2014 5th IEEE RAS & EMBS International Conference on
Biomedical Robotics and Biomechatronics (BioRob)
August 12-15, 2014. São Paulo, Brazil

Hindlimb splitbelt treadmill walking of a rat based on a neuromusculoskeletal model

Soichiro Fujiki[1], Shinya Aoi[1,6], Dai Yanagihara[2,6], Tetsuro Funato[3,6], Nozomi Tomita[4,6], Naomichi Ogihara[5,6], Kei Senda[1], and Kazuo Tsuchiya[1,6]

Abstract— **In this study, we conducted computer simulation of splitbelt treadmill walking by the hindlimbs of a rat based on a neuromusculoskeletal model. We developed the skeletal model based on anatomical data and constructed the nervous system model for locomotion based on the physiological findings of muscle synergy, central pattern generator, and sensory regulation by phase resetting. Our simulation results show that even in asymmetric environment due to the speed discrepancy between the left and right belts of a splitbelt treadmill, the rat model produced stable walking. The sensory regulation model contributed to generation of adaptive splitbelt treadmill walking while inducing the modulation of locomotion parameters, such as relative phase between the legs and duty factors, as observed in splitbelt treadmill walking of humans and animals. This helps understanding of the adaptation mechanism in locomotion through dynamic interactions among the nervous system, the musculoskeletal system, and the environment.**

I. INTRODUCTION

Animals manipulate their complicated and redundant musculoskeletal systems and show highly adaptive walking in diverse environments. To produce adaptive locomotion, interlimb coordination is crucial factor. The splitbelt treadmill has been often used to investigate the mechanism of controlling the interlimb coordination during walking in humans and animals [1], [2], [3], [4], [5], [6], [7]. It has two parallel belts to produce tied configuration (same speed between the belts) and splitbelt configuration (different speeds between the belts) by controlling the belts independently. This artificially creates asymmetric environment for locomotion. It has been reported that two types of adaptations are observed in splitbelt treadmill walking [5]. One is called early adaptation, which is an instant adaptation observed soon after the tied configuration is switched into the splitbelt configuration. The other is called late adaptation, which is gradual adaptation observed after the early adaptation. However, the underlying mechanism of these adaptations remains unclear.

By constructing mathematical models based on physiological findings, the adaptation mechanism in splitbelt treadmill walking has been studied. Ito *et al*. [8] represented four limb motions of a cat by four oscillators and proposed an oscillator network model, which modulates the relative phases among the oscillators depending on the treadmill configuration. Otoda *et al*. [9] modeled human splitbelt treadmill walking using a biped robot on sagittal plane. Although these models show similar adaptive behaviors to humans and animals, their models have limitations to explain the adaptation mechanism during splitbelt treadmill walking. Ito's model did not include body dynamics and Otoda's model is based on a robot, which uses different actuators from biological muscles. To more clearly investigate adaptation mechanism, integrating the nervous system and musculoskeletal system is crucial.

To overcome the limitations, neuromusculoskeletal models for locomotion of humans and animals have been developed, which consist of the nervous system model based on brain and spinal cord and the body mechanical model based on musculoskeletal system [10], [11], [12], [13], [14], [15], [16]. In our previous work [17], we constructed a neuromusculoskeletal model of the hindlimb of a rat, where the musculoskeletal part of the model was based on anatomical data of the rat and the nervous system model was based on the physiological findings of muscle synergy [18], [19], [20], [21], [22], [23], [24], [25], central pattern generator (CPG) [26], [27], [28], and sensory regulation by phase resetting [29], [30], [31], [32], [33], [34]. We confirmed the validity of our model in terms of dynamics by comparing the simulation results with measured kinematics and electromyographic data of actual rats, and investigated the functional roles of the nervous system by focusing on the obstacle avoidance task.

In this study, we conducted dynamic simulation of splitbelt treadmill walking by the hindlimbs of a rat using our neuromusculoskeletal model [17]. When we changed the treadmill configuration from the tied to splitbelt configuration, adaptive locomotor behavior appeared due to the sensory regulation model. This adaptation shows qualitatively similar trend to the early adaptation of humans and animals, which helps understanding of the adaptation mechanism in locomotion through dynamic interactions among the nervous system, the musculoskeletal system, and the environment.

[1]Soichiro Fujiki, Shinya Aoi, Kei Senda, and Kazuo Tsuchiya are with the Department of Aeronautics and Astronautics, Graduate School of Engineering, Kyoto University, Kyoto daigaku-Katsura, Nishikyo-ku, Kyoto 615-8540, Japan. fujiki.soichiro.25s@st.kyoto-u.ac.jp

[2]Dai Yanagihara is with the Department of Life Sciences, Graduate School of Arts and Sciences, The University of Tokyo, 3-8-1 Komaba, Meguro-ku, Tokyo 153-8902, Japan.

[3]Tetsuro Funato is with the Department of Mechanical Engineering and Intelligent Systems, Graduate School of Informatics and Engineering, The University of Electro-Communications, 1-5-1 Choufugaoka, Choufu-shi, Tokyo 182-8585, Japan.

[4]Nozomi Tomita is with the Department of Mathematics, Graduate School of Science, Kyoto University, Kitashirakawa-oiwakecho, Sakyo-ku, Kyoto 606-8502, Japan.

[5]Naomichi Ogihara is with the Department of Mechanical Engineering, Faculty of Science and Technology, Keio University, 3-14-1 Hiyoshi, Kohoku-ku, Yokohama 223-8522, Japan.

[6]Shinya Aoi, Dai Yanagihara, Tetsuro Funato, Nozomi Tomita, Naomichi Ogihara, and Kazuo Tsuchiya are with JST, CREST, 5 Sanbancho , Chiyoda-ku, Tokyo 102-0075, Japan.

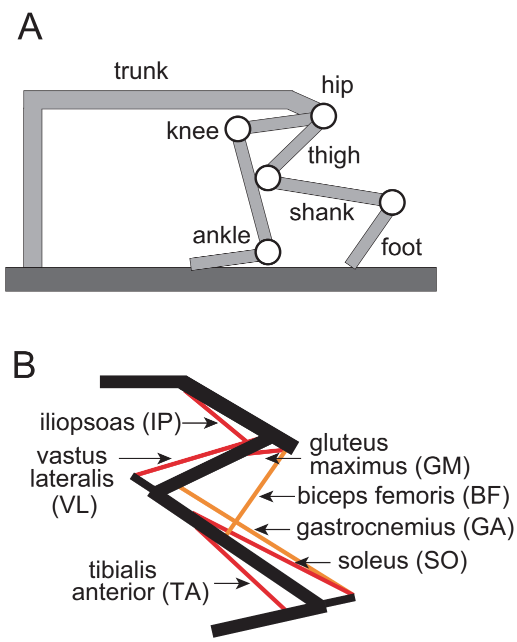

Fig. 1. Musculoskeletal model (**A**: skeletal model, **B**: muscle model)

II. Muscloskeletal model

In this study, we use the musculoskeletal model developed in our previous work. We briefly introduce the model in this section (for detail, see [17]).

A. Skeletal model

Figure 1A shows the skeletal model, which consists of seven rigid links representing the trunk and hindlimbs. It is a two-dimensional model in sagittal plane. The ground reaction force is modeled using viscoelastic elements. Because we focus on locomotion by the hindlimbs, the forelimbs are fixed on the trunk and slide on the ground without friction.

B. Muscle model

The muscle model uses seven principal muscles for each hindlimb (IP, GM, VL, TA, SO, BF, and GA) (Fig. 1B). The mathematical model of the muscle tension is given by

$$F_m = F_m^{\max}(F_m^{\mathrm{l}} F_m^{\mathrm{v}} a_m + F_m^{\mathrm{p}}) \tag{1}$$

where F_m (m = IP, GM, VL, TA, SO, BF, and GA) is the muscle tension, $F_m^{\max}$ is the maximum muscle tension, a_m is the muscle activation ($a_m \geq 0$), F_m^{l} is the force-length relationship, F_m^{v} is the force-velocity relationship, and F_m^{p} is the passive component. The muscle tension forces generate torques acting to each joint. Muscle activation a_m is determined by the motor command u_m from the nervous system model through a low pass filter.

III. Nervous system model

We use the nervous system model (Fig. 2) developed in our previous work [17], where motor commands are determined by the following three components; 1) limb movement control, which produces motor commands in a feedforward fashion at the spinal cord level to create periodic limb movements for forward motion, 2) sensory regulation of locomotion phase and rhythm, which regulates timing to produce the feedforward signals of the limb movement control at the spinal cord level based on sensory signals, and 3) posture control, which creates motor commands in a feedback fashion based on somatosensory information at the brainstem and cerebellar levels to regulate postural behavior. We denote that motor commands generated in the limb movement control by Mov_m and in the posture control by Pos_m, respectively. The motor command u_m to produce muscle activation a_m is given by the summation of these two elements;

$$u_m = Mov_m + Pos_m \tag{2}$$

A. Limb movement control

The limb movement control is modeled based on the physiological findings of the CPG in the spinal cord, which has two layered structure with rhythm generator (RG) and pattern formation (PF) networks [35], [33]. For the RG model, we used two phase oscillators, which generate basic rhythm and phase of locomotion of the corresponding leg. We denote the phase by ϕ_i ($0 \leq \phi_i < 2\pi$, $i = left, right$). The oscillator phase is governed by the following dynamics;

$$\begin{aligned}\dot{\phi}_{left} &= \omega - K_\phi \sin(\phi_{left} - \phi_{right} - \pi)\\ \dot{\phi}_{right} &= \omega - K_\phi \sin(\phi_{right} - \phi_{left} - \pi)\end{aligned} \tag{3}$$

where ω is basic frequency and we used $\omega = 8\pi$. K_ϕ is gain parameter so that the relative phase between the oscillators is antiphase. We used a small value of K_ϕ to allow the relative phase to move from antiphase due to the sensory regulation in Sec. III-B.

Related to muscle synergy, physiological studies suggested that muscle activation patterns during locomotion can be explained by the combination of small number of basic patterns [22], [24]. It is suggested that CPG generates such basic patterns projected to motor neurons through interneurons [24]. For the PF model, we used four rectangular pulses and their bust timings were determined by the oscillator phase from the RG model based on [11] (Fig.3).

$$CPG_i(\phi) = \begin{cases} 1 & \phi_i^{\mathrm{Start}} < \phi \leq \phi_i^{\mathrm{Start}} + \Delta\phi_i \\ 0 & \text{otherwise} \end{cases} \qquad i = 1, \cdots, 4 \tag{4}$$

where $CPG_i(\phi)$ ($i = 1, ..., 4$) is the rectangular pulse, ϕ_i^{Start} is the phase value to start bursting, and $\Delta\phi_i$ is the duration of the rectangular pulse. The motor command Mov_m is given by the summation of these four rectangular pulses with weighting coefficients;

$$Mov_m = \sum_{i=1}^{4} w_{m,i} CPG_i(\phi) \tag{5}$$

where $w_{m,i}$ is the weighting coefficient.

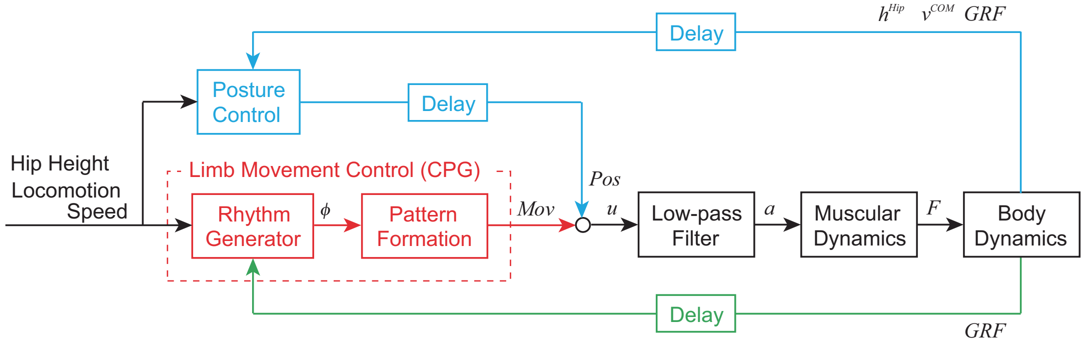

Fig. 2. Nervous system model. Red blocks and arrows show the limb movement control, blue blocks and arrows show posture control and green and arrows show sensory regulation.

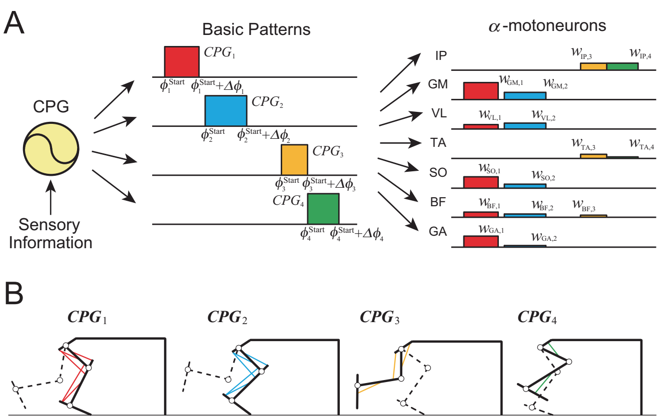

Fig. 3. CPG produces four basic patterns delivered to α-motoneurons and manages their firing timing based on sensory information. **A** shows four rectangular pulses and command signals composed of combination of four rectangular pulses. **B** shows activated muscles by four rectangular pulses.

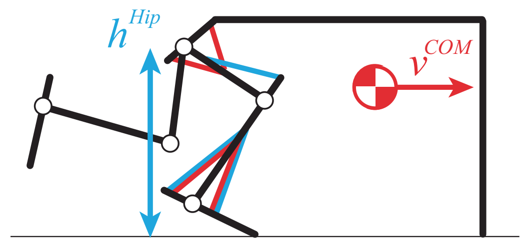

Fig. 4. Posture control based on hip height h^{Hip} and horizontal center of mass velocity v^{COM}.

B. Sensory regulation by phase resetting

Physiological findings suggest that CPG manages the timing to generate the basic patterns based on the kinematic event, such as foot contact [24] and that the RG network in CPG modulates its basic rhythm by producing phase shifts and rhythm resetting based on sensory information (phase resetting) [32], [33]. As cutaneous afferents were observed to contribute to these phase-shift and rhythm resetting behaviors [30], [34], we modeled this by resetting the oscillator phase ϕ_i $(i = left, right)$ based on foot contact event and modified the phase dynamics (3) by

$$\begin{aligned}\dot{\phi}_{left} &= \omega - K_\phi \sin(\phi_{left} - \phi_{right} - \pi) \\ &\quad -(\phi_{left} - \phi^{\text{Contact}})\delta(t - t^{\text{Contact}}_{left} - \tau^{\text{Contact}}) \\ \dot{\phi}_{right} &= \omega - K_\phi \sin(\phi_{right} - \phi_{left} - \pi) \\ &\quad -(\phi_{right} - \phi^{\text{Contact}})\delta(t - t^{\text{Contact}}_{right} - \tau^{\text{Contact}})\end{aligned} \tag{6}$$

where $\delta(\cdot)$ is Dirac's delta function, t_i^{Contact} $(i = left, right)$ is the time when the foot lands on the ground, and ϕ^{Contact} is the phase value to be reset at foot contact. We set the transmission delay τ^{Contact} at 10 ms. Due to this phase resetting based on the foot contact event, the generation timing of the feedforward motor commands of the limb movement control is modulated.

C. Posture control

At the levels of the brainstem and cerebellum, command signals are produced to regulate postural behavior based on somatosensory information. For the locomotor behavior of the rat, it is crucial to maintain the hip height and forward velocity during locomotion. For the postural control of the hip height h^{Hip}, we used a simple feedback control Hgt_m by the muscles VL, TA, and SO of the standing limb to maintain the hip height during locomotion (Fig. 4). For the postural control of the center of mass velocity v^{COM}, we used a simple feedback control COM_m by the muscles IP, GM, TA, and SO of the standing limb (Fig. 4). The motor command by the posture control Pos_m is given by

$$\begin{aligned}Pos_m(t) &= Hgt_m(t - \tau^{\text{Ascend}} - \tau^{\text{Descend}}) \\ &\quad + COM_m(t - \tau^{\text{Ascend}} - \tau^{\text{Descend}})\end{aligned} \tag{7}$$

where τ^{Ascend} and τ^{Descend} represent the ascending and descending delays in transmission of somatosensory information, respectively. We used $\tau^{\text{Ascend}} + \tau^{\text{Descend}} = 15$ ms.

IV. Splitbelt Treadmill Model

To simulate the walking of our model on a splitbelt treadmill, we prepared two belts for the left and right legs to contact and moved the belts independently. We used

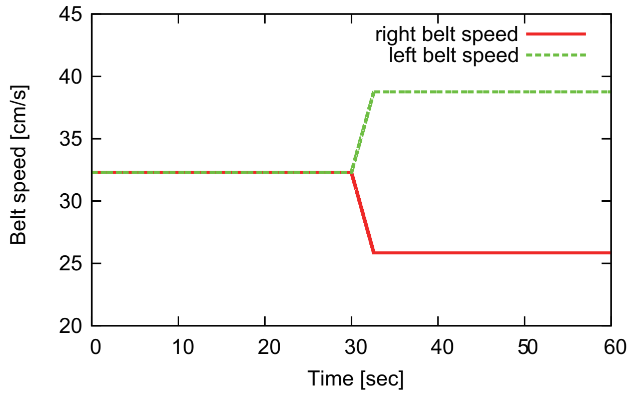

Fig. 5. The speeds of each belt.

viscoelastic elements for modeling the foot contact and reaction forces.

By following [4], [5], we used two types of speed conditions for the splitbelt treadmill: 1. tied configuration with $v_{left} = v_{right} = 32.3$ cm/s and 2. splitbelt configuration with $v_{left} = 38.8$, and $v_{right} = 25.8$ cm/s, where v_{left} is left belt speed and v_{right} is right belt speed. Because our model has bilateral symmetry, we examined only the configuration ($v_{left} \geq v_{right}$). To clearly see the difference of the locomotor behavior between these speed conditions, firstly our model walked on the tied configuration. After our model established steady walking, we changed the speed condition from the tied configuration to splitbelt configuration (Fig. 5).

Some characteristic locomotion parameters change in splitbelt treadmill walking of humans and animals [4], [5]. Based on these observations, we focus on the following five parameters.

1) Stride length, which is the distance from the foot-contact to lift-off positions of one leg.

2) Step length, which is the distance between the foot positions of two legs at the foot contact of one leg.

3) Duty factor, which is the ratio of the stance phase duration relative to one gait cycle duration.

4) Percent of double support duration, which is the ratio of the time duration when both feet are in contact with the belt relative to one gait cycle. (fast/slow double support duration is defined as occurring at the end of the fast/slow limb's stance.)

5) Relative phase between the left and right legs. We used the relative phase between the oscillators.

V. Results

We determined the control parameters so that our model produced stable walking in the tied configuration without depending on the use of phase resetting. When the configuration of the treadmill was switched from the tied to splitbelt configuration, the gait of our model without phase resetting was much disturbed and our model did not establish stable walking. On the other hand, our model with phase resetting recovered soon after being disturbed by the change of the

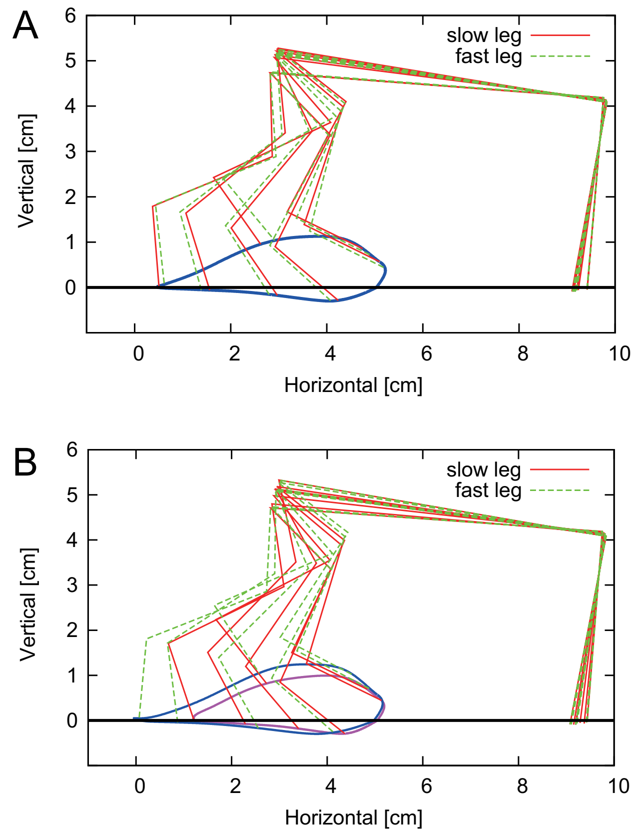

Fig. 6. Stick diagrams during the (A) tied and (B) splitbelt configurations.

splitbelt configuration and continued stable walking. Figure 6A and B show the stick diagrams of legs during the tied and splitbelt configurations.

Figure 7A shows the stride length of each step. During the tied configuration, the values on the fast and slow sides were identical. However, during the splitbelt configuration, they increased on the fast side and decreased on the slow side. This is because moving distances of the feet changed depending on the belt's speed. Figure 7B shows the step length of each step. The values were also identical between the fast and slow sides during the tied configuration. During the splitbelt configuration, they decreased on the fast side and increased on the slow side. It means that, during the splitbelt configuration, the slow side leg contacted the belt when the fast side leg was pulled more backward (this made step length longer) and the fast side leg contacted the belt when the slow side leg was not pulled so much (this made step length shorter).

Figure 8A shows duty factor. The values were identical between the fast and slow sides during the tied configuration. During the splitbelt configuration, they decreased on the fast side and increased on the slow side. This reason is considered as follows: foot-contact timing of the slow side leg became earlier because the horizontal speed of the fast side leg away from the COM position became faster, while foot-contact timing of the fast side leg became later because the horizontal

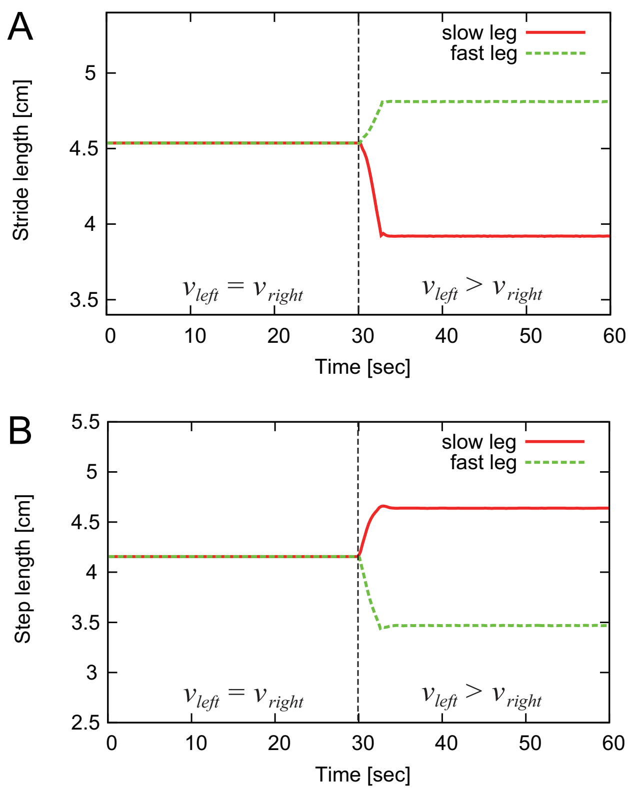

Fig. 7. Simulation results of (**A**) stride length and (**B**) step length. Stride length is the distance from the foot-contact to lift-off positions of one leg. Step length is the distance between the foot positions of two legs at the foot contact of one leg. (fast/slow step length refers to the step length measured at fast/slow leg landing.)

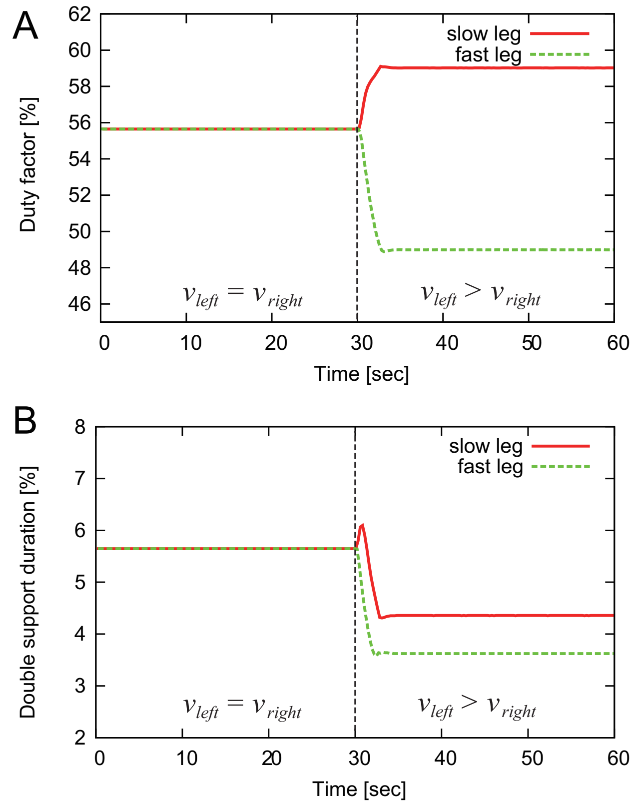

Fig. 8. Simulation results of (**A**) duty factor and (**B**) percent of double support duration. Duty factor is the ratio of the stance phase duration relative to one gait cycle duration. Percent of support duration is the ratio of the time duration when both feet are in contact with the belt relative to one gait cycle. (fast/slow double support duration is defined as occurring at the end of the fast/slow limb's stance.)

speed of the slow side leg away from the COM position became slower. As a result, the stance duration on the fast side became shorter and the stance duration on the slow side became longer. Figure 8B shows the percent of double support duration. During the tide configuration, the values also were identical between the fast and slow sides. During the splitbelt configuration, they decreased on the both side but the value on the fast side was smaller than the slow side. This means that the body weight shifted from the fast to slow side leg quickly while the body weight shifted from the slow to fast side leg slowly.

Figure 9 shows the relative phase between the oscillators. During the tide configuration, the value was π. However, during the splitbelt configuration, it shifted from antiphase. This is caused by the asymmetry of the leg movements between the left and right sides as shown in above adaptations.

Adaptation trends of these five parameters are qualitatively similar to those of early adaptation in human splitbelt treadmill walking [4], [5]. Duty factor and percent of double support duration showed qualitatively similar trends to those of early adaptation in cat splitbelt treadmill walking (there is no data for the other parameters) [8]. In our model, late adaptation was not observed.

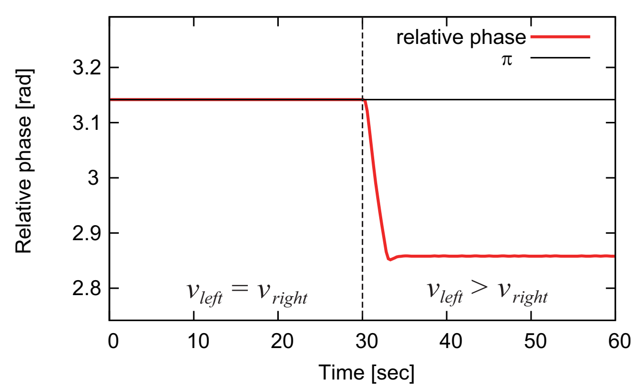

Fig. 9. Simulation result of relative phase between the oscillators.

VI. Conclusion

In this study, we conducted computer simulation of splitbelt treadmill walking by the hindlimbs of a rat based on a neuromusculoskeletal model. When the speed configuration of the treadmill changed from the tied to splitbelt configuration, our model continued stable walking by sensory regulation based on phase resetting and adaptations appear in kinematics and rhythm of locomotion.

In the nervous system model, when we changed the speed configuration of the treadmill, we did not change the control parameters, such as ϕ_i^{Start}, $\Delta\phi_i$, and $w_{m,i}$. The environmental change influenced the body dynamics as shown in the changes of the locomotion parameters and phase resetting contributed to producing stable walking while inducing the changes of foot-contact timing. When we did not use phase resetting, the locomotion parameters were largely disturbed, which caused falling down of our model.

It is suggested that the late adaptation, which was not observed in our model, is caused by cerebellum function [4]. In future works, we should improve our model by including cerebellum model to clarify functional roles of the nervous system in generating adaptive locomotion. In addition, to verify our neuromusculoskeletal model, we should compare the simulation results with the data of rats walking on a splitbelt treadmill. Through such improvement and comparison, the simulation study with a neuromusculoskeletal model will be expected to be a useful tool to investigate the mechanisms in generation of locomotion.

ACKNOWLEDGMENT

This paper is supported in part by a Grant-in-Aid for Scientific Research (B) No. 23360111 from the Ministry of Education, Culture, Sports, Science, and Technology of Japan.

REFERENCES

[1] J.T. Choi and A.J. Bastian, *Adaptation reveals independent control networks for human walking*, Nat. Neurosci., 10(8):1055–1062, 2007.

[2] A. Frigon, MF. Hurteau, Y. Thibaudier, H. Leblond, A. Telonio, and G. D'Angelo, *Split-belt walking alters the relationship between locomotor phases and cycle duration across speeds in intact and chronic spinalized adult cats*, J. Neurosci., 33(19):8559–8566, 2013.

[3] F. Mawase, T. Haizler, S. Bar-Haim, and A. Karniel, *Kinetic adaptation during locomotion on a split-belt treadmill*, J. Neurophysiol., 26(36):9107–9116, 2006.

[4] S.M. Morton and A.J. Bastian, *Cerebellar contributions to locomotor adaptations during splitbelt treadmill walking*, J. Neurosci., 26(36):9107–9116, 2006.

[5] D.S. Reisman, H.J. Block, and A.J. Bastian, *Interlimb coordination during locomotion: What can be adapted and stored?*, J. Neurophysiol., 94:2403–2415, 2005.

[6] D. Yanagihara, M. Udo, I. Kondo, and T. Yoshida, *A new learning paradigm: adaptive changes in interlimb coordination during perturbed locomotion in decerebrate cats*, Neurosci. Res., 18:241–244, 1993.

[7] D. Yanagihara and I. Kondo, *Nitric oxide plays a key role in adaptive control of locomotion in cat*, Proc. Natl. Acad. Sci. USA, 93:13292–13297, 1996.

[8] S. Ito, H. Yuasa, Z. Luo, M. Ito, and D. Yanagihara, *A mathematical model of adaptive behavior in quadruped locomotion*, Biol. Cybern., 78, 337–347, 1998.

[9] Y. Otoda, H. Kimura, and K. Takase, *Construction of a gait adaptation model in human split-belt treadmill walking using a two-dimensional biped robot*, Adv. Robot., 23(5):535–561, 2009.

[10] Ö. Ekeberg and K. Pearson, *Computer simulation of stepping in the hind legs of the cat: An examination of mechanisms regulating the stance-to-swing transition*, J. Neurophysiol., 94:4256–4268, 2005.

[11] S. Jo and SG. Massaquoi, *Amodel of cerebrocerebello-spinomuscular interaction in the sagittal control of human walking*, Biol. Cybern., 96:279–307, 2007.

[12] N. Ogihara and N. Yamazaki, *Generation of human bipedal locomotion by a bio-mimetic neuro-musculo-skeletal model*, Biol. Cybern., 84:1–11, 2001.

[13] G. Taga, Y. Yamaguchi, and H. Shimizu, *Self-organized control of bipedal locomotion by neural oscillators in unpredictable environment*, Biol. Cybern., 65:147–159, 1991.

[14] G. Taga, *A model of the neuro-musculo-skeletal system for human locomotion I. Emergence of basic gait*, Biol. Cybern., 73:97–111, 1995.

[15] S. Yakovenko, V. Gritsenko, and A. Prochazka, *Contribution of stretch reflexes to locomotor control: A modeling study*, Biol. Cybern., 90: 146–155, 2004.

[16] T. Yamasaki, T. Nomura, and S. Sato, *Possible functional roles of phase resetting during walking*, Biol. Cybern., 88:468–496, 2003.

[17] S. Aoi, T. Kondo, N. Hayashi, D. Yanagihara, S. Aoki, H. Yamaura, N. Ogihara, T. Funato, N. Tomita, K. Senda, and K. Tsuchiya, *Contributions of phase resetting and interlimb coordination to the adaptive control of hindlimb obstacle avoidance during locomotion in rats: a simulation study*, Biol. Cybern., 107:201–216, 2013.

[18] A. Danna-dos-Santos, K. Slomka, V.M. Zatsiorsky, and M.L. Latash, *Muscle modes and synergies during voluntary body sway*. Exp. Brain. Res., 179:533–550, 2007.

[19] A. d'Avella, P. Saltiel, and E. Bizzi, *Combinations of muscle synergies in the construction of a natural motor behavior*, Nat. Neurosci., 6:300–308, 2003.

[20] A. d'Avella and E. Bizzi, *Shared and specific muscle synergies in natural motor behaviors*, Proc. Natl. Acad. Sci. USA, 102(8):3076–3081, 2005.

[21] T. Drew, J. Kalaska, and N. Krouchev, *Muscle synergies during locomotion in the cat: a model for motor cortex control* J. Physiol., 586(5):1239–1245, 2008.

[22] Y.P. Ivanenko, R.E. Poppele, and F. Lacquaniti, *Five basic muscle activation patterns account for muscle activity during human locomotion*, J. Physiol., 556:267–282, 2004.

[23] Y.P. Ivanenko, G. Cappellini, N. Dominici, R.E. Poppele, and F. Lacquaniti, *Coordination of locomotion with voluntary movements in humans*, J. Neurosci., 25(31):7238–7253, 2005.

[24] Y.P. Ivanenko, R.E. Poppele, and F. Lacquaniti, *Motor control programs and walking*, Neuroscientist., 12(4):339–348, 2006.

[25] L.H. Ting and J.M. Macpherson, *A limited set of muscle synergies for force control during a postural task*, J. Neurophysiol., 93:609–613, 2005.

[26] S. Grillner, *Locomotion in vertebrates: central mechanisms and reflex interaction*, Physiol. Rev., 55(2):247–304, 1975.

[27] G.N. Orlovsky, T. Deliagina, and S. Grillner, *Neuronal control of locomotion: from mollusc to man*, Oxford University Press, 1999.

[28] M.L. Shik and G.N. Orlovsky, *Neurophysiology of locomotor automatism*, Phsyiol. Rev., 56(3):465–501, 1976.

[29] B.A. Conway, H. Hultborn, and O. Kiehn, *Proprioceptive input resets central locomotor rhythm in the spinal cat*, Exp. Brain. Res., 68:643–656, 1987.

[30] J. Duysens, *Fluctuations in sensitivity to rhythm resetting effects during the cat's step cycle*, Brain. Res., 133(1):190–195, 1977.

[31] P. Guertin, M.J. Angel, M.-C. Perreault, and D.A. McCrea, *Ankle extensor group I afferents excite extensors throughout the hindlimb during fictive locomotion in the cat*, J. Physiol., 487(1):197–209, 1995.

[32] M. Lafreniere-Roula and D.A. McCrea, *Deletions of rhythmic motoneuron activity during fictive locomotion and scratch provide clues to the organization of the mammalian central pattern generator*, J. Neurophysiol., 94:1120–1132, 2005.

[33] I.A. Rybak, N.A. Shevtsova, M. Lafreniere-Roula, and D.A. McCrea, *Modelling spinal circuitry involved in locomotor pattern generation: insights from deletions during fictive locomotion*, J. Physiol., 577(2):617–639, 2006.

[34] E.D. Schomburg, N. Petersen, I. Barajon, and H. Hultborn, *Flexor reflex afferents reset the step cycle during fictive locomotion in the cat*, Exp. Brain Res., 122(3):339–350, 1998.

[35] R.E. Burke, A.M. Degtyarenko, and E.S. Simon, *Patterns of locomotor drive to motoneurons and lastorder interneurons: Clues to the structure of the CPG*, J. Neurophysiol., 86:447–462, 2001.