Comparison of Efficiency of Translation Between a Deformable Swimmer Versus a Rigid Body in a Bounded Fluid Domain: Consequences for Subcellular Transport

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Abstract. In this paper, we compare the translation efficiencies of a deformable circle that swims by means of low amplitude periodic tangential surface waves versus a rigid circle, moving in a bounded fluid domain. The swimmer is found to be much more efficient than the rigid body. We believe that this result gives some support to the active hypothesis of subcellular transport, where it is supposed that the organelle can generate by itself a propulsive flux, (by changes of form or metabolic activities) instead of just being carried by the motion of an external agent, like a molecular motor.

Key words: microswimming, Stokes fluids, organelle transport

1. Introduction

Subcellular particles such as mitochondria and vesicles move inside the cell in a non-random way. In the eucaryotic cell, mitochondria go to places of high energy demand, while vesicles transport different classes of cell materials, for example from the Golgi apparatus to the cell membrane.

Nowadays there are five different hypotheses regarding the mechanism of subcellular motion. They can be classified either as active or passive. An active translation mechanism is when it is supposed that the organelle can generate, by itself, a propulsive hydrodynamic flux, while in a passive one there is another agent that carries the organelle with it. Examples of an active mechanism are the generation of a propulsive flux by means of metabolic activities or actual changes of form in the organelle [1–3], while organelles carried by molecular motors [4, 5], random fluid motion [4–6] or self-organized cytoskeleton structures [7] are examples of passive mechanisms. In Cell Biology, the current status of this hypothesis is very different, since the idea of organelles carried by molecular motors prevails over all others in spite of the fact that no other hypothesis has been completely discarded yet.

We want to compare the hydrodynamic efficiency of an active versus a passive translation mechanism, as helpful theoretical criteria in deciding which one has a better chance to exist in the actual eucaryotic cell.

As a model of an organelle inside a cell, we took a bidimensional eccentric annulus where, *a priori*, the fluid patterns derived from an active translation mechanism would be very different from the ones arising from a passively dragged object. Independently of the complexities of the underlying dynamics of a truly passive deterministic transport mechanism, it can be assumed that the organelle is moving essentially as a rigid body while dragged. In the particular case of molecular motors is possible to make the simplifying hypothesis that the organelle is being rigidly translated throughout the fluid by an agent of negligible mass and size. As for an active mechanism, in principle its characteristic fluid pattern can be obtained by an appropriate oscillating membrane, which in this case is supposed to be subject to small amplitude tangential periodic deformations.

There are numerous models of microorganism locomotion based on the idea that they can deform their bodies in a periodic way [8–16]. All these models, which are part of the subject known as microswimming, place the organism in a infinite fluid domain, a condition that can't be taken as a good approximation to the situation of a subcellular particle, no matter how small or far away from the cell membrane it is, because of expected wall effects, which at low Reynolds number Re are believed to be significant [17].

2. Method

The definition of hydrodynamic efficiency η that we use is:

$$\eta = \frac{|V|}{E} \quad (1)$$

where V is the speed with which the object is moving and E is the power or energy dissipated per second during the motion. For a swimmer that moves using low amplitude surface traveling waves, V and E are taken as the speed and power per stroke and η is known as “naïve” efficiency [18]. In this case, definition (1) is closely related to the quantity D/E (D , displacement), that appears as a Lagrange multiplier while solving the linear variational problem of finding an optimal swimming strategy, the one that produces the largest displacement with minimum energy expenditure for a given stroke period T [18]. Dividing D/E by T gives a definition independent of time-size rescaling.

Naïve efficiency is deeply embedded in the geometry of phase space Q , the set of all possible space-time localized shapes whose basic starting form is S_0 . Space Q is formally the infinite dimensional manifold of embeddings of S_0 into the Euclidean d -space. In Q one can describe the trajectories followed by a swimmer that performs a certain stroke. At each point on a trajectory $q(t)$ it is possible to

define the instantaneous deformation $\mathbf{U} = dq(t)/dt$, and the set of all $\mathbf{U}$ forms the tangent space $T_q Q$ at each $q \in Q$. Displacement is calculated from the curvature of the connection in Q and power sets a metric on $T_q Q$ [19].

We need to calculate η for different tangential oscillation modes in selected positions along the radial direction that goes from the center of the cell to its boundary (or membrane). Next, we calculate η for a rigid translation that has the same speed as the tangential swimmer at every position and compare both results.

Therefore, it is only necessary to calculate the ratio of efficiencies:

$$P \equiv \frac{\eta_{tg}}{\eta_{rg}} = \frac{E_{rg}}{E_{tg}} \quad (2)$$

which reduces to a quotient of powers, where subscript tg refers to the tangential swimmer and rg to the rigidly translated body. Notice that one can arrive to the same expression for P given in (2) starting with another efficiency definition different from the naïve [Eq. (1)]. For example, the same ratio P would be obtained with Lighthill's definition [16], as long as one has the same starting shape for both, deformable and rigid bodies.

In general, the power generated by a shape S moving in a fluid whose velocity field is $\mathbf{v}$ is given by the integral:

$$E(\mathbf{v}) = \int_S \mathbf{v} \cdot \boldsymbol{\Pi}(\mathbf{v}) \cdot \mathbf{n} dS \quad (3)$$

where $\boldsymbol{\Pi}$ is the stress tensor associated with such field and $\mathbf{n}$ is the exterior normal vector to the area element dS . For a Newtonian incompressible fluid, $\boldsymbol{\Pi} = -p\mathbf{I} + \mu\mathbf{D}$, where $\mathbf{I}$, $\mathbf{D}$ are the identity and strain tensors while μ , p are the fluid's dynamic viscosity and pressure, respectively.

As explained in the next section, the velocity vector field $\mathbf{v}$ that results from the motion of the body throughout the fluid is a solution of the Stokes equation, and is known as the Stokes extension.

2.1. STOKES PROBLEM

Considering typical size and speed figures of some organelles one obtains $Re \approx 10^{-8}$. For comparison, microorganisms swim at $Re \approx 10^{-5}$. In this regime of low Re , viscous forces are much greater than inertial ones and fluid dynamics is accurately described by the Stokes equation, which will be solved under the conditions:

$$\mu \nabla^2 \mathbf{v} = \nabla p; \quad \nabla \cdot \mathbf{v} = 0; \quad \mathbf{v}|_{C_1} = \mathbf{U}; \quad \mathbf{v}|_{C_2} = \mathbf{0}, \quad (4)$$

where μ is dynamic viscosity and p is pressure. Therefore, the fluid is assumed incompressible and contained by a cell wall C_2 , immobile and impenetrable. Fluid velocity v has to match the deformation rate $\mathbf{U}$ on the swimmer's boundary C_1 , a non-slip condition. In the case of rigid motion, $\mathbf{U}$ is reduced to a constant vector field.

The Stokes problem (2) can be equivalently restated as a biharmonic problem where one tries to find a stream function Ψ satisfying the biharmonic equation:

$$\nabla^4 \Psi = 0$$

with definite Neumann (NBC) or Dirichlet (DBC) boundary conditions on the fluid's domain [20]. For a bidimensional setting, once the stream function is found, the components ν_1, ν_2 of the Stokes extension are obtained by means of the relations:

$$\nu_1 = h_2 \frac{\partial \Psi}{\partial q_2}; \quad \nu_2 = -h_1 \frac{\partial \Psi}{\partial q_1} \quad (5)$$

where q_i are coordinates in a particular coordinate system and h_1, h_2 are their metric coefficients.

3. Calculations

The fluid domain Ω is here an eccentric ring in the Cartesian plane, where the outer circle C_2 represents cell membrane while the inner circle C_1 represents the organelle. Thus Ω 's complete boundary is $\partial\Omega = C_1 \cup C_2$ (Figure 1).

We restrict ourselves to study displacement along the y -axis (Figure 1), and so a natural coordinate frame for domain Ω is the bipolar coordinate system (α, β) with $\alpha = \ln(r_1/r_2)$ and $\beta = \theta_1 - \theta_2$ (Figure 2). Circles C_1, C_2 are defined now by a pair of non-intersecting coaxial circles corresponding to constant values of α (α_1 for C_1 and α_2 for C_2 with $\alpha_1 > \alpha_2$), which in the bipolar complex plane $\zeta = \alpha + i\beta$ correspond to vertical lines mod 2π . The single metric coefficient of this coordinate system is $h = |\frac{\partial \zeta}{\partial z}| = [\cosh(\alpha) - \cos(\beta)]/a$ where $a > 0$. The parameter a is constant for each eccentric position of the swimmer and defines the scale of the system.

The complete solution to the bidimensional biharmonic problem in bipolar coordinates, and in terms of Jeffery's function $h\Psi$, is given in [21]. In order to avoid multivalued stream functions and to exclude trivial deformation cases, we restrict our solutions to the form:

$$h\Psi = \sum_{k=1}^{\infty} F_k(\alpha) \cos(k\beta) + G_k(\alpha) \sin(k\beta) \quad (6)$$

Figure 1. Fluid domain Ω in the Cartesian plane. Circles C_2 with radius R_2 and C_1 with radius R_1 have a distance d_C between their centers and represent the cell membrane and the swimmer's boundary, respectively.

Figure 2. Bipolar circles α_1, α_2 in the Cartesian plane and their representation in the bipolar complex plane ζ . Angle β , unitary bipolar vectors $\hat{e}_\alpha, \hat{e}_\beta$ and the conformal mappings $\zeta(z), z(\zeta)$ between both planes are also shown, as well as the angles θ_1, θ_2 and lengths r_1, r_2 that define $\beta = \theta_1 - \theta_2$ and $\alpha = \ln(r_1/r_2)$, respectively.

where:

$$F_1(\alpha) = A_1 \cosh(2\alpha) + B_1 + C_1 \sinh(2\alpha) + D_1 \alpha, \quad (7)$$

$$G_1(\alpha) = \tilde{A}_1 \cosh(2\alpha) + \tilde{B}_1 + \tilde{C}_1 \sinh(2\alpha) + \tilde{D}_1 \alpha, \quad (8)$$

and, for $k > 1$,

$$F_k(\alpha) = A_k \cosh[(k+1)\alpha] + B_k \cosh[(k-1)\alpha] + C_k \sinh[(k+1)\alpha] + D_k \sinh[(k-1)\alpha], \quad (9)$$

$$G_k(\alpha) = \tilde{A}_k \cosh[(k+1)\alpha] + \tilde{B}_k \cosh[(k-1)\alpha] + \tilde{C}_k \sinh[(k+1)\alpha] + \tilde{D}_k \sinh[(k-1)\alpha]. \quad (10)$$

3.1. TANGENTIAL SWIMMER

In order to produce a net translation, the deformation mode $\mathbf{U}$ in Eq. (4) has to be described by at least a pair of linearly independent autonomous vector fields on C_1 : $\boldsymbol{\nu}_1, \boldsymbol{\nu}_2$ (swimming strategy). Otherwise, a reciprocal motion is produced; a swimming stroke that only reverses its initial sequence of deformations to come back to the initial form. Reciprocal motions fail to produce net translation at low Reynolds number [10].

In this way, and assuming separability of time dependence, a minimal swimming stroke is determined by a linear combination of two base modes: $a_1(t)\boldsymbol{\nu}_1 + a_2(t)\boldsymbol{\nu}_2$ where coefficients $a_1(t), a_2(t)$ represent the time periodic contribution of each mode $\boldsymbol{\nu}_i$ at instant t . For simplicity, in the following we take $a_1(t) = \cos(2\pi\nu t)$, $a_2(t) = \sin(2\pi\nu t)$ where ν is the frequency of the oscillation. The actual low amplitude deformation of a circle ξ of radius R_1 is given by:

$$\xi \rightarrow \xi + R_1 \varepsilon (a_1(t)\boldsymbol{\nu}_1(\xi) + a_2(t)\boldsymbol{\nu}_2(\xi)) \quad (11)$$

where ε is a small positive number giving the relative size of the deformation in R_1 units and ξ is the parameterization of circle C_1 in bipolar coordinates, that is: $\xi = (x, y - a \coth \alpha_1)$ with $R_1 = a \cosh \alpha_1$, and

$$x = x(\alpha, \beta) = \frac{a \sin(\beta)}{\cosh(\alpha) - \cos(\beta)}; \quad y = y(\alpha, \beta) = \frac{a \sinh(\alpha)}{\cosh(\alpha) - \cos(\beta)}$$

that for C_1 are evaluated at α_1 .

Thus, the velocity vector field $\mathbf{U}$ which is the boundary condition in (4) is obtained by differentiating (11) with respect to t :

$$\mathbf{U} = R\varepsilon(\dot{a}_1(t)\boldsymbol{\nu}_1 + \dot{a}_2(t)\boldsymbol{\nu}_2). \quad (12)$$

As a basis $\boldsymbol{\nu}_1, \boldsymbol{\nu}_2$ for tangential deformations we took the normalized vector fields:

$$\boldsymbol{\nu}_i = \frac{\mathbf{w}_i}{\|\mathbf{w}_i\|} \quad (13)$$

with $i = 1, 2$ and:

$$\mathbf{w}_i = \sigma_i(n) \hat{e}_\beta$$

where $\hat{e}_\beta$ is the bipolar basis vector for angle β which, as seen in Figure 2, is tangential at each point on any circle α , and:

$$\sigma_1(n) = \cos(n\beta); \quad \sigma_2(n) = \sin(n\beta).$$

Also:

$$\|\mathbf{w}_i\| = \sqrt{\int_{-\pi}^{\pi} \langle \mathbf{w}, \mathbf{w} \rangle \frac{d\beta}{h}} = \sqrt{\pi a \operatorname{csch}(\alpha) (1 \pm e^{-2n\alpha})}$$

is the L^2 norm of each $\mathbf{w}_i$ where plus sign corresponds to $i = 1$.

Under the action of this boundary field according to Eq. (11), a point in C_1 will move cyclically back and forth from its initial position following the direction of the tangent at that point. The phase difference between consecutive points will produce alternating zones of compression and extension around the circle C_1 , more numerous as the wave number n increases.

3.1.1. Stokes Extension

According to the procedure detailed in the appendix, the Dirichlet and Neumann boundary conditions for $h\Psi$ on the circle α_1 are:

$$h\Psi|_{\alpha_1} = 0 \tag{14}$$

$$\left. \frac{\partial(h\Psi)}{\partial\alpha} \right|_{\alpha_1} = -\sigma_i(n) \tag{15}$$

and on the boundary α_2 :

$$h\Psi|_{\alpha_2} = 0, \tag{16}$$

$$\left. \frac{\partial(h\Psi)}{\partial\alpha} \right|_{\alpha_2} = 0. \tag{17}$$

Following the standard procedure of equating coefficients of the general solution with the boundary conditions and solving for coefficients $A_n, \dots, D_n$ and $\tilde{A}_n, \dots, \tilde{D}_n$ of Eqs. (9) and (10), as explained in the appendix, gives the solutions:

$$\Psi_i = \frac{\Lambda_i^n(\alpha) \sigma_i(n)}{h} \tag{18}$$

where if $i = 1$, $\Lambda_i^n(\alpha)$ represents Eq. (9) while if $i = 2$, it represents Eq. (10).

For bipolar coordinate, Eq. (5) is

$$\nu_\alpha = h \frac{\partial \Psi}{\partial \beta} \quad (19)$$

$$\nu_\beta = -h \frac{\partial \Psi}{\partial \alpha} \quad (20)$$

and so, components w_α, w_β of Stokes extension $\mathbf{w}_i$ are obtained from (19) and (20) together with (18):

$$w_\alpha = \Lambda_i^n(\alpha) \left[\frac{-\sigma_i(n) \sin(\beta)}{ah} + \sigma_i'(n) \right]; \quad w_\beta = \sigma_i(n) \left[\frac{\Lambda_i^n(\alpha) \sinh(\alpha)}{ah} - \Lambda_i^m(\alpha) \right],$$

for each $i = 1$ or 2 . Therefore, the Stokes extension corresponding to the normalized deformation vector field $\mathbf{v}_i$, is obtained simply by dividing $\mathbf{w}_i$ by its corresponding norm.

As a careful calculation of the total force $\mathbf{F}_T$ and torque $\mathbf{T}_T$ on the swimmer's boundary α_1 shows, the Stokes extensions $\mathbf{v}_i$, here calculated are horizontal as such, that is: $\mathbf{F}_T = \mathbf{T}_T = \mathbf{0}$, which is a physical prerequisite for swimming at low Re [10]. This is no surprise, since all rigid motion terms in (6) are excluded from the beginning. The zero total force and torque prerequisite is known as the “non-bootstrap” condition and physically means that the swimmer can deform its shape but not pushes or pulls on itself in any way [10].

3.1.2. Power

When the pressure term is too complicated, calculating the power E with Eq. (3) can be difficult. Applying the divergence theorem to (3) for an incompressible Stokes fluid in the absence of body forces one gets:

$$E(\mathbf{v}) = \int_{\Omega} \Phi dV,$$

where $\Phi = 2\mu \mathbf{D}:\mathbf{D}$ is the dissipative function of mechanical energy integrated over region Ω , $\mathbf{D}$ is the strain tensor and where $\mathbf{D}:\mathbf{D}$ denotes the double dot product of the dyadic $\mathbf{D}$ (rank 2 tensor) with itself [17]. Thus, in bipolar coordinates:

$$E(\boldsymbol{\nu}) = 2\mu \int_{\alpha_1}^{\alpha_2} \int_{-\pi}^{\pi} \frac{\Phi}{h^2} d\alpha d\beta. \quad (21)$$

Calculating (21) with the Stokes extensions $\mathbf{w}_i$ of the tangential deformations gives:

$$\begin{aligned} E(w_i) = & -n\pi\mu(-8 \cosh[n(\alpha_1 - \alpha_2)] \sinh[n(\alpha_1 - \alpha_2)]^3 \\ & + n\{-n^2 \sinh[4(\alpha_1 - \alpha_2)] + 2(n^2 - 1) \sinh[2(\alpha_1 - \alpha_2)]\} \\ & + (n - 1) \sinh[2(n - 1)(\alpha_1 - \alpha_2)] - 2n \sinh[2n(\alpha_1 - \alpha_2)] \\ & + (n - 1) \sinh[2(n + 1)(\alpha_1 - \alpha_2)] / \{\cosh[2n(\alpha_1 - \alpha_2)] \\ & - n^2 \cosh[2(\alpha_1 - \alpha_2)] + n^2 - 1\}^2. \end{aligned} \quad (22)$$

Therefore for a normalized deformation given by (13):

$$E(\boldsymbol{\nu}_i) = \frac{E(\mathbf{w}_i)}{\|\mathbf{w}_i\|^2} \quad (23)$$

since the quadratic form (3) corresponds to a bilinear operator of velocity vector fields.

The quadratic $E(\boldsymbol{\nu})$ gives the power generated by the rate at which the stresses acting on the boundary of shape S provide work do to the instantaneous deformation specified by the vector field $\boldsymbol{\nu}$. The total average energy E_T dissipated during the cycle of deformations that constitutes a swimming stroke, is obtained by integrating, over the stroke period T , the individual contributions to energy dissipation that each shape gives through the cycle [22]:

$$E_T = \frac{1}{T} \int_0^T E(\boldsymbol{\nu}) dt$$

which also is our definition for E_{tg} in (2). Applying the bilinearity properties of the power operator:

$$\mathbf{E}(\boldsymbol{\nu}, \mathbf{u}) = \int_S \boldsymbol{\nu} \cdot \Pi(\mathbf{u}) \cdot \mathbf{n} dS,$$

together with the fact that tangential base vector fields are autonomous and since $\boldsymbol{\nu}$ on S is given by (12) one gets [22]:

$$E_{tg} \equiv E_T = 2 \left(\frac{\pi d}{T} \right)^2 (E[\boldsymbol{\nu}_m, \boldsymbol{\nu}_m] + E[\boldsymbol{\nu}_n, \boldsymbol{\nu}_n]) \quad (24)$$

where $\boldsymbol{\nu}_m, \boldsymbol{\nu}_n$ are two different tangential oscillation modes and $d = R_1 \varepsilon$ is the absolute deformation size.

3.2. RIGID MOTION

Here $\mathbf{U} = \hat{j}$ in (2) corresponding to the Cartesian frame (Figure 1). In bipolar coordinates the unitary Cartesian base vector is $\mathbf{w} = \hat{j}(\alpha, \beta) = w_\alpha \hat{e}_\alpha + w_\beta \hat{e}_\beta$ with:

$$w_\alpha = (ah)^{-1} [1 - \cos(\beta) \cosh(\alpha_1)] \quad (25)$$

$$w_\beta = -(ah)^{-1} \sin(\beta) \sinh(\alpha_1) \quad (26)$$

restricted to the circle α_1 . One can have a normalized vector field $\boldsymbol{\nu}$:

$$\boldsymbol{\nu} = \frac{\mathbf{w}}{\|\mathbf{w}\|}$$

where L^2 norm of w is:

$$\|\mathbf{w}\| = \sqrt{\int_{-\pi}^{\pi} (w_{\alpha}^2 + w_{\beta}^2) \frac{d\beta}{h}} = \sqrt{2\pi a \cosh(\alpha)}. \quad (27)$$

3.2.1. Stokes Extension

As shown in the appendix, the boundary conditions in this case are, on circle α_1 :

$$h\Psi = -\sin(\beta), \quad (28)$$

$$\frac{\partial(h\Psi)}{\partial\alpha} = 0, \quad (29)$$

and on circle α_2 are given by Eqs. (16–17).

Equating coefficients of corresponding terms in the general solution and the boundary conditions and solving for coefficients $\tilde{A}_1, \dots, \tilde{D}_1$ of Eq. (8), as shown in the appendix, gives the solution:

$$\Psi = \frac{G_1(\alpha) \sin(\beta)}{h} \quad (30)$$

where G_1 is given by Eq. (8). After substitution and simplification the last expression gives:

$$\Psi = h^{-1} \sin(\beta) \frac{[(\alpha - \alpha_2) \cosh(\alpha_1 - \alpha_2) - \cosh(\alpha - \alpha_1) \sinh(\alpha - \alpha_2)]}{[(\alpha_2 - \alpha_1) \cosh(\alpha_1 - \alpha_2) + \sinh(\alpha_1 - \alpha_2)]} \quad (31)$$

and components w_{α}, w_{β} of the Stokes extension $\mathbf{w}$ can be obtained using Eqs. (19–20), with Φ given as in Eq. (31). Again, the Stokes extension $\mathbf{v}$ corresponding to a normalized boundary condition is $\mathbf{w}$ divided by its norm (27).

3.2.2. Power

With formula (21), the power $E(\mathbf{w})$ is given by:

$$E(\mathbf{w}) = \frac{4\pi\mu \cosh(\alpha_1 - \alpha_2)}{(\alpha_1 - \alpha_2) \cosh(\alpha_1 - \alpha_2) - \sinh(\alpha_1 - \alpha_2)}. \quad (32)$$

Hence, for a normalized boundary condition $\mathbf{v}$ on circle C_1 one has:

$$E_{rg}(\mathbf{v}) = \frac{1}{\|\mathbf{w}\|^2} E(\mathbf{w}) = \frac{1}{2\pi R_1} E(\mathbf{w}) \quad (33)$$

according to (27). Our calculations show that, except for locations very near to the wall, data from Eq. (32) are in close agreement with those obtained using the formula for power published in [23].

Figure 3. Tangential power E_{tg} versus oscillation mode m at station five ($\gamma = 0.5$). Calculations of E_{tg} according to Eq. (26) where made with $R_1 = 10^{-5}$ cm, $\varepsilon = 0.01$, $\nu = 500 \text{ s}^{-1}$ and $\mu = 1$ cP.

3.3. SCALING

To bring bipolar circles α_1, α_2 to the real cellular scale, one needs to calculate parameter a of metric coefficient h at each swimmer's eccentric position.

To do so, first we find a pair of bipolar circles α_1, α_2 with radii ρ_1, ρ_2 , that have the same ratio ρ_2/ρ_1 and whose centers $(0, \coth \alpha_i)$ are at the same proportional distance γ as the ones in the Cartesian model, where it is assumed that $R_2/R_1 = 100$ and $\gamma = d_C/R_2$ is the relative eccentricity (d_C , distance between centers of circles C_1, C_2).

Once the system

$$\begin{aligned} a[\cot h(\alpha_2) - \cot h(\alpha_1)] &= \gamma a \cos h(\alpha_2), \\ \cos h(\alpha_2) \sinh(\alpha_1) &= 100, \end{aligned}$$

is solved for α_1, α_2 the parameter a is calculated from $\rho_1 = a \cos h \alpha_1$ knowing that $R_1 = 10^{-5}$ cm.

4. Results

For each eccentricity value $\gamma = 0.1, 0.2, \dots, 0.98$, (also referred to as stations 1,2,...,10) we run numeric calculations for modes m, n with $1 < m \leq 100$ and $n = m + 1$ for the tangential swimmer. After assigning values to m, n and calculating parameters α_1, α_2 and a for each bipolar circle, as explained in Sec. 3.3, we evaluate rigid power E_{rg} using formulas (32–33) and tangential power E_{tg} with Eqs. (22–24).

As shown in Figure 3 for $\gamma = 0.5$, the average stroke power E_{tg} raises linearly as the oscillation mode m increases. This behavior is the same at every other station.

Figure 4. Tangential power E_{tg} for the coupling of modes $m=5, n=6$ versus relative eccentricity γ using the same parameter values as in Figure 3. The axis for E_{tg} only shows its range of values.

Calculation where made with a frequency $\nu = 500 \text{ s}^{-1}$, which is similar to the ones reported for molecular motors [24].

As the swimmer moves from the center of the cell to its boundary, E_{tg} increases ever so slowly until in the final station it shows a slightly higher increase (Figure 4). The difference between the lowest ($\gamma = 0.1$) and the highest value ($\gamma = 0.98$) is more noticeable for lower modes ($m < 5$) where it reaches a peak of 14% when $m = 2$ and is only of 0.02% at $m = 5$, but it becomes progressively insignificant ($\sim 10^{-5}$ for $m = 10$, $\sim 10^{-15}$ for $m = 50$) as m grows higher. Therefore, it is safe to say that even for moderately high oscillation modes, E_{tg} can be considered, for every purpose, constant throughout the whole journey.

The qualitative behavior of E_{rg} is similar to the E_{tg} as γ increases, the difference being quantitative in both the rate at which power increases and in its absolute magnitude at each station (Figure 5). As a consequence, the tangential swimmer is thousands of times hydrodynamically more efficient in its motion than the rigidly translated circle, and the difference grows as the body gets closer to the wall, as shown in Figure 6 where P is given by Eq. (2). In this graph we pick the highest dissipative oscillation mode, corresponding to the coupling of $m = 100, n = 101$. Since, according to Figure 3, lower modes dissipate less energy per second than higher ones, by using those lower modes, the quotient of efficiencies P will be much bigger, in favor of the tangential swimmer.

5. Discussion

At low Re , viscous forces prevail over inertial ones, and so the former are the kind of forces that a moving body has to use to propel itself throughout a fluid. In such a dynamic regime, resistance and changes in resistance in a particular direction

Figure 5. Rigid power E_{rg} calculated with Eqs. (33–34) versus relative eccentricity γ . The axis for E_{rg} starts from 556.

Figure 6. Efficiency ratio P calculated according to Eq. (2) for the coupling $m = 100$, $n = 101$, versus relative eccentricity γ . The first point is at $P = 2.83$.

could lead to propulsion. For example, an oscillatory membrane at low Re basically uses the fluid's viscosity to permit purchase [12, 25–26]. The oscillatory swimming strategy given by (11), whose corresponding Stokes extensions v_i were obtained in Sec. 3.1.1, does generate significant net displacement per swimming stroke along the chosen radial direction [27]. At every station, the maximum displacement is always reached when $n = m + 1$ are coupling, which is the reason why we calculate power in the tangential case only for those modes.

Since, for a given length of the membrane, the higher the oscillation's wave number n , the higher the number of regions on it that strongly interact with the fluid through stress generation, one would expect that this sort of “grabbing” of

the fluid by the swimmer's frontier would produce a proportionally higher energy dissipation per stroke, as shown in Figure 3. This trend is also present in different models of oscillatory membranes in an unbounded fluid domain, such as sheets, filaments, spheres and circles [10, 15, 22] and is recovered here too in the bounded case for tangential deformations.

The difference in energy dissipation between the tangential swimmer and the rigidly translated body has to do with the fact that the deformable body is subject to low amplitude oscillations. On one hand, surface oscillations cause those variables such as speed and stress change periodically, going from maximum to minimum values (including zero) at each point around the swimmer's boundary. As a result, a variable such as the power, defined by (3), is an actual space average that flattens out extreme values of the quantities involved. In contrast, a rigidly translated body has, for example, a constant drag on its boundary. On the other hand, since power is proportional to oscillation amplitude, here defined by $\varepsilon = 0.01$ in Eq. (11), a low level of energy dissipation is expected from the start. But, with $R_1 \sim 10^{-5}\text{cm}$ and $\varepsilon = 0.01$ the absolute deformation is in the nanometer scale of small biopolymers, and one can think of them as minimal deformation or metabolic units able to generate a hydrodynamic flux around a subcellular particle. Besides, taking higher values for ε will invalidate the low amplitude approximation that leads to formula (24) for stroke power.

For both the rigid and the deformable circle, the magnitude of the velocity field dies out slowly at a geometrical pace as one moves away from the body, at least in a region of significant size around it in all stations. Therefore, in any case there is always a layer of fluid with noticeable speed around the body. However, while for the rigid circle the thickness of this layer remains constant and therefore a considerable volume of fluid set in motion goes along with the body, for an oscillating membrane with wave number n , such thickness is $O(n^{-1})$ [10]. As a consequence, even for low oscillation modes it can be said that the velocity field is non-zero only in a very small region around the swimmer while the remaining fluid in the domain stays at rest. Therefore, one would expect a lower power generation in the whole fluid domain Ω as a result of the motion of the tangential swimmer as compared with a rigid body. In conclusion, the tangential swimmer is both kinematically "silent" and energetically "cold" inside a finite domain, not perturbing the fluid but in a small neighborhood. One can think that this is a desirable characteristic in the overpacked living cell, where thousands of energetically costly processes are running at the same time. Take for example the docking process of vesicles at the cell's membrane, where a delicate intertwining interaction has to happen between proteins in both membranes before a vesicle fuses with the cell membrane to pour out its contents [4]. A reasonable assumption here is that a significant fluid velocity field around the vesicle could only impair the whole process.

As shown in Figure 6, the tangential swimmer is more efficient than the rigid body. Following [28], we expect this result to be independent in some degree of the definition of efficiency, as long as such definitions also take into account the quotient

D/E (see Sec. 2). We also expect the same result to hold for other non-tangential low amplitude swimming strategies since, as shown elsewhere [27], some of them are even more efficient than the tangential ones.

It is worthwhile to remember here the fact that the calculated efficiency ratio is only hydrodynamic, resulting from stress generation in the fluid alone, irrespective of the energies that certainly would be needed to generate a propulsive flux around the moving body. If the energy dissipated by elastic and/or metabolic processes in charge of stirring the fluid is taken into account, the picture can turn around completely, maybe by offsetting the factor of thousands favoring the tangential swimmer. Also, one has to be careful when extrapolating bidimensional results to the real world. We certainly do not believe that a bidimensional model is more relevant than a three-dimensional one for subcellular transport. Our work here is a first step in applying microswimming theory to bounded fluid domains and we adopt the bidimensional approach based on relative mathematical simplicity. To deal with the three-dimensional case would be the subject of a completely new research.

In terms of the molar concentration of ATP [ATP], taking into account maximal (close to the cell wall) and minimal (close to cell center) power data with an ATP free energy $\Delta G = 12$ Kcal/mol, and using the same values as in Figure 3 for the rest of the parameters, with the formula:

$$[\text{ATP}] = (K_1/\Delta G)(E\Theta)^{1/2},$$

where K_1 is a unit conversion factor, E is given by Eq. (24) or (33) and Θ is the vesicle's volume, one gets for tangential deformations a range of $[\text{ATP}] \sim 10^{-8}$ M, while for rigid motion $[\text{ATP}] \sim 10^{-4}$ M. Compare this data with 10^{-3} M, a typical value of intracellular [ATP] or with the measured saturated concentration of ATP needed to achieve maximal speed in individual molecular motors *in vitro*, $[\text{ATP}] \sim 10^{-4}$ M [24].

Notice that the molar concentration of ATP for the rigid body and the molecular motor are in the same order of magnitude, suggesting that rigid body translation may be the average end result of all the complex oscillating dynamics that supposedly underlies the motion of molecular motors (for example see [29]).

Efficiency is an important concept in biology since any living being has a limited amount of space, time, matter and energy at its disposal to achieve growth, maintenance and reproduction of its body in both their structural and functional aspects [30]. That is why an efficient use of its resources has to have a significant survival value. Therefore, one would like to conclude that in view of its higher efficiency level, tangential deformations or, for that matter, other more efficient deformations had a better chance to be selected over rigid translation during living cells' evolutionary process.

However, is not always obvious, when a biological situation it is being interpreted in terms of efficiency that evolution is trying to solve the particular optimization

problem involved. So here, we adopt the point of view, also expressed in [15], that naïve efficiency can be one of perhaps many parameters that can be useful in evaluating experimental data.

Still, in view of the later discussion, one can think that a truly efficient translation mechanism needs to include some sort of oscillation agents in organelle's membrane, capable of creating a propulsive flux by stirring water around in a non-reciprocal way. One candidate are the molecular motors themselves. Even if nowadays nobody knows how many of those motors are attached to a membranous organelle *in vivo*, one can suggest that maybe some of them could stir the water in a propulsive way while other(s) walk on the cytoskeleton fibers, in the way it is believed today that they do.

Another candidate to such role is the organelle's membrane itself, since deformations do occur during organelles transport. This is a long recognized fact for mitochondria, where even the precise sequence of deformations has been described [2]. Transport vesicles had been also observed changing their form during transport along the axon of nerve cells [4]. In this latter case, it was not clear if the deformations were a cause or an effect of the motion of the vesicle, but that is hardly an issue in the case of mitochondria, since the observed changes of form were periodic. Of course, in both cases the observed deformations were large, but it is argued that large deformations are even more efficient than infinitesimal ones [31], at least in an unbounded fluid domain.

6. Conclusion

We have shown that the fluid pattern generated by a deformable circular body subject to low amplitude periodic tangential waves is clearly a hydrodynamically more efficient translation mechanism than simple rigid motion in a bounded fluid domain. This result seems to give some support to the active subcellular transport hypothesis against the deterministic passive ones, specifically to the idea of an organelle being transported by a single molecular motor walking on microfilaments as the sole translation agent. In addition, it points out the possibility that an organelle's translation mechanism may need to include some sort of swimming to be truly efficient. Such swimming mechanism could be based in the work of molecular motors as stirring agents or in the periodic deformation of organelle's membrane. On the theoretical front, still much more work is required to prove such a hypothesis, for example by including the elastic/metabolic energies involved in the actual generation of the propulsive flux or by dealing with the problem in three dimensions.

Appendix

STOKES EXTENSION. TANGENTIAL SWIMMER

Since $\mathbf{w}_i$ is purely tangential, then $\mathbf{w}_i = w_\alpha \hat{e}_\alpha + w_\beta \hat{e}_\beta$ with $w_\alpha = 0$ and $w_\beta = \sigma_i(n)$. A convenient characteristic of tangential deformations is that swimmer's boundary can be set equal to a streamline

where Ψ is constant, and so:

$$\Psi|_{\alpha_1} = 0 \quad (\text{A.1})$$

Therefore the DBC on α_1 for Jeffery's function is:

$$h\Psi|_{\alpha_1} = 0. \quad (\text{A.2})$$

A NBC for $h\Psi$ on boundary α_1 is obtained with:

$$\frac{\partial(h\Psi)}{\partial\alpha}\bigg|_{\alpha_1} = \left(h \frac{\partial\Psi}{\partial\alpha}\bigg|_{\alpha_1} + \Psi \frac{\partial h}{\partial\alpha}\bigg|_{\alpha_1} \right) \quad (\text{A.3})$$

and using (20) together with (A1) gives:

$$\frac{\partial(h\Psi)}{\partial\alpha}\bigg|_{\alpha_1} = -w_\beta = -\sigma_i(n). \quad (\text{A.4})$$

On boundary α_2 , being immobile and impenetrable, DBC and NBC for $h\Psi$ are:

$$\Psi|_{\alpha_2} = 0 \Rightarrow h\Psi|_{\alpha_2} = 0, \quad (\text{A.5})$$

$$\frac{\partial(h\Psi)}{\partial\alpha}\bigg|_{\alpha_2} = 0. \quad (\text{A.6})$$

After equating coefficients in solution (6) with DBCs (14) on α_1 and (16) on α_2 and coefficients of:

$$\frac{\partial(h\Psi)}{\partial\alpha} = \sum_{k=2}^{\infty} F'_k(\alpha) \cos(k\beta) + G'_k(\alpha) \sin(k\beta) \quad (\text{A.7})$$

with NBCs (15), (17) on both circles [where in (A.7) the apostrophe means derivative with respect to α], the only non-homogeneous linear system occurs when $k = n$ and is:

$$\Lambda_i^n(\alpha_1) = 0; \quad \Lambda_i^n(\alpha_2) = 0; \quad \Lambda_i'^n(\alpha_1) = -1; \quad \Lambda_i''^n(\alpha_2) = 0, \quad (\text{A.8})$$

where if $i = 1$, $\Lambda_i^n(\alpha)$ represents Eq. (9) while if $i = 2$, it represents Eq. (10).

Solving for coefficients $A_n, \dots, D_n$ and $\tilde{A}_n, \dots, \tilde{D}_n$ in each system, one obtains the solutions for Ψ_i given in Eq. (18).

STOKES EXTENSION. RIGID BODY

Using (19) with (25) and integrating leads to:

$$\Psi|_{\alpha_1} = \int \frac{\partial\Psi}{\partial\beta}\bigg|_{\alpha_1} d\beta = -h^{-1} \sin(\beta). \quad (\text{A.9})$$

Therefore DBC on circle α_1 for Jeffery's function is:

$$h\Psi = -\sin(\beta). \quad (\text{A.10})$$

A NBC for $h\Psi$ on boundary α_1 is obtained using Eq. (A.3) and (20) with (A8), which after simplification gives:

$$\frac{\partial(h\Psi)}{\partial\alpha} = 0. \quad (\text{A.11})$$

Boundary conditions on circle α_2 are as given in Eqs. (16), (17). After equating corresponding coefficients in solution (6) with DBCs (A.9) on α_1 and (16) on α_2 and coefficients of (A.7) with NBCs (A.10), (17), the only non-homogeneous linear system occurs when $k = 1$ and is:

$$G_1(\alpha_1) = -1; \quad G_1(\alpha_2) = 0; \quad G'_1(\alpha_1) = 0; \quad G'_1(\alpha_2) = 0. \quad (\text{A.12})$$

where G_1 is given by (8). Solving for coefficients $\tilde{A}_1, \dots, \tilde{D}_1$ of G_1 one obtains the solution given by Eq. (30).

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