

Paper:

A Dynamic Body Model of the Nematode *C. elegans* with Neural Oscillators

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The nematode *Caenorhabditis elegans* (*C. elegans*), a relatively simple organism in structure, is one of the most well-studied multicellular organisms. We developed a virtual *C. elegans* based on the actual organism to analyze motor control. We propose a dynamic body model, including muscles, controlled by a neural circuit model based on the actual nematode. The model uses neural oscillators to generate rhythmic movement. Computer simulation confirmed that the virtual *C. elegans* realizes motor control similar qualitatively to that of the actual organism. Specified classes of neurons are killed in the neural circuit model corresponding to actual *unc* mutants, demonstrating that resulting movement of the virtual *C. elegans* resembles that of actual mutants.

Keywords: *C. elegans*, neural circuit model, dynamic body model, neural oscillator, computer simulation

1. Introduction

An approach for analyzing the functional mechanism of organisms recently proposed uses computer simulation with a mathematical model [1]. Computational analysis is essential for understanding complex organism mechanisms. In analysis using a mathematical model, *virtual* organism, instead of the *actual* one, environmental conditions are changed easily and behavior analyzed repeatedly under the same conditions. This is useful in the study of biology and applicable to engineering work such as establishment a brain-like machine based on organisms.

Organisms relatively easy to analyze are called model organisms, and include colibacilli, saccharomyces cerevisiae, nematodes and drosophila. In molecular biology, model organisms have been thoroughly analyzed and experimental evidence applied to analyzing higher organisms. Our group has developed computer models of the unicellular colibacilli and paramecium based on biology and engineering knowledge [2–4].

This paper deals with multicellular organisms as the

next step in this approach, focusing on the nematode *Caenorhabditis elegans* (*C. elegans*), one of the most well-analyzed multicellular organisms targeting a computer model based on studies at the nervous system level.

Among the many studies on the *C. elegans* model, Ferrée et al. [6] simulated a simplified neural circuit that processes external information on chemicals. Cangelosi et al. [5] and Kawamura et al. [7] developed neural circuit models for processing touch stimuli. Since their work focused only on sensing and processing external stimuli, the movement produced was extremely simplified.

Bryden et al. proposed a body model of motion simulation [8] that dealt only with forward and backward movement for a simplified neural-circuit structure of motoneurons.

We developed a neural circuit model for stimulation response and a kinematic model of movement of the nematode itself, integrating the two for whole body simulation [9]. The model ignored body and environment dynamics, but realized five patterns of movement. Here, we discuss the motor control model of *C. elegans* based on the actual organism including neural circuit models of motoneurons and a dynamic model of the nematode itself [10].

Researchers such as Grillner developed motor control models of animals, such as the lamprey and salamander, showing sinusoidal movement [11–15]. These very complex structures, have not, however, involved body models controlled by neural circuits based on the actual animal structure. Now that the other hand, since the complete genome sequence, complete cell lineage, and nervous-system connections of *C. elegans* have been determined [16–18], we model its neural circuit based on biological evidence, targeting actual phenomena using a model based on the actual structure unlike studies designing a structure to reproduce actual phenomena, our model is used for simulation analyzing the relationship between the structure and the motor control mechanism. This point differs from other studies which aim to design the structure so as to reproduce the actual phenomena.

This paper is organized as follows: Section 2 gives an overview of *C. elegans*. Sections 3 and 4 detail two neural circuit models of motoneurons and a dynamic model of

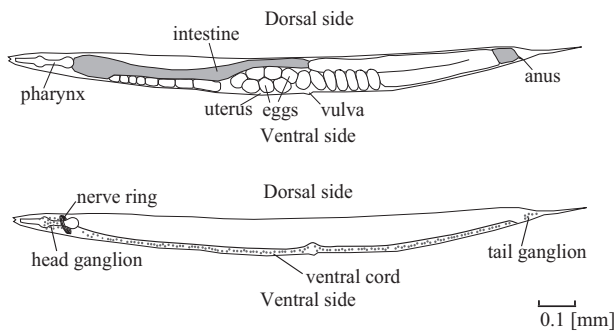


Fig. 1. Organization of *C. elegans* (revised from the figure in [7]).

the organism. Section 5 confirms the feasibility of this model through a series of computer simulations whose results are compared to the actual organism. Section 6 presents conclusions.

2. *C. elegans*

2.1. Structure

Caenorhabditis elegans, a non parasitic soil nematode, is shaped like a simple cylindrical approximately 1mm long. It consists of 959 cells and includes such basic organs as a nervous system, muscles, a pharynx, a hypodermis, an alimentary canal and genitalia (**Fig.1**). Its body-wall muscles are internal and the musculature consists of four quadrants of striated muscles. Each quadrant consists of two closely apposed rows of muscle cells [17]. It moves sinusoidally by dorso-ventrally flexing these muscles. Pharyngeal muscles play a role in behavior, e.g., by opening and closing the mouth and in swallowing and manducation.

The nervous system consists of 302 neurons, the head and tail ganglia, and the ventral cord, which runs longitudinally down the ventral side (**Fig.1**). The neural circuit processes information from internal and external stimuli, and produces motion corresponding to individual stimuli, e.g., avoiding obstacles and repellent chemicals. These neurons are classified functionally into three main groups: sensory neurons, interneurons, and motoneurons. Sensory neurons detect external stimuli first, then interneurons process information from stimuli. Motoneurons control muscles based on signals from interneurons. These neural circuits play an important role in sensing, information processing, and motor control.

Note that head and tail ganglia consist of the three types of neurons. The head ganglion has functions similar to the brains of higher organisms. The ventral cord consists of motoneurons that innervate the muscles and control some motion patterns. The nerve ring, the center of the nervous system, encompasses the pharynx with nerve axons from the ganglion and the ventral cord. Information from the sensory neurons and interneurons is integrated here.

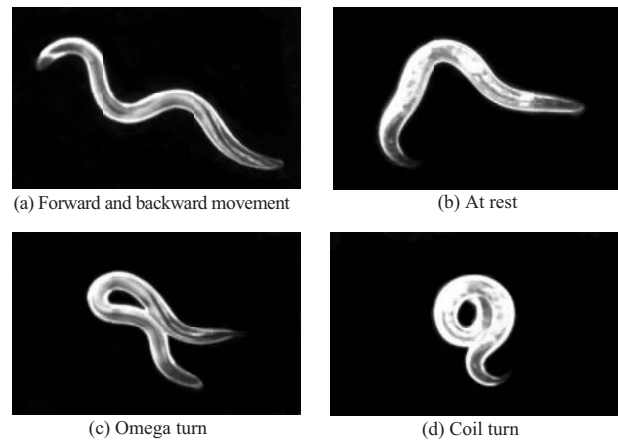


Fig. 2. Movement patterns of *C. elegans*.

2.2. Movement

C. elegans sidles sideways and ambulates similar to a snake. Its five patterns of movement are forward and backward, rest, the omega turn, and the coil turn (**Fig.2**). *C. elegans* chooses suitable patterns move in search of food. It moves forward and backward (**Fig.2(a)**) by wriggling in sinusoidal waves. Its rest posture (**Fig.2(b)**) is led by a kink from the tail [19]. The omega turn is a distinctive feature in worm movement. The worm usually executes an omega (Ω) shape on agar (**Fig.2(c)**). The coil turn, in which the body forms a flat spiral [19] (**Fig.2(d)**) occurs typically in water. *C. elegans* moves forward continuously changing patterns spontaneously or in response to by external stimuli-movements controlled by motoneurons in the head ganglion and the ventral cord. The motoneurons in the ventral cord also reportedly replay an important role in movement [20].

Neural circuit models consisting of motoneurons in the head ganglion and the ventral cord are constructed to recreate these patterns of movement as explained in the next section.

3. Neural Circuit Models

Motoneurons in the head ganglion and the ventral cord innervate the ventral and dorsal body-wall muscles of *C. elegans*, which moves sinusoidally by rhythmical dorso-ventral flexure of these muscles [17]. The neural circuits of motoneurons play a significant role in contract these muscles rhythmically. A neural circuit model of motoneurons in the head ganglion and the ventral cord is explained in the sections that follow.

3.1. Model of Motoneurons in the Head Ganglion

While the sinusoidal movement suggests the existence of neural circuits that generate rhythmic signals, the anatomical positions of these pattern generators have yet to be identified. It seems unlikely that the circuits for the pattern generator exist in the ventral cord because even *unc-25* mutants, whose inhibitory neurons in the ventral

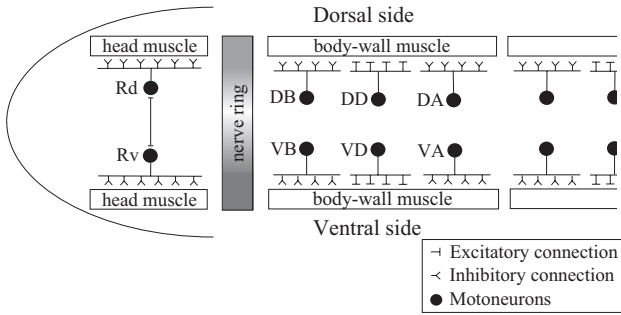


Fig. 3. Motoneuronal circuit innervating muscles of *C. elegans*.

cord are unable to function, generate rhythmic sinusoidal movement, although with reduced amplitude [20]. Inhibitory neurons play a role in generating a rhythmic pattern [21], so we assume here that circuits for the rhythmic pattern generator exist in the head ganglion.

The head ganglion contains 32 motoneurons [17], although their functions are not clear. It is estimated that two motoneurons RME(R/L) in this ganglion act as cross-inhibitors [17], so we infer that the circuit consists of motoneurons in the head ganglion that generates a rhythmic pattern. Therefore, the neural circuit is simplified using a pattern generation circuit model consisting of two neurons, Rv and Rd (Fig.3). To generate alternating oscillation, the internal states M_j ($j \in \{Rv, Rd\}$) of motoneurons are expressed by the following equations based on the Matsuoka's neural oscillator [21]:

$$T_r \frac{dM_j}{dt} = -M_j + \sum_n w_{j,k} \cdot V_k + s_j - b_j \cdot f_j$$

$$T_a \frac{df_j}{dt} = -f_j + V_j \quad \dots \quad (1)$$

$$V_j = \begin{cases} M_j & (M_j \geq 0) \\ 0 & (M_j < 0) \end{cases}$$

where T_r and T_a are time constants; $w_{j,k}$ ($j, k \in \{Rv, Rd\}; j \neq k$) is the connection weight from Rv to Rd (or from Rd to Rv); V_j is the output state of the j -th neuron; s_j is a constant input from neurons connected to Rv or Rd; b_j is a fatigue coefficient; and f_j is the state of fatigue in motoneurons.

Input signals to the ventral body-wall muscle of the head, I_1^v , and to the dorsal muscle, I_1^d , are calculated using internal states M_j ($j \in \{Rv, Rd\}$) of the motoneurons as follows:

$$I_1^v = W_{1,Rv} \cdot M_{Rv} \quad \dots \quad (2)$$

$$I_1^d = W_{1,Rd} \cdot M_{Rd} \quad \dots \quad (3)$$

where $W_{1,Rv}$ and $W_{1,Rd}$ are the connection weight from Rv to the ventral head muscle and that from Rd to the dorsal head muscle.

Table 1. Six classes of body-wall muscle motoneurons.

VB	VB1 VB2 VB3 VB4 VB5 VB6 VB7 VB8 VB9 VB10 VB11
VA	VA1 VA2 VA3 VA4 VA5 VA6 VA7 VA8 VA9 VA10 VA11 VA12
DB	DB1 DB2 DB3 DB4 DB5 DB6 DB7
DA	DA1 DA2 DA3 DA4 DA5 DA6 DA7 DA8 DA9
VD	VD1 VD2 VD3 VD4 VD5 VD6 VD7 VD8 VD9 VD10 VD11 VD12 VD13
DD	DD1 DD2 DD3 DD4 DD5 DD6

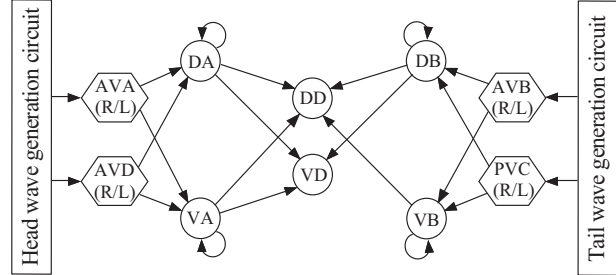


Fig. 4. The schematic diagram of the neural circuit organized by interneurons and motoneurons.

3.2. Model of Motoneurons in the Ventral Cord

The 58 motoneurons in the ventral cord required for movement are divided into six classes, VB, VA, DB, DA, VD, and DD (Table 1). VB and DB are used in forward movement and VA and DA in backward movement [20]. VB, VA, DB, and DA are excitatory motoneurons, while VD and DD are inhibitory motoneurons. VB, VA, and VD innervate ventral body-wall muscles and DB, DA, and DD dorsal muscles (Fig.3). Connections between neurons are determined based on ref.[17]. Fig.4 maps the neural circuit consisting of interneurons (hexagons) and motoneurons (circles).

Sinusoidal forward and backward wave in movement require wave signals to interneurons connected to motoneurons in the ventral cord.

We assume that wave signals are transmitted from the head and tail wave generation circuits connected to interneurons. Wave signals are sent to motoneurons included in VB and DB from interneurons AVB(R/L) and PVC(R/L) and are also sent to motoneurons included in VA and DA from AVA(R/L) and AVD(R/L) as shown in Fig.4. Motoneurons fire rhythmically in correspondence to interneuron rhythm.

Internal states M_l and M_k of interneurons l and k ($l \in \{AVB(R/L), PVC(R/L)\}$, $k \in \{AVA(R/L), AVD(R/L)\}$), which connect to the tail and head wave generation circuits, are assumed for simplicity by the following equations:

$$M_k = \begin{cases} \sin(\alpha_k \cdot t + T_k) & (\text{forward movement}) \\ 0 & (\text{backward movement}), \end{cases}$$

$$M_l = \begin{cases} 0 & (\text{forward movement}) \\ \sin(\alpha_l \cdot t + T_l) & (\text{backward movement}), \end{cases}$$

where α_k, α_l, T_k and T_l are constants.

Internal states M_m of each motoneuron m ($\in \{VB, VA, DB, DA, VD, DD\}$) are described by the following equation:

$$T_m \frac{dM_m}{dt} = -M_m + \sum w_{m,n} \cdot M_n \quad \dots \quad (4)$$

where $w_{m,n}$ is the connection weight from neuron n ($\in \{AVB(R/L), PVC(R/L), AVA(R/L), AVD(R/L), VB, VA, DB, DA, VD, DD\}$) to motoneuron m , and T_m is the time constant. Using internal states M_m , input signals to ventral body-wall muscle and dorsal muscle, I_i^v and I_i^d ($i = 2, 3, \dots, 12$), are calculated by

$$I_i^v = \sum W_{i,m}^v \cdot M_m \quad \dots \quad (5)$$

$$I_i^d = \sum W_{i,m}^d \cdot M_m \quad \dots \quad (6)$$

where $W_{i,m}^v$ and $W_{i,m}^d$ represent connection weights from motoneuron m to the i -th ventral and dorsal body-wall muscles. For excitatory motoneurons VB, VA, DB, and DA, connection weights are positive, while for inhibitory motoneurons VD and DD, connection weights are negative.

Section 4 explains how we derive a dynamic model of *C. elegans* using input signals of body-wall muscles I_i^v and I_i^d ($i = 1, 2, \dots, 12$) calculated by the neural circuit models of motoneurons above.

4. Dynamic Body Model

In this paper, the body of a *C. elegans* is expressed by a multi-joint rigid link model with twelve rotational joints, J_i ($i = 1, 2, \dots, 12$), in the two dimensional space (**Fig.5(a)**) based on ref.[20], assuming that joint movement is controlled by signals I_i^v and I_i^d input from motoneurons.

4.1. Dynamic Equations

Link model movement can be expressed by:

$$\mathbf{M}(\mathbf{q})\ddot{\mathbf{q}} + \mathbf{h}(\mathbf{q}, \dot{\mathbf{q}}) + \mathbf{g}(\mathbf{q}) = \boldsymbol{\tau} + \boldsymbol{\tau}_f \quad \dots \quad (7)$$

where $\mathbf{M}(\mathbf{q})$ is the inertia matrix, $\mathbf{h}(\mathbf{q}, \dot{\mathbf{q}})$ the non-linear term including joint torque due to rifugal and Coriolis forces, $\mathbf{g}(\mathbf{q})$ joint torque due to gravity, $\mathbf{q} = [q_1, q_2, \dots, q_{12}]^T$ is the vector of joint rotation angle (**Fig.5(a)**), $\boldsymbol{\tau} = [\tau_1, \tau_2, \dots, \tau_{12}]^T$ the vector of joint torque, and $\boldsymbol{\tau}_f = [\tau_{f1}, \tau_{f2}, \dots, \tau_{f12}]^T$ the vector of torque due to force generated between the body and the floor. i -th torque τ_i ($i = 1, 2, \dots, 12$) is expressed as follows based on ref.[22]:

$$\tau_i = \beta_i(M_i^v - M_i^d) - K_i(M_i^v + M_i^d + \gamma_i)(q_i - \theta_{ei}) - B_i\dot{q}_i \quad \dots \quad (8)$$

where K_i is stiffness of i -th rotational joint, B_i viscosity, β_i force generation gain, and γ_i passive stiffness coefficient. θ_i is equilibrium angle, where θ_1 corresponds to the direction of movement. M_i^v and M_i^d are internal states of the

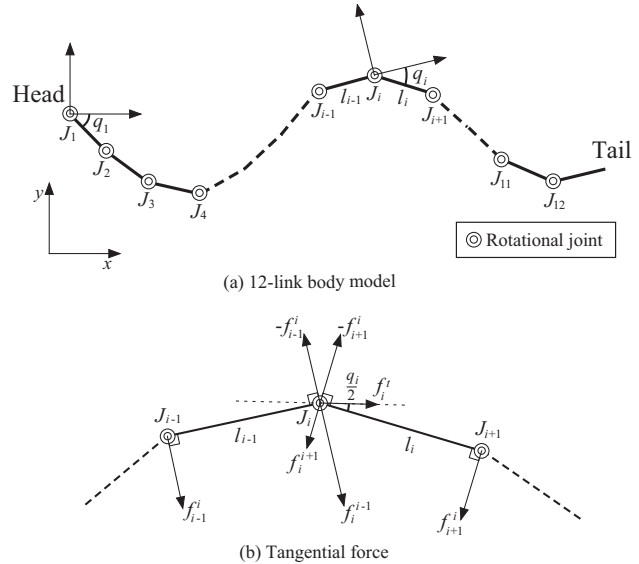


Fig. 5. *C. elegans* link model.

i -th ventral and dorsal muscles given by:

$$M_i^v = h_i(I_i^v) \quad \dots \quad (9)$$

$$M_i^d = h_i(I_i^d) \quad \dots \quad (10)$$

$h_i(x)$ is the characteristic of the i -th ventral and dorsal muscles expressed by the following function:

$$h_i(x) = \frac{1}{1 + \exp(-a_i(x - b_i))} \quad \dots \quad (11)$$

where a_i is an inclination with the function and b_i is the value of the input signal at which the internal state of the muscle takes a central value. These parameters for muscle characteristics are set by trial and error. Furthermore, τ_{fi} in Eq.(7) is given by the following equation for viscous friction B_{fi} :

$$\tau_{fi} = -B_{fi} \left(\sum_{h=1}^i \dot{q}_h \right) \quad \dots \quad (12)$$

4.2. Propulsion

C. elegans requires propulsion to go forward or backward, although the mechanism for generating this force has yet to be clarified. Therefore motion dynamics of a snake [23] is applied to our model of *C. elegans*. Also, it assumes that propulsion F_{head} acts on the head in forward movement and F_{tail} on the tail in backward movement. Propulsion F_p ($p = head, tail$) is calculated from tangential force on the body shaft, f_i^t ($i = 1, 2, \dots, 12$), which results from $f_{i-1}^{i-1}, f_i^{i+1} - f_{i-1}^i$ and $-f_{i+1}^i$ on the joint J_i , where the tangential direction on the body shaft is defined as that of a continuous curve that divides joint angle q_i into two [23]. f_{i-1}^i , generated on joint J_{i-1} by i -th torque τ_i on joint J_i is perpendicular to the $(i - 1)$ -th link (**Fig.5(b)**). Tangential force f_i^t on joint J_i is calculated

by [23]

$$f_i^t = \{(f_i - f_{i+1}) + (f_{i-1} - f_i)\} \sin \frac{q_i}{2} \quad \dots \quad (13)$$

$$(i = 2, 3, \dots, 12)$$

where

$$f_i = \frac{\tau_i}{l_i} \quad \dots \quad (14)$$

l_i is the link length (**Fig.5(a)**), and sets $l_1 = l_2 = \dots = l_{12} = l$. Note that $f_1^t = f_{13}^t = 0$ in Eq.(13) when the tangential direction on end of the head and tail denote 1st and 12-th links.

Propulsion F_p ($p = head, tail$) can be given by summing f_i^t :

$$F_p = \begin{cases} -\sum_{i=2}^{12} f_i^t \cos\left(\sum_{h=1}^i q_h - \frac{q_i}{2}\right) \\ \quad (p = head, \text{ forward movement}) \\ \sum_{i=2}^{12} f_i^t \cos\left(\sum_{h=i}^{12} q_h - \frac{q_i}{2}\right) \\ \quad (p = tail, \text{ backward movement}) \end{cases} \quad \dots \quad (15)$$

In this model, propulsion F_p ($p = head, tail$) is converted to propulsion velocity of the head or the tail v_p as follows:

$$m_c \dot{v}_p + B_f v_p = F_p \quad (p = head, tail) \quad \dots \quad (16)$$

where m_c is the worm's weight, and B_f the friction between the worm and the floor.

The dynamic behavior of the *virtual C. elegans* is calculated using the Appell method [24].

5. Simulation

To verify the effectiveness of our proposed model, *virtual C. elegans*, a series of computer simulations are carried out.

5.1. Parameter Setting

Although many parameters included in *virtual C. elegans* should be adequately determined, little biological data is applicable to these parameters, main by due to the extreme difficulty of quantitatively measuring the electrophysiological states of neurons and muscular forces. In this paper, almost of the parameters here are determined by trial and error based on *actual C. elegans* movement.

Virtual C. elegans is simulated using parameters tuned in advance. Differential equations included in *virtual C. elegans* are calculated every 0.001s by using the fourth-order Runge-Kutta method [25].

5.2. Patterns of Movement

The results of patterns generated in forward and backward movement and the omega turn are discussed below. Note that since we deal only with movement on land, the

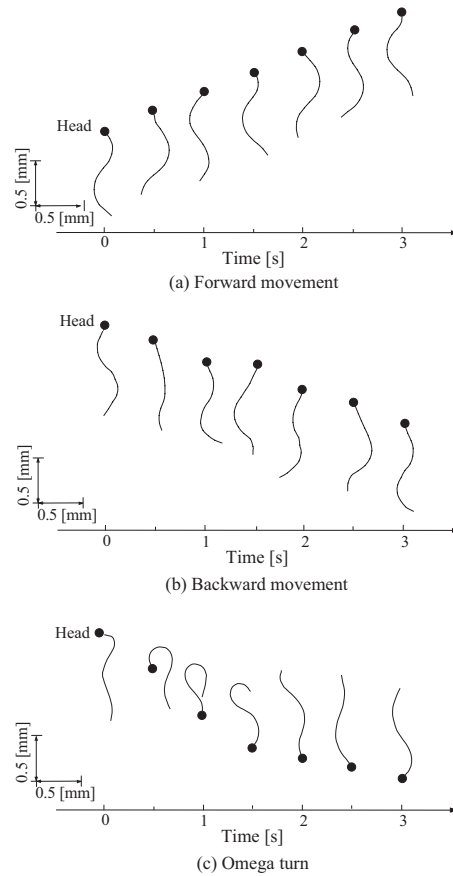


Fig. 6. Movement patterns of the *virtual C. elegans*.

coil turn in water was ignored. The change in patterns is planned in advance because information processing determining such changes has not been considered here.

Figure 6(a) shows how *virtual C. elegans* moves forward for 3s every 0.5sec, where ● expresses the head. *Virtual C. elegans* can reproduce the sinusoidal waves similar to that of *actual C. elegans*. In backward movement (**Fig.6(b)**), *virtual C. elegans* is sinuated from the tail to forward movement, although it moves sideways slightly. When *virtual C. elegans* turns π rad (**Fig.6(c)**), it has started to turn at 0.5sec, and forms an Ω (**Fig.2(c)**).

These results confirm that our proposed *virtual C. elegans* recreates *actual* patterns of movement well.

5.3. Comparison to Actual C. elegans

The validity of *virtual C. elegans* is demonstrated by comparing (i) time profiles for the translational velocity of the head, and (ii) joint angular change to those of *actual C. elegans*. The video images of *actual C. elegans* are used to determine head velocity and angular change using image processing software, Scion Image (Scion Corporation) [26]. The velocity of *actual C. elegans* is calculated from changes in head positions measured each six frames per second. The angle of i -th rotational joint q_i ($i = 2, 3, \dots, 12$) is measured as follows:

- Extract a picture from video images each three frames per second.

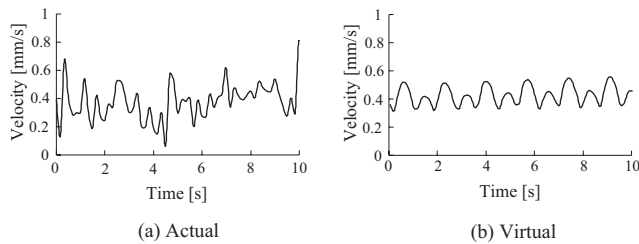


Fig. 7. Head velocities of the *actual* and *virtual* *C. elegans* worms.

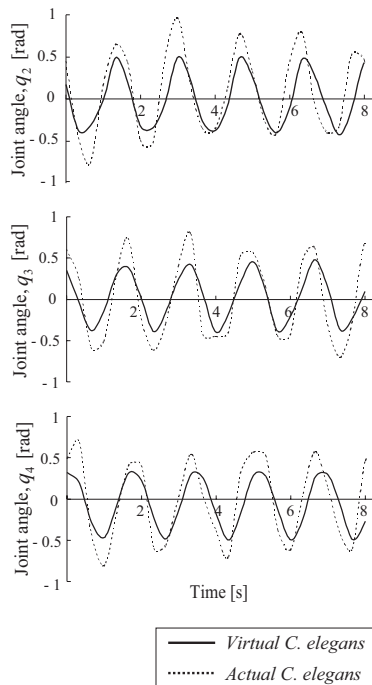


Fig. 8. Joint angles of *actual* and *virtual* *C. elegans*.

- Skeletonize the body of *C. elegans* in the picture using image processing software.
- Divide the skeletonized line into twelve parts.
- Measure angles between adjoined links using the same software.

In head velocity for *actual* and *virtual* worms (**Fig.7(a),(b)**), the velocity of *actual* *C. elegans* oscillates within 0.2 to 0.6mm/s. The velocity of *virtual* *C. elegans* varies within this range, but cycles of *actual* and *virtual* worms differ considerably. In this model, propulsion is defined in Eq.(15). Although propulsion may play a primary role in moving forward or backward, other factors may affect it when the body expands and contracts longitudinally as with an earthworm. Propulsion must be revised in future work. In time courses for joint angles q_2 , q_3 and q_4 of *actual* and *virtual* *C. elegans* (**Fig.8**), dotted lines show angles for an *actual* worm and solid lines that for *virtual* worm. **Fig.8** confirms that cycles of angular change and phase difference in *virtual* *C. elegans* correspond to those of *actual* *C. elegans*. In both , an-

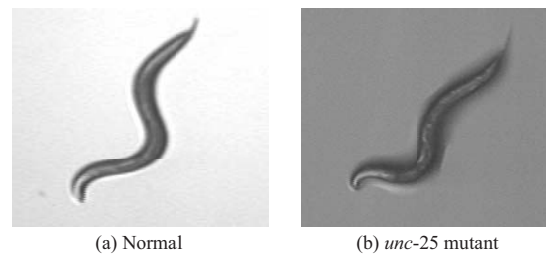


Fig. 9. Normal and *unc-25* mutant of *actual* *C. elegans*.

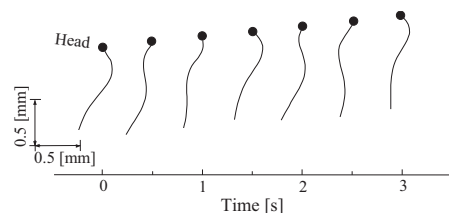


Fig. 10. Body forms of *virtual* *unc-25* mutant of *C. elegans*.

gles change with a cycle of about two seconds, and these phases shift bit by bit from the head toward the center of the body. The phase difference between time profiles of joint angles produce sinusoidal waves of *C. elegans*, although amplitudes of *virtual* *C. elegans* are smaller than those of *actual* *C. elegans*.

If torque τ_i in *virtual* *C. elegans* increases by tuning parameters in Eq.(8), amplitudes could become larger, but movement of *virtual* *C. elegans* would then no longer correspond to *actual* movement. It is thus necessary to analyze effects and sensitivity of individual parameters.

5.4. Can *Virtual C. elegans* Predict the Motion of the *unc-25* Mutant?

The mutants of *C. elegans* are dealt to examine the function of our neural circuit model. The mutant, an organism with gene mutations, sheds light on neuron, or gene, functions when compared to the normal worm [20]. Corresponding classes of neurons in the neural circuit model of *virtual* *C. elegans* are killed to simulate the neural structure of *unc* mutants. Since this study deals with the movement of *C. elegans*, *virtual* *C. elegans* with the mutated circuit model is compared to *actual* *unc* mutants.

A *unc-25* mutant lacks all inhibitory motoneurons in VD and DD in the ventral cord [20], forming a sinusoidal wave with a small amplitude in forward or backward movement (**Fig.9**). A difference of amplitudes in sinusoidal form is seen in body shape. The neural circuit model of the ventral cord is constructed based on the *unc-25* mutant as noted in Section 3. In simulation, all inhibitory motoneurons in VD and DD are removed from the circuit model in **Fig.4**. Note that parameters are the same as those used in the above normal simulation.

Figure 10 shows the *virtual* *unc-25* mutant of *C. elegans* in forward movement every 0.5s. Compared to

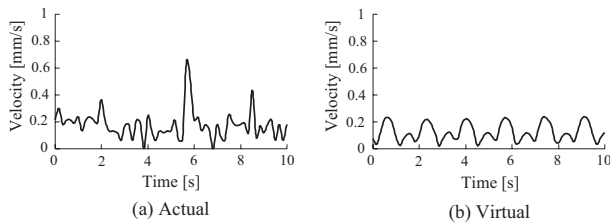


Fig. 11. Head velocity of *actual* and *virtual unc-25* mutants of *C. elegans*.

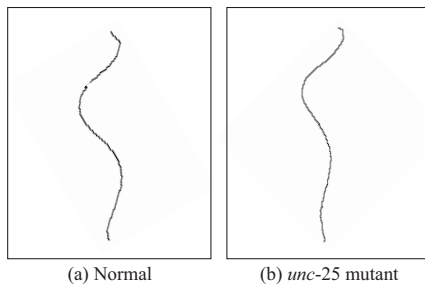


Fig. 12. Body forms of two *actual C. elegans*.

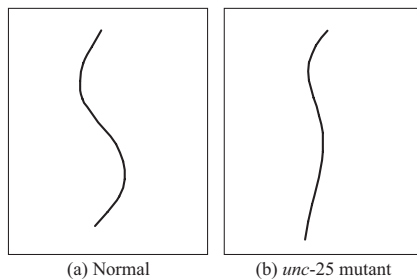


Fig. 13. Body forms of two *virtual C. elegans*.

result of the normal worm (**Fig.6(a)**), the *virtual unc-25* mutant forms sinusoidal waves with a smaller amplitude. In velocity of *actual* and *virtual* mutants (**Fig.11**), both are slower in the normal worm in **Fig.7**. The worm moves forward or backward and velocity varies with the wave amplitude.

In *actual C. elegans* in **Fig.12, (a)** is the normal worm and **(b)** the *unc-25* mutant. Note that the mutant amplitude is smaller than that of the normal worm and that the tail curves little remaining almost straight. **Fig.13(a), (b)** confirms similar characteristics in *virtual C. elegans*, indicating that the rhythmic pattern generator may not consist of motoneurons in the ventral cord.

Few factors are analyzable experimentally with *actual* organisms, so computer simulation such as in this study will effectively overcome such a problem.

6. Conclusions

In this paper, a motor control model of *C. elegans*, the simplest multicellular organism, was constructed based on biological evidence from *actual C. elegans*. This *virtual C. elegans* consists of two neural circuit models of motoneurons and a dynamic model.

Computer simulation confirmed the effectiveness of the proposed model as follows:

- Patterns of movement such as forward and backward and the omega turn, are re-created by this model.
- The behavior of the proposed model quantitatively corresponds to that of *actual C. elegans*.
- The function of the neural circuit in the ventral cord is well approximated by this model.

Computer simulation effectively enables the study of unknown factors in biology.

The following three points remain to be clarified:

- Roles of individual head ganglion motoneurons
- Details of pattern generator circuits for movement
- Propulsion for forward and backward movement

Future research will be directed at reconstructing and revising the motor control model using the latest data on molecular biology and electrophysiology. We hope to construct a computer model of *C. elegans* by integrating this motor control model and the conventional sensory-information processing model.

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