

# A model of the neuro-musculo-skeletal system for anticipatory adjustment of human locomotion during obstacle avoidance

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**Abstract.** Theoretical studies on human locomotion have shown that a stable and flexible gait emerges from the dynamic interaction between the rhythmic activity of a neural system composed of a neural rhythm generator (RG) and the rhythmic movement of the musculo-skeletal system. This study further explores the mechanism of the anticipatory control of locomotion based on the emergent properties of a neural system that generates the basic pattern of gait. A model of the neuro-musculo-skeletal system to execute the task of stepping over a visible obstacle with both limbs during walking is described. The RG in the neural system was combined with a system referred to as a discrete movement generator (DM), which receives both the output of the RG and visual information regarding the obstacle and generates discrete signals for modification of the basic gait pattern. A series of computer simulations demonstrated that an obstacle placed at an arbitrary position can be cleared by sequential modifications of gait: (1) modulating the step length when approaching the obstacle and (2) modifying the trajectory of the swing limbs while stepping over it. This result suggests that anticipatory adjustments are produced not by the unidirectional flow of the information from visual signals to motor commands but by the bi-directional circulation of information between the DM and the RG. The validity of this model is discussed in relation to motor cortical activity during anticipatory modifications in cats and the ecological psychology of visuo-motor control in humans.

## 1 Introduction

Neurophysiological experiments in animals have revealed that rhythmic movements such as locomotion are generated by central pattern generators (CPGs), which exist at a relatively low level of the central nervous system such as the spinal cord (Grillner 1985). Although movements that are generated by CPGs are stereotypical, this does not necessarily mean that motor patterns are strictly programmed and that movements lack flexibility and adaptability. Theoretical studies on locomotor control have shown that CPGs are complex adaptive systems where movements emerge

from the dynamic interaction among the neural system, the body and the environment in a self-organized manner (Taga et al. 1991). Such emergent properties of the system provide some adaptability to unpredictable changes in the environment. However, it is still unclear how movements are planned based on anticipation when confronted with drastic changes in the environment. For instance, when we step over an obstacle during walking, the path of limb motion must be quickly and precisely controlled so as to place the foot in a specific spatial location while avoiding the obstacle along the path. In this case, on-going movements must be adjusted in an anticipatory manner using visual information. A question addressed in this paper is how the emergent generation and the anticipatory planning of movements are reconciled in the task of obstacle avoidance during walking.

A model of the neuro-musculo-skeletal system for human locomotion (Taga 1995a) demonstrated that generation of the basic gait over even terrain takes the form of a limit cycle attractor which emerges from global entrainment between the rhythmic activity of a neural system composed of a neural rhythm generator and the rhythmic movement of the musculo-skeletal system. As long as the stability of the attractor is maintained, the locomotor system can generate an adaptive gait even in an unpredictable environment (Taga 1995b). Based on the structural stability of the attractor, it is also possible for a higher center in the neural system to plan and produce various locomotor patterns depending on the task requirements (Taga 1995b). However, this type of control is valid only when changes in the environmental and task constraints occur relatively slowly compared with the time scale of the rhythm of walking, or when the ability to walk is not severely affected by transient states of movements which occur after sudden changes in the constraints. In obstacle avoidance during walking, the basic gait pattern must be quickly modified to clear an obstacle safely, and transient states after clearing the obstacle must be suppressed to maintain the stability of locomotion. The purpose of this paper is to explore the mechanisms that overcome these problems to produce anticipatory adjustments of locomotion.

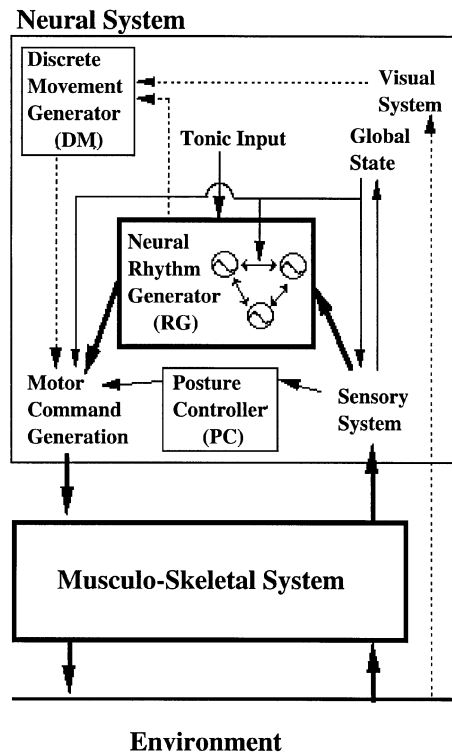
There now exists abundant evidence in cats that the motor cortex is involved in anticipatory changes in limb move-

ment during walking. The discharge frequency of neurons within the motor cortex markedly increases in visually initiated modifications of gait when animals are required to step over obstacles (Drew 1988). Furthermore, it has been shown that the motor cortex supplies detailed information about the altered step that is needed to modify the activity patterns of different groups of muscles at different times during gait modification (Drew 1993, 1994). Considering that decerebrated cats are only able to produce steady walking, the motor cortex must play a specific role in the discrete modification of rhythmic movements based on visual information.

Although studies of locomotion in humans have focused on the steady state of gait, volitional aspects of locomotor control in a changing environment are progressively attracting more attention. When subjects intend to walk at a given speed, that speed is attained with an invariant combination of the step length and frequency in the steady state (Nilsson and Thorstensson 1987). This invariant relationship can be intentionally modulated given external cues. Bonnard and Pailhous (1993) showed that when subjects were required to change their step length temporarily, they could execute such tasks very quickly without changing their step frequency. Zijlstra et al. (1995) showed that if either the step length or frequency is constrained by external cues, the other tends to remain unchanged. Patla et al. (1989) focused on the effect of the timing of visual cues for changing step length by analyzing changes in ground reaction forces. These studies demonstrated that only specific parameters of locomotion can be quickly and precisely modulated. On the other hand, an analysis of limb movements in clearing an obstacle during walking showed specific changes in the patterns of ground reaction forces, joint torques and electromyograms (EMGs) (McFadyen and Winter 1991; Patla et al. 1991; McFadyen et al. 1993). These experiments suggest that not only the modulation of specific parameters of locomotion but also the modification of the basic gait pattern occurs in obstacle avoidance.

The computational theories of motor control have claimed that goal-directed movements are generated in a feedforward manner by using an internal model of the body and the environment, which might be acquired through learning by the cerebellum (Kawato et al. 1987; Jordan 1990). Along this line, McFadyen et al. (1994) proposed an algorithm to calculate joint angle trajectories in an obstructed gait from a stereotypic unobstructed pattern in human locomotion based on experimental data, and to generate the necessary joint torque based on feedforward and feedback control. However, this model is only valid under the assumption that the planning of joint trajectories and the generation of motor commands are independent and sequential processes in the central nervous system. If the joint trajectories of the basic gait emerge from the non-linear dynamics of the system in which kinematics and dynamics are inseparable (Taga et al. 1991; Taga 1995a), a central question is how the anticipatory mechanism and the pattern-generating mechanism interact with each other to produce relevant movements.

In this paper, I focus on obstacle avoidance during walking and examine whether combining a new mechanism for anticipatory control with the previous model of the neuro-musculo-skeletal system that generates the basic gait pattern



**Fig. 1.** A model of the neuro-musculo-skeletal system for the anticipatory control of walking. The basic structure is the same as that described by Taga (1995a). The discrete movement generator (DM) and the flow of information illustrated by the *dotted arrows* are combined with the previous model

(Taga 1995a) can produce rapid adjustments of locomotion to execute the task.

## 2 Model of the neuro-musculo-skeletal system for an obstructed gait

### 2.1 Outline of the model

Figure 1 shows the outline of the model of obstacle avoidance during walking. Steady-state walking on flat ground is generated by the model of the neuro-musculo-skeletal system (Taga 1995a). The model is composed of two dynamical systems: a musculo-skeletal one and a neural one. The musculo-skeletal system is modeled as eight rigid segments: HAT (head, arms and trunk), pelvis and the lower limbs, each of which consists of a thigh, shank and foot. Twenty muscles are considered: six single-joint muscles and three double-joint muscles for one limb and two trunk muscles. The triangular foot interacts with the ground at its heel and/or toe. The equations of motion in the sagittal plane are derived using the Newton-Euler method. The body parameters reflect those of an adult. The neural system contains a neural rhythm generator (RG), which is composed of seven pairs of neural oscillators, each of which controls the movement of a corresponding joint of the body. Each neural oscillator takes the form of a half-center model which is expressed by a set of differential equations. The activity of all the neural oscillators in the RG is regulated by tonic input. Sensory signals which indicate the current state of the musculo-skeletal

system and the environment are processed and sent to the RG. The steady-state gait within a step cycle is represented by a cyclic sequence of six global states which are calculated from the sensory signals. The global states are used to modulate the amplitude of the motor commands and sensory signals and the connections between neural oscillators in the RG. In parallel with the RG, the posture controller (PC) regulates the impedance of the joints to maintain the static stability of the stance limbs and the upright posture of the HAT. These parts of the model generate a steady-state gait in the form of a limit cycle attractor.

Let us consider a task which consists of approaching an obstacle during steady-state walking, modulating the step length to provide better placement of a stance limb, stepping over it with a swing limb, straddling it with both limbs, clearing it with the other limb and continuing to walk. Although visual information processing is one of the essential elements of this task, advance information about obstacles and their location is postulated to be available. Since an obstacle can be seen at least several seconds before executing the task, there is enough time to perceive it and plan modifications of the ongoing movement. In this paper, a discrete movement generator (DM) is newly incorporated to achieve anticipatory adaptation to changes in the environment. It is assumed that the DM perceives the location of the obstacle and decides when to initiate adjustments of on-going walking patterns. The control problem is then divided into two sub-tasks: to modulate the step length before clearing an obstacle to provide stable and better placement of the foot, and to modify the basic gait pattern while clearing the obstacle. The DM sequentially generates motor signals for these sub-tasks.

## 2.2 Modulation of step length

Although there are several strategies for regulating step length, it is assumed that only the last step before clearing an obstacle is shortened or lengthened according to the location of the obstacle. There are several possible ways to control the step length within the framework of this model. Changes in the value of the tonic input to the RG produce changes in the walking speed with a specific combination of step length and frequency (Taga 1995b). This characteristic corresponds to the observation that human subjects prefer a certain combination of step length and frequency at a given speed (Nilsson and Thorstensson 1987). However, the transition from one step length to another due to changes in the level of the tonic input requires considerably long transient states. A similar observation in human subjects was made by Bonnard and Pailhous (1993). This mechanism, therefore, is not appropriate for making rapid changes in the step length. Another way to control the step length is to change the gain level of the RG's output to the muscles. Changes in all the values of the gain parameters in a nonspecific way are also followed by considerably long transient states before the step length is changed. In contrast, specific changes in the gain level of specific muscles provide rapid changes in the step length. For instance, slight changes in the timing and strength of the hip and ankle extensor activity greatly affect the step length, since these muscles are responsible for generating

forces for forward progression. We adopt this mechanism involving the specific modulation of muscle torque as the means by which the DM produces temporal changes in step length.

In ordinary walking, the muscle torque generated by the output of the RG can be written in a general form as

$$\begin{aligned} T_{mr} &= p s_g f(u) \\ (f(u) &= \max(0, u)) \end{aligned} \quad (1)$$

where  $p$  sets the gain level of the output of the RG to the muscle,  $s_g$  is the global state which takes a value 0 or 1, and  $u$  is the activity of the RG. The muscle torque modulated by the DM is defined in general form as

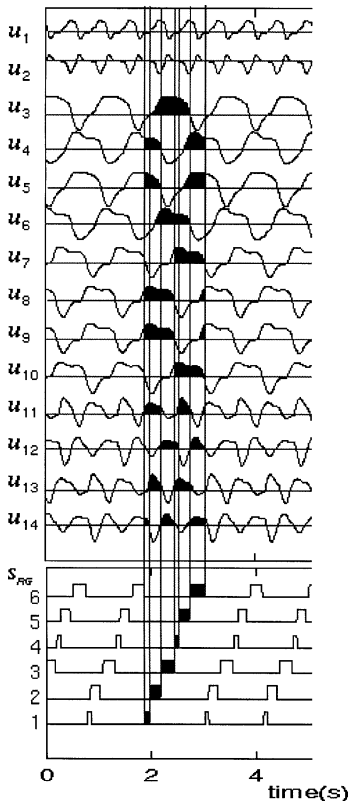
$$q(t) = \begin{cases} q & (t_1 \leq t \leq t_2) \\ 0 & (t < t_1, t > t_2) \end{cases} \quad (2)$$

$$T'_{mr} = p s_g (1 - q(t) s_{RG}) f(u) \quad (3)$$

where  $q$  determines the strength of the modulation of the output of the RG. In ordinary walking,  $q$  is zero. When the step length is modulated,  $q$  takes a specific value that is determined according to the location of the obstacle. Muscle torque decreases when  $q$  has a positive value, while muscle torque increases when  $q$  has a negative value;  $t_1$  and  $t_2$  are roughly chosen so that they only set the initiation and termination of the entire process of the modulation of the step length. The precise timing of the generation of modulation signals is determined by the ongoing activity of the RG. The current state of the RG within a step cycle is abbreviated as the RG global state  $s_{RG}$ . Each step cycle is represented as a cyclic sequence of six RG global states: the double-support phase, which begins with the right limb striking the ground (state 1), the first half of the single-support phase with left limb swinging (state 2), the second half of the single-support phase (state 3), and the subsequent three states which are symmetrical to the former three states (states 4, 5 and 6). The value of  $s_{RGi}$  is chosen such that  $s_{RGi} = 1$  only when the current state is the  $i$ th state of the gait cycle; otherwise,  $s_{RGi} = 0$ . Each RG global state is defined by multiplication of a set of active neurons, as shown in Appendix A. Figure 2 demonstrates the activity of neurons of the RG and the RG global state in the steady state of walking obtained by computer simulation. In summary, the DM receives both visual information regarding the obstacle and the current state of the activity of the RG, as shown in Fig. 1, and produces modulation signals for a specific muscle torque at specific times.

## 2.3 Modification of the gait pattern

The joint torque estimated from the joint trajectory (McFadyen et al. 1993) and the EMG (Patla et al. 1991) while clearing an obstacle in human subjects suggests the reorganization of motor strategies toward active knee flexion which is not observed in walking on level terrain. Such reorganization cannot be achieved simply by modulating motor commands through changes in the tonic input and the output gain of the RG. Here it is assumed that the DM generates a sequence of discrete motor signals for specific muscles and that the final



**Fig. 2.** The activity of the neural rhythm generator (RG) and the RG global state. A result of the computer simulation of the steady-state walking is shown.  $u_i$  ( $i = 1, 14$ ) shows the activity of each neuron of the RG;  $u_1$  trunk flexor,  $u_2$  trunk extensor,  $u_3$  hip flexor (right),  $u_4$  hip extensor (right),  $u_5$  hip flexor (left),  $u_6$  hip extensor (left),  $u_7$  knee flexor (right),  $u_8$  knee extensor (right),  $u_9$  knee flexor (left),  $u_{10}$  knee extensor (left),  $u_{11}$  ankle flexor (right),  $u_{12}$  ankle extensor (right),  $u_{13}$  ankle flexor (left) and  $u_{14}$  ankle extensor (left).  $s_{RG}$  was calculated by multiplication of the activity of neurons, as shown in the Appendix A. Vertical lines and areas painted black in the figure indicate the relationship between the activity of the RG and the RG global state. Neural activities which are painted black determine the value of the specific RG global state. For instance, when  $u_4, u_5, u_8, u_9, u_{11}, u_{14}$  are active,  $s_{RG1} = 1$

muscle activation pattern is determined by the weighted sum of the signals from the RG and the DM.

The modified muscle torque for clearing an obstacle is defined in general form as

$$r = \begin{cases} r & (t_3 \leq t \leq t_4) \\ 0 & (t < t_3, t > t_4) \end{cases} \quad (4)$$

$$T'_{mr} = p s_g f(u) + r(t) s_{RG} (= T_{mr} + r(t) s_{RG}) \quad (5)$$

where  $r$  determines the strength of the modification signal according to the obstacle height. Like parameter  $q$ ,  $r$  takes a specific value when the gait pattern is modified;  $t_3$  and  $t_4$  are roughly chosen so that they only set the initiation and termination of the entire process of gait modification;  $r$  is multiplied by the  $s_{RG}$  so that the precise timing of the initiation and termination of the generation of the modification signals is determined by the RG global states. The same modification is applied to the second limb that passes over the obstacle. The first and second limbs that pass over an obstacle are called the lead and trail limbs, respectively. When

an obstacle is placed at an arbitrary position and modulation of the step length is required, it is assumed that modulation of the step length and modification of the gait pattern are executed sequentially.

## 2.4 Method for the computer simulation

A series of computer simulations was conducted. The differential equations of the neural and musculo-skeletal system were integrated numerically. The fourth-order Runge-Kutta-Gill method was used for the integration, with a time step of 0.25 ms. The inverse matrix of the equations of motion of the musculo-skeletal system was calculated by the Cholesky decomposition method. See Taga (1995a) for details of the equations. Calculations were performed on a JP4 workstation (Japan Computer Corp.).

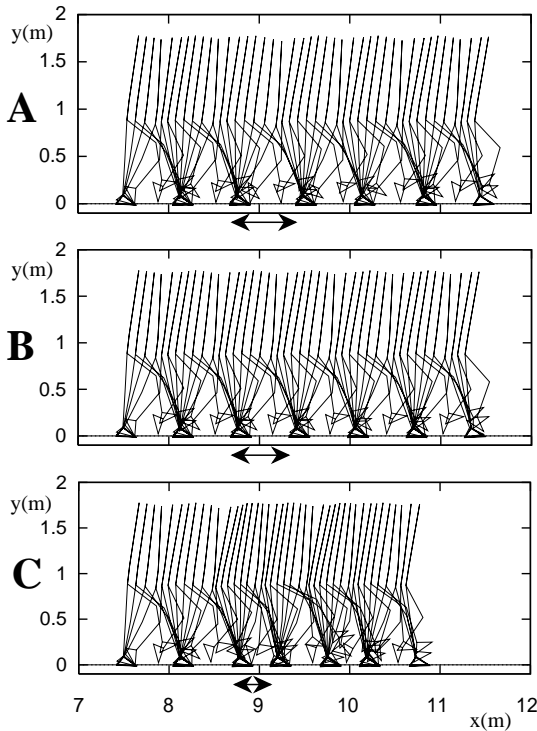
## 3 Results of computer simulation

### 3.1 Modulation of step length

As a first step toward obstacle avoidance, modulation of the step length during steady-state walking was simulated by computer. To realize rapid modulation of the step length by the action of the DM, modulations of various muscles at timings determined by various RG global states were examined. When the modulation signals did not match the motor signals for basic locomotion, they disturbed the stable limit cycle of the basic gait, and this was followed by very long transient states or falling down. It was found that an effective strategy for controlling the step length was to modulate specifically the ankle extensor torque, which is responsible for forward progression, at the end of the stance phase and the hip flexor torque at the beginning of the swing phase. When the position of contact of the left limb was controlled, the action by the DM was applied to the ankle extensor of the left limb in states 6 and 1 and to the hip flexor of the same limb in states 1 and 2. Equations that define DM signals are shown in Appendix B(a). For simplicity, the same values of  $q$  were used to modulate ankle and hip torque. The computer simulation showed that the step length could be controlled continuously by monotonous changes in the value of  $q$ . Figure 3 shows typical examples of stick figures of walking with various values of  $q$ . While the step length of the unmodulated gait ( $q = 0$ ) was 64.5 cm, the shortest step length was 39.6 cm ( $q = 0.7$ ), and the longest step length was 72.6 cm ( $q = -0.2$ ). Within this range for the value of  $q$ , the step length changed quickly and stable walking was maintained. Modulations with a value of  $q$  outside this range caused instability and falling down.

### 3.2 Modification of gait pattern

Movements for clearing an obstacle were simulated under the special condition in which the obstacle occurred at the mid-point of swing and the step length did not need to be controlled. It was found that an effective way to obtain a smooth change in gait pattern was to activate the knee flexor



**Fig. 3A–C.** Stick figures of the modulation of step length during walking. The first two steps show walking in the steady state. The step length of the third step is then modulated. **A** Lengthening of the step length,  $q = -0.2$ . **B** Walking without modulation,  $q = 0$ . **C** Shortening of the step length,  $q = 0.6$ . Arrows in **A** and **C** show the modulated step length, which can be compared with the arrow in **B**, which indicates the step length in unobstructed walking

torque of the limb that passes over the obstacle from the end of the double-support phase until the beginning of the swing phase, and to activate the knee extensor torque of the same limb at the middle of the single-support phase. It was assumed that the same modification signals were applied to the trail limb. The RG global state that is generated by the efferent signals from the RG is responsible for determining the timing of the generation of modification signals. When the right limb was the lead limb and the left limb was the trail limb, modification by the DM was sequentially applied to (1) the knee flexor of the lead limb in state 4, (2) the knee extensor of the trail limb in state 5, (3) the knee flexor of the trail limb in state 1, and (4) the knee extensor of the trail limb in state 2. Equations that define the DM signals are shown in Appendix B(b). The amplitude of the modification signal for each was referred to as  $r_1, r_2, r_3, r_4$ , respectively. These four parameters had to be adjusted to produce a smooth and coordinated change in gait. The stick figures of movements shown in Fig. 4 demonstrate that the height of the trajectory of the toe can be controlled by changes in the values of  $r$ .

Activation of the torque of the knee flexor contributed to the active bending of the knee joint, which produced changes in the trajectory of the toe to go over the obstacle. Although obstacle avoidance was successfully achieved by modifying the torques of only single-joint muscles of the knee, modifications of other muscles can contribute to this task. For example, single-joint muscles of the hip and double-joint

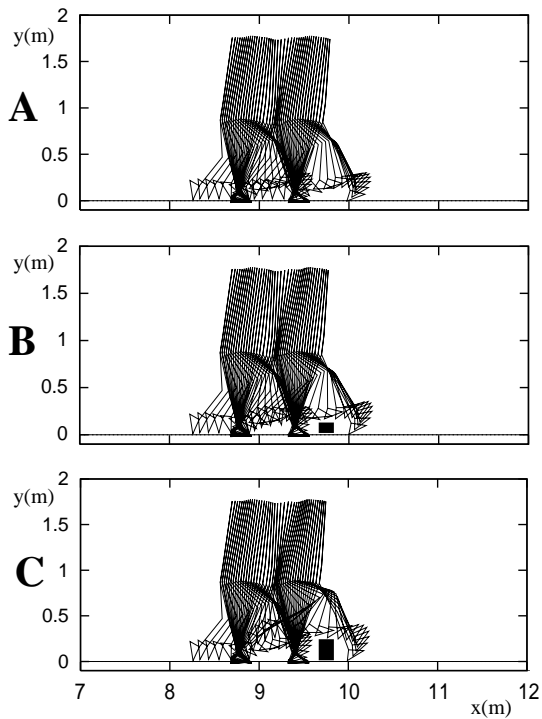
muscles of the hip and knee should be involved in this task. In fact, a combination of modification signals of the muscle torque of the hip flexor and the hamstrings (hip extensor and knee flexor) could produce the same modified torque of knee flexion. Given the redundant character of the muscular system, in which activation of different sets of muscles can generate the same joint torque, the results of the simulations indicate that the simplest case was successful in performing this task.

Activation of the torque of the knee extensor was also found to be necessary for stable movement, since walking was strongly perturbed and resulted in falling down when the modification signals were not applied to the knee extensors following active knee flexion. The extensor torque contributed to the quick positioning of the foot on the ground. It should be noted that the active extension of the knee joint is absent during the swing phase of walking on level ground. From a dynamical point of view, the role of the active extension of the knee joints of the swing limb is to return the system's state, which is perturbed by active flexion of the knee, back to the steady state as quickly as possible.

### 3.3 Obstacle avoidance

Finally, movement in clearing an obstacle placed in an arbitrary position was simulated. The height of the obstacle was fixed at 15 cm. The location of the obstacle was systematically determined as follows. The walking pathway along one step length which was estimated from the steady-state walking was divided into six sections. The width of the obstacle was then set at 10.8 cm. The obstacle was placed at one of the sections from the near position to the far position. When the obstacle was placed at the near and far positions, which overlap with those of foot contact during unobstructed walking, anticipatory regulation of the stride length is required to avoid collision. It was assumed that the DM generates the modulation signal for regulating the step length according to the location of the obstacle and subsequently generates modification signals for stepping over the obstacle by the lead and trail limbs. The final activation pattern of the muscles is the weighted sum of the descending signals from the DM and the intrinsic properties of the RG.

Figure 5 shows typical examples of stick pictures of the movements in obstacle avoidance. When the obstacle was placed at the middle position, as shown in Fig. 5A, regulation of the step length was not required, and the obstacle was cleared at the mid-point of the swing. When the obstacle was placed at the near position, as shown in Fig. 5B, the step length was shortened by choosing a positive value of  $q$ , and the gait pattern was subsequently modified to go over the obstacle. Since the trajectory of the toe that steps over the obstacle in the near position must reach the maximal height earlier than when the obstacle is in the middle position, a slight adjustment of parameters  $r$  was required to increase the muscle torque of the flexor and extensor of the knee. When the obstacle was placed at the far position, the step length was lengthened by choosing a negative value of  $q$ , as shown in Fig. 5C. In this case, a slight adjustment of  $r$  was required to maintain the stability of locomotion which was disturbed by the change in step length. From



**Fig. 4A–C.** Stick figures of the modification of the gait pattern with various step heights. **A** Stepping without modification,  $r_i = 0 (i = 1, 4)$ . **B** Stepping over a low obstacle,  $r_1 = 22.5$ ,  $r_2 = 7.5$ ,  $r_3 = 22.5$ ,  $r_4 = 7.5$ . **C** Stepping over a high obstacle,  $r_1 = 54.0$ ,  $r_2 = 18.0$ ,  $r_3 = 54.0$ ,  $r_4 = 18.0$

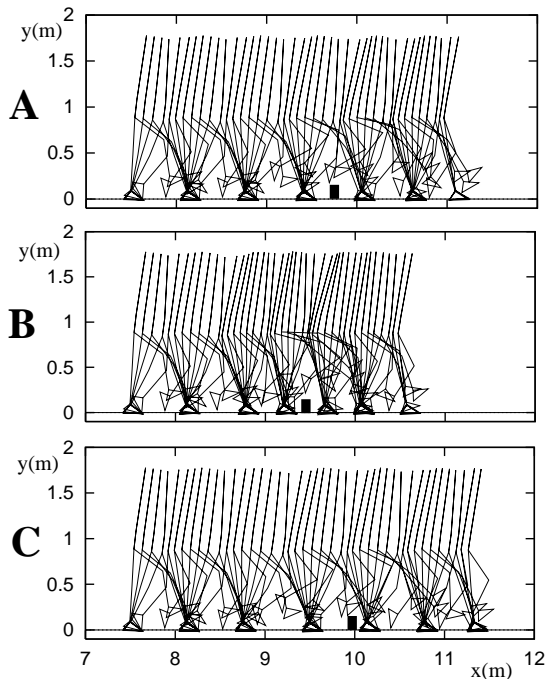
these simulations, it was found that an obstacle placed at various proximities can be cleared when appropriate values of the parameters  $q$  and  $r$  are chosen. In Fig. 6, the RG global state and the muscle torque of the steady-state gait over even terrain (Fig. 6A) are compared with those when clearing an obstacle placed at the near position (Fig. 6B). Only the muscle torques which are modulated or modified by the DM are presented. The time courses of the RG global states were almost the same in both cases, indicating that signals from the DM were chosen so as not only to execute the task but also to suppress transient states and maintain the stability of locomotion.

## 4 Discussion

### 4.1 Emergent generation and anticipatory control of movements

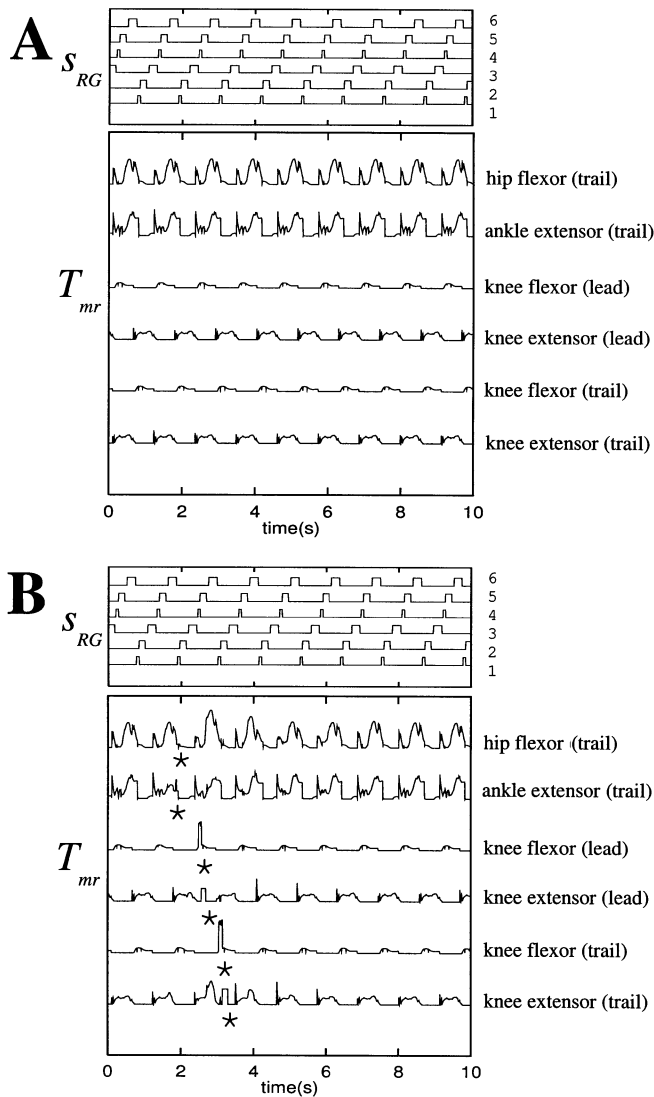
This model gives a concrete example of how environmental information relates to the internal dynamics of the neural system to adapt to a changing environment. The essential point is that the DM integrates both advance information regarding the obstacle and the current state of the RG to produce appropriate signals for modification of the gait. This mechanism makes it possible not only to produce quick adjustments of movements depending on task requirements, but also to establish the stability of locomotion for the entire system.

A series of computer simulations demonstrated anticipatory adjustments of locomotion, which can be compared with those of human subjects. The earlier study showed that most



**Fig. 5A–C.** Stick figures of stepping over obstacles placed at various positions. The height of the obstacle is 15 cm and the width is 10.8 cm. **A** Middle condition,  $q = 0$ ,  $r_1 = 45.0$ ,  $r_2 = 15.0$ ,  $r_3 = 45.0$ ,  $r_4 = 15.0$ . **B** Near condition,  $q = 0.6$ ,  $r_1 = 45.0$ ,  $r_2 = 25.0$ ,  $r_3 = 55.0$ ,  $r_4 = 30.0$ . **C** Far condition,  $q = -0.25$ ,  $r_1 = 45.0$ ,  $r_2 = 15.0$ ,  $r_3 = 35.0$ ,  $r_4 = 15.0$

of the simulated variables in the steady state of locomotion are comparable to the experimental variables in human subjects (Taga 1995a), although there are some differences such as a high floor clearance of the foot and a large impact on the ground reaction forces in the vertical direction. These differences do not affect the points of the present simulations, since the height of the obstacle was chosen to be sufficiently high as compared with the height of the floor clearance of the foot in the absence of obstructions. The active flexion of the knee during obstacle avoidance in this paper is comparable to the previous reports on human subjects performing a similar task. The predicted joint torque from human subjects (McFadyen and Winter 1991) showed an increase in the flexor torque at the knee joint. The analysis of the EMG (McFadyen and Winter 1991; Patla et al. 1991) showed that double-joint muscles are involved in the active knee flexion. Although this paper used the modification of only the single-joint muscles, the same net joint torque can be obtained by a combination of activation of single-joint and double-joint muscles. Concerning the changes in the stride length when clearing the obstacle with variable proximities, McFadyen et al. (1993) reported that the stride length remained unchanged from unobstructed walking when an obstacle was placed near the foot. However, the position of the obstacle in their experiment does not overlap with that of the foot contact during unobstructed walking, in contrast with the near obstacle of the present paper which forces a change in stride length to avoid collision. Validation of the strategy for modulation of the step length should be addressed in future experimental studies.



**Fig. 6A,B.** Time courses of the RG global states and the muscle torques during the unobstructed and obstructed gaits. **A** Time courses of the RG global states and the muscle torques of the unobstructed gait for reference. **B** Time courses of the RG global states and the muscle torques when clearing the obstacle under the near condition shown in Fig. 5B. Only the muscle torques which are modified by the discrete movement generator (DM) are shown. Asterisks indicate the timing of the application of the signals from the DM

In their model of anticipatory locomotor adjustments, McFadyen et al. (1994) claimed that an obstructed gait can be planned from a stereotypic unobstructed gait pattern. The weighting functions that they proposed have similar roles as those of the DM in the present model, since the DM can be viewed as a kind of internal model that estimates movements capable of clearing the obstacle. However, the two models differ in the basic organization of the movement pattern formation. The model of McFadyen et al. (1994) requires detailed planning of joint angle trajectories and calculation of torque based on the forward or inverse dynamics of the body as the models of motor control by the cerebellum (Kawato et al. 1987; Jordan 1990). In contrast, within the present paper's framework, one does not need to plan a new trajectory for the limb when clearing an obstacle dur-

ing walking. Only the magnitude of the modification of the gait pattern is determined in advance, and the details of the pattern of the obstructed gait emerge from the real-time interaction between the RG and DM. This implies that the indeterminacy problem in the voluntary control of the limbs might be relieved if the intrinsic dynamics of the lower level of the neural system are used to produce voluntary movements. Georgopoulos and Grillner (1989) and Kalaska and Drew (1993) showed neurophysiological evidence that the lower level of the neural system might be used in generating both stereotypical movements such as locomotion and voluntary movements such as reaching.

By extending the present model of the anticipatory control of locomotion, various types of motor control can be explained by a general framework in which the neural system is composed of interacting subsystems: the RG, the DM and the posture controller (PC). The RG consists of coupled neural oscillators and generates various patterns of activity in a self-organized manner. It is responsible for the dynamic stability of movements. On the other hand, the PC is responsible for the stability of the static posture. By coactivating the antagonistic muscles, the PC also regulates the number of effective degrees of freedom of the joints of the body depending on task requirements. In addition to the RG and the PC, the DM generates control signals for discrete movements and regulates transient states of the system. The present results showed that the movements in obstacle avoidance during walking are generated by interaction between the RG and the DM. In other types of movement control, such interactions are important. When humans initiate walking from an upright posture, a steady-state gait is reached within a few steps (Breniere and Do 1986). This implies that the neural system contains a DM that actively controls transient states, and that the interplay between the RG and the DM produces a smooth initiation of gait.

Although the role of the PC was not a focus of the present study, the interaction between the PC and the DM plays a central role in the anticipatory adjustment of posture. For instance, if a voluntary movement of an upper limb is planned and executed independent of the posture control of the entire body, the limb's movement affects the stability of the standing posture. It is known that such a disturbance is prevented by feedforward changes in posture (Massion 1992). This suggests that the anticipatory adjustment of posture is generated by interaction between the PC and the DM. Another example is voluntary movements of the upper limbs during walking, which involve phase-dependent modifications of postural adjustments (Hirschfeld and Forssberg 1991). The anticipatory adjustment of posture during walking suggests that interaction among the RG, the PC and the DM produces such complex behaviors. A study of rhythmical and discrete movements about a single joint (Adamovich et al. 1994) showed that different motor patterns can be superimposed, which is also within the scope of the present framework composed of three subsystems.

#### 4.2 Neural mechanism of obstacle avoidance during locomotion

The well-known phenomenon of infant stepping (Forssberg 1985) and recent studies on adult patients with paraplegia

(Calancie et al. 1994; Dietz et al. 1995) suggest that the mechanism of the generation of the stepping rhythm within the spinal cord might be shared by humans and other animals. However, the fact that patients with cerebral palsy have abnormal gait patterns (Leonard et al. 1991) shows that supraspinal centers might be involved in the generation of the basic pattern of gait in humans, which is in contrast to the mechanism in cats. Although there has been no clear evidence that humans and cats have the same neural architecture for locomotor control, the model of human locomotion based on the neural rhythm generator suggests that the generation of the basic pattern of locomotion is governed by a common principle called global entrainment (Taga et al. 1991; Taga 1995a).

The present model of the obstructed gait in humans demonstrated that a concrete form of interplay between advance information about the obstacle and the on-going dynamics of the neural system produces anticipatory movements. The functional role and the organization of the DM in this model can be compared to those of the motor cortex of cats performing an obstacle avoidance task. The neurons of the primary motor cortex of cats can be divided into different populations of cells that are active at different times during gait modification; one group is associated with the initial flexion of the limb that is needed to bring it above and over the obstacle (phase I), and the second group is associated with increased wrist dorsiflexor muscle activity before foot contact (phase II) (Drew 1993). This strategy for the modification of muscle activity is exactly the same as that of the active flexion and extension of the knee joint induced by signals from the DM in this model. Drew (1993) suggested that the motor cortex takes into account the inherent timing constraints imposed by the spinal network and that the time of the onset of the discharge of neurons is probably determined by the interaction between the central command and information ascending from the spinal cord, and possibly relayed by the cerebellum. The mechanism by which the DM modifies the basic gait pattern in this model is fundamentally in agreement with such mechanisms in cats. Since the cerebellum in cats receives both the output of the CPG and sensory signals (Arshavsky et al. 1984), information regarding the global state and the RG global state in this model might be represented in some form by the interplay among the spinal cord, the cerebellum and the motor cortex.

### 4.3 Ecological theory of action and perception

An essential point of the present paper is that anticipatory behaviour is not produced by unidirectional processing of information from the visual signal to the motor command but rather by the integration of external signals from the visual system with the internal state of the RG by the action of the DM. As to the mechanism for the integration, an obstacle placed at various proximities can be cleared when the value of  $q$  for the control of the step length and the value of  $r$  for the obstacle clearance are appropriately chosen. From a neurophysiological point of view, it is difficult to validate how such parameters in the DM are determined based on the perception of the obstacle. However, it is possible to discuss the relationship between the visual information and

the self-motion at a phenomenological level, which ecological psychology has studied.

Based on the rate of divergence of optical flow that specifies properties about self-motion in relation to the environment, it is possible to detect a simple parameter, tau ( $\tau$ ), that specifies the time-to-contact to obstacles (Lee and Reddish 1981). Does the locomotor system always monitor the time-to-contact to an obstacle and initiate modification of on-going movement when  $\tau$  reaches a certain value? The present model suggests that the parameter  $\tau$  alone does not specify the time of the initiation of gait modification. Since the modulation of on-going movement is possible only at specific phases of the gait cycle during walking, not only  $\tau$  but also information regarding the phase of locomotion constrains the strategy for the anticipatory adjustment of movement. In the present model, the step length can be successfully modulated if a single parameter  $q$  is chosen appropriately according to the relationship between the location of the obstacle and the phase of locomotion at a certain time before the modulation occurs. One way to explicitly relate  $q$  to information about the obstacle is to determine the value of  $q$  as a function of  $\tau$  at a certain RG global state. Since the change in the step length is a monotonous function of  $q$ , it is possible to define  $q$  as a monotonous function of  $\tau$ . Moreover, if the step cycle  $T$  is relatively constant with changes in walking speed,  $\tau$  with reference to the step cycle  $T$  specifies the invariant relationship between the internal phase of the walking movement and the distance to the obstacle. In summary, the parameter  $q$  of the DM can be obtained by using the information on the time-to-contact to the obstacle and the step cycle.

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## Appendix A. The RG global state

The steady gait within a single step cycle is represented as a cyclic sequence of six RG global states. Each RG global state is defined by multiplication of a set of active neurons as follows.

$$s_{RG1} = 1(u_4) 1(u_5) 1(u_8) 1(u_9) 1(u_{11}) 1(u_{14}) \quad (A1)$$

$$s_{RG2} = 1(u_4) 1(u_5) 1(u_8) 1(u_9) 1(u_{11}) 1(u_{13}) \quad (A2)$$

$$s_{RG3} = 1(u_3) 1(u_6) 1(u_8) 1(u_9) 1(u_{12}) 1(u_{14}) \quad (A3)$$

$$s_{RG4} = 1(u_3) 1(u_6) 1(u_7) 1(u_{10}) 1(u_{12}) 1(u_{13}) \quad (A4)$$

$$s_{RG5} = 1(u_3) 1(u_6) 1(u_7) 1(u_{10}) 1(u_{11}) 1(u_{13}) \quad (A5)$$

$$s_{RG6} = 1(u_4) 1(u_5) 1(u_7) 1(u_{10}) 1(u_{12}) 1(u_{14}) \quad (A6)$$

$$1(u) = \begin{cases} 1 & (0.01 < u) \\ 100u & (0 \leq u \leq 0.01) \\ 0 & (u < 0) \end{cases}$$

where  $u_i$   $i = 3, 14$  are the activities of neurons of the RG.



## Appendix B. Muscle torque that is modulated and modified by the DM

### (a) Modulation of the step length

The muscle torques of the hip flexor and ankle extensor are modulated by the DM as follows:

$$T'_{mr-hip-fl-1} = \{p_1 s_{lon} (1 - q(t) s_{RG1}) + p_2 s_{loff} (1 - q(t) s_{RG2})\} f(u_5) \quad (B1)$$

$$T'_{mr-ank-ex-1} = \{p_3 s_{lon} (1 - q(t) s_{RG6} - q(t) s_{RG1}) + p_4 s_{loff}\} f(u_{14}) \quad (B2)$$

where  $T'_{mr-hip-fl-1}$  and  $T'_{mr-ank-ex-1}$  are the modulated muscle torques of the hip flexor of the left limb and the ankle extensor of the left limb, respectively,  $p_1$ ,  $p_2$ ,  $p_3$ , and  $p_4$  are constant parameters which determine the strength of the torque,  $s_{lon}$  and  $s_{loff}$  are global states which indicate the timing of the stance and swing phases of the left limb, respectively, and  $u_5$  and  $u_{14}$  are activities of the neural oscillators for the hip flexor and the ankle extensor of the left limb, respectively.

### (b) Modification of the gait pattern

The muscle torques of the knee flexor and extensor of both limbs are modified by the DM as follows:

$$T'_{mr-knee-fl-r} = T_{mr-knee-fl-r} + r_1(t) s_{RG4} \quad (B3)$$

$$T'_{mr-knee-ex-r} = T_{mr-knee-ex-r} + r_2(t) s_{RG5} \quad (B4)$$

$$T'_{mr-knee-fl-l} = T_{mr-knee-fl-l} + r_3(t) s_{RG1} \quad (B5)$$

$$T'_{mr-knee-ex-l} = T_{mr-knee-ex-l} + r_4(t) s_{RG2} \quad (B6)$$

where  $T'_{mr-knee-fl-r}$  and  $T'_{mr-knee-ex-r}$  are the modified and unmodified muscle torques of the knee flexor of the right limb,  $T'_{mr-knee-ex-r}$  and  $T'_{mr-knee-ex-r}$  are the modified and unmodified torques of the knee extensor of the right limb,  $T'_{mr-knee-fl-l}$  and  $T'_{mr-knee-fl-l}$  are the modified and unmodified muscle torques of the knee flexor of the left limb, and  $T'_{mr-knee-ex-l}$  and  $T'_{mr-knee-ex-l}$  are the modified and unmodified torques of the knee extensor of the left limb, respectively.

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