A mathematical model of adaptive behavior in quadruped locomotion

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Abstract. Locomotion involves repetitive movements and is often executed unconsciously and automatically. In order to achieve smooth locomotion, the coordination of the rhythms of all physical parts is important. Neurophysiological studies have revealed that basic rhythms are produced in the spinal network called, the central pattern generator (CPG), where some neural oscillators interact to self-organize coordinated rhythms. We present a model of the adaptation of locomotion patterns to a variable environment, and attempt to elucidate how the dynamics of locomotion pattern generation are adjusted by the environmental changes. Recent experimental results indicate that decerebrate cats have the ability to learn new gait patterns in a changed environment. In those experiments, a decerebrate cat was set on a treadmill consisting of three moving belts. This treadmill provides a periodic perturbation to each limb through variation of the speed of each belt. When the belt for the left forelimb is quickened, the decerebrate cat initially loses interlimb coordination and stability, but gradually recovers them and finally walks with a new gait. Based on the above biological facts, we propose a CPG model whose rhythmic pattern adapts to periodic perturbation from the variable environment. First, we design the oscillator interactions to generate a desired rhythmic pattern. In our model, oscillator interactions are regarded as the forces that generate the desired motion pattern. If the desired pattern has already been realized, then the interactions are equal to zero. However, this rhythmic pattern is not reproducible when there is an environmental change. Also, if we do not adjust the rhythmic dynamics, the oscillator interactions will not be zero. Therefore, in our adaptation rule, we adjust the memorized rhythmic pattern so as to minimize the oscillator interactions. This rule can describe the adaptive behavior of decerebrate cats well. Finally, we propose a mathematical framework of an adaptation in rhythmic motion. Our framework consists of three types of dynamics: environmental, rhythmic motion, and adaptation dynamics. We conclude that the time scale of adaptation dynamics should be much larger than that of rhythmic motion dynamics, and the repetition of rhythmic motions in a stable environment is important for the convergence of adaptation.

1 Introduction

Basic movements of animals, such as walking, swimming, breathing, and feeding, are important for their existence and are executed very frequently. It is possible to perform these movements unconsciously, in other words, automatically. They consist of reproducible and repetitive movements of several physical parts of the body. Such periodic motions are influenced by the rhythmic pattern produced in the nervous system. Neurophysiological studies indicate that the basic rhythms are intrinsically generated in spinal neuronal networks, which include neural oscillators (Grillner 1975; Delcomyn 1980).

Such a rhythm generator is called a central pattern generator (CPG), and it has been mathematically modeled using coupled oscillator dynamics in many studies (Cohen et al. 1982; Schöner et al. 1990; Yuasa and Ito 1990; Kimura et al. 1993, 1994; Collins and Richmond 1994; Taga 1995a, b). However, discussion on how the rhythmic behavior changes in a variable environment is insufficient. Animals actually show adaptive behaviors to a new environment. Such adaptation requires coordination of the rhythms, which is important for the smooth execution of rhythmic motions.

Neurophysiological studies focusing on the adaptability of quadrupedal locomotion to environmental changes have recently been reported (Yanagihara et al. 1993; Yanagihara and Kondo 1996). These studies were performed on decerebrate cats that exhibited stable locomotion on a treadmill as well as on the floor, in the same manner as intact cats. Once the treadmill belts began to move, decerebrate cats automatically per-

formed stable locomotion. The treadmill consisted of three moving belts. As shown in Fig. 1, in the experiment, the left forelimb (LF) and the left hindlimb (LH) of the cat were positioned on two independent belts, and the two right limbs [right forelimb (RF) and right hindlimb (RH)] were both positioned on the remaining belt. In the unperturbed case, when the three belts were driven at the same slow speed, the cat maintained a stable gait pattern called walk. Then, the speed of the LF belt was increased by 1.7 times (61 cm/s) that of the others (36 cm/s). In this case, whenever the cat placed its left forelimb onto the belt, the limb was subject to a perturbation. During the initial stage of perturbation, locomotion was not stable, i.e., there was an enhancement in the fluctuations of the step cycle durations. However, the cat gradually adapted to the perturbed environment and began to walk with a new steady gait pattern (Fig. 2c).
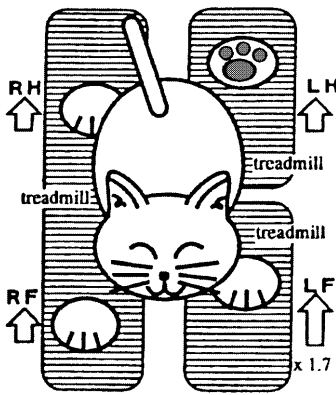

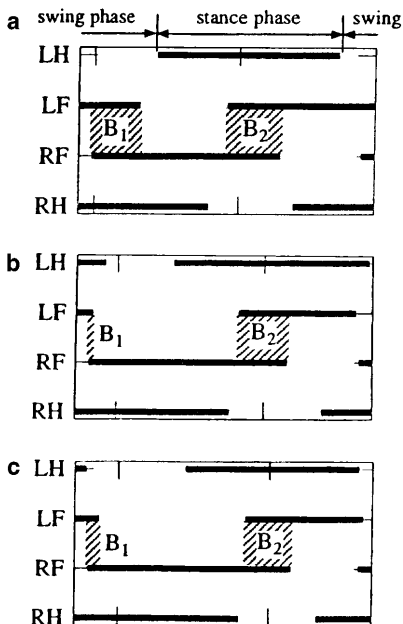Fig. 1. Perturbed locomotion of a decerebrate cat

Fig. 2a–c. Gait diagrams of cat locomotion. They change according to perturbation as well as adaptation. **a** Normal locomotion, **b** before adaptation, **c** after adaptation

The result of adaptation can also be seen in the duration of the bisupport phase of the two forelimbs. The experimentally obtained gait diagrams are shown in Fig. 2. There are two bisupport phases in one step cycle, marked by B_1 and B_2. In the B_1 bisupport phase, the left forelimb first provides support, followed by the right forelimb. Conversely, in the B_2 bisupport phase, the right forelimb first provides support, followed by the left forelimb. It was found that, during normal locomotion, the two bisupport phases are of equal duration (Fig. 2a). However, perturbation makes B_1 shorter than B_2 (Fig. 2b). This difference tends to decrease after the cat has adapted to the new environmental conditions (Fig. 2c). This indicates that the interlimb coordination, which is disturbed by perturbation, is regained after many steps. This interlimb coordination is important in the execution of smooth and stable locomotion. Yanagihara and Kondo (1996) have also shown, using this experimental paradigm, that nitric oxide (NO) in the cerebellum plays a key role in motor learning. They first confirmed that N^G-monomethyl-D-arginine [D-NMMA], which has no inhibitory effect on NO synthase, did not abolish an adaptation. Next, they injected haemoglobin, a NO scavenger, or N^G-monomethyl-L-arginine L-NMMA a NO synthase inhibitor, into the cerebellar cortical locomotion area. In each case, no adaptation occurred, i.e., locomotion did not become steady, and interlimb coordination was not achieved. They considered that plasticity of synaptic transmission efficacy, which is affected by NO concentration, is essential in motor learning. Although their work was on both the cellular and the behavioral level, we focus here on the behavioral level and undertake to explain it mathematically.

The essence of the adaptation mechanism is to adjust an attractor corresponding to the memorized motion pattern to render the motion more suitable for the new environment. It was found in the experiment that at the next trial after a rest, a decerebrate cat can walk under the perturbed environment with the gait shown in Fig. 2c immediately without a learning period. This means that the decerebrate cat memorized the new gait pattern, although it had memorized the gait pattern shown in Fig. 2a before the adaptation. Thus, once learning is achieved, the new stable pattern emerges immediately since the new memorized locomotion pattern becomes an attractor. However, some training is necessary to change an attractor. In the experiment, a number of steps was required before the decerebrate cat acquired the new stable gait pattern.

We propose a mathematical model of adaptation to periodic perturbation in quadruped locomotion. In the next section, we compose a mathematical model of CPG and define its dynamics, followed by our concept of adaptation. Simulation yields results similar to those of the experiments with a decerebrate cat. Extending the previous model, we will next consider common features of adaptation in typical rhythmic motions and propose a mathematical framework applicable to them. In the fourth section, we mention the significance of this work among other related studies. It should be finally noted

that our CPG model is merely a mathematical model of animal behavior to explain our concept of adaptation.

2 Pattern generation in quadruped locomotion

2.1 Model of CPG

Considering gait patterns, we pay attention to the relative phases among movements of four limbs. Although each limb movement is dynamic and periodic, the relative phases will be constant if the gait pattern is stationary. Since the relative phases are specific to each gait, we can regard the gait as fixed points in a relative phase space. If the relative phases can be set to any value, we can design a gait pattern generator in locomotion systems.

Yuasa and Ito (1990) used a gradient system to describe the dynamics of relative phases. A gradient system is one whose dynamic property can be described by a potential function. The potential function is defined on the state space of a system and provides potential energy at the system state. The gradient system evolves in a manner in which the potential energy decreases maximally. If the potential energy cannot decrease, then the system no longer evolves. Accordingly, minimum points of the potential function correspond to the stationary states of the gradient system. Yuasa and Ito (1990) defined one potential function in the relative phase space so that the relative phases of gait (walk, trot, and gallop) become its minimum point, and simulated the locomotion pattern transition by changing the shape of the potential function. In their approach, interactions among oscillators (oscillator interactions) are represented by a gradient force.

Although Yuasa and Ito (1990) provided the necessary and sufficient conditions which ensure that dynamics in the relative phase space can be described as a gradient system, they did not examine how rhythm patterns adapt to environmental changes. Thus, we add here the adaptation mechanism to their approach so as to treat adaptation in quadruped locomotion.

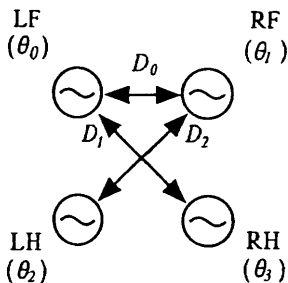As shown in Fig. 3, we model the rhythm generator of limb movement as four coupled oscillators. According to Yuasa and Ito's approach, we can uniquely design the interactions using the potential function in the relative phase space. Note that this kind of connection (in Fig. 3) is used only for mathematical convenience and may not always coincide with the actual CPG connections in animals. However, it does not influence the essence of the problem.

In Fig. 4, the oscillator phase θ_i $(i = 0, 1, 2, 3)$ represents a limb state in one cycle of movement. Here, we have assumed that the oscillator phase coincides with the phase of limb movement. Each limb can be in one of two states: swing phase and stance phase. We divide the phase space of oscillators $[0, 2\pi)$ into two parts and assign them to the swing phase and the stance phase. As shown in Fig. 4, the range of $\cos \theta_i \geq \gamma$ corresponds to the stance phase and the range of $\cos \theta_i < \gamma$, to the swing phase. Here γ is determined from the duty factor β, which denotes the proportion of the stance phase in one step cycle. The relation between γ and β is described by

$$\gamma = \cos \pi \beta \tag{1}$$

2.1.1 Dynamics in stance phase In the stance phase, limbs are always in contact with the treadmill and cannot move freely. Thus, we describe the dynamics of the supporting limbs as

$$\dot{\theta}_i = \rho_i \quad (i = 0, 1, 2, 3) \tag{2}$$

where ρ_i $(i = 0, 1, 2, 3)$ is a variable representing the speed of the treadmill belt. Equation (2) means that the limb movement is forced by the treadmill.

2.1.2 Dynamics in swing phase In this phase, limbs can move freely. Thus, it is possible to adjust the phase of limb movement according to interactions among oscillators.

$$\dot{\theta}_i = \omega_i + f_i \quad (i = 0, 1, 2, 3) \tag{3}$$

Here ω_i $(i = 0, 1, 2, 3)$ denotes angular velocity in the swing phase, and f_i $(i = 0, 1, 2, 3)$ denotes the interaction term. According to Yuasa and Ito (1990), f_i $(i = 0, 1, 2, 3)$ is given as
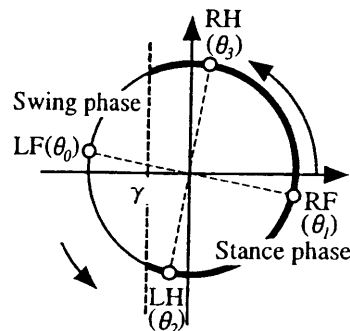

Fig. 3. Connection of oscillators in our central pattern generator (CPG) model (*LF*: left forelimb, *RF*: right forelimb, *LH*: left hindlimb, *RH*: right hindlimb)

Fig. 4. Stance phase and swing phase. In this case, only the LF (θ_0) is in the swing phase, and the others (LH, RF, RH) are in the stance phase
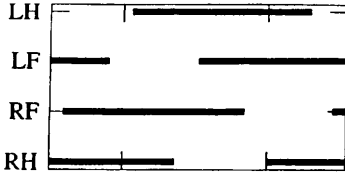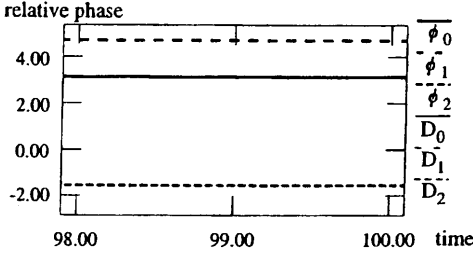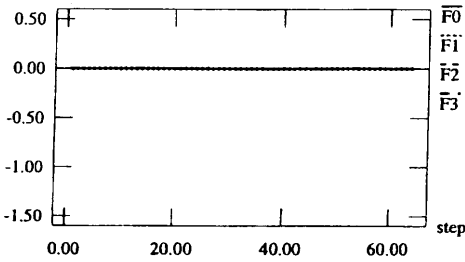
Fig. 5. Normal locomotion

Fig. 6. The time series of relative phases ϕ_0, ϕ_1, ϕ_2 and their desired values D_0, D_1, D_2 in normal locomotion

Fig. 7. Oscillator interactions during normal locomotion: No interaction occurs

Fig. 8. Perturbed locomotion without adaptation

Fig. 9. The time series of relative phases ϕ_0, ϕ_1, ϕ_2 and their desired value D_0, D_1, D_2 in perturbed locomotion without adaptation
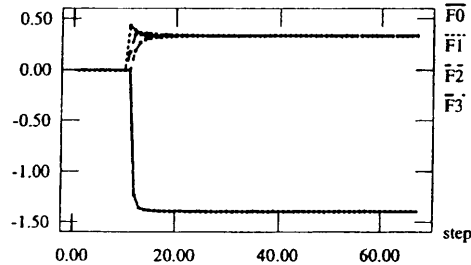
Fig. 10. Oscillator interactions in perturbed locomotion. Interactions occur, so locomotion should converge to the memorized pattern

$$f_0 = \tau_\theta(\theta_1 + \theta_3 - 2\theta_0 - D_0 - D_1) \tag{4}$$

$$f_1 = \tau_\theta(\theta_0 + \theta_2 - 2\theta_1 + D_0 - D_2) \tag{5}$$

$$f_2 = \tau_\theta(\theta_1 - \theta_2 + D_2) \tag{6}$$

$$f_3 = \tau_\theta(\theta_0 - \theta_3 + D_1) \tag{7}$$

where τ_θ is a constant parameter which determines the magnitude of oscillator interaction, and D_0, D_1, D_2 are the desired values of the relative phases $\phi_0 = \theta_0 - \theta_1$, $\phi_1 = \theta_0 - \theta_3$, $\phi_2 = \theta_1 - \theta_2$, respectively.[1] Appendix A shows their potential function and minimum point. It should be noted that if the relative phases equal the desired values, then the interactions will be zero, i.e., they never work.

2.1.3 Treadmill dynamics For the case of a decerebrate cat walking on the treadmill, the rotation velocity of the treadmill corresponds to its environment. We describe it as

$$\rho_i = \mu_i \quad (i = 0, 1, 2, 3) \tag{8}$$

where μ_i $(i = 0, 1, 2, 3)$ is the parameter describing the environment.

2.2 Simulations without adaptation

2.2.1 Normal locomotion When all the treadmill belts are driven at the same slow speed, then

$$\mu_0 = \mu_1 = \mu_2 = \mu_3 = \omega \tag{9}$$

and the decerebrate cat walks with the normal locomotion pattern 'walk' shown in Fig. 2a. This indicates that this pattern has been memorized in CPG as the one suitable for its environment. In our model, if we choose

$$\omega_0 = \omega_1 = \omega_2 = \omega_3 = \omega \tag{10}$$

and

$$D_0 = \pi, \quad D_1 = \tfrac{3}{2}\pi, \quad D_2 = -\tfrac{1}{2}\pi \tag{11}$$

then we can realize the same locomotion pattern as in Fig. 2a.

We select the duty factor from Fig. 2a ($\beta \cong 2/3$). Thus, using (1), we get $\gamma = -0.5$. Figure 5 shows the

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[1] Strictly speaking, they are the desired relative phase when the natural frequencies of oscillators are equal, $\omega_0 = \omega_1 = \omega_2 = \omega_3$. See Appendix A for details.
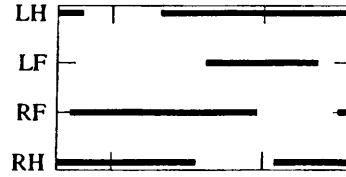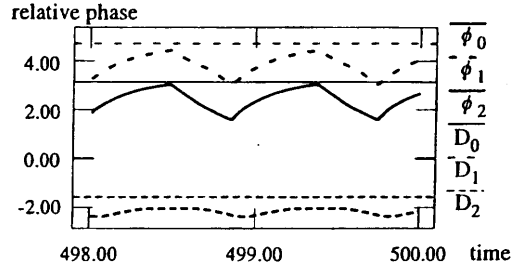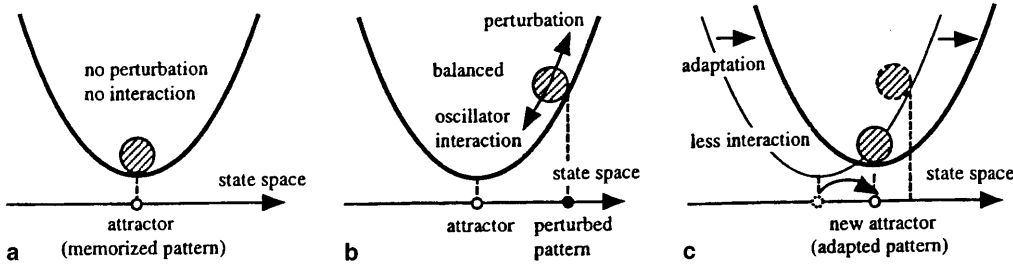
Fig. 11a–c. Mechanism of adaptation in perturbed locomotion. **a** Normal locomotion, **b** perturbed locomotion without adaptation, **c** perturbed locomotion with adaptation

simulation result of the gait diagram when the treadmills are driven at the same speed. Figure 6 shows the time series of the relative phases ϕ_0, ϕ_1, ϕ_2 and their desired values D_0, D_1, D_2. In normal locomotion, the relative phases exactly coincide with their desired values. In this state, the desired pattern has been generated, and thus the oscillator interactions are equal to zero. This is shown in Fig. 7, which is a plot of

$$F_i = \int_T f_i \, dt \quad (i = 0, 1, 2, 3) \tag{12}$$

that is, an integration of the interaction f_i during one step cycle. The potential function with the above minimum **(10, 11)** corresponds to the memorized locomotion pattern (Fig. 2a) in the normal environment.

2.2.2 Perturbed locomotion When the treadmill belt of the left forelimb (LF) is driven faster (1.7 times) than the others, that is,

$$\mu_0 = 1.7\omega, \mu_1 = \mu_2 = \mu_3 = \omega \tag{13}$$

and if we still use (10) and (11), then we obtain the simulation result shown in Figs. 8–10. As shown in Fig. 9, the relative phases are not equal to their desired values because of the periodic perturbation. Then, oscillator interactions, which can be approximately estimated by the difference between relative phases and their desired values, never reach zero. This is shown in Fig. 10, where oscillator interactions always exist.

3 Adaptation mechanism in perturbed locomotion

3.1 Adaptation mechanism

In the simulation described in the previous section (Fig. 8), although we can achieve a stable pattern in the changed environment, we cannot regard this gait pattern as a result of adaptation. In the biological experiments, it was suggested that, first, before the cat can walk stably in the perturbed environment, training with many steps is necessary; and second, after learning, the cat can memorize the new gait pattern that is adapted to the new perturbed environment. However, the mathematical model described in the above section was not sufficient to explain these two important aspects.

In order to explain our concept of the adaptation mechanism, we use Fig. 11, where the oscillator interactions correspond to the gradient of potential. Ac-

cordingly, at the minimum point, the oscillator interaction does not work since the gradient of the potential vanishes. Then, the desired motion pattern is generated if it is set to the minimum point. It should be noted that this figure is conceptual, and thus it is different from the potential function given by (26).

The oscillator interactions work in such a manner that the relative phases converge to the attractor, i.e., the minimum point of potential in Fig. 11. This ensures the stability of the desired locomotion pattern. Here we assume that there is a periodic perturbation. Then the state of the relative phase will be shifted from the attractor, i.e., the minimum point of potential. In this case, the gradient force acts to lead the state back to the attractor. However, since perturbation is periodic, it may disturb the state before converging to a minimum point of potential. As a result, a new state emerges, where perturbation and gradient force, i.e., oscillator interactions, are balanced (see Fig. 11b). This corresponds to the gait pattern given in Fig. 8. If the new pattern is generated as a result of the balance between the oscillator interactions and periodic perturbation, then the oscillator interactions will always be necessary. This kind of pattern generation is not effective, even from the point of view of energy loss. Therefore, we propose that in the perturbed environment, the potential function (26) should be adjusted so that, when performing adapted movement, the interactions among all oscillators tend toward zero. As shown in Fig. 11c, this is equivalent to changing the minimum point of the potential function with respect to the environmental changes.

In our model, we define oscillator dynamics separately in the swing phase and stance phase. Therefore, the whole dynamics of the relative phase is not strictly following the gradient system. However, we may consider this situation as follows: Basically, the gradient dynamics governs the relative phase dynamics, and the forcing oscillation resulting from the stance phase dynamics is regarded as periodic disturbance applied to this gradient dynamics. The relations of phases, i.e., relative phases, are disturbed in the stance phase, but the desired relations of phases are regained in the swing phase, where the gradient dynamics is dominant.

In summary, our adaptation mechanism is the adjustment of the parameter of oscillator dynamics, especially the minimum point of potential function, which corresponds to the memorized motion pattern. The adjusted parameters in oscillator dynamics determine the emerging motion pattern, whereas the adjustment process corresponds to learning.

3.2 Dynamics of adaptation mechanism

We now study how to adjust the parameters of the locomotion pattern: The angular velocity in the swing phase ω_i $(i = 0, 1, 2, 3)$ as well as the desired relative phase D_j $(j = 0, 1, 2)$. A criterion for parameter adjustment is to decrease the oscillator interactions. Then the adaptation dynamics should be slower than that of locomotion, because it is necessary first to evaluate the current pattern before adjusting the parameters. The resultant adjustment rules are given as

$$\omega_i^{(n+1)} = \omega_i^{(n)} + \tau_\omega \int_T f_i \, dt \, (i = 0, 1, 2, 3) \tag{14}$$

$$D_0^{(n+1)} = D_0^{(n)} + \tau_D \int_T (f_0 - f_1) \, dt \tag{15}$$

$$D_1^{(n+1)} = D_1^{(n)} + \tau_D \int_T (f_0 - f_3) \, dt \tag{16}$$

$$D_2^{(n+1)} = D_2^{(n)} + \tau_D \int_T (f_1 - f_2) \, dt \tag{17}$$

where n denotes the number of step cycles, T is the duration of one step cycle, f_i $(i = 0, 1, 2, 3)$ is the force given by (4)–(7), and τ_ω and τ_D are parameters that influence the convergence of ω_i and D_j, respectively. This adaptation dynamics is applied in every step cycle.

Equation (14) controls the natural frequency of each oscillator ω_i. We can show that F_i, the integrated value of interaction f_i for one cycle, decreases according to (14) (see Appendix B). On the other hand, (15)–(17) balance the magnitude of the oscillator interactions. Consequently, these equations reduce the cost function V_D,

$$V_D = \int_T \sum_{i=0}^{3} \left\{ \frac{1}{2\tau_\theta} f_i^2 \right\} dt \tag{18}$$

that is, the integration of the squared sum of interaction f_i. As a result, the minimization of F_i and V_D reduces the interaction f_i. It should be noted that if the change of ω_i is slow enough, then the dynamics of the relative phases will still remain as the gradient system.

3.3 Simulations

We executed new simulations by applying the above adaptive mechanism. In the simulation, we set time constants as $\tau_\theta = 2.0$, $\tau_\omega = 0.25$, and $\tau_D = 0.02$.

Figure 12 shows the simulated gait diagram, which is very similar to the experimental result in Fig. 2c for the decerebrate cat. Figure 13 shows the time series of relative phases. This graph implies that the oscillator in-
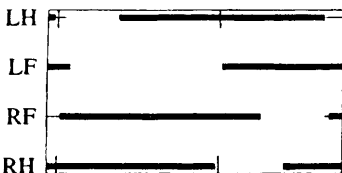

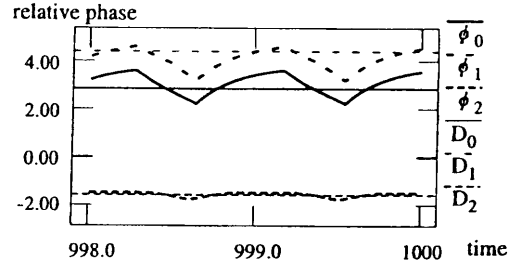**Fig. 12.** Adapted locomotion to perturbation

Fig. 13. The time series of relative phases, ϕ_0, ϕ_1, ϕ_2 and their desired values D_0, D_1, D_2 in adapted locomotion
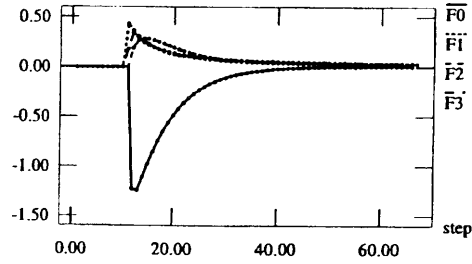

Fig. 14. Oscillator interactions in adapted locomotion. Interactions decrease with adaptation
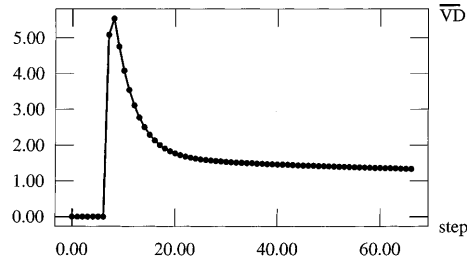

Fig. 15. Evaluation function V_D, which decreases with adaptation

teractions decrease in comparison with the unadapted locomotion in Fig. 9 since the relative phases oscillate near their desired values. This oscillation necessarily occurs even in the adapted locomotion, because the relative phases are disturbed in the stance phase of left forelimb, which is driven faster than the others. Figures 14 and 15 show the time evolutions of F_i (12) and V_D (18), respectively. Figures 16 and 17 show the adjustment of angular velocity ω_i and the desired relative phase D_j. These figures indicate that the parameters of the locomotion pattern are changed, which led to decrement of oscillator interactions. In addition, Fig. 18 shows the durations of the swing phase, stance phase, and step cycle in our simulation. These durations change considerably with perturbation and adaptation. Similar tendencies can also be found in the experimental result for the decerebrate cat (Fig. 19).

3.4 Aftereffect of adaptation

We now come to analyze the aftereffect of adaptation. In the biological experiment, it was shown that after the
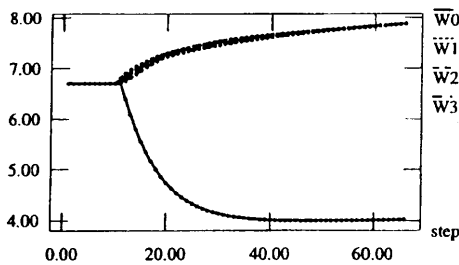
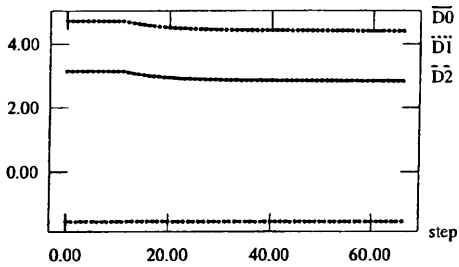**Fig. 16.** Change of $\omega_i (i = 0, 1, 2, 3)$ due to adaptation

Fig. 17. Change of $D_j (j = 0, 1, 2)$ due to adaptation

decerebrate cat adapted to the perturbed environment and returned to walking under normal conditions where all the treadmill belts were driven with the same speed, the cat walked with the gait pattern shown in Fig. 20a. Compared with the gait pattern of Fig. 2a, the bisupport phase B_1 in Fig. 20a was longer than B_2. Therefore, the memorized motion pattern was changed by the adaptation. As shown in Fig. 2, the difference between the two successive bisupport phases, which is due to the perturbation, decreases upon adaptive learning. This
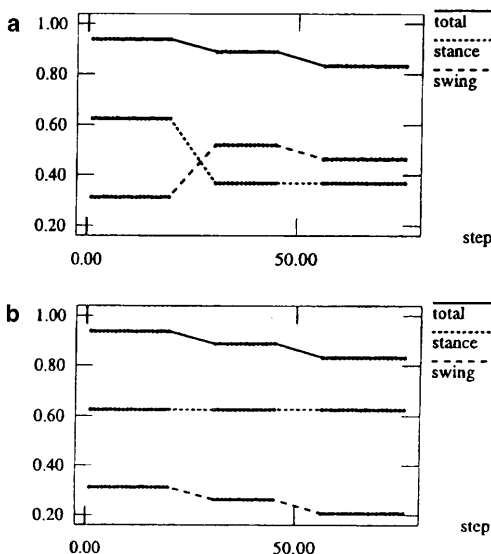
decrement is feasible through interlimb coordination in which, in the swing phase, the left forelimb moves slower while the right forelimb moves faster than before. Such an aftereffect can, however, be eliminated by readaptation, if the decerebrate cat continues to walk on the treadmill. Figure 20b shows the same result of 'walk' as in the initial experiment of Fig. 2a. On the other hand, Fig. 21 shows the durations of the swing phase, stance phase, and step cycle in this experiment. These results imply that the 'walk' gait is more suitable than any other gait in the normal environment.

Our model provides a similar computer simulation result to the above experiment. Figure 22 shows a gait diagram and Fig. 23 the durations of each phase in the simulation. These results indicate that the parameters of locomotion patterns have been readjusted to return to the initial values.

4 Basic framework of adaptation in rhythmic motions

4.1 Common features

We have described our concept of the adaptive mechanism in rhythmic movements. There are two types of parameters that determine the rhythmic motion pattern: Those representing the subsystem's natural characteristics and those describing the relation among subsystems. In the locomotion example, the former is $\omega_i (i = 0, 1, 2, 3)$ and the latter is $D_j (j = 1, 2, 3)$. If these parameters are adjusted, the attractor of motion dynamics will change, which, in our concept, corresponds to adaptation. In order to clarify the essence of adaptation, we summarize several common features in the adaptation of rhythmic movement.

Fig. 18a, b. The durations of swing phase, stance phase, and step cycle for left and right forelimbs (*LF* and *RF*) determined by simulation. **a** Left forelimb (LF), **b** right forelimb (RF). The first stage (20 steps) is normal locomotion, the second stage (15 steps) is perturbed locomotion without adaptation, and the last stage (20 steps) is adapted locomotion
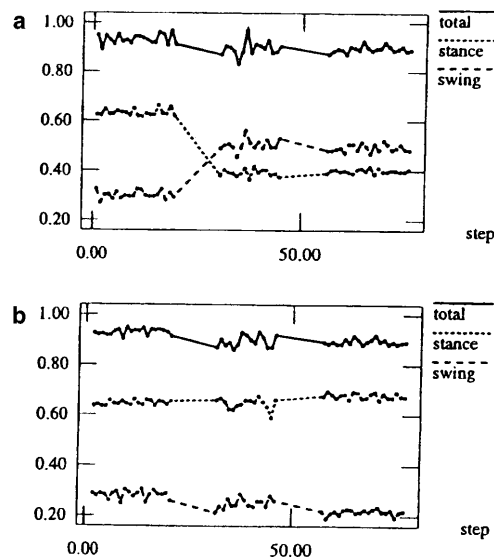

Fig. 19a, b. Durations of swing phase, stance phase, and step cycle for left and right forelimbs (*LF* and *RF*) obtained experimentally from a decerebrate cat. **a** Left forelimb (LF), **b** right forelimb (RF). The stages are the same as in Fig. 18
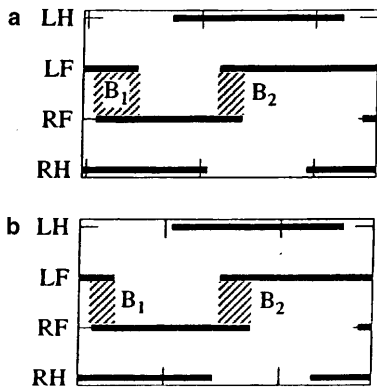
Fig. 20a, b. Change of locomotion pattern experimentally, where treadmill belt under LF was changed from 61 cm/s back to 36 cm/s. **a** Gait just after change of treadmill speed, **b** adapted gait to changed treadmill speed
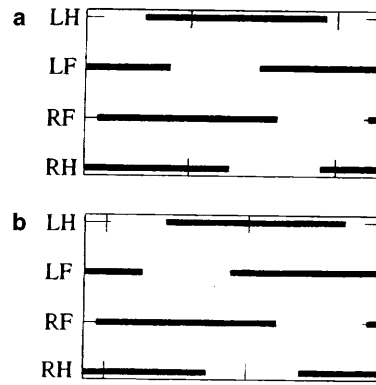

Fig. 22a, b. Change of locomotion pattern determined by simulation, where the environment of *LF*, i.e., μ_0, was changed from 1.7ω back to ω. **a** Gait without adaptation after change of treadmill speed, **b** adapted gait to changed treadmill speed
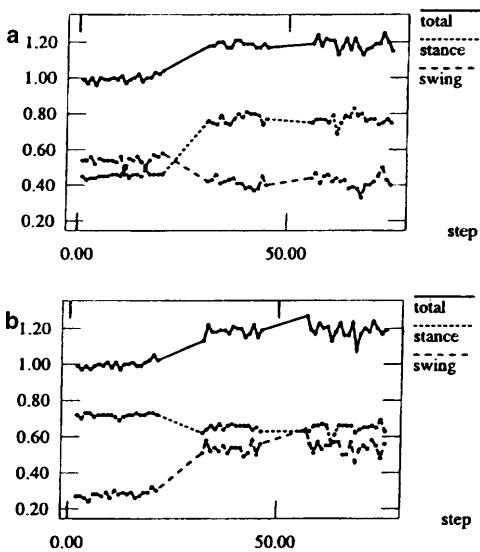

Fig. 21a, b. Durations of swing phase, stance phase, and step cycle for left and right forelimbs (*LF* and *RF*) in experiment, where treadmill belt under LF was changed from 61 cm/s back to 36 cm/s. **a** Left forelimb (LF), **b** right forelimb (RF). The stages are the same as in Fig. 18
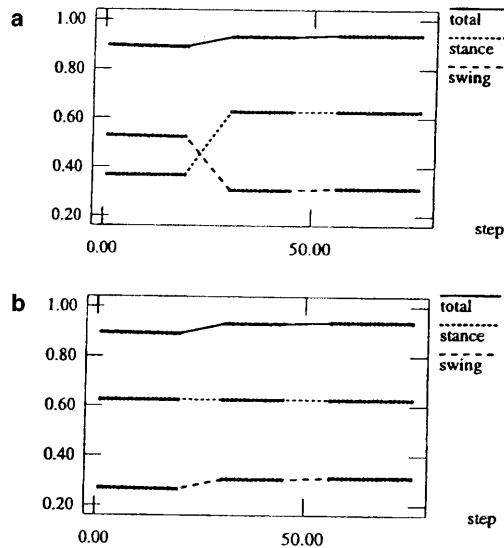

Fig. 23a, b. Durations of swing phase, stance phase, and step cycle for left and right forelimbs (*LF* and *RF*) determined by simulation, where environment of LF, i.e., μ_0, was changed from 1.7ω back to ω. **a** Left forelimb (LF), **b** right forelimb (RF). The stages are the same as in Fig. 18

Memorization of rhythmic motion patterns. The fact that the same rhythms can be generated reproducibly in the same environment indicates that patterns are memorized in some form. In the locomotion example, the natural frequency of the oscillator and the desired relative phases among oscillators are stored in the memory.

Adjustment of rhythmic motion pattern in memory. It is impossible to memorize all motion patterns in order to adapt to any unknown environment. When working in a new environment, the corresponding new pattern should be acquired by adjusting the memorized pattern.

Environmental changes. CPG basically produces rhythms in a feedforward manner, since it does not use any sensory feedback or command from the upper nervous system (Grillner 1975). If the environment is always changing at random, such a feedforward rhythm gen-

eration will be impossible because the environment must be identified using sensory feedback. Therefore, in order to adjust the CPG so that it generates the appropriate rhythmic pattern with respect to the specific environment, the environment itself should not fluctuate faster than the rate of adaptation.

Time scale of adaptation. Adaptation requires the evaluation of current motion. Before pattern adjustment, it is necessary to know how suitable the current pattern is. Therefore, the dynamics of adaptation must be slow compared with that of the rhythmic motion dynamics.

Convergency of adaptation. If adaptation progresses slowly, rhythmic motion must continue for a long time. The repetition of rhythmic motion is important for the convergence of adaptation.

4.2 A framework for adaptation in rhythmic motion

Based on the above consideration, we propose, as shown in Fig. 24, a framework for an adaptation mechanism in rhythmic movements. Here, x denotes the state of rhythmic movement, y denotes the environment, λ affects the rhythmic pattern, and parameter μ specifies the environment. In the above case of locomotion, for example, the parameters are $x = [\theta_0, \theta_1, \theta_2, \theta_3]$, $y = [\rho_0, \rho_1, \rho_2, \rho_3]$, $\lambda = [\omega_0, \omega_1, \omega_2, \omega_3, D_0, D_1, D_2]$, and $\mu = [\mu_0, \mu_1, \mu_2, \mu_3]$, respectively.

Environmental dynamics. The dynamics of the environment varies according to μ. Thus, μ must at least be constant for convergence of adaptation. In the case of locomotion, environmental dynamics is described by (8).

Rhythmic motion dynamics. The rhythmic motion pattern is an attractor within the space of x. It is determined from λ of the rhythmic motion pattern. In addition, it is also affected by y. Accordingly, the dynamics of x contain not only x but also y and λ. In the case of locomotion, rhythmic motion dynamics are described by (2)–(7).

Adaptation dynamics. The rhythmic motion is directly influenced by the environment. The fact that adaptation achieves 'better' motions implies the existence of some evaluation function $E(x)$ (V_D and F_i in the case of locomotion) of the motion pattern. In order to improve the evaluation, λ must be adjusted. Then, the dynamics of λ must be sufficiently slower than that of x, so that it is possible to adjust λ according to the evaluation of the motion pattern. In the case of locomotion, adaptation dynamics is described by (14)–(17).

In this framework, adaptation can be defined as the correspondence of λ to μ, i.e., finding adequate parameters of the rhythmic pattern relative to the given environment. This process is influenced by the rhythmic motion dynamics.

5 Discussion

By analyzing the perturbed locomotion, we proposed a mathematical model of oscillator coordination, in which the potential function of the relative phase dynamics is
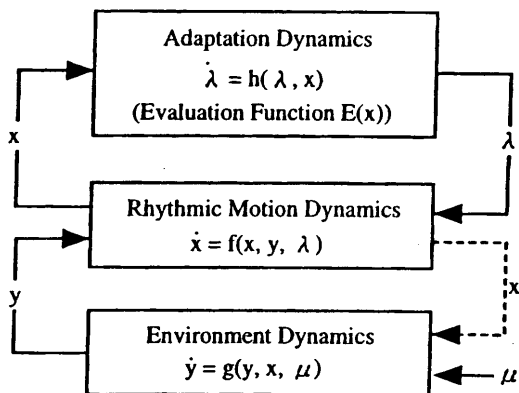

Fig. 24. Basic framework for adaptation in rhythmic movements

adjusted. This kind of adjustment minimizes the interactions between subsystems (oscillators) and allows the system (CPG) to memorize the new motion pattern with respect to the corresponding environment. It is important to note that the environmental perturbation considered in this paper is regular and periodic. If it is an impulsive perturbation, the locomotion, because it is stable, will return to the original pattern. If, on the other hand, perturbations are irregular, the steady locomotion pattern will never appear. In our adaptive mechanism, it is necessary for the time scales of adaptation dynamics, τ_ω and τ_D, to be much larger than that of the rhythmic motion dynamics τ_θ.

Our model can also explain the aftereffect of adaptation well (Sect. 3.4). It is understood that if we do not adjust the potential function, the memorized gait pattern will not change, i.e., remain 'walk' (Fig. 2a), even if periodic perturbation was applied. In this case, if we return the cat to walking under the normal condition again, that is, to drive all treadmills with the same speed, the decerebrate cat will walk with the normal pattern immediately as shown in Fig. 2a. However, the result from the biological experiment tells us that the cat did not immediately walk with the normal pattern of Fig. 2a; it walked with the pattern of Fig. 20a. This fact indicates that the memorized pattern has been changed.

For locomotion pattern generation, Kimura et al. (1993, 1994) simulated the change in the walking pattern of insects against locomotion speed, load effect, and limb amputation. They designed the oscillator coordination such that the load of each limb was distributed evenly. Their coordination dynamics was also slower in comparison with oscillator dynamics. This approach can be summarized within our framework. Taga (1995a, b), on the other hand, considered human locomotion as an entrainment between the neural system and the musculoskeletal system. He showed, in his simulation, that locomotion changes with walking speed and load effect, which he has called a real-time adaptability. This formulation, however, did not include the concept of slow dynamics of parameter adjustment according to environmental changes. The emergence of the locomotion pattern in his work is equivalent to the balance between perturbation and interaction, as shown in Fig. 11b. Because no parameter has been adjusted, that is, no information about the changed environment has been memorized, it is then difficult for this approach to realize the immediate adaptation to unknown environmental changes.

The adaptation demonstrated in this paper, in which a new gait pattern was acquired under the changed environment condition, is different from the adaptation observed as pattern transition with increasing locomotion speed, e.g., walk to trot to gallop. This kind of adaptation merely switches between gait patterns which are already acquired. Thus, this adaptation can be achieved in a short time. We have proposed the pattern transition model of quadruped locomotion based on energy consumption (Ito et al. 1996), where we used the same CPG model as in this work. Since the two different kinds of adaptation can be described by the same CPG

model, both adaptations could be possibly explained by the similar principle. However, in both cases, it is assumed that some locomotion patterns are memorized beforehand, and therefore the question of how they are initially acquired arises. Reflex stepping (Thelen and Smith 1994) seen in infants enables us to infer that a mechanism of rhythm generation may be inherent for automatic movement, originally.

6 Conclusions

We studied the adaptation mechanism of rhythmic movement to a variable environment. As rhythmic movement, we mainly considered automatic movement, i.e., rhythmic movements which are produced by the rhythm generator with neuronal oscillators. However, there is the possibility that, if the common features described in Sect. 4.1 are satisfied, our framework is applicable to other kinds of movements. Thus, it is necessary to discuss the criterion of parameter adjustment.

In one of our future projects, we will take the actual dynamics of limbs or the body into consideration. In the present study, we implicitly assume that the phase of the limb movement is equal to that of the oscillator. However, they are not always equal. Therefore, the problem of how to deal with the difference in these two phases arises. Furthermore, postural balance, because of body dynamics, will be another problem, since the interlimb coordination is acquired through postural balance. The stability of the body would also have an important effect on the determination of quadruped gait, e.g., walk, trot, and gallop.

Appendix

A Dynamics of relative phases

Rewriting (3)–(7), we obtain

$$\dot{\theta}_0 = \omega_0 + \tau_\theta(\theta_1 + \theta_3 - 2\theta_0 - D_0 - D_1) \tag{19}$$
$$\dot{\theta}_1 = \omega_1 + \tau_\theta(\theta_0 + \theta_2 - 2\theta_1 + D_0 - D_2) \tag{20}$$
$$\dot{\theta}_2 = \omega_2 + \tau_\theta(\theta_1 - \theta_2 + D_2) \tag{21}$$
$$\dot{\theta}_3 = \omega_3 + \tau_\theta(\theta_0 - \theta_3 + D_1) \tag{22}$$

Using these equations, we calculate the dynamics of the relative phases $\phi_0 = \theta_1 - \theta_0$, $\phi_1 = \theta_3 - \theta_0$, $\phi_2 = \theta_2 - \theta_1$:

$$\dot{\phi}_0 = \omega_1 - \omega_0 + \tau_\theta(-\phi_0 + \phi_2 + D_0 - D_2)$$
$$\quad - \tau_\theta(\phi_0 + \phi_1 - D_0 - D_1) \tag{23}$$
$$\dot{\phi}_1 = \omega_3 - \omega_0 + \tau_\theta(-\phi_1 + D_1) - \tau_\theta(\phi_0 + \phi_1 - D_0 - D_1) \tag{24}$$
$$\dot{\phi}_2 = \omega_2 - \omega_1 + \tau_\theta(-\phi_2 + D_2) - \tau_\theta(-\phi_0 + \phi_2 + D_0 - D_2) \tag{25}$$

It is obvious that they are the gradient dynamics whose potential function is defined by the following function:

$$V = \frac{1}{2}\tau_\theta\left[\left(\phi_0 + \phi_1 - D_0 - D_1 + \frac{\omega_0}{\tau_\theta}\right)^2\right.$$
$$+ \left(-\phi_0 + \phi_2 + D_0 - D_2 + \frac{\omega_1}{\tau_\theta}\right)^2$$
$$\left. + \left(-\phi_2 + D_2 + \frac{\omega_2}{\tau_\theta}\right)^2 + \left(-\phi_1 + D_1 + \frac{\omega_3}{\tau_\theta}\right)^2\right] \tag{26}$$

In fact, (23)–(25) can be derived from $\dot{\phi}_0 = -\partial V/\partial\phi_0$, $\dot{\phi}_1 = -\partial V/\partial\phi_1$, and $\dot{\phi}_2 = -\partial V/\partial\phi_2$. Therefore, the minimum points of potential function $\partial V/\partial\phi_0 = \partial V/\partial\phi_1 = \partial V/\partial\phi_2 = 0$ can be given as solutions of the equations $\dot{\phi}_0 = \dot{\phi}_1 = \dot{\phi}_2 = 0$. After some computation, we can obtain the solution,

$$\begin{bmatrix} \phi_0 \\ \phi_1 \\ \phi_2 \end{bmatrix} = \begin{bmatrix} D_0 \\ D_1 \\ D_2 \end{bmatrix} + \frac{1}{4\tau_\theta}\begin{bmatrix} 4 & -2 & 2 \\ -2 & 3 & -1 \\ 2 & -1 & 3 \end{bmatrix}\begin{bmatrix} \omega_1 - \omega_0 \\ \omega_3 - \omega_0 \\ \omega_2 - \omega_1 \end{bmatrix}$$
$$= \begin{bmatrix} D_0 \\ D_1 \\ D_2 \end{bmatrix} + \frac{1}{4\tau_\theta}\begin{bmatrix} -2\omega_0 + 2\omega_1 + 2\omega_2 - 2\omega_3 \\ -\omega_0 - \omega_1 - \omega_2 + 3\omega_3 \\ -\omega_0 - \omega_1 + 3\omega_2 - \omega_3 \end{bmatrix} \tag{27}$$

It should be noted that, if $\omega_0 = \omega_1 = \omega_2 = \omega_3$, which is the case for normal locomotion in our simulation, the relative phases ϕ_0, ϕ_1, ϕ_2 converge to D_0, D_1, D_2.

B Adjustment of angular velocity in the swing phase

The dynamics of the oscillator in the swing phase is given by

$$\dot{\theta}_i = \omega_i + f_i \quad (i = 0, 1, 2, 3) \tag{28}$$

Integrating them during the swing phase, we obtain

$$\theta_i(t) = \omega_i t + F_i \quad (i = 0, 1, 2, 3) \tag{29}$$

where

$$F_i = \int_{T_{sw}} f_i \, dt \quad (i = 0, 1, 2, 3) \tag{30}$$

and T_{sw} is the duration of the swing phase. If $F_i > 0$ (or < 0), then θ_i is accelerated (or decelerated). In order to reduce the interaction F_i, we adjust ω_i in proportion to F_i,

$$\omega_i^{(n+1)} = \omega_i^{(n)} + \tau_\omega F_i \quad (i = 0, 1, 2, 3) \tag{31}$$

If $F_i = 0$, then we do not change ω_i because ω_i is neither small nor large.

Since interactions do not work in a stance phase, we can change (30) as follows:

$$F_i = \int_T f_i \, dt \quad (i = 0, 1, 2, 3) \tag{32}$$

C Modification of desired relative phase

When the cost function is given by (18), we can adjust the minimum of the potential function D_j as

$$\frac{dD_j}{dt} = -\tau_D \prime \frac{\partial V_D}{\partial D_j} \quad (j = 0, 1, 2) \tag{33}$$

It can be expressed in the discrete form

$$D^{(n+1)} = D^{(n)} + \tau \frac{dD_j^{(n)}}{dt}$$
$$= D^{(n)} - \tau_D \frac{\partial V_D}{\partial D_j} \tag{34}$$

Thus, (15–17) can be derived from (4–7).

For example, we derive (15). The evolution equation becomes

$$\frac{\partial V_D}{\partial D_0} = \int_T \frac{\partial}{\partial D_0} \sum_{i=0}^{3} \left\{ \frac{1}{2\tau_\theta} f_i^2 \right\} dt$$
$$= \int_T \sum_{i=0}^{3} \frac{\partial}{\partial D_0} \left\{ \frac{1}{2\tau_\theta} f_i^2 \right\} dt$$
$$= \int_T \sum_{i=0}^{3} \left\{ \frac{f_i}{\tau_\theta} \frac{\partial f_i}{\partial D_0} \right\} dt \tag{35}$$

where, from (4)–(7),

$$\frac{\partial f_0}{\partial D_0} = -\tau_\theta, \quad \frac{\partial f_1}{\partial D_0} = \tau_\theta, \quad \frac{\partial f_2}{\partial D_0} = \frac{\partial f_3}{\partial D_0} = 0 \tag{36}$$

Substituting them in (35), we get

$$\frac{\partial V_D}{\partial D_0} = -\int_T (f_0 - f_1) \, dt \tag{37}$$

Thus, we obtained (15).

References

Cohen AH, Holmes PJ, Rand RH (1982) The nature of the coupling between segmental oscillators of the lamprey spinal generator for locomotion: a mathematical model. J Math Biol 13:345–369

Collins JJ, Richmond SA (1994) Hard-wired central pattern generators for quadrupedal locomotion. Biol Cybern 71:375–385

Delcomyn F (1980) Neural basis of rhythmic behavior in animals. Science 210:492–498

Grillner S (1975) Locomotion in vertebrates: central mechanisms and reflex interaction. Phy Rev 55:247–304

Ito S, Yuasa H, Ito K, Ito M (1996) Energy-based pattern transition of quadrupedal locomotion with oscillator and mechanical model. Proc. of 1996 IEEE Int. Conf. on System, Man and Cybernetics, pp 2321–2326

Kimura S, Yano M, Shimizu H (1993) A self-organizing model of walking patterns of insects. Biol Cyber 69:183–193

Kimura S, Yano M, Shimizu H (1994) A self-organizing model of walking patterns of insects. II. Biol Cybern 70:505–512

Schöner G, Jiang WY, Kelso JAS (1990) A synergetic theory of quadrupedal gaits and gait transitions. J Theor Biol 142:359–391

Taga G (1995a) A model of the neuro-musculo-skeletal system for human locomotion. I. Emergence of basic gait. Biol Cybern 73:97–111

Taga G (1995b) A model of the neuro-musculo-skeletal system for human locomotion. II. Real-time adaptability under various constraints. Biol Cybern 73:113–121

Thelen E, Smith LB (1994) A dynamic system approach to the development of cognition and action. MIT Press, Cambridge, Mass.

Yanagihara D, Kondo I (1996) Nitric oxide plays a key role in adaptive control of locomotion in cat. Proc Natl Acad Sci USA 93:13292–13297

Yanagihara D, Udo M, Kondo I, Yoshida T (1993) A new learning paradigm: adaptive changes in interlimb coordination during perturbed locomotion in decerebrate cats. Neurosci Res 18:241–244

Yuasa H, Ito M (1990) Coordination of many oscillators and generation of locomotory patterns. Biol Cybern 63:177–184