

# A Motor Control Model of the Nematode *C. elegans*

Michiyo Suzuki, Takeshi Goto, and Toshio Tsuji  
Graduate School of Engineering  
Hiroshima University  
Higashi-Hiroshima, JAPAN  
Email: {suzuki / tsuji}@bsys.hiroshima-u.ac.jp

Hisao Ohtake  
Graduate School of Engineering  
Osaka University  
Suita, JAPAN  
Email: hohtake@bio.eng.osaka-u.ac.jp

**Abstract**—This paper focuses on the nematode *C. elegans*, which has a relatively simple structure, and is one of the most analyzed organisms among multicellular ones. We aim to develop a mathematical model of this organism to analyze control mechanisms with respect to locomotion. First, a new motor control model of the *C. elegans* is proposed, which includes both of the neuronal circuit model and the dynamic model of the body. Then, the effectiveness of the proposed model is verified through a series of computer simulations.

**Keywords**—*C. elegans*; motor control; neuronal circuit model; dynamic model; computer simulation

## I. INTRODUCTION

Recently, a new approach for analyzing functional mechanism of a living organism has been proposed, in which computer simulation of a mathematical model is utilized [1], [2]. With the recent development of computer technology, such a computational analysis has been essential to understand the complex mechanisms of organisms [2]. In this analysis using a *virtual* organism instead of the corresponding *actual* one, it is possible to change environmental conditions easily and to analyze their behavior repeatedly under the same conditions. This is not only useful to the study of biology, but also possible to be applied to the area of engineering such as establishment of a new brain-like machine based on the mechanism of living organisms.

The organisms which are relatively easy to be analyzed are called “model organisms” such as colibacilli, *saccharomyces cerevisiae*, nematode and drosophila. In molecular biology, the model organisms have been thoroughly analyzed, and the experimental evidence has been applied to the analysis of higher organisms. In the approach using a *virtual* organism, analysis of ‘simple’ organisms is necessary to understand systems of higher ones. Thereunder, our group has developed computer models of two kinds of unicellular organisms, colibacilli and paramecium, based on the knowledge of both biology and engineering [3], [4].

This paper deals with multicellular organisms as the next step of the above-mentioned approach. Among multicellular organisms, this study focuses on the nematode *Caenorhabditis elegans* (*C. elegans*), whose complete genome sequence, complete cell lineage and connection structure of the neuronal system have been determined [5]–[7]. Since the *C. elegans* is one of the most analyzed organism among multicellular ones, we aim to develop a mathematical model of this organism based on the previous studies at the neuronal level.

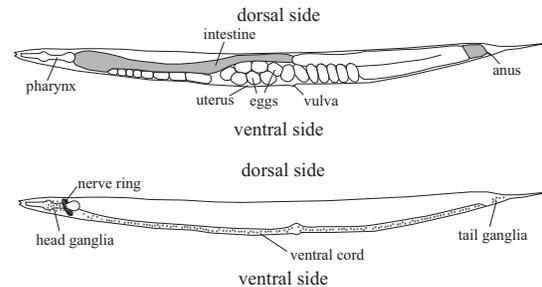


Figure 1. Organization of the *C. elegans* (revised from the figure in [7]).

So far, many studies of the *C. elegans* model have been reported. Ferrée *et al.* [8] simulated a simplified neuronal circuit which processes external information on chemicals. Cangelosi *et al.* [9] and Kawamura *et al.* [10] also developed neuronal circuit models concerned with processing mechanical stimuli. However, since they focused on only sensing and processing external stimuli, the locomotions which are appeared were extremely simplified. In other words, they have not dealt with a series of the processes occurred in the motor control system, in which the motoneurons receive the input from internal processing systems and control the muscles, and so that the *C. elegans* moves. In modeling the *C. elegans*, the motor control system with respect to locomotory responses have to be considered as well as the internal processing system. Consequently, the motor control model of the *C. elegans* should be established, which includes neuronal circuit models of the motoneurons and a dynamic model of the body [11].

This paper is organized as follows: In Section 2, the overview of the *C. elegans* is explained. In Sections 3 and 4, two neuronal circuit models of the motoneurons and a dynamic model of the *C. elegans* body are described in detail. In Section 5, the effectiveness of this model is verified through a series of computer simulations. Also the simulation results are compared with the actual organism. Finally, Section 6 concludes the paper.

## II. *C. elegans*

### A. Structure of the *C. elegans*

The *C. elegans* (the non-parasitic and soil nematode) has a simple cylindrical body whose length is about one millimeter. The body is composed of 959 cells and has fundamental organs such as hypodermis, muscles, alimentary

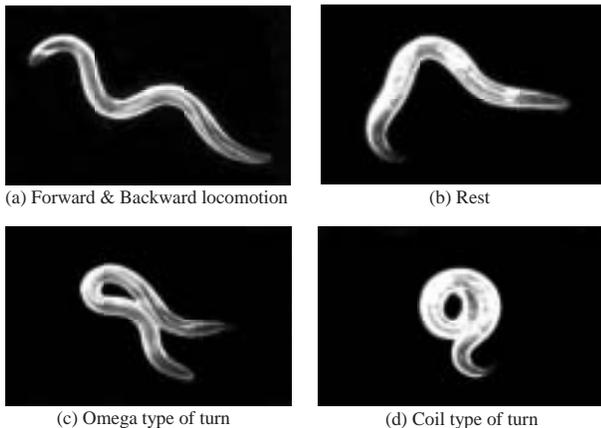


Figure 2. Locomotion patterns of the *C. elegans*.

canal and nervous systems (Fig. 1). The body-wall muscles exist inside the body and the body musculature consists of four quadrants of striated muscles. Each quadrant consists of two closely apposed rows of muscle cells [7]. Sinusoidal locomotion is achieved by the dorso-ventral flexures of these muscles. Also, the pharynx muscles play a role in the behavior (e.g., opening or closing of the mouth, swallowing and manducation).

The nervous system is comprised of 302 neurons, and consists of the head and tail ganglia and the ventral cord which runs down the ventral side longitudinally as shown in Fig. 1. The neuronal circuit processes information from various kinds of stimuli inside and outside the body, and produces locomotion corresponding to each stimulus, for example, avoiding obstacles or repellent chemicals. These neurons are classified into three main groups by the function: sensory neurons, interneurons and motoneurons. The sensory neurons detect external stimuli first, and then the interneurons process information from the stimuli. Finally, the motoneurons control the muscles based on signals from interneurons. These neuronal circuits play an important role for sensing, information processing, and motor control.

Note that the head and tail ganglia consist of the above-mentioned three types of neurons. The head ganglion has similar functions of brains of higher organisms. The ventral cord consists of only motoneurons that innervate the muscles and control some patterns of locomotion. Also, the nerve ring, the center of the nervous system, encompasses the pharynx with the neurites from the ganglion and the ventral cord. The information from the sensory neurons and interneurons is integrated here.

### B. Locomotion of the *C. elegans*

The *C. elegans* sidles sideways and sinuates similar to that of a snake. As shown in Fig. 2, there are 5 patterns of locomotion; the forward and backward locomotion, the rest, the omega type of turn and the coil type of turn. The *C. elegans* chooses the suitable locomotion from these patterns to search for food. Fig. 2 (a) shows the posture at forward or backward locomotion. From the figure, it can be seen that the locomotion is achieved by wriggling the body in sinusoidal waves. The rest posture as shown in Fig. 2 (b) is led by a kink from the tail [12]. The omega type of turn is the distinguished feature in locomotion of

the *C. elegans* worms. As shown in Fig. 2 (c), the body of a *C. elegans* usually executes an “ $\Omega$ ” shape on agar. The coil type of turn, in which the body forms a flat spiral posture [12], shown in Fig. 2 (d) occurs typically in water. The *C. elegans* always goes forward, and the pattern of locomotion is changed spontaneously or by external stimuli. These movements are controlled by the motoneurons in the head ganglion and the ventral cord. In addition, it has been reported that the motoneurons in the ventral cord play an important role in locomotion [13].

In the next section, the neuronal circuit models consisting of the motoneurons in the head ganglia and the ventral cord are constructed to recreate these patterns of locomotion.

### III. NEURONAL CIRCUIT MODELS

The motoneurons in the head ganglion and the ventral cord innervate the ventral and dorsal body-wall muscles of the *C. elegans*. Sinusoidal locomotion is achieved by rhythmical dorso-ventral flexures of these muscles [7]. The neuronal circuits of the motoneurons play significant roles to contract these muscles rhythmically. A neuronal circuit model of the motoneurons in the head ganglion and the ventral cord is explained in this Section.

#### A. Neuronal circuit model of motoneurons in the head ganglion

The sinusoidal locomotion of the *C. elegans* suggests the existence of the neuronal circuits that generate rhythmic signals. However, anatomical positions of these pattern generators have never been identified. In contrast, it seems unlikely that the circuits with respect to the pattern generator exist in the ventral cord, because even the *unc-25* mutants, whose inhibitory neurons in the ventral cord are unable to function, generate rhythmic sinusoidal locomotion albeit with a reduced amplitude [14]. The inhibitory neurons play a role to generate a rhythmic pattern [15]. Therefore, in this paper, it is assumed that the circuits with respect to the pattern generator exist in the head ganglion.

32 motoneurons are found in the head ganglion [7], although their functions are not clear. Since it has been estimated that two motoneurons RME(R/L) in this ganglion act as cross-inhibitors [7], it can be inferred that the circuit consisted of the motoneurons in the head ganglion generates a rhythmic pattern. Therefore, the neuronal circuit is simplified using the pattern generating circuit model consisting of two neurons (Rv, Rd) as shown in Fig. 3. To generate alternating oscillation, the internal states  $V_r$  ( $r \in \{Rv, Rd\}$ ) of the motoneurons are expressed by the following equations based on the CPG model [15]:

$$\left. \begin{aligned} T_r \frac{dV_r}{dt} &= -V_r + \sum_n \omega_{r,n} \cdot V_n^o - \beta_r \cdot V_r^\phi + S_r \\ T_r^\phi \frac{dV_r^\phi}{dt} &= -V_r^\phi + V_r^o \\ V_r^o &= \begin{cases} V_r & (V_r \geq 0) \\ 0 & (V_r < 0) \end{cases} \end{aligned} \right\}, \quad (1)$$

where  $V_r^o$  is the output of the motoneurons  $r$ ;  $V_r^\phi$  is the state of fatigue in the motoneurons;  $\omega_{r,n}$  ( $r, n \in \{Rv, Rd\}; r \neq n$ ) is the connection weight from Rv to Rd

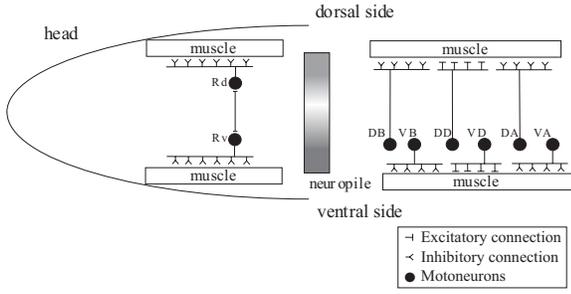


Figure 3. The schematic diagram of the motoneuronal circuit innervating muscles of the *C. elegans*.

(or from Rd to Rv).  $\beta_r$  denotes a fatigue coefficient;  $T_r$  and  $T_r^\phi$  time constants;  $S_r$  a constant input from neurons connecting with Rv or Rd.

The input signal to the ventral body-wall muscle of the head,  $M_1^v$ , and that to the dorsal muscle,  $M_1^d$ , are calculated using the internal states  $V_r$  as follows:

$$M_1^v = W_{1,Rv} \cdot V_{Rv}, \quad (2)$$

$$M_1^d = W_{1,Rd} \cdot V_{Rd}, \quad (3)$$

where  $W_{1,Rv}$  and  $W_{1,Rd}$  are the connection weights from Rv to  $M_1^v$  (or from Rd to  $M_1^d$ ).

### B. Neuronal circuit model of motoneurons in the ventral cord

58 motoneurons in the ventral cord are required for locomotion and divided into six classes, i.e.,

$$VB = \{VB1, VB2, VB3, VB4, VB5, VB6, VB7, VB8, VB9, VB10, VB11\},$$

$$VA = \{VA1, VA2, VA3, VA4, VA5, VA6, VA7, VA8, VA9, VA10, VA11, VA12\},$$

$$DB = \{DB1, DB2, DB3, DB4, DB5, DB6, DB7\},$$

$$DA = \{DA1, DA2, DA3, DA4, DA5, DA6, DA7, DA8, DA9\},$$

$$VD = \{VD1, VD2, VD3, VD4, VD5, VD6, VD7, VD8, VD9, VD10, VD11, VD12, VD13\},$$

$$DD = \{DD1, DD2, DD3, DD4, DD5, DD6\}.$$

VB and DB are used in forward locomotion, and VA and DA in backward locomotion [14]. Also, VB, VA, DB and DA are excitatory motoneurons, while VD and DD are inhibitory motoneurons. Furthermore, VB, VA and VD innervate the ventral body-wall muscles; and DB, DA and DD the dorsal muscles (Fig. 3).

In this paper, the connections between neurons are determined according to [7]. Fig. 4 shows the neuronal circuit map consisting of the interneurons and the motoneurons, where the motoneurons are shown as circles and the interneurons as hexagons. The rhythmic pattern signals generated in the head or tail ganglion are sent to the motoneurons VB and DB from interneuron AVB(R/L) and PVC(R/L), and sent to VA and DA from AVA(R/L) and AVD(R/L) as shown in Fig. 4. The motoneurons fire rhythmically corresponding to the interneurons rhythm. The internal states  $V_a$  of the interneuron  $a$  ( $\in \{AVB(R/L), PVC(R/L), AVA(R/L), AVD(R/L)\}$ ) are assumed by the

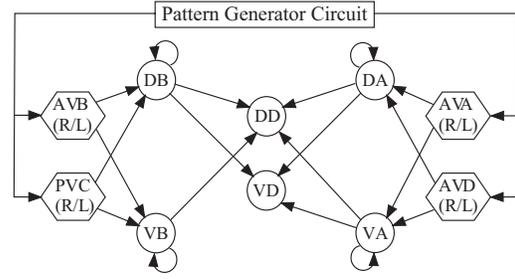


Figure 4. The schematic diagram of the neuronal circuit organized by interneurons and motoneurons.

following equations for simplicity:

$$V_a = \begin{cases} \sin(\xi_a \cdot t + T_a) & \text{(forward locomotion)} \\ 0 & \text{(backward locomotion)} \end{cases} \quad (a \in \{AVB(R/L), PVC(R/L)\}), \quad (4)$$

$$V_a = \begin{cases} 0 & \text{(forward locomotion)} \\ \sin(\xi_a \cdot t + T_a) & \text{(backward locomotion)} \end{cases} \quad (a \in \{AVA(R/L), AVD(R/L)\}), \quad (5)$$

where  $\xi_a$  and  $T_a$  denote the constants.

The internal states  $V_k$  of each motoneuron  $k$  ( $\in \{VB, VA, DB, DA, VD, DD\}$ ) are described by the following equation:

$$T_k \frac{dV_k}{dt} = -V_k + \sum_m w_{k,m} \cdot V_m, \quad (6)$$

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

$$M_i^v = \sum_k W_{i,k}^v \cdot V_k, \quad (7)$$

$$M_i^d = \sum_k W_{i,k}^d \cdot V_k, \quad (8)$$

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

In Section 4, the dynamic model of the *C. elegans* is derived by using the input signals of the body-wall muscles  $M_i^v$  and  $M_i^d$  ( $i = 1, 2, \dots, 12$ ) that are calculated by the neuronal circuit model of the motoneurons as mentioned above.

## IV. DYNAMIC 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 as shown in Fig. 5 (a) on the basis of the [14]. It is assumed that the joint motions are controlled by the signals from the motoneurons,  $M_i^v$  and  $M_i^d$ .

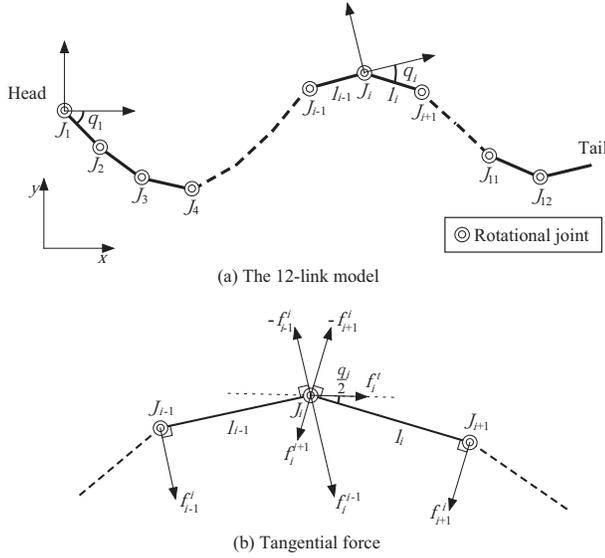


Figure 5. The link model of the *C. elegans*.

### A. Dynamic equation

The motion of the link model can be expressed by the following equation [16]:

$$\mathbf{M}(\mathbf{q})\ddot{\mathbf{q}} + \mathbf{h}(\mathbf{q}, \dot{\mathbf{q}}) + \mathbf{g}(\mathbf{q}) = \boldsymbol{\tau} + \mathbf{F}, \quad (9)$$

where  $\mathbf{M}(\mathbf{q})$  is the inertia matrix,  $\mathbf{h}(\mathbf{q}, \dot{\mathbf{q}})$  the non-linear term including the joint torque due to the centrifugal and Coriolis forces,  $\mathbf{g}(\mathbf{q})$  the joint torque due to the gravity, and  $\mathbf{F} = [F_1^{env}, F_2^{env}, \dots, F_{12}^{env}]^T$  the term of the friction between the body and the floor.  $\mathbf{q} = [q_1, q_2, \dots, q_{12}]^T$  is the vector of the joint rotation angle as shown Fig. 5 (a), and  $\boldsymbol{\tau} = [\tau_1, \tau_2, \dots, \tau_{12}]^T$  the vector of the joint torque. The  $i$ -th torque  $\tau_i$  is expressed by the following equation based on [16] as:

$$\tau_i = \alpha_i(M_i^v - M_i^d) - K_i(M_i^v + M_i^d + \gamma_i)(q_i - \theta_{ei}) - B_i\dot{q}_i \quad (10)$$

where  $K_i$  is the stiffness of the  $i$ -th rotational joint,  $B_i$  the viscosity,  $\alpha_i$  the force generation gain, and  $\gamma_i$  the passive stiffness coefficient.  $\theta_{ei}$  is the equilibrium angle, where  $\theta_{e1}$  corresponds to the desired direction of locomotion.

$F_i^{env}$  is given by the following equation with respect to the viscous friction  $B_i^{env}$ :

$$F_i^{env} = -B_i^{env} \left( \sum_{h=1}^i \dot{q}_h \right). \quad (11)$$

### B. Propulsive force

The *C. elegans* requires a propulsive force to go forward or backward. Thus far the mechanism for generating this force has not yet been revealed. Hence, the motion dynamics of a snake [17] is applied to our model of the *C. elegans*. Also, it assumes that a propulsive force  $F_{head}$  acts on the head in forward locomotion, and  $F_{tail}$  on the tail in backward locomotion. The propulsive forces  $F_n$  ( $n = head, tail$ ) are calculated from the tangential force on body shaft,  $f_i^t$ , which is the resultant force of  $f_i^{i-1}$ ,  $f_i^{i+1} - f_{i-1}^i$  and  $-f_{i+1}^i$  on joint  $J_i$ , where the tangential direction on the body shaft is defined as that of the continuous curve

which divides the joint angle  $q_i$  into two [17]. In addition,  $f_{i-1}^i$  which is generated on the joint  $J_{i-1}$  by the  $i$ -th torque  $\tau_i$  on the joint  $J_i$  is perpendicular to the  $(i-1)$ -th link (Fig. 5 (b)). The tangential force  $f_i^t$  on the joint  $J_i$  is calculated by [17]

$$f_i^t = \{(f_i - f_{i+1}) + (f_{i-1} - f_i)\} \sin \frac{q_i}{2} \quad (12)$$

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

where

$$f_i = \frac{\tau_i}{l_i}. \quad (13)$$

$l_i$  denotes the link length as shown in Fig. 5 (a), and sets  $l_1 = l_2 = \dots = l_{12} = l$  in this paper. Note that  $f_1^t = f_{13}^t = 0$  in (12) when tangential directions on tips of the head and tail denote those of 1st and 12-th links, respectively.

Therefore, the propulsive forces  $F_n$  ( $n = head, tail$ ) can be given by the sum of  $f_i^t$  as:

$$F_n = \begin{cases} -\sum_{i=2}^{12} f_i^t \cos\left\{\left(\sum_{h=2}^{i-1} q_h + \frac{q_i}{2}\right)\right\} \\ \quad (n = head; \text{forward locomotion}) \\ \sum_{i=2}^{12} f_i^t \cos\left(\sum_{h=i+1}^{12} q_h + \frac{q_i}{2}\right) \\ \quad (n = tail; \text{backward locomotion}) \end{cases}. \quad (14)$$

In this model, the propulsive forces  $F_n$  ( $n = head, tail$ ) are converted into the propulsive velocity of the head or the tail  $v_n$  by the following equation:

$$m_c \dot{v}_n + B_c v_n = F_n \quad (n = head, tail), \quad (15)$$

where  $m_c$  is the body weight of a *C. elegans*, and  $B_c$  the friction between a *C. elegans* and the floor.

The dynamic behavior of the virtual model is calculated by using the Appell method [18].

## V. SIMULATION

In order to verify the effectiveness of the proposed model, the *virtual C. elegans*, a series of computer simulations are carried out.

### A. Setting of parameters

Although many parameters included in our model should be adequately determined, there is little biological data that can be applied to these parameters. The main reason for this is the extreme difficulty to measure quantitatively the electrophysiological states of neurons and muscular forces. In this paper, almost of all parameters are determined by trial and error based on the locomotion of the *actual C. elegans*.

Simulations of this model are carried out using the parameters tuned in advance. The differential equations included in this model are calculated every 0.001 [s] by using the fourth-order Runge-Kutta method [19].

## B. Locomotion patterns

In this section, the results of the generated patterns in forward and backward locomotion and the omega type of turn are shown. Note that since we deal with only locomotion on land, the coil type of turn in water was ignored. In addition, the change of locomotion patterns is determined in advance because the information processing system which determines such changes has not been included in this model.

Fig. 6 (a) shows the postures of this model in forward locomotion for 3 [s] at every 0.5 [s], where “□” in the figure expresses the head of the *virtual C. elegans*. It is obvious that this model can reproduce the sinusoidal waves similar to that of the actual organism. The postures in backward locomotion are shown in Fig. 6 (b). In the figure, it can be observed that the proposed model is sinuated from the tail contrary to forward locomotion. However, it moves sideways slightly. Finally, the postures when the *virtual C. elegans* turned  $\pi$  [rad] are shown in Fig. 6 (c), where it has started to turn at 0.5 [s], and formed an “Ω” shape as shown in Fig. 2 (c).

From these results, it can be confirmed that the proposed model in this paper can well recreate the locomotion patterns of the *actual C. elegans*.

## C. Comparison with the actual *C. elegans*

The validity of the *virtual C. elegans* is then demonstrated by comparison of (i) time profiles of the translational velocity of the head and (ii) the joint angular change with those of the *actual C. elegans*. The video images of the *actual C. elegans* in motion has been employed for estimating the head velocity and the angular changes with the aid of the image processing software, Scion Image (Scion Corporation [20]). The velocity of the *actual C. elegans* is calculated from the changes of the head position measured at every six frames per second. The angle of the  $i$ -th rotational joint  $q_i$  ( $i = 2, 3, \dots, 12$ ) is also measured along the following procedure:

- Extract a picture from the video images at every three frames per second.
- Skeletonize the body of a *C. elegans* on the picture using the image processing software.
- Divide the skeletonized line into twelve parts.
- Measure the angles between the adjoined links using the same software.

The head velocities of the *actual* and *virtual C. elegans* are respectively shown in Fig. 7 (a), (b). From Fig. 7 (a), it is obvious that the velocity of the *actual* organism oscillates within 0.2 to 0.6 [mm/s]. Similarly, the velocity of the *virtual C. elegans* varies periodically within this range. However, there are considerable differences between these cycles of the *actual* and *virtual C. elegans*. In this model, a propulsive force has been defined as (14). Although such propulsive force may play a primary role to go forward or backward, other factors may affect it when the body of a *C. elegans* expands and contracts longitudinally like an earthworm. In future research, a propulsive force should be revised.

Next, the time courses of joint angles,  $q_2, q_3, \dots, q_{12}$ , of the *actual* and *virtual C. elegans* are shown in Fig. 8. In

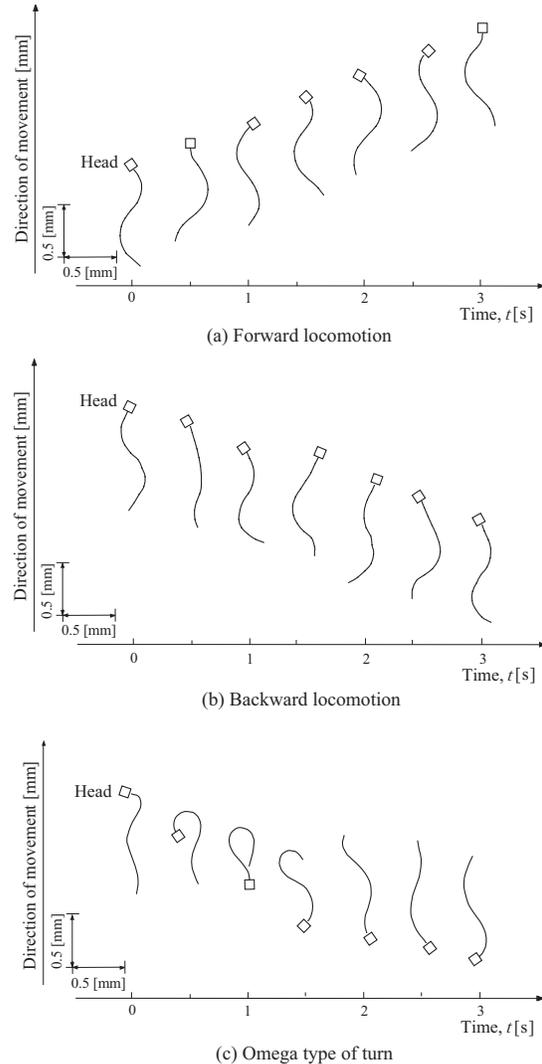


Figure 6. Locomotion patterns of the *virtual C. elegans*.

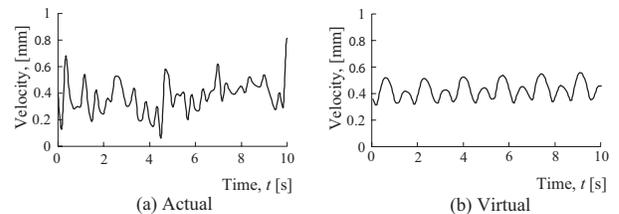


Figure 7. Head velocities of the *actual* and *virtual C. elegans*.

the figure, the dotted and full lines show the angles of the *actual* and *virtual C. elegans*, respectively. From Fig. 8, it is obvious that in the *actual C. elegans* the angles change with a cycle of about two seconds, and these phases shift by bits from the head toward the tail. The phase differences between time profiles of joint angles produce the sinusoidal waves of the *C. elegans*. Then, the amplitudes of angular changes near the tail are smaller than those near the head.

The cycles of the angular change and the phase difference in the *virtual C. elegans* correspond well with those of the *actual C. elegans*, although considerable differences can be observed in some joints such as  $q_2, q_3, q_4$ , and  $q_6$ .

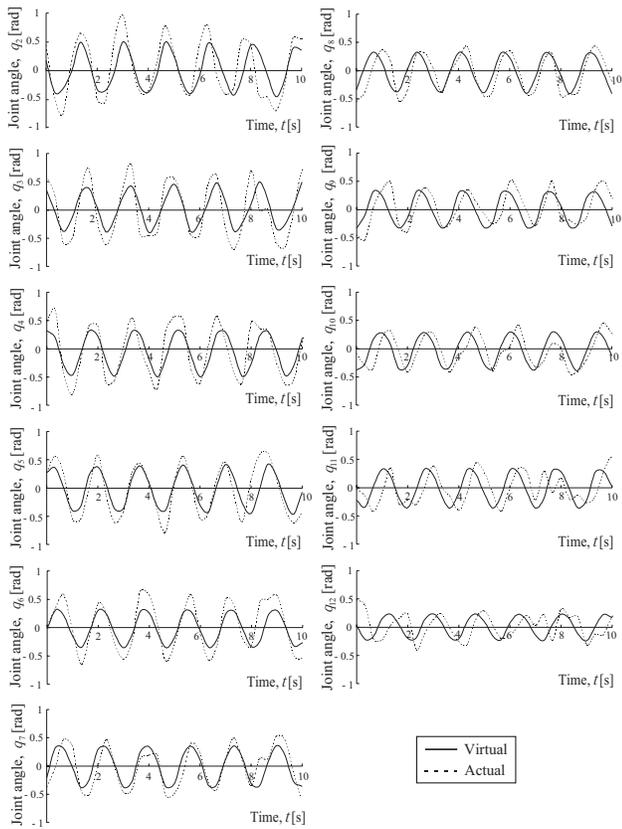


Figure 8. Joint angles of the *actual* and *virtual C. elegans*.

Also, the *virtual C. elegans* can reproduce the actual characteristic that the angular amplitude in the head is larger than in the tail, although the angular amplitudes in the *virtual C. elegans* are smaller than those in the *actual* organism on the whole. If the torque  $\tau_i$  is increased by tuning the parameters included in (10), the amplitudes could become larger. However, the locomotion of this model could not correspond with the *actual* locomotion of a *C. elegans* any longer. It is necessary to analyze effects and sensitivity of each parameter.

## VI. CONCLUSIONS

In this paper, the motor control model of the *C. elegans*, which is the simplest multicellular organism, has been constructed based on the biological evidence of the actual *C. elegans*. This model is composed of two neuronal circuit models of the motoneurons and the dynamic model.

Through the computer simulations, the effectiveness of the proposed model has been clarified as follows:

- The locomotion patterns, such as forward and backward locomotion and the omega type of turn, can be re-created by this model.
- The behavior of the proposed model quantitatively corresponds to that of the actual *C. elegans*.
- The function of the neuronal circuit in the ventral cord is well approximated by this model.

The computer simulation can be an effective approach to investigate the unknown factors in biology. Future research will be directed to reconstruct and revise the motor control model using the latest data on the molecular biology and

electrophysiology. Then, it is hoped that the whole model of the *C. elegans* will be constructed by integrating this motor control model and the conventional sensory-information processing model.

## ACKNOWLEDGMENT

A part of this study was supported by a Grant-in-Aid for Scientific Research (No. 1605189) by the Research Fellowships of the Japan Society for the Promotion of Science for Young Scientists.

## REFERENCES

- [1] H.Ohtake, "Software of Organisms," KYORITSU SUPPAN, 1998 (in Japanese).
- [2] H.Kitano ed., "Development of System Biology -New Biological Approach-," Springer-Verlag Tokyo, 2001 (in Japanese).
- [3] T.Tsuji, K.Hashigami, M.Kaneko and H.Ohtake, "Emerging Chemotaxis of Virtual Bacteria using Genetic Algorithm," T. IEE Japan, Vol.122-C, No.2, pp.201-207, 2002 (in Japanese).
- [4] A.Hirano, T.Tsuji, N.Takiguchi and H.Ohtake, "A Model of Paramecia Accumulate for Attractants," Proc. of the 16th Bioengineering Conference, pp.327-328, 2004 (in Japanese).
- [5] The *C. elegans* Sequencing Consortium, "Genome Sequence of the Nematode *C. elegans*: A Platform for Investigating Biology," Science, Vol.282, pp.2012-2018, 1998.
- [6] J.E.Sulston, E.Schierenberg, J.G.White and J.N.Thomson, "The Embryonic Cell Lineage of the Nematode *Caenorhabditis elegans*," Developmental Biology, Vol.100, pp.64-119, 1983.
- [7] J.G.White, E.Southgate, J.N.Thomson and S.Brenner, "The Structure of The Nervous System of Nematode *Caenorhabditis elegans*," Phil. Trans. Royal Soc. London, series B, Boil. Scien. Vol.314, Issue-1165, pp.1-340, 1986.
- [8] T.C.Ferrée and R.Lockery, "Computational rules for chemotaxis in the nematode *C. elegans*," Journal of Computational Neuroscience, Vol. 6, pp 263-277, 1999.
- [9] A.Cangelosi and D.Parisi, "A neural network model of *Caenorhabditis elegans*: The circuit of touch sensitivity," Neural Processing Letters, Vol. 6, pp. 91-98, 1997.
- [10] Keio University Science and Technology CCEP ed., "A Study of Nerve System of *C. elegans* for Bio-infomation System," Keio University Science and Technology, pp.123-144, 2001 (in Japanese).
- [11] T.Goto, M.Suzuki, T.Tsuji, N.Takiguchi and H.Ohtake, "Locomotion Patterns Generated by a Neural Circuit Model Innervating Muscle of *C. elegans*," Proc. of the 16th Bioengineering Conference, pp.449-450, 2004 (in Japanese).
- [12] N.A.Croll, "Components and patterns in the behaviour of the nematode *Caenorhabditis elegans*," Journal of Zoology, London, Vol.176, pp159-176, 1975.
- [13] Y.Kohara ed., "The Nematode [A Symphony of 1000 Cells]," KYORITSU SYUPPAN, 1997 (in Japanese).
- [14] Donald L.Riddle, Thomas Blumenthal, Barbara J.Meyer, James R.Priess, "*C. elegans* II," Cold Spring Harbor Laboratory Press, 1998.
- [15] K.Matsuoka : "Mechanisms of Frequency and Pattern Control in the Neural Rhythm Generators," Biological Cybernetics, Vol.56, pp.345-353, 1987.
- [16] K.Ito and M.Ito, "Motor Control for Living Organisms and Robots," the Society of Instrumentation and Control Engineers, 1991 (in Japanese).
- [17] S.Hirose, "Biological and Mechanical Engineering -Basis and Application of Flexible Robots-," Kougyou Chosakai Publishing, 1987 (in Japanese).
- [18] V.Potkonjak and M.Vukobratovic, "Two new methods for computer forming of dynamic equation of active mechanisms," Mech Mach Theory, Vol.14, pp.189-200, 1979.
- [19] W.H. Press, S.A. Teukolsky, W.T. Vetterling, B.P. Flannery (K.Tankei, H.Okumura, T.Satoh, M.Kobayashi, trans.) "Numerical Recipes in C:The Art of Scientific Computing," Gijutsu-Hyohron, 1993 (in Japanese) (Original work published in 1993).
- [20] Scion Corporation, <http://www.scioncorp.com/>