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Crawlers in viscous environments: Linear vs non-linear rheology

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Keywords: Cell motility Cell migration Self-propulsion Crawling motility Motility on a solid substrate Soft biomimetic robots We study model self-propelled crawlers which derive their propulsive capabilities from the tangential resistance to motion offered by the environment. Two types of relationships between tangential forces and slip velocities are considered: a linear, Newtonian one and a non-linear one of Bingham-type. Different behaviors result from the two different rheologies. These differences and their implications in terms of motility performance are discussed. Our aim is to develop new tools and insight for future studies of cell motility by crawling.

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1. Introduction

This paper studies model locomotors that exploit shape changes and mechanical interactions with the environment (adhesive, viscous, or frictional resistance) for self-propulsion. We focus on one-dimensional systems that can execute shape changes by propagating stretching or contraction waves along their bodies, and that interact with the environment through tangential forces whose density at a point depends on the velocity at that point.

We consider two force-velocity laws: a linear, Newtonian one and a non-linear one of Bingham-type. The first one requires that some slip must occur for the tangential force to be non-zero. The second one requires that a force threshold be overcome for slip to occur, and it leads to stick-slip behavior at the interface between the locomotor and its environment.

The model system studied in this paper, and briefly described above, arises in a variety of physical situations. The most direct examples are those of crawlers moving on a solid substrate lubricated by a thin layer of a viscous fluid, with the fluid being either Newtonian or of Bingham-type. Studies of these systems aim to discover the principles of the locomotion strategy of snails and to replicate them with artificial prototypes [17,28,29]. Further examples include low Reynolds number swimming of slender organisms (in the Newtonian version, if hydrodynamic interactions are treated with the local drag approximation [26] of Resistive Force Theory), and cells migrating on or within solid substrates, matrices and tissues ([3], with a Bingham-like force– velocity law [31] arising from the adhesion dynamics of receptor– ligand binding). The idea we pursue in this paper is to combine recent progress in the non-linear mechanics of soft and biological matter [12,14,22,25,32] with the insight afforded by the (non-linear) Geometric Control Theory approach to self-propulsion [4–8,19]. Using these tools, new progress towards the understanding of key principles of limbless locomotion in natural and engineered systems can be obtained.

The main results of this paper are the following. We show that, contrary to opposite claims in the literature (see the discussion in [21]), it is possible to obtain net advancement with cyclic shape changes even in the context of a linear, purely Newtonian interaction with a substrate. This requires that non-linearities arising from large deformations are correctly taken into account and exploited. On the other hand, at given gait (a fixed traveling wave of contraction), the displacements available with non-linear Bingham-type interactions are consistently larger. Motion is oscillatory in time in the Newtonian case while the displacement of a typical material point is monotonic in time in the Bingham case. Finally, the sign of the displacement can be inverted, at fixed gait, by changing the rheology of the interactions with the environment.

2. Kinematics

We consider a straight one-dimensional crawler (worm) moving along a straight line. It is important to analyze the system within the non-linear framework of large deformations, i.e., to distinguish between material (Lagrangian) vs spatial (Eulerian) velocities. Our developments here follow closely those in [21] and, in turn, [16] where a general three-dimensional shape-changing body surrounded by a (Stokes) viscous fluid is considered.

We denote by *X* the coordinate along the worm's body in the reference configuration, in which the left end coincides with the origin $(X_1 = 0)$ and *L* is the reference length $(X_2 = L)$, see Fig. 1.

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Fig. 1. Kinematics of the one-dimensional worm.



We thus have $0 \le X \le L$ and the one-dimensional motion of the worm is described by

$$x(X,t) = x_1(t) + s(X,t) \quad \text{with } s(0,t) \equiv 0, s'(X,t) > 0 \ \forall X \in (0,L),$$
(2.1)

where a prime denotes the derivative with respect to X and

$$x_1(t) \coloneqq x(X_1, t), \quad x_2(t) \coloneqq x(X_2, t).$$
 (2.2)

We also have

$$l(t) = \int_0^L s'(X,t) \, dX,$$
(2.3)

where l(t) is the current length of the crawler at time t. Here, x_1 describes the position of the worm (with respect to the fixed lab frame) and s, the arc-length parameter in the deformed configuration, describes the shape of the worm (configuration in the body frame, i.e., as seen by an observer moving with the worm). In this paper, we will consider shape as freely controllable, by assigning

$$S'(X,t) = \gamma^*(X,t),$$
 (2.4)

where γ^* is a prescribed function of space and time such that

$$\gamma^*(X,t) > 0 \quad \forall X \in (0,L).$$

$$(2.5)$$

In conclusion, note that the (Eulerian) velocity at position *x* in the current configuration of the worm is given by

$$\nu(x,t) = \dot{x}(X,t) \Big|_{X = s^{-1}(x-x_1(t),t)} = \dot{x}_1(t) + \dot{s}(s^{-1}(x-x_1(t),t),t).$$
(2.6)

3. Equations of motion (force balance)

We neglect inertia, so that the equations of motion reduce to the vanishing of the component along the *x*-axis of the total force. Our model worm can only exploit shape changes (extensions and contractions along its axis) and tangential interactions with a substrate, see Fig. 2. These are described by a force-velocity relationship, giving the density per unit current length $\mathbf{f}(s,t)$ at time *t* and at the point identified by arc-length *s*, as a function of the velocity $\mathbf{v}(s,t)$ at that point and time. The corresponding density per unit reference length is given by

$$\mathbf{f}^{ref}(X,t) = \mathbf{f}(s,t) \Big|_{s = s(X,t)} s'(X,t).$$
(3.1)

In what follows, we will only consider the components of **v**, **f**, and \mathbf{f}^{ref} along the axis of motion, oriented from left to right, denoted simply by v, f, and f^{ref} . One example (Newtonian case) is



Fig. 3. Newtonian (black solid line) and Bingham (red dashed lines) force-velocity interaction laws. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the linear viscous law shown in black in Fig. 3 and given by $f(s,t) = -\mu v(s,t).$

$$(s,t) = -\mu v(s,t),$$
 (3.2)

where $\mu > 0$ is a viscosity or friction coefficient.

Another possibility (see the red dashed curve in Fig. 3), useful to model stick-slip behavior, is the Bingham case described by

$$f(s,t) = \begin{cases} -\tau_y - \mu_1 v(s,t) & \text{if } v(s,t) > 0, \\ \tau \in [-\tau_y, \tau_y] & \text{if } v(s,t) = 0, \\ \tau_y - \mu_1 v(s,t) & \text{if } v(s,t) < 0. \end{cases}$$
(3.3)

Denoting by N(X,t) the axial stress at point X and time t, the pointwise force balance reads

$$N'(X,t) = -f^{ref}(X,t)$$
(3.4)

and, assuming that no external forces are applied at the two ends, we also have

$$N(0,t) = 0, \quad N(L,t) = 0.$$
 (3.5)

Using the equations above we obtain the global force balance

$$0 = F(t) = \int_0^L f^{ref}(X,t) \, dX = \int_0^{l(t)} f(s,t) \, ds.$$
(3.6)

In the Newtonian case (3.2), the total force on the worm is

$$F(t) = -\mu \int_0^{l(t)} \nu(s,t) \, ds$$

= $-\mu \left(l(t)\dot{x}_1(t) + \int_0^{l(t)} \dot{s}(s^{-1}(s,t),t) \, ds \right)$
= $-\mu \left(l(t)\dot{x}_1(t) + \int_0^L \dot{s}(X,t)s'(X,t) \, dX \right)$ (3.7)

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