

Self-organized control of bipedal locomotion by neural oscillators in unpredictable environment

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Abstract. A new principle of sensorimotor control of legged locomotion in an unpredictable environment is proposed on the basis of neurophysiological knowledge and a theory of nonlinear dynamics. Stable and flexible locomotion is realized as a global limit cycle generated by a global entrainment between the rhythmic activities of a nervous system composed of coupled neural oscillators and the rhythmic movements of a musculo-skeletal system including interaction with its environment. Coordinated movements are generated not by slaving to an explicit representation of the precise trajectories of the movement of each part but by dynamic interactions among the nervous system, the musculo-skeletal system and the environment. The performance of a bipedal model based on the above principle was investigated by computer simulation. Walking movements stable to mechanical perturbations and to environmental changes were obtained. Moreover, the model generated not only the walking movement but also the running movement by changing a single parameter nonspecific to the movement. The transitions between the gait patterns occurred with hysteresis.

1 Introduction

Biological systems are characterized by their behavioral patterns with complexity of large degrees of freedom that will be stably and flexibly generated depending on the state of the environment. One of the fascinating examples is found in locomotion. Elucidation of locomotor behavior gives us an important clue as to how the motor pattern is generated through the interplay of motor and sensory systems. On the other hand, the general picture of motor control is that of the controlled body faithfully responding to the commands of the nervous system in a master-slave manner. Since the real environment is generally more complex than can be explicitly represented, a flexible mechanism of the control is necessary to generate the coordinated motor patterns in real time in an indefinite environment.

Neurophysiological studies have revealed that a hi-

erarchical structure is present in locomotor systems. Shik et al. (1966) demonstrated that decerebrate cats could be made to walk on a treadmill by steady electrical stimulation to the midbrain region. Moreover, the animals adopt different gaits depending on the stimulation strength and the speed of the treadmill. This shows that a complex type of behavior can be controlled by a simple type of top-down signal, while it is not determined uniquely by the signal but is influenced by functional and environmental constraints.

Furthermore, rhythmic motor patterns are coordinated by neural circuits referred to as central pattern generators (Grillner 1975, 1985; Selverston 1985 for review). This has inspired theoretical studies of motor pattern generation in isolated neural networks in the absence of sensory feedback (Miller and Scott 1977; Friesen and Stent 1977; Kawahara and Mori 1982; Matsuoka 1985, 1987; Kleinfeld and Sompolinsky 1988; Yuasa and Ito 1990). On the other hand, neurophysiological studies of insect locomotion suggest that sensory feedback is involved in patterning motor activity and that it is more than the modulation of the centrally generated pattern (Bässler 1986; Pearson 1987). How sensory feedback interacts with the central pattern generator to adapt to the environment is still an open question.

Spatio-temporal patterns in nonequilibrium open systems emerge spontaneously from the cooperation among the system's components in a so-called self-organized fashion (Nicolis and Prigogine 1977; Haken 1983). The slaving principle proposed by Haken (1983) has been successfully applied to explain motor coordination at the macroscopic level of observation under fixed constraints (Kelso 1984; Haken et al. 1985; Schöner and Kelso 1988). However we must go one step further to clarify the mechanism of how the macroscopic order of motor patterns is relevantly generated from the interactions of microscopic elements such as neural, musculo-skeletal, and sensory systems under variable constraints of the environment.

The purpose of this paper is to present the principle of such adaptive control of locomotor systems, where neural, musculo-skeletal, and sensory systems behave

cooperatively to adapt immediately to unpredictable changes of environments. For this purpose, we will focus our study on the control of legged locomotion.

In a system of legged locomotion, not only a nervous system controlling locomotion but also a musculo-skeletal system controlled by the nervous system has oscillatory dynamics. The latter is naturally validated by the effects of gravity and inertia. In the case of a biped, models of passive walking in the absence of torque have been studied (Mochon and McMahon 1980; McGeer 1989). Since both the nervous system and the musculo-skeletal system have their own nonlinear dynamics, the appropriate interaction between them would be necessary to generate stable and flexible movements. Anderson and Grillner (1983) demonstrated that imposed rhythmic movements of the legs of spinal cats can entrain central rhythms over a wide range of frequency. This will be a crucial cue for the mechanism of flexible sensorimotor control.

An important point in the present study is the recursive dynamics that occurs between a nervous system and a musculo-skeletal system during locomotion in an environment. A mutual entrainment between them is focused on as the principle of flexible control of the locomotion. As the entrainment is spontaneously established through the interaction with its environment, we may hypothesize that the principle is responsible for the global stability of the movement in real time in its environment, where conditions are unpredictable.

In the present paper, the principle is applied to a model of bipedal locomotion in which a nervous system composed of coupled neural oscillators works as an autonomous controller. Through computer simulations, we shall demonstrate that locomotion is stably realized under variable conditions and that a gradual change in speed of locomotion induces a drastic transition of the gait pattern.

2 Outline of the model

2.1 The structure of the model

The information flows in our model of bipedal locomotion are indicated by arrows in Fig. 1. The bipedal musculo-skeletal system, which is composed of interconnected rigid links, is represented by Newton-Euler equations, where the environment is modeled as a reaction force from the ground to the legs with or without mechanical perturbation. The locomotor movement results from torques acting at each joint. These torques are generated according to signals of the neural rhythm generator, which is constructed by extending a hypothetical model of the neural network of the spinal cord proposed by Grillner (1981) for quadrupedal locomotion. The neural rhythm generator consists of coupled neural oscillators, each of which controls movement of a leg joint. Our network is represented by differential equations. The feedback pathway from the bipedal musculo-skeletal system to the neural rhythm generator is modeled on the basis of a simple type of reflex in

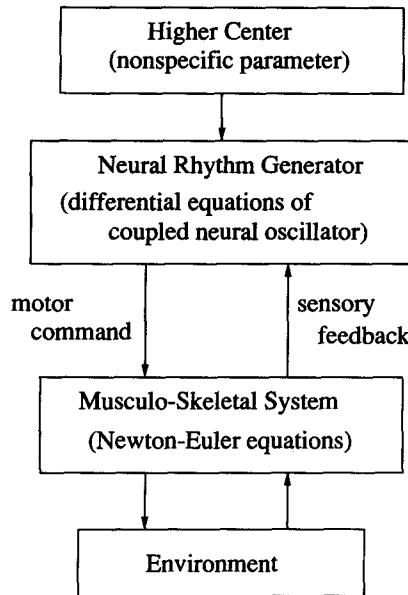


Fig. 1. The general model for control of the locomotor system

vertebrates. The higher center is represented by a single parameter which sets the level of activity of the neural rhythm generator in a nonspecific manner. The higher center may be compared to the brain stem activating the spinal cord (Shik et al. 1966; Mori 1987).

2.2 The strategy of control

Our strategy of control is as follows:

(a) The mutual entrainment among the neural oscillators is responsible for the flexible coordination among rhythmic movements of the joints of the legs. Some aspects of timing are established by sensory feedback.

(b) Not only the neural rhythm generator but also the musculo-skeletal system has oscillatory dynamics owing to reaction forces from the ground and to inertial forces. What is responsible for the dynamic stability of the whole system is a mutual entrainment between the neural rhythm generator and the musculo-skeletal system. Since the entrainment has a global characteristic of being spontaneously established through interaction with the environment, we call it *global entrainment*. This means that the interaction with the environment takes part in the generation of a stable limit cycle called a global limit cycle. If the whole system can generate the global limit cycle by *global entrainment*, the movements will become stable against mechanical perturbations within the range of the orbital stability of the global limit cycle. Furthermore, the stability against environmental changes will be obtained within the structural stability of the global limit cycle.

(c) If the locomotor movements are structurally stable, hierarchical control will become possible by a single parameter of the higher center. In such cases, the speed of locomotion is expected to be controlled by changing the value of the parameter. Furthermore, if

the system acquires a qualitatively different stable state by changing its speed, the nonspecific control of the motor pattern will become possible. Transitions of gait patterns are expected to be realized as a bifurcation between different types of global limit cycles of the whole system.

3 The model of bipedal locomotion

3.1 Musculo-skeletal system

The bipedal musculo-skeletal system is constructed by an interconnected chain of rigid links, as shown in Fig. 2. The model is confined to move in the sagittal plane. A leg is composed of a thigh and shank, and has three joints: at the hip, knee, and ankle. The mass of the remainder of the body is given by a point mass at the hip joint. The feet are omitted because their low inertial properties render their influence minimal in the swing phase and they do not enter into the dynamics in the stance phase during which they are planted firmly on the ground. Some bipedal models similar to this have been studied (Beuter et al. 1986; Pandy and Berme 1988). Torques acting at the joints are assumed to be induced by the output of the neural rhythm generator. The torque at the ankle joint is assumed to be generated only when the ankle makes contact with the ground. To avoid mechanical coupling between the legs, one leg is detached from the other at the hip. Nonlinear friction forces are assumed in the hip and knee joints, and elastic forces in the knee. The former are the pathway of energy dissipation and the latter restricts the bending of the knee.

The ground is modeled as a two-dimensional spring and damper. Each time the ankle touches the ground, the rest position of the spring is reset to the point at which the ankle first touches (Raibert 1984). To simu-

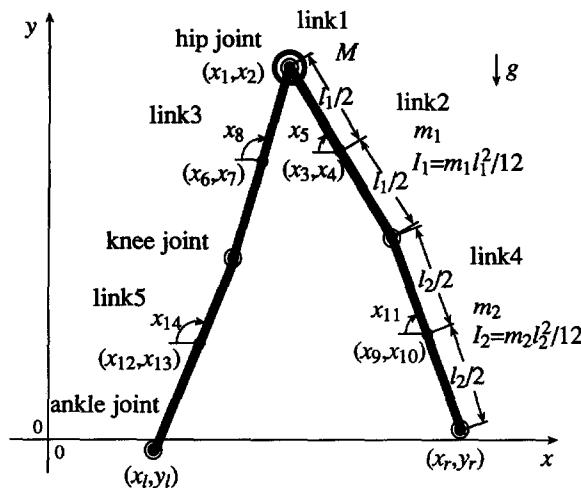


Fig. 2. Musculo-skeletal system. A dynamic model of a bipedal musculo-skeletal system is shown. Link 2, 3 represents the thigh and shank. Link 4, 5 represents the shank. Link 1 represents the remainder of the body which is given as a point mass

late locomotion not only on flat ground but also on a slope, a two-dimensional model of the terrain is described by a function which determines the profile of the ground in the sagittal plane.

The equations of motion for the musculo-skeletal system are derived by means of the Newton-Euler method. The general form of the equations may be written as

$$\ddot{\mathbf{x}} = P(\mathbf{x})\mathbf{F} + \mathbf{Q}(\mathbf{x}, \dot{\mathbf{x}}, \mathbf{T}_r(y), \mathbf{F}_g(\mathbf{x}, \dot{\mathbf{x}})), \quad (1)$$

where \mathbf{x} is a (14×1) vector of the inertial positions of 5 links and the inertial angles of 4 links; P is a (14×8) matrix; \mathbf{F} is a (8×1) vector of constraint forces; \mathbf{Q} is a (14×1) vector; \mathbf{T}_r is a (6×1) vector of torques; \mathbf{F}_g is a (4×1) vector of forces on the ankle which depend on the state of the terrain; and y is a (12×1) vector of the output of the neural rhythm generator to be explained in the next section. The details of (1) are presented in the Appendix.

The equations of kinematic constraints are also shown in the Appendix. To obtain the constraint forces, we differentiate the equations of kinematic constraints twice with respect to time. They can be written in a general form:

$$C(\mathbf{x})\ddot{\mathbf{x}} = \mathbf{D}(\mathbf{x}, \dot{\mathbf{x}}), \quad (2)$$

where C is a (8×14) matrix and \mathbf{D} is a (8×1) vector. The derivation of (2) is also given in the Appendix.

By substituting (1) into (2), we get

$$\begin{aligned} \mathbf{F} &= [C(\mathbf{x})P(\mathbf{x})]^{-1}[\mathbf{D}(\mathbf{x}, \dot{\mathbf{x}}) \\ &\quad - C(\mathbf{x})\mathbf{Q}(\mathbf{x}, \dot{\mathbf{x}}, \mathbf{T}_r(y), \mathbf{F}_g(\mathbf{x}, \dot{\mathbf{x}}))]. \end{aligned} \quad (3)$$

Substitution of (3) into (1) gives the required accelerations by

$$\begin{aligned} \ddot{\mathbf{x}} &= P(\mathbf{x})[C(\mathbf{x})P(\mathbf{x})]^{-1}[\mathbf{D}(\mathbf{x}, \dot{\mathbf{x}}) \\ &\quad - C(\mathbf{x})\mathbf{Q}(\mathbf{x}, \dot{\mathbf{x}}, \mathbf{T}_r(y), \mathbf{F}_g(\mathbf{x}, \dot{\mathbf{x}}))] \\ &\quad + \mathbf{Q}(\mathbf{x}, \dot{\mathbf{x}}, \mathbf{T}_r(y), \mathbf{F}_g(\mathbf{x}, \dot{\mathbf{x}})). \end{aligned} \quad (4)$$

We are able to obtain the motion of the bipedal musculo-skeletal system, provided that the output of the neural rhythm generator y is given.

3.2.1 Neural oscillator model. Before we consider the neural rhythm generator for bipedal locomotion, it would be instructive to discuss a neural oscillator model used as the element of the neural rhythm generator. One of the simplest neural network models which generate oscillatory activity consists of two tonically excited neurons, with the adaptation or self-inhibition effect, linked reciprocally via inhibitory connections. This model was originally proposed by Brown (1914) to account for the alternating activation of flexor and extensor muscles of a cat's limbs during walking. The model can be mathematically

represented by the following differential equations (Matsuoka 1985, 1987):

$$\begin{aligned}\tau \dot{u}_1 &= -u_1 - w y_2 - \beta v_1 + u_0, \\ \tau \dot{u}_2 &= -u_2 - w y_1 - \beta v_2 + u_0, \\ \tau' \dot{v}_1 &= -v_1 + y_1, \\ \tau' \dot{v}_2 &= -v_2 + y_2, \\ y_i &= f(u_i) \quad (f(u_i) = \max(0, u_i)) \quad (i = 1, 2),\end{aligned}\quad (5)$$

where u_i is the inner state of the i th neuron; y_i is the output of the i th neuron; v_i is a variable representing the degree of the adaptation or self-inhibition effect of the i th neuron; u_0 is an external input with a constant rate; w is a connecting weight; and τ and τ' are time constants of the inner state and the adaptation effect, respectively.

Conditions under which the network generates oscillatory activity are found by investigating differential equations obtained by linearizing (5) in the vicinity of stationary solutions (Matsuoka 1985). The time constants τ and τ' change the frequency, while the constant input u_0 changes not the frequency but the amplitude.

3.2.2 Neural rhythm generator. By using the neural oscillator model described above as a unit oscillator, a neural rhythm generator, composed of six unit oscillators, for bipedal locomotion is constructed as illustrated in Fig. 3. The six unit oscillators have inhibitory connections. Each unit oscillator induces a torque at a

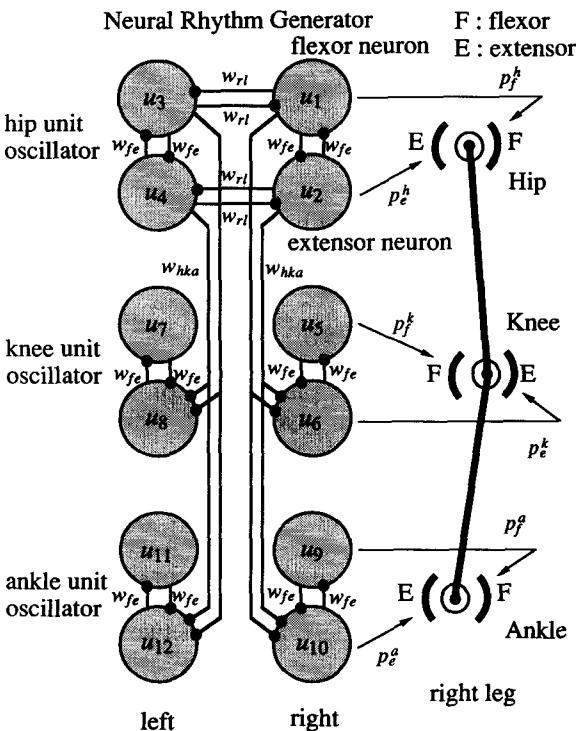


Fig. 3. Neural rhythm generator. The output of the neural rhythm generator to the right leg joints is shown. w_{fe} , w_{rl} , and w_{hka} represent the weights of interconnections between subunit neurons of unit oscillators

specific joint. The two neurons of each unit oscillator alternately induce torques in opposite directions: the directions of contraction of flexor and extensor muscles. It is assumed that the torque generated at the joint is proportional to the output of the subunit neurons. This model is consistent with a hypothetical model for the spinal network for locomotion proposed by Grillner (1981).

The neural rhythm generator is represented by the following differential equations:

$$\begin{aligned}\tau_i \dot{u}_i &= -u_i + \sum_{ij=1}^{12} w_{ij} y_j - \beta v_i + u_0 + F_{eedi}(\mathbf{x}, \dot{\mathbf{x}}, \mathbf{F}_g(\mathbf{x}, \dot{\mathbf{x}})), \\ \tau'_i \dot{v}_i &= -v_i + y_i, \\ y_i &= f(u_i) \quad (f(u_i) = \max(0, u_i)) \quad (i = 1, 12),\end{aligned}\quad (6)$$

where F_{eedi} is a feedback signal from the musculo-skeletal system, as explained in the next section. The other parameters in (6) were given in (5).

The values of the parameters for the unit oscillators and for the interconnections between them are specified so that the patterns of activity are generated consistently with the observed motion of the human biped, as is described below.

Serial angular patterns of movements of the human biped can be characterized as follows: within each walking cycle, the hip pattern shows one excursion of flexion and extension; the knee and ankle patterns, on the other hand, show two excursions of flexion and extension (Murray 1967). In the present model, the values of τ and τ' of the hip unit oscillators are chosen to be twice those of the knee and ankle unit oscillators so that the frequency of the latter is twice that of the former. The frequency of the hip unit oscillators is chosen to be slightly slower than the characteristic frequency of a damped pendulum corresponding to a straight leg with no knee joint. Since the amplitude of the leg's oscillation forced by the unit oscillator becomes large owing to the resonance effect under this condition, the mutual entrainment between the unit oscillator and the leg is expected to become stable.

The inhibitory connections between hip unit oscillators on the contralateral side produce alternate excitations to give the alternation between the movements of the two legs. In order to produce relative phases appropriately in ipsilateral joints, the interconnections between unit oscillators on the ipsilateral side are chosen in such a way that the extensor neurons of the knee and ankle unit oscillators are inhibited by the flexor and extensor neurons of the hip unit oscillators. Then the extensor neurons of the knee and ankle unit oscillators are excited each time they are disinhibited.

3.3 Feedback pathway

The human motor system receives two different types of sensory information: proprioceptive and exteroceptive information. The former is the sense of the positions and movements of different parts of the body, while the latter is constituted of visual, somatic, and vestibular

information and is important for monitoring the relationship between the body and the environment.

Two obvious choices for kinematic state variables are the anatomical and inertial angles. The anatomical angles may be sensed only by proprioceptors. To get inertial angles, however, both the proprioceptive and exteroceptive information are needed. Information on the proprio-extero relationship seems to be crucial for adaptation to the environment.

In this model, we will postulate explicit representations of sensory signals of inertial angles, angular velocities, and somatic senses. Figure 4A illustrates the feedback pathway to each unit oscillator. Here the inertial angles of the thigh and the shank and the angular velocity of the shank are assumed to be signaled. The somatic senses are signaled only when the ankle is in contact with the ground.

The design of the feedback pathway is mainly based on a simple mechanism, shown in Fig. 4B, which is an extended form of the stretch reflex in vertebrates. Let us consider a simplified system composed of a unit oscillator, a pendulum controlled by antagonistic muscles,

and a pair of receptors called the angle receptors. It is assumed that each angle receptor is activated when the inertial angle of the pendulum exceeds the upright position and the strength of the activity is proportional to the angle. The afferent signal from the angle receptor on one side enhances the activity of the ipsilateral neuron and suppresses the activity of the contralateral one. This stretch-reflex like feedback is responsible for the entrainment between the activity of the unit oscillator and the movement of the pendulum. As illustrated in Fig. 4A, the hip and ankle unit oscillators have this type of feedback. The stretch-reflex like feedback is also extensively used in the inter joint feedback pathways, which are important for generating appropriate phase relationships among the movements of the joints. It is noted that the signals of the somatic sense are used for taking account of only the relevant phases of the signals of the stretch-reflex like feedback, so that the inertial angles of the ankle joints are signaled only when the ankle is in contact with the ground. The feedback of the angular velocities and the somatic senses are expected to be effective for the stability of locomotion.

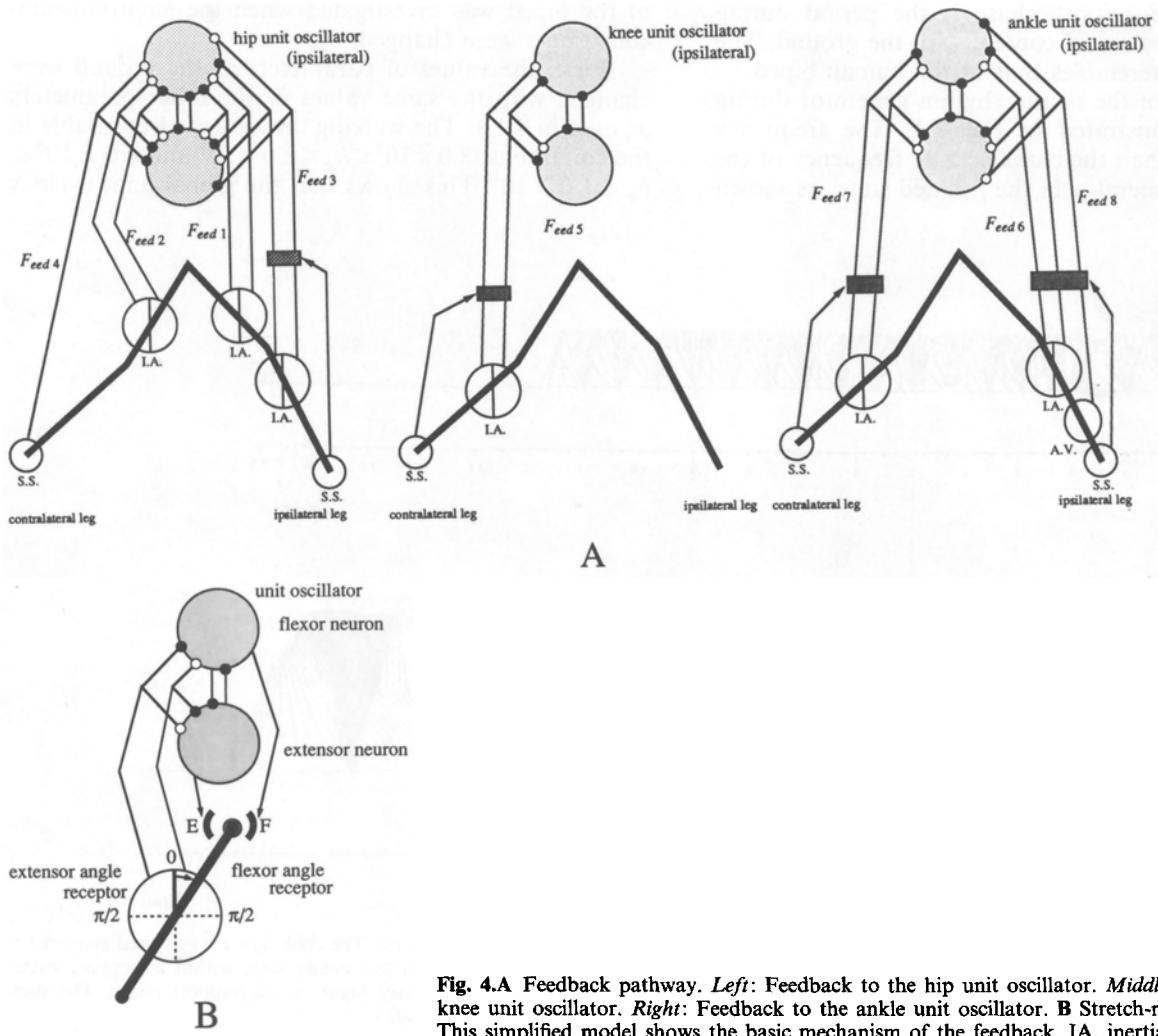


Fig. 4.A Feedback pathway. *Left:* Feedback to the hip unit oscillator. *Middle:* Feedback to the knee unit oscillator. *Right:* Feedback to the ankle unit oscillator. **B** Stretch-reflex like feedback. This simplified model shows the basic mechanism of the feedback. IA, inertial angle; AV, angular velocity; SS, somatic sense

4 Results

In this section, some of the results of the computer simulation using the HITACHI M-680/682H system at the Computer Center of University of Tokyo will be presented. Equations (4) and (6) were implemented in Fortran using the fourth-order Runge-Kutta-Gill method for integration. The inverse matrix in (4) was solved by using the Gauss-Jordan method. Given a certain set of initial conditions and a function describing the terrain, our bipedal model generated locomotor patterns as a completely autonomous system.

4.1 Generation of walking movements

4.1.1 Walking pattern. Figure 5 shows the simulated motion of the legs on level ground. As clearly demonstrated in Fig. 5A, the equations for this autonomous system have a stable limit cycle solution for an appropriate set of initial conditions. The pattern of movement within a stepping cycle is shown in Fig. 5B, where the single- and double-support phases are separately illustrated. The single-support phase is the period during which only one ankle is in contact with the ground, while the double-support phase is the period during which both ankles are in contact with the ground. The walking pattern resembles that of the human biped.

The activity of the neural rhythm generator during walking is demonstrated in Fig. 6A. The frequency becomes higher than the characteristic frequency of the neural rhythm generator in the isolated state, as shown

in Fig. 6B. This shows that the neural rhythm generator and the musculo-skeletal system are mutually entrained. Therefore this motion of the system is the global limit cycle, as was noted in 2.2. The phase relationships among the unit oscillators during walking are more complex than those in the isolated state. This means that the neural rhythm generator is not entirely responsible for establishing the relative timing of motor activity, but some contribution is made by sensory feedback.

4.1.2 Responses to perturbation. Mechanical perturbations to a part of the body were examined (Fig. 7). The results demonstrate that the system returns to steady walking within a few step cycles after instantaneous perturbations. The stability against the perturbations is attributed to the orbital stability of the global limit cycle. The biped fell down for such a large perturbation as that which forces the system to move beyond the separatrix of the stable limit cycle. Many of the details of trajectory responding to perturbation arise directly from the structure of the dynamical system and need not be controlled by higher levels of the nervous system.

4.1.3 Stability to environmental changes. The behavior of the biped was investigated when the environmental constraints were changed.

First, the values of parameters of the ground were changed with the same values of the other parameters as used in 4.1.1. The walking movements were stable in the conditions; $8.0 \times 10^3 \leq k_g \leq 2.0 \times 10^4$ and $8.0 \times 10^2 \leq b_g \leq 1.0 \times 10^4$. This shows that the global limit cycle is

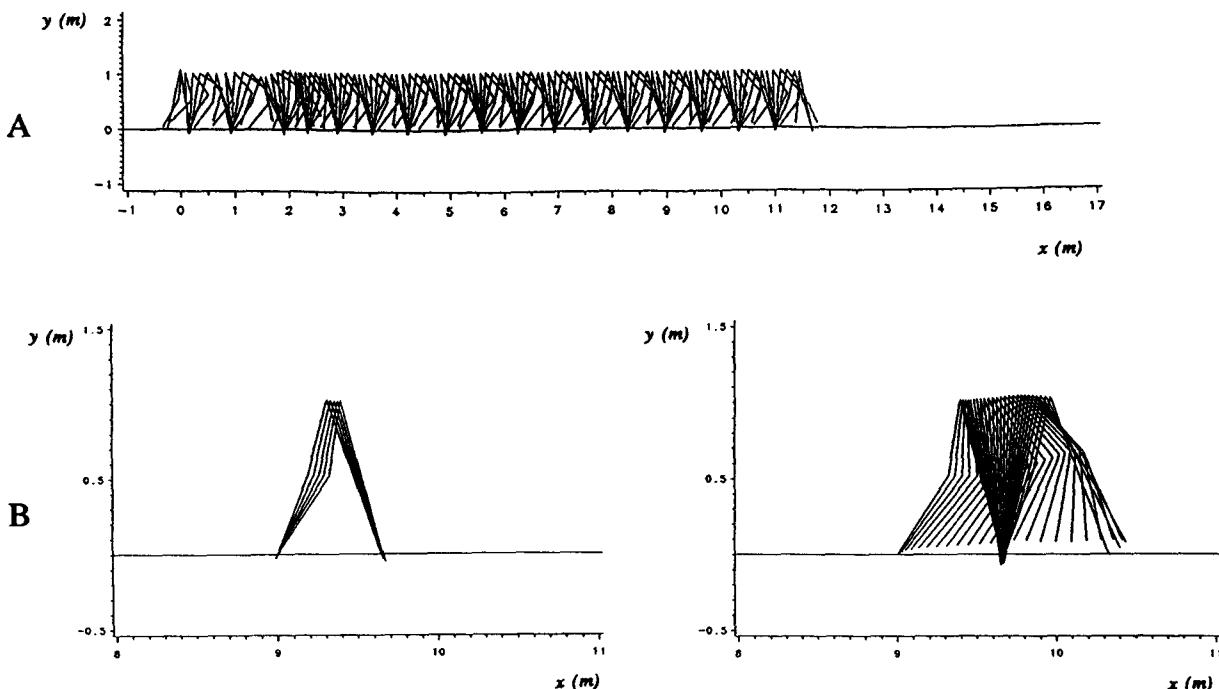


Fig. 5A, B. The stick figure of the walking movement on level ground. $u_0 = 5.5$. The values of the other parameters of the system and the initial conditions are shown in the Appendix. **A** The walking movement over 10 s. Given a set of initial conditions, the system was

asymptotic to steady walking. The stick figure was traced every 0.1 s. **B** The walking pattern in the steady state within a stepping cycle. *Left:* Double-support phase. *Right:* Single-support phase. The stick figure was traced every 0.02 s

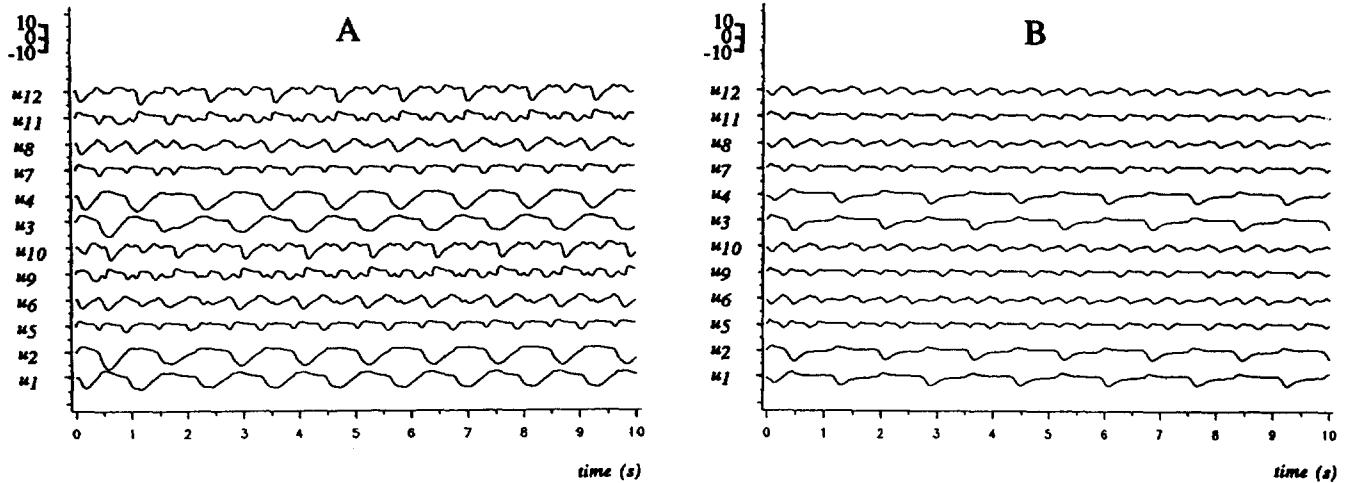


Fig. 6. **A** The activity of the neural rhythm generator during walking. Each inner state of neuron u_i is shown. **B** The activity of the neural rhythm generator in the isolated state. $F_{eedi} = 0$

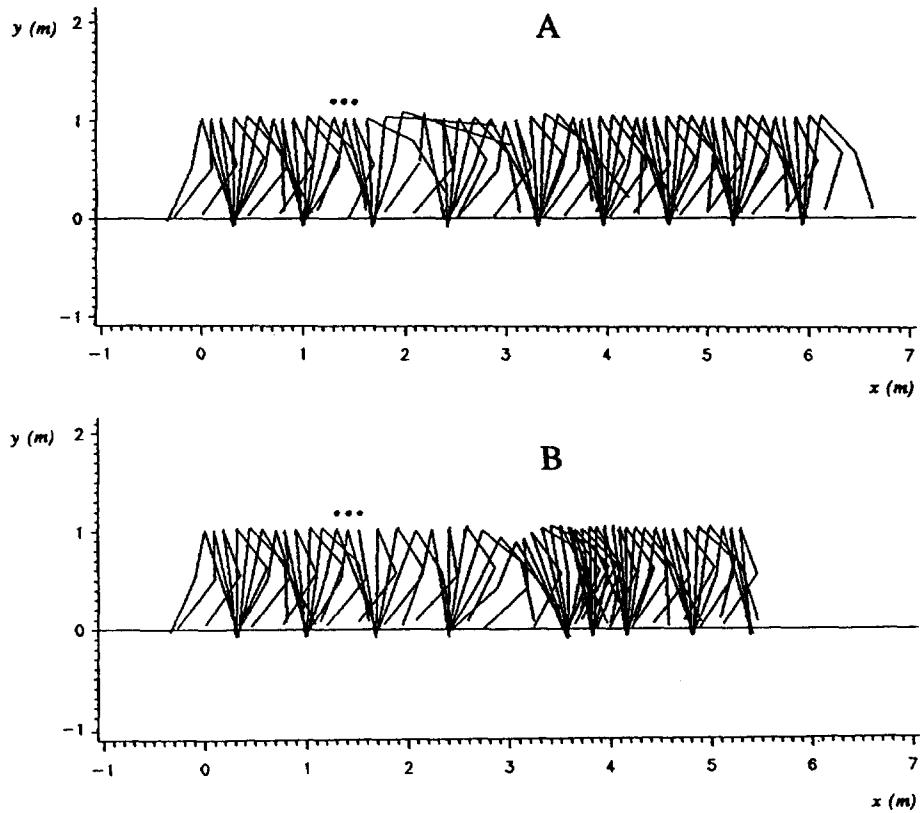


Fig. 7. **A, B.** The walking movement when mechanical perturbation was applied. The values of the parameters of the system were the same as those of 4.1.1. The initial condition was chosen to be the value of the steady state. Dots show the time when a mechanical force was applied.

The stick figure was traced every 0.1 s. **A** Perturbation to the leg. A force of 200 N in the forward direction was applied to the center of the mass of link5 during swinging for 0.2 s. **B** Perturbation to the head. A force of 288 N in the forward direction was applied to link1 for 0.2 s

structurally stable to the wide range of the parameter changes.

Secondly, uphill walking on a shallow slope was examined with the same values of parameters as used in 4.1.1 (Fig. 8). The upper limit of the slope that the biped could walk on was 6%. The biped fell down on a

downhill slope, because the torque strong enough to support the upright body was generated before the swing leg touched the ground, which caused balance loss. The stability against environmental changes is attributed to the structural stability of the global limit cycle in the whole system.

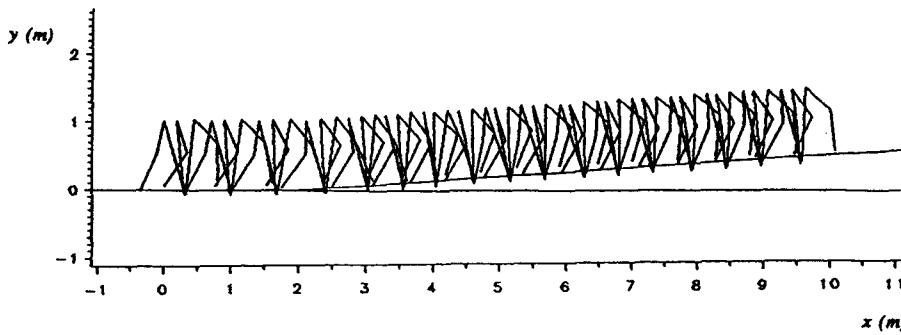


Fig. 8. Uphill walking. The walking movement on a 6% uphill slope is shown. The values of the parameters and the initial condition were the same as those of 4.1.2

4.2 Control of speed and transition of gait pattern

Human bipeds adopt a walking gait over a wide range of velocities. The adaptation to increasing speed is accomplished by an increase in both frequency and amplitude of the movement. Above a certain speed, a man changes his gait from walking to running (Nilsson et al. 1985), just as quadrupeds change gaits from walking to trotting to galloping.

Hierarchical control by the higher center was examined as follows. The constant input parameter u_0 , setting the activity level of the neural rhythm generator, was changed continuously. This may be compared to the experiments by Shik et al. (1966) on the electrical stimulation to the midbrain region of decerebrate cats. The result showed that the biped changed not only its speed but also the gait pattern between walking and running.

The simulated motion for a large value of u_0 is demonstrated in Fig. 9A. It was categorized as a running mode for the following reason. The stepping cycle can be divided into the flight phase and the single-sup-

port phase, as shown in Fig. 9B. Comparing this motion with that shown in Fig. 5B, walking and running can be distinguished from each other by the presence of the double-support phase and the flight phase, respectively. As the present model does not take account of the stiffness of the leg storing elastic energy, the duration of the flight phase is, therefore, shorter than that of the human biped. The activity of the neural rhythm generator in the running mode is shown in Fig. 10. The fine structure of the activity is different from that in the walking mode shown in Fig. 6A.

The change of the gait between the walking and running modes was not continuous but abrupt. The bifurcation diagrams, established numerically as indicated in Fig. 11, represent the steady-state stride length, the stride cycle duration and the speed as a function of the constant input u_0 . The abrupt transition occurs with hysteresis. The coexistence of two stable limit cycles in the same condition provides the capability of switching back and forth between the gaits upon appropriate perturbation or parameter change. This hys-

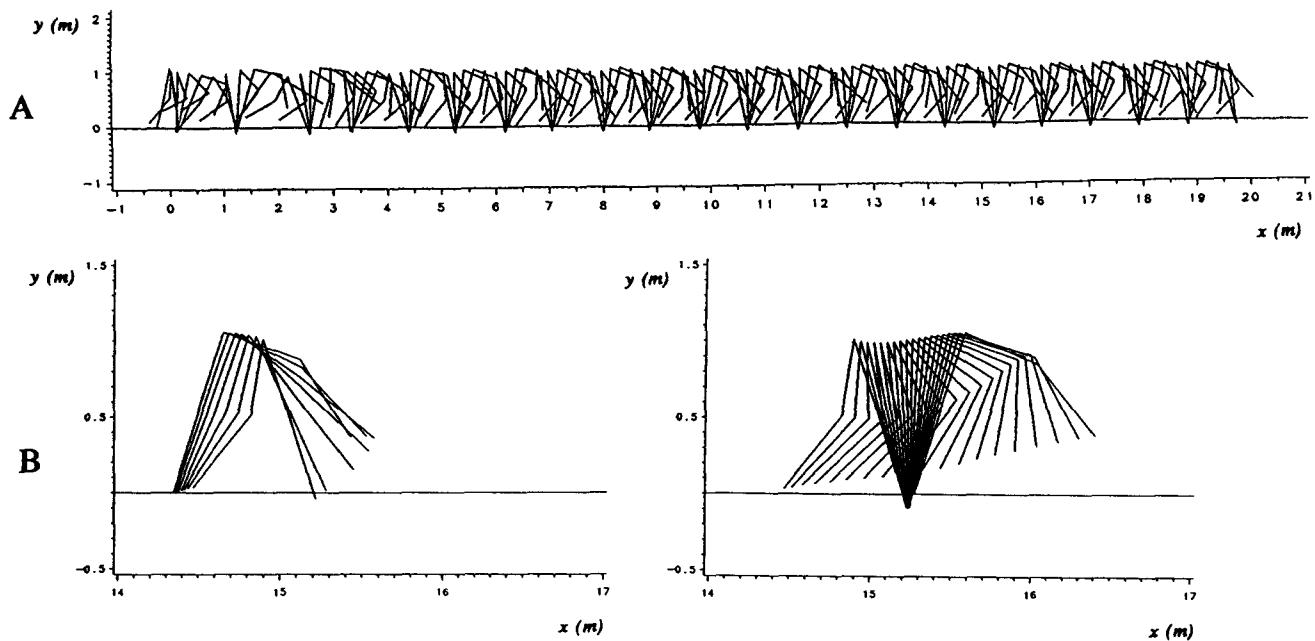


Fig. 9A, B. The stick figure of the running movement. $u_0 = 8.3$. The values of the other parameters of the system and the initial conditions were the same as those of 4.1.1. **A** The running movement over 10 s.

The stick figure was traced every 0.1 s. **B** The running pattern in the steady state within a stepping cycle. *Left:* Flight phase. *Right:* Single-support phase. The stick figure was traced every 0.02 s

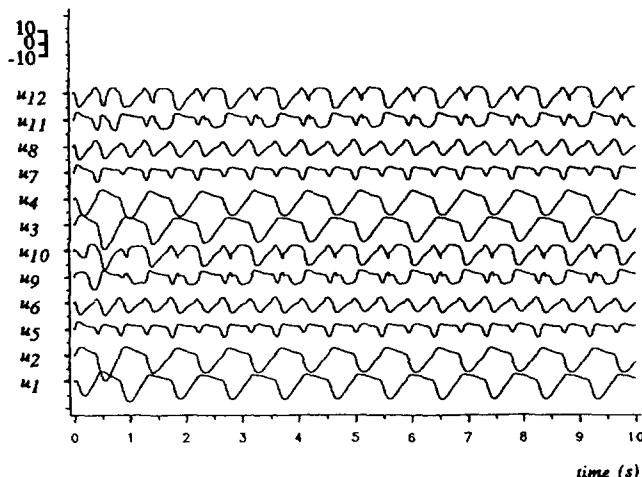


Fig. 10. The activity of the neural rhythm generator during walking. Each inner state of neuron u_i is shown

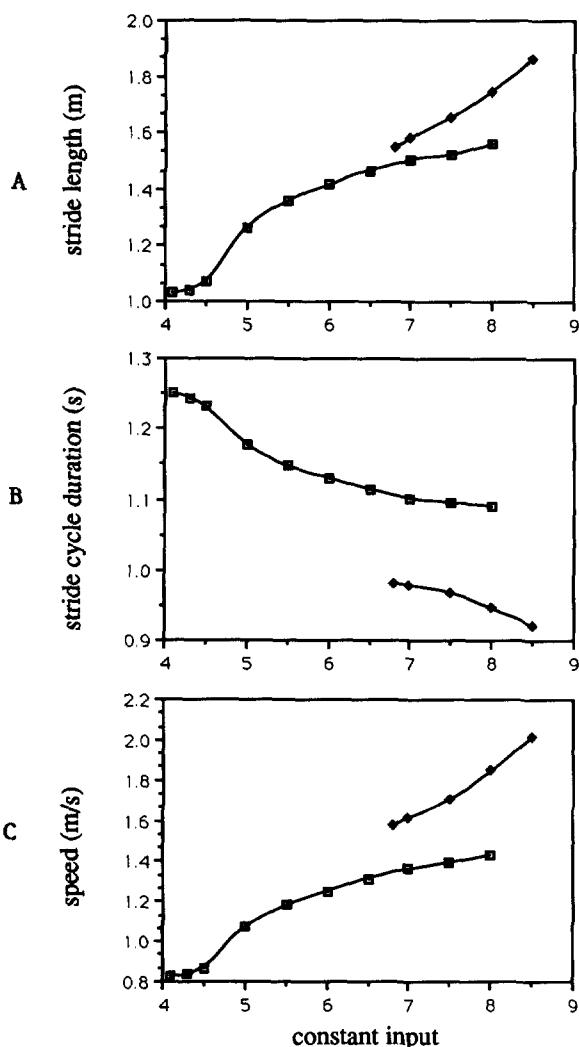


Fig. 11A–C. The gait changes between walking and running. The bifurcation diagrams were numerically established. **A** The stride length is the distance between successive contact points of the same leg with the ground. **B** The stride cycle duration as a function of u_0 . **C** The speed as a function of u_0 . The stride length divided by the stride cycle duration makes the speed. \square , walking; \diamond , running

teresis phenomenon is typical for a nonlinear dynamical system.

5 Discussion

In summary, the following generalized principles for locomotor control are derived from the present study, though the structure of our model was abstracted from neurophysiological knowledge. (1) Self-organized relationships among nonlinear oscillators in a locomotor system due to their mutual entrainment are the basis for the flexible generation of motor patterns. (2) Dynamic stability for the locomotor system is produced by a *global entrainment* between the control system composed of nonlinear oscillators and the controlled system which has oscillatory dynamics. This entrainment generates a global limit cycle in the whole system including the environment. (3) Gait patterns can be hierarchically controlled by changes of a nonspecific parameter in the form of bifurcations between different types of global limit cycles.

These principles may work in animal locomotion, including not only walking and running but also such diverse forms as swimming, crawling, and flying. It is suggested from the present study that the control of rhythmic movements is not merely switching on or preexisting motor programs, nor reflex chains, but generative phenomena; neural, sensory, and musculo-skeletal systems behave cooperatively to adapt to what is happening to the system in real time.

The transitions of the gait patterns in our model are caused not only by the internal dynamics of the nervous system, but also by the external dynamics of the environment. As the relationship between the dynamics of the nervous system and the dynamics of the musculoskeletal system is gradually varied, a critical point may be reached at which a transition to a qualitatively different pattern of movement occurs. Haken et al. (1985) proposed that gait changes can be regarded as nonequilibrium phase transitions in a synergetic system. Inspired by this view, Schöner et al. (1990) showed theoretically, only on the kinematic level of observation, that different patterns arise from the same underlying nonlinear dynamical structure and that a pattern switch can be brought about by nonspecific parameter change. The present model demonstrates a possible mechanism underlying gait transitions; gait patterns are flexibly generated through the interplay of motor and sensory systems.

With regard to the motor performance, the cerebellum is known to play a crucial role (Ito 1984 for review). The cerebellum receives detailed information concerning the activity of an executive motor apparatus: the phase and degree of contraction of various muscles, joint angles, and contact with the ground (Arshavsky et al. 1984). As the explicit processing of such sensory signals is treated in our model, the functions of the cerebellum might be partly involved. Kawato et al. (1987) proposed an inverse-dynamics model of the cerebellum for control and learning of voluntary arm movements. However, the dynamical coupling between the cerebellum and the spinal net-

work for locomotion is still an open question. Furthermore, the relationship between voluntary movements and rhythmic movements remains for further experimental and theoretical research.

Although motor development and learning have not been considered, our model will provide insight into this problem. Thelen (1988) characterizes infant motor development as self-organizing phenomena; infants seek stable solutions of walking patterns which would be given as a result of cooperative interactions among their physical as well as neural subsystems. This view is consistent with our model that stable walking is realized as a global limit cycle of the whole system. How locomotor systems develop to find stable states interacting with the environment remains a problem for further theoretical research. Recurrent neural network models for learning limit cycles (Doya and Yoshizawa 1989; Williams and Zipser 1989; Pearlmuter 1989) might be applied to motor learning.

As a final note, we would like to stress that the strategy for the motor control presented in this paper is strikingly different from that for the robotic control. Many kinds of bipedal robots have been studied using the conventional control theory (Kato 1983 for survey). In these approaches, planning and execution of movements are strictly separated and sequentially solved. The planning of a desirable trajectory, however, is time consuming. Direct encoding of the trajectory is the source of inflexibility. Kato and Mori (1984) proposed a flexible control of a bipedal robot in which a trajectory is realized as a stable limit cycle. However, a desirable trajectory is uniquely defined by the torque given as a function of the state of the movement, and the dynamics of the control system is not considered. In the view presented in this paper, the control and controlled systems are coupled dynamically and are inseparable. Coordinated rhythmic movements emerge as a result of the dynamic interaction of the *global entrainment* between the control and controlled systems. Therefore, the planning and execution are performed in parallel with constant interactions with the environment. The present principle of motor control in an unpredictable environment is expected to exploit a novel paradigm.

Appendix

A The equations of motion for the bipedal musculo-skeletal system

The equations of motion of the bipedal musculo-skeletal system are derived using the Newton-Euler method. All variables and conventions correspond to those shown in Fig. 2 and Fig. 12.

$$M\ddot{x}_1 = F_1 + F_3 ,$$

$$M\ddot{x}_2 = F_2 + F_4 - Mg ,$$

$$m_1\ddot{x}_3 = -F_1 + F_5 ,$$

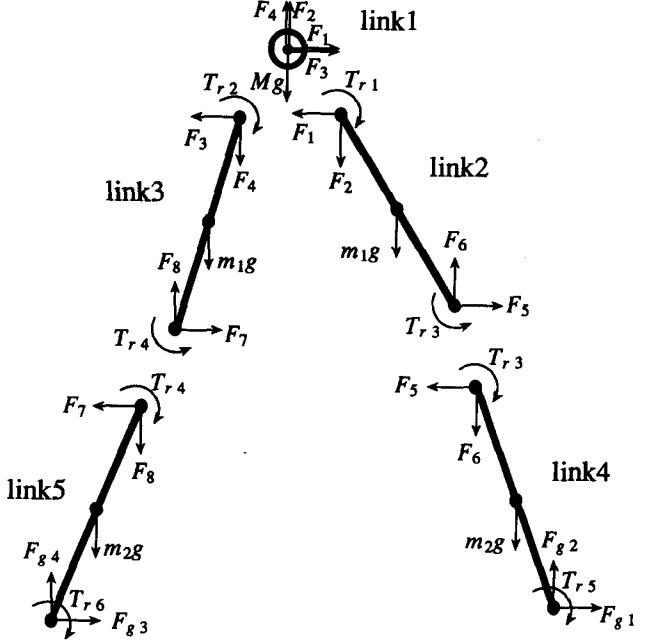


Fig. 12. Dynamics of each link

$$m_1\ddot{x}_4 = -F_2 + F_6 - m_1g ,$$

$$\begin{aligned} I_1\ddot{x}_5 &= -F_1(l_1/2) \sin x_5 - F_2(l_1/2) \cos x_5 \\ &\quad - F_5(l_1/2) \sin x_5 - F_6(l_1/2) \cos x_5 \\ &\quad - b_1|x_5 - \pi/2|\dot{x}_5 - \{b_2 + b_k f(x_5 - x_{11})\}(\dot{x}_5 - \dot{x}_{11}) \\ &\quad - k_k h(x_5 - x_{11}) + T_{r1} + T_{r3} , \end{aligned}$$

$$m_1\ddot{x}_6 = -F_3 + F_7 ,$$

$$m_1\ddot{x}_7 = -F_4 + F_8 - m_1g ,$$

$$\begin{aligned} I_1\ddot{x}_8 &= -F_3(l_1/2) \sin x_8 - F_4(l_1/2) \cos x_8 \\ &\quad - F_7(l_1/2) \sin x_8 - F_8(l_1/2) \cos x_8 \\ &\quad - b_1|x_8 - \pi/2|\dot{x}_8 - \{b_2 + b_k f(x_8 - x_{14})\}(\dot{x}_8 - \dot{x}_{14}) \\ &\quad - k_k h(x_8 - x_{14}) + T_{r2} + T_{r4} , \end{aligned}$$

$$m_2\ddot{x}_9 = -F_5 + F_{g1} ,$$

$$m_2\ddot{x}_{10} = -F_6 + F_{g2} - m_2g ,$$

$$\begin{aligned} I_2\ddot{x}_{11} &= -F_5(l_2/2) \sin x_{11} - F_6(l_2/2) \cos x_{11} \\ &\quad - F_{g1}(l_2/2) \sin x_{11} - F_{g2}(l_2/2) \cos x_{11} \\ &\quad - \{b_2 + b_k f(x_5 - x_{11})\}(\dot{x}_{11} - \dot{x}_5) \\ &\quad + k_k h(x_5 - x_{11}) - T_{r3} - T_{r5} , \end{aligned}$$

$$m_2\ddot{x}_{12} = -F_7 + F_{g3} ,$$

$$m_2\ddot{x}_{13} = -F_8 + F_{g4} - m_2g ,$$

$$\begin{aligned}
I_2 \ddot{x}_{14} &= -F_7(l_2/2) \sin x_{14} - F_8(l_2/2) \cos x_{14} \\
&\quad - F_{g3}(l_2/2) \sin x_{14} - F_{g4}(l_2/2) \cos x_{14} \\
&\quad - \{b_2 + b_k f(x_8 - x_{14})\}(\dot{x}_{14} - \dot{x}_8) \\
&\quad + k_k h(x_8 - x_{14}) - T_{r4} - T_{r6}, \\
f(x) &= \max(0, x), \quad h(x) = \begin{cases} 0 & (x \leq 0) \\ 1 & (x \geq 0) \end{cases}.
\end{aligned}$$

Horizontal and vertical forces on the ankles are given by:

$$\begin{aligned}
F_{g1} &= \begin{cases} -k_g(x_r - x_{r0}) - b_g \dot{x}_r & \text{for } y_r - y_g(x_r) < 0 \\ 0 & \text{otherwise,} \end{cases} \\
F_{g2} &= \begin{cases} -k_g(y_r - y_{r0}) + b_g f(-\dot{y}_r) & \text{for } y_r - y_g(x_r) < 0 \\ 0 & \text{otherwise,} \end{cases} \\
F_{g3} &= \begin{cases} -k_g(x_l - x_{l0}) - b_g \dot{x}_l & \text{for } y_l - y_g(x_l) < 0 \\ 0 & \text{otherwise,} \end{cases} \\
F_{g4} &= \begin{cases} -k_g(y_l - y_{l0}) + b_g f(-\dot{y}_l) & \text{for } y_l - y_g(x_l) < 0 \\ 0 & \text{otherwise,} \end{cases}
\end{aligned}$$

where $y_g(x)$ is the function which represents the terrain. When the ground is level, $y_g(x) = 0$. (x_r, y_r) and (x_l, y_l) represent the positions of the ankles, which are given by:

$$\begin{aligned}
(x_r, y_r) &= (x_9 + (l_2/2) \cos x_{11}, x_{10} - (l_2/2) \sin x_{11}), \\
(x_l, y_l) &= (x_{12} + (l_2/2) \cos x_{14}, x_{13} - (l_2/2) \sin x_{14}).
\end{aligned}$$

Torques generated at each joint are given by:

$$\begin{aligned}
T_{r1} &= p_e^h y_2 - p_f^h y_1, \quad T_{r2} = p_e^h y_4 - p_f^h y_3, \\
T_{r3} &= p_e^k y_6 - p_f^k y_5, \quad T_{r4} = p_e^k y_8 - p_f^k y_7, \\
T_{r5} &= (p_e^a y_{10} - p_f^a y_9)h(F_g 2), \\
T_{r6} &= (p_e^a y_{12} - p_f^a y_{11})h(F_g 4),
\end{aligned}$$

where p is the positive constant.

These equations can be written in the compact form shown in the text.

$$\ddot{\mathbf{x}} = P(\mathbf{x})\mathbf{F} + \mathbf{Q}(\mathbf{x}, \dot{\mathbf{x}}, \mathbf{T}_r(\mathbf{y}), \mathbf{F}_g(\mathbf{x}, \dot{\mathbf{x}})). \quad (1)$$

B The equations of the kinematic constraints

$$\begin{aligned}
x_1 &= x_3 - (l_1/2) \cos x_5, \quad x_2 = x_4 + (l_1/2) \sin x_5, \\
x_1 &= x_6 - (l_1/2) \cos x_8, \quad x_2 = x_7 + (l_1/2) \sin x_8, \\
x_3 + (l_1/2) \cos x_5 &= x_9 - (l_2/2) \cos x_{11}, \\
x_4 - (l_1/2) \sin x_5 &= x_{10} + (l_2/2) \sin x_{11}, \\
x_6 + (l_1/2) \cos x_8 &= x_{12} - (l_2/2) \cos x_{14}, \\
x_7 - (l_1/2) \sin x_8 &= x_{13} + (l_2/2) \sin x_{14}.
\end{aligned}$$

The equations of the kinematic constraints are differentiated twice and we obtain:

$$\begin{aligned}
\ddot{x}_1 - \ddot{x}_3 - (l_1/2) \sin x_5 \ddot{x}_5 &= (l_1/2) \cos x_5 \dot{x}_5^2, \\
\ddot{x}_2 - \ddot{x}_4 - (l_1/2) \cos x_5 \ddot{x}_5 &= -(l_1/2) \sin x_5 \dot{x}_5^2, \\
\ddot{x}_1 - \ddot{x}_6 - (l_1/2) \sin x_8 \ddot{x}_8 &= (l_1/2) \cos x_8 \dot{x}_8^2, \\
\ddot{x}_2 - \ddot{x}_7 - (l_1/2) \cos x_8 \ddot{x}_8 &= -(l_1/2) \sin x_8 \dot{x}_8^2, \\
\ddot{x}_3 - (l_1/2) \sin x_5 \ddot{x}_5 - \ddot{x}_9 - (l_2/2) \sin x_{11} \ddot{x}_{11} &= \\
&= (l_1/2) \cos x_5 \dot{x}_5^2 + (l_2/2) \cos x_{11} \dot{x}_{11}^2, \\
\ddot{x}_4 - (l_1/2) \cos x_5 \ddot{x}_5 - \ddot{x}_{10} - (l_2/2) \cos x_{11} \ddot{x}_{11} &= \\
&= -(l_1/2) \sin x_5 \dot{x}_5^2 - (l_2/2) \sin x_{11} \dot{x}_{11}^2, \\
\ddot{x}_6 - (l_1/2) \sin x_8 \ddot{x}_8 - \ddot{x}_{12} - (l_2/2) \sin x_{14} \ddot{x}_{14} &= \\
&= (l_1/2) \cos x_8 \dot{x}_8^2 + (l_2/2) \cos x_{14} \dot{x}_{14}^2, \\
\ddot{x}_7 - (l_1/2) \cos x_8 \ddot{x}_8 - \ddot{x}_{13} - (l_2/2) \cos x_{14} \ddot{x}_{14} &= \\
&= -(l_1/2) \sin x_8 \dot{x}_8^2 - (l_2/2) \sin x_{14} \dot{x}_{14}^2.
\end{aligned}$$

These equations can be written in the compact form as shown in the text.

$$C(\mathbf{x})\ddot{\mathbf{x}} = \mathbf{D}(\mathbf{x}, \dot{\mathbf{x}}) \quad (2)$$

C Feedback pathway

Feedback signals from the musculo-skeletal system to the neural rhythm generator are given by:

$$\begin{aligned}
F_{eed1} &= a_1(x_5 - \pi/2) - a_2(x_8 - \pi/2) \\
&\quad + a_3(x_{11} - \pi/2)h(F_{g2}) + a_4h(F_{g4}), \\
F_{eed2} &= a_1(\pi/2 - x_5) - a_2(\pi/2 - x_8) \\
&\quad + a_3(\pi/2 - x_{11})h(F_{g2}) - a_4h(F_{g4}), \\
F_{eed3} &= a_1(x_8 - \pi/2) - a_2(x_5 - \pi/2) \\
&\quad + a_3(x_{14} - \pi/2)h(F_{g4}) + a_4h(F_{g2}), \\
F_{eed4} &= a_1(\pi/2 - x_8) - a_2(\pi/2 - x_5) \\
&\quad + a_3(\pi/2 - x_{14})h(F_{g4}) - a_4h(F_{g2}), \\
F_{eed5} &= a_5(\pi/2 - x_{14})h(F_{g4}), \\
F_{eed6} &= a_5(x_{14}\pi/2)h(F_{g4}), \\
F_{eed7} &= a_5(\pi/2 - x_{11})h(F_{g2}), \\
F_{eed8} &= a_5(x_{11} - \pi/2)h(F_{g2}), \\
F_{eed9} &= a_6(\pi/2 - x_{11})h(F_{g2}) + a_7(\pi/2 - x_{14})h(F_{g4}) \\
&\quad - a_8\dot{x}_{11}h(F_{g2}), \\
F_{eed10} &= a_6(x_{11} - \pi/2)h(F_{g2}) + a_7(x_{14} - \pi/2)h(F_{g4}) \\
&\quad + a_8\dot{x}_{11}h(F_{g2}), \\
F_{eed11} &= a_6(\pi/2 - x_{14})h(F_{g4}) + a_7(\pi/2 - x_{11})h(F_{g2}) \\
&\quad - a_8\dot{x}_{14}h(F_{g4}), \\
F_{eed12} &= a_6(x_{14} - \pi/2)h(F_{g4}) + a_7(x_{11} - \pi/2)h(F_{g2}) \\
&\quad + a_8\dot{x}_{14}h(F_{g4}).
\end{aligned}$$

D Simulation parameters

Musculo-skeletal system

$$M = 48.0 ,$$

$$m_1 = 7.0 , \quad l_1 = 0.5 , \quad I_1 = m_1 l_1^2 / 12 ,$$

$$m_2 = 4.0 , \quad l_2 = 0.6 , \quad I_2 = m_2 l_2^2 / 12 ,$$

$$b_1 = 10.0 , \quad b_2 = 10.0 , \quad b_k = 1000.0 ,$$

$$k_k = 10000.0 , \quad g = 9.8 ,$$

$$k_g = 10000.0 , \quad b_g = 1000.0 ,$$

$$p_f^h = 15.0 , \quad p_e^h = 85.0 , \quad p_f^k = 15.0 ,$$

$$p_e^k = 15.0 , \quad p_f^a = 100.0 , \quad p_e^a = 75.0 .$$

neural rhythm generator

$$\tau_1, \tau_2, \tau_3, \tau_4 = 0.05 ,$$

$$\tau'_1, \tau'_2, \tau'_3, \tau'_4 = 0.60 ,$$

$$\tau_5, \tau_6, \tau_7, \tau_8, \tau_9, \tau_{10}, \tau_{11}, \tau_{12} = 0.025 ,$$

$$\tau'_5, \tau'_6, \tau'_7, \tau'_8, \tau'_9, \tau'_{10}, \tau'_{11}, \tau'_{12} = 0.30 ,$$

$$\beta = 2.5 ,$$

$$w_{12}, w_{21}, w_{34}, w_{43}, w_{56}, w_{65}, w_{78}, w_{87}, w_{910}, w_{109},$$

$$w_{1112}, w_{1211} = w_{fe} = -2.0 ,$$

$$w_{13}, w_{31}, w_{24}, w_{42} = w_{rl} = -1.0 ,$$

$$w_{61}, w_{62}, w_{83}, w_{84}, w_{101}, w_{102}, w_{123}, w_{124} = w_{hka}$$

$$= -1.0 ,$$

$$\text{otherwise } w_{ij} = 0.0 .$$

feedback

$$a_1 = 1.5 , \quad a_2 = 1.0 , \quad a_3 = 1.5 , \quad a_4 = 1.5 ,$$

$$a_5 = 3.0 , \quad a_6 = 1.5 , \quad a_7 = 3.0 , \quad a_8 = 1.5 .$$

E Initial condition

$$x_1 = 0.0 , \quad x_2 = 1.09 , \quad x_5, x_{11} = 0.45\pi ,$$

$$x_8, x_{14} = 0.57\pi ,$$

$$x_3 = x_1 + (l_1/2) \cos x_5 , \quad x_4 = x_2 - (l_1/2) \sin x_5 ,$$

$$x_6 = x_1 + (l_1/2) \cos x_8 , \quad x_7 = x_2 - (l_1/2) \sin x_8 ,$$

$$x_9 = l_1 \cos x_5 + (l_2/2) \cos x_{11} ,$$

$$x_{10} = x_2 - l_1 \sin x_5 - (l_2/2) \sin x_{11} ,$$

$$x_{12} = l_1 \cos x_8 + (l_2/2) \cos x_{14} ,$$

$$x_{13} = x_2 - l_1 \sin x_8 - (l_2/2) \sin x_{14} ,$$

$$\dot{x}_i = 0.0 \quad (i = 1, 14) ,$$

$$\dot{u}_i, \dot{v}_i = 0.0 \quad (i = 1, 12) .$$

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