Dissipative shocks behind bacteria gliding

Epifanio G. Virga

Dipartimento di Matematica, Università di Pavia, Via Ferrata 5, 27100 Pavia, Italy

Gliding is a means of locomotion on rigid substrates used by a number of bacteria, including myxobacteria and cyanobacteria. One of the hypotheses advanced to explain this motility mechanism hinges on the role played by the slime filaments continuously extruded from gliding bacteria. This paper solves, in full, a nonlinear mechanical theory that treats as **dissipative shocks** both the point where the extruded slime filament comes into contact with the substrate, called the filament’s *foot*, and the pore on the bacterium outer surface from where the filament is ejected. I prove that kinematic compatibility for shock propagation requires that the bacterium uniform gliding velocity (relative to the substrate) and the slime ejecting velocity (relative to the bacterium) must be equal, a coincidence that seems to have already been observed.

1. Introduction

For living cells, motility is as essential to their life as are the nutrients that sustain it. If food becomes scarce in the vicinity of a cell, this must move to survive. As explained in Wolgemuth’s [1] recent review, cell motion involves interaction with the environment: to move, a cell must exert an active force on its environment, which is counteracted by a resistive force, or reaction. At the cellular length scale, inertia is negligible, hence a motion results only from the balance of the active force produced by the cell and the reactive force exerted by the environment. A cell that stops producing a propelling force is brought to a halt virtually in no time.

One way of classifying cellular motion is by distinguishing the environments against which a cell moves into two gross categories: fluids and solids. In the former case, a cell is a swimmer, as it moves within a resistive fluid; in the latter case, it is a surfer, as it moves about a rigid surface. Like most gross classifications, this also joins the advantage of simplicity
to the disadvantage of inexactness. According to Nan & Zusman [2], what is called a surfer actually may exhibit one or more of the following different motility patterns, namely, swarming, twitching, sliding and gliding. This paper will be concerned only with the latter. I shall adopt here the neat definition of gliding given by Jarosch [3] in 1962 (also reproduced in [4]):

Gliding is ‘the active movement of an organism in contact with a solid substratum where there is neither a visible organ responsible for the movement nor a distinct change in the shape of the organism’.1

As remarked by Fritsch [6] in 1945, gliding movements are usually associated with the secretion of mucilage (also called slime), which has often been regarded as the very cause of movement [4]. Here, I am mainly concerned with modelling quantitatively the possible connection between slime extrusion and thrust force on the bacterium that secretes it. It should be clear from the start that the mechanism that I shall envisage is different from that of jet propulsion in the absence of inertia that has recently been studied in [7] for swimming bacteria: in this view, it is not the slime extrusion that generates the propelling thrust, but the adhesion of the secreted slime on the rigid substrate that sustains the advancing motion. I shall return later to the gliding mechanism modelled in this paper, after having briefly reviewed the families of bacteria to which it could be potentially applied.

Many bacteria glide over surfaces, including cyanobacteria and myxobacteria [8]. The former are among the fastest gliders, with a velocity as high as 10 \( \mu \text{ms}^{-1} \) [5], whereas the latter are among the slowest, with Myxococcus xanthus going at most at a speed of 4 \( \mu \text{mm} \text{min}^{-1} \), 1000 times slower than typical flagellated bacteria [9–11].

Myxococcus xanthus is presumably the most studied among gliding bacteria for the variety of propulsion mechanisms it exhibits and the complexity of its life cycle. It is a common Gram-negative bacterium that lives in the soil [12,13]; it is rod-shaped with typical length and diameter of 5–7 \( \mu \text{m} \) and 0.5 \( \mu \text{m} \), respectively. \( M. \text{xanthus} \) makes use of two genetically distinct mechanisms for gliding; either or both may be present in an individual cell [14]. One mechanism, called social, is characteristic of synergetic, coordinated motions involving a colony of cells [15–17], while the other, called adventurous, is typical of single cells living at the outskirts of a colony [18]. What distinguishes social from adventurous gliding in \( M. \text{xanthus} \) is not just the collective character of the former, as opposed to the solipsism of the latter. They also differ in their mechanics. Extrusion and retraction of pili are involved in social gliding: each cell emits a filament, typically of nearly 6 nm in diameter and a few micrometres in length, which adheres to either the supporting substrate or to another cell nearby; by retracting the adhered filament, a cell propels itself in coordination with those in its vicinity.

If social gliding of \( M. \text{xanthus} \) is rather well understood, its adventurous gliding remains a mystery. Apart from not being powered by pili, little is known about the actual mechanism of adventurous gliding of myxobacteria, as none of the hypotheses advanced so far has proved to be able to explain the full body of available experimental evidence. One such hypothesis, put forward nearly 90 years ago [19,20], hinges on the observation that myxobacteria secrete slime [21,22]. More recently, Wolgemuth et al. [23] gave direct evidence that slime extrusion is associated with the adventurous gliding of \( M. \text{xanthus} \): the micrographs in figure 1, which lately have been repeatedly reproduced, are rather striking illustrations of the slime filaments ejected by the cell. A mathematical model was also proposed in [23] to describe the extrusion of slime from the cell’s nozzles; it is treated as a polyelectrolyte gel and it is assumed that its extrusion results from the swelling induced by a hydration process taking place within the nozzle’s body. This rather sophisticated jet emission mechanism allowed for an estimate of the propelling force, which

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1Perhaps a more concise but equivalent definition is given in [2]: Gliding motility is ‘the active and smooth translocation of cells on a surface without the aid of flagella or pili’. Finally, a similar definition taken from Reichenbach [5] is also used in [1], that is, ‘the translocation in the long axis of the bacterium when in contact with a surface’.
Figure 1. Examination of the slime secretion process in wild-type M. xanthus cells. (a) Fluorescent light micrograph of gliding M. xanthus cells (capable of both adventurous and social gliding: strain DK1622). During locomotion, the cells leave slime trails behind, which can be stained by acridine orange. The slime trails originate at the rear poles of the individual cells (small arrows). Photograph taken after 1 h at 2000×. (b) Electron micrograph of the cell pole of a gliding M. xanthus cell. At higher magnification, it can be seen that the slime trails are composed of several slime bands, which are secreted from the sites at the cell pole, where the nozzles are located (large arrow). Adapted from [23], © 2002 Copyright Elsevier (Licence no. 3347720296046, granted on 14 March 2014).

was found to be sufficient to explain the observed gliding velocity for both myxobacteria and cyanobacteria.2

An opposing hypothesis has recently been advanced, according to which adventurous motility is provided by protein motors distributed along the length of the cell, which tend to form complexes that remain stationary relative to the supporting rigid substrate while the bacterium moves [11,25–28]. Such focal adhesion complexes seem to require slime secreted underneath the cell both to produce specific adhesion sites and to lubricate the area of contact between cell and substrate, as also confirmed by some other recent observations [29]. Also, compromising hypotheses have been proposed to the effect of regarding both slime extrusion and focal adhesion as viable coexisting mechanisms for myxobacteria gliding. It is no wonder that, in such a state of affairs, controversies have grown [2]. One, in particular, concerned the necessity for a gliding cell to rotate along its long axis while advancing: this was first believed to be the case for the focal adhesion theory to be confirmed, as the M. xanthus cytoskeleton along which the motive proteins are supposed to move is helicoidal, with axis coincident with the cell’s long axis [11,30]. Very recently, evidence has been brought against cell rotation [31], though per se this would neither rule out completely the focal adhesion hypothesis [32], nor prove the slime extrusion hypothesis.

Even if this latter hypothesis is not universally accepted as an explanation for the gliding of myxobacteria, since the work of Hoiczyk and Baumeister [18], it is well established as an explanation for the gliding of cyanobacteria. These latter are filamentous bacteria (blue-green algae) with a number of septa, for which the slime extrusion hypothesis assumes that slime filaments are ejected through the pores that surround each cell septum (see also [9]). Hoiczyk and Baumeister showed in [18] how slime formed bands about the cell surface that could be removed.

2See also [24] for the explanation of their experimental findings within this theoretical framework.
by a fluid flow. They were also able to establish that the slime was extruded at a rate of $3 \mu m \, s^{-1}$, which compared well with the gliding velocity (a coincidence to which I shall return later).

A previous study had shown the distribution of pores (14–16 nm in diameter) close to the cyanobacteria septa [33]. These pores were recognized in [18] as parts of a more complex system (called junctional pore complex) that appeared to constitute the extrusion organelles [34]. Figure 2 presents recent optical images illustrating the gliding of a *Nostoc* cyanobacterium, belonging to the Nostocales, a group that contains most of the cyanobacteria capable of gliding [35].

The general mathematical model put forward in [23] builds on the assumption that external fluids perfuse into the nozzle-like organelles hydrating the polysaccharide material constituting the slime; the swelling thus produced forces the slime out of the pores and causes the swollen gel to fall on the substrate and adhere to it. This, as it were, produces a footing for the cell to advance in a way that only superficially resembles walking [1]. Though the extrusion mechanism and the force associated with the gel swelling are fairly well described by the model in [23], to my knowledge, the forces associated with both adhesion and footing have not yet been studied. In particular, it would be desirable to know how the propelling force should be determined by the full gliding mechanism, which includes slime extrusion, adhesion and footing.

This will be the subject of this paper, which builds on a theory that has recently been proved to be useful to explain the forces at play in the popular, fascinating phenomenon of the chain fountain [36], a common chain that under the action of gravity alone raises spontaneously out of the pot that contains it before plunging down towards the floor [37]. The feature of the theory presented in [36] that distinguishes it from the earlier theory of Biggins & Warner [40] and Biggins [41] is the assumption that the pickup and putdown points of the steady, shape-preserving motion of the chain fountain are standing shocks that dissipate energy at the rate dictated by a classical law for internal impacts. Here, the same theory is applied to the extruded slime filament, which comes into contact with the substrate over which a bacterium glides. Both the foot, where contact is established between filament and substrate, and the pore, where the filament is extruded

Figure 2. Optical snapshots of a *Nostoc* bacterium gliding upon a glass slide. The scale is given by the black reference bar (corresponding to 10 μm). The bacterium is moving from right to left as indicated by the displacement of the arrow landmark. Image (b) is taken 12 s after image (a). Both images are reproduced from [35]. It should be noted that the resolution of these images is at least 100 times poorer than that of the images shown in figure 1, and so the slime filaments cannot be seen. (Online version in colour.)
from the bacterium, will be treated as dissipative shocks, though they are of two different natures. Figure 3 illustrates the model: a cigar-shaped bacterium glides on a flat substrate with constant velocity $u$ while ejecting a slime filament from its back (actually, the bacterium is apolar and its temporary back is just the end opposite to the direction of its motion).

In a steady gliding motion, the foot itself glides over the substrate and the filament shape is dislocated in time in the substrate rest frame. However, in the bacterium rest frame, both the filament shape and its foot remain unchanged as time elapses, making the extruded filament completely analogous to the ‘ejected’ chain studied in [36]. In this frame, both the ejecting pore and the adhering foot of the filament will be regarded as standing shocks; they will be treated following a paper of O’Reilly & Varadi [42] who, elaborating on earlier work of Green & Naghdi [43–46], proposed an elegant and rather comprehensive theory of shocks in one-dimensional continua, which in §2 is extended to the case in hand.

Section 2, which is largely based on [36] and serves the purpose of making the development here self-contained, is split into several subsections to make it easier for the reader to retrace the different elements of the theory developed here. In §3, I shall describe in quantitative terms the solution that the theory recalled in §2 affords for a gliding bacterium. In particular, I shall compute both the bacterium gliding velocity and the force resulting on it from the complete motion of the extruded slime filament. One simple result, which has already echoed in the observations recalled above, will follow from a kinematic compatibility condition on shock propagation, that is, that the absolute gliding velocity must equal the relative extrusion velocity.\(^5\) The analysis in §2 does not neglect gravity and in a way treats the ejected slime filament macroscopically, as if it were composed of coherent chain links fired away from an orifice. This assumption is discussed in §3d together with the consequences of relaxing it. Finally, the paper is closed with §4, where I collect the theoretical conclusions reached here and comment on the need for their experimental scrutiny.

2. Dissipative shocks

In this section, I recall the theory presented in [36], adapting it to the special problem envisaged here. Think of a slime filament as an inextensible string with uniform mass density $\lambda$ per unit length, parametrized in the reference configuration by the arc-length $s$. The position in space occupied by a material point of the filament is represented by the mapping $p = p(s, t)$. Here, $s$, which designates the convected variable, could also be used to designate the arc-length in the present configuration. Correspondingly, the velocity $v$ is defined by $v := \dot{p}$, where a superimposed dot represents differentiation with respect to time $t$. Similarly, $a := \ddot{v}$ is the acceleration. Let $f$ denote the external force acting per unit length of the filament and $\tau \geq 0$ the internal tension that arises as a reaction to the inextensibility constraint. The balance of linear momentum along any smooth arc of the filament is expressed by

$$\lambda a = f + (\tau t)', \tag{2.1}$$

where $t$ is the unit tangent and a prime $'$ denotes differentiation with respect to $s$ (see, for example, [47, section 34]). Equation (2.1) is written for an observer gliding at uniform speed along with the bacterium. Though the bacterium gliding motion on the substrate will be assumed to

\(^{5}\)The former is taken by an observer at rest on the substrate, whereas the latter is taken by an observer at rest on the gliding bacterium.
Figure 4. The present shape at time *t* of the filament. The points *p*(s₁, *t*) and *p*(s₂, *t*), with *s₂ > s₁*, delimit the arc under consideration. The point *p*(s₀, *t*) is a singular point, where the unit tangent *t* is discontinuous, with traces *t⁺* and *t⁻* on the two sides. (Online version in colour.)

have uniform speed as a result of neglecting its inertia, in describing the filament’s motion, with the objective of determining the bacterium thrust, I shall neglect neither the filament’s inertia nor the gravity (which I regard somehow on the same footing); I refer the reader to §3d for a quantitative discussion of this assumption.

(a) Shock equations

In this context, a shock propagating along the filament is described by a function, *s₀ = s₀(*t*), identifying the point in the reference configuration carrying a discontinuity in speed. Specifically, assume that *p* is continuous at *s₀*, because the ejected filament breaks nowhere, but *v* is discontinuous. Similarly, both the unit tangent *t*, the principal unit normal *n*, and the curvature *c* of the curve representing the present shape (at time *t*) of the filament are discontinuous at *p*(s₀(*t*), *t*), as illustrated in figure 4. I shall call *p*(s₀, *t*) a singular point. I denote by *t⁺* and *t⁻* the two limiting values of *t* across a singular point. Here, and below, for any quantity *Ψ*, superscripts ± refer to the traces of *Ψ* across *p*(s₀, *t*) from the sides of increasing and decreasing *s*, respectively. Also, I shall employ the customary notation \[ \Psi^± \] for the jump of *Ψ* across a singular point.

The shock speed is \( \dot{s}_0 \) relative to both the reference and present shapes (as a consequence of the filament’s inextensibility). A kinematic compatibility condition arises for the jump of *v*, as a result of the requirement that the velocity of the geometric point that instantaneously coincides in space with a singular point can be expressed in two different, but equivalent, ways (see e.g. [42,48]):

\[
\| v \| + \dot{s}_0 \| t \| = 0. \quad (2.2)
\]

The balance of linear momentum for an arbitrary small arc enclosing a singular point (that is, for *s₂ → s₂⁺* and *s₁ → s₁⁻* in figure 4) requires that

\[
\| t \| \dot{s}_0 \| v \| + \Phi = 0, \quad (2.3)
\]

where *Φ* is the concentrated supply of momentum that must be provided at a singular point to sustain the shock. In a similar way (see again [42,48] for more details), the energy balance at a singular point results in the following equation:

\[
\| t \cdot v \| + \frac{1}{2} \lambda \dot{s}_0 \| v^2 \| + W_s = 0, \quad (2.4)
\]

where *Wₛ* is the concentrated power supply involved in the shock.⁶ For a dissipative shock, *Wₛ* is negative and measures the energy lost per unit time by the internal friction that hampers the shock as it goes by. While in this setting the force *Φ* will be provided by the contact of the slime filament

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⁶Equation (2.4) is a specialization to the athermal case treated here of equation (2.7) of [42]; what here is denoted by *Wₛ* was denoted by *Φ₂* in that work. For *Wₛ < 0*, energy is lost in the shock. According to the treatment of chains in Sommerfeld’s book [49] (see pp. 28–29 and Problem 1.7, pp. 241, 257), the energy loss in chain dynamics is a concept first introduced by Lazare Carnot, the father of Sadi (this latter is known for his contributions to the theory of heat), who was a writer on mathematics and mechanics (besides later becoming one of the most loyal of Napoleon’s generals). See also [50, p. 52; 51; 52].
with the external world, $W_s$ is of a constitutive nature, which needs to be further specified (see §2b). Equations (2.3) and (2.4) express only the mechanical balances at a singular point. The former is also known as the Rankine–Hugoniot jump condition for one-dimensional continua [53, p. 29].

Interesting versions of the jump conditions in (2.2)–(2.4) above occur when the material constituting the filament is amorphously quiescent on one side of the shock. In this context, for definiteness, I shall refer to such a shock as external, while the shock described so far will be referred to as internal. An external shock is an attempt at formalizing the notion of continually imparted impacts introduced in the work of Cayley [55]; as such, it is more than just an internal shock with vanishing velocity on one side. At an external shock, mass is not conserved, as the filament there is in contact with a slime reservoir, where a shapeless deposit of matter serves as a supply of mass abruptly injected into the moving filament. More generally, the moving system receives from the external reservoir supplies of mass, linear momentum and energy, which enter the corresponding balance laws. This concept will inspire my mathematical treatment of the extrusion process that takes place at the bacterium pore whence the slime filament is extruded.

Assuming that, at the pore, where mass is instantaneously ejected with velocity $v$ along the direction $t_0$, a shock is propagating with speed $s$, the same kinematic condition that led to (2.2) now requires that

$$v + s \, t_0 = 0.$$  

(2.5a)

Similarly, by applying the balance laws of linear momentum and energy to an arbitrarily small arc of the ejected filament near the pore, one obtains

$$\tau_0 t_0 + \lambda s \, t_0 v + \Phi_0 = 0,$$  

(2.5b)

$$\tau_0 t_0 \cdot v + \frac{1}{2} \lambda s \, t_0 v^2 + W_0 = 0,$$  

(2.5c)

where the filament’s tension at the pore has been denoted by $\tau_0$, and $\Phi_0$ and $W_0$ are the appropriate supplies. Combining (2.5a)–(2.5c), it can be seen that

$$\begin{aligned}
&v = v t_0, \quad s = -v, \\
&\Phi_0 = -(\tau_0 - \lambda v^2) t_0, \quad W_0 = -\left(\tau_0 - \frac{1}{2} \lambda v^2\right) v.
\end{aligned}$$  

(2.6)

Equation (2.6), in particular, allows one to interpret $\Phi_0$ as the continuous-impact force envisaged by Cayley [55] to describe mechanical systems in which particles of infinitesimal mass are continuously taken into ‘connection’. An external shock is propagating backwards relative to the filament at the same scalar velocity as the material in the filament, with the result that the shock is steady in space. The complementary expressions for $W_0$ give the energy lost (or gained) by the filament being set in motion instantaneously.

(b) Shock dissipation

When the shock is internal, that is, the singular point is both followed and preceded by mass in motion, the shock dissipation $W_s$ should depend only on the impact mechanism responsible for the abrupt change in velocity. As in [36], to posit a constitutive law for $W_s$, one must seek inspiration in the laws of impact, which were already introduced in 1668 by Wallis & Wren [56], as recounted, for example, in Whittaker’s [57, p. 234] treatise.

When, in a system of mass-points, all impacts happen to be characterized by the same restitution coefficient $0 \leq e \leq 1$, the kinetic energy after a single impact decreases by $(1 - e)/(1 + e)$ times the kinetic energy of the lost motion, the motion that would have been composed with the

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7 The reader is further referred to [42,48] for a general thermodynamic theory of strings, which also features an additional jump condition for the entropy imbalance. A formulation of shock waves for general three-dimensional continua can also be found in §§32 and 33 of [54].

8 In particular, equation (2.5a) is nothing but the statement that slime is ejected along the tangent to the present shape of the filament. This is a necessary boundary condition for the existence of a steady solution of the dynamics of the filament that preserves its shape in the bacterium rest frame.

9 It should perhaps be recalled that equations (2.2)–(2.6) are all valid in the bacterium rest frame.
Figure 5. Snapshot of an idealized bacterium gliding over a fixed, flat substrate. In the Cartesian frame \((e_x, e_y)\), the gliding velocity is \(\mathbf{u} = -u e_x\). The points \(p_0\) and \(p_1\) represent the ejecting pore and the filament’s foot, respectively; their difference in height is \(h\). The force \(\Phi_0\) is applied in \(p_0\) to the extruded filament, so that \(-\Phi_0\) is the force transmitted to the bacterium; its component along \(e_x\) is the effective propelling force. \(\Phi_1\) is the linear momentum supply transferred to the internal shock in \(p_1\) by the substrate. (Online version in colour.)

motion before the impact to reproduce the motion after the impact [57, p. 235]. By applying this law to the elementary transfer of mass through the shock suffered by a filament, interpreted as an internal impact, I justify setting

\[ W_s := -\frac{1}{2} f \lambda |\dot{s}_0| \mathbf{v}^2, \]  

where \(0 \leq f \leq 1\) will be treated as a phenomenological parameter.\(^{10}\) In the ideal limit where \(f \to 0^+\), the shock is not dissipative. On the other hand, for \(f = 1\), the shock is maximally dissipative. In practice, for a slime filament, \(f\) should depend on the material that constitutes it.\(^{11}\)

(c) Inverted catenary

Before solving the balance equations for an ejected slime filament, one needs to specify, albeit in an idealized fashion, the mechanisms at work at both pore and foot. Figure 5 illustrates the view taken here. The points \(p_0\) and \(p_1\), which represent the pore and foot, respectively, are thought of as steady shocks, external the former and internal the latter; their kinematic compatibility with the dynamic solution is still to be established.

The dynamics of a smooth arc of a slime filament is governed by equation (2.1), while equations (2.2)–(2.6) are to be enforced at the two singular points identified above. I shall seek the solution to the problem within a special class, that of steady motions. To this end, I assume that the trajectory followed by the slime in the filament is invariable in time and that the spatial velocity field \(\mathbf{v}\) on it takes the form \(\mathbf{v} = \mathbf{v}_t\), with \(\mathbf{v}\) constant.

Projecting both sides of equation (2.1) along the tangent \(t\), the principal normal \(n\) and the binormal \(b := t \times n\) to the filament’s steady shape, one arrives at

\[ \tau' + f_t = 0, \quad (\lambda \mathbf{v}^2 - \tau)c = f_n, \quad f_b = 0, \]  

where \(c\) is the shape’s curvature and \(f_t, f_n\) and \(f_b\) are the components of \(f\) along \(t, n\) and \(b\), respectively (see also [58]).

Letting \(f\) lie in the \((x, y)\) plane, \(f_b\) vanishes identically as long as the filament’s shape lies in that plane as well. Figure 6a describes a generic arc of the filament. Denoting by \(\vartheta\) the angle that \(t\)

\(^{10}\)Letting for a moment \(f := (1 - e)/(1 + e)\), I note that, for a plastic impact, \(e = 0\) and \(f = 1\), whereas, for a perfectly elastic impact, \(e = 1\) and \(f = 0\). However, in the absence of a microscopic mechanism illuminating the origin of \(W_s\), these correspondences are purely formal and \(f\) remains a constitutive parameter of the filament.

\(^{11}\)It might be suggested that \(W_s\) could equally well be regarded as an external energy sink, instead of the energy lost in an internal impact. This interpretation could indeed provide a better justification in the present context for the explicit law posited in (2.7), as the impact model recalled in the text, if appropriate for chain links, may be a bit too strained for a slime filament.
Figure 6. Blow-ups of different significant portions of the steady shape of a slime filament. (a) Generic arc with the local, movable frame \((t, n)\) and a fixed, Cartesian frame \((e_x, e_y)\). (b) Arc leaving the pore \(p_0\); the dots represent the slime supply. (c) Arc around the foot \(p_1\). The different unit tangent vectors are described analytically by (3.3) and (3.9). In the terminology here, \(p_0\) designates an external shock; a force \(\Phi_0\) is supplied there to the ejected slime filament, related to \(t_0\) via (2.6). Similarly, \(\Phi_1\) is a realization of the momentum supply \(\Phi\) featuring in (2.3). (Online version in colour.)

makes with \(e_y\), one can represent \(t\) and \(n\) as

\[
t = \sin \vartheta e_x + \cos \vartheta e_y \quad \text{and} \quad n = \cos \vartheta e_x - \sin \vartheta e_y,
\]

whence it follows that \(c = \vartheta'\). Thus, as long as \(c\) does not vanish, \(\vartheta\) and \(s\) can equally be employed to parametrize the filament's shape: in the setting described by figures 5 and 6b,c, \(\vartheta_0 \leq \vartheta \leq \vartheta_1\). Expressing both \(f_t\) and \(f_n\) as functions of \(\vartheta\), for \(f_n \neq 0\), one readily obtains from (2.8) that

\[
\ln |\lambda v^2 - \tau| = \int_{t_0}^{t} f_t f_n \, d\vartheta, \quad c = \frac{f_n}{\lambda v^2 - \tau}.
\]

If \(f = -\lambda g e_y\), where \(g\) is the acceleration of gravity, then \(f_t = -\lambda g \cos \vartheta\), \(f_n = -\lambda g \sin \vartheta\), and (2.10) yields

\[
\tau = \lambda v^2 - \frac{a^2}{\sin \vartheta}, \quad c = \frac{\lambda g}{a^2} \sin^2 \vartheta,
\]

where \(a^2\) is an as yet unknown, positive integration constant. As already remarked in [59, p. 64], the shape described in (2.11) is an inverted catenary. Moreover, for \(\tau\) not to be negative somewhere, it suffices that \(\tau_1 := \tau(\vartheta_1) \geq 0\), that is,

\[
a^2 \leq \lambda v^2 \sin \vartheta_1.
\]

By integrating in \(\vartheta\), with the aid of (2.11), the equations

\[
\frac{dx}{d\vartheta} = \frac{\sin \vartheta}{c}, \quad \frac{dy}{d\vartheta} = \frac{\cos \vartheta}{c},
\]

which follow from (2.9), one arrives at

\[
x(\vartheta) = \frac{a^2}{\lambda g} \left( \ln \frac{1 - \cos \vartheta}{\sin \vartheta} - \ln \frac{1 - \cos \vartheta_0}{\sin \vartheta_0} \right), \tag{2.14a}
\]

\[
y(\vartheta) = \frac{a^2}{\lambda g} \left( \frac{1}{\sin \vartheta_0} - \frac{1}{\sin \vartheta} \right), \tag{2.14b}
\]

Incidentally, neglecting both the filament’s inertia and gravity would result in setting \(\lambda\) equal to zero and all components of \(f\) in (2.8), thus leaving \(\tau > 0\) constant along a straight line and raising a geometric compatibility issue for the choice of the ejection angle \(\vartheta_0\), which would no longer be free.

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which parametrize the filament’s steady shape in the Cartesian plane \((x,y)\) with the origin at \(p_0\). Likewise, the correspondence between \(\vartheta\) and \(s\) is expressed explicitly by

\[
s(\vartheta) = \frac{a^2}{\lambda t} (\cot \vartheta_0 - \cot \vartheta).
\]

(2.15)

So far, I have considered both the ejecting velocity \(v \geq 0\) and the ejecting angle \(0 \leq \vartheta_0 \leq \pi/2\) as parameters of the solution sought. The solution of the balance equation for linear momentum along the ejected slime filament has identified two further parameters, \(a^2\) and \(\vartheta_1\), subject to the bound (2.12). In the next section, by use of appropriate boundary conditions, I shall resolve the shocks and devise a strategy to determine all four unknowns encountered here.

3. Gliding mechanics

Here, the theory is applied to describe the gliding of bacteria powered by slime extrusion. First, I introduce boundary conditions for which all balance equations of the theory can be solved. Then, I shall illustrate the solution thus found in a special case with a number of quantitative details.

(a) Motion resolution

In the substrate rest frame, the gliding motion of the bacterium with constant velocity \(u\) is governed by the equation

\[-k_0 u - (\Phi_0 \cdot e_x) e_x = 0,\]

(3.1)

which balances the viscous drag force, \(-k_0 u\), arising from the environment resistance and the effective propelling force, \(F = -(\Phi_0 \cdot e_x) e_x\), arising from the extruded slime filament. In (3.1), \(k_0\) is a viscosity coefficient characterizing the gliding bacterium and its environment, while \(F\) is determined by (2.6) in the form

\[F = -\lambda v^2 - \tau_0 \sin \vartheta_0 e_x,\]

(3.2)

where \(v\) is the ejecting velocity and, in accord with (2.9), use has been made of the following representation for \(t_0\):

\[t_0 = \sin \vartheta_0 e_x + \cos \vartheta_0 e_y.\]

(3.3)

Denoting by

\[F_0 := \lambda v^2 - \tau_0\]

(3.4)

the propelling thrust, which is the total force felt by the bacterium, I rewrite (3.2) as \(F_0 = -F_0 \sin \vartheta_0 e_x\). In (3.4), the tension \(\tau_0\) of the filament at the pore is still to be determined; it will follow from the complete resolution of the shock equations. A comment is called upon by (3.4): since \(\tau_0 \geq 0\), \(F_0\) does not exceed \(\lambda v^2\), which according to [49, p. 29] corresponds to the thrust that would be imparted by the jet propulsion of incoherent matter extruded at the rate \(\lambda v\). This shows already that, however, one determines \(\tau_0\), the resulting thrust on the bacterium provided by an unbroken slime filament partially adhered to a rigid substrate will be less than that provided by pure jet propulsion. Letting \(u = -ue_x\) and combining (3.1), (3.2) and (2.11), one arrives at

\[u = \frac{a^2}{k_0},\]

(3.5)

where \(a^2\) is yet to be determined.

Now I resolve the two shocks shown in figure 5 by applying equations (2.2)–(2.4) to \(p_1\) and (2.6) to \(p_0\). In the bacterium rest frame, the slime filament is seen to approach the substrate with velocity \(v^- = vt_1^-\) before adhesion and to glide on the substrate with velocity \(v^+ = ut_1^+\) after adhesion; here the unit vectors \(t_1^\pm\) are as shown in figure 6e, \(v\) is the ejecting velocity and \(u\) is the gliding velocity.
By (2.2), one immediately concludes that \( u = v \) and \( s_0 = -v \). Thus, kinematic compatibility requires that, in a steady motion that preserves the filament’s shape, the bacterium gliding velocity \( u \) (relative to the substrate) must coincide with the slime ejecting velocity \( v \) (relative to the bacterium). Thus, (3.5) is turned into an equation for the admissible ejecting velocity:

\[
v = \frac{a^2}{k_0},
\]

which depends on the filament’s shape through the unknown constant \( a^2 \).

At \( p_1 \), equation (2.3) can now be enforced in the form

\[
\left\{ \left( \tau - \lambda v^2 \right) s_1 \right\} + \Phi_1 = 0.
\]

(3.7)

In a similar way, with the aid of (2.7), at \( p_1 \) (2.4) becomes

\[
\left\{ \tau \right\} = \frac{1}{2f} \lambda v^2 \left\{ s_1 \right\}^2.
\]

(3.8)

It is expedient to record here that, in accord with (2.9), the explicit expressions for the unit vectors \( t_1^\pm \) featuring in (3.7) and (3.8) are

\[
\begin{align*}
t_1^+ &= e_x \\
t_1^- &= \sin \vartheta_1 e_x + \cos \vartheta_1 e_y.
\end{align*}
\]

(3.9)

While equation (3.7) determines the momentum supply \( \Phi_1 \), the jump condition (3.8) ties \( a^2 \) to \( \vartheta_1 \) via (2.11). Overall, there are four unknowns that need to be determined to identify completely the steady solution sought here, namely, \( \vartheta_1, v, a^2 \) and \( \tau^+ \), where the latter designates the tension in the adhered filament, just after its foot \( p_1 \) (figure 5). The bacterium equation of motion and the shock kinematic compatibility condition combined in (3.6) together with the jump condition (3.8) provide only two equations: two others are missing.

One missing equation comes from the geometric condition

\[
y(\vartheta_1) = -h,
\]

(3.10)

which prescribes the total downfall of the filament (figure 5). The other is the boundary condition that must be required at the filament’s foot \( p_1 \) to reflect the contact mechanism with the substrate envisaged in the model. Here, to the purpose of showing that theoretically gliding is also possible on smooth substrates, I shall assume that the reactive supply of linear momentum \( \Phi_1 \) can only be directed vertically upwards, \( \Phi_1 = \Phi_{1y} e_y \), with \( \Phi_{1y} \geq 0 \). Thus, the second missing equation will be

\[
\Phi_{1x} = \Phi_1 \cdot e_x = 0.
\]

(3.11)

There are two compatibility conditions that a solution must meet to be acceptable: both concern the positivity of the tension \( \tau \). One is (2.12), which amounts to requiring that \( \tau_1 \geq 0 \), and the other is

\[
\tau^+ \geq 0.
\]

(3.12)

To expedite the search for solutions and to retrace more easily in them signs of universality, it is advisable to scale all lengths to \( h \) and all velocities to \( v_0 = \frac{k_0}{\lambda} \)

(3.13)

which represents a velocity characteristic of both the environment opposing the bacterium gliding and the material constituting the extruded slime. Thus, \( v \) will be replaced by

\[
v := \frac{v}{v_0}.
\]

(3.14)

By (3.14) and (3.13), one can readily rewrite (3.6) as

\[
a^2 = \lambda \nu v_0^2.
\]

(3.15)
by which (2.12) reduces to

\[ \nu \sin \vartheta_1 \geq 1. \]  

(3.16)

By inserting (3.15) into (3.10), one obtains the following expression, for \( \pi - \vartheta_0 \leq \vartheta_1 \leq \pi \):

\[ \frac{1}{\sin \vartheta_1} = \frac{1}{\sin \vartheta_0} + \frac{\eta^2}{2\nu}, \]  

(3.17)

where

\[ \eta := \frac{\sqrt{2gh}}{v_0}, \]  

(3.18)

which represents the velocity acquired by any body falling from rest over the distance \( h \) scaled to \( v_0 \), combines in a dimensionless parameter both \( h \) and \( v_0 \). Similarly, using both (3.7) and (3.8), one can easily see that (3.11) amounts to

\[ \nu = \frac{1}{f \sin \vartheta_1}, \]  

(3.19)

which makes (3.16) automatically satisfied since \( 0 \leq f \leq 1 \).

Making use of (3.19) in (3.17), I finally determine \( \nu \) as

\[ \nu = \nu^* := \frac{1}{2f} \left( \frac{1}{\sin \vartheta_0} + \frac{1}{\sin^2 \vartheta_0} + 2f\eta^2 \right), \]  

(3.20a)

in terms of which all other unknowns are expressed:

\[ \vartheta_1 = \pi - \arcsin \left( \frac{1}{f\nu^*} \right), \]  

(3.20b)

\[ \tau^+ = \lambda v_0^2 \nu^*(\nu^* - 1), \]  

(3.20c)

\[ \Phi_{1y} = \lambda v_0^2 \nu^* \sqrt{(f\nu^*)^2 - 1}. \]  

(3.20d)

Equation (3.20c), combined with (3.19), shows in particular that \( \tau^+ \) satisfies the inequality (3.12). Similarly, it follows from (3.20d) that \( \Phi_{1y} \geq 0 \). I record here for later use that by (3.15) the thrust in (3.4) can also be expressed as

\[ F_0 = \frac{\lambda v_0^2 \nu^*}{\sin \vartheta_0}. \]  

(3.21)

(b) Energy balance

This is an active system, and so the energy dissipated in the gliding process must come from the bacterium itself. The theory developed here identifies with \( W_0 \) the rate at which such an active energy is produced to sustain the bacterium locomotion. In the bacterium rest frame, where the kinetic energy of the slime filament extruded between pore and foot is constant in time, balance of energy requires that

\[ \dot{K} = W_0 + W_s + W_g + \tau^+ v, \]  

(3.22)

where \( K \) is the extra kinetic energy associated with the sliding motion of the filament on the substrate. In (3.22), \( W_0 \) is the power supply at the bacterium pore, given by (2.6), \( W_s \) is the concentrated power supply involved in the dissipative internal shock at the filament’s foot, given by (2.7), \( W_g \) is the power expended by the gravitational forces and \( \tau^+ v \) is the power expended by the free end of the adhered filament (seen gliding with velocity \( v \) in the bacterium rest frame). All these powers can be computed explicitly. To this end, I found it expedient to scale them to \( \lambda v^3 \).
Figure 7. Sketch illustrating the solution in (3.20). The filament’s shape is drawn for the following choice of parameters: $\vartheta_0 = \pi/2$, $f = 1$, $\eta = 0.77$; the distance $w$ scaled to $h$ is $w/h = 2.9$. (Online version in colour.)

By combining (2.6) with (2.11) and replacing (3.15) with
\[ a = \lambda v^2 \sin \vartheta_1, \] (3.23)
by use of both (3.14) and (3.19), one obtains
\[ W_0 = \lambda v^3 \left( f \frac{\sin \vartheta_1}{\sin \vartheta_0} - \frac{1}{2} \right). \] (3.24)

Directly from (2.7), one has
\[ W_s = -\lambda v^3 f (1 - \sin \vartheta_1). \] (3.25)

Moreover, it is easily seen (for example, in [36]) that $W_g = (\tau_0 - \tau_1) v$, which by (2.11) and (3.23) becomes
\[ W_g = \lambda v^3 f \left( 1 - \frac{\sin \vartheta_1}{\sin \vartheta_0} \right). \] (3.26)

Likewise, by (3.8) and (3.23), one can write
\[ \tau^+ v = \lambda v^3 (1 - f \sin \vartheta_1). \] (3.27)

Inserting equations (3.23)–(3.27) into (3.21), one readily arrives at
\[ \dot{K} = \frac{1}{2} \lambda v^3, \] (3.28)
which is indeed justifiable by a direct computation. Considering the ever extending string of slime on the substrate, which moves at the speed $v$, one can see that at time $t$ later it is carrying the extra kinetic energy $K = \frac{1}{2} \lambda v^3 t$ on account of being longer. By differentiating $K$ with respect to time, one recovers immediately (3.28).

In the following subsection, I shall explore some quantitative aspects of this solution in the simpler case where $\vartheta_0 = \pi/2$ and $f$ and $\eta$ remain the only free parameters.

(c) Horizontal ejection

To illustrate the solution in (3.20), here I set $\vartheta_0 = \pi/2$; the situation I envisage is sketched in figure 7, where $w$ denotes the distance between the filament’s foot $p_1$ and the projection onto the substrate of the ejecting pore $p_0$.

The plots of $v^*$, $\vartheta_1$, $\tau^+$ and $\Phi_{1y}$ as functions of $\eta$ are shown in figure 8 for three indicative values of $f$, namely, 1/4, 1/2 and 1. It should be noted that by (3.21), for $\vartheta_0 = \pi/2$, $v^*$ also represents the thrust on the bacterium expressed in terms of $\lambda v_0^2$. All the graphs in figure 8 describe increasing functions of $\eta$. Moreover, for a given $\eta$, increasing $f$ results in a decrease in $v^*$, $\tau^+$ and $\Phi_{1y}$, and in an increase of $\vartheta_1$. Thus, for a less dissipative shock, all the forces increase and so also does the gliding velocity, while the slime filament becomes steeper in approaching its foot.

(d) Neglecting gravity

The inverted catenary solution described in §2c is characterized by gravity. One may sensibly argue that gravity has no role to play at the small length scales characteristic of bacteria. To put
Figure 8. The graphs of (a) $\nu^*$, (b) $\vartheta_1$, (c) $\tau^+$ and (d) $\Phi_1^y$ as functions of $\eta$ for $f = \frac{1}{4}$ (dotted lines), $f = \frac{1}{2}$ (dashed lines) and $f = 1$ (solid lines). Here, as discussed in §3c, $\vartheta_0 = \pi/2$. (Online version in colour.)

this objection into a quantitative perspective, I consider here what survives of the analysis in the limit as the dimensionless parameter $\eta$ introduced in (3.18) tends to zero; I interpret this to be either the zero-gravity limit or the zero-thickness limit, in view of the way both $g$ and $h$ feature
in (3.18). By use of (3.20), it is a simple matter to show that, for \( \eta \to 0 \), \( v^* \), \( \vartheta_1 \), \( \tau^+ \) and \( \Phi_{1y} \) are, respectively, delivered by

\[
(v^*)_0 = \frac{1}{f \sin \vartheta_0},
\]

\[
(\vartheta_1)_0 = \vartheta_0,
\]

\[
(\tau^+)_0 = \frac{\lambda v_0^2}{f^2 \sin \vartheta_0} (1 - f \sin \vartheta_0)
\]

and

\[
(\Phi_{1y})_0 = \frac{\lambda v_0^2}{f \sin^2 \vartheta_0} \cos \vartheta_0.
\]

Correspondingly, by (3.18), (3.15) and (2.14b), for any \( \eta \), the function \( y(\vartheta) \) that describes the inverted catenary can be recast in the form

\[
y(\vartheta) = h = \frac{1 - \sin \vartheta_0 / \sin \vartheta}{\sin \vartheta_0 / \sin \vartheta_1 - 1}.
\]

Since by (3.29b) \( \vartheta_1 \) tends to \( \vartheta_0 \) as \( \eta \) tends to 0, (3.30) shows that in that limit the inverted catenary solution makes no sense, and so the filament’s shape remains undetermined (as was perhaps to be expected). Nevertheless, all formulas (3.29) remain perfectly valid and carry a definite mechanical meaning, which is presumably most appropriate at bacterial length scales.

4. Conclusion

I have proposed a mathematical model to describe the mechanics of gliding, a means used by some bacteria to move on a rigid substrate. The theory attempted to prove the propelling ability of the slime filaments extruded by some cells, such as myxobacteria and cyanobacteria, which are known to adopt gliding as a locomotion mechanism.

Seen in the bacterium rest frame, an extruded slime filament was treated as a flexible, inextensible string with uniform linear mass density, flowing along its own shape and meeting the substrate at a kink, which was called the foot, where a dissipative internal shock travels backwards in the string reference configuration to remain still relative to the moving bacterium. The extruding pore was instead treated as an external shock, as new mass is continuously supplied there to the moving filament, together with linear momentum and energy. This distinction between internal and external shocks was taken from [36]; the mathematical formalism put forward there was adapted to an ideal bacterium gliding over a flat, rigid substrate.

I proved that the kinematic compatibility condition for shock propagation requires the gliding velocity (in the substrate rest frame) to equal the extrusion velocity (in the bacterium rest frame), a result that seems to be supported by some experimental evidence [1]. Essentially, this is a consequence of the assumption on the filament’s inextensibility, in favour of which I was not able to produce any direct experimental validation. Perhaps, one should consider the observed coincidence between gliding and extruding velocities as an indirect one. I also determined completely the bacterium gliding motion by solving explicitly a nonlinear problem. I obtained both the velocity compatible with the assumption of uniform gliding and the propelling thrust on the bacterium in terms of a few parameters. Though not numerous, these latter are not directly accessible, so that no reliable estimate of the mechanical quantities involved in the bacterium motion could be proposed. In the analysis, gravity was not neglected, whereas both viscous forces on the extruded filament and its bending rigidity were. As for the first assumption, which might be considered inappropriate at the typical length scales of bacteria, I proved that in the zero-gravity limit only the specific inverted catenary structure of the solution does not survive (as was perhaps to be expected), whereas all the mechanical quantities of interest have a definite limit, so that gravity appears here as an analytic regularizing device that just makes the filament’s shape
definite. As for the other two assumptions, I simply plead guilty of having no better justification than the simplicity they afford to the analysis.13

At this stage, this remains just a viable mathematical hypothesis on the role of slime extrusion in bacteria gliding. I was content with proving theoretically that continuously extruded slime filaments exert a thrust on the bacterium through their footing on the substrate, for which I can afford a precise quantitative description. Whether this contributes to clarifying the mystery of bacteria gliding still remains to be seen.

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References

13It was already shown in [58] that viscous forces make the simple catenary problem far more complicated, though still solvable analytically in some special cases.
34. Dhahri S, Ramonda M, Marlière C. 2013 In-situ determination of the mechanical properties of gliding or non-motile bacteria by atomic force microscopy under physiological conditions without immobilization. PLoS ONE 8, e61663. (DOI:10.1371/journal.pone.0061663)