An elasto-hydrodynamical model of friction for the locomotion of Caenorhabditis elegans

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Abstract

Caenorhabditis elegans (C. elegans) is one of the most studied organisms by biologists. Composed of around one thousand cells, easy to culture and to modify genetically, it is a good model system to address fundamental physiological questions and in particular to investigate neuromuscular processes. Many C. elegans mutants can be distinguished by their locomotion phenotype and it then important to understand the biomechanics of their locomotion and in particular the mechanics of their undulating crawling motion on agar aqueous gels where they are commonly grown and observed. In this article, we present a mechanical model of the friction of the worms on their substrate where we have included capillarity (which pins the worm of the gel), the hydrodynamics of the lubrication film (between worm and gel) and the substrate/body elasticity. We determine the ratio of the transverse to longitudinal friction coefficients of the worm body on the culture gel as a function of a control parameter which describes the relative role of the deformation of the gel and the viscous dissipation in the lubrication film. Experimentally this ratio is – for soft gels – larger than the maximal value predicted by our model (this maximum is equal to 2, the value for an infinite cylinder in bulk liquid) and we propose to include the plasticity of the gel (i.e. the dissipation of the deformation of the gel) for a better description of the worm/gel interaction.

1. Introduction

Caenorhabditis elegans (C. elegans), is a free-living soil nematode, 1 mm in length at the adult stage (Riddle et al., 1997). Its sensory system responds to numerous stimuli such as chemical and thermal gradients and mechanical perturbations. The complete knowledge of the neuronal connectivity of the worm associated with modern genetic tools has made it possible to determine the cellular and molecular basis of the worm behaviour. C. elegans has hence reached the status of a biological model comparable to Drosophila melanogaster or Escherichia coli.

In the laboratory C. elegans is usually kept on flat substrates such as agar aqueous gels, upon which it slides, forwards and backwards, describing a sine-shaped trajectory. Since this movement is apparently very simple, and since the C. elegans organism is composed of only about a thousand cells, one could reasonably address the possibility to build a complete model of the neuromuscular system. Of the 959 cells which make up the adult hermaphrodite, 302 are neurons whose connectivity pattern has been mapped out, and 95 are muscular cells. Due to the intrinsic relationship between neuronal activity patterns and muscular activity, our understanding of the neuromuscular processes can be advanced by the study of the locomotion of the worm and of its sensitivity to external mechanical constraints. This investigation requires an understanding of the contact mechanics between the worm and its environment.

There are very few studies on the influence of the mechanical environment on worm locomotion: Wallace (1958) reported the influence of the thickness of the wetting film coating the worm substrate and underlined the role of capillarity; Alexander (2002) reported the kinematic description of the undulating swimming motion originally presented by Gray and Lissmann (1964) and outlined the role of the anisotropy of the viscous friction but ignored the deformation of the substrate and capillary phenomena. Some models have been developed which incorporate the neural wiring of the worm (Niebur and Erdos, 1991) but these still ignore the physics of the worm–substrate interactions.

Until very recently, the rare quantitative experimental studies of C. elegans locomotion have consisted of attempts to establish qualitative markers (frequency, amplitude and wave length) in order to distinguish between different mutant strains. Locomotion characteristics constitute the major phenotype of C. elegans (Stetina...
et al., 2005) and there is now an increased interest in the biomechanics of C. elegans: for instance recent studies have considered the modulation of the swimming gait of C. elegans by the viscosity of the liquid (Fang-Yen et al., 2010) or the motion of C. elegans in wet granular media (Juarez et al., 2010). But, to our best knowledge, no studies have focussed on the mechanical interaction between the worm and its substrate, and its effect on locomotion.

In this paper, we address the problem of C. elegans locomotion from a purely mechanical point of view and propose an initial method of calculating friction coefficients, taking into account elements of the worm environment, specifically hydrodynamics, capillarity and elasticity. This is a necessary step to build a general mechanical model for the locomotion of C. elegans which could allow to describe the different crawling behaviours of the worms on different substrates.

2. Locomotion model

2.1. Introduction: the Alexander model

A locomotion model for slender body organisms has been proposed for swimming spermatozoa (Gray and Hancock, 1955) and then applied to the locomotion of nematodes (Gray and Lissmann, 1964). This model was presented by McNeill Alexander (Alexander, 2002) in a recent review. Worms move by generating a wave which, because of viscous friction, generates a force in the direction opposite to the direction of propagation of the wave. Because of the geometry of the worm, the friction is asymmetric and two friction coefficients ($C_1$ and $C_2$) can be distinguished depending on the direction of sliding of the worm’s body on its substrate (cf Fig. 1).

Fig. 1. Definition of the friction coefficients $C_1$ and $C_2$. $V_1^*$ and $V_2^*$, respectively, are the longitudinal and transverse velocities of the worm body with respect to the substrate for a sliding worm or to the liquid for a swimming worm. $F_1^* = -C_1 V_1^*$ and $F_2^* = -C_2 V_2^*$, respectively, are the longitudinal and transverse friction forces (per unit length) acting on the cylindrical worm.

The calculation of these coefficients (with dimension [ML$^{-1}$T$^{-1}$], i.e. the dimension of dynamic viscosity) is a classic exercise of hydrodynamics for cylinders in bulk liquids (Lamb, 1916), which could be applied to the motion of immersed swimming worms (Lighthill, 1976) and where $C_1/C_2 \approx 2$.

A point of the body of the worm is localized by its coordinates in the lab frame $(x(s,t), y(s,t))$, where $s$ is the arc length, measured tail-wards along the body of the worm (Fig. 2). If the worm is moving in the negative $x$ direction with velocity $U$ (counted positively), generating a sine wave from head to tail with velocity $\omega/q$ then

$$x(s,t) = s - Ut$$

$$y(s,t) = a \sin(\omega t - qs)$$

where $a$ is the undulation amplitude, $\omega$ the angular frequency and $q$ the wavenumber. This expression assumes small amplitude undulations, i.e. $a \ll q^{-1}$. When the worm moves at constant velocity, the sum of the viscous forces must equal zero: this yields the average horizontal velocity (Alexander, 2002):

$$U = -\frac{(C_2/C_1) - 1}{(C_1/C_2) + 2(aq)^2} \frac{\omega}{q} = \gamma \frac{\omega}{q}$$

where we have introduced the efficiency coefficient $\gamma$, representing the ratio of velocity of the worm to the phase velocity. The values of the friction coefficients depend on the contact mechanics of the worm on its substrate and are assumed to be independent of the worm velocity. In the following section, we develop a new model to determine these coefficients as a function of the elasticity of the substrate, the surface tension of the film covering the substrate and the hydrodynamics of the lubricating film.

2.2. Elasto-capillary-hydrodynamical model

C. elegans is a worm which is unsegmented, bilaterally symmetrical, with a cylindrical cuticle. We modelize the body of the worm by a homogeneous elastic cylinder of radius $R$ and Young modulus $E_w$, ignoring the surface texture of the cuticle and the alae (longitudinal ridges along the body of a gut worms) (Page and Johnstone, 2007). Note that the actual elasticity of the worm, which can be considered as a cylindrical shell (the shell being the cuticle) has been measured quite recently (Park et al., 2007). Since the length of the adult worm is about twenty times the diameter, the mechanical problem can be reduced to an essentially 2D problem as sketched on Fig. 3. The substrate is assumed to be semi-infinite, i.e. the thickness of the gel is much larger than any other length of the problem, with Young modulus $E_s$.

Fig. 2. A microphotograph of C. elegans (adult), with body parameterized by arc length $s$. The worm moves with velocity $U$ (Eq. (1a)); the wave propagates backwards in the frame of the worm with velocity $\omega/q$ (Eq. (1b)). Note the visible groove left by the worm on this soft gel.
2.2.1. Elasto-hydrodynamics problem

The Reynolds number $Re$ of the flow in the lubrication film is given by $Re = \rho Vu/\eta$ with $\rho$ the volumic mass of the fluid ($\approx 10^3$ kg m$^{-3}$), $V$ the velocity of the worm ($\leq$ one body length per second), $u$ the characteristic lubrication film thickness ($< a$ few micrometers) and $\eta$ the dynamic viscosity of water ($\eta \approx 10^{-3}$ Pa s), i.e. $Re < 10^{-3}$: C. elegans is another specimen of Life at low Reynolds numbers (Purcell, 1977) where the effects of viscosity effects dominate those of inertia.

Since the worm length is much larger than its radius $R$, the velocity field does not depend on $X$ and we can neglect the gradient of the pressure $P$ in the $X$ direction ($\partial X P = 0$). Using $Re \ll 1$, the lubrication approximation (Landau and Lifshitz, 1959), we have

$$V_X(Y,Z) = \frac{V_\perp Z}{H(Y)} \tag{3a}$$

$$\partial Y V_Y(Y,Z) = \frac{V_\perp}{\eta} \partial Y P(Y) \tag{3b}$$

$$V_Z = 0 \tag{3c}$$

Integrating Eq. (3b) with no-slip boundary conditions ($V_Y(Y,0) = 0$ and $V_Y(Y,H(Y)) = V_\perp$ where $V_\perp$ is the transverse velocity of the worm and $H(Y)$ the thickness of the film (Fig. 3)), we obtain the velocity profile of the film between the worm and the gel:

$$V_Y(Y,Z) = \frac{1}{2\eta} (Z^2 - ZH(Y)) \partial Y P(Y) + V_\perp \frac{Z}{H(Y)} \tag{4}$$

The mass flux of the fluid in the film must be conserved: by integrating Eq. (4) in the $Z$-direction between the substrate ($Z = 0$) and the worm body ($Z = H(Y)$) we obtain

$$\partial Y P(Y) = 6\eta V_\perp \frac{H(Y) - H_0}{H(Y)^3} \tag{5}$$

where $H_0$ is the film thickness at which the pressure gradient is zero. Eq. (5) is the Reynolds equation (Landau and Lifshitz, 1959).

Without elastic deformation of the gel or the worm, $H(Y)$ is parabolic: $H(Y) = H_0 + Y^2/2R$. Nevertheless, the liquid flow generates a pressure gradient, which in turn induces deformation of both cylinder and substrate. A very localized pressure applied to the surface of a two dimensional elastic medium gives a logarithmic deformation (Landau and Lifshitz, 1987); the film thickness then reads

$$H(Y) = H_0 + \frac{Y^2}{2R} - \frac{1}{\pi E} \int_{-\infty}^{+\infty} P(Y') \ln|Y-Y'| \, dY' \tag{6}$$

where $E$ is a composite Young’s modulus (Landau and Lifshitz, 1987) given by $1/E = (1 - \nu_0^2)/E_w + (1 - \nu_1^2)/E_v$; $E_w$ and $E_v$ are the Young’s moduli associated, respectively, with the worm ($w$) and the substrate ($s$) and $\nu_0$ and $\nu_1$ the associated Poisson’s ratios. Assuming for convenience the incompressibility of both worm and substrate (i.e. $v_w = v_s = 1/2$), we get $2/3 = 1/\left(E_w + 1/E_v\right)$.

The system of Eqs. (5) and (6) is the basis of the elasto-hydrodynamics theory as introduced in the seminal article of Herrebrugh (1968); nonetheless the boundary conditions are still to be defined. Far away from the worm, the pressure is equal to the atmospheric pressure and set to zero for convenience. In a recent work (Skotheim and Mahadevan, 2004) this boundary condition has been used to give insights into elasto-hydrodynamics. It has, however, been shown that for a rigid sphere it may not represent what occurs in reality since an adverse pressure may be generated in the film (Herrebrugh, 1968). It is then suitable to introduce $Y_e$ defined by $\partial Y P(Y_e) = 0$ and $P(Y) = 0$ for $Y > Y_e$. We are now left with three unknown quantities $P(Y), H(Y)$ and $Y_e$ for two equations and three boundary conditions:

$$\begin{aligned}
\partial Y P(Y) &= 6\eta V_\perp \frac{H - H_0}{H^3} \\
\partial Y P(Y) &= 1 \frac{1}{R} \int_{-\infty}^{+\infty} P(Y') \, dY' \\
P(\infty) &= 0 \\
P(Y_e) &= 0 \\
\partial Y P(Y_e) &= 0
\end{aligned} \tag{7}$$

The problem can be adimensionalised using the characteristic horizontal scale $\sqrt{RH_0}$ and the reduced variables $y$, $p$, and $h$ defined by

$$\begin{aligned}
Y &= \sqrt{RH_0} y \\
P &= \frac{6\eta V_\perp}{R \sqrt{E_s h}} \sqrt{p} \\
H &= H_0 h
\end{aligned} \tag{8}$$

The elasto-hydrodynamics system of Eq. (7) can be rewritten as

$$\begin{aligned}
\partial Y p(y) &= \frac{h-1}{h^3} \\
\partial Y h(y) &= y - \lambda \int_{-\infty}^{+\infty} p(y') \, dy' \\
p(\infty) &= 0 \\
p(Y_e) &= 0 \\
\partial Y p(Y_e) &= 0
\end{aligned} \tag{9}$$

where we have introduced the control parameter $\lambda$:

$$\lambda = \frac{6\eta V_\perp R}{\pi EH_0^2} \tag{10}$$

which represents the ratio of viscous stresses to elastic stresses. When $\lambda \ll 1$ the elastic deformation is negligible and the system behaves like a rigid cylinder dragged across a rigid substrate; conversely when $\lambda \gg 1$, the elastic stresses become dominant and the deformed system can be described within the frame of Hertz (1982) contact theory.

The integro-differential system of Eq. (9) can be solved using a finite difference scheme (Herrebrugh, 1968). For a given value of the parameter $\lambda$, the unknown $y_e$ is chosen such that all boundary conditions are verified: this is done by using a Newton–Raphson method (Press et al., 1986). The spatial dependence of the film thickness and the pressure is presented in Fig. 4(a) and (b). As expected, when $\lambda$ is small, the viscous shear is not large enough to

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$^2$ Common culture gels are made with 2% agar. These gels are less rigid than the worms, i.e. $E_i < E_w$, so that $E \approx 4/3E_w$.  

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Fig. 3. Schematic representation of a cross-section of the worm. The worm (of radius $R$) is pinned down on the substrate by capillary forces created by the meniscus; the thickness of the lubrication film is noted $H(Y)$ and the components of the velocity of the body section (with respect to the substrate) are $V_\perp$ and $V_\parallel$.  

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**References**

induce elastic deformations. On the contrary, as $\lambda$ increases, the film tends to flatten and the spatial variation of the pressure becomes localized like in Hertz contact.

2.2.2. Inclusion of capillarity

The worm radius $R$ ($\approx 20$ $\mu$m) is much smaller than the capillary length of water ($\approx 1$ mm) and, as such, capillary forces exceed gravity forces at the worm scale. The derivation of the force $F_c$ (per unit length) which pins the worm on its substrate is given in the Appendix and reads

$$F_c = 4\sigma \frac{\sin \theta}{1 - \cos \theta}$$

(11)

where $\sigma$ is the surface tension of the liquid and $\theta$ measures the size of the meniscus. It is noticeable that for vanishing $\theta$ values, the capillary force $F_c$ becomes very large: the worm is stuck on its substrate and should then move with great difficulty as observed experimentally for eel-worms by Wallace (1958).

In a stationary regime, this force should be balanced by the hydrodynamic lift and thus

$$F_c = \int_{-\infty}^{\infty} P(Y)\ dy = 6\eta \frac{R}{\mu_c} \int_{-\infty}^{\infty} p(y)\ dy$$

(12)

and finally

$$\frac{F_c}{(6\pi\eta RV)\sqrt{2}} \equiv \lambda^{1/2} \int_{-\infty}^{+\infty} p(y)\ dy = g(\lambda)$$

(13)

g(\lambda) is a function of the sole control parameter $\lambda$ and is shown in Fig. 5.

2.2.3. Friction coefficients

We can now extract the friction coefficients $C_l$ and $C_r$ from our model. We have

$$\begin{align*}
F_l &= C_l V_l = \int_{-\infty}^{+\infty} \eta \partial_{\bar{Z}} V_{\bar{Z}}(Z = H)\ dY \\
F_r &= C_r V_r = \int_{-\infty}^{+\infty} \eta \partial_{\bar{Z}} V_{\bar{Z}}(Z = H)\ dY
\end{align*}$$

(14)

We introduce the adimensionalized friction coefficients $c_l$ and $c_r$ by

$$\begin{align*}
c_l &= \frac{H}{H_e} \sqrt{\frac{R}{\mu_c} c_l} \\
c_r &= \frac{H}{H_e} \sqrt{\frac{R}{\mu_c} c_r}
\end{align*}$$

(15)

The expression of $c_l$ in obtained thanks to Eq. (3a) and that of $c_r$ is deduced from Eqs. (4) and (5):

$$\begin{align*}
c_l &= \int_{-\infty}^{+\infty} \frac{h - 3}{h^2} \ dy \\
c_r &= \int_{-\infty}^{+\infty} \frac{1}{h} \ dy
\end{align*}$$

(16)

These friction coefficients are presented in Fig. 6. It is worth noticing that, as $\lambda \to 0$, the ratio $c_l/c_r \approx 2$, ending towards one as $\lambda$ is increased; in terms of change of rigidity of the substrate, this would indicate that the efficiency of propulsion $\gamma$ decreases as the rigidity $E$ decreases (cf. Fig. 7).

2.3. Application of the model to the locomotion of C. elegans

Our model should be used as follows. If the radius $R$ and the rigidity $E_w$ of the worm are known, along with the characteristics of the substrate (rigidity $E_s$, viscosity $\eta$ and surface tension $\sigma$) and an experimental value for $V_{\bar{Z}}$ is found, this makes it possible to determine the value of the function $g(\lambda)$ (Eq. (13)), and hence the value of the control parameter $\lambda$ (cf. Fig. 5). Once the value of $\lambda$ is known, we can determine the friction coefficients and check the validity of the model by comparing the measured and computed efficiency $\gamma$ and thus obtain the thickness $H_e$ of the lubrication film. The transverse velocity $V_{\bar{Z}}$ can be obtained directly from the kinematics of the worm (Eq. (1a)). By elimination of the curvilinear abscissa $s$, we obtain the shape of the worm as a function of time $t$:

$$y(x,t) = a \sin((\omega - Ut)x - \omega t)$$

(17)
For small undulation amplitudes, i.e. when \(aq < 1\), it is easy to check that the transverse velocity along the body of the worm is given in a first approximation by

\[
\begin{align*}
V_{\perp} &= a(qU) \cos((qU)t - qx) \\
V_{\parallel} &= A(qU)
\end{align*}
\]

Eq. (18)

and is then maximizes in the less curved part of the worm by

\[
V_{\perp} = A(qU)
\]

Eq. (19)

or, introducing the efficiency \(\gamma\):

\[
V_{\perp} = AqU\frac{1-\gamma}{\gamma}
\]

Eq. (20)

Our theory is a self-consistent description of the locomotion since from the value of \(V_{\parallel}\), we obtain the value of the control parameter \(\lambda\) which is then used to determine the coefficients of friction \(C_{\perp}\) and \(C_{\parallel}\). Finally these coefficients can be used to determine the velocity \(U\) (using Eq. (2)) and then \(V_{\parallel}\) (using Eq. (19)).

Karbowski et al. (2006) have recently reported experiments where they vary the agar concentration of the gel substrate of the worms and consequently the rigidity \(E_s\) of the substrate: they observed a slight decrease of the \(\gamma\) efficiency from 0.75 to 0.63 upon increasing the agar concentration from 2 to 8%. We have also studied the locomotion of \textit{dauer} larvae of \textit{C. elegans} on 2% agar gels with the addition of surfactant (SDS) which reduces the surface tension\(^3\): the measured efficiency \(\gamma\) stayed very close to 1 while the surface tension \(\sigma\) was changed by a factor 2. This is in accordance with the original observations of Gray and Lissman (Gray and Lissmann, 1964; Alexander, 2002) which reported \(\gamma\)–values in the range of 0.77 to 0.90 on jelly. Our model does not predict \(\gamma\)–values larger than 0.25 from the smallest \(\lambda\)–values (cf. Fig. 7). There is clearly an element missing in our analysis which cannot predict \(c_{\perp}/c_{\parallel}\)–values larger than 2, i.e. the value for an elongated cylinder in a bulk liquid. Note that worms crawling on rigid surfaces (such as moist glass) do exhibit very low efficiencies (Alexander, 2002).

2.4. Tentative inclusion of gel dissipation

It has been already mentioned (Fig. 3) that the worms carve a groove behind them: this shows that the gel undergoes a plastic deformation and that the energy produced by the worm to deform the gel is lost. We can compare the energies associated with longitudinal and transverse deformations (Fig. 8). The increase of deformed area is equal to \(2Rv dt\) (a) and \(Lv dt\) (b) (\(v\) is the velocity of the considered body part with respect to the substrate). From these expressions, we can give an estimate of the ratio of the friction coefficients associated with the dissipations of the gel deformations \((c_{\perp}/c_{\parallel})\) by \(L/(2R)\). This ratio is of order 40 for adult worms and our prediction certainly is an overestimation. Note that it is only valid when the stresses associated with the gel deformations are larger than the viscous stress, i.e. when \(\lambda < 1\), and that it will lead to large efficiency coefficients, close to one.

Conflict of interest statement

There are no conflicts of interest.

\(^3\) \textit{Dauer} constitute an alternative state of the development of \textit{C. elegans}\ induced, for instance, by starving the worm: the larvae are smaller that the adult worms, they do not feed and can be considered \textit{waterproof}. This allows the use of surfactants which are toxic for ordinary worms.
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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jbiomech.2011.01.026.

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