Sensory regulation of stance-to-swing transition in generation of adaptive human walking: a simulation study

Shinya Aoi[1,5], Naomichi Ogihara[2,5], Tetsuro Funato[3], and Kazuo Tsuchiya[4,5]

[1] *Dept. of Aeronautics and Astronautics, Graduate School of Engineering, Kyoto University, Yoshida-honmachi, Sakyo-ku, Kyoto 606-8501, Japan*
[2] *Dept. of Mechanical Engineering, Faculty of Science and Technology, Keio University, 3-14-1 Hiyoshi, Kohoku-ku, Yokohama 223-8522, Japan*
[3] *Dept. of Mechanical Engineering and Science, Graduate School of Engineering, Kyoto University, Yoshida-honmachi, Sakyo-ku, Kyoto 606-8501, Japan*
[4] *Dept. of Energy and Mechanical Engineering, Faculty of Science and Engineering, Doshisha University, 1-3 Tatara, Miyakodani, Kyotanabe, Kyoto 610-0394, Japan*
[5] *JST, CREST, 5 Sanbancho, Chiyoda-ku, Tokyo 102-0075, Japan*

Abstract

In this paper, we investigated sensory mechanisms to regulate the transition from the stance to swing phases in the generation of adaptive human bipedal walking based on a neuromusculoskeletal model. We examined the contributions of the sensory information from the force-sensitive afferents in the ankle extensor muscle and from the position-sensitive afferents from the hip, inspired by a neuro-mechanical simulation for the stepping of the hind legs of cats. Our simulation results showed that the sensory signals related to the force in the ankle extensor muscle make a larger contribution than sensory signals related to the joint angle at the hip to produce robust walking against disturbances, as observed in the simulation results of cat locomotion. This suggests that such a sensorimotor mechanism is a general property and

is also embedded in the neuro-control system of human bipedal walking.

1. Introduction

Humans and animals produce adaptive walking in diverse environments by cooperatively and skillfully manipulating their complicated and redundant musculoskeletal systems. Many studies have been conducted to elucidate their neuro-control mechanisms. Physiological studies using lampreys and decerebrate cats have greatly contributed to elucidating locomotor mechanisms by examining the configurations and activities of neural systems [13, 25, 29, 34, 37, 41]. However, completely clarifying the mechanisms in terms of the nervous system alone is difficult because locomotion is a well-organized motion generated through dynamic interactions among the body, the nervous system, and the environment. To overcome limitations, simulation studies have recently attracted attention, since physiological and anatomical findings allow us to construct reasonably realistic mathematical models of musculoskeletal and nervous systems and to investigate the neuro-mechanical interactions in locomotor behavior [6, 9, 10, 17, 30, 32, 38, 39, 40, 42, 44].

Elucidating sensorimotor interactions is important to clarify the mechanisms to create adaptive locomotor behavior. During cat locomotion, two types of sensory information are used for the phase transition from stance to swing: force-sensitive afferents in the ankle extensor muscles [8, 43] and position-sensitive afferents from the hip [12, 15]. Ekeberg and Pearson [9] performed computer simulations with a musculoskeletal model of the hind limbs of cats to investigate the roles of such sensory information by preparing four phases for the leg movements: swing, touchdown, stance, and liftoff. They determined the muscle activation patterns depending on the phases and switched them based on the following triggering rules:

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1. from swing to touchdown phase: threshold of hip and knee joint angles

2. from touchdown to stance phase: ground contact information

3. from stance to liftoff phase: unloading rule or hip extension rule

4. from liftoff to swing phase: loss of ground contact information,

where the unloading rule indicates that when the force in the ankle extensor muscle is low, the liftoff phase starts. The hip extension rule means that when the hip joint is sufficiently extended, the liftoff phase commences. They examined these two rules to regulate the transition from the stance to liftoff phases and showed that stable locomotion was not established when the hip extension rule was used alone. They demonstrated that the unloading rule makes a larger contribution than the hip extension rule to the generation of robust locomotor behavior against disturbances, which gives a great insight for sensorimotor integration to produce adaptive locomotor behavior for animals.

In our previous work [1], we constructed a neuromusculoskeletal model for human bipedal walking and examined the roles of the phase transitions based on foot-contact information, similar to the transitions from the touchdown to stance phases and from the liftoff to swing phases in [9]. In this paper, we modified our neuromusculoskeletal model, especially the phase transition rule, and investigated the contributions of the sensory information from the force-sensitive afferents in the ankle extensor muscles and from the position-sensitive afferents from the hip for the stance-to-swing transition to create adaptive human bipedal walking. That is, we examined the roles of the unloading and hip extension rules for human bipedal walking. Our simulation results showed that the unloading rule contributes more than the hip exten-

sion rule to produce robust bipedal walking against disturbances, as observed in [9], suggesting that such a sensorimotor mechanism is a general property and is also embedded in the neuro-control system of human bipedal walking.
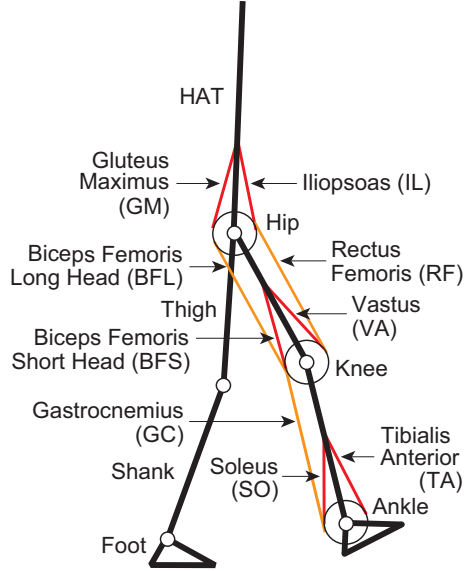
Figure 1: Musculoskeletal model [1, 2]. The skeletal model is composed of seven rigid links that represent HAT (head, arms, and trunk), thighs, shanks, and feet and the muscle model for one leg is composed of nine principal muscles; six muscles (IL, GM, VA, BFS, TA, and SO) are uniarticular, and three (RF, BFL, and GC) are biarticular.

2. Model

2.1. Musculoskeletal model

We used the musculoskeletal model in [1, 2], originally constructed in [28] (Fig. 1). For the skeletal model, we used seven rigid links that represent the HAT (head, arms, and trunk), thighs, shanks, and feet. For the muscle model, we used nine principal muscles for each leg; six muscles (IL, GM, VA, BFS, TA, and SO) are uniarticular, and three (RF, BFL, and GC) are biarticular.

A muscle receives command signals from its corresponding α-motoneuron and generates muscle tension depending on the force-length and force-velocity

relationships. We modeled muscle tension F_m (m = IL, GM, VA, BFS, TA, SO, RF, BFL, and GC) based on a contractile element, and passive elastic and damping elements parallel to the contractile element [1, 2]. Muscle activation for the contractile element is given by a low-pass filter for the output from the α-motoneuron determined in the nervous system model.

2.2. Nervous system model

We used the nervous system model for human bipedal walking constructed in our previous work [1] (Fig. 2) and modified the phase transition rule based on phase resetting to investigate sensory mechanisms to regulate the transition from the stance to swing phases. In our model, the output from α-motoneuron consists of the following three components: 1) movement control, 2) phase resetting, and 3) posture control. The movement control produces periodic signals in a feedforward fashion at the spinal cord level to create periodic limb movements for forward motion. The phase resetting regulates the timing to produce the feedforward signals of the movement controller at the spinal cord level based on sensory signals. The posture control creates command signals in a feedback fashion based on somatosensory information at the brainstem and cerebellar levels to regulate postural behavior. The output from α-motoneuron u_m is given by

$$u_m = Mov_m + Pos_m \qquad (1)$$

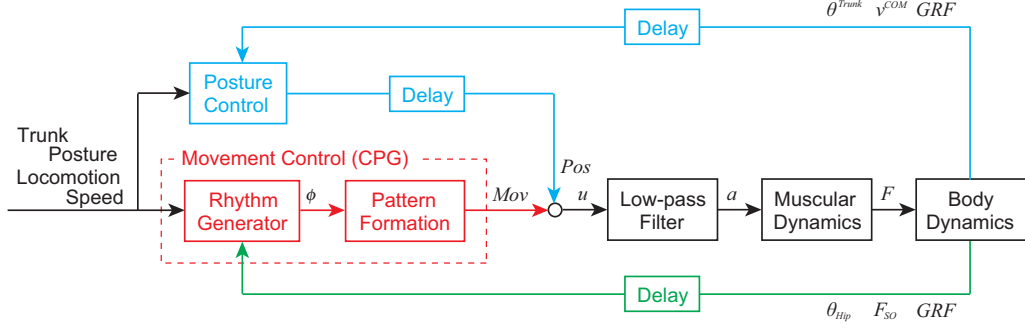where Mov_m and Pos_m are the outputs of the movement and posture controls, respectively.

Figure 2: Nervous system model. Red blocks and arrows indicate movement control, blue blocks and arrows indicate posture control, and green blocks and arrows indicate phase resetting.

2.2.1. Movement control

Physiological studies suggest that central pattern generators (CPGs) in the spinal cord strongly contribute to rhythmic limb movements, such as locomotion [13, 29, 37]. Their organization remains unclear, and various CPG models have been proposed [14, 24]. However, recent neurophysiological findings suggest that CPGs consist of hierarchical networks composed of rhythm generator (RG) and pattern formation (PF) networks [5, 23, 35, 36]. The RG network generates the basic rhythm and alters it by producing phase shift and rhythm resetting based on sensory afferents and perturbations (phase resetting). The PF network shapes the rhythm into spatiotemporal patterns of the activation of the motoneurons through interneurons. CPGs separately control the locomotor rhythm and the pattern of the motoneuron activation in the RG and PF networks, respectively.

We constructed a locomotor CPG model based on a two-layered hierarchical network model. For the RG model, we employed two phase oscillators

that follow the dynamics

$$\dot{\phi}_{left} = \omega - K_\phi \sin(\phi_{left} - \phi_{right} - \pi)$$
$$\dot{\phi}_{right} = \omega - K_\phi \sin(\phi_{right} - \phi_{left} - \pi) \qquad (2)$$

where ϕ_i $(i = left, right)$ is the oscillator phase for the corresponding leg $(0 \le \phi_i \le 2\pi)$, ω is the basic frequency, and K_ϕ is the gain parameter.

From analysis regarding muscle synergy, Ivanenko *et al.* [18, 19] showed that although the electromyographic data recorded during human bipedal walking are complex, they can be accounted for by a combination of only five basic patterns. They suggested that CPGs produce the basic patterns and manage the timing based on sensory information. The basic patterns are delivered to the α-motoneurons through interneurons, and the α-motoneurons receive combinations of the basic patterns. Based on this suggestion, we used five rectangular pulses $CPG_i(\phi)$ $(i = 1, \ldots, 5)$ for the basic patterns for the PF model inspired by [20, 21], whose timing of the initiation of bursting and duration depend on oscillator phase ϕ from the RG model (Fig. 3**A**)

$$CPG_i(\phi) = \begin{cases} 1 & \phi_i^{Start} \le \phi < \phi_i^{Start} + \Delta\phi_i \\ 0 & \text{otherwise} \end{cases} \quad i = 1, \ldots, 5 \qquad (3)$$

where ϕ_i^{Start} is the phase value when the rectangular pulse starts to burst and $\Delta\phi_i$ is the duration of the rectangular pulse. These five pulses are delivered to the α-motoneurons, and the output of movement control Mov_m is given by

$$Mov_m = \sum_{i=1}^{5} w_{mi} CPG_i(\phi) \qquad (4)$$

where w_{mi} is the weighting coefficient $(w_{mi} \ge 0)$. As shown in Fig. 3**B**, $CPG_3(\phi)$ contributes to the liftoff of the stance leg to start the swing phase.
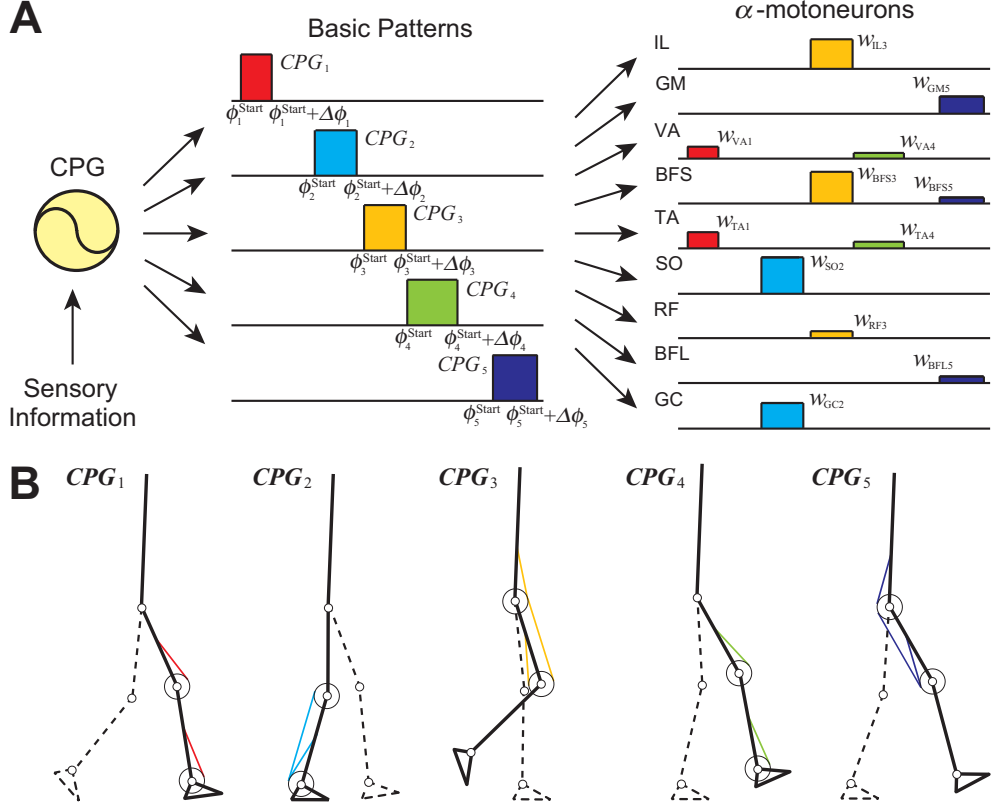
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Figure 3: CPG produces five basic patterns delivered to α-motoneurons and manages timing of firing based on sensory information. **A** shows five rectangular pulses and command signals of movement controller composed of combination of five rectangular pulses. **B** shows activated muscles by five rectangular pulses.

2.2.2. Phase resetting to regulate the stance-to-swing transition

Physiological findings suggest that CPGs manage the timing of firing of the basic patterns [19]. In addition, the RG network in CPGs probably modulates its basic rhythm by producing phase shifts and rhythm resetting based on sensory information (phase resetting) [23, 35].

In this paper, we investigated the roles of the unloading and hip extension rules to regulate the transition from the stance to swing phases in the

generation of adaptive bipedal walking. For that purpose, we reset oscillator phase ϕ to start firing basic pattern $CPG_3(\phi)$ based on these rules. For the unloading rule, we used the muscle tension of ankle extensor muscle F_{SO} and reset oscillator phase ϕ when $F_{SO} < F_{SO}^*$. For the hip extension rule, we used hip joint angle θ_{Hip} and reset oscillator phase ϕ when $\theta_{Hip} < \theta_{Hip}^*$. To incorporate phase resetting, we modified oscillator phase dynamics (2) by

$$
\begin{aligned}
\dot{\phi}_{left} &= \omega - K_\phi \sin(\phi_{left} - \phi_{right} - \pi) - (\phi_{left} - \phi^{Lift})\delta(t - t_{left}^{Lift} - \tau^{Delay}) \\
\dot{\phi}_{right} &= \omega - K_\phi \sin(\phi_{right} - \phi_{left} - \pi) - (\phi_{right} - \phi^{Lift})\delta(t - t_{right}^{Lift} - \tau^{Delay})
\end{aligned}
$$

$$(5)$$

where $\delta(\cdot)$ is Dirac's delta function and t_i^{Lift} $(i = left, right)$ and ϕ^{Lift} are the time and phase values to be reset when the condition for the rule is satisfied. This phase resetting depends on the sensory information of the force of the ankle extensor muscle for the unloading rule and the hip joint angle for the hip extension rule. To incorporate the delay in the spinal cord that receives the sensory information, we set the transmission delay τ^{Delay} to 30 ms.

2.2.3. Posture control

For posture control to regulate postural behavior at the brainstem and cerebellar levels, we focused on two factors to maintain a vertical trunk pitch and move the center of mass forward at the desired velocity [1].

For the trunk pitch, we determined the command Tru_m using muscles IL and GM of the standing leg by

$$
Tru_m = \begin{cases} -K_m^{Trunk}(\theta^{Trunk} - \hat{\theta}^{Trunk}) - D_m^{Trunk}\dot{\theta}^{Trunk} & \text{when } GRF > 0 \\ 0 & \text{otherwise} \end{cases} \tag{6}
$$

where θ^{Trunk} and $\dot{\theta}^{Trunk}$ are the trunk pitch angle and angular rate, $\hat{\theta}^{Trunk}$ is the reference angle, K_m^{Trunk} and D_m^{Trunk} are the gain parameters ($K_m^{Trunk} = D_m^{Trunk} = 0$ when $m \neq$ IL or GM), and GRF is the vertical ground reaction force.

For the COM velocity, we determined the command COM_m using muscles TA and SO of the standing leg by

$$COM_m = \begin{cases} -K_m^{\text{COM}}(v^{\text{COM}} - \hat{v}^{\text{COM}}) & \text{when } GRF > 0 \\ 0 & \text{otherwise} \end{cases} \quad (7)$$

where v^{COM} is the COM velocity, $\hat{v}^{\text{COM}}$ is its desired value, and K_m^{COM} is the gain parameter ($K_m^{\text{COM}} = 0$ when $m \neq$ TA or SO).

By incorporating the transmission delay, we determined the output of the posture control Pos_m by

$$Pos_m(t) = Tru_m(t - \tau^{Somato} - \tau^{Descend}) + COM_m(t - \tau^{Somato} - \tau^{Descend}) \quad (8)$$

where τ^{Somato} and $\tau^{Descend}$ are the delays in receiving transmission of somatosensory information at the brainstem and cerebellar levels and sending the command signal to the spinal cord level, respectively.

3. Results

3.1. Generation of steady walking

We conducted a numerical simulation based on our neuromusculoskeletal model. To fairly compare the contributions of the unloading and hip extension rules, we determined parameters F_{SO}^*, θ_{Hip}^*, and ϕ^{Lift} for phase resetting to establish identical steady walking both with and without phase resetting, similar to [1], as follows: $F_{SO}^* = 1.97 \times 10^3$ N, $\theta_{Hip}^* = -0.207$ rad, and $\phi^{Lift} = 2.53$ rad, which allows us to clearly investigate the difference only of the response to the perturbations. We used the same value for the other parameters of the nervous system model as our previous work [1]. Figure 4 shows the simulation results. **A** shows the joint angles, where HC and TO indicate heel contact and toe off, respectively. For the hip extension rule, when the hip joint extends to be $\theta_{Hip} < \theta_{Hip}^*$ before the end of the stance phase, the oscillator phase is reset to regulate the transition from the stance to swing phases. **B** illustrates simulated walking behavior with a stick diagram and a display interval of 0.1 s. **C** shows the muscle tensions and the command signals of the movement controller (MC) composed of a combination of five rectangular pulses. For the unloading rule, when the muscle tension of the ankle extensor muscle F_{SO} is less than F_{SO}^* before the end of the stance phase, the oscillator phase is reset.

3.2. Roles of unloading and hip extension rules in tolerance of perturbing forces

To investigate the roles of the unloading and hip extension rules, we examined adaptability to the perturbing forces by comparing three cases: without
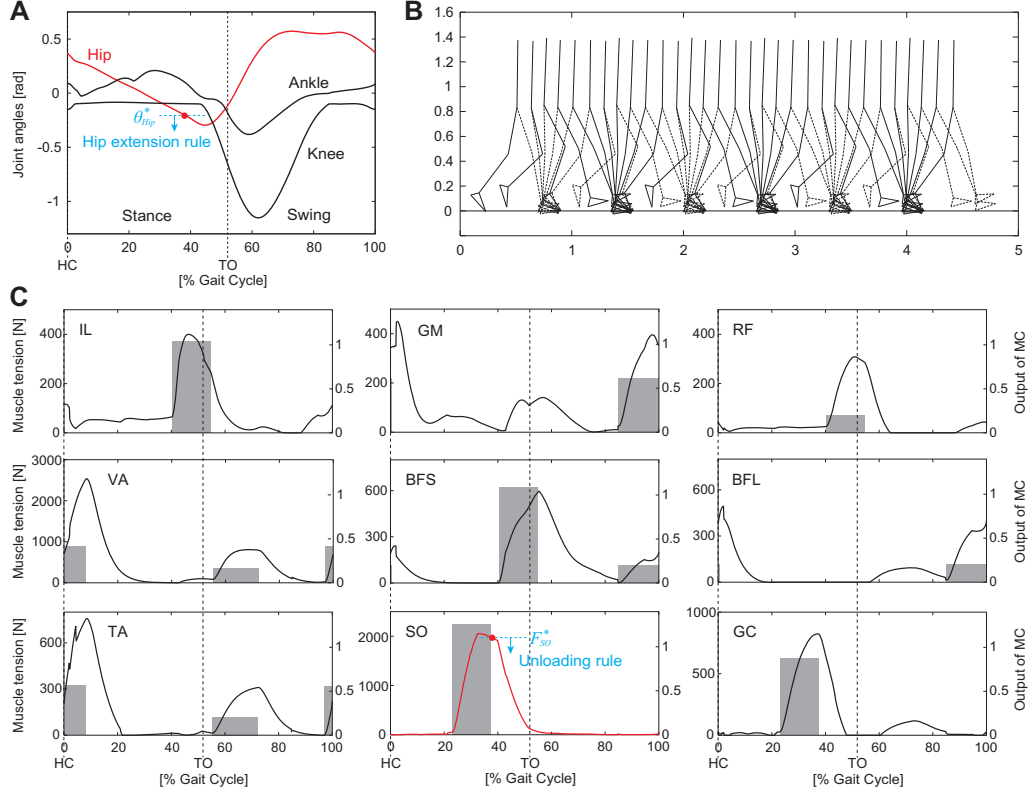
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Figure 4: Simulation results of steady walking. **A**: joint angles, **B**: stick diagram, and **C**: muscle tensions (lines) and command signals of movement controller (MC) (gray blocks). HC and TO indicate heel contact and toe off. θ^*_{Hip} and F^*_{SO} are thresholds for hip extension and unloading rules, respectively.

phase resetting, phase resetting based on the hip extension rule, and phase resetting based on the unloading rule. Specifically, after the walking model established steady walking, we added a perturbing force for 100 ms to the center of the mass of HAT in the horizontal direction (forward or backward) and used various magnitudes and timings of perturbation to thoroughly examine the robustness of the responses.

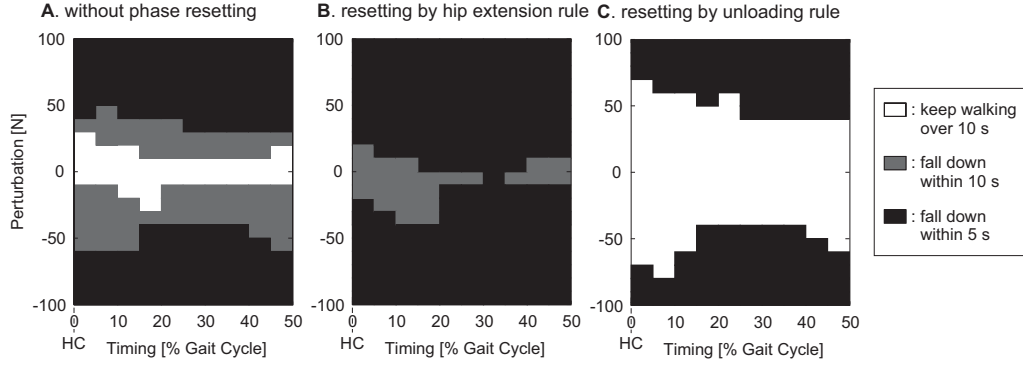Figure 5 shows the simulation results, where white boxes indicate that

Figure 5: Tolerance of perturbing forces. **A** shows results without phase resetting, **B** shows phase resetting based on hip extension rule, and **C** shows phase resetting based on unloading rule.

the walking model continued walking over 10 s after being disturbed, gray boxes indicate that it fell down within 10 s after being disturbed, and black boxes indicate that it fell down within 5 s after being disturbed. When we used phase resetting based on the hip extension rule, the model easily fell down compared to the results without it. On the other hand, when we used phase resetting based on the unloading rule, the model kept walking longer, indicating that the unloading rule increased the robustness of the responses.

4. Discussion

In this paper, we investigated the sensory mechanisms to regulate the transition from the stance to swing phases in the generation of adaptive human bipedal walking by modifying the phase resetting model in our previous neuromusculoskeletal model [1]. In particular, we examined the contributions of the unloading and hip extension rules, inspired by neuro-mechanical simulations for stepping in the hind legs of cats by Ekeberg and Pearson [9]. They prepared muscle activation patterns for four phases (swing, touchdown, stance, and liftoff) related to limb movements and switched the phases based on triggering rules. We prepared five basic patterns for muscle activations inspired by the analysis of muscle synergy [18, 19] and controlled the timing to start bursting of the basic pattern based on the unloading or the hip extension rule. Our simulation results showed that the unloading rule makes a larger contribution than the hip extension rule to produce robust walking against disturbances (Fig. 5), as observed in [9].

In the steady walking, the basic pattern of the movement controller related to the liftoff of the stance leg (CPG_3) starts bursting before the force of the ankle extensor muscle becomes low (Fig. 4), which caused us to use a relatively high value for threshold F_{SO}^* of the unloading rule and to reset the oscillator phase just after the force of the ankle extensor muscle starts to decrease. In addition, different from [9], our model has an intrinsic rhythm by using a CPG model and uses the coupling between the phase oscillators in (5) that helps produce stable alternating leg movements [1]. Of course, there are also differences in the musculoskeletal systems of cats and humans, but our simulation results showed that the unloading rule increases the robust-

ness of the responses more than the hip extension rule, as observed in [9], which suggests that such sensory mechanism is a general property for producing locomotor behavior and is also embedded in the neuro-control system of human bipedal walking.

Humans and animals integrate various sensory information and create motor commands. To produce adaptive and efficient movements, the kind of sensory information they use and when and how they use it is crucial. Modulating the timing to produce motor commands based on sensory information during locomotion allows both humans and animals to regulate the locomotor rhythm and movements depending on the situations. However, different sensory information causes different dynamic characteristics in locomotor behavior, as investigated in this paper and [9]. Humans and animals must use adequate sensory information at proper timing. Computer simulation seems a useful tool to examine sensorimotor integration mechanisms during locomotion.

Many studies have elucidated the adaptation mechanisms in humans and animals. Physiological studies have investigated the configurations and activities of neural networks that contribute to locomotor behavior, revealing the important roles in controlling movements in nervous systems [13, 25, 29, 34, 37, 41]. However, there are limitations to fully elucidate the mechanisms from nervous systems alone, since locomotion is a well-organized motion produced through dynamic interactions among the body, the nervous system, and the environment. To surmount limitations, various approaches have been conducted. One approach is a simulation study to investigate neuromechanical interactions by constructing neuromusculoskeletal models based

on physiological and anatomical findings, as performed in this paper. Another is a robotic study to demonstrate real-world dynamic characteristics by constructing legged robots and their control systems based on physiological findings [7, 11, 16, 22, 27, 31, 33]. Although many sophisticated robots have recently been developed, a clear design principle has not been established to create adaptive locomotor behavior, as in humans and animals. When the functional roles in the neuro-control mechanisms are clarified from the simulation studies, those findings can be applied to improve the control systems of robots. Actually, the phase resetting mechanism in this paper has been used for robot controllers to produce adaptive walking [3, 4, 26, 27]. Constructive approaches using computer simulations and robots are expected to improve the understanding of the neuro-control mechanisms in humans and animals.

Acknowledgements

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