When do shape-changers swim upstream?

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Using multiple-scale analysis, Walker *et al.* (2022) obtain the long-time behaviour of a shape-changing swimmer in Poiseuille flow. They show that the behaviour falls into one of three categories: endless tumbling at increasing distance from the midline of the flow; preserved initial behaviour of the swimmer; or convergence to upstream rheotaxis, where the swimmer is situated at the midline of the flow. Furthermore, a single swimmer-dependent constant is identified that determines which of the three behaviours is realised.

Key words: Micro-organism dynamics, Low-Reynolds number flows, Nonlinear Dynamical Systems

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1. Introduction

Understanding the behaviour of microswimmers in flow environments has a wide-range of applications; from upstream contamination by bacteria in medical devices (Figueroa-Morales *et al.* 2020), to the vertical migration of phytoplankton in turbulence (Lovecchio *et al.* 2019). To predict how a micro-swimmer moves through a flow environment, we need to track the swimmer's orientation and position; these are coupled because changes in orientation can depend on space if the flow field is non-uniform, and changes in position occur due to swimming, which depends on orientation, as well as advection by the fluid.

Because of their small size, microswimmers typically live in the world of low Reynolds number, where inertial effects can be neglected (Purcell 1977). In this Stokes flow limit, the motion of spheroidal particles in simple shear was first described by Jeffery (1922), and shown to be valid for all axi-symmetric particles by Bretherton (1962). These results have been used to study hydrodynamic phenomena in microswimmer suspensions (e.g. Pedley & Kessler 1992). In general, for swimmer with orientation $\mathbf{p}$, the change in orientation is governed by

$$\frac{d\mathbf{p}}{dt} = \frac{1}{2}\mathbf{\Omega} \times \mathbf{p} + B\mathbf{p} \cdot \mathbf{E} \cdot (\mathbf{I} - \mathbf{pp}) \tag{1.1}$$

where $\mathbf{\Omega}$ is the vorticity, $\mathbf{E}$ is the rate-of-strain tensor, and B is the Bretherton constant. Microswimmers can display interesting dynamics that are distinct from passive colloids, as highlighted by Zoettl & Stark (2013) who used a dynamical systems approach to identify that elongated swimmers in Poiseuille flow can undergo either tumbling or swinging behaviour.

Microswimmers typically propel themselves through fluid environments by changing their shape in a periodic manner, for example by the beating of long whip-like flagella, or shorter cilia which cover the surface of the swimmer (Elgeti *et al.* 2015). Walker *et al.* (2022) (WIMGD) take a minimal model to account for shape-changing; they use the model of Jeffery, equation (1.1), but allow the Bretherton constant, B, and swimming

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speed to be an oscillatory function of time. WIMGD show that this simple model can capture key long-time dynamics of swimmers, in particular they are able to identify a single shape parameter which captures whether swimmers undergo rheotaxis, that is stably orientate themselves to swim upstream.

2. Overview

Applying equation (1.1) to planar Poiseuille flow, Omori *et al.* (2021) introduced and numerically analysed the following system of ordinary differential equations describing the transverse coordinate y and swimmer orientation θ, with $\theta = 0$ corresponding to the direction of flow and $y = 0$ the centreline:

$$\frac{dy}{dt} = \omega u(\omega t) \sin\theta, \tag{2.1}$$

$$\frac{d\theta}{dt} = \gamma y(1 - B(\omega t)\cos 2\theta). \tag{2.2}$$

The shape-changing nature of the swimmers is captured here by allowing the swimming speed, u, and Bretherton constant, B, to be oscillatory functions, where $\omega \gg 1$ is the high frequency period of the oscillations. The parameter γ is a fixed (positive) characteristic shear rate of the flow.

In order to understand the observed dynamics, WIMGD define $z(t) = y(t)/w^{1/2}$ and, inspired by Zoettl & Stark (2013), introduce a Hamiltonian-like quantity:

$$H(t) := \frac{\gamma}{2\langle u\rangle} z^2 + g(\theta), \tag{2.3}$$

where g is a closed form analytic function that only depends on B, and $\langle(\cdot)\rangle$ denotes the average value over an oscillatory period.

WIMGD introduce fast and intermediate timescales: $T = \omega t; \tau = \omega^{1/2} t$, and implement a multiple-scale analysis, formally defining $z(t) = z(T, \tau, t)$ and $\theta(t) = \theta(T, \tau, t)$, treating each time variable as independent. At leading order, WIMGD find that the intermediate timescale dynamics directly correspond to the dynamics for a fixed shape particle:

$$z_{0\tau} = \langle u\rangle \sin\theta_0, \tag{2.4}$$

$$\theta_{0\tau} = \gamma z_0(1 - \langle B\rangle \cos 2\theta_0). \tag{2.5}$$

Over the intermediate timescale τ, this yields the result that the leading order expression for the Hamiltonian-like quantity given by $H_0(t)$ (equal to $H(t)$ with $z = z_0$ and $\theta = \theta_0$) is conserved. Now, on considering H_0 as a fixed quantity, as identified by Zoettl & Stark (2013) and illustrated in figure 1, two types of behaviours are observed: if $H_0 > g(0)$ the swimmers tumble and there is monotonic evolution of θ_0; else if $H_0 < g(0)$ the swimmers exhibit swinging motion with θ_0 oscillating between two values. Also note in figure 1 the existence of the unique equilibrium point $(z_0, \theta_0) = (0, \pi)$ which corresponds to rheotaxis and H_0 taking its minimum value of $g(\pi)$.

In order to examine the long-time dynamics of the swimmers, WIMGD examine the full dynamics of $H(t)$. Specifically, they introduce the function $h(T, \tau, t) = H_{2T} + H_{1\tau} + H_{0t}$ to represent the $O(1)$ terms in the full derivative dH/dt. Averaging over a period in T and then period in τ yields the long-time evolution equation:

$$\frac{dH_0}{dt} = \gamma f(H_0)W, \tag{2.6}$$

where W is a constant that can be calculated purely from the shape properties of the

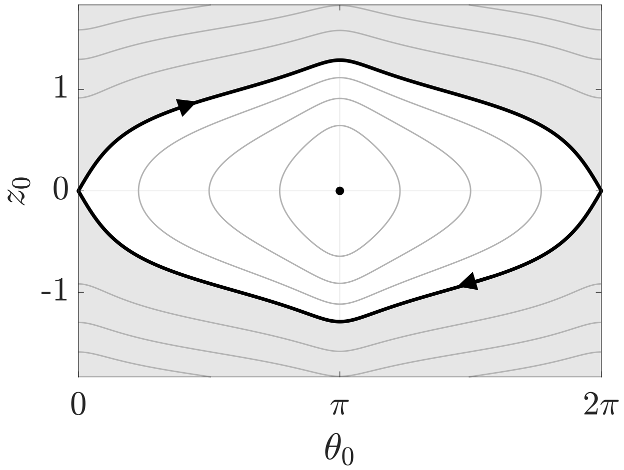

FIGURE 1. Phase portrait on the intermediate timescale, τ, showing contours of H_0. Solutions in the shaded region where $H_0 > g(0)$ correspond to tumbling motion whereas trajectories with $H_0 < g(0)$ exhibit swinging motion. The stationary point $(z_0, \theta_0) = (0, \pi)$ corresponds to upstream swimming, i.e. rheotaxis, with $H_0 = g(\pi)$. Taken from WIMGD.

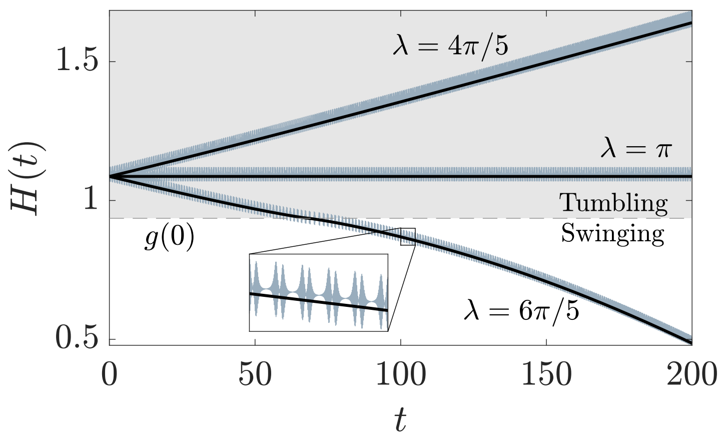

FIGURE 2. The value of H as computed from the full numerical solution (blue), equations (2.1-2.3) and approximate solution (black), equation (2.6), for three phase shifts $\lambda \in \{4\pi/5, \pi, 6\pi/5\}$ and parameters $(\alpha, \beta, \delta, \mu) = (1, 0.5, 0.32, 0.3)$. Adapted from WIMGD.

swimmer. The quantity $f(H_0)$ is shown to be negative for all H_0 and so the sign of $\frac{dH_0}{dt}$ is determined by the constant W. Specifically the fixed point $H_0 = g(\pi)$ corresponding to the rheotactic configuration $(z_0, \theta_0) = (0, \pi)$ is globally stable if $W > 0$ and unstable if $W < 0$.

WIMGD illustrate the asymptotic calculations with the specific example of $u(T) = \alpha + \beta \sin T$ and $B(T) = \delta + \mu \sin(T + \lambda)$. In this case, if $\beta\mu > 0$ then $\lambda \in (0, \pi)$ corresponds to $W < 0$ and tumbling, whereas $\lambda \in (\pi, 2\pi)$ corresponds to $W > 0$ and rheotaxis as illustrated in figure 2 which also demonstrates the good agreement between the full solutions of the dynamical system with the asymptotic approximation.

3. Future

The elegant analysis of WIMGD has the potential to be applied and extended to a wide range of topical questions in the field of active biofluids, and there are open questions to determine the range of applicability of the results. In particularly, WIMGD assumed shape-changing can be be modelled through periodic oscillations in the Bretherton constant (valid for axi-symmetric particles in steady Stokes flow) and swimming speed. When considering individual micro-swimmers, the detailed mechanisms of propulsion, for example gait, can affect the swimming speed as demonstrated theoretically and recently experimentally by using dynamically-similar robotic models (Diaz *et al.* 2021). Furthermore, swimmers can swim in chiral patterns when propulsive torque and propulsive force are not aligned, and the unsteady nature of Stokes flow and external fields can also affect their swimming velocity and rotation rate (Maity & Burada 2022). The role of external fields, such as gravity, light or chemical gradients is also incorporated in recent work by Lauga *et al.* (2021) who identified a new instability in suspensions of biased microswimmers. Because of the ability of swimmers to cross streamlines, their dispersion is quite different to passive colloids, and current work aims to identify the correct population-level transport models for micro-swimmers (Fung *et al.* 2022, e.g); incorporating the shape-changing effects of WIMGD would be an interesting development in such population-level models.

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