

Hindlimb obstacle avoidance during rat locomotion based on a neuromusculoskeletal model

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Abstract—We investigated the obstacle avoidance in locomotion of the rat using a neuromusculoskeletal model. We constructed a musculoskeletal model of the hindlimbs based on the measured anatomical data and constructed a nervous system model based on the central pattern generator and muscle synergy. We incorporated sensory regulation models based on interlimb coordination and phase resetting and investigated their functional roles during obstacle avoidance in locomotion. Our simulation results show that the phase regulation based on interlimb coordination contributes to stepping over a high obstacle and show that the phase regulation based on phase resetting contributes to quick recovery after obstacle avoidance. These results suggest the importance of sensory regulation in generation of successful obstacle avoidance in locomotion.

I. INTRODUCTION

Animals produce adaptive locomotion in diverse environments by skillfully manipulating their complicated and redundant musculoskeletal systems. Stepping over obstacles in locomotion is an essential movement for safe and smooth locomotion, where animals must recognize the information of obstacle and determine how to manipulate their limbs to avoid a collision with the obstacle while maintaining their posture. This task needs highly coordinated control of spatiotemporal patterns of command signals.

The abilities of animals to create adaptive movements have been investigated based on the configurations and activities of neural systems [10], [20], [26], [31], [32]. However, since locomotion is a well-organized motion generated through dynamic interactions among the body, the nervous system, and the environment, it is difficult to fully elucidate locomotion mechanisms only from the nervous system. As well as the nervous system, it is crucial to analyze dynamic characteristics in the body. To conduct integrative studies of the musculoskeletal and nervous systems, simulation studies

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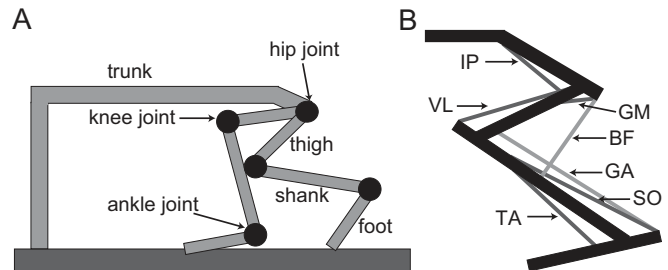


Fig. 1. Musculoskeletal model of the hindlimb of the rat (A: Skeletal model, B: Muscle model)

have recently been performed [1], [9], [14–16], [19], [27–29], where physiological and anatomical findings allow us to construct reasonably realistic models of the musculoskeletal and nervous systems.

In this paper, we investigated the stepping over an obstacle in locomotion of the rat using a neuromusculoskeletal model. We constructed a musculoskeletal model of the hindlimbs of the rat based on the measured anatomical data and developed a nervous system model based on the central pattern generator (CPG) and muscle synergy. We compared the simulation results with the measured kinematic data of a rat during the stepping over an obstacle. In addition, we incorporated sensory regulation models based on interlimb coordination and phase resetting and examined their functional roles in obstacle avoidance in locomotion.

II. MODEL

A. Musculoskeletal model

Due to their geometrical similarity [4], [17], we constructed the musculoskeletal model of the hindlimbs of the rat based on the model of the cat [9]. The skeletal model is composed of planar seven rigid links that represent the trunk and the hindlimbs (Fig. 1A). Since we focus on the locomotion of the hindlimbs, the forelimbs are fixed on the trunk and slide on the ground without friction. We determined the physical parameters of the skeletal model based on the measured anatomical data [18].

We developed the muscle model using seven principal muscles for each hindlimb (Fig. 1B); five muscles are uniaxial: hip flexion (iliopsoas (IP)), hip extension (gluteus maximus (GM)), knee extension (vastus lateralis (VL)), ankle flexion (tibialis anterior (TA)), and ankle extension (soleus (SO)), and two muscles are biarticular: hip extension and knee flexion (biceps femoris (BF)), and knee flexion and

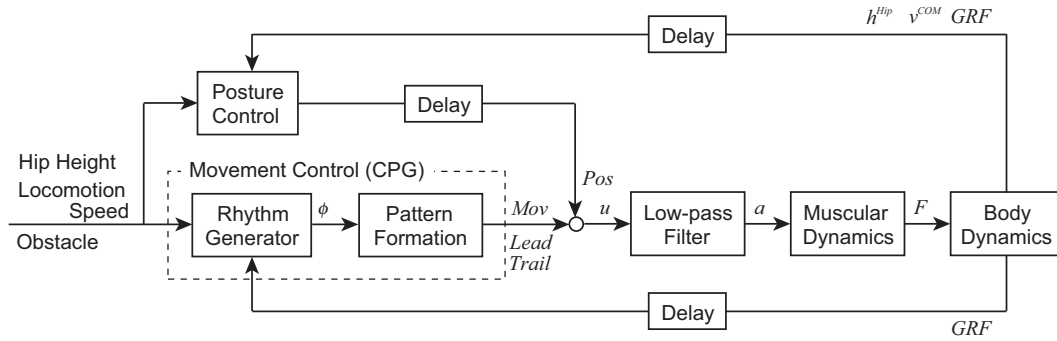


Fig. 2. Nervous system model for locomotion and obstacle avoidance by the hindlimbs of the rat

ankle extension (gastrocnemius (GA)). A muscle receives command signals from the corresponding α -motoneuron and generates muscle tension depending on the force-length and force-velocity relationships. We used the model in [9], composed of contractile and passive elements, by

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

where F_m ($m = \text{IP, GM, VL, TA, SO, BF, and GA}$) 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. We determined the physical parameters of the muscle model based on the measured anatomical data [18].

Muscle activation a_m is determined through the low-pass filter [29]

$$\dot{a}_m + \frac{1}{\tau_{\text{act}}} \left\{ \frac{\tau_{\text{act}}}{\tau_{\text{deact}}} + \left(1 - \frac{\tau_{\text{act}}}{\tau_{\text{deact}}} \right) u_m \right\} a_m = \frac{1}{\tau_{\text{act}}} u_m \quad (2)$$

where τ_{act} and τ_{deact} are activation and deactivation time constants (11 and 18 ms, respectively) and u_m is the output from the α -motoneuron from the nervous system model.

B. Nervous system model

Command signals are projected to the α -motoneuron in the spinal cord by integrating signals from upper centers and sensory signals. We determined the output u_m from the α -motoneuron from the following three components by improving our previous model [1] (Fig. 2): 1. Movement control, which produces command signals in feedforward fashion at the spinal cord level to create periodic limb movements for forward motion and to create intended movements for obstacle avoidance, 2. Phase modulation, which regulates timing to produce the feedforward signals in the movement control at the spinal cord level based on sensory signals; and 3. Posture control, which creates command signals in feedback fashion based on somatosensory information at the brainstem and cerebellar levels to regulate postural behavior. The output u_m is given by

$$u_m = Mov_m + Pos_m + Lead_m + Trail_m \quad (3)$$

where Mov_m is the output of the movement control for the periodic limb movements, Pos_m is the output of the

posture control, and $Lead_m$ and $Trail_m$ are the outputs of the movement control used only for one duration of the obstacle avoidance.

1) *Movement control for periodic limb movements:* Physiological studies suggest that the CPGs in the spinal cord greatly contribute to rhythmic limb movement, such as locomotion [10], [20], [26]. The organization of CPGs remains unclear. However, recent physiological findings suggest that CPGs consist of hierarchical networks, which include rhythm generator (RG) and pattern formation (PF) networks [3], [22], [23]. The RG network generates the basic rhythm and alters it based on sensory afferents and perturbations. The PF network shapes the rhythm into spatiotemporal patterns of activation of motoneurons through interneurons. That is, CPGs separately control the locomotor rhythm and pattern of motoneuron activation in the RG and PF networks, respectively.

We modeled the movement control based on this two-layered hierarchical network. For the RG model, we used two simple phase oscillators, each of which produces a basic rhythm and phase information for the corresponding limb. We define the oscillator phase by ϕ_i ($i = \text{left, right}$) ($0 \leq \phi_i \leq 2\pi$), which follows the dynamics

$$\begin{aligned} \dot{\phi}_{\text{left}} &= \omega - K_\phi \sin(\phi_{\text{left}} - \phi_{\text{right}} - \pi) \\ \dot{\phi}_{\text{right}} &= \omega - K_\phi \sin(\phi_{\text{right}} - \phi_{\text{left}} - \pi) \end{aligned} \quad (4)$$

where ω is the basic frequency and K_ϕ is the gain parameter. We used $\omega = 8\pi$ rad/s to generate locomotion with a gait cycle of 250 ms. The second term on the right side maintains the interlimb coordination pattern so that the hindlimbs move out of phase.

Physiological studies also suggest the important concept of muscle synergy, which explains the coordinated structure in muscle activities and is viewed as one means of coping with redundancy problem. Although the electromyographic data measured during locomotion are complex, they can be accounted for by the combination of only small number of basic patterns [6], [7], [11–13]. For the PF model, we prepared four rectangular pulses for the basic patterns of locomotion [1], [15], [16], whose timing of initiation of bursting and duration depend on oscillator phase ϕ from the

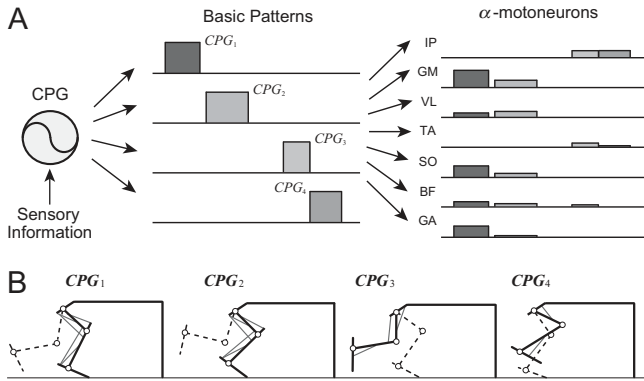


Fig. 3. CPG model. **A** shows four rectangular pulses and command signals composed of combination of four rectangular pulses. **B** shows activated muscles by four rectangular pulses.

RG model, and which are given by

$$CPG_i(\phi) = \begin{cases} 1 & \phi_i^{\text{Start}} < \phi \leq \phi_i^{\text{Start}} + \Delta\phi_i \\ 0 & \text{otherwise} \end{cases} \quad i = 1, \dots, 4 \quad (5)$$

where $CPG_i(\phi)$ ($i = 1, \dots, 4$) is the rectangular pulse, ϕ_i^{Start} the phase value when the rectangular pulse starts to burst, and $\Delta\phi_i$ the duration of the rectangular pulse (Fig. 3). These four patterns are delivered to the α -motoneurons, and the output Mov_m of this movement control is given by

$$Mov_m = \sum_{i=1}^4 w_{m,i} CPG_i(\phi) \quad (6)$$

where $w_{m,i}$ is the weighting coefficient for delivery of the four basic patterns to α -motoneurons ($w_{m,i} \geq 0$).

2) *Phase regulation by phase resetting*: CPGs are suggested to manage the timing of firing of the basic patterns based on kinematic events [12]. In addition, the RG network in CPGs modulates its basic rhythm by producing phase shifts and rhythm resetting based on sensory information (phase resetting) [22]. Since cutaneous afferents contribute to the phase shift and rhythm resetting behaviors [8], [25], we modeled such phase resetting by resetting oscillator phase ϕ_i based on foot-contact events. More specifically, we modified the oscillator phase dynamics (4) by

$$\begin{aligned} \dot{\phi}_{\text{left}} &= \omega - K_\phi \sin(\phi_{\text{left}} - \phi_{\text{right}} - \pi) \\ &\quad - (\phi_{\text{left}} - \phi_{\text{Contact}}) \delta(t - t_{\text{left}}^{\text{Contact}} - \tau^{\text{Contact}}) \\ \dot{\phi}_{\text{right}} &= \omega - K_\phi \sin(\phi_{\text{right}} - \phi_{\text{left}} - \pi) \\ &\quad - (\phi_{\text{right}} - \phi_{\text{Contact}}) \delta(t - t_{\text{right}}^{\text{Contact}} - \tau^{\text{Contact}}) \end{aligned} \quad (7)$$

where $\delta(\cdot)$ is Dirac's delta function, t_i^{Contact} ($i = \text{left, right}$) is the time when the foot lands on the ground, and ϕ_{Contact} is the phase value to be reset when the foot touches the ground. This phase resetting depends on the tactile sensor on the foot and the delay in the spinal cord receiving the sensory signal. We set the transmission delay τ^{Contact} at 10 ms.

3) *Posture control*: Command signals are produced to regulate postural behavior based on somatosensory information in the brainstem and cerebellum levels. For the locomotor in rat, it is crucial to maintain the hip height and move the center of mass (COM) forward at the desired velocity. For simplicity, we focused on these two factors for the posture control.

For the postural control of the hip height, we used simple feedback control by muscles VL, TA, and SO of the standing leg,

$$Hgt_m = \begin{cases} -K_m^{\text{Hgt}}(h^{\text{Hip}} - \hat{h}^{\text{Hip}}) - D_m^{\text{Hgt}}\dot{h}^{\text{Hip}} & \text{when } GRF > 0 \\ 0 & \text{otherwise} \end{cases} \quad (8)$$

where h^{Hip} and \dot{h}^{Hip} are the hip height and its rate, \hat{h}^{Hip} is the reference height, K_m^{Hgt} and D_m^{Hgt} are the gain parameters ($K_m^{\text{Hgt}} = D_m^{\text{Hgt}} = 0$ when $m \neq \text{VL, TA, or SO}$), and GRF is the vertical ground reaction force.

For the postural control of COM velocity, we used simple feedback control by muscles IP, GM, TA, and SO of the standing leg,

$$COM_m = \begin{cases} -K_m^{\text{COM}}(v^{\text{COM}} - \hat{v}^{\text{COM}}) & \text{when } GRF > 0 \\ 0 & \text{otherwise} \end{cases} \quad (9)$$

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

Since this posture control is managed at the brainstem and cerebellar levels, the command signals are delayed and the output Pos_m of the posture control is given by

$$Pos_m(t) = Hgt_m(t - \tau^{\text{Somato}} - \tau^{\text{Descend}}) + COM_m(t - \tau^{\text{Somato}} - \tau^{\text{Descend}}) \quad (10)$$

where τ^{Somato} and τ^{Descend} are the transmission delays. We used $\tau^{\text{Somato}} + \tau^{\text{Descend}} = 15$ ms.

4) *Strategy for stepping over an obstacle*: Different from usual locomotion, obstacle avoidance is a skillful intended movement, where the rat must recognize the information of obstacle, such as distance and height, and determine how to manipulate the limbs to avoid colliding with the obstacle while maintaining the posture. Analysis of muscle synergy has shown that the addition of a basic pattern to the basic patterns of locomotion explains the muscle activation patterns for the obstacle avoidance [12], [13]. Jo [16] evaluated this hypothesis for the stepping over an obstacle by one leg based on a neuromusculoskeletal model of human locomotion.

In the obstacle avoidance during locomotion, the lead limb steps over an obstacle and the trail limb follows it and clears the obstacle. Therefore, to complete this task, both lead and trail limbs must step over an obstacle without colliding with the obstacle. In this paper, we focused on stepping over an obstacle during locomotion by the hindlimbs without modulating the stride length before the obstacle avoidance, where we neglect the collision of the forelimbs with the obstacle. Since the tip of the lead limb is distant from an obstacle at the liftoff from the ground, the lead limb steps

over the obstacle at the posterior half of the swing phase. On the other hand, the tip of the trail limb is closer to the obstacle at the liftoff and the trail limb clears the obstacle at the anterior half of the swing phase. The movement of the lead limb differs from that of the trail limb and the roles of the lead and trail limbs are not identical.

We prepared an additional rectangular pulse for each lead and trail limbs and used them only once for the obstacle avoidance. The additional rectangular pulse $CPG_{lead}(\phi_{lead})$ for the lead limb and $CPG_{trail}(\phi_{trail})$ for the trail limb are given by

$$CPG_i(\phi_i) = \begin{cases} 1 & \phi_i^{Start} < \phi_i \leq \phi_i^{Start} + \Delta\phi_i \\ 0 & \text{otherwise} \end{cases} \quad i = \text{lead, trail} \quad (11)$$

where ϕ_i^{Start} ($i = \text{lead, trail}$) is the phase value when the rectangular pulse starts to burst and $\Delta\phi_i$ is the duration of the rectangular pulse. For the obstacle avoidance, the rat must not only swing the limb more than usual but also support the body by the contralateral limb. Therefore, the additional rectangular pulse contributes to the contralateral supporting limb as well as the ipsilateral swinging limb. The additional rectangular pulse is delivered to the α -motoneurons, and the outputs $Lead_m^{Ipsi}$ for the lead limb, $Lead_m^{Contra}$ for the contralateral limb of the lead limb, $Trail_m^{Ipsi}$ for the trail limb, $Trail_m^{Contra}$ for the contralateral limb of the trail limb are given by

$$\begin{aligned} Lead_m^{Ipsi} &= w_{m,lead}^{Ipsi} CPG_{lead}(\phi_{lead}) \\ Lead_m^{Contra} &= w_{m,lead}^{Contra} CPG_{lead}(\phi_{lead}) \\ Trail_m^{Ipsi} &= w_{m,trail}^{Ipsi} CPG_{trail}(\phi_{trail}) \\ Trail_m^{Contra} &= w_{m,trail}^{Contra} CPG_{trail}(\phi_{trail}) \end{aligned} \quad (12)$$

where $w_{m,lead}^{Ipsi}$, $w_{m,lead}^{Contra}$, $w_{m,trail}^{Ipsi}$, and $w_{m,trail}^{Contra}$ are the weighting coefficients for delivery of the additional rectangular pulses to α -motoneurons (Fig. 4).

In this paper, after our model produced steady walking, we added these additional inputs only once. Since these additional inputs change the kinematics of the lead and trail limbs, we determined the height of the obstacle that our model steps over without collision from the resultant simulated kinematics of the lead and trail limbs, where we assumed that the depth of the obstacle is zero.

5) *Regulation of interlimb coordination pattern during obstacle avoidance:* As explained above, supporting the body by the contralateral limb is important for the obstacle avoidance. When the lead or trail limb starts stepping over an obstacle without supporting by the contralateral limb, this task will fail. The interlimb coordination depending on the contralateral limb is crucial for the success of the trial.

To control this interlimb coordination, we regulate the phase of the ipsilateral limb by setting $\dot{\phi}_i = 0$ ($i = \text{lead, trail}$) when $\phi_i \geq \phi_i^{Start}$ and the ground reaction force of the contralateral limb is zero. This aims to delay the additional rectangular pulse for stepping over an obstacle until the contralateral limb supports the body.

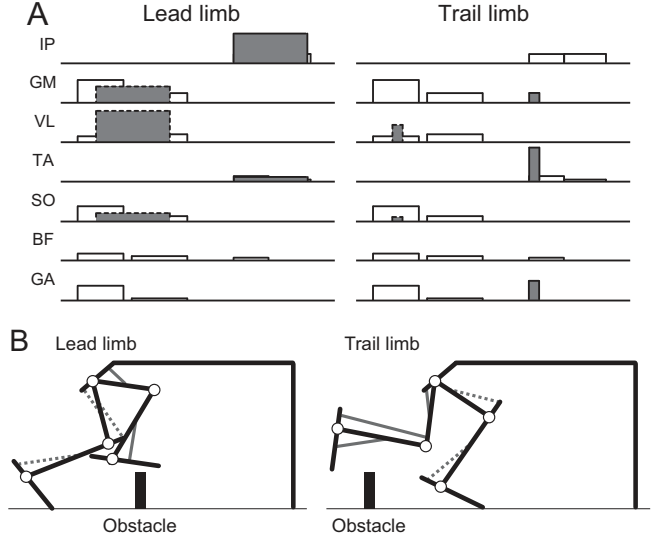


Fig. 4. Additional rectangular pulses for obstacle avoidance. **A** shows the command signals delivered to α -motoneurons for lead and trail limbs. Gray rectangular pulses are additional inputs. Bold and dotted lines correspond to the contributions to the swinging and supporting limbs, respectively. **B** shows the activated muscles by the additional rectangular pulses.

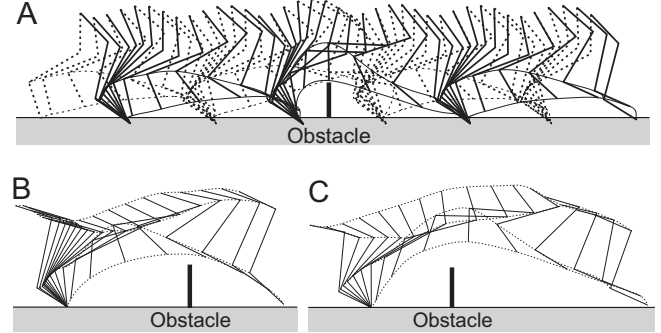


Fig. 5. Stick diagram during obstacle avoidance. **A**: simulated behavior. **B**: measured kinematics of the lead limb of a rat. **C**: measured kinematics of the trail limb of a rat.

III. RESULTS

A. Stepping over an obstacle

We first determined the parameters of our nervous system model to produce stable locomotion in a similar way to our previous study [1]. Then, we simulated the obstacle avoidance using additional rectangular pulses. Figure 5 shows the result with a stick diagram, where **A** is the simulated behavior and **B** and **C** are the measured kinematics of the lead and trail limbs of a rat, respectively, which step over an obstacle [24]. By comparing with the measured data, the simulation result shows similar behavior for stepping over an obstacle.

B. Contribution of sensory regulations

To investigate the contribution of the phase modulation based on phase resetting and interlimb coordination during obstacle avoidance, we used various magnitudes of the

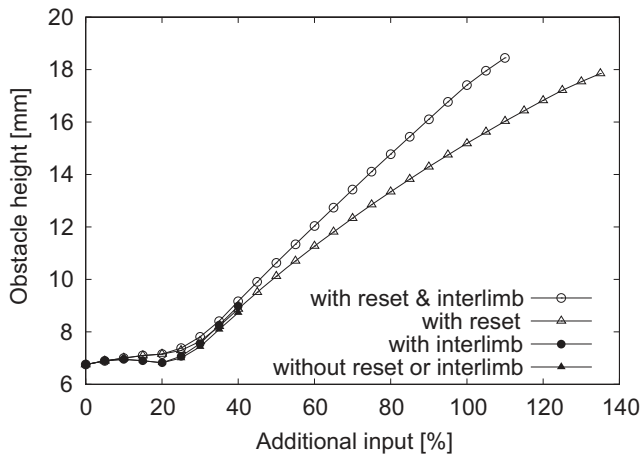


Fig. 6. Comparison of obstacle height between with and without phase regulations based on phase resetting and interlimb coordination

additional rectangular pulses and examined what height of obstacle our model steps over without falling down. In particular, we compared four cases; 1. without phase modulation; 2. with phase modulation based on interlimb coordination; 3. with phase modulation based on phase resetting; and 4. with phase modulation based on both phase resetting and interlimb coordination.

Figure 6 shows the height of the obstacle that our model stepped over for various magnitudes of the additional inputs. When we did not use the phase modulation based on phase resetting, our model easily fell down and could step over an obstacle of at best 9 mm (40% of additional inputs), showing that the phase modulation based on phase resetting contributes to quick recovery after stepping over the obstacle. The phase regulation based on interlimb coordination allowed our model to clear high obstacles. Although our model with the phase modulation by phase resetting also could step over high obstacles, it needs more magnitude of additional inputs than our model with both phase resetting and interlimb coordination. By using the phase modulation based on both phase resetting and interlimb coordination, our model cleared higher obstacles than the other three cases using the same additional inputs without falling over after stepping over obstacles.

The contribution of the phase modulation based on phase resetting to quick recovery after being disturbed has been demonstrated in the previous study [1], [29], [30]. To investigate the contribution of the phase modulation based on interlimb coordination, we examined the relationship between the times for the foot-contact of the lead limb and the onset of the additional input of the trail limb for the case without phase modulation based on interlimb coordination. Figure 7 shows this relationship. As the additional input for the lead limb increases, the tip height of the lead limb increases and the foot-contact of the lead limb is delayed. When the additional input is larger than 20%, the foot-contact of the lead limb is behind the onset of the additional input for the trail limb. In this case, our model starts stepping

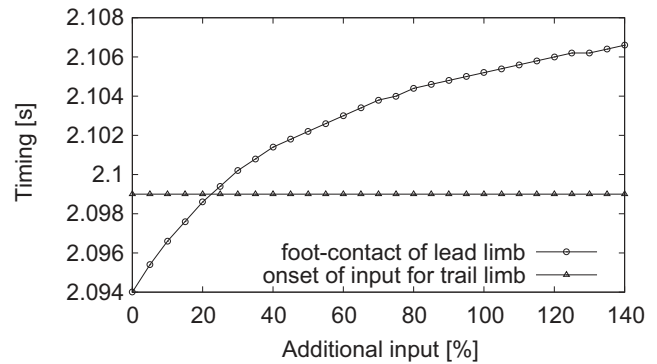


Fig. 7. Relationship between times for foot contact of lead limb and onset of input of trail limb for the case without phase regulation based on interlimb coordination

over an obstacle without supporting by the contralateral limb. This decreases the performance of the obstacle avoidance.

IV. CONCLUSION

In this paper, we investigated the obstacle avoidance in locomotion of the rat using a neuromusculoskeletal model. We constructed a musculoskeletal model of the hindlimbs based on the measured anatomical data and constructed a nervous system model based on CPG and muscle synergy. In addition, we incorporated sensory regulation models based on interlimb coordination and phase resetting and investigated their functional roles during obstacle avoidance in locomotion.

For a successful obstacle avoidance in locomotion, the following two factors are crucial; 1. the lead and trail limbs step over an obstacle without collision and 2. the walking behavior recovers soon after obstacle avoidance [28]. As the obstacle height increases, the toe height of the lead and trail limbs have to be increased, which disturbs the postural behavior and causes instability and falling down. Therefore, stepping over a high obstacle and recovery soon after stepping over the obstacle are not consistent. In this paper, we employed two sensory regulation models; 1. based on phase resetting using the foot-contact information of the ipsilateral limb and 2. based on interlimb coordination using the foot-contact information of the contralateral limb. Our simulation results show that the phase regulation based on interlimb coordination contributes to stepping over a high obstacle and that the phase modulation based on phase resetting contributes to quick recovery after stepping over the obstacle.

In this paper, we focused on the implementation of stepping over an obstacle using additional inputs. However, the modification of walking behavior during the approach phase prior to reaching the obstacle is also important [2], [5], [21], [24], [28]. In addition, we confined our musculoskeletal model to two dimensions and did not use the forelimbs or phalangeal part of feet in the hindlimbs. We should incorporate more plausible and sophisticated models in future studies.

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REFERENCES

- [1] S. Aoi, N. Ogihara, T. Funato, Y. Sugimoto, and K. Tsuchiya, *Evaluating functional roles of phase resetting in generation of adaptive human bipedal walking with a physiologically based model of the spinal pattern generator*, Biol. Cybern., 102(5):373–387, 2010.
- [2] G.P. Austin, G.E. Garrett, and R.W. Bohannon, *Kinematic analysis of obstacle clearance during locomotion*, Gait Posture, 10:109–120, 1999.
- [3] R.E. Burke, A.M. Degtyarenko, and E.S. Simon, *Patterns of locomotor drive to motoneurons and last-order interneurons: Clues to the structure of the CPG*, J. Neurophysiol., 86:447–462, 2001.
- [4] T.J. Burkholder and T.R. Nichols, *Three-dimensional model of the feline hindlimb*, J. Morphol., 261(1):118–129, 2004.
- [5] L.S. Chou and L.F. Draganich, *Increasing obstacle height and decreasing toe-obstacle distance affect the joint moments of the stance limb differently when stepping over an obstacle*, Gait Posture, 8:186–204, 1998.
- [6] 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.
- [7] 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.
- [8] J. Duysens, *Fluctuations in sensitivity to rhythm resetting effects during the cat's step cycle*, Brain Res., 133(1):190–195, 1977.
- [9] 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.
- [10] S. Grillner, *Locomotion in vertebrates: central mechanisms and reflex interaction*, Physiol. Rev., 55(2):247–304, 1975.
- [11] 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.
- [12] Y.P. Ivanenko, R.E. Poppele, and F. Lacquaniti, *Motor control programs and walking*, Neuroscientist, 12(4):339–348, 2006.
- [13] 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.
- [14] D.G. Ivashko, B.I. Prilutsky, S.N. Markin, J.K. Chapin, and I.A. Rybak, *Modeling the spinal cord neural circuitry controlling cat hindlimb movement during locomotion*, Neurocomputing, 52-54:621–629, 2003.
- [15] S. Jo and S.G. Massaquoi, *A model of cerebrocerebello-spinomuscular interaction in the sagittal control of human walking*, Biol. Cybern., 96:279–307, 2007.
- [16] S. Jo, *Hypothetical neural control of human bipedal walking with voluntary modulation*, Med. Bio. Eng. Comput., 46:179–193, 2008.
- [17] W.L. Johnson, D.L. Jindrich, R.R. Roy, and V.R. Edgerton, *A three-dimensional model of the rat hindlimb: Musculoskeletal geometry and muscle moment arms*, J. Biomech., 41(3):610–619, 2008.
- [18] T. Kondo, S. Aoi, D. Yanagihara, S. Aoki, H. Yamaura, N. Ogihara, A. Ichikawa, and K. Tsuchiya, *Development of a musculoskeletal model of the hind legs of the rat based on anatomical data and generation of locomotion based on kinematic data*, Proc. SICE Ann. Conf., pp. 2308–2310, 2010.
- [19] S.N. Markin, A.N. Klishko, N.A. Shevtsova, M.A. Lemay, B.I. Prilutsky, and I.A. Rybak, *Afferent control of locomotor CPG: insights from a simple neuromechanical model*, Ann. N.Y. Acad. Sci., 1198:21–34, 2010.
- [20] G.N. Orlovsky, T. Deliagina, and S. Grillner, *Neuronal control of locomotion: from mollusc to man*, Oxford University Press, 1999.
- [21] A.E. Patla and M. Greig, *Any way you look at it, successful obstacle negotiation needs visually guided on-line foot placement regulation during the approach phase*, Neurosci. Lett., 397:110–114, 2006.
- [22] 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.
- [23] I.A. Rybak, K. Stecina, N.A. Shevtsova, and D.A. McCrea, *Modelling spinal circuitry involved in locomotor pattern generation: insights from the effects of afferent stimulation*, J. Physiol., 577(2):641–658, 2006.
- [24] Y. Sato, S. Aoki, and D. Yanagihara, *Gait modification during approach phase when stepping over an obstacle in rats*, Neurosci. Res., in press.
- [25] 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.
- [26] M.L. Shik and G.N. Orlovsky, *Neurophysiology of locomotor automatism*, Physiol. Rev., 56(3):465–501, 1976.
- [27] G. Taga, *A model of the neuro-musculo-skeletal system for human locomotion I. Emergence of basic gait*, Biol. Cybern., 73: 97–111, 1995.
- [28] G. Taga, *A model of the neuro-musculo-skeletal system for anticipatory adjustment of human locomotion during obstacle avoidance*, Biol. Cybern., 78:9–17, 1998.
- [29] S. Yakovenko, V. Gritsenko, and A. Prochazka, *Contribution of stretch reflexes to locomotor control: A modeling study*, Biol. Cybern., 90: 146–155, 2004.
- [30] T. Yamasaki, T. Nomura, and S. Sato, *Possible functional roles of phase resetting during walking*, Biol. Cybern., 88:468–496, 2003.
- [31] 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(3):241–244, 1993.
- [32] 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.