Biophysics

Bacteria swim faster when obstacles keep them in line

Raphaël Jeanneret & Marco Polin

Adding particles or polymers to a fluid can make bacteria swim straighter — and therefore faster — than they do through water, by inducing a torque that changes their body alignment. **See p.819**

It might come as a surprise that bacteria can swim tens of times their body length in a single second. This is equivalent to a human swimming 100 metres in less than 5 seconds. Even more surprising, however, is that bacteria sometimes swim even faster — not slower — than this when the fluid around them is filled with myriad obstacles that increase its viscosity. Such fluids are known as complex fluids, and they are found, for example, in our lungs and lining our stomach. On page 819, Kamdar *et al.*[1] show that the mysterious ability of bacteria to swim faster in complex fluids is actually the result of a remarkably simple effect: they swim straighter.

Complex fluids contain polymers or colloidal particles that endow the liquids with peculiar mechanical properties ranging between those of solids and simple liquids. Although such fluids might seem almost exotic, in reality they are quite common. The study of complex fluids in a biological context is an active interdisciplinary endeavour straddling the fields of soft condensed matter, microhydrodynamics, microbiology and cell biology. Besides existing in complex fluids in our bodies, polymers are abundant in the ocean, which is the largest ecosystem on the planet. There, they can assemble into gels spanning micrometres, and influence the physics and biology at the air–water interface, as well as the global sequestration of carbon to the ocean depths[2].

The first observations that mixing polymers into a fluid could increase bacterial swimming speeds were made 62 years ago[3]. The effect was initially attributed to changes in the shape of the bacterial flagella[4] — the flexible helical filaments that bacteria use for swimming. Bacteria are single-celled organisms, typically measuring a few thousandths of a millimetre. Those that can swim have one or more flagella, each connected to its own rotary motor on the surface of the cell through a flexible hook structure. These flagella are helical, like a corkscrew, so when the rotary motor twists them, they generate thrust, propelling the bacterium forwards.

When all of the motors rotate in the same direction, the flagella form a bundle that rotates as a single structure. This means that the cell body must also rotate to balance the motion of the bundle. Sometimes, one or more of the motors can temporarily reverse, causing the bundle to separate and the cell to tumble and change direction. The mechanics of this process can temporarily change the pitch (the distance of one complete turn) or even the handedness of flagella, affecting their efficiency as propellers. That polymers in solution could affect bacterial swimming speed by altering flagellar shape was therefore a plausible idea. But there has been no evidence to support this original proposal.

Fast-forward several decades, and two potential alternative mechanisms have emerged. The first concerns the fact that flagella can rotate hundreds of times per second, which means that they should experience a lower viscosity in a complex fluid than that felt by the cell body. This should, in turn, change the ratio of flagellar rotation to cell rotation in a way that is equivalent to the bundle rotating faster[5].

The second mechanism is based on the fact that flagellar rotation should stretch the suspended polymers, generating an elastic recoil. This is what makes honey climb up a rotating spoon. For bacteria, these extra forces should decrease the natural misalignment between the cell body and the overall direction of motion, leading to faster swimming[6]. As it turns out, the key to the problem lies with this misalignment.

The imprecise alignment between the flagellar bundle and the cell body causes bacteria to move along helical, rather than straight, trajectories (Fig. 1). When viewed under a microscope, this 3D motion looks like a 'wobble' of the cell body around a straight trajectory. Kamdar *et al.* showed that this wobbling is strongly reduced when nanometre- or micrometre-sized objects are suspended in the liquid, regardless of whether they are polymers or solid particles.

Reduced wobbling allows cells to move along straighter trajectories, leading to higher

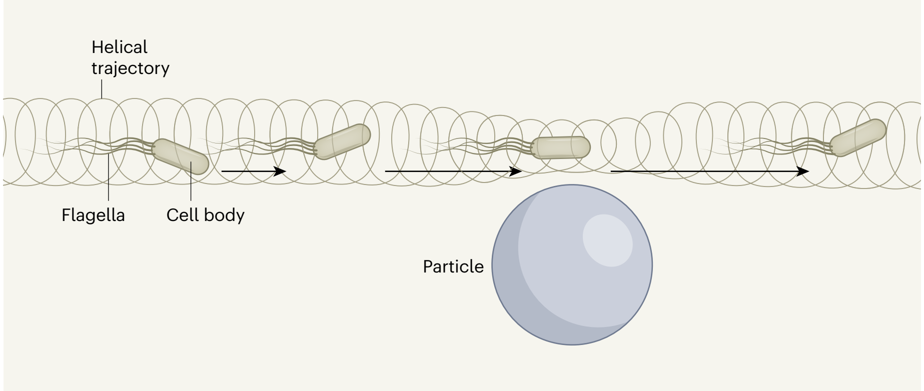

Figure 1 | Bacteria swim faster through fluids filled with particles. Bacteria are propelled forwards by helical filaments known as flagella, which are each attached to the cell body by a flexible hook structure (not shown). The cell body is angled in a direction that is not perfectly aligned with the flagella, and this causes bacteria to move along helical, rather than straight, trajectories. Kamdar *et al.*[1] showed that, when a bacterium encounters a particle, a hydrodynamic phenomenon known as boundary-induced torque bends the hooks, reducing the misalignment between the flagella and the cell body. The result is straighter, faster swimming, which has long been observed in fluids containing objects such as particles or polymers[3].

speeds along the axis of the helix. To understand this point, imagine that the bacterium's trajectory follows the helical shape of a spring. Pulling on the spring increases its length and decreases its radius, which means that the bacterium travels farther along the stretched spring than it does along the relaxed spring in the same amount of time.

But why do these cells swim on straighter trajectories when they are embedded in complex fluids? Kamdar and colleagues' experiments ruled out the polymer-induced elastic stresses suggested previously, because the team also observed the phenomenon when the fluids contained colloids rather than polymers. The authors showed instead that the trajectories were straighter because of a hydrodynamic phenomenon known as boundary-induced torque, which is experienced by particles in a fluid when they move close to a solid boundary. It results from the difference in drag between the sections of the particle closer and farther away from the wall.

In the case of bacteria moving through a complex fluid, each particle in the suspension – whether it's a polymer or a colloid – acts like a solid surface, inducing a torque on the moving bacteria. This torque bends the flagellar hooks, reducing the misalignment between the flagellar bundle and the cell body. The result is straighter, faster swimming. Together with their experiments, Kamdar and colleagues' mathematical model improves our understanding of bacterial wobbling, which had so far been overlooked despite the fact that it held the key to interpreting decades of observations of bacteria in complex fluids.

Nonetheless, the authors' findings need to be tested further in different experiments. An intriguing direction of study would be to investigate bacterial wobbling as a function of the hook length, which could be achieved by using genetically engineered mutants[7]. Changing the hook length modifies its resistance to bending, which should directly affect the magnitude of the speed increase. Beyond bacterial motion, Kamdar and co-workers' results could contribute to the design of versatile, self-propelled microrobots whose translational speed could be modulated by changing the angle between the propulsion machinery (synthetic flagella) and the body axis.

Raphaël Jeanneret is in the Laboratoire de Physique de l'Ecole Normale Supérieure, Université PSL, CNRS, Sorbonne Université, Université de Paris, F-75005 Paris, France. **Marco Polin** is at the Mediterranean Institute for Advanced Studies (UIB-CSIC), 07190 Esporles, Spain, and in the Department of Physics, University of Warwick, Coventry, UK.
e-mails: raphael.jeanneret@phys.ens.fr; mpolin@imedea.uib-csic.es

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Earth science

Mobile mantle could explain volcanic hotspots

Allen K. McNamara

Ancient records of Earth's magnetic field seem to contradict a conceptual picture of how regions of volcanic activity form. Statistical modelling now reconciles these data with our understanding of mantle fluid dynamics. **See p.846**

The speed of seismic waves can reveal the temperature of structures beneath Earth's surface, with faster waves indicating cooler temperatures and slower waves, warmer ones. Unusually low wave speeds have been measured[1] beneath the African continent and the Pacific Ocean, and these regions are known as large low-shear-velocity provinces (LLSVPs). Palaeomagnetic data provide an ancient record of Earth's magnetic field, and have been interpreted as evidence that the LLSVPs have remained fixed in their current positions for several hundred million years[2,3]. But this conclusion is at odds with our understanding of how mantle convects[4]. On page 846, Flament and colleagues[5] report simulations showing that palaeomagnetic data cannot distinguish between fixed and mobile LLSVPs – a finding that reconciles these observations with mantle fluid dynamics.

> **"As a tectonic plate moves over a hotspot, a chain of volcanoes is created, such as those on the Hawaiian Islands."**

When tectonic plates collide, one plate sinks into the deep interior, forming a region known as a subduction zone. Perhaps unsurprisingly, the regions of Earth's mantle that experience higher-than-average seismic-wave speeds lie beneath these boundaries. The LLSVPs are found in the deepest parts of Earth's lower mantle, nested between these regions of sinking tectonic plates. Seismic data suggest that LLSVPs have well-defined, sharp boundaries, providing evidence that their composition might be distinct from that of the surrounding mantle[1].

The area above the LLSVPs hosts the majority of Earth's volcanic hotspots; these are localized regions of volcanic activity seemingly unrelated to plate tectonics. And many of these hotspots lie directly over the LLSVP boundaries[2,6–8] (Fig. 1a). Hawaii's Big Island is an example of an active hotspot. Compared with the speed of tectonic plates, hotspot locations are relatively slow-moving. As a tectonic plate moves over a hotspot, a chain of volcanoes is created, such as those on the Hawaiian Islands. The volcano directly above a hotspot is active, whereas the older volcanoes along the chain have become extinct, which means that they are considered unlikely to erupt again.

Hotspot lavas have a different trace-element chemistry from other lavas, such as those generated at divergent plate boundaries, where new plates are formed. This observation has led to the hypothesis that hotspots are caused by hot plumes rising from Earth's lower mantle, probably from regions of the deep mantle that have a different, perhaps more primitive chemistry compared with that of their surroundings[9]. The fact that the LLSVPs are compositionally distinct from their surroundings in the lowermost mantle has implicated them in this hypothesis: one popular conceptual model of Earth's interior has LLSVPs as the source of this anomalous hotspot chemistry, delivered to the surface by rising mantle plumes[10] (Fig. 1b).

It's straightforward to connect the location of active hotspots with the LLSVPs, but what do we know about extinct volcanoes caused by hotspots that existed in the geological past? This is where palaeomagnetism comes into play. Volcanic rocks typically contain a small amount of the iron oxide mineral magnetite, which has a magnetic field that aligns itself with Earth's magnetic field. After a