change their shape is elementary at small Reynolds numbers. If large strokes are allowed then the swimmer has superior efficiency to other models of artificial swimmers. The change of shape resembles the wriggling motion known as *metaboly* of certain protozoa.

Swimming at low Reynolds numbers can be remote from common intuition because of the absence of inertia [1, 2]. In fact, even the direction of swimming may be hard to foretell. At the same time, and not unrelated to this, it does not require elaborate designs: Any stroke that is not self-retracing will, generically, lead to some swimming [3]. A simple model that illustrates these features is the three linked spheres [4], Fig. 1 (right), that swim by manipulating the distances $\ell_{1,2}$ between neighboring spheres. The swimming stroke is a closed, area enclosing, path in the $\ell_1 - \ell_2$ plane.

Swimming efficiently is an issue for artificial micro-swimmers. As we have been cautioned by Purcell [2] not to trust common intuition at low Reynolds numbers, one may worry that efficient swimming may involve unusual and nonintuitive swimming styles. The aim of this letter 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, Fig. 1 (left). It swims by cyclically changing the volume of the bladders and the distance between them. For the sake of simplicity and concreteness we assume that the total volume is conserved: The bladders exchange volumes in each stroke. The swimming stroke is a closed path in the $v - \ell$ plane where v is the volume of, say, the left bladder and ℓ the distance between them. We shall make the further simplifying assumption that the viscosity of the fluid in the bladders is negligible compared with the viscosity of the ambient fluid [1]. 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 that the distance between the spheres is large, i.e. when $\varepsilon = a/\ell \ll 1$. ($a$ stands for the sphere radii and ℓ for the distances between the spheres.) When $\varepsilon = O(1)$ Stokes equations do not seem to have an explicit solution in terms of elementary functions. We assume that the Reynolds number $R = \rho a v/\mu \ll 1$, and also that the distances between the balls are not too large: $\ell v \ll \mu$. The second assumption is not essential and is made for simplicity only. (To treat large ℓ one needs to replace the Stokes solution, Eq. (11), by the more complicated, but still elementary, Oseen-Lamb solution [9].)

Pushmepullyou is simpler than the three linked spheres: It involves two spheres rather than three; it is more intuitive and is easier to solve mathematically. It is also remarkably more efficient if large strokes are allowed. It can even outperform conventional models of biological swimmers that swim by beating a flagellum [10]. If only small strokes are allowed then pushmepullyou, like all squirmers [11], becomes rather inefficient.

The swimming velocity is defined by $\dot{X} = (U_1 + U_2)/2$ where U_i are the velocities of the centers of the two spheres. To solve a swimming problem one needs to find the (linear) relation between the response, dX, and the (shape) controls $(d\ell, dv)$. This relation, as we shall show, takes the form:

$$2\, đX = \frac{a_1 - a_2}{a_1 + a_2}\, d\ell \; + \frac{1}{2\pi \ell^2}\, dv, \tag{1}$$

where a_1, a_2 are the radii of the left and right spheres respectively and v is the volume of the left bladder. ($đX$ stresses that the differential describing the change in the location of the swimmer, does not integrate to a function on shape space. Rather $X(\gamma)$ depends on the path γ in shape space.) The first term 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. The second term says that the swimming is in the direction of the contracting sphere: The expanding sphere acts as a source pushing away the shrinking

[1] Saffman pointed out [8] that a bladder *with inertia* can swim also in a superfluid.

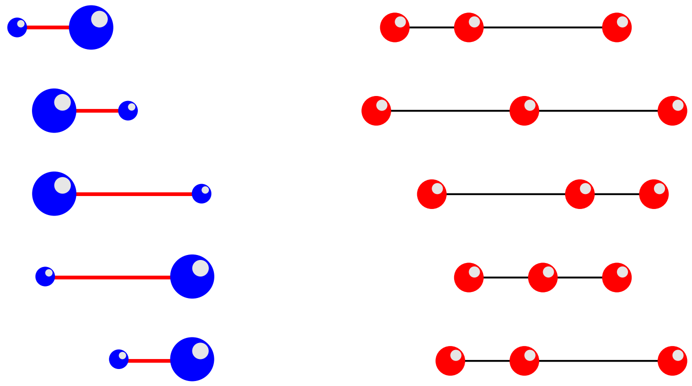

Figure 1: *Five snapshots of the pushmepullyou swimming stroke (left) and the corresponding strokes of the three linked spheres (right). Both figures are schematic. After a full cycle the swimmers resume their original shape but are displaced to the right. Pushmepullyou is both more intuitive and more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

sphere which acts as a sink to pull the expanding sphere. This is why the swimmer is dubbed pushmepullyou.

Certain protozoa and species of *Euglena* perform a wriggling motion known as *metaboly* where, like pushmepullyou, body fluids are transferred from a large spheroid to a small spheroid [7]. Metaboly is, at present not well understood and while some suggest that it plays a role in feeding [5] others argue that it is relevant to locomotion [6]. The pushmepullyou model shows that at least as far as fluid dynamics is concerned, metaboly is a viable method of locomotion. Racing tests made by Triemer [5] show that Euglenoids swim 1-1.5 their body length per stroke. This is in agreement with Eq. (1) and (6) for reasonable choices of stroke parameters. Since Euglena resemble deformed pears — for which there is no known solution to the flow equations — more than disconnected spheres the theory, if correct, has limited predictive value. Pushmepullyou is therefore, at best, a biological over-simplification. It has the virtue that admits complete analysis.

To gain further insight into the pushmepullyou swimmer consider the special case of small strokes near equal bi-spheres. Using Eq. (1) one finds, dropping sub-leading terms in $\varepsilon = a_i/\ell$:

$$\delta X = \frac{1}{6}\, d\log v \wedge d\ell \tag{2}$$

Note that the swimming distance *does not* scale to zero with ε. This is in contrast with the three linked spheres where the swimming distance of one stroke is proportional to ε. For small cycle in the $\ell_1 - \ell_2$ plane Najafi et. al. find (Eq. (11) in [4]):

$$\delta X = 0.7\varepsilon\, d\log \ell_2 \wedge d\ell_1 \tag{3}$$

When the swimmer is elementary, (=when ε is small), it is also poor.

The second step in solving a swimming problem is to find the dissipation rate P. 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. We find

$$\frac{P}{6\pi\mu} = \left(\frac{1}{a_1} + \frac{1}{a_2}\right)^{-1} \dot{\ell}^2 + \frac{2}{9\pi}\left(\frac{1}{v_1} + \frac{1}{v_2}\right)\dot{v}^2 \tag{4}$$

Note that the dissipation associated with $\dot{\ell}$, is dictated by the *small* sphere and decreases as the radius of the small sphere shrinks. (It can not get arbitrarily small and must remain much larger than the atomic scale for 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.

The drag coefficient is a natural measure to compare different swimmers. It measures the energy dissipated in swimming a fixed distance at fixed speed. (One can always decrease the dissipation by swimming more slowly.) Choosing the stroke period as the unit of time the drag is formally defined by [10, 12]:

$$\delta(\gamma) = \frac{\int_0^1 P dt}{6\pi\mu X^2(\gamma)}\,. \tag{5}$$

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

Consider now a large stroke associated with the closed rectangular path enclosing the box $\ell_s \le \ell \le \ell_L,\ v_s \le v_1, v_2 \le v_L \equiv v_0 - v_s$, 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 Eq. (1), $X(\gamma)$ is essentially $\ell_L - \ell_s$:

$$X(\gamma) = \left(\frac{a_L - a_s}{a_L + a_s}\right)\ (\ell_L - \ell_s)\left(1 + O(\varepsilon^3)\right) \tag{6}$$

To compute the dissipation for the rectangular path we need to choose rates for traversing it. The optimal rates are constant on each leg provided the coordinates are chosen as $(\ell, \arcsin\sqrt{\frac{v}{v_0}})$. 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 Eq. (4) is quadratic in $(\dot{\ell}, \dot{x})$, like the ordinary kinetic Lagrangian of non relativistic mechanics. It is a common fact that the optimal path of quadratic Lagrangian has constant speed. From Eq. (4) we find, provided also $\ell_L^2 \gg \ell_s^2,\ \ell_L/a_s \gg \sqrt{v_L/v_s}$

$$\frac{1}{6\pi\mu}\int P dt \approx \frac{2a_s\ell_L^2}{T_\ell}\left(1 + O\left(\varepsilon^2 \frac{v_L}{v_s}\frac{T_\ell}{T_v}\right)\right), \quad T_\ell + T_v = 1/2 \tag{7}$$

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 then the much larger $(a_L/\ell_s)^2$. Also note that the second term in Eq. (4) contributed $O(v_L/T_\ell)$ rather then $O(v_L^2/(v_s T_\ell))$ as one may have expected from Eq. (4) 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 Eq. (5) this gives the drag

$$\delta \approx 4a_s \tag{8}$$

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.* To beat dragging, we need $a_s = a/4$, which means that most of the volume, 63/64, must be shuttled between the two bladders in each stroke.

It is instructive to compare this mode of swimming with the swimming efficiency of models of (spherical) micro-organisms that swim by beating flagella. These have been extensively studied by the school of Lighthill and Taylor [10, 13] where one finds $\delta \geq 100\,a$. This is much worse than dragging. (We could not find estimates for the efficiency δ for swimming by ciliary motion [14], but we expect that they are rather poor, as for all squirmers [11].) For models of bacteria that swim by propagating longitudinal waves along their surfaces Stone and Samuel [12] established the (theoretical) lower bound $\delta \geq \frac{4}{3}a$. (Actual models of squirmers do much worse that the bound.) If the pushmepullyou swimmer is allowed to make large strokes, it can beat the efficiency of all of the above [2].

[2] A mechanical model that has been carefully studied is Purcell's two hinge model [15]. One can not make a meaningful comparison between it and pushmepullyou since their shapes are so different.

It is likely that some artificial micro-swimmers will be constrained to make only small (relative) strokes. Small strokes necessarily lead to large drag [11], but it is still interesting to see how large. Suppose $\delta \log \ell \sim \delta \log v,\ a_1 \sim a_2$. The dissipation in one stroke is then

$$\frac{\int P dt}{6\pi\mu} = (\delta\ell)^2 \left(\frac{a}{T_\ell}\right)\left(1 + O\left(\varepsilon^2 \frac{T_\ell}{T_v}\right)\right) \tag{9}$$

From Eq. (2) one finds

$$\delta \approx \frac{72}{(\delta \log v)^2}\ a\ . \tag{10}$$

We shall now outline how the key results, Eqs. (1,4), are derived. A solution to the Stokes equation for a single sphere of radius a dragged by a force f and dilated at rate $\dot{v}$ is

$$\pi\vec{u}(\vec{x}; a, f, \dot{v}) = \frac{1}{6\mu|x|}\left(\left(3 + \frac{a^2}{x^2}\right)\vec{f} + \left(1 - \frac{a^2}{x^2}\right)3(\vec{f}\cdot\hat{x})\hat{x}\right) + \frac{\dot{v}}{x^2}\hat{x}. \tag{11}$$

$\vec{u}(\vec{x}; a, f, \dot{v})$ is the velocity field at a position $\vec{x}$ from the center of the sphere. The left term is the known Stokes solution. (A Stokeslet, [9], 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 determine the velocities U_i of the centers of the two spheres:

$$U_i = \vec{u}(a_i\hat{f}; a_i, (-)^j f, 0) + \vec{u}((-)^i\ell\hat{f}; a_j, (-)^i f, (-)^i\dot{v}), \quad i \neq j \in \{1, 2\} \tag{12}$$

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 velocities and forces are parallel to the axis connecting the centers of the two spheres, and can be taken as scalars. To leading order in ε Eq. (12) reduces to

$$2\pi U_i = (-)^j \frac{f}{\mu}\left(\frac{1}{3a_i} - \frac{1}{2\ell}\right) + \frac{\dot{v}}{2\ell^2} \tag{13}$$

Using $\dot{\ell} = -U_1 + U_2$, and dropping sub-leading terms in ε, gives the force in the rod

$$f = -6\pi\mu \left(\frac{1}{a_1} + \frac{1}{a_2}\right)^{-1} \dot{\ell} \tag{14}$$

and Eq. (1).

We now turn to Eq. (4). 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

$$\sigma = -\frac{2\mu\dot{v}}{4\pi}\left(\frac{1}{x^2}\right)' = \frac{\mu\dot{v}}{\pi a^3} \tag{15}$$

The power requisite to expand one sphere is then

$$4\pi a^2 \sigma \dot{a} = \sigma\dot{v} = \frac{4\mu}{3v}(\dot{v})^2 \tag{16}$$

Since there are two spheres, this give the second term in Eq. (4). Finally, we note that there can not be 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 can not be coupled to give a scalar.

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