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Forces and shapes as determinants of micro-swimming: effect on synchronisation and the utilisation of drag†

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In this analytical study we demonstrate the richness of behaviour exhibited by bead-spring micro-swimmers, both in terms of known yet not fully explained effects such as synchronisation, and hitherto undiscovered phenomena such as the existence of two transport regimes where the swimmer shape has fundamentally different effects on the velocity. For this purpose we employ a micro-swimmer model composed of three arbitrarily-shaped rigid beads connected linearly by two springs. By analysing this swimmer in terms of the forces on the different beads, we determine the optimal kinematic parameters for sinusoidal driving, and also explain the pusher/puller nature of the swimmer. Moreover, we show that the phase difference between the swimmer's arms automatically attains values which maximise the swimming speed for a large region of the parameter space. Apart from this, we determine precisely the optimal bead shapes that maximise the velocity when the beads are constrained to be ellipsoids of a constant volume or surface area. On doing so, we discover the surprising existence of the aforementioned transport regimes in micro-swimming, where the motion is dominated by either a reduction of the drag force opposing the beads, or by the hydrodynamic interaction amongst them. Under some conditions, these regimes lead to counter-intuitive effects such as the most streamlined shapes forming locally the slowest swimmers.

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In recent years, the motion of self-propelled micro-objects has, in all senses, come under the microscope, with various experimental,^{1–12} theoretical,^{13–19} and simulation^{20–24} studies being performed to investigate their behaviour in various environments (for reviews see ref. 25 and 26). This is mainly with two complementary objectives in mind: understanding the biomechanics of natural micro-organisms, and designing controllable micro-machines. With increased analysis, many fundamental features of motion at these scales have come to light, such as the 'pusher' or 'puller' nature of many autonomous swimmers and synchronisation effects amongst the propulsive body elements such as flagella that help to make the swimming more efficient. This latter effect is a signature of the way that notions of energy loss and efficiency are important at the micro-scale,^{27–29} contrary to what was initially believed.³⁰

While the existence of these phenomena is undeniable, the mechanisms underlying them remain on the whole a mystery. The effects of the body shape on micro-swimming are only rudimentarily known,^{28,31} and while some success has been achieved in giving a physical basis to synchronisation among the swimmer body elements,¹⁷ more insight is needed before the construction of efficient micro-swimmers becomes a realisable possibility.

In this work, we aim to explain some fundamental features of micro-swimming through the analytical study of a simple micro-swimmer. The model that we choose consists of three beads of any shape linked linearly by two springs and following a defined periodic stroke (Fig. 1). This swimmer is a good candidate for forming the basis of future micro-carriers, a claim supported as much by its simplicity of design as by the number of experimental micro-swimmer systems that are based on linearly connected beads.^{1,3–5,7,12} A simpler variant of this design,

Fig. 1 A bead-spring swimmer with ellipsoidal beads.

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the three-sphere swimmer introduced by Najafi and Golestanian,³² has already proved its immense utility by establishing many basic properties of micro-swimming in spite of sparseness of body elements.^{33–36}

Starting with a force-based description³⁷ and considering only ellipsoids of revolution for the beads in our swimmer, we here determine the optimal forcing parameters as well as the ellipsoidal aspect ratios that lead to the fastest and the most efficient swimming. This, as we shall see, allows us to present conditions predicting the pusher or puller nature of the swimmer, and also to exhibit the fact that synchronisation between the arms emerges naturally, even in such a simple design, so as to maximise the swimming speed. Finally, we report and explain the existence of two swimming regimes where changes in the drag force on the swimmer, induced by changes in bead shape, have fundamentally different effects upon the velocity, deepening our understanding of the dichotomous roles that drag force plays in micro-swimming.

The beads in our swimmer are assumed to be (prolate or oblate) ellipsoids of revolution constrained to be of either a constant volume or a constant surface area (Fig. 1). This constraint is motivated by the foreseen application of the beads as payload-carrying sites in future micro-carriers; depending on whether the payload were placed on the surface of the beads or in their interior, one would conceivably want them to have a certain volume or surface area. We choose to study this bead-spring design starting from the forces acting upon it,³⁷ instead of from the deformation of the bead-to-bead distances as in the three-sphere model.^{32,38} The force-based approach allows us to consider individually the effect of the different forces acting on the swimmer, and is arguably more fundamental than the stroke-based one, since it is the forces on the beads that cause the arms to deform. For instance, this approach shows that micro-swimmers can sometimes swim faster in more viscous fluids.³⁷

We assume the forces driving the motion of the individual beads to be sinusoidal and given by

$$\mathbf{F}_1^d(t) = A \sin(\omega t) \hat{\mathbf{z}}; \quad (1)$$

$$\mathbf{F}_2^d(t) = -\mathbf{F}_1^d(t) - \mathbf{F}_3^d(t); \quad (2)$$

$$\mathbf{F}_3^d(t) = B \sin(\omega t + \alpha) \hat{\mathbf{z}}, \text{ with } \alpha \in [-\pi, \pi]. \quad (3)$$

Here t is the time, ω is the force frequency, α is the phase shift between the forces $\mathbf{F}_1^d$ and $\mathbf{F}_3^d$ acting on the end-beads, and A and B are their amplitudes. The springs in the swimmer as well as the driving forces $\mathbf{F}_i^d$ are along the $\hat{\mathbf{z}}$ -direction (Fig. 1). To ensure that the swimming occurs independently, we explicitly set the force $\mathbf{F}_2^d$ on the middle sphere to be the negative sum of the other two forces, making the net driving force on the swimmer zero at all instants. This is in accordance with the approach widely adopted in the literature, including for mechanical swimmers with ellipsoidal components.^{39–41} One may note that any sinusoidal forces driving the beads can be cast in the form of eqn (1)–(3) as long as the condition of autonomous swimming is satisfied.

Given this driving force description, we have in previous work determined analytically the velocity of a three-bead swimmer with rigid beads of any shape under the assumption of the bead separations being much larger than their characteristic dimensions.³⁷ This velocity may be expressed as

$$\mathbf{v} = \frac{7\lambda[AB(\kappa^2 + 12\lambda^2)\sin\alpha + 2(A^2 - B^2)\kappa\lambda]}{24l^2\pi^2\eta^2\omega(\kappa^4 + 40\kappa^2\lambda^2 + 144\lambda^4)} \hat{\mathbf{z}}. \quad (4)$$

Here κ is the ‘reduced spring constant’ and λ is the ‘reduced friction coefficient’ of the beads, these being respectively defined by

$$\kappa = \frac{k}{\pi\eta\omega}, \text{ and } \lambda = \frac{\gamma}{6\pi\eta}, \quad (5)$$

where η is the fluid viscosity, ω is the frequency of driving the beads, l is the mean distance between the beads, and γ is the full friction coefficient of each bead. The reduced friction coefficient λ carries the signature of the bead shape under the far-field assumption of the bead separations being much larger than their dimensions (*i.e.* $\lambda \ll l$). Note that this assumption means that the flow fields around any bead are not directly affected by the shapes of the other beads.

In brief, our approach is to maximise the swimmer velocity using eqn (4) for different driving parameters, and for a varying aspect ratio and orientation of the ellipsoids comprising the different families. This allows us to find the optimal ellipsoids for the construction of a bead-spring micro-swimmer, and leads to the discovery of the aforementioned swimming regimes.

Effect of driving parameters on the velocity and nature of swimming

We first study the effects on the swimming that the driving parameters have, irrespective of the shape of the beads. From eqn (4), the velocity magnitude $|\mathbf{v}|$ is the highest when the phase difference α is $\pi/2$ if $A \geq B$, and $-\pi/2$ if $A < B$. If one increases the force amplitudes, there is a corresponding quadratic increase in the velocity.

The force-based approach has the important consequence of allowing analytical prediction of the pusher or puller nature of the swimmer. We find that this nature depends upon the relation

$$\left(\frac{B}{A} - \frac{A}{B}\right)^{-1} \sin\alpha \gtrless \frac{2\kappa\lambda}{\kappa^2 + 12\lambda^2}. \quad (6)$$

When the left hand side of relation (6) is larger, then the swimmer moves in the direction of the bead with the higher force amplitude, and is consequently a puller. On the other hand, if the right hand side is larger, then the swimmer moves in the opposite direction, and is a pusher. This is borne out by the analysis of the obtained flow-fields. The above relation fails to hold when the velocity becomes very low; in this case, the nature of the swimmer is not clearly defined.

Relation (6) says that the same swimmer following essentially similar strokes may be a pusher or a puller depending on the precise parameter values of the forces it faces. For instance, the nature of the swimmer can be changed by simply applying the driving at a different rate (Fig. 2(a)). Similarly, this nature may change on changing the magnitude of the forces. For the force amplitudes A and B , if the force phase difference α is positive (i.e. $\alpha \in [0, \pi]$), then the swimmer is a pusher if $A > B$ (Fig. 2(b)). If $B > A$, the swimmer is a puller at small B , and becomes a pusher at large B .

Fig. 2 also shows the dependence of the velocity magnitude on the force parameters. For a changing ratio of B/A , due to the quadratic nature of the velocity curve, the global maximum of the velocity magnitude is always in the pusher regime. For other parameter changes (ω , α , κ , η), this does not necessarily hold true.

Since the swimming stroke results from the forces on the swimmer, we are also able to determine the stroke parameters from our approach. Doing this is very instructive as it shows the relationship between the motions of the two arms, and sheds light on phenomena such as their relative amplitudes and their synchronisation. By assuming a swimming stroke, Golestanian and co-workers have found the velocity of the three-sphere swimmer³⁸ to be

$$\mathbf{v} = G d_1 d_2 \omega \sin \beta \hat{\mathbf{z}}. \quad (7)$$

Here G is a geometric factor, d_1 and d_2 are the amplitudes of the oscillations of the swimmer's arms, and β gives the phase difference between the sinusoidal deformations of the arms. From our force-based formulation, we can express d_1 , d_2 and β explicitly as functions of the different driving and swimmer parameters (plotted in Fig. 2, lower panels; see the *Mathematica* notebook in the ESI† for full expressions).

We find that as the force amplitude ratio B/A varies with α fixed at $\pi/2$, the stroke amplitude ratio d_2/d_1 becomes one at a

point when the swimmer transitions from a pusher to a puller (Fig. 2(b)). Moreover, the maximum in the d_2/d_1 curve coincides with the other transition from a puller to a pusher. Similarly, as the driving frequency ω varies with A and B held fixed, when the relative difference between the arm oscillation amplitudes d_2 and d_1 is the largest then again the swimmer has a transition point between being a puller and a pusher (Fig. 2(a)).

An especially significant effect that we observe on studying the dependence of the stroke on the force parameters is the near locking of the stroke phase shift β for large parts of the parameter space. This is highlighted when the force amplitude ratio B/A is varied (lower panel of Fig. 2(b)), when $\sin \beta$ automatically assumes the optimal values of $+1$ or -1 . This suggests that the swimmer has the ability to automatically synchronise its two beating arms for much of the phase space so as to achieve efficient propulsion, and is reminiscent of the phase locking observed in *Chlamydomonas* flagella when elastic connections are included.⁴²

Effect of shape

For ellipsoidal beads, we now investigate how their aspect ratio affects the swimming velocity for fixed driving parameters. The ellipsoids are formed by revolving an ellipse of semi-axes a and b around a , with aspect ratio $e = a/b$ and their major axis either parallel or perpendicular to the springs (Fig. 1). We consider prolate ($e \geq 1$) and oblate ($e \leq 1$) ellipsoids separately, and have therefore four families, namely prolates and oblates of a constant volume and a constant surface area.

Friction coefficients of beads under constraints

General expressions for the friction coefficients of ellipsoids of revolution are available in the literature,^{43,44} from which we determine the reduced friction coefficients λ for the above four

Fig. 2 Velocity $\mathbf{v}$, armlength ratio d_2/d_1 and stroke phase difference $\sin \beta$ of a swimmer as a function of (a) frequency ω , and (b) force ratio B/A . Here $\alpha = \pi/2$. Note that $\mathbf{v} \sim \omega$ for $\omega \rightarrow 0$ and $\mathbf{v} \sim 1/\omega$ for $\omega \rightarrow \infty$, in contrast to the linear dependence of the swimming velocity $\mathbf{v}$ on the driving frequency ω for all ω , when the stroke is pre-set.³⁸

families (Table 1). For three of these families – namely prolates of a constant volume and a constant surface area and oblates of a constant volume – the smallest reduced friction coefficient $\lambda_{\min}$ is attained for an ellipsoid oriented parallel to the direction of motion and with an aspect ratio close to one (Fig. 3(a) and Table 2). In the thin body limit ($e \rightarrow \infty$ for prolates and $e \rightarrow 0$ for oblates), λ diverges as some body dimension becomes infinite. In contrast, for oblates of a constant surface area, both the smallest and the largest values of λ are attained in the thin body limits ($e \rightarrow 0$), depending on the ellipsoid orientation (Fig. 3(c) and Table 2). This is because the limiting shape in this case is a finite two-sided circular disc with the area of each side being $S/2$, where $S = 4\pi r_0^2$ is the constant surface area. It is easy to show that in this case the friction coefficients have boundary extrema given by

$$\lambda_{\min} = \frac{16\sqrt{2}r_0}{9\pi},$$

and

$$\lambda_{\max} = \frac{8\sqrt{2}r_0}{3\pi}. \quad (8)$$

Geometric optimisation for fixed driving

For the above families, to determine the effect of bead shape upon the swimming, we analyse the equation

$$\frac{d|\mathbf{v}|}{de} = 0 = \frac{d|\mathbf{v}|}{d\lambda} \frac{d\lambda}{de}. \quad (9)$$

Using the chain rule, we have broken up the relation for the velocity extrema into

$$d\lambda/de = 0, \quad (10)$$

and

$$d|\mathbf{v}|/d\lambda = 0. \quad (11)$$

Looking at these two relations separately is instructive. Eqn (10) yields the aspect ratio $e_{\min}$ of the ellipsoid with the smallest effective hydrodynamic radius $\lambda_{\min}$ as determined earlier (Table 1). Since this condition relates only to the geometry of the beads and not to the forces acting on the swimmer, the velocity curve always has an extremum $\mathbf{v}_{\lambda_{\min}}$ at the aspect ratio $e_{\min}$. This value $\mathbf{v}_{\lambda_{\min}}$ is given by eqn (4), with λ replaced by $\lambda_{\min}$ for the appropriate case (Table 1). This smallest effective hydrodynamic radius $\lambda_{\min}$ defines a global critical value κ_c of the reduced spring constant, given by

$$\kappa_c = 2\sqrt{3}\lambda_{\min}. \quad (12)$$

As we shall see, depending on whether the reduced spring constant of the swimmer is larger or smaller than this critical value, the extremum $\mathbf{v}_{\lambda_{\min}}$ in the velocity–aspect ratio curve may be a maximum or a minimum.

Eqn (11) allows us to connect the optimal shapes to the different forces acting on the beads, since its solutions relate the effective radius to the spring constant, the driving frequency and the fluid viscosity. Let the springs in the swimmer have a reduced spring constant given by

$$\kappa = \kappa_s. \quad (13)$$

Then, there is a shape with the reduced friction coefficient given by

$$\lambda_s^{-1} = \kappa_s / (2\sqrt{3}), \quad (14)$$

such that λ_s^{-1} is a solution to eqn (11). This leads to the velocity extremum

Table 1 The reduced friction coefficients λ of prolate and oblate ellipsoids in different orientations and under different constraints in terms of the ellipsoidal aspect ratio e

Shape and orientation	Pre-factor P	λ for constant volume $V (V = (4/3)\pi r_0^3)$	λ for constant surface area $S (S = 4\pi r_0^2)$
$\frac{(4/3)(e^2 - 1)}{(2e^2 - 1)} \log(e + \sqrt{e^2 - 1}) - e$	$P \times \frac{r_0}{e^{1/3}}$	$P \times \frac{\sqrt{2}r_0}{\sqrt{1 + \frac{e^2}{\sqrt{e^2 - 1}} \sin^{-1}\left(\frac{\sqrt{e^2 - 1}}{e}\right)}}$
$\frac{(8/3)(e^2 - 1)}{(2e^2 - 3)} \log(e + \sqrt{e^2 - 1}) + e$	$P \times \frac{r_0}{e^{1/3}}$	$P \times \frac{\sqrt{2}r_0}{\sqrt{1 + \frac{e^2}{\sqrt{e^2 - 1}} \sin^{-1}\left(\frac{\sqrt{e^2 - 1}}{e}\right)}}$
$\frac{(8/3)(1 - e^2)}{(3 - 2e^2)} \tan^{-1}\left(\frac{\sqrt{1 - e^2}}{e}\right) - e$	$P \times \frac{r_0}{e^{1/3}}$	$P \times \frac{\sqrt{2}r_0}{\sqrt{1 + \frac{e^2}{\sqrt{1 - e^2}} \tanh^{-1}(\sqrt{1 - e^2})}}$
$\frac{(4/3)(1 - e^2)}{(1 - 2e^2)} \tan^{-1}\left(\frac{\sqrt{1 - e^2}}{e}\right) + e$	$P \times \frac{r_0}{e^{1/3}}$	$P \times \frac{\sqrt{2}r_0}{\sqrt{1 + \frac{e^2}{\sqrt{1 - e^2}} \tanh^{-1}(\sqrt{1 - e^2})}}$

Fig. 3 (a) Reduced friction coefficient λ for prolate ellipsoids of a constant volume or surface area and oblate ellipsoids of a constant volume. (b) The corresponding velocity v curves, for either $A = B$ or $\alpha = \pi/2$ if $A \geq B$ (or $\alpha = -\pi/2$ if $A < B$). (c) λ for oblate ellipsoids of a constant surface area. (d) The corresponding velocity v curves, for either $A = B$ or $\alpha = \pi/2$ if $A \geq B$ (or $\alpha = -\pi/2$ if $A < B$). In (a) and (b), 'I' and 'II' denote the drag-dominated and the interaction-dominated regimes, respectively, while in (c) and (d), 'Ia' and 'Ib' denote the drag-dominated regime and 'II' denotes the interaction-dominated one.

$$v_{\lambda_s^{-1}} = \frac{7(2\sqrt{3}AB \sin \alpha + A^2 - B^2)}{768\pi^2\eta^2\Gamma^2\omega\kappa_s} \hat{z}. \quad (15)$$

If λ_s^{-1} is the only solution to eqn (11), then one can show (see Appendix) that if $\kappa_s < \kappa_c$, the magnitude of the velocity has only one maximum obtained from the geometric condition which determines the most streamlined shape (solid curve, labelled 'I', in Fig. 3(b)). We call this regime 'drag-dominated', as here the velocity is maximised upon minimising the drag. On the other hand, if $\kappa_s > \kappa_c$, then the velocity curve has two more extrema (one in the case of oblates of a constant surface area), which are degenerate and are attained for the ellipsoids whose reduced hydrodynamic radius equals λ_s^{-1} (dashed curve, labelled 'II', in Fig. 3(b)). In this case, the magnitude of these latter velocity extrema is globally the maximum. We label this regime as 'interaction-dominated', as here the velocity is maximised at an

intermediate value of the drag, where the hydrodynamic interaction between the beads becomes important. In this regime, in fact, one sees the highly counter-intuitive effect of the most streamlined shape forming locally the slowest swimmer (as the dashed curve in Fig. 3(b) has a local minimum at $e_{\min}$).

The fact that these two regimes exist can be attributed to the two conflicting effects that drag has upon a swimmer: while on one hand it resists motion through the fluid, on the other hand it promotes the fluid's agitation, resulting in hydrodynamic interaction among the beads and ultimately in swimming. In the interaction-dominated regime, where the spring constant (and consequently κ_s) is relatively high, most of the input work is consumed in deforming the springs, and so an increased drag is beneficial for a heightened hydrodynamic interaction among the bodies. Therefore, the swimmer with ellipsoids of an effective radius $\lambda_{\min}$, which agitates the fluid the least, is locally the slowest. In contrast, in the drag-dominated regime, where the spring constant is low, most of the input work is transferred directly onto the agitation of the fluid, so having a high drag only slows the swimmer down.

Phase diagram

More generally, eqn (11) can have several solutions for λ depending on the force parameters A , B and α . Then the velocity – seen as a function of the ellipsoid's aspect ratio e and its orientation – can have upto seven extrema (see Appendix for details). In this case, too, we can identify the drag-dominated and the interaction-dominated regimes, as the regimes respectively where the highest velocity magnitude is attained for

Table 2 Critical values of $e_{\min}$ and their respective $\lambda_{\min}$, for prolate and oblate ellipsoids subject to a constant total volume (V) or surface area (S) constraint

Shape	Constant volume ($V = (4/3)\pi r_0^3$)		Constant surface area ($S = 4\pi r_0^2$)	
	$e_{\min}$	$\lambda_{\min}$	$e_{\min}$	$\lambda_{\min}$
1.95	$0.95r_0$	4.04	$0.89r_0$
0.70	$0.99r_0$	0.00	$0.80r_0$

Fig. 4 Phase diagrams and solution maps for the forcing parameters A/B vs. α , for particular values of κ_s . If $\kappa_s/\lambda_{\min} < 2\sqrt{3}$, then for some parameters we have $\mathbf{v}_{\max} = \mathbf{v}_{\lambda_{\min}}$ (i.e. the drag-dominated regime), and if $\kappa_s/\lambda_{\min} > 2\sqrt{3}$ the whole phase space is interaction-dominated.

the most stream-lined bead shapes and for the bead shapes where a higher drag causes a sufficiently positive hydrodynamic interaction to lead to an increase in the velocity. Fig. 4 shows phase diagrams identifying these two regimes (top graph in each panel), and solution maps showing the number of velocity extrema (bottom graph), as a function of the driving parameters and for different values of the reduced spring constant κ_s . Since the velocity magnitude is unchanged under the transformation $\{A \leftrightarrow B, \alpha \rightarrow -\alpha\}$, we restrict these diagrams to $-\pi \leq \alpha \leq 0$.

These diagrams show that, in general, as the reduced spring stiffness κ_s increases, the swimmer goes from the drag-dominated regime to the interaction-dominated one. In particular, for $\kappa_s = 0$, the swimmer is always in the drag dominated regime (light blue in the phase diagrams), irrespective of the other parameters. There is only one velocity extremum (light green in the solution maps), at $\lambda = \lambda_{\min}$. As κ_s increases, two more extrema, associated with λ_s^2 (see Appendix), appear in the velocity curve for some values of the driving parameters (shown by purple in the solution maps), and parts of the corresponding phase diagrams enter the interaction-dominated regime (indicated by dark blue). This holds true as long as $\kappa_s < \kappa_c$. As soon as κ_s becomes larger, upto four extrema, associated with λ_s^1 and λ_s^3 (see Appendix), appear in the velocity-shape curve (shown by yellow and orange in the solution maps) depending on the force parameters, and the whole phase diagram enters the interaction-dominated regime.

Transport efficiency

To quantify the ability of swimmers to carry cargo, we define the transport efficiency ε_T as the ratio of the reduced transport energy $|\mathbf{v}|^2$ and the input power $\frac{1}{T} \int_0^T \sum_{j=1}^3 \mathbf{F}_j(t) \cdot \mathbf{v}_j(t) dt$, giving

$$\varepsilon_T = \left| \frac{AB(\kappa_s^2 + 12\lambda^2) \sin \alpha - 2(B^2 - A^2)\kappa_s \lambda}{(A^2 + B^2)(\kappa_s^2 + 12\lambda^2) - AB(\kappa_s^2 - 12\lambda^2) \cos \alpha} \right|.$$

This definition favours fast swimmers, but penalises ones which require a high power input. It is also bounded as a function of ω , κ_s and λ , thus ensuring that it does not diverge on, for example, increasing the time period. It is more suitable than the simple ratio of the current (which is proportional to $\mathbf{v}$) to the

Fig. 5 Velocity v (dashed blue curve) and transport efficiency ε_T (solid orange curve) of constant-volume prolate swimmers, with $B = 3A$ and $\alpha = \pi/4$. The λ_v written near each velocity extremum ($\lambda_v = \lambda_s^i$ or $\lambda_{\min}$) specifies that the respective extremum is attained at $\lambda = \lambda_v$. For the definition of λ_s^2 and λ_s^3 and the corresponding velocity extrema, please see the Appendix.

input work (as in ref. 45), which is insensitive to changes in shape for fixed driving in the far-field approximation. Also, the Lighthill efficiency⁴⁶ is unsuitable because it penalises swimmers facing a high drag, and this is inapt for the interaction-dominated swimming regime.

In spite of the natural correlation between the transport velocity and efficiency, the most efficient swimmer is not necessarily the fastest one (Fig. 5). This is particularly important in the interaction dominated regime, where designs which propagate with the same speed can have significantly different efficiencies due to a different repartition of the input work on the fluid and the compression of springs. For instance, in Fig. 5, ε_T at λ_s^3 is much less than at λ_s^2 , although $\mathbf{v}_{\lambda_s^2} = \mathbf{v}_{\lambda_s^3}$. In contrast, in the drag-dominated regime, the input work consumed by the elastic components is negligible, and so optimally-shaped swimmers are typically the most efficient.

Conclusion

Here we showed that starting from a fixed driving protocol of micro-swimmers allows one to describe several important phenomena, such as the puller or pusher behaviour of the swimmer and the synchronisation of its body parts that drive

the motion. We used this protocol to find the best driving force parameters and the optimal ellipsoidal shapes that lead to the fastest swimming. We identified two heretofore undiscovered regimes of transport, one where the fastest swimming occurs when the drag on the bodies is minimal, and the other where the swimming is promoted by strong body interactions caused by the body drag. Our results will be useful in the construction of relatively efficient bead-spring swimmer models, and more generally, in understanding the fundamental effects of drag and body shape on micro-swimming.

Appendix

Here we show the calculation of the critical value κ_c of the reduced spring constant and of the general extrema in the velocity–aspect ratio curve (which also takes the ellipsoid orientation into account, as in Fig. 3). First we consider the three special cases of (i) $A = B$, (ii) $\alpha = \pi/2$ with $A > B$, and (iii) $\alpha = -\pi/2$ with $A < B$. For these cases, it can be easily shown that λ_s^{-1} (eqn (14)) is the only solution to eqn (11). Therefore, if the springs are so soft that $\kappa_s < 2\sqrt{3}\lambda_{\min}$, then there can be no ellipsoid with the effective radius λ_s^{-1} , since in that case $\lambda_s^{-1} = \kappa_s/(2\sqrt{3})$ would be smaller than $\lambda_{\min}$, which is impossible. On the other hand, if the springs are stiff enough so that $\kappa_s > 2\sqrt{3}\lambda_{\min}$, then – for prolate ellipsoids of a constant volume, as in Fig. 3(a) – exactly two ellipsoids have the effective radius λ_s^{-1} (with aspect ratios given by e_1 and e_2 in regime II, Fig. 3(a)). Therefore, $\kappa_c = 2\sqrt{3}\lambda_{\min}$ acts as a critical value of κ .

The above discussion is identical for prolates of a constant surface area and for oblates of a constant volume. The case of oblates of a constant surface area is slightly different, since $e_{\min} = 0$ and $\lambda_{\max}$ is finite. In this case, if the springs are too soft, *i.e.* with $\kappa_s < 2\sqrt{3}\lambda_{\min}$ or too stiff, with $\kappa_s > 2\sqrt{3}\lambda_{\max}$, then there is no ellipsoid with the effective radius λ_s^{-1} . Moreover, since $e_{\min}$ equals 0, the velocity curves are monotonic functions of the aspect ratio e . For soft springs, this function decreases with e (regime Ia in Fig. 3), while for stiff springs it increases (regime Ib). If, however, the spring stiffness is intermediate, *i.e.* $2\sqrt{3}\lambda_{\min} < \kappa_s < 2\sqrt{3}\lambda_{\max}$, then there is one velocity maximum obtained from the condition in eqn (11).

For a general choice of parameters, eqn (11) provides two further pairs of solutions, namely $\{\lambda_s^{-2}, \lambda_s^{-3}\}$ (when the relation between the force amplitudes is $B < A$), and $\{\lambda_s^{-4}, \lambda_s^{-5}\}$ (when $A < B$). These solutions can be ordered as $\lambda_s^{-2} < \lambda_s^{-1} < \lambda_s^{-3}$ and $\lambda_s^{-4} < \lambda_s^{-1} < \lambda_s^{-5}$. A solution λ_s^{-i} of eqn (11) for the effective drag coefficient is physically relevant only if $\lambda_s^{-i} \in R$ and $\lambda_s^{-i} \geq \lambda_{\min}$. Each such physically relevant solution λ_s^{-i} provides two degenerate velocity extrema $\mathbf{v}_{\lambda_s^{-i}}$. Furthermore, the degeneracy extends over the solution pairs, with $\mathbf{v}_{\lambda_s^{-2}} = \mathbf{v}_{\lambda_s^{-3}}$ and $\mathbf{v}_{\lambda_s^{-4}} = \mathbf{v}_{\lambda_s^{-5}}$. These extrema values are given by

$$|\mathbf{v}_{\lambda_s^{-i}}| = \frac{7 \left(F_{>}^2 - F_{<}^2 - \sqrt{F_{>}^4 + F_{<}^4 - 2F_{>}^2 F_{<}^2 \cos(2\alpha)} \right)}{384\pi^2 \eta^2 l^2 \omega \kappa_s}, \quad (16)$$

where $i = 2, \dots, 5$ and $F_{>}$ and $F_{<}$ denote the larger and the smaller of the force amplitudes A and B , respectively. Consequently, the

velocity $\mathbf{v}$ as a function of the aspect ratio e has, in addition to one extremum from $\lambda_{\min}$, up to 3 pairs of extrema from λ_s^{-i} .

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