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Discrete one-dimensional crawlers on viscous substrates: Achievable net displacements and their energy cost

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ABSTRACT

We study model one-dimensional crawlers, namely, model mechanical systems that can achieve self-propulsion by controlled shape changes of their body (extension or contraction of portions of the body), thanks to frictional interactions with a rigid substrate. We evaluate the achievable net displacement and the related energetic cost for self-propulsion by discrete crawlers (i.e., whose body is made of a discrete number of contractile or extensile segments) moving on substrates with either a Newtonian (linear) or a Bingham-type (stick-slip) rheology. Our analysis is aimed at constructing the basic building blocks towards an integrative, multi-scale description of crawling cell motility.

1. Introduction

This paper discusses the mechanics of model one-dimensional crawlers, namely, model systems that are capable of self-propulsion. This is powered by shape changes of their body (controlled extension or contraction of portions of the body), thanks to frictional interactions with a rigid substrate. The motivations for this study stem from the quantitative study of biological locomotion at the micron scale (crawling or swimming motility of cells and unicellular organisms), and the quest for engineered, biomimetic systems capable of reproducing micron-scale motility in artificial devices. Devices of this type would have countless applications, for example in the fields of bio-engineering and miniaturized bio-medical devices.

The framework employed to study the problem is that of Geometric Control Theory, used e.g. in Alouges et al. (2008, 2009), and, more recently, in Alouges et al. (2013a) to study microscopic (low Reynolds number) swimmers. In fact, as discussed in DeSimone et al. (2013), the mechanics of swimming and crawling can be treated in a unified way, at least as long as the local approximation of Resistive Force Theory can be used to model hydrodynamic forces.

The study of the locomotion strategies of microscopic, unicellular organisms has received enormous attention in recent years, and a lot is known about the mechanisms on which self-propulsion is based, up to the minute details of the molecular motors powering them. By comparison, the development of integrative multi-scale models at the whole cell scale is in its infancy. The goal of our research is the construction of the basic building blocks of such synthetic models, by focusing initially on model systems in which the kinematics of the locomotor and its mechanical interactions with the environment are coarse-grained.

In this work, we consider the case in which the crawler body is made of a discrete number of contractile or extensile segments, in a spirit similar to Alouges et al. (2013b), where propulsion powered by bending waves traveling in a flagellum is analyzed. We believe that our approach is quite general, and that it will be possible to extend it in the future to different types of crawler–substrate interactions (e.g. dry-friction, Bigoni and Noselli, 2011) and to concrete biological examples (such as unicellular swimming protists, Arroyo et al., 2012 and crawling cells, Cardamone et al., 2011).

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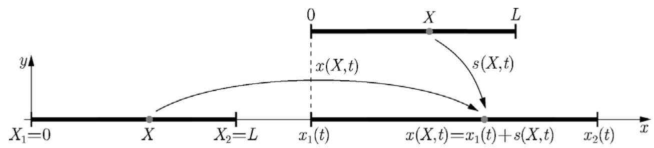

Fig. 1. Kinematics of the one-dimensional crawler.

2. One-dimensional crawlers: kinematics, equation of motion and energetic cost

We consider a one-dimensional crawler constrained to move along a straight line. The system is analyzed within the non-linear framework of large deformations, i.e., we distinguish between material (Lagrangian) and spatial (Eulerian) velocities. Our developments here follow closely those in DeSimone and Tatone (2012) and, in turn, Dal Maso et al. (2011) 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).

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

$$x(X, t) = x_1(t) + s(X, t), \tag{2.1}$$

with $s(0, t) = 0$, $s'(X, t) > 0 \; \forall X \in (0, L)$, where a prime denotes derivative with respect to X, and $x_1(t) := x(X_1, t)$, $x_2(t) := x(X_2, t)$. We also have

$$l(t) = \int_0^L s'(X, t)\, dX, \tag{2.2}$$

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

$$s'(X, t) = \gamma^*(X, t), \tag{2.3}$$

where γ^* is a prescribed function of space and time such that $\gamma^*(X, t) > 0 \; \forall X \in (0, L)$. Note that the Eulerian velocity at position x in the current configuration of the worm is given by

$$v(x, t) = \dot{x}(X, t)|_{X = s^{-1}(x - x_1(t), t)} = \dot{x}_1(t) + \dot{s}(s^{-1}(x - x_1(t), t), t). \tag{2.4}$$

In this study the system is analyzed in the quasi-static approximation, such that inertial forces are neglected and the equations of motion reduce to the vanishing of the component along the x-axis of the total force acting on the crawler in its current configuration. 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 can be introduced as follows

$$\mathbf{f}_{\mathrm{r}}(X, t) = \mathbf{f}(s, t)|_{s = s(X, t)} s'(X, t), \tag{2.5}$$

and in the following analyses we will only consider the components of $\mathbf{v}$, $\mathbf{f}$, and $\mathbf{f}_{\mathrm{r}}$ along the axis of motion, oriented from left to right, denoted simply by v, f, and f_{r}. One interesting case is the Newtonian linear viscous law given by

$$f_{\mathrm{N}}(s, t) = -\mu_{\mathrm{N}} v(s, t), \tag{2.6}$$

where $\mu_{\mathrm{N}} > 0$ is a constant viscosity coefficient. Another possibility, useful to model stick-and-slip behavior, is the Bingham case described by

$$f_{\mathrm{B}}(s, t) = \begin{cases} -\tau_y - \mu_{\mathrm{B}} v(s, t) & \text{if } v(s, t) > 0, \\ \tau \in [-\tau_y, \tau_y] & \text{if } v(s, t) = 0, \\ \tau_y - \mu_{\mathrm{B}} v(s, t) & \text{if } v(s, t) < 0. \end{cases} \tag{2.7}$$

Force–velocity laws of this type arise, for instance, in the study of snail locomotion (see e.g. Chan et al., 2005; Denny, 1980, 1981; DeSimone et al., 2013).

Denoting by $N(X, t)$ the axial force at point X and time t, the pointwise force balance in the reference configuration reads

$$N'(X, t) = -f_{\mathrm{r}}(X, t) \tag{2.8}$$

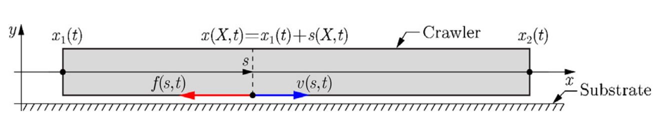

Fig. 2. A sketch of the forces per unit length $f(s, t)$ acting on the one-dimensional crawler.