Chapter 8
Neuromusculoskeletal Modeling for the Adaptive Control of Posture During Locomotion

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Abstract People and animals produce adaptive locomotion in diverse environments by cooperatively and skillfully manipulating their complicated and redundant musculoskeletal systems. To establish such locomotion, the control of leg movement to transport the entire body against gravity and the control of posture to prevent falling are required. However, these controls affect one another for the posture of the body during locomotion because leg movement disturbs the posture. The underlying mechanism for stabilizing posture during locomotion remains unclear. In this chapter, simulation studies are presented to investigate the functional roles of the nervous system to maintain the posture of the body during locomotion by focusing on the adaptive walking of humans during disturbances and on obstacle avoidance during walking by the hind legs of rats. Neuromusculoskeletal models for humans and rats were constructed by integrating the musculoskeletal model using anatomical data and the nervous system model based on physiological findings. The leg movement control was modeled based on the physiological concepts of central pattern generators and muscle synergy and on sensory regulation by phase resetting and interlimb coordination. The posture control was also modeled to regulate the postural behavior using somatosensory information. We also examine how these controls contribute to stabilizing posture during locomotion.

Keywords Neuromusculoskeletal model · Human · Rat · Locomotion · Obstacle avoidance · Posture · Central pattern generator (CPG) · Muscle synergy · Phase resetting · Interlimb coordination

8.1 Introduction

People and animals produce adaptive locomotion in diverse environments by cooperatively and skillfully manipulating their complicated and redundant musculoskeletal systems. To put it simply, locomotion involves moving the entire body against

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B. I. Prilutsky, D. H. Edwards (eds.), *Neuromechanical Modeling of Posture and Locomotion,* Springer Series in Computational Neuroscience,
DOI 10.1007/978-1-4939-3267-2_8

gravitational force by using the legs. To establish locomotion, leg movement needs to be controlled to transport the entire body and posture needs to be controlled to prevent falling during locomotion. However, although posture is maintained via the posture control, the movement of the legs disturbs the posture. In other words, the controls of posture and movement affect one another during locomotion, making the adequate balancing of these controls very important. The underlying mechanism for stabilizing posture during locomotion remains unclear.

So far, the abilities of humans and other animals to generate adaptive movements have been investigated by examining the structure and activities of neural systems. For example, physiological studies on lampreys and cats have greatly contributed to the elucidation of locomotor mechanisms (Grillner 1975; Shik and Orlovsky 1976; Orlovsky et al. 1999). However, locomotion is a well-organized motion generated through dynamic interactions among the nervous system, the musculoskeletal system, and the environment. It is difficult to fully analyze locomotor mechanisms solely in terms of the nervous system. In addition to understanding the nervous system, it is crucial to elucidate the dynamic characteristics inherent in the musculoskeletal system. Integrative studies of the nervous and musculoskeletal systems are required to clarify locomotor mechanisms. Physiological and anatomical findings now enable the construction of reasonably realistic models of the nervous and musculoskeletal systems. Thus, to overcome the limitations of behavioral studies based only on the nervous system, simulation studies have recently investigated specific functional roles of the nervous system in locomotor behavior (Taga et al. 1991; Ogihara and Yamazaki 2001; Ivashko et al. 2003; Yamasaki et al. 2003; Yakovenko et al. 2004; Ekeberg and Pearson 2005; Pearson et al. 2006; Jo and Massaquoi 2007; Prochazka and Yakovenko 2007; Jo 2008; Nomura et al. 2009; Markin et al. 2010).

In an actual travel path, obstacles that must be stepped over to continue locomotion are often encountered. Stepping over obstacles to avoid tripping is an essential movement for safe, smooth locomotion. Such obstacle avoidance is a skillful, intentional movement, whereby humans and other animals must recognize the dimensions of an obstacle, and determine how to control their legs to avoid colliding with it while maintaining their posture. This task requires a highly coordinated control of the leg movements and posture, which highlights the relationship between movement and postural controls.

In this chapter, the functional roles of the nervous system in maintaining posture during locomotion are investigated by focusing on the adaptive walking of humans during applications of perturbing forces and sudden environmental variations (Aoi et al. 2010, 2012) and on obstacle avoidance by the hind legs of rats during walking (Aoi et al. 2013). Neuromusculoskeletal models for humans and rats were constructed by integrating the anatomically realistic musculoskeletal model and the physiologically based nervous system model. The leg movement control was modeled based on the physiological concepts of central pattern generators (CPGs) and muscle synergy and on sensory regulation by phase resetting and interlimb coordination. The posture control was modeled to regulate the postural behavior using

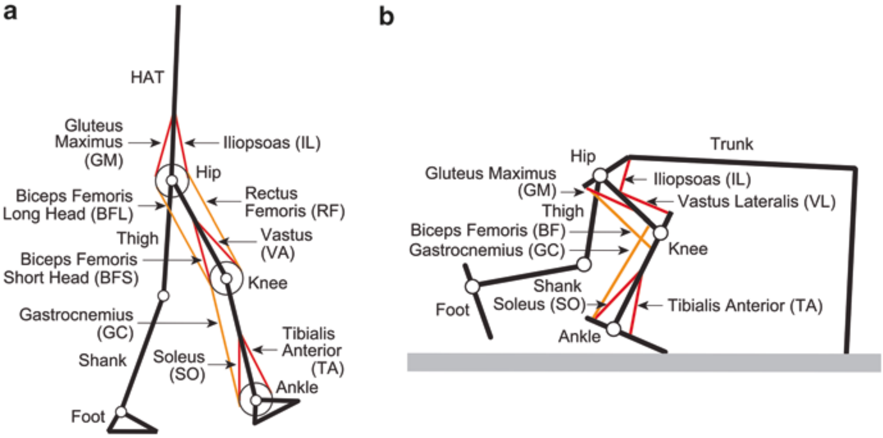

Fig. 8.1 Musculoskeletal models for humans (**a**) and rats (**b**)

somatosensory information. We have examined how these controls contribute to stabilizing posture during locomotion.

8.2 Neuromusculoskeletal Model

8.2.1 Musculoskeletal Model

Figure 8.1a and b show the musculoskeletal models for humans and rats, respectively. The human skeletal model consists of seven rigid links that represent the HAT (head, arms, and trunk), thighs, shanks, and feet. For the rat skeletal model, seven rigid links were used for the trunk and hind legs, where the front legs are fixed on the trunk and slide on the ground without friction, which is similar to the models of previous studies (Yakovenko et al. 2004; Ekeberg and Pearson 2005; Pearson et al. 2006; Prochazka and Yakovenko 2007). The current two models are two-dimensional and the walking behaviors are constrained in the sagittal plane. The contact between their feet and the ground was modeled using viscoelastic elements. Physical parameters of the skeletal models were determined from measured anatomical data.

The human model has nine principal muscles for each leg, including uniarticular and biarticular muscles. The rat model has seven principal muscles for each hind leg. Each muscle receives signals from the corresponding motoneuron and generates muscle tension depending on the force-length and force-velocity relationships and muscle activation. The muscle tension was modeled based on a contractile element and passive elements parallel to the contractile element. The muscle activation for the contractile element is given through a low-pass filter to motor commands of

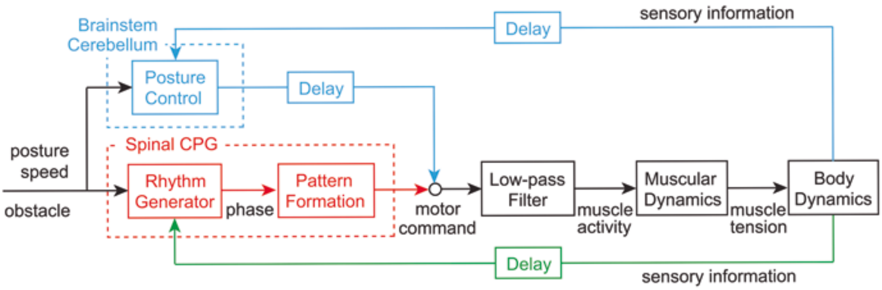

Fig. 8.2 Nervous system model for the human and rat

the motoneuron determined in the nervous system model. The physical parameters of the muscle models were determined from the measured anatomical data.

8.2.2 Nervous System Model

A nervous system model at the brainstem, cerebellar, and spinal cord levels was developed based on the physiological findings (Fig. 8.2), which were used for both the human and rat models.

8.2.2.1 Central Pattern Generators

Physiological studies suggest that CPGs in the spinal cord strongly contribute to rhythmic leg movements, such as locomotion (Grillner 1975; Shik and Orlovsky 1976; Orlovsky et al. 1999). Although the organization of CPGs remains unclear, physiological findings suggest that CPGs consist of hierarchical networks, including rhythm generator (RG) and pattern formation (PF) networks (Burke et al. 2001; Lafreniere-Roula and McCrea 2005; Rybak et al. 2006a, b). The RG network generates the basic rhythm and alters it by producing phase shifts and rhythm resetting based on sensory afferents and perturbations. The PF network shapes the rhythm into spatiotemporal patterns of activated motoneurons through interneurons. CPGs separately control the locomotor rhythm and pattern of motoneuron activation in the RG and PF networks, respectively.

Such a two-layered hierarchical network was created for the CPG model. For the RG model, two simple phase oscillators, each of which produces basic rhythm and phase information for the corresponding leg, were used. In the PF model, the motor commands for the motoneurons were determined to produce periodic leg movements using the oscillator phase based on the physiological concept of muscle synergy, which is explained in the next section.

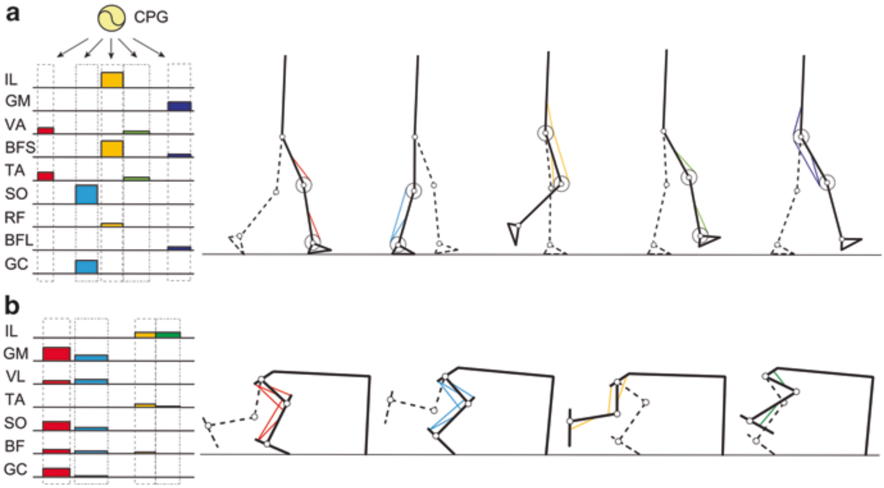

Fig. 8.3 Rectangular pulses from the CPG model delivered to the muscles of the human model (**a**) and rat model (**b**). Five pulses were used for the human model and four pulses were used for the rat model to generate the basic patterns of locomotion

8.2.2.2 Muscle Synergy

Physiological studies have suggested an important concept of muscle synergy, which explains the coordinated structure of muscle activity and is viewed as one way of coping with motor redundancy by decreasing the number of degrees of freedom (Todorov and Jordan 2002; d'Avella et al. 2003; d'Avella and Bizzi 2005; Ting and Macpherson 2005; Drew et al. 2008; Latash 2008). In regards to muscle synergy for locomotion, many studies have shown that although the recorded electromyography (EMG) data during locomotion are complex, they can be accounted for by the combination of only a small number of basic patterns (Ivanenko et al. 2004; Ivanenko et al. 2005; Cappellini et al. 2006; Ivanenko et al. 2006; Dominici et al. 2011).

For the PF model of the CPG model, five rectangular pulses for the human model and four rectangular pulses for the rat model were used for the basic patterns of the motor commands for walking (Fig. 8.3), which is similar to the models of a previous study (Jo and Massaquoi 2007). The timing of the initiation of bursting and the burst duration were determined in accordance with the oscillator phase of the RG model. The rectangular pulses were delivered to muscles by using weighting coefficients.

Muscle synergy analysis has also shown that the addition of another pattern to the basic patterns for walking explains the muscle activities for obstacle avoidance during walking (Ivanenko et al. 2005, 2006), which means that this additional pattern controls the intralimb (intersegmental) coordination of the leg movement to step over an obstacle. To establish the obstacle avoidance task in the rat model,

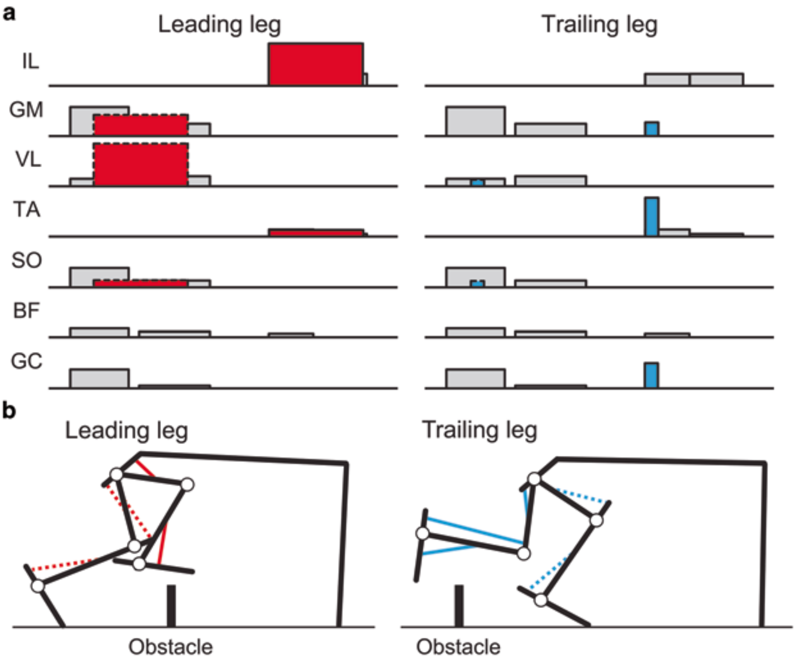

Fig. 8.4 Additional rectangular pulses for obstacle avoidance (**a**) and muscles activated by the additional pulses (**b**). *Solid* and *dotted lines* correspond to the contributions to the swinging and supporting legs, respectively

another rectangular pulse, similar to that used in a previous study (Jo and Massaquoi 2007), was used. Because the leading and trailing legs have different roles during obstacle avoidance, different rectangular pulses for the leading and trailing legs were used (Fig. 8.4). To step over an obstacle, a rat must not only swing its legs more than usual, but also support its body with its contralateral legs. The additional rectangular pulses contribute to both the swinging and supporting legs.

8.2.2.3 Phase Resetting

Because basic motor patterns for walking and obstacle avoidance are produced by rectangular pulses, adequate timing to generate these pulses is crucial. Although CPGs can produce oscillatory behaviors even in the absence of rhythmic input and proprioceptive feedback, CPGs must use sensory information to produce adaptive and effective locomotion. In particular, from the muscle synergy analysis, physiological findings suggest that CPGs manage the timing to produce the basic patterns based on events, such as foot contact, to achieve adaptive locomotion (Ivanenko et al. 2006).

The locomotor rhythm and phase have been shown to be modulated by producing phase shifts and rhythm resetting based on sensory afferents and perturbations (Duysens 1977; Conway et al. 1987; Guertin et al. 1995; Schomburg et al. 1998;

Lafreniere-Roula and McCrea 2005; Rybak et al. 2006b). As cutaneous afferents were observed to contribute to these phase shifts and rhythm resetting behaviors (Duysens 1977; Schomburg et al. 1998), they were modeled by resetting the oscillator phase in the RG model based on foot-contact information (phase resetting) for the sensory regulation model.

In cat locomotion, two types of sensory information are suggested to be used for the phase transition from stance to swing: force-sensitive afferents in the ankle extensor muscles (Duysens and Pearson 1980; Whelan et al. 1995) and position-sensitive afferents from the hip (Grillner and Rossignol 1978; Hiebert et al. 1996). When the force in the ankle extensor muscle is low (unloading rule) or when the hip joint is sufficiently extended (hip extension rule), the phase changes from the stance to the swing. However, it is unclear which rule has more contribution to the generation of robust walking (Ekeberg and Pearson 2005; Pearson et al. 2006). To investigate the sensory mechanism to regulate this transition for adaptive walking, the oscillator phase was reset not only based on foot-contact information but also on the unloading and hip extension rules in the human model.

8.2.2.4 Control of Interlimb Coordination

Because locomotor behavior is produced by alternating leg movements between the left and right legs, interlimb coordination is an important factor. In the discussed above models, weak potential was used in the oscillator dynamics to stabilize the antiphase movement of the oscillators.

During obstacle avoidance, when the swinging leg steps over an obstacle, the contralateral leg must support the entire body to maintain its posture. Because obstacle avoidance will fail without this support, interlimb coordination is crucial for the success of this task. To satisfy this adequate interlimb coordination during obstacle avoidance, the oscillator phase was regulated to delay the additional rectangular pulse for stepping over an obstacle until the contralateral leg contacted the ground to support the body.

8.2.2.5 Posture Control

At the brainstem and cerebellum levels, postural behavior is regulated based on the somatosensory information. For the walking motion of a human, it is crucial to maintain a vertical trunk pitch and move the center of mass (COM) forward at the desired velocity. For the walking motion of a rat, it is important to maintain a constant hip height and forward velocity. For posture control, these factors were focused on for simplicity and motor commands were produced in a feedback fashion using specific muscles to regulate posture during locomotion (Fig. 8.5). Because this posture control is managed at the brainstem and cerebellar levels, receiving the somatosensory information at the brainstem and cerebellar levels and sending the signal to the spinal cord level are delayed. Due to these delays, gain parameters of

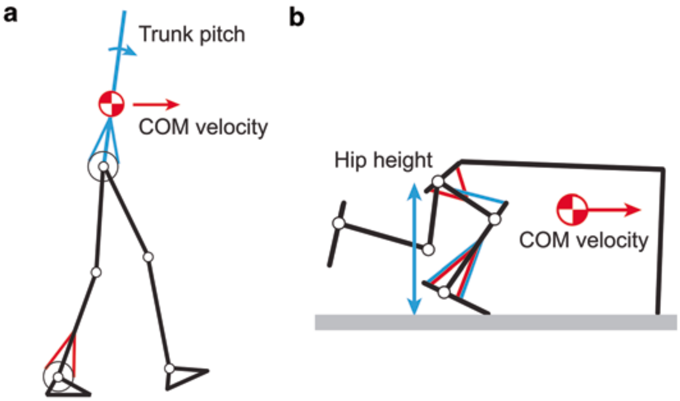

Fig. 8.5 Posture control for the human model (**a**) and rat model (**b**)

the posture control were small, so that the contribution of the posture control was smaller than that of the muscle synergy.

The motor commands for motoneurons were given by the summation of the rectangular pulses based on muscle synergy and the motor commands given by the posture control (Fig. 8.2).

8.3 Results

The dynamic characteristics of our neuromusculoskeletal models for humans and rats that were obtained via forward dynamic simulations are described in this section.

8.3.1 Locomotion in the Human Model

Here we verify our model by comparing the simulation results with the measured data obtained during human walking and investigate the functional roles of the nervous system.

8.3.1.1 Generation of Walking

Stable walking was established by adequately determining the model parameters. To verify our model, we compared the simulation results with the measured data obtained during human walking (Fig. 8.6), where the recorded joint angles and ground reaction forces were taken from (Winter 2004) and the EMG data from (Inman 1953). The properties of the simulation results are similar to those of the measured data, and in particular the vertical reaction force has a double-peaked shape also seen in the human walking results.

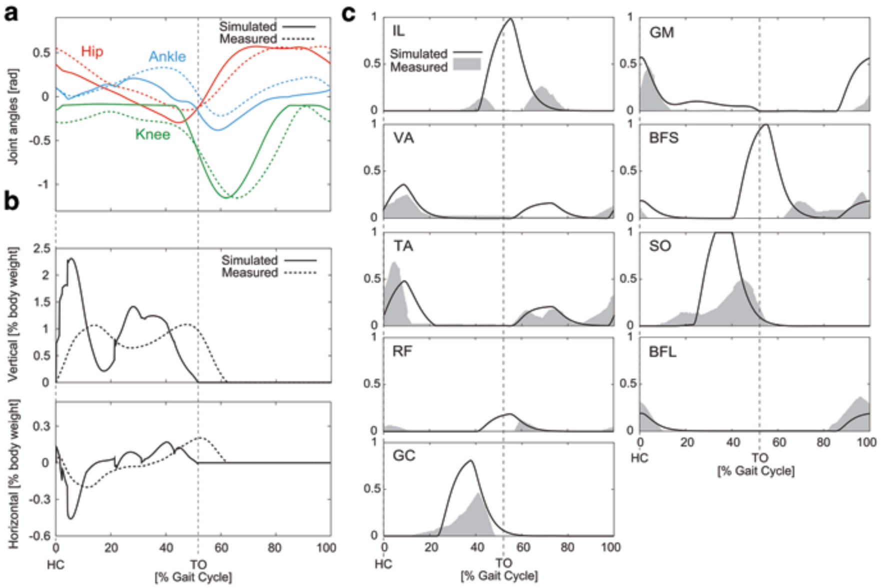

Fig. 8.6 Comparison between the simulation results and the measured data that were obtained during human walking (**a**: joint angles, **b**: ground reaction forces, and **c**: muscle activities). *HC* and *TO* indicate heel contact and toe-off, respectively, for the simulation results

8.3.1.2 Contribution of the Posture Control

While the motor commands are given by the summation of the rectangular pulses and posture control, the contribution of the posture control was only a few percent during steady walking. This contribution appears relatively small, but the human model easily fell when the posture control was eliminated from our nervous system model. This shows that the posture control plays an important role in the generation of walking.

8.3.1.3 Contribution of Phase Resetting Based on Foot-Contact Information

To determine the contribution of sensory regulation by phase resetting to the generation of adaptive walking, we examined the ability of our model to adapt to the perturbing forces; that is, we determined if the human model could recover after being perturbed. More specifically, after steady walking was established in the model, a perturbing force was applied for 0.1 s to the COM of HAT in the horizontal direction (forward or backward) using various magnitudes and timings of the perturbation. In particular, four cases were compared: (1) without the use of phase resetting, (2) use of phase resetting only at foot off, (3) use of phase resetting only at foot contact, and (4) use of phase resetting at both foot off and foot contact. Figure 8.7 shows the results, where the white boxes indicate that the human

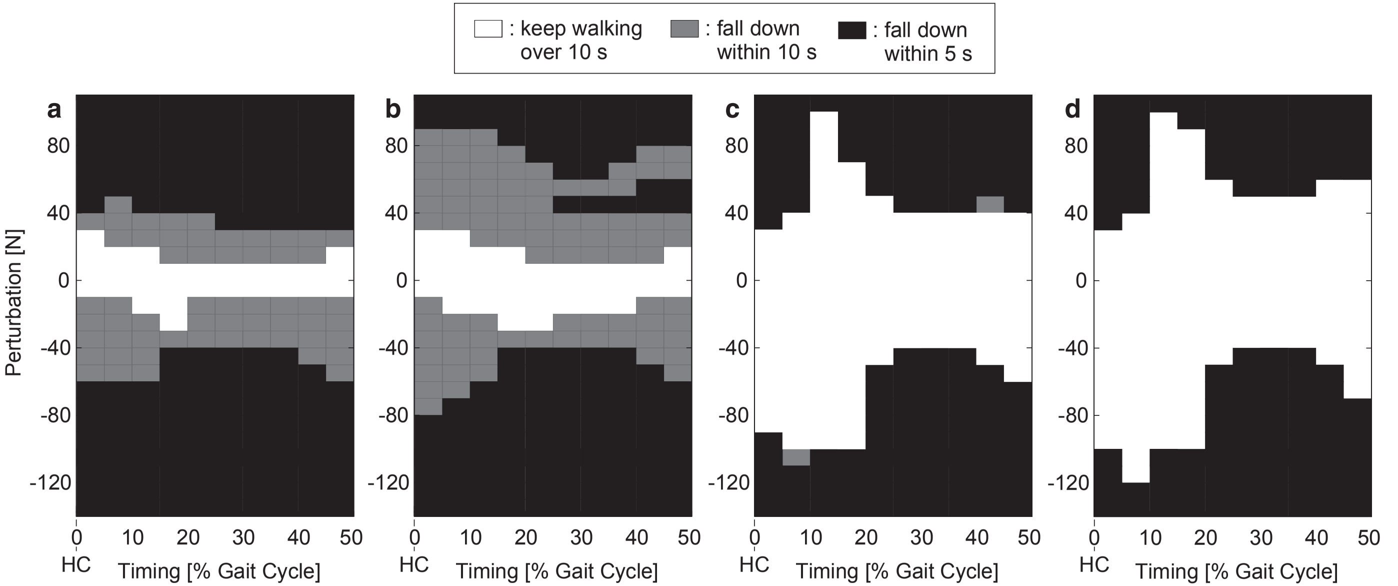

Fig. 8.7 Tolerance to the perturbing forces. (**a**) without the use of phase resetting, (**b**) use of phase resetting only at foot off, (**c**) use of phase resetting only at foot contact, and (**d**) use of phase resetting at both foot off and foot contact

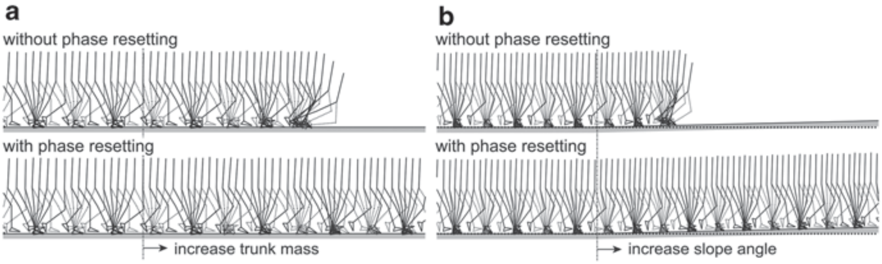

Fig. 8.8 Simulated walking behavior for the sudden environmental changes, with and without the phase resetting. **a** Sudden increase in the trunk mass, and **b** sudden increase in the slope angle

model continued walking for over 10 s after the disturbance was applied, the gray boxes indicate that the human model fell within 10 s after the disturbance was applied, and the black boxes indicate that the human model fell within 5 s after the disturbance was applied. When phase resetting was not incorporated, the human model easily fell. The human model walked longer when phase resetting was applied. The number of white boxes suggests that the application of phase resetting at foot contact contributes more significantly to counteracting the perturbing forces than when phase resetting was applied at foot off. The use of phase resetting at both foot off and foot contact yielded the greatest degree of robustness among the four cases.

The ability of our model to adapt to sudden environmental changes was also investigated. To alter the environment, the trunk mass (Fig. 8.8a) and slope angle (Fig. 8.8b) were instantaneously increased for the cases with and without phase resetting. The human model without the phase resetting easily fell after the sudden environmental changes. In contrast, the human model with the phase resetting continued walking against the environmental variations. These environmental changes induced a decrease in walking speed and changes in the joint motions through the sensory regulation of the motor patterns.

8.3.1.4 Unloading Rule vs. Hip Extension Rule

To investigate the roles of the unloading and hip extension rules that regulate the stance-to-swing transition during walking, the ability of our model to adapt to the perturbing forces was examined. The following three cases of model walking were compared: (1) without the use of phase resetting, (2) use of phase resetting based on the hip extension rule, and (3) use of phase resetting based on the unloading rule (Fig. 8.9). The human model for case 2 easily fell after being disturbed, compared to the model without phase resetting. However, for case 3, the human model walked longer, which indicates that the unloading rule increased the robustness of the responses, similar to the results of a previous modeling study of cat locomotion (Ekeberg and Pearson 2005; Pearson et al. 2006).

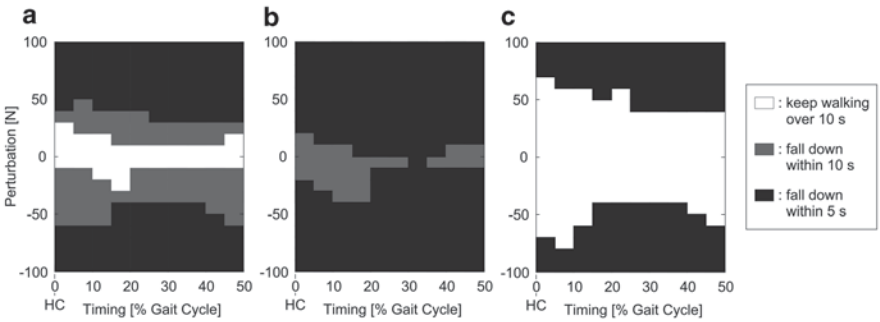

Fig. 8.9 Tolerance to the perturbing forces. **a** Without the use of phase resetting, **b** use of phase resetting based on the hip extension rule, and **c** use of phase resetting based on the unloading rule

8.3.2 Locomotion in the Rat Model

In this section, the neuromusculoskeletal model of rats is verified by comparing the simulation results with the measured data obtained during rat walking, and the functional roles of the nervous system during walking and obstacle avoidance are investigated.

8.3.2.1 Generation of Walking

An adequate determination of the model parameters produced stable walking of the rat. We verified our model by comparing the simulation results with the measured data obtained during rat walking (Aoi et al. 2013; Fig. 8.10). The properties of the simulation results are similar to those of the measured data.

8.3.2.2 Contribution of the Posture Control

In the rat model, the contribution of the posture control was only a few percent for the motor commands during steady walking. However, the rat model fell when the posture control was removed from the nervous system model. This indicates the importance of the posture control to generate walking, which was similarly shown in the human model.

8.3.2.3 Stepping Over an Obstacle

By using additional rectangular pulses, the rat model stepped over an obstacle and the walking behavior of the rat soon recovered after the obstacle avoidance process (Fig. 8.11c). Figure 8.11a and b show stick diagrams of the measured kinematics of the leading and trailing legs, respectively, during the obstacle avoidance process of the rat (Aoi et al. 2013) as a comparison with the simulation results. When the

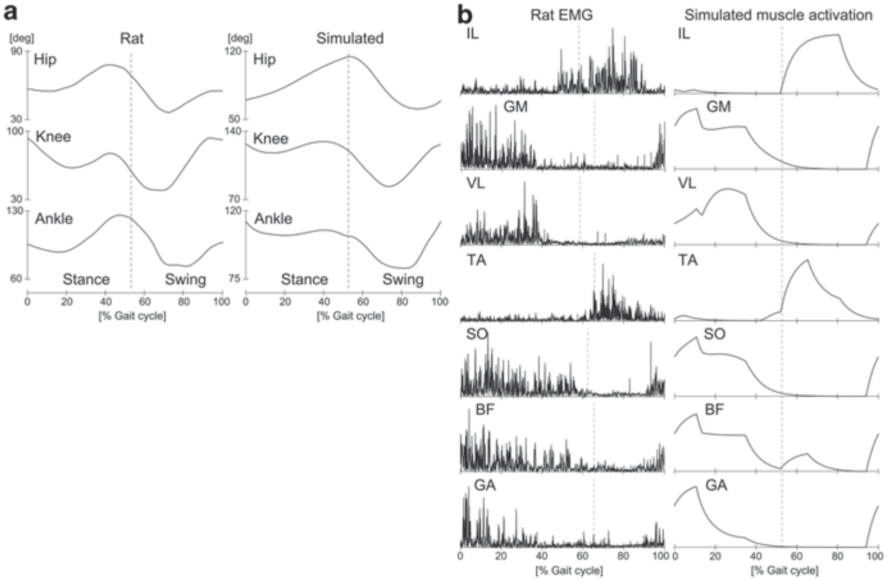

Fig. 8.10 Comparison between the simulation results and the measured data obtained during the rat walking (**a**: joint angles and **b**: muscle activities)

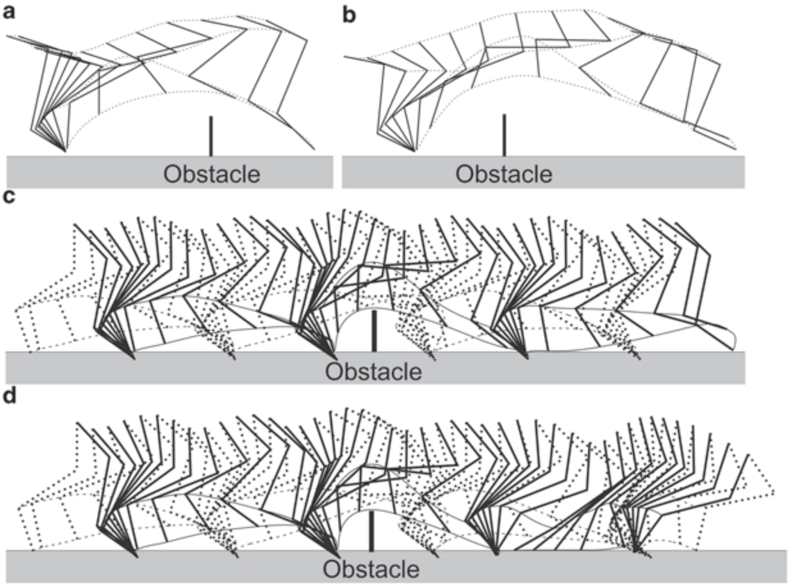

Fig. 8.11 Stick diagrams during obstacle avoidance. **a** Measured kinematics of the leading leg, **b** measured kinematics of the trailing leg, **c** simulated obstacle avoidance behavior, and **d** falling after stepping over an obstacle due to the lack of phase resetting

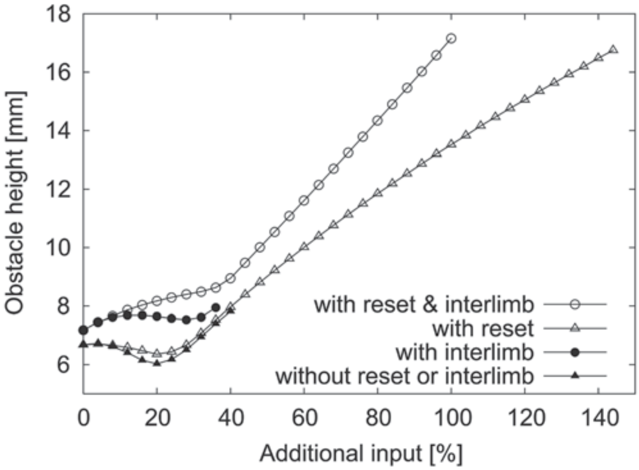

Fig. 8.12 Comparison between obstacle height with and without phase resetting and control of interlimb coordination

phase resetting based on foot contact was not incorporated, the rat model fell after stepping over an obstacle (Fig. 8.11d).

8.3.2.4 Contribution of Phase Resetting and Interlimb Coordination During Obstacle Avoidance

To investigate the contribution of the sensory regulation based on phase resetting and interlimb coordination during obstacle avoidance, various magnitudes of the additional rectangular pulses were used and the height of an obstacle that a rat could step over without falling was examined. The height of an obstacle that a rat could step over without collision was determined from the resultant simulated kinematics of the leading and trailing legs, in which the obstacle was assumed to be a zero-width bar in the sagittal plane. In particular, the following four cases were compared: (1) without phase resetting or control of interlimb coordination, (2) with the use of control of interlimb coordination, (3) with the use of phase resetting, and (4) with the use of both phase resetting and control of interlimb coordination. Figure 8.12, in which various magnitudes of the additional inputs are used, shows the height of an obstacle that the rat model could clear. When phase resetting was not used, the rat model stepped over an obstacle of 8 mm (40 % of additional inputs) at best. Phase resetting contributed to a quick recovery after the obstacle was cleared. The control of interlimb coordination allowed the model to clear higher obstacles. Although the rat model with phase resetting also stepped over higher obstacles, the magnitudes of the additional inputs for the model needed to be higher than those of the model with both phase resetting and control of interlimb coordination, which cleared high obstacles by using small additional inputs without falling after stepping over the obstacles.

8.4 Discussion

To investigate the functional roles of the nervous system for the stabilization of posture during locomotion, our models focus on the leg movement control, which is based on the physiological concepts of CPGs and muscle synergy and on sensory regulation by phase resetting and interlimb coordination, and the posture control to regulate the postural behavior via somatosensory information.

8.4.1 Control of the Leg Movement and Posture

To establish locomotion, it is necessary to control the leg movement needed to move the entire body and the posture needed to prevent the body from falling during locomotion. In our models, the leg movement control uses basic motor command patterns that are based on the physiological concepts of CPGs and muscle synergy, which are regulated through sensory information based on phase resetting and interlimb coordination. In contrast, the posture control regulates the postural behavior in a feedback fashion by using somatosensory information.

When the sensory regulation in the leg movement control was eliminated, the human and rat models fell easily and the robustness against the force disturbances and sudden environmental variations decreased. When the posture control was eliminated from the nervous system model, the human and rat models fell easily. By adequately integrating these controls in the nervous system model, our models produced adaptive locomotor behaviors.

8.4.2 Leg Movement Control Based on Muscle Synergy

Humans and other animals produce adaptive movements from a combination of various degrees of freedom, from which they must solve the motor redundancy problem. Physiological studies suggest the importance of muscle synergies for controlling movements (Todorov and Jordan 2002; d’Avella et al. 2003; Ivanenko et al. 2004; d’Avella and Bizzi 2005; Ivanenko et al. 2005; Ting and Macpherson 2005; Ivanenko et al. 2006; Drew et al. 2008; Latash 2008; Dominici et al. 2011), which is viewed as one solution to the redundancy problem. Muscle synergy is related to the co-variation of muscle activities. Humans and other animals share some basic patterns for producing muscle activation patterns among various movements (e.g., the jumping,, and walking patterns of frogs and the walking, obstacle avoidance, kicking motion, and running of humans) and produce these various movements with the addition of other patterns (Ivanenko et al. 2004; d’Avella and Bizzi 2005; Ivanenko et al. 2005; Cappellini et al. 2006; Ivanenko et al. 2006). This means that some degrees of freedom are functionally connected depending on the task, which reduces the number of degrees of freedom and solves the problem of motor redundancy.

CPGs are considered to produce such basic patterns in a feedforward fashion to create various movements, and by adding another pattern to the basic patterns for walking, the motor control of stepping over an obstacle is achieved (Ivanenko et al. 2005, 2006). In addition, the timing to produce the basic patterns is managed by CPGs based on events, such as foot contact (Ivanenko et al. 2006). Based on these physiological findings and hypotheses, we developed a simple rectangular pulse model for walking and obstacle avoidance and modulated the rectangular pulses by incorporating a sensory regulation model based on phase resetting and interlimb coordination.

For successful obstacle avoidance during locomotion, two factors are crucial; the leading and trailing legs must clear the obstacle without collision and the walking behavior must recover soon after stepping over the obstacle. As the obstacle height increases, the toe heights of the leading and trailing legs must also increase, which disturbs the posture and causes instability and falling. Therefore, the processes of stepping over a high obstacle and recovering soon after obstacle avoidance are not consistent. The simulation results of the rat model showed that the sensory regulation based on phase resetting, which was achieved by using the foot-contact information, contributed to a quick recovery after stepping over an obstacle and the sensory regulation based on interlimb coordination contributed to efficiently stepping over a high obstacle.

8.4.3 Sensory Regulation by Phase Resetting

For the sensory regulation model, phase resetting was used. Although physiological evidence showed that locomotor rhythm and phases are modulated by phase shifts and rhythm resetting that is produced based on sensory afferents and perturbations (Duysens 1977; Conway et al. 1987; Guertin et al. 1995; Schomburg et al. 1998; Rybak et al., 2006b), such rhythm and phase modulations have been investigated, for the most part, during fictive locomotion in cats, and their functional roles during actual locomotion remain unclear. However, spinal cats produce locomotor behaviors on treadmills and change their gaits depending on the belt speed (Forssberg and Grillner 1973; Orlovsky et al. 1999), suggesting that the tactile sensory information between their feet and the belt influences the locomotion phase and rhythm generated by the CPG (Duysens et al. 2000). In addition, cutaneous afferents were observed to contribute to phase resetting (Duysens 1977; Schomburg et al. 1998). Our sensory regulation model, in which phase resetting is utilized, is consistent with these observations. Furthermore, previous neuromechanical models have demonstrated that phase resetting contributes to the generation of adaptive walking (Yamasaki et al. 2003; Nomura et al. 2009).

Locomotor behavior can be determined from the spatiotemporal patterns of motor commands and phase resetting manages the temporal regulation based on foot-contact events. Even if the timing of the foot-contact event is affected by disturbances, the phase resetting regulates the timing to generate motor commands based on the event. Early foot contact induces a phase shift in the periodic motor commands to interrupt the locomotor rhythm, and delayed foot contact results in a phase shift in the periodic motor commands to prolong the locomotor rhythm. Phase resetting creates various phase profiles and locomotor rhythms depending on the situation, thus improving the stability and robustness of the locomotion.

People and animals integrate sensory information to produce motor commands. Different sensory information causes different dynamic characteristics in locomotor behavior. To produce adaptive and efficient movements, the type of sensory information they use and when and how they use the sensory information are crucial. Our simulation results showed that sensory regulation based on foot-contact information helps maintain posture during locomotion and the unloading rule related to the force information in the ankle extensor muscle increased the robustness of locomotion more than the hip extension rule that is related to the angle information of the hip joint. Computer simulations are useful to examine sensorimotor integration mechanisms during locomotion.

8.4.4 Sensory Regulation Based on Interlimb Coordination

During obstacle avoidance, as the additional input for the leading leg increases, the toe height of the leading leg increases and its contact with the ground is delayed. When the delay is longer than the onset of the additional input for the trailing leg, the rat model begins to step over an obstacle without support from its contralateral leg. This reduces the performance of obstacle avoidance. The sensory regulation to produce adequate interlimb coordination to support the body by the contralateral leg allowed the rat model to clear a high obstacle with little additional input.

Although the sensory regulation based on this interlimb coordination increased the performance of obstacle avoidance, it shifted the relative phase of the rectangular pulses for the basic patterns of locomotion between the legs from an antiphase state. Because this shift causes instability and falling during walking, the relative phase should return to antiphase after stepping over an obstacle. Weak potential was used in the oscillator dynamics to stabilize the antiphase movement of the oscillators, which increased the robustness of locomotion. Adequate control of the interlimb coordination is required during walking and obstacle avoidance.

8.5 Conclusion

Simulation studies that were conducted by integrating musculoskeletal models based on anatomical and biomechanical findings and nervous system models based on physiological findings have become useful tools to elucidate the locomotor mechanisms in biological systems, which overcome the limitations of behavioral studies based only on the nervous system. In this chapter, we constructed the neuromusculoskeletal models of humans and rats to investigate the functional roles of the nervous system for stabilizing the posture of the body during locomotion. The physical structure of the musculoskeletal models is simple and is constrained in the two- dimensional sagittal plane. The nervous system is limited to the brainstem, cerebellar, and spinal cord levels and only focuses on the leg movement control that is based on CPGs, muscle synergy, and sensory regulation via phase resetting and interlimb coordination, and focuses on the posture control by using somatosensory information. To further elucidate adaptive functions in the locomotion dynamics of biological systems, we intend to employ a more sophisticated and plausible model in the future.

Acknowledgements This chapter is based on collaboration studies with Kazuo Tsuchiya, Naomichi Ogihara, Dai Yanagihara, Tetsuro Funato, Nozomi Tomita, Takahiro Kondo, Naohiro Hayashi, Sho Aoki, Hiroshi Yamaura, Yasuhiro Sugimoto, and Kei Senda. This chapter is supported in part by KAKENHI (23360111, 26120006) from MEXT, Japan, by JST, CREST, Japan, and by Uehara Memorial Foundation, Japan.

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