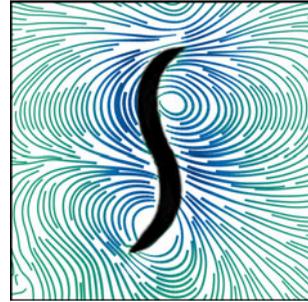


## The bearable gooeyness of swimming

Eric Lauga†

Department of Applied Mathematics and Theoretical Physics,  
Centre for Mathematical Sciences, University of Cambridge,  
Wilberforce Road, Cambridge CB3 0WA, UK



Understanding biolocomotion in fluids has long been a focus of fluid dynamicists. One method to quantify the impact of environmental stresses on locomotion is to systematically change the mechanical properties of the surrounding medium, and measure how that change influences swimming kinematics and energetics. In a recently published investigation, Gagnon *et al.* (*J. Fluid Mech.*, vol. 758, 2014, R3) employ that approach to investigate the locomotion of the nematode *Caenorhabditis elegans* in complex fluids. Specifically, they characterize experimentally how the presence of shear-thinning rheology influences the flow around the organism and its swimming ability. Surprisingly, while they measure an important change to the flow structure around the organism, they find no change in its waving motion and the speed at which it is able to swim. While ‘gooeyness’ is a universal feature of natural biological and environmental media, *C. elegans* seems to find it perfectly bearable.

**Key words:** biological fluid dynamics, micro-organism dynamics, non-Newtonian flows

### 1. Introduction

At some point in our lives, we invariably end up making a fool of ourselves by performing the following stunt. A child asks us to demonstrate how to swim properly. Since the question will be asked when we are not at the pool but in our living room, we lie down to support our weight and proceed to demonstrate how to swim like an Olympian. But whereas the motion feels natural in water, pretend swimming in air feels oddly off, and one is often not able to coordinate legs and arms properly. When we are used to one specific environment (water), swimming under different conditions (air) does not feel quite right.

Encountering changes in the mechanical properties of one’s environment occurs very frequently for small organisms swimming at low Reynolds numbers (Lighthill 1975). Three ubiquitous examples can be given: during infection, bacteria have to self-propel through multi-layered viscoelastic host tissues (Madigan *et al.* 2010); in open water, planktonic micro-organisms are surrounded by chemically inhomogeneous

† Email address for correspondence: [e.lauga@damtp.cam.ac.uk](mailto:e.lauga@damtp.cam.ac.uk)

particle suspensions (Guasto, Rusconi & Stocker 2012); and along their journey to the ovum, mammalian spermatozoa have to progress through different types of mucus with large variations in viscosity and relaxation times (Suarez & Pacey 2006).

Understanding locomotion in complex media is therefore a problem of genuine biological importance. Furthermore, from a biophysical point of view, changes in the environment can allow one to gain insight into the force generation mechanisms at the heart of biological behaviour. A famous example is that devised by Chen & Berg (2000), who linked bacterial flagella to external beads in fluids of varying viscosity. The resulting change in the mechanical resistance to rotation then allowed them to determine the torque–speed relationship of the bacterial rotary motor (Berg 2003).

Driven by a combination of new experimental techniques, affordable high-frame-rate cameras and sophisticated numerical algorithms, a number of groups have recently investigated various aspects of small-scale locomotion in complex fluids. Most work has focused on model elastic fluids with constant viscosities (termed Boger fluids). Asymptotic studies suggest that swimmers driven by small-amplitude waving undergo a systematic decrease in their swimming speed (Lauga 2007), confirmed by experiments with *C. elegans* (Shen & Arratia 2011). For larger waving amplitudes, a transition can take place to a swimming enhancement (Teran, Fauci & Shelley 2010; Liu, Powers & Breuer 2011; Spagnolie, Liu & Powers 2013), although small-amplitude enhancement is also possible (Lauga 2014). Other biomimetic experiments show that adding elasticity always allows the swimmer to move faster (Dasgupta *et al.* 2013; Espinosa-Garcia, Lauga & Zenit 2013).

Less attention has been paid to another class of fluids, namely inelastic fluids, whose material properties depend nonlinearly on the rate of deformation. A theoretical study at small amplitude showed that the impact of shear-dependent rheology should be effectively, if not exactly, zero (Vélez-Cordero & Lauga 2013). In contrast, self-propelled waving sheets showed a very systematic decrease of propulsion for shear-thinning fluids (Dasgupta *et al.* 2013), while numerics for a two-dimensional model spermatozoon cell with a head and increasing waving amplitude shows faster locomotion (Montenegro-Johnson, Smith & Loghin 2013).

This is the context in which the new experimental study by Gagnon, Keim & Arratia (2014) appears, and it attempts to answer a simple but fundamental question: How would a real biological organism behave in a shear-thinning fluid?

## 2. Overview

Gagnon *et al.* (2014) consider the locomotion of the millimetre-sized nematode *C. elegans* in a variety of shear-thinning fluids (figure 1a). They measure the locomotion kinematics and the fluid mechanisms around the organism using tracer particles for two kinds of fluids: (a) solutions of the rod-like polymer xanthan gum, which show rheological data consistent with a Carreau fluid with power indices  $n$  ranging from 0.3 to 0.9 (i.e. at large shear rates  $\dot{\gamma}$ , the viscosity  $\mu$  varies as  $\mu \sim \dot{\gamma}^{n-1}$ , with  $n < 1$  indicating shear-thinning behaviour); and (b) Newtonian fluids with a large range of viscosities (from that of water to a few hundred times above). In all cases, the Reynolds numbers characterizing the flow were well below unity.

The experimental investigation obtained two main results. First, despite such a large change in the fluid rheology, the cells behave in exactly the same way in a complex fluid and in a Newtonian one. The authors found no measurable change in the worm waving amplitude, the speed of the waves, the waving frequency and the swimming speed. These results are consistent with the asymptotic study of Vélez-Cordero &

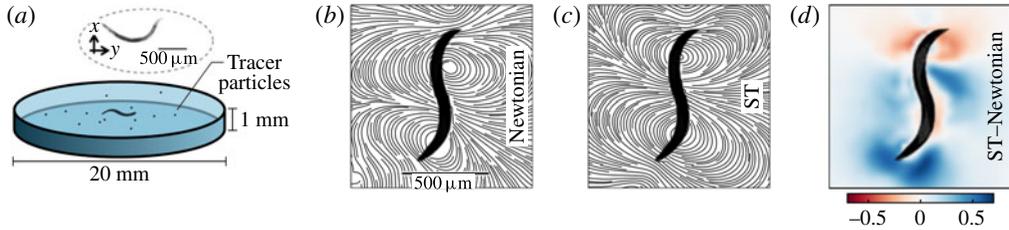


FIGURE 1. (a) Sketch of the experiment studied by Gagnon *et al.* (2014). (b) Streamlines around the swimming worm in a Newtonian fluid. (c) Streamlines in a shear-thinning fluid. (d) Difference between the normalized velocities in the shear-thinning and Newtonian flows, showing flow decrease near the head and increase near the tail of the swimmer.

Lauga (2013) on the small-amplitude waving locomotion of an inextensible sheet, but not with the numerical results of Montenegro-Johnson *et al.* (2013). However, that study focused on swimming spermatozoa-like waveforms with a head and increasing head-to-tail amplitude, whereas the waving motion of the head-less *C. elegans* has actually a decreasing amplitude.

The second main result is that, despite undergoing no change in their swimming kinematics, the organisms generate flows that display a number of important differences. To characterize the flows, the authors employ velocimetry with small tracer particles seeding the fluids. In the Newtonian case, the instantaneous flow streamlines around the organism are shown in figure 1(b) at the moment in the beating cycle where the instantaneous shear rates are the largest. In contrast, the flow induced in the shear-thinning fluid is displayed in figure 1(c) at the same instant in the waving motion. The main difference between the two is the displacement of the head and tail vortices, which have moved towards the head and display stronger flow gradients. Using measurements of the vorticity field, the authors further confirm that the head vortex increases in both size and magnitude in the non-Newtonian fluid.

In order to further contrast the two flows, the authors compute the difference between the velocity magnitudes (normalized by their maximum values) in the shear-thinning fluid and in the Newtonian one. These results are shown in figure 1(d), and as is quantified in more detail in the paper, show that non-Newtonian stresses impact the swimmer in an asymmetric way. The fluid velocities undergo a decrease near the head of the swimmer and an increase near the tail. Furthermore, this asymmetry in the velocity profile is seen to increase with the amount of shear thinning in the fluid until the typical rate of deformation is of the same order as the critical shear rate at which the shear viscosity displays a transition from Newtonian to non-Newtonian.

### 3. Future

Like many thought-provoking experiments, the study by Gagnon *et al.* (2014) leads to more questions than answers. The worms are self-propelled, and it is the balance between waving propulsion and drag that leads to their swimming speed (Lauga & Powers 2009). For the speed to remain unchanged, the stresses leading to both drag and thrust would need to change in exactly the same manner with changes in the rheology. How this is possible while at the same time undergoing significant changes in the flow structure is not clear. Using headless synthetic swimmers with

constant-amplitude waveforms, Dasgupta *et al.* (2013) found a systematic decrease of the swimming speed in shear-thinning fluids. Why such a different answer?

Biologically, how do the results of this study extend to much smaller organisms, such as flagellated algae or bacteria? One key difference lies perhaps in the flexibility of the organisms. The nematode *C. elegans* is large and uses muscular contractions to generate waving, and has bending rigidities  $B$  in the range  $B \approx 10^{-16}$ – $10^{-13}$  N m<sup>2</sup> (Backholm, Ryu & Dalnoki-Veress 2013). In contrast, eukaryotic flagella are orders of magnitude softer, with  $B \approx 10^{-23}$ – $10^{-21}$  N m<sup>2</sup> (Hines & Blum 1983). The waving motion of small cells is therefore likely to be impacted by changes in the fluid rheology, leading to an additional feedback mechanism for the fluid rheology to affect locomotion. These small cells might find so much gooeyness to be unbearable.

## References

- BACKHOLM, M., RYU, W. S. & DALNOKI-VERESS, K. 2013 Viscoelastic properties of the nematode *Caenorhabditis elegans*, a self-similar, shear-thinning worm. *Proc. Natl Acad. Sci. USA* **110**, 4528–4533.
- BERG, H. C. 2003 The rotary motor of bacterial flagella. *Annu. Rev. Biochem.* **72**, 19–54.
- CHEN, X. & BERG, H. C. 2000 Torque–speed relationship of the flagellar rotary motor of *Escherichia coli*. *Biophys. J.* **78**, 1036–1041.
- DASGUPTA, M., LIU, B., FU, H. C., BERHANU, M., BREUER, K. S., POWERS, T. R. & KUDROLLI, A. 2013 Speed of a swimming sheet in Newtonian and viscoelastic fluids. *Phys. Rev. E* **87**, 013015.
- ESPINOSA-GARCIA, J., LAUGA, E. & ZENIT, R. 2013 Fluid elasticity increases the locomotion of flexible swimmers. *Phys. Fluids* **25**, 031701.
- GAGNON, D. A., KEIM, N. C. & ARRATIA, P. E. 2014 Undulatory swimming in shear-thinning fluids: experiments with *C. elegans*. *J. Fluid Mech.* **758**, R3.
- GUASTO, J. S., RUSCONI, R. & STOCKER, R. 2012 Fluid mechanics of planktonic microorganisms. *Annu. Rev. Fluid Mech.* **44**, 373–400.
- HINES, M. & BLUM, J. J. 1983 Three-dimensional mechanics of eukaryotic flagella. *Biophys. J.* **41**, 67–79.
- LAUGA, E. 2007 Propulsion in a viscoelastic fluid. *Phys. Fluids* **19**, 083104.
- LAUGA, E. 2014 Locomotion in complex fluids: integral theorems. *Phys. Fluids* **26**, 081902.
- LAUGA, E. & POWERS, T. R. 2009 The hydrodynamics of swimming microorganisms. *Rep. Prog. Phys.* **72**, 096601.
- LIGHTHILL, J. 1975 *Mathematical Biofluidynamics*. SIAM.
- LIU, B., POWERS, T. R. & BREUER, K. S. 2011 Force-free swimming of a model helical flagellum in viscoelastic fluids. *Proc. Natl Acad. Sci. USA* **108**, 19516–19520.
- MADIGAN, M. T., MARTINKO, J. M., STAHL, D. & CLARK, D. P. 2010 *Brock Biology of Microorganisms*, 13th edn. Benjamin Cummings.
- MONTENEGRO-JOHNSON, T. D., SMITH, D. J. & LOGHIN, D. 2013 Physics of rheologically-enhanced propulsion: Different strokes in generalized Stokes. *Phys. Fluids* **25**, 081903.
- SHEN, X. N. & ARRATIA, P. E. 2011 Undulatory swimming in viscoelastic fluids. *Phys. Rev. Lett.* **106**, 208101.
- SPAGNOLIE, S. E., LIU, B. & POWERS, T. R. 2013 Locomotion of helical bodies in viscoelastic fluids: enhanced swimming at large helical amplitudes. *Phys. Rev. Lett.* **111**, 068101.
- SUAREZ, S. S. & PACEY, A. A. 2006 Sperm transport in the female reproductive tract. *Hum. Reprod. Update* **12**, 23–37.
- TERAN, J., FAUCI, L. & SHELLEY, M. 2010 Viscoelastic fluid response can increase the speed and efficiency of a free swimmer. *Phys. Rev. Lett.* **104**, 038101.
- VÉLEZ-CORDERO, J. R. & LAUGA, E. 2013 Waving transport and propulsion in a generalized Newtonian fluid. *J. Non-Newtonian Fluid Mech.* **199**, 37–50.