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When do shape changers swim upstream?

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Using a multiple-scale analysis, Walker *et al.* (*J. Fluid Mech.*, vol. 944, 2022, R2) obtain the long-time behaviour of a shape-changing swimmer in a 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

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 microswimmer 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 numbers, 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 axisymmetric particles by Bretherton (1962). These results have been used to study hydrodynamic phenomena in microswimmer suspensions (e.g. Pedley & Kessler 1992). In general, for a swimmer with orientation $\boldsymbol{p}$, the change in orientation is governed by

$$\frac{\mathrm{d}\boldsymbol{p}}{\mathrm{d}t} = \frac{1}{2}\boldsymbol{\Omega} \times \boldsymbol{p} + B\boldsymbol{p}\cdot\boldsymbol{E}\cdot(\boldsymbol{I} - \boldsymbol{pp}), \tag{1.1}$$

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where $\boldsymbol{\Omega}$ is the vorticity, $\boldsymbol{E}$ is the rate-of-strain tensor and B is the Bretherton constant (which ranges from zero for a sphere to unity for an infinitely thin rod). Microswimmers can display interesting dynamics distinct from the dynamics exhibited by 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, Winkler & Gompper 2015). Walker *et al.* (2022) (WIMGD) take a minimal model to account for shape changing; they use the model of Jeffery, (1.1), but allow the Bretherton constant, B, and swimming speed to be an oscillatory function of time. WIMGD show that this simple model can capture the 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 that the swimmers stably orientate themselves to swim upstream.

2. Overview

Applying (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:

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \omega u(\omega t)\sin\theta, \tag{2.1}$$

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

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 time scales: $T = \omega t$; $\tau = \omega^{1/2}t$, 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 time scale dynamics directly corresponds 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 time scale 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

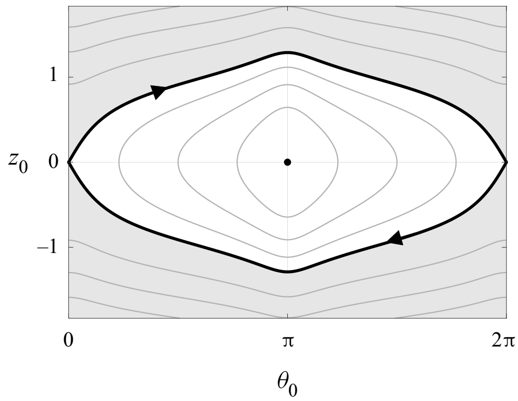

Figure 1. Phase portrait on the intermediate time scale, τ, showing contours of H_0. Solutions in the shaded region where $H_0 > g(0)$ correspond to tumbling motion whereas trajectories with $H_0 < g(0)$ exhibit swinging motion. The stationary point $(z_0, \theta_0) = (0, \pi)$ corresponds to upstream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

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 a 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 $\mathrm{d}H/\mathrm{d}t$. Averaging over a period in T and then period in τ yields the long-time evolution equation

$$\frac{\mathrm{d}H_0}{\mathrm{d}t} = \gamma f(H_0) W, \tag{2.6}$$

where W is a constant that can be calculated purely from the shape properties of the swimmer. The quantity $f(H_0)$ is shown to be negative for all H_0 and so the sign of $\mathrm{d}H_0/\mathrm{d}t$ 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 particular, WIMGD assumed shape changing can be modelled through periodic oscillations in the Bretherton constant (valid for axisymmetric particles in steady Stokes flow) and swimming speed. When considering individual microswimmers, the detailed mechanisms of propulsion, for example gait, can affect the swimming speed, as demonstrated theoretically and recently experimentally by

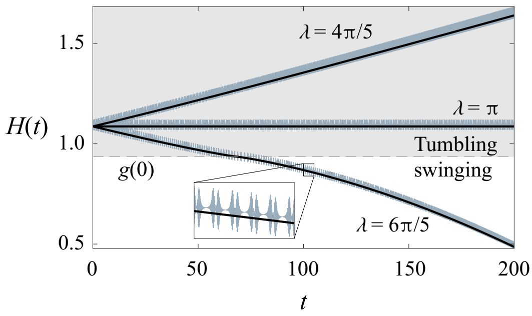

Figure 2. The value of H as computed from the full numerical solution (blue), (2.1)–(2.3) and approximate solution (black), (2.6), for three phase shifts $\lambda \in \{4\pi/5, \pi, 6\pi/5\}$ and parameters $(\alpha, \beta, \delta, \mu) = (1, 0.5, 0.32, 0.3)$. Adapted from WIMGD.

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, Dang & Ishikawa (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 microswimmers (e.g. Fung, Bearon & Hwang 2022); incorporating the shape-changing effects of WIMGD would be an interesting development in such population-level models.

Declaration of interests. The author report no conflict of interest.

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