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Learning model for coupled neural oscillators

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Abstract. Neurophysiological experiments have shown that many motor commands in living systems are generated by coupled neural oscillators. To coordinate the oscillators and achieve a desired phase relation with desired frequency, the intrinsic frequencies of component oscillators and coupling strengths between them must be chosen appropriately. In this paper we propose learning models for coupled neural oscillators to acquire the desired intrinsic frequencies and coupling weights based on the instruction of the desired phase pattern or an evaluation function. The abilities of the learning rules were examined by computer simulations including adaptive control of the hopping height of a hopping robot. The proposed learning rule takes a simple form like a Hebbian rule. Studies on such learning models for neural oscillators will aid in the understanding of the learning mechanism of motor commands in living bodies.

1. Introduction

Results of neurophysiological studies have shown that many motor commands, including those for basic locomotor patterns, such as swimming and walking (Getting 1981, Grillner *et al* 1991, Pearson 1976), mastication (Lund and Enomoto 1988) and movement of gastric mills (Flamm and Harris-Warrick 1986), are generated by coupled oscillatory components, such as a neural cell and a neural circuit. Such dynamic behaviours of neural activities are also reported in sensory systems, the olfactory system (Freeman 1987) and the visual system (Gray *et al* 1989). To coordinate the component oscillators and generate a desired phase pattern with desired frequency, intrinsic frequencies of the oscillators and coupling weights between them must be well chosen. In the generation of motor commands the coordination between coupled neural oscillators and the body components, such as a leg, must be also taken through the motor command and sensory feedback signals.

Some studies motivated by the existence of coupled neural oscillators generating locomotor patterns in the central nervous systems have proposed learning models to acquire the desired phase pattern in coupled neural oscillators. Doya and Yoshizawa (1992) proposed an adaptive rule to control a physical system by a neural oscillator and Ermentrout and Kopell (1994) proposed a learning rule to acquire an instructed phase pattern in an oscillatory network. These works showed that the desired motor command can be acquired by simple learning rules for coupling weight between component oscillators or between the oscillator and a physical system. However, we still have problems in these learning rules. The first problem is that no learning rule for intrinsic frequencies of component oscillators is proposed, therefore we must expect that the intrinsic frequencies are set at a desired value before learning. The second is that the proposed learning rules cannot be easily generalized to other neural oscillators because these models have considered a specific neural oscillator and required *a priori* knowledge of its dynamics in the derivation of the learning rules. The third is that the factors on the success of the learning rules have not been analysed.

We have previously proposed learning models for phase oscillators (Nishii and Suzuki 1994, Nishii 1997, 1998, in press). In these studies, learning rules for the coupling strengths between oscillators and intrinsic frequencies of component oscillators are investigated, and conditions on the proposed learning model's acquisition of the desired phase pattern were analysed. The dynamics of many nonlinear systems which have an orbitally asymptotically stable limit cycle can be expressed as a phase oscillator (Ermentrout and Kopell 1991). Therefore we can expect that the learning rules for a class of coupled nonlinear oscillators will be derived from our phase-oscillator learning rules. In this paper we discuss the derivation and propose learning rules for neural oscillators which are nonlinear oscillators composed of neural cells. The perfomance of the proposed learning rule is examined by computer simulations including adaptive control of a one-dimensional hopping robot.

The paper is organized as follows. In section 2, the proposed learning models for phase oscillators are briefly summarized. In section 3, the relation between the dynamics of a phase oscillator and a nonlinear oscillator is discussed. Based on the result, learning rules for neural oscillators are proposed. Section 4 provides the results of computer simulations.

2. Learning models for coupled phase oscillators

We previously proposed learning rules for coupled phase oscillators in two different situations. In the first case the desired phase pattern for each component oscillator was explicitly instructed as a teacher signal (Nishii and Suzuki 1994, Nishii 1998), and in the second case the target phase pattern was not explicitly given, but an evaluation signal which is a function of the phase difference between oscillators was given (Nishii 1997, in press). In both cases the intrinsic frequencies of the component oscillators and the coupling weights between component oscillators were tuned according to the proposed learning rules so as to acquire a desired phase pattern. In this section we briefly summarize these learning rules.

In the first case, we assume the phase dynamics of coupled oscillators without recurrent connection as

$$\begin{cases} \dot{\theta}_i = \omega_i + R_i + F_i \\ \dot{\tilde{\theta}}_i = \Omega_i \end{cases} \qquad i = 1, \ldots, N \tag{1}$$

where

$$R_i \equiv \begin{cases} 0 & i = 1 \\ \displaystyle\sum_{k \in J_i} \sum_{l=1}^{L_{ik}} w_{ik}^l R_{ik}^l & i \neq 1 \end{cases} \tag{2}$$
$$R_{ik}^l \equiv R(\theta_i, \theta_k - \psi_{ik}^l) \qquad F_i \equiv F(\theta_i, \tilde{\theta}_i)$$

and $\theta_i, \tilde{\theta}_i \in \mathbf{S}$†, $(i = 1, \ldots, N)$ are the phases of component oscillators and the teacher signal, respectively, N is the number of the component oscillators, J_i indicates the ensemble of indices of oscillators sending signals to the oscillator i $(\forall k \in J_i, k < i)$, ω_i is the intrinsic frequency of the oscillator i, and Ω_i is the frequency of the teacher signal for oscillator i. We assume various phase delayed couplings between oscillators, w_{ik}^l and ψ_{ik}^l $(l = 1, \ldots, L_{ik})$ show the coupling strength and the phase delay of the lth coupling from the kth to the ith oscillator, respectively, where $\sum_{k \in J_i} \sum_{l=1}^{L_{ik}} w_{ik}^l \ll 1$, i.e., the total effect of the signals from the coupled oscillator is

† Here, we define $\mathbf{S} = \mathbf{R} \pmod 1$.

much less than the effect of the intrinsic dynamics. L_{ik} indicates the number of different phase delayed couplings from the kth to the ith oscillator. $R(\theta_i, \theta_k - \psi_{ik}^l)$ and $F(\theta_i, \tilde{\theta}_i)$ are functions showing the effects of signals from the coupled oscillator and the teacher signal on the phase dynamics, respectively.

The proposed learning rule for the coupling weight w_{ij} and the intrinsic frequency ω_i to obtain the same phase pattern as the instructed teacher signal takes the form

$$\begin{cases} \dot{\omega}_i = \varepsilon \langle F_i + R_i \rangle \\ \dot{w}_{ij}^l = \varepsilon\gamma \langle F_i \rangle \cdot \langle R_{ij}^l \rangle \end{cases} \qquad i = 1, \ldots, N, \ \ j \in J_i \tag{3}$$

where $\varepsilon, \gamma \ll 1$ are constants determining the learning velocity and $\langle * \rangle$ shows the time averaged term. This learning rule implies that the intrinsic frequency changes according to the total effect of the input signals and adapts to the current frequency of the oscillator. The coupling strength changes according to the correlation between the effects of the signal from the coupled oscillator and the teacher signal. With this learning rule, the same phase pattern and frequency as for the teacher signal are obtained in the coupled oscillators under certain conditions (for details see Nishii 1998).

In the second case, we assume that the phase dynamics of the coupling oscillators are in the same form as in equation(1) with the exception of the term of the effect of the teacher signal, which is

$$\dot{\theta}_i = \omega_i + R_i \qquad i = 0, \ldots, N. \tag{4}$$

We propose the following learning rule for acquiring a desired phase relation in the oscillators based on the evaluation function E_i $(i = 1, \ldots, N)$, which satisfies $\forall i = 1, \ldots, N$, $\exists s_i < i$, $E_i = E_i(\theta_i, \theta_{s_i})$:

$$\begin{aligned} \dot{\omega}_i &= \varepsilon \langle R_i \rangle \\ \dot{w}_{ij}^l &= \varepsilon\gamma \langle E_i \rangle \cdot \langle R_{ij}^l \rangle \end{aligned} \qquad i = 1, \ldots, N, \ \ j \in J_i. \tag{5}$$

The learning rule for the intrinsic frequency takes the same form as equation (3); that is, it changes according to the total effect of the input signals. The learning rule for coupling weights also takes a similar form to equation (3), i.e., it changes according to the correlation between the evaluation function and the effect of the input signal. With this learning rule, a desired phase pattern which satisfies $\forall i$, $\langle E_i \rangle = 0$ is obtained under certain conditions (for details see Nishii 1997, in press).

Although conditions for the learning by equations (3) and (5) are analysed under the assumption that no recurrent connections exist between oscillators, the simulation results show that the learning rules work well even if such connections exist.

3. Learning models for coupled neural oscillators

In this section we derive learning models for neural oscillators from learning rules (3) and (5). When each component oscillator is composed of neural cells, we must determine the relation between the state of the cells and the function R, which shows the effect of the input signal on the phase dynamics in equations (3) and (5).

3.1. The effect of the input signal on the phase dynamics

Consider two-dimensional dynamics with a limit cycle around an origin by Hopf bifurcation and receiving a small input signal $\boldsymbol{\epsilon} = (\epsilon, 0)^t$, $(\epsilon \ll 1)$:

$$\dot{\boldsymbol{u}} = \boldsymbol{f}(\boldsymbol{u}) + \boldsymbol{\epsilon} \tag{6}$$

where $\boldsymbol{u} = (u_1, u_2)^t \in \mathbf{R}^n$ is the state vector, $\boldsymbol{f} : \mathbf{R}^2 \to \mathbf{R}^2$ is a C^∞ function which satisfies $\boldsymbol{f}(\mathbf{0}) = \mathbf{0}$, and the Jacobian matrix $Df(\mathbf{0})$ has eigen values $\lambda_1 = \alpha + i\omega$, $\lambda_2 = \bar{\lambda}_1$, $(\alpha > 0, \omega > 0)$. Here there exists a matrix P which satisfies

$$P^{-1}(D\boldsymbol{f}(0))P = \begin{pmatrix} \alpha & -\omega \\ \omega & \alpha \end{pmatrix} \equiv \Omega. \tag{7}$$

Setting

$$\boldsymbol{u} = P\tilde{\boldsymbol{u}} \qquad \tilde{\boldsymbol{u}} = (\tilde{u}_1, \tilde{u}_2)^t \tag{8}$$

the system (6) becomes

$$\dot{\tilde{\boldsymbol{u}}} = \Omega\tilde{\boldsymbol{u}} + P^{-1}\boldsymbol{\epsilon} + \mathcal{O}(\tilde{\boldsymbol{u}}^2). \tag{9}$$

By setting

$$\xi = \tilde{u}_1 + i\tilde{u}_2 \qquad \lambda = \alpha + i\omega \qquad P^{-1} \equiv \{p_{ij}\} \qquad p_j e^{2\pi i\gamma_j} \equiv (p_{1j} + ip_{2j}) \tag{10}$$

equation (9) is transformed to

$$\dot{\xi} = \lambda\xi + p_1 e^{2\pi i\gamma_1}\epsilon + V(\xi, \bar{\xi}), \tag{11}$$

where $V(\xi, \bar{\xi}) = \mathcal{O}(|\xi|^2)$. Here, there exists a nonlinear transformation

$$\xi = z + \chi(z, \bar{z}) \tag{12}$$

by which equation (11) is reduced to the normal form with disturbance (Hassard and Wan 1978):

$$\dot{z} = \lambda z + Cz^2\bar{z} + p_1 e^{2\pi i\gamma_1}\epsilon + \mathcal{O}(|z|^5) \tag{13}$$

where $C \in \mathrm{C}$ is a constant. By ignoring the higher orders and setting

$$z \equiv r e^{2\pi i(\theta+\gamma_1)}, \tag{14}$$

where $r \in \mathbf{R}$ and $\theta \in \mathbf{S}$, equation (13) can be transformed to

$$\begin{cases} \dot{\theta} = \omega + C_i r^2 - \epsilon \dfrac{p_1}{r} \sin 2\pi\theta \\ \dot{r} = \alpha r + C_r r^3 + \epsilon p_1 \cos 2\pi\theta \end{cases} \tag{15}$$

$$C_r = \mathrm{Re}\{C\} \qquad C_i = \mathrm{Im}\{C\}$$

where $C_r < 0$, $\alpha > 0$ from the assumption that the above dynamics have an oscillatory solution. By substituting the expansions of θ, r by ϵ, i.e.,

$$\begin{cases} \theta = \theta_0 + \epsilon\theta_1 + \epsilon^2\theta_2 + \cdots \\ r = r_0 + \epsilon r_1 + \epsilon^2 r_2 + \cdots \end{cases} \tag{16}$$

into (15) we obtain

$$\dot{\theta}_0 = \omega + C_i r_0^2 \qquad \dot{\theta}_1 = 2C_i r_0 r_1 - \frac{p_1}{r_0} \sin 2\pi\theta_0 \tag{17}$$

$$\dot{r}_0 = \alpha r_0 + C_r r_0^3 \qquad \dot{r}_1 = \alpha r_1 + 3C_r r_0^2 r_1 + p_1 \cos 2\pi\theta_0. \tag{18}$$

This result suggests that if the dynamics is in the steady state ($r_0 = \sqrt{-\alpha/C_r}$) and if r_0 is sufficiently small ($r_0 \ll 1$), i.e., the system is close to the bifurcation point, the effect $R_1(\theta, \epsilon)$ of disturbance $\boldsymbol{\epsilon} = (\epsilon, 0)$ on the phase dynamics is given by the following form in the lowest approximation:

$$R_1(\theta, \epsilon) = -\epsilon \frac{p_1}{r_0} \sin 2\pi\theta_0. \tag{19}$$

We next consider the relation between equation (19) and state variables (u_1, u_2) of the oscillator (6). From (8), (10) and (12), we obtain

$$\begin{aligned} z &= \xi + O(|z|^2) \\ &= \tilde{u}_1 + \mathrm{i}\tilde{u}_2 + O((\tilde{u}_1, \tilde{u}_2)^2) \\ &= \sum_{j=1}^{2} p_j \mathrm{e}^{\mathrm{i}\gamma_j} u_j + O((u_i)^2). \end{aligned} \tag{20}$$

Comparing equation (20) with equation (14) and ignoring the higher-order terms, we obtain the following relation:

$$r\mathrm{e}^{2\pi\mathrm{i}\theta} = \sum_{j=1}^{2} p_j \mathrm{e}^{2\pi\mathrm{i}(\gamma_j - \gamma_1)} u_j. \tag{21}$$

By expanding r, θ, u_j for ϵ in the above equation, we obtain at $O(\epsilon)$

$$\begin{cases} r_0 \cos\theta_0 = p_1 u_{1,0} + p_2 u_{2,0} \cos 2\pi(\gamma_j - \gamma_1) \\ r_0 \sin\theta_0 = p_2 u_{2,0} \sin 2\pi(\gamma_2 - \gamma_1) \end{cases} \tag{22}$$

where r_0, θ_0, and u_{j0} are zero order terms of r, θ and x_j for ϵ. By comparing equations (19) and (22), we obtain

$$R_1(\boldsymbol{u}, \epsilon) \simeq \epsilon \frac{p_1 p_2}{r_0^2} u_{2,0} \sin 2\pi(\gamma_2 - \gamma_1). \tag{23}$$

This relation implies that the effect of the input signal is given by using the state variable which is not affected by the input directly. In order to apply this expression to the learning rule for neural oscillators we must at least determine the sign of the r.h.s. of equation (23), that is, the sign of $\sin 2\pi(\gamma_2 - \gamma_1)$, which requires knowledge about the dynamics of the oscillator. We therefore consider another expression for the function R.

Because $\dot{\theta}_0 \simeq \omega$ for $r_0 \ll 1$ from equation (17), the time derivative of the first equation in (22) is given by

$$-r_0\omega \sin\theta_0 = p_1 \dot{u}_{1,0} + p_2 \dot{u}_{2,0} \cos 2\pi(\gamma_j - \gamma_1). \tag{24}$$

By comparing the above equation and equation (19), we obtain

$$R_1(\boldsymbol{u}, \epsilon) \simeq \epsilon \frac{p_1^2}{r_0^2 \omega} \dot{u}_{1,0} \tag{25}$$

under the following condition:

$$\cos 2\pi(\gamma_2 - \gamma_1) \ll 1. \tag{26}$$

We have considered the effect of the input signal $\boldsymbol{\epsilon} = (\epsilon, 0)^t$ on the phase dynamics, we can also express the effect $R_2(\boldsymbol{u}, \epsilon)$ for the input signal $\boldsymbol{\epsilon} = (0, \epsilon)^t$ in a similar form. We can thus approximately express the effect of the input signal ϵ on the ith state variable by

$$R_i(\boldsymbol{u}, \epsilon) \simeq \epsilon \frac{p_i^2}{r_0^2 \omega} \dot{u}_{i,0} \sim \epsilon \dot{u}_{i,0}. \tag{27}$$

When the oscillator is composed of neural cells and each state variable shows the state of component cells, the above equation is interpreted as follows: the phase shift of a neural oscillator caused by an input signal can be given in the lowest approximation by the product of the amplitude of the input signal and the temporal change of the state of the postsynaptic cell which receives the input signal.

Then, we explain that the condition (26) is satisfied if the shape of the limit cycle in the space $\boldsymbol{u} = (x, y)^t$ is nearly circular or if the axes of the elliptic shape of the limit cycle match the xy axes.

The matrix P in equation (7) maps the space of $\tilde{\boldsymbol{u}}$, where the shape of the limit cycle is almost circular, to the space of $\boldsymbol{u}$, where the shape is elliptic. Therefore, the ratio of the norms of the two column vectors of the matrix P shows the extent of the distortion of the elliptic shape of the limit cycle in $\boldsymbol{u}$. Because the formula of the inverse matrix indicates that the norms of the first- and second-row vectors of P^{-1} are proportional to the norms of the second- and first-column vectors of P, respectively, the ratio of the norms of the two row vectors of P^{-1} also indicates the distortion of the limit cycle. Low distortion of the elliptic shape of the limit cycle is represented by $p_{11}^2 + p_{12}^2 \simeq p_{21}^2 + p_{22}^2$. Because the column vectors of P are orthogonal, the row vectors of P^{-1} are also orthogonal, that is, $p_{11}p_{21} + p_{12}p_{22} = 0$. From these two equations we obtain $p_{12}^2 \simeq p_{21}^2$ and $p_{11}p_{12} + p_{21}p_{22} = -p_{12}^2 p_{22}/p_{21} + p_{21}p_{22} \simeq 0$, which implies that equation (26) is satisfied, since $\cos 2\pi(\gamma_2 - \gamma_1) = (p_{11}p_{12} + p_{21}p_{22})/p_1 p_2$. In this case, we also obtain $p_1^2 \simeq p_2^2$, which implies that the coefficients of $\dot{u}_{i0}$ in equation (27) take the same value for $i = 1, 2$. Therefore the total effect of input signals $\boldsymbol{\epsilon} = (\epsilon_1, \epsilon_2)$ on the phase dynamics $R(\boldsymbol{u})$ is given by the linear combination of equation (27) in the lowest approximations, i.e.,

$$R(\boldsymbol{u}, \boldsymbol{\epsilon}) \sim \boldsymbol{\epsilon}^t \cdot \dot{\boldsymbol{u}}_0 \tag{28}$$

where $\boldsymbol{u}_0 = (u_{1,0}, u_{2,0})^t$.

If the axes of the elliptic shape of the limit cycle almost match the xy axes, the non-diagonal elements of matrices P and P^{-1} would be sufficiently small, that is, $p_{12}, p_{21} \sim 0$, which also implies $\cos 2\pi(\gamma_2 - \gamma_1) \sim 0$, and therefore condition (26) would be satisfied.

Thus we have proved that equation (27) gives a good approximation if the shape of the limit cycle in the space $\boldsymbol{u}$ is nearly circular or if the axes of the limit cycle match the xy axes.

The meaning of the relation (27) can be explained geometrically as follows. Suppose that the state changes in an anti-clockwise direction along the circular limit cycle in the xy plane (figure 1). If the input signal $\boldsymbol{\epsilon} = (\epsilon, 0)$ is given when $y = 0$, the phase is not affected. If the input signal is given when $x = 0$ and y takes its maximum value, the phase is delayed considerably. On the other hand, the phase is advanced considerably if the input signal is

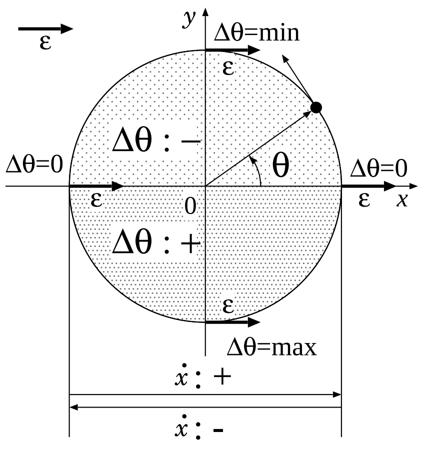

Figure 1. Effect of an input signal on phase dynamics. When the limit cycle is circular on the xy plane, the PRC for the input $\epsilon = (\epsilon, 0)$ is given by $\Delta\theta \sim \dot{x}$ or $\Delta\theta \sim \pm cx$.

given when $x = 0$ and y assumes its minimum value. As the input signal grows larger, its effect on the phase also increases. From such considerations, we obtain $R_1(\boldsymbol{u}, \epsilon) \sim \epsilon\dot{x}$, where $\boldsymbol{u} = (x, y)$. Although it is also established that $R_1(\boldsymbol{u}, \epsilon) \sim -\epsilon y$, the sign of the r.h.s. changes if the state changes in a clockwise direction; that is, the sign cannot be determined without a knowledge of the dynamics of the oscillator, as mentioned above.

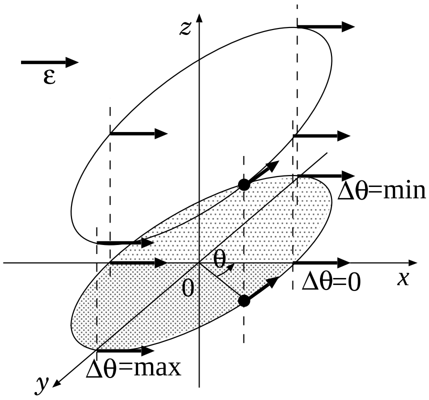

Figure 2. Effect of an input signal on the phase dynamics of a limit cycle in three-dimensional space.

When a limit cycle exists in $N(\geqslant 3)$-dimensional space, the same analysis would be possible by considering the projection of the limit cycle on the plane containing the x_i axis for a small input vector parallel to the x_i axis (figure 2), provided that the state variable x_i contributes to the oscillation; that is, we obtain $R_i(\boldsymbol{u}, \epsilon) \sim \epsilon\dot{u}_i$.

3.2. Learning rule for neural oscillators

We now formulate a learning rule for coupled neural oscillators. Here we assume that the dynamics of the neural oscillator can be essentially expressed by two variables which show the states of the component cell, and that the distortion of the limit cycle is small. We replace the dynamics of a component oscillator in equation (1) with the following form:

$$\dot{\boldsymbol{u}}_i = \boldsymbol{f}(\boldsymbol{u}_i) + \boldsymbol{s}_i + \tilde{\boldsymbol{y}}_i \tag{29}$$

where $\boldsymbol{f}(\boldsymbol{u}_i) = (f^1(\boldsymbol{u}_i), f^2(\boldsymbol{u}_i))^t$, and we regard each element of the state vector $\boldsymbol{u}_i = (u_i^1, u_i^2)^t$ as the state of a component cell. $\boldsymbol{s}_i = (s_i^1, s_i^2)^t$ shows the input signals from coupled oscillators:

$$\boldsymbol{s}_i \equiv \left(\sum_{j\in J_i} \sum_{l=1}^{2} w_{1j}^{1l} y_j^l, \sum_{j\in J_i} \sum_{l=1}^{2} w_{2j}^{2l} y_j^l \right)^t \tag{30}$$

where $y_j^l = y(\boldsymbol{u}_j^l)$ denotes the output signal from the lth cell in the oscillator j, w_{ij}^{kl} denotes the coupling weight of the signal y_j^l to the kth cell in oscillator i and $\tilde{\boldsymbol{y}}_i = (\tilde{y}_i^1, \tilde{y}_i^2)^t$ is the teacher signal to the oscillator.

The learning rule (3) can be transformed to

$$\begin{cases} \dot{\omega}_i = \varepsilon\langle \boldsymbol{p}_i^t \cdot (\boldsymbol{s}_i + \tilde{\boldsymbol{y}}_i)\rangle \\ \dot{w}_{ij}^{kl} = \varepsilon\gamma\langle p^k(\boldsymbol{u}_i)\tilde{y}_i^k\rangle\langle p^k(\boldsymbol{u}_i)y_j^l\rangle \end{cases} \tag{31}$$

where $\boldsymbol{p}_i = (p^1(\boldsymbol{u}_i), p^2(\boldsymbol{u}_i))^t$ shows the effect of the input signal to the oscillator i on the phase dynamics and p^k takes the following form based on equation (27):

$$p^k(\boldsymbol{u}_i) = \dot{u}^k_{i0} = f^k(\boldsymbol{u}_i). \tag{32}$$

The derived learning rule is based on the time averaged effect of the input signals, which is given by the product of the input signal and the temporal change of the state in the postsynaptic cell that receives the signal.

The learning rule for neural oscillators corresponding to equation (5) is given in the same manner, i.e.,

$$\begin{cases} \dot{\omega}_i = \varepsilon \langle \boldsymbol{p}_i^t \cdot \boldsymbol{s}_i \rangle \\ \dot{w}^{kl}_{ij} = \varepsilon\gamma \langle E_i \rangle \cdot \langle p^k(\boldsymbol{u}_i) \cdot y^l_j \rangle \end{cases} \tag{33}$$

for similar dynamics to those in equation (29), except for the term of the teacher signal.

When the weight w^{kl}_{ij} is the function of a parameter α^{kl}_{ij}, an adequate value for α^{kl}_{ij} can also be learned in the same manner by replacing $w^{kl}_{ij} = W(\alpha^{kl}_{ij})$ with α^{kl}_{ij} in equations (31) and (33), if the C^1 function $W : \mathbf{R} \to \mathbf{R}$ satisfies $\forall s \in \mathbf{R}$, $W'(s) > 0$ (Nishii 1998).

In this section we regarded the state variable as a state of a component cell. However, it is possible to regard it as a state of an ensemble of neural cells which work as a component of a neural oscillator.

4. Results of computer simulations

In this section, we show the results of simulations in which the proposed learning rules were applied. For these simulations, a Wilson–Cowan-type oscillator was used as a neural oscillator. The oscillator is composed of two cells, an excitatory cell and an inhibitory cell, and its dynamics are given by

$$\begin{cases} \tau_i \dot{u}^E_i = -u^E_i + g^{EE} y^E_i - g^{IE} y^I_i + s^E_i \\ \tau_i \dot{u}^I_i = -u^E_i + g^{EI} y^E_i - g^{II} y^I_i + s^I_i \end{cases} \tag{34}$$

where the subscript i indicates the index of the oscillator, the superscripts (E, I) indicate the excitatory cell and the inhibitory cell, respectively, τ_i is the time constant, $\boldsymbol{u}_i = (u^E_i, u^I_i)$ is the state vector which shows the states of the component cells, $y^E_i = h(u^E_i)$ and $y^I_i = h(u^I_i)$ are the output signals from the cells, h is a function giving the output, g^{EE}, g^{EI}, g^{IE}, and g^{II} are the coupling weights between component cells, and s^E_i and s^I_i are the external input signals to the cells. The dynamics in (34) show periodic activities for some parameter sets when h is a sigmoidal function (Amari 1972). In this simulation we set $h(x) = 2/(1 + \exp(-x)) - 1$, $g^{EE} = 6.0$, $g^{EI} = 5.0$, $g^{IE} = 5.0$, and $g^{II} = 0.0$ such that equation (34) has a limit cycle solution as shown in figure 3, although the shape does not satisfy the condition for the learning discussed in the previous section.

If the values of the coupling weights between oscillators become too large by learning, the large effect of input signals on the dynamics of the neural oscillator may suspend the oscillation. To avoid such a situation we give the coupling weight w^{kl}_{ij} by using a sigmoidal function of the parameter α^{kl}_{ij} so as to restrict the range of the value in the simulations; i.e., $w^{kl}_{ij} = W(\alpha^{kl}_{ij})$, $W(\alpha) = 2w_{\max}/(1 + \exp(-\alpha/T)) - 1$, ($w_{\max}$, T: constant). To restrict the range of the coupling strength would also be a natural assumption from the viewpoint of neurophysiology. Because the intrinsic frequency is not explicitly given in equation (34), we apply the learning rules of the frequency in equations (31) and (33) to the time constant $\tau_i \sim 1/\omega_i$. In summary, we used

$$\begin{cases} \dot{\tau}_i = -\varepsilon \cdot (\tau_i)^2 \langle \boldsymbol{p}_i^t \cdot (\boldsymbol{s}_i + \tilde{\boldsymbol{s}}_i) \rangle \\ \dot{\alpha}^{kl}_{ij} = \varepsilon\gamma \langle p^k(\boldsymbol{u}_i) \tilde{y}^t_i \rangle \langle p^k(\boldsymbol{u}_i) y^l_j \rangle \end{cases} \tag{35}$$

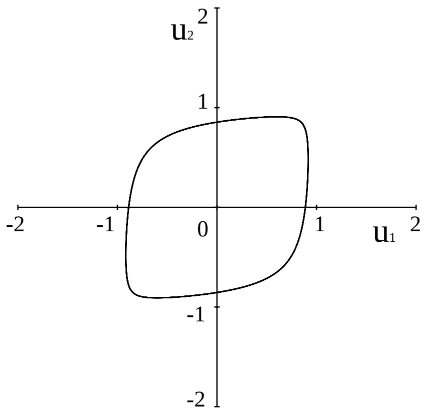

Figure 3. The limit cycle of the neural oscillator used in simulations.

instead of equation (31), and

$$\begin{cases} \dot{\tau}_i = -\varepsilon \cdot (\tau_i)^2 \langle \boldsymbol{p}_i^t \cdot \boldsymbol{s}_i \rangle \\ \dot{\alpha}_{ij}^{kl} = \varepsilon\gamma \langle E_i \rangle \cdot \langle p^k(\boldsymbol{u}_i) \cdot y_j^l \rangle \end{cases} \tag{36}$$

instead of equation (33), where $\boldsymbol{p}_i = (p^E(\boldsymbol{u}_i), p^I(\boldsymbol{u}_i))^t$ and

$$p^E(\boldsymbol{u}_i) = (-u_i^E + g^{EE} y_i^E - g^{IE} y_i^I)/\tau_i \qquad p^I(\boldsymbol{u}_i) = (-u_i^E + g^{EI} y_i^E - g^{II} y_i^I)/\tau_i$$

by equation (32). The time averaged terms in the learning rules are obtained by the first-order low-pass filter, $\tau_0 \dot{\langle * \rangle} = -\langle * \rangle + *$, where τ_0 is a time constant.

4.1. Learning a phase pattern instructed by a teacher signal

The oscillators with all-to-all coupling were examined to learn an instructed phase pattern. Each excitatory cell in component cells receives signals from all other cells in the coupling oscillators; hence the input signals to the kth oscillator s_k^E, s_k^I, $(k = 1, \ldots, N)$ in the learning mode are given by

$$s_k^E = \sum_{j \neq k}^{N} (w_{kj}^{EE} y_j^E + w_{kj}^{EI} y_j^I) + \tilde{y}_k(t) \qquad s_k^I = 0 \quad k = 1, \ldots, N \tag{37}$$

where $\tilde{y}_k(t) = \epsilon_f \cos 2\pi(t - k/N)$ (ϵ_f: constant) is the teacher signal for the kth oscillator, which means that the equal phase difference between neighbouring oscillators is the desired one (figure 4(a)). The time constants of the oscillators τ_i were set randomly in a range from 0.2 to 0.133 s, which corresponds to a frequency range of about 1 to 1.5 Hz. The time constant τ_i and coupling weights $w_{ij}^{El}(i, j = 1, \ldots, N, i \neq j, l = I, E)$ are learned by equation (35).

The phase pattern was almost random before learning, as seen in figure 4(b), where the dots show the time when the state of each excitatory cell in the oscillators changes from a negative to a positive value. By applying the teacher signal, the phase pattern becomes in phase with the teacher signal which gives the forcing oscillation (figure 4(c), (d)), and the learned pattern is stably recalled after learning from random initial states of cells (figure 4(e)).

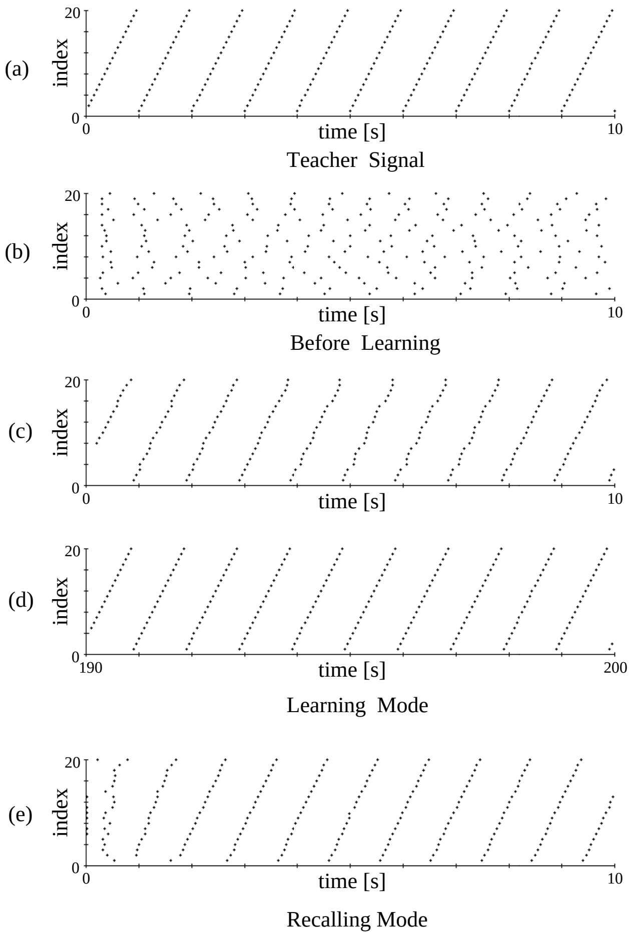

Figure 4. The firing pattern of the coupled neural oscillators during learning and after learning: (a) phase pattern of teacher signal; (b) before learning; (c), (d) during learning; (e) after learning (recalling mode). The ordinate shows the index of oscillators, and the dots show the time when the state of each excitatory cell in the oscillators changes from a negative value to a positive one. At $t = 200$ s, learning was stopped and random state values were assigned to each oscillator. Parameters: $\Omega = 1$ Hz, $w_{\max} = 1.0$, $T = 0.2$, $\epsilon_f = 4.0$, $\varepsilon = 0.005$, $\gamma = 0.1$, $\tau_0 = 3$ s.

4.2. Learning a phase pattern based on evaluation

Living bodies must acquire and generate a desired motor command to obtain a desired motor pattern based on evaluations of the performance. In this section we will show the results of applying equation (36) for computer simulations of adaptive control of phase relations between oscillators and a one-dimensional hopping robot.

4.2.1. Learning a phase difference between two neural oscillators Here we show the results of simulations intended to obtain a desired phase relation between two neural oscillators. We assume the connections from the excitatory cell in oscillator 1 to the cells in oscillator 2. The input signals s_k^E and s_k^I are given by

$$s_1^E = 0 \qquad s_1^I = 0 \qquad s_2^E = w_{21}^{EE} y_1^E \qquad s_2^I = w_{21}^{IE} y_1^E. \tag{38}$$

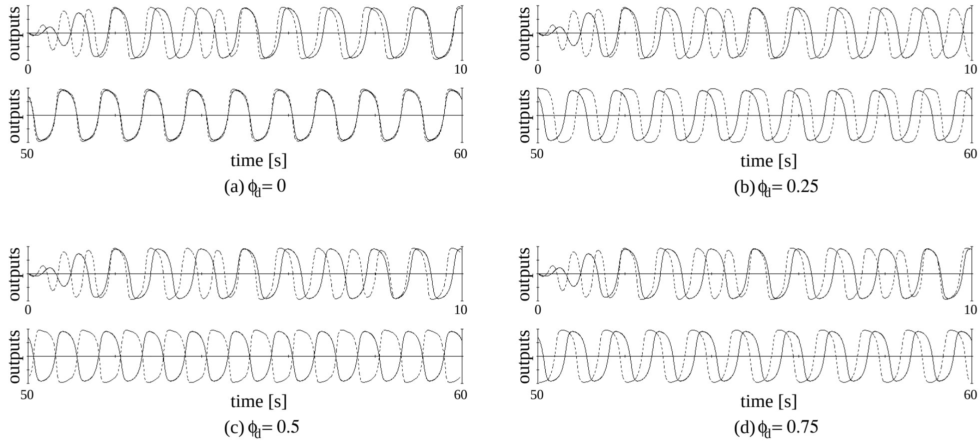

Figure 5. Results of simulations. The full curve and the dotted curve show the outputs of the excitatory cell of oscillators 1 and 2, respectively. Parameters: $\varepsilon = 0.003$, $\gamma = 1.0$, $\tau_1 = 0.2$, $w_{\max} = 5.0$, $T = 3.0$, $w^{EE} = 6.0$, $w^{EI} = 5.0$; $w^{IE} = 5.0$, $w^{II} = 0.0$, $\tau_0 = 25\tau_2$. Initial conditions: $\tau_2 = 1/7.5$, $\alpha^l_{21}E = 1.0$ $(l = I, E)$.

The evaluation function is given by $E = \sin 2\pi((t_1 - t_2)/T_1 - \phi_d)$, where ϕ_d is the desired phase difference between oscillators, t_i $(i = 1, 2)$ is the time when the output signal of the excitatory cell, y_i^E $(i = 1, 2)$, changes from a negative to a positive value, T_1 is the period of oscillator 1, and ϕ_d is the desired phase difference.

Figure 5 shows that the desired phase differences $\phi_d = 0$, 0.25, 0.5, 0.75 were adaptively obtained within 50 s by the proposed learning rule (36).

4.2.2. Adaptive control of a one-dimensional hopping robot by a neural oscillator We previously proposed that the learning rule (5) can be applied to the adaptive control of a periodic movement by regarding a physical system as an oscillator (Nishii in press). Here, we report the result of a computer simulation of the adaptive control of a one-legged hopping robot using Wilson–Cowan-type oscillator by applying the learning rule (36).

Our robot is composed of a trunk with a mass and a leg which has a spring component, a damping component, and a thruster (figure 6). The thruster generates a force between the trunk and the toe according to the input signal from an oscillator. The dynamics of the robot are the same as in our previous study (Nishii in press). The dynamics of the oscillator is given by equation (34), and the input signals to component cells are given by

$$s^E = w^E \hat{v} \qquad s^I = w^I \hat{v}$$

where w^E and w^I are the coupling weight of the feedback signal from the robot $\hat{v}$ to the excitatory and the inhibitory cell, respectively. The feedback signal $\hat{v}$ is the normalized velocity of the trunk of the robot and is given by $\hat{v} = \dot{x}_0/\langle v_0\rangle$, $\tau_v\langle\dot{v}_0\rangle = -\langle v_0\rangle + |\dot{x}_0|$, where x_0 is the position of the trunk and τ_v is a time constant. The purpose of the learning is to induce the time averaged height of the trunk $\langle x_0\rangle$ to approach the desired value, x_d. The evaluation function is given by $E = x_d - \langle x_0\rangle$.

Figure 7 shows the simulation results. In order to obtain a steady relation between the oscillator and the robot, the learning was started 20 s after the simulation. The desired hopping heights $x_d = 0.6$, 0.7, 0.8, 0.9 [m] were achieved within about 100 seconds by the learning.

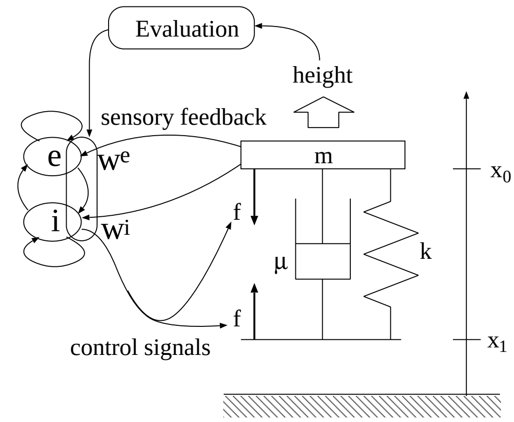

Figure 6. One-dimensional hopping robot. The robot consists of a trunk with mass m and a leg with a spring component (elastic coefficient k), a damping component (damping coefficient μ), and a thruster. The oscillator sends control signals to the thruster which generates the force f between the trunk and the toe and receives the sensory feedback signals from the robot.

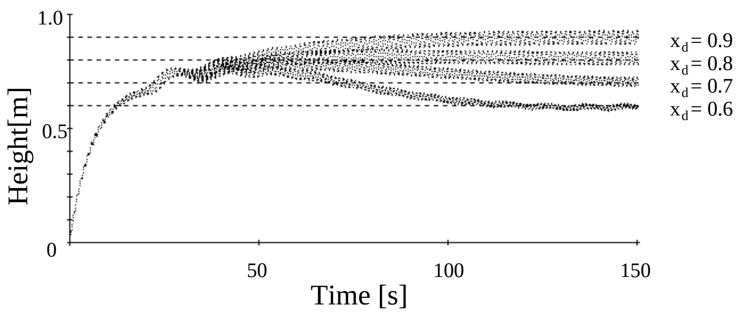

Figure 7. Time profile of the time averaged height $\langle x_0 \rangle$ of the trunk of the hopping robot. Parameters: $\epsilon = 0.06$, $\gamma = 2/3$, $\tau_0 = 25\tau$, where τ is the time constant of the oscillator, and $\tau_v = 5.0$ s. Initial conditions, $\tau(0) = 5.0$ s, $\alpha^l(0) = -3.0$, ($l = e, i$), $x_1(0) = 0.1$ m, $x_0(0) = x_1 + l = 0.8$ m.

5. Proposed learning rule and conventional learning models

Sutton and Barto (1982) proposed a learning model that improved the Hebbian rule so as to solve the problem of the infinite increase of the coupling weight by the learning. Their model takes the form

$$\Delta w_i(t) = c\Delta u(t-1)\bar{y}_i(t) \tag{39}$$

where $\Delta w_i(t) = w_i(t+1) - w_i(t)$, $\Delta u(t) = u(t+1) - u(t)$, $\bar{y}_i(t+1) = \alpha\bar{y}_i(t) + y_i(t)$; y_i is the signal from the ith presynaptic cell, u is the state of the postsynaptic cell, and $\alpha < 1$ is a positive constant. If we write the above equation as a continuous time model, we obtain

$$\dot{w}_i = c\dot{u}(t)\bar{y}_i(t) \tag{40}$$

where $\bar{y}_i(t)$ can be considered a time average of the signal y_i with amplification. This model thus constitutes the learning model without a teacher based on the association between the input signal and the time derivative of the state of the postsynaptic cell. The learning rules for the coupling weights in equations (31) and (33) can therefore be regarded as an extension of the Sutton–Barto model with a teacher, in which the direction of the learning is given by the effect of an instructed teacher signal or an evaluation signal, since y_i^l in equations (31) and (33) corresponds to the time averaged firing ratio over a short period of time.

Ermentrout and Kopell (1994) proposed a learning model for neural oscillators with unidirectional nearest-neighbour coupling to acquire an instructed desired phase pattern. In their learning rule, as in equation (31), the coupling weights between oscillators were also modulated according to the correlation between the time derivative of the state of the postsynaptic cell and the teacher signal. They determined the direction of the learning based on *a priori* knowledge of the dynamics of the neural oscillator, while, in our model, the direction is given by the effect of the input signal. Therefore, our learning rules for coupling weights take a generalized form of those proposed by Ermentrout and Kopell.

6. Conclusion

We proposed learning models for coupled neural oscillators, and their performance was confirmed by computer simulations. Although the shape of the limit cycle of the neural oscillator used in the simulations is not an ideal form to satisfy the condition for the learning, desired phase relations were achieved by the proposed learning rule. The simulation also suggested that we can use a first-order low-pass filter, a mechanism which only requires first-order dynamics, to obtain the time averaged term required in our learning rule.

The derived learning rule for the coupling weight was given by a simple associative rule, that uses the first derivative of the state of the postsynaptic cell, as in the Sutton–Barto model and the learning model of Ermentrout and Kopell. The Hebbian rule is a learning rule based on zero-order derivatives of the states of presynaptic and postsynaptic neurons. The learning rule of the neural system in living bodies would depend on many-order derivatives of the states of cells, although the contribution of the higher orders has been neglected in most learning models of neural circuits. The contribution of each order could be tuned according to the required signal processing.

The intrinsic frequency of the neural oscillator was learned by changing the time constant of the dynamics of the oscillator in the simulations. It has been reported that the frequency of a neural oscillator can be modified by changing the amplitude of the tonic input signal to component cells and by modulations of the chemical environment (Harris-Warrick 1988, Grillner *et al* 1991, Buchanan 1992). The learning of the time constant might correspond to the latter case. If there is an input signal modulating the frequency, the learning of the weight for the signal can also be carried out by the proposed learning rule.

Theoretical studies for conventional neural networks composed of static components have suggested the high ability of static information processing in nervous systems. We expect that studies of the dynamical features of neural cells will clarify the mechanism of dynamic information processing in nervous systems.

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