An Estimation Method for Environmental Friction Based on Body Dynamic Model of *Caenorhabditis elegans*

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Abstract

*Caenorhabditis elegans* is a small worm which is approximately 1.3 mm in length. The present study proposes an estimation method for frictional force using locomotion information obtained from video analysis of actual worms. The results indicate that the body model driven by the estimated frictional force can trace the locomotion of the worm within 4% of the body length. The proposed method may be able to be applied to analyze the relationship between friction and gait control.

**Keywords:** *Caenorhabditis elegans*, frictional force, dynamics model, video analysis, locomotion

1. Introduction

*Caenorhabditis elegans* is a small soil-dwelling worm with a slender translucent body composed of around 1,000 cells. It is approximately 1.3 mm long and weighs 5.0 µg (Figure 1(a)). Its neural network, which is composed of only 302 neurons, allows the processing of environmental information such as temperature and chemical gradients so that the worm can act in response to its surroundings. Due to the small scale of its neural network, *C. elegans* has become a favored model organism for the analysis of information processing mechanisms hidden inside neural networks, especially since White et al. revealed a connective structure between its neurons and muscle cells.1

In this context, the mechanism of gait control is an interesting analysis target among various life phenomena because commands generated by neural networks can be easily observed through body locomotion. Accordingly, the worm’s information processing mechanism can be investigated by recording its behavior and examining the internal states of its neural network. Recently, dopamine was identified as a key chemical2 intermediating the distinctive gait changes observed when the worm swims in water and crawls on agar.3,4 It was also revealed that dopamine-related changes are induced by mechanical stimuli5. However, experimental conditions and current technology limit measurement of the amount of force that can be applied to the worm without

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influencing its behavior. As a result, the input for its neural network system remains unclear.

Computer simulation provides a potential solution to this problem because the worm's thrust is generated by reaction force based on the friction between its body and its environment in the absence of other external forces, and can be calculated using motion equations. The body dynamics model of C. elegans first proposed by Niebur and Erdos⁵ was able to simulate the worm's undulatory locomotion so that a model worm could travel as fast as a real one. As friction cannot be measured from an actual worm, the friction coefficients included in the model were estimated from the friction measured between glass fiber and agar⁶. Recently, more precise friction coefficients in a gelatin solution and water were calculated by Berri et al. and Szmitman et al. based on the principles of fluid dynamics.⁷⁻⁹ However, previous methods have limitations in terms of the range of environments in which they can be applied. An algorithm to determine friction independent of environmental conditions is therefore needed to support estimation of the mechanical stimuli affecting C. elegans.

In this paper, the authors propose a body dynamics model incorporating the considerations of dynamic and viscous friction. An estimation method for friction coefficients based on the model is then proposed. As this method requires only locomotion information obtained from video analysis of worms, it enables estimation of friction regardless of the environment and the worm's behavior. Chapter 2 describes the body dynamics model of C. elegans and the estimation method for environmental friction. Chapter 3 covers verification of the proposed algorithm and reports on the results of environmental friction estimation. Chapter 4 discusses the relationship between translational force and friction force, and Chapter 5 details the conclusion and outlines future work.

2. Materials and Methods

When C. elegans moves on a solid surface such as an agar plate or swims in liquid, it is exposed to different environmental drag forces. As these forces are the basis of propulsion, different drag characteristics or strengths produce different propulsive movements. Drag force can therefore be derived by observing the motion of worms to solve dynamic problems. The following section describes the materials and methods used to record worm motions, and highlights the algorithms used to estimate drag force.

2.1. Strains and culture

The C. elegans wild-type Bristol N2¹⁰ and the Escherichia coli OP50 strain were obtained from the Caenorhabditis Genetics Center. Using standard methods¹⁰ worms were grown at 20°C on 6-cm plates containing 10 ml of nematode growth medium (NGM) agar spread with E. coli (food). Well-fed worm at the young adult stage were used in all assays.

2.2. Sample preparation

6-cm plates containing 4 ml of NGM agar for assay were prepared on the same day of experiments. The plate for the crawling assay (plate A) was uncovered and placed on a clean bench for approximately 1h to dry up excess fluid from the surface. The plate for the swimming assay (plate B) was not dried up and was added 300 μl of S basal buffer¹¹. A worm was picked up from a culture plate and washed twice in a few drops of S basal buffer. Immediately after wash, a worm was transferred to an assay plate A or B.

2.3. Rigid link model

To estimate the drag forces acting between C. elegans and its environment, the worm's body was first approximated using the N rigid link model shown in
driving each link, and the second term represents friction, where $\mathbf{f}_j^T$ is the Jacobean matrix of the $j$-th joint with a representative point. $\mathbf{F}_j = (f_{j,\text{c}}, f_{j,n})^T$ represents the drag force acting on the gravity point of each joint, and can be described in arbitrary form depending on the surrounding environment. In this study, drag force was modeled using the properties of Coulomb friction and viscous drag in a Newtonian fluid as follows:

$$f_{j,a} = -\mu_d \frac{v_{j,a}}{|v_{j,a}|} - \eta_d v_{j,a}$$

(3)

where $d \in \{t, n\}$ denotes the tangential and normal directions related to the link, $v_{j,a}$ are the velocities at the gravity point of link $j$, $\mu_d$ is the coefficient of Coulomb friction, and $\eta_d$ is the viscous drag coefficient.

Equation (2) indicates that the drag coefficients and torque $\boldsymbol{\tau}$ driving each joint can be derived from local bending angles and the related velocities and accelerations $(\mathbf{q}, \dot{\mathbf{q}}, \ddot{\mathbf{q}})$ and translational acceleration $\ddot{\mathbf{r}}_g$, which can be determined from video analysis. Based on this equation, an algorithm for friction coefficient estimation is proposed below.

2.4. Friction estimation algorithm

The motion equations (1) and (2) can be solved for drag coefficients given the motion information $(\mathbf{q}, \dot{\mathbf{q}}, \ddot{\mathbf{q}})$ and position $\mathbf{r}_g$. Among these values, the local bending angle $\mathbf{q}$ and the position $\mathbf{r}_g$ can be determined by recording the motion of a worm and analyzing the resulting video, and the related time derivations can be used to determine velocity and acceleration. The information obtained can then be used to solve the motion equations for the drag coefficients in relation to each video. However, there are two problems in the implementation of this calculation.

Firstly, it is an ill-posed problem because only $N+2$ coupled equations can be derived from Equations (1) and (2), while there are four unknown drag coefficients plus $N$ unknown torque values $\mathbf{r} \in \mathbb{R}^{N-1}$. To solve this problem, the proposed algorithm involves simultaneous analysis of two different motions of a worm placed in the same environment in which identical drag coefficients are assumed. In this manner, the number of unique coupled equations can be doubled without increasing the number of unknown drag coefficients.

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Secondly, the drag coefficients calculated from only one sampling can be significantly affected by video analysis measurement error. To reduce this impact, the proposed algorithm involves the solution of a motion equation for \( \bar{r}_d \) and \( q_0 \) for the time duration \( T \) with different drag coefficients. The coefficients that generate the paths closest to those of the actual worm are then explored by minimizing the following evaluation function:

\[
E = \frac{1}{2(t_{\text{max}} + 1)} \sum_{t=0}^{T} \sum_{i=1}^{l} \sum_{j=1}^{2} ||x_i^j(t) - r_i^j(t)||, \tag{4}
\]

Where \( x_i^j \) represents the position of the \( i \)-th evaluation point on the worm, \( r_i^j \) represents the corresponding position on the rigid-link body model, and subscript \( j \) denotes an individual worm.

The proposed algorithm is applied to estimate the drag coefficients for a worm swimming in liquid and crawling on an agar surface. The proposed algorithm consists of four blocks as outlined below.

**Block 1: Video analysis**

To analyze the body form of *C. elegans* in crawling and swimming, the worm on an assay plate (A for crawling and B for swimming) was video-recorded using a digital camera EXILIM EX-F1 (CASIO COMPUTER CO., LTD., Tokyo) mounted on a stereomicroscope for approximately 10 seconds at 300 frames per second. The resolution of each frame was 512 x 384 pixels. Distinct worms picked up from a culture plate were used for crawling assays and swimming assays. The body form in crawling and swimming of *C. elegans* was analyzed off-line based on the previous method\(^7\) as shown in Figure 2. Briefly, each frame of the video was processed using the following procedures: (i) binarization, (ii) denoising, (iii) skeletonizing, and (iv) division of body line into the 13 parts. After image processing, time-series data concerning with the body form were obtained using the following procedures: (v) length-scale calibration, (vi) acquisition of the x- and y-coordinates of each point on the body, and (vii) calculation of values concerning with the body form such as the relative angle between adjacent dividing points. Video analyses described above were carried out using the following software: Wriggle Tracker (Library Co. Ltd., Tokyo) for procedures (i)-(iv) and Move-tr/2D (Library Co. Ltd., Tokyo) for procedures (v)-(vii).

**Block 2: Selection of drag coefficient**

In this block, a set of coefficients is selected in three phases as described below.

**[Phase 1]**

In Phase 1, drag coefficients are selected from the set \( \{ \mu_n, \mu_r, \eta_n, \eta_r \} \) \( \in \{ (N_1 \Delta \mu, N_2 \Delta \mu, N_3 \eta, N_4 \eta) | N_1, N_2, N_3, N_4 = 0,1, \ldots, N_{\text{max}} \} \) based on iterative alteration of \( N_1, N_2, N_3, N_4 \).

After the search for all combinations is complete, \( d_i \) % of the drag coefficients \( \{ \mu_n, \mu_r, \eta_n, \eta_r \} \) with smaller evaluation values (Equation (4)) are selected, and the iteration proceeds to Phase 2, where \( a = 1,2, \ldots, d_i(N_{\text{max}} + 1)^2/100 \).

**[Phase 2]**

In Phase 2, better drag coefficients are sought from the set selected in Phase 1. The search is carried out with the set \( \{ \mu_n, \mu_r, \eta_n, \eta_r \} \) \( \in \{ (N_1 \Delta \mu, N_2 \Delta \mu, N_3 \eta, N_4 \eta) | N_{i=4} = \{-1,0,1\} \) . After the search for all combinations is complete, \( d_2 \) % of the drag coefficients \( \{ \mu_n, \mu_r, \eta_n, \eta_r \} \) with smaller evaluation values (Equation (4)) are selected, and the iteration proceeds to Phase 3, where \( b = 1,2, \ldots, 3d_i(N_{\text{max}} + 1)^2/10000 \).

**[Phase 3]**

In this phase, the generalized reduced gradient method\(^9\) is applied for the selection of drag coefficients \( \{ \mu_n, \mu_r, \eta_n, \eta_r \} \) as initial values so that the friction coefficients with the smallest evaluation values are calculated.

**Block 3: Calculation of Motion Equations**

In this block, calculation for the path of two rigid-link body models in the time span \( T \) s is performed with the friction coefficients selected in Block 2. Calculation to solve Equations (1) and (2) for \( q_0, r \) is carried out using ADAMS (MSC Software Corporation, Tokyo) multi-body dynamics simulator.
Table 1 Parameters used in simulation

<table>
<thead>
<tr>
<th>$l_{\text{max}}$</th>
<th>5 s</th>
<th>$\Delta \mu$</th>
<th>$1.0 \times 10^{-1}$</th>
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<tbody>
<tr>
<td>$l$</td>
<td>3</td>
<td>$\Delta \eta$</td>
<td>$1.0 \times 10^{-2}$</td>
</tr>
<tr>
<td>$m$</td>
<td>$3.84 \times 10^{-7}$ g</td>
<td>$d_1$</td>
<td>1.0 %</td>
</tr>
<tr>
<td>$\Delta l_{\text{max}}$</td>
<td>10</td>
<td>$d_2$</td>
<td>0.2 %</td>
</tr>
</tbody>
</table>

Fig. 3. Estimated results of friction coefficients

Fig. 4. Estimated paths

Block 4: Evaluation of Drag Coefficients

In Block 4, evaluation is performed for drag coefficients by substituting the paths calculated in Block 3 into an evaluation function (Equation (4)), and the iteration returns to Block 2.

3. Experiments

As a way of verifying the performance of the proposed body dynamics model and the estimation algorithm for friction coefficients, testing was performed to determine whether the algorithm enabled estimation of artificially preset friction coefficients. Such coefficients were then estimated for worms crawling on agar and swimming in a drop of water. Major headings should be typeset in boldface with the first letter of important words capitalized.

Fig. 5. Locomotion of *C. elegans*

3.1. Verification

The locomotion of the body model was simulated using Equations (1) and (2) with artificially preset friction coefficients and time-dependent joint angles. The paths determined from this simulation were then used with the proposed algorithm for friction coefficient estimation. Finally, the errors observed between the preset and estimated friction coefficients were calculated to verify the performance of the algorithm. Here, time-dependent joint angles with the following four patterns were chosen: $q_{t+1} - q_t = 0.4 \sin(5t - 0.6i), 0.6 \sin(5t - 0.6i), 0.4 \sin(5t - 0.6i) + 0.1, 0.6 \sin(5t - 0.6i) + 0.1$ which are respectively denoted as Locomotion 1–4. In addition, 10 sets of friction coefficients ($F_1$–$F_10$) were chosen as uniform random numbers in the range of [0, 1] for dynamic friction coefficients and [0, 0.01] for viscous friction coefficients. The locomotion pair of 1 and 2 was simulated with the friction coefficients of $F_1$–$F_5$ and the other pair (Locomotion 3 and 4) was simulated with the friction coefficients of $F_6$–$F_{10}$. The parameters of the body dynamics model and the proposed estimation algorithm are shown in Table 1.
3.2. Estimation of friction coefficients of actual worms

Friction coefficients for actual worms were estimated using video of their movement on agar and in a drop of water (Figures 5). Each of the time-dependent joint angles determined from image processing was smoothed using a two-order Butterworth low-pass filter (high cutoff frequency: 5 Hz) for denoising. The analysis times for crawling and swimming were respectively set as $t_{max}=4$ s, 1 s, and the other parameters were the same as those used in the verification simulation.
Fig. 10. Estimated friction coefficients (Water) direction shown in (A1) was much larger than that shown in (A3). The next section discusses this friction coefficient variability.

4. Discussion

This section discusses the cause of variances found in the estimated friction coefficients A1, A2 and A3 (Fig. 10) or the same worm on the same agar plate.

To compare the effects of different friction coefficients adopted for the same joint motion, the time-dependent joint angles $\mathbf{q}^A(t)$ extracted from the locomotion of A1 were substituted into Equations (1) and (2), and paths with the friction coefficients of A2 and A3 were calculated. Figure 11 shows paths resulting from simulation under the time-dependent joint angles $\mathbf{q}^A(t)$ and the friction coefficients A2 and A3. The errors observed between the actual and simulated worm’s paths are also shown in Figure 12(b), which indicates that the average path error was about 4% of the worm’s length even when different friction coefficients (A1, A2 and A3) were used. Figure 12(a) highlights the friction force at each link accumulated at the point of the head tip. The right-hand side of Equation (2) shows this calculation. From the figure, it can be seen that the total friction generated from friction coefficient A1 showed a strong correlation and similar values to that generated from friction coefficients A2 and A3. As the total friction reactive force is the basis of the propulsion force the worm uses to crawl and swim, this result indicates that the proposed algorithm with path errors as an evaluation function can be used to estimate propulsion force.

In previous studies regarding the dynamic modeling of C. elegans, it was reported that a worm’s path can be determined from the ratio between the normal and tangential friction coefficient.57 Indeed, the friction coefficient ratio is a dominant factor in determining worm paths. However, according to the simulation performed here, identical locomotion cannot be
generated if the same ratio but different friction coefficients are adapted. Figure 13 shows locomotion paths observed when the dynamic friction coefficients were kept at a constant ratio \( \mu_d = \mu_s \) and the viscous friction coefficient was set to 0 \( \eta = 0 \). It can be seen that there were path differences depending on the value of \( \mu_s \), even though the dynamic friction coefficients were kept at a constant ratio. This suggests that if image processing on actual worms can be carried out with a high degree of accuracy, friction coefficients can be specifically determined because verification simulation under artificially preset configurations (3.1) enabled the estimation of friction coefficients close to actual values with an acceptable level of accuracy.

Finally, the effect of friction in different environments was quantified. Figure 14 shows the average RMS value of the total friction forces as calculated from the crawling and swimming simulation results. The result of a t-test to determine the RMS between crawling and swimming showed a significant difference between the two \( p < 0.001 \). Fig. 15 indicates that worms experience stronger friction forces when swimming than when crawling. Using results obtained from the proposed estimation algorithm allows estimation of the mechanisms behind gait control \(^8\) at the friction level.

5. Conclusion and Future Work

This paper proposed a method for estimating friction coefficients based on a body dynamics model and video images of *C. elegans*. The study verified that the proposed algorithm can be used to estimate friction coefficients under artificially preset configurations, and the results of experiments using actual worms confirmed that it can also be used to generate locomotions with small errors and track worm paths closely. The algorithm can be used to estimate true friction coefficient values under ideal noise-free conditions. Although estimation results were affected by noise contamination from image processing, the propulsion forces affecting locomotion paths could be estimated.

In future works, the authors plan to improve the robustness of the proposed method to support the calculation of time-dependent friction changes acting on worms, and will analyze the mechanisms behind gait control against environmental factors in the context of body dynamics.

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References


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