A Dynamic Body Model of the Nematode
C. elegans with a Touch-response Circuit

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Abstract - **The nematode *Caenorhabditis elegans* (*C. elegans*), a relatively simple organism in structure, is one of the most welll-studied multicellular organisms. In this study, we develop a *virtual C. elegans* based on the actual nematode to analyze motor control which uses neuronal circuits and muscles. Although *C. elegans* processes many kinds of external stimuli, we focus on gentle touch stimulation. *Virtual C. elegans* consists of both a neuronal circuit model for touch-response and a dynamic body model, and is capable of reproducing a series of information processing from stimulation reception to generation of movement. The effectiveness of our model is discussed through simulation results.**

Keywords - **C. elegans; motor control; touch-response circuit model; dynamic body model; computer simulation**

I. INTRODUCTION

Living organisms such as human beings have mechanisms to adapt to various conditions of external environments. In the field of molecular biology, one research strategy uses comparatively simple organisms to analyze complicated organisms in detail. A gene that has an important function in the nervous system, for example, was identified in human beings after being discovered in nematodes, and the effectiveness of the analysis of simple organisms is widely recognized. However, despite experimental techniques of biology, even the simple nematode has never been fully clarified.

In this study, we focus on *Caenorhabditis elegans* (*C. elegans*) among multicellular organisms to model a series of mechanisms from processing of stimulation information to representation of behavior. By using such a model, the behavior of an actual organism can be reproduced on the computer. The multicellular organism differs mainly from unicellular organisms in that it processes information by using neuronal circuits, in addition to a difference in the number of cells. All neuronal cells (neurons) of *C. elegans* have been identified, and neuronal connections have been approximately clarified [1].

Several computer models of the neuronal circuit of *C. elegans* based on biological data have been proposed in recent years [2],[3],[4]. On the other hand, much interest is centered on the control of movement by *C. elegans*, which uses only four muscles to realize various movements, as shown in Fig. 1, and several body models for motor control have been proposed [5],[6]. So far, authors also

(a) Forward and backward movement (b) At rest
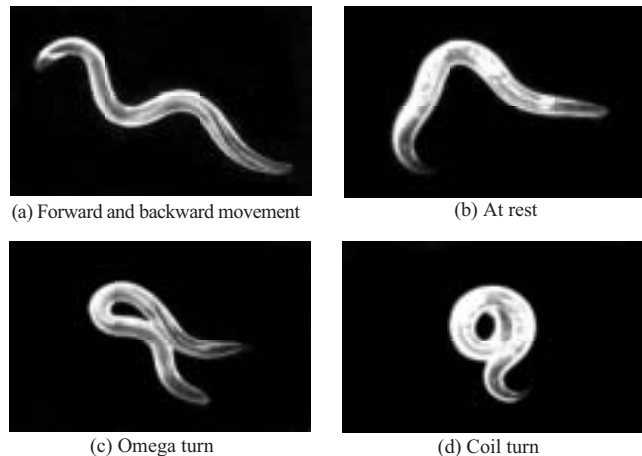
(c) Omega turn (d) Coil turn

Figure 1. Movement patterns of *C. elegans*.

have proposed a dynamic body model for motor control of *C. elegans* [7]. However, a model that aims only at limited functions like information processing or motor control cannot express a series of mechanisms from the reception of stimuli to the generation of movement specifically. Then, we developed a neuronal circuit model for stimulation response and a kinematic model of movement of the nematode itself, integrating the two for whole body simulation [8],[9]. The model ignored body and environment dynamics, but realized a series of information processing from reception of stimulation to generation of movement.

In this paper, as the next step of the above model, we newly construct a whole body model of *C. elegans* by integrating the both a neuronal circuit model for touch response and a dynamic model of the body. In this model, the waving movement of *C. elegans* are reproduced, and forward and backward movement are controlled based on stimulation information.

This paper is organized as follows: Section II gives an overview of *C. elegans* . Sections III and IV detail a neuronal circuit model for the waving movement and a dynamic model of *C. elegans* body, respectively. In Section V, to control the body model corresponding to external stimulation, a touch-response circuit model is proposed. Section VI verifies behavior of *virtual C. elegans* through a series of computer simulations. Finally, Section VII concludes the paper.
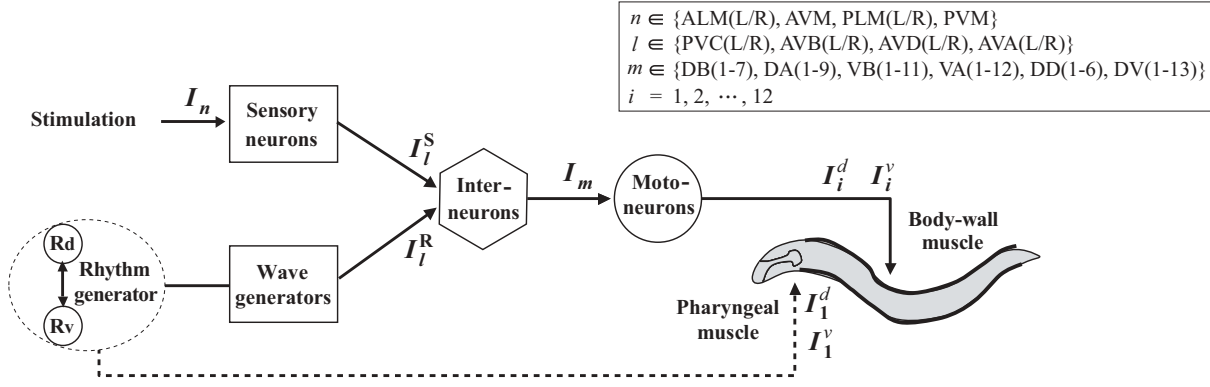
$n \in \{$ALM(L/R), AVM, PLM(L/R), PVM$\}$
$l \in \{$PVC(L/R), AVB(L/R), AVD(L/R), AVA(L/R)$\}$
$m \in \{$DB(1-7), DA(1-9), VB(1-11), VA(1-12), DD(1-6), DV(1-13)$\}$
$i = 1, 2, \cdots, 12$

Figure 2. Schematic diagram of the proposed model.

II. Nervous System and Movement of *C. elegans*

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 [10]. 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 [1].

In 1986, J.G. White *et al.* published a neuronal circuit map that includes 302 neurons, about 5000 chemical synaptic connections, about 600 gap junctions and about 2000 connections between neurons and muscles [1]. The neural circuit processes information from internal and external stimuli, and produces movement 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. The sensory neurons detect external stimuli first, and then interneurons process information from the stimuli. Finally, motoneurons control the muscles on the basis of signals from interneurons. These neuronal circuits play an important role in sensing, information processing and motor control.

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. 1). *C. elegans* chooses suitable patterns move in search of food. *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. Motoneurons in the ventral cord also reportedly replay an important role in movement [10].

III. Neuronal Circuit Model for Waving Movement

Pharyngeal muscles play a important role in the rhythmic behavior. Also, the waving movement is achieved by dorso-ventral flexure of body-wall muscles. These movements are controlled by motoneurons. Motoneurons in the head ganglion innervate pharyngeal muscles, and ones in the ventral cord innervate dorsal and ventral body-wall muscles. In this model, a rhythm generator of pharyngeal muscles and sinusoidal wave generators of body-wall muscles are constructed separately.

A. Motor control of pharyngeal muscles

The head ganglion contains 32 motoneurons [1], although their functions are not clear. While the waving movement suggests the existence of neural circuits that generate rhythmic signals, the anatomical positions of these pattern generators have yet to be identified. It can be inferred that the circuit consisted of motoneurons in the head ganglion generates a rhythmic pattern. Therefore, the neuronal circuit is simplified using the pattern generation circuit model consisting of two motoneurons, Rd and Rv. The rhythmic signals are transmitted to pharyngeal muscles, and the pharynx moves rhythmically.

To generate alternating oscillation, ontputs M_j ($j \in \{$Rd, Rv$\}$) of pharyngeal motoneurons are expressed by the following equations based on the Matsuoka's neuronal oscillator [11]:

$$
\left.
\begin{aligned}
T_r \frac{dM_j}{dt} &= -M_j + \sum_n w_{j,k} \cdot V_k - b_j \cdot f_j + s_j \\
T_a \frac{df_j}{dt} &= -f_j + V_j \\
V_j &= \begin{cases} M_j & (M_j \geq 0) \\ 0 & (M_j < 0) \end{cases}
\end{aligned}
\right\}, \quad (1)
$$

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

Input signals, I_1^d and I_1^v, to the dorsal and ventral pharyngeal muscles (dotted line in Fig. 2) are calculated using outputs M_j ($j \in \{$Rv, Rv$\}$) of pharyngeal motoneurons as follows:

$$
\begin{aligned}
I_1^d &= W_{1,\text{Rd}} \cdot M_{\text{Rd}}, &(2) \\
I_1^v &= W_{1,\text{Rv}} \cdot M_{\text{Rv}}, &(3)
\end{aligned}
$$

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

B. Motor control of body-wall muscles

The 58 motoneurons in the ventral cord are required for movement and divided into six classes as shown in Table I. DB and VB are used in forward movement, and DA and VA in backward movement [10]. Also, DB, DA, VB and VA are
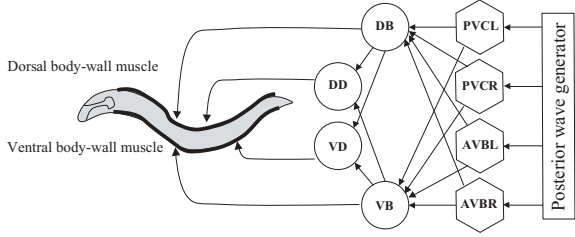
(a) Neuronal circuit for forward movement
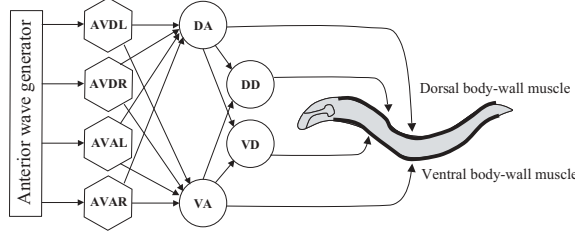
(b) Neuronal circuit for backward movement

Figure 3. Schematic diagram of the neural circuit organized by interneurons and motoneurons.

TABLE I

CLASSES OF BODY-WALL MUSCLE MOTONEURONS.

DB	DB1 DB2 DB3 DB4 DB5 DB6 DB7
DA	DA1 DA2 DA3 DA4 DA5 DA6 DA7 DA8 DA9
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
DD	DD1 DD2 DD3 DD4 DD5 DD6
VD	VD1 VD2 VD3 VD4 VD5 VD6 VD7 VD8 VD9 VD10 VD11 VD12 VD13

excitatory motoneurons, while DD and VD are inhibitory motoneurons. Body-wall muscles are controlled by motoneurons connected with interneurons. Motoneurons, DB, DA, and DD, innervate dorsal body-wall muscles; VB, VA, and VD ventral muscles, (Fig. 3). Motor control of body-wall muscles can be divided into 11 parts. Therefore, in this model, body-wall muscles are dealt as 11 small muscles, i-th muscle ($i = 2, \cdots, 12$), where the pharyngeal muscle is the 1st muscle. In this paper, connections between neurons are determined according to the reference [1].

Sinusoidal forward and backward waves in movement require wave signals to interneurons connected to motoneurons in the ventral cord. We assume that wave signals are generated in the anterior and posterior wave generators and transmitted to interneurons. On the other hand, sensory neurons for stimulation reception connect with interneurons and transmit signals for stimulation response (see Fig. 2). Therefore, the interneuron l ($l \in \{\mathrm{PVC(L/R)}, \mathrm{AVB(L/R)}, \mathrm{AVD(L/R)}, \mathrm{AVA(L/R)}\}$) in this model receives signals I_l^{R} and I_l^{S} from wave generators and sensory neurons (Fig. 2). The output M_l and the total input I_l of each interneuron are expressed by:

$$M_l = h_l(I_l), \tag{4}$$
$$I_l = I_l^{\mathrm{R}} - I_l^{\mathrm{S}}, \tag{5}$$

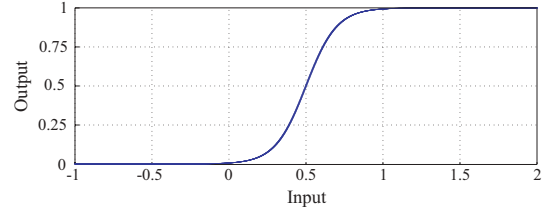where $h_l(x)$ is characteristics of neurons and is expressed

Figure 4. Input-output caracteristics of interneurons.

by the following function based on a general neuron model [12]:

$$h_l(x) = \frac{1}{1 + \exp(-a_l(x - b_l))}, \tag{6}$$

where a_l is an inclination with output function, and b_l is the value of the stimulation input at which the output of the neuron takes a central value.

The wave signals, I_l^{R}, from posterior and anterior wave generators are sent to interneurons. As shown in Fig. 3, the posterior wave generator transmit signals to interneurons PVC(L/R) and AVB(L/R), which connect with motoneurons for forward movement, and also the anterior wave generator transmit signals to AVD(L/R) and AVA(L/R) for backward movement. In this paper, the following sinusoidal wave signals are generated and transmit to each interneuron:

$$I_l^{\mathrm{R}} = \frac{1}{2}(\sin(\alpha_l \cdot t + T_l) + 1), \tag{7}$$

where α_l and T_l denote the constants, and I_l^{R} is the continuation value of [0, 1].

Although these sinusoidal inputs are always given to interneurons, forward and backward movements could never happen at the same time, since the neuronal circuit for stimulation response controls only one among anterior and posterior inputs to be effective. In this study, we assume that I_l^{S} in Eq.(5), which is determined by various kinds of external stimuli, plays a role in motor control inhibiting either wave signals corresponding to stimuli. Then we design the characteristic of interneurons in Eq.(6) as shown in Fig. 4, where $a_l = 10$, $b_l = 0.5$. In this model, for example, if the input I_l^{S} to interneurons l ($l \in \{\mathrm{PVC(L/R)}, \mathrm{AVB(L/R)}\}$), which connect with motoneurons included in the forward circuit (Fig.3 (a)), is 1 and orver, the total input I_l in Eq.(5) obtains negative because the range of the wave signal I_l^{R} obtains [0, 1] as given in Eq.(7). Therefore, the interneuron in this model outputs 0 when the input is negative as shown in Fig. 4. In this manner, the sinusoidal signal I_l^{R} from the posterior wave generator is inhibited and only the signal from the anterior wave generator becomes effective. Although I_l^{S} is determined by various kinds of external stimuli, we especially deal with gentle touch stimuli in this paper. The details of the touch-response circuit, which transmits signals I_l^{S} to interneurons, is described in Section V.

Outputs M_m of each motoneuron m ($m \in \{\mathrm{DB}, \mathrm{DA}, \mathrm{VB}, \mathrm{VA}, \mathrm{DD}, \mathrm{VD}\}$) are described by the following equa-
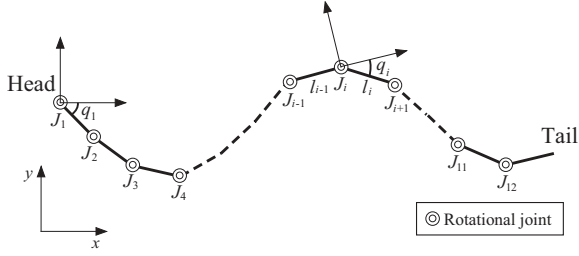
Figure 5. 12-link body model of *C. elegans*.

tions:

$$T_m \frac{dM_m}{dt} = -M_m + h_m(I_m), \qquad (8)$$

$$I_m = \sum W_{l,m} \cdot M_l, \qquad (9)$$

where $W_{l,m}$ is the connection weight from interneuron l ($l \in$ {PVC(L/R), AVB(L/R), AVD(L/R), AVA(L/R)}) to motoneuron m ($m \in$ {DB, DA, VB, VA, DD, VD}), and T_m the time constant.

By using outputs M_m, both input signals I_i^d and I_i^v ($i = 2, 3, \cdots, 12$), to the dorsal body-wall muscle and to the ventral muscle (solid line in Fig. 2) are calculated respectively by

$$I_i^d = \sum W_{i,m}^d \cdot M_m, \qquad (10)$$

$$I_i^v = \sum W_{i,m}^v \cdot M_m, \qquad (11)$$

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

The dynamic model of *C. elegans* mentioned in the next section, is derived using input signals of body-wall muscles I_i^d and I_i^v ($i = 1, 2, \cdots, 12$) that are calculated by the neuronal circuit model of motoneurons as mentioned above.

IV. DYNAMIC BODY MODEL

In this paper, the body of a *C. elegans* is approximated by a multi-joint rigid link model with twelve rotational joints J_i ($i = 1, 2, \ldots, 12$) (Fig. 5) based on the actual nematode [10], assuming that joint movement is controlled by signals I_i^d and I_i^v input from motoneruons.

Dynamic equation of link model in contact with its environment can generally be expressed by:

$$\mathbf{M(q)\ddot{q}} + \mathbf{h(q, \dot{q})} + \mathbf{g(q)} = \tau + \tau_{\mathbf{f}}, \qquad (12)$$

where $\mathbf{M(q)}$ is the inertia matrix, $\mathbf{h(q, \dot{q})}$ the nonlinear term including the joint torque due to centrifugal and Coriolis forces, $\mathbf{g(q)}$ the joint torque due to gravity, $\mathbf{q} = [q_1, q_2, \cdots, q_{12}]^T$ the vector of the joint rotation angle as shown in Fig. 5, $\tau = [\tau_1, \tau_2, \cdots, \tau_{12}]^T$ the vector of the joint torque, and $\tau_{\mathbf{f}} = [\tau_{f1}, \tau_{f2}, \ldots, \tau_{f12}]^T$ is the torque due to the force generated between the body and the floor. Since joint torque is determined by the difference of the contraction forces of ventral and dorsal muscles and the joint stiffness should depend on the contraction forces, i-th torque $\tau_i (i = 1, 2, \cdots, 12)$ can be expressed by the

following equation based on the reference [13] as:

$$\tau_i = \beta_i(M_i^v - M_i^d) - K_i(M_i^v + M_i^d + \gamma_i)(q_i - \theta_{ei}) - B_i\dot{q}_i \quad (13)$$

where K_i and B_i are stiffness and viscosity of i-th rotational joint generated by muscles, β_i force generation gain, and γ_i passive stiffness coefficient. θ_i is equilibrium angle. M_i^v and M_i^d are outputs of i-th ventral and dorsal muscles calculated from inputs I_i^v and I_i^d. In this paper, τ_{fi} is approximated by the following equation with viscous friction coefficient B_{fi} for simplicity:

$$\tau_{fi} = -B_{fi}\left(\sum_{h=1}^{i} \dot{q}_h\right). \qquad (14)$$

C. elegans requires a propulsion to go forward or backward. Thus far the mechanism for generation this force has not yet been revealed. Therefore, motion dynamics of a snake, whose movement is similar to *C. elegans* and has been analyzed dynamically [14], is applied to our model of *C. elegans*. Also, it assumes that a propulsion $\mathbf{F_{head}}$ acts on the head in forward movement, and $\mathbf{F_{tail}}$ on the tail in backward movement. The propulsion $\mathbf{F_p}$ ($p = head, tail$) can be given by the sum of tangential force, f_i^t, on i-th link. The details are given in the reference [7]. The head position in forward movement, $\mathbf{X_{head}} = [x_1, y_1, z_1]^T$, is calculated from the propulsion $\mathbf{F_{head}}$ as follows:

$$m_c\ddot{\mathbf{X}}_{\mathbf{head}} + B\dot{\mathbf{X}}_{\mathbf{head}} = \mathbf{F_{head}}, \qquad (15)$$

$$\mathbf{F_{head}} = -\sum_{i=2}^{12}\left(f_i^t \begin{bmatrix} \cos\left(\sum_{h=1}^{i} q_h - q_i/2\right) \\ \sin\left(\sum_{h=1}^{i} q_h - q_i/2\right) \\ 0 \end{bmatrix}\right), \qquad (16)$$

where m_c is the body weight of a *C. elegans*, and B the viscosity between a *C. elegans* and the floor. The tail position in backward movement, $\mathbf{X_{tail}}$, is calculated in the same manner.

The dynamic behavior of the model is calculated using the Appell method [15].
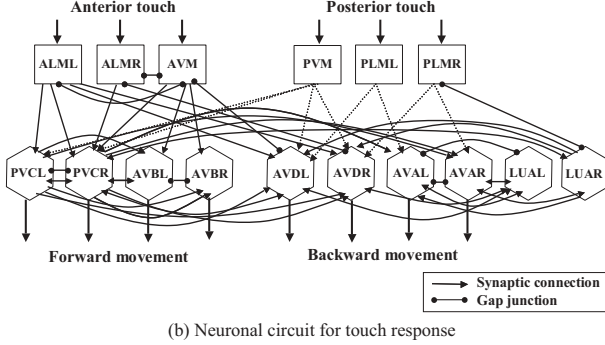
V. MOTOR CONTROL WITH A NEURONAL CIRCUIT MODEL FOR TOUCH RESPONSE

Movement patterns are changed by internal or external stimulation. Although *C. elegans* processes various kinds of stimuli, this paper focuses on the response to gentle touch stimuli.

When *C. elegans* receives gentle touch stimulation on the anterior part of the body, it moves backward, and it also moves forward when stimulated on the posterior part of the body. Gentle touch stimulation on the anterior part of the body is received by three sensory neurons: ALML, ALMR and AVM. Similarly, gentle touch stimulation on the posterior part of the body is received by PLML, PLMR and PVM. The positions of these sensory neurons are shown in Fig. 6(a) [1],[10],[16]. Fig. 6(b) show the proposed neuronal circuit model of *C. elegans* for gentle touch stimuli consisting of six sensory neurons (rectangles) and interneurons (hexagons). Furthermore, since some parts of connections with respect to PLM(L/R) and PVM have
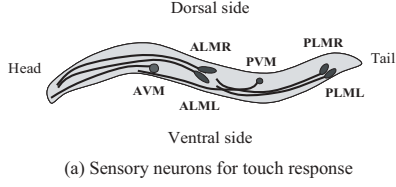
(a) Sensory neurons for touch response

(b) Neuronal circuit for touch response

Figure 6. The touch-response circuit model.

Figure 7. Forward movement of the proposed model.

Figure 8. Joint torques in forward movement.

never been clarified, the connections are determined according to those of ALM(L/R) and AVM.

Sensory neurons ALML and ALMR receive gentle touch stimuli on the anterior part of the body. In particular, ALML receives stimuli on the left side and ALMR on the right side. Similarly, PLML and PLMR receive gentle touch stimuli on the posterior part of the body. Furthermore, AVM and PVM receive gentle touch stimuli on anterior and posterior parts of the body, respectively. Output characteristics of sensory neurons are also represented by Eq.(6).

Touch stimulation input I_n to the sensory neuron n ($n \in \{\text{ALM(L/R)}, \text{AVM}, \text{PLM(L/R)}, \text{PVM}\}$) are stepless inputs of the range of [0, 1] which quantifies the strength of the stimulation. Therefore, each neuron outputs the continuation value of [0, 1] which is normalized by the maximum output from the actual neuron. In this paper, it is assumed that ALM(L/R) and PLM(L/R) have the same characteristic for simplicity. Considering characteristics of actual *C. elegans*, stimulation inputs to AVM and PVM are averages of those of ALML and ALMR and averages of PLML and PLMR, respectively, and their reception sensitivities are 1/2 of ALM(L/R) and PLM(L/R).

The input I_l^{S} in Eq.(5) to the interneuron l ($l \in \{\text{PVC(L/R)}, \text{AVB(L/R)}, \text{AVD(L/R)}, \text{AVA(L/R)}\}$) is the sum of a value that multiplies the connection weight by the output of connected neurons i as follows:

$$I_l^{\text{S}} = \sum w_{i,l} \cdot M_i + \sum g_{i,l} \cdot M_i, \qquad (17)$$

where $w_{i,l}$ and $g_{i,l}$ are the connection weights of synaptic connections (one-way) and gap junctions (interactive), respectively ($w_{i,l} \neq w_{l,i}$, and $g_{m,l} = g_{l,m}$).

In this model, I_l^{S} ($l \in \{\text{PVC(L/R)}, \text{AVB(L/R)}\}$) becomes 0 when touch stimuli are given on the posterior part of the body, and is negative on the anterior part. In the same way, I_l^{S} ($l \in \{\text{AVD(L/R)}, \text{AVA(L/R)}\}$) becomes 0 when touch stimuli are given on the anterior part of the body, and is negative on the posterior part. Connection weights included in the model are required to tune in order that
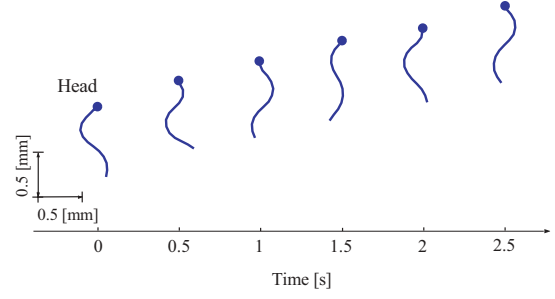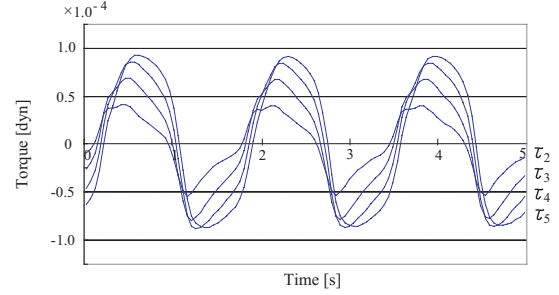
I_l^{S} obtain the above values corresponding to stimulation inputs.

VI. SIMULATION

A. Behavior of the body model

Before integrating the touch-response circuit model described in Section V, the behavior of the body model in Section IV was confirmed. The forward movement of the model for 2.5 [s] is plotted every 0.5 [s] in Fig. 7. Considering the body size of *C. elegans*, the length of each link was set as $l_1 = l_2 = \cdots = l_{12} = 0.08$ [mm] and the weight $m_c = 0.7$ [µg] based on the reference [1]. Also, differential equations included in the model were calculated every 1.0×10^{-3} [s] using the fourth-order Runge-Kutta method [17]. In the figure, ● is the head of *C. elegans*. The figure shows that the waving movement of *C. elegans* can be expressed by the proposed model.

In addition, joint torques τ_2, τ_3, τ_4 and τ_5 in forward movement are shown in Fig. 8. Parameters for τ in Eqs.(12) and (13) were determined after a process of trial and error based on data such as video images of actual *C. elegans*. From Fig. 8, each joint torque has cyclic ups and downs, and is out of phase with adjacent angles by the constant degrees. This enables the model to realize the waving movement as shown in Fig. 7.

B. Integration of the touch-response circuit model and the body model

Connection weights included in the touch-response circuit model must be appropriately set to realize the desired output according to the stimulation. However, it is impossible to measure these values by biological experiments with actual organisms. Therefore, in this paper, a real-coded genetic algorithm (GA) [9],[18] was employed, in which
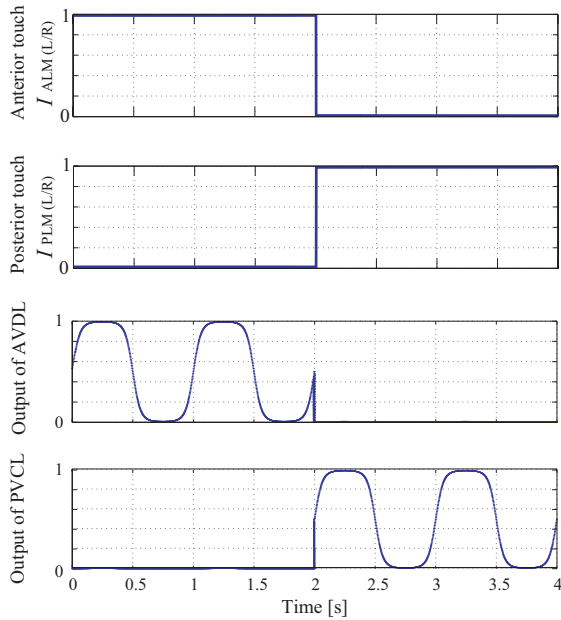
Figure 9. Outputs of interneurons for touch stimulation.

the mechanism of heredity or the evolution of organisms is simulated, in order to adjust connection weights of 47 chemical synaptic connections and 9 gap junctions. The touch-response circuit model was optimized by 3 patterns of touch stimulation inputs, that is, anterior touch, posterior touch and no-touch.

In the simulation, anterior touch stimuli are given for the first 2 [s], and then, posterior touch stimuli for 2 [s]. Figure 8 shows outputs of AVDL and PVCL to motoneurons in which connection weights tuned by the GA. Results of the other interneurons, which are concerned with anterior or posterior touch stimulation, were similar to those of AVDL or PVCL. From Fig. 9, it is confirmed that when anterior touch stimuli are given, posterior sinusoidal inputs such as $I_{\text{PVCL}}^{\text{R}}$ from a posterior wave generator are inhibited and only anterior sinusoidal signals become effective. As the result, *C. elegans* moves backward. Similarly, when posterior touch stimuli are given, anterior sinusoidal inputs such as $I_{\text{AVDL}}^{\text{R}}$ are inhibited and only posterior sinusoidal signals become effective. Motor control in forward and backward movements can be well realized by outputs of touch-response circuit.

VII. CONCLUSIONS

In this paper, we developed a whole body model, *virtual C. elegans*, based on the biological evidence of the actual nematode. *virtual C. elegans* consists of a neuronal circuit model for touch response and a dynamic model of the body for movement. By integrating the two models, motor control based on stimulation information was realized. Since dynamics of *C. elegans* and environments are considered, it became capable of realizing motor control similar to that of the actual nematode on some extent.

Further research will be required to compare the behavior of our model with that of actual *C. elegans* in detail. It is also necessary to adopt actual characteristics based on experimental biological data to the model. Furthermore, if a neuronal circuit can be constructed to model not only the touch-response circuit but also various functional circuits such as those concerned with chemotaxis and direction control, it will be possible to realize a more realistic model that represents complex mechanisms of behavior as responses to various stimuli in external environments.

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