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

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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 [1–6]. 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 [7–17].

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 [18,19] and position-sensitive afferents from the hip [20,21]. Ekeberg and Pearson [8] 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:

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

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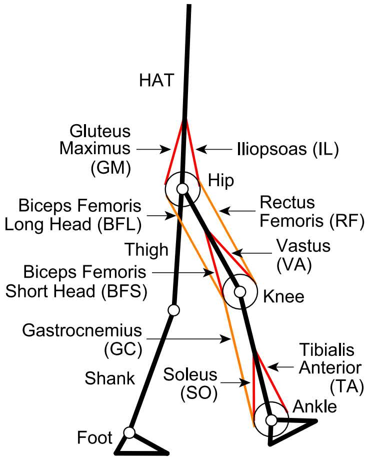

Fig. 1. Musculoskeletal model [22,23]. The skeletal model is composed of seven rigid links that represent HAT (head, arms, and trunk), thighs, shanks, and feet and the muscle model for one leg is composed of nine principal muscles; six muscles (IL, GM, VA, BFS, TA, and SO) are uniarticular, and three (RF, BFL, and GC) are biarticular.

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 [22], 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 [8]. 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 extension rule to produce robust bipedal walking against disturbances, as observed in [8], suggesting that such a sensorimotor mechanism is a general property and is also embedded in the neuro-control system of human bipedal walking.

2. Model

2.1. Musculoskeletal model

We used the musculoskeletal model in [22,23], originally constructed in [24] (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 [22,23]. 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 [22] (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

$$u_m = Mov_m + Pos_m \tag{1}$$

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

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 [1,3,5]. Their organization remains unclear, and various CPG models have been proposed [25,26]. However, recent neurophysiological findings suggest that CPGs consist of hierarchical networks composed of rhythm generator (RG) and pattern formation (PF) networks [27–30]. 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

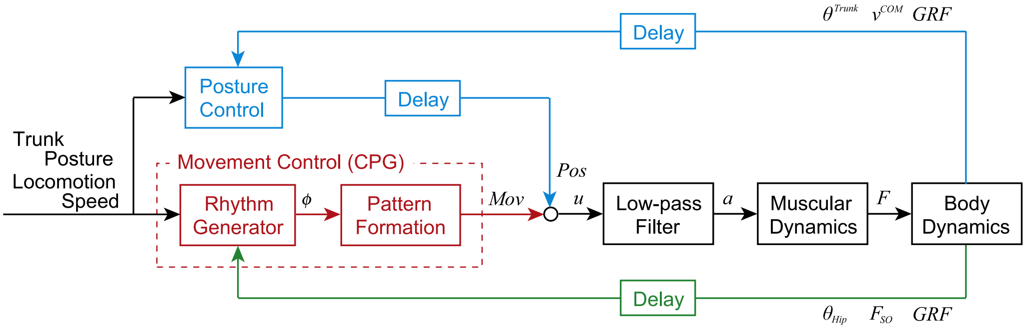

Fig. 2. Nervous system model. Red blocks and arrows indicate movement control, blue blocks and arrows indicate posture control, and green blocks and arrows indicate phase resetting (see color figure in the web version).