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Two Coupled Oscillators as a Model for the Coordinated Finger Tapping by Both Hands

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Abstract. Recently, it was found that rhythmic movements (e.g. locomotion, swimmeret beating) are controlled by mutually coupled endogeneous neural oscillators (Kennedy and Davis, 1977; Pearson and Iles, 1973; Stein, 1974; Shik and Orlovsky, 1976; Grillner and Zangger, 1979). Meanwhile, it has been found out that the phase resetting experiment is useful to investigate the interaction of neural oscillators (Perkel et al., 1963; Stein, 1974). In the preceding paper (Yamanishi et al., 1979), we studied the functional interaction between the neural oscillator which is assumed to control finger tapping and the neural networks which control some tasks. The tasks were imposed on the subject as the perturbation of the phase resetting experiment. In this paper, we investigate the control mechanism of the coordinated finger tapping by both hands. First, the subjects were instructed to coordinate the finger tapping by both hands so as to keep the phase difference between two hands constant. The performance was evaluated by a systematic error and a standard deviation of phase differences. Second, we propose two coupled neural oscillators as a model for the coordinated finger tapping. Dynamical behavior of the model system is analyzed by using phase transition curves which were measured on one hand finger tapping in the previous experiment (Yamanishi et al., 1979). Prediction by the model is in good agreement with the results of the experiments. Therefore, it is suggested that the neural mechanism which controls the coordinated finger tapping may be composed of a coupled system of two neural oscillators each of which controls the right and the left finger tapping respectively.

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1. Introduction

Organisms must control temporal and spatial activity patterns of motor units in order to achieve well coordinated movement. Some neural networks carry out these control. Probably, rhythmic movement is controlled by a certain oscillatory neural network. In invertebrates it has been found that rhythmic movement (e.g. heart beat, respiration, locomotion or flight) can be controlled endogenously by neural oscillators without the sensory feedback from the periphery. A neural oscillator may consist of one or more pacemaker cells or bursting cells. Otherwise it may be a neural network consisting of many neurons. Stein (1974) has found that the coordinated movement of swimmerets in the crayfish is controlled by the neural oscillators interacting with each other. A pair of neural oscillators in each abdominal ganglion innervates the corresponding swimmerets. He studied interactions between neural oscillators by measuring phase response curves. In vertebrates, the notion of endogenous neural oscillators has been also developed. Shik and Orlovsky (1976) and Grillner and Zangger (1979) indicated that coordinated locomotion of the cat is controlled by the reciprocal action of the stepping centers in the spinal cord.

In the preceding paper (Yamanishi et al., 1979), assuming that the human finger tapping is controlled by an oscillatory neural network, we studied the functional interaction between the finger tapping neural network and neural networks which control some psychological tasks imposed on the subject as perturbations of the phase resetting experiments. By the way, there are many coordinated movements which are performed by both hands in our daily life. Playing a piano, or typewriting are typical examples for coordinated finger tapping by both hands. What kind of neural networks are responsible for these coordinated movements? In the previous paper, we have assumed

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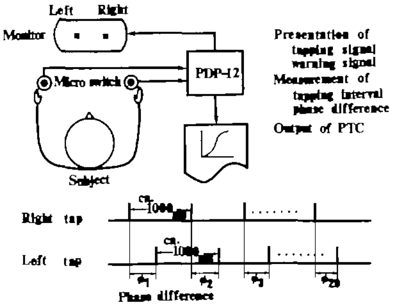

Fig. 1. Experimental system of coordinated tapping by both hands

that the finger tapping by the left hand is controlled by one oscillatory neural network and the finger tapping by the right hand by other oscillatory neural network. By measurement of phase transition curves, we studied the properties of these two neural networks. Here we assume that coordinated finger tapping by both hands is controlled by these two neural networks which interact with each other.

In this paper, we will examine this assumption by psychological experiments and by a model study. First, the performance of both hands finger tapping with a constant phase difference was studied quantitatively. The subjects were requested to tap their both hands with one of 10 various phase differences. We found that subjects can perform the synchronous rhythm and the alternate rhythm more easily and accurately than others. Second, we propose two coupled neural oscillators as a model for these coordinated finger tapping. Under the assumption that two coupled neural oscillators control the coordinated finger tapping by both hands, dynamical behavior of the model system is analyzed by using phase transition curves which were measured on one hand finger tapping in the previous experiment (Yamanishi et al., 1979).

2. Experiment

2.1. Method

The experimental system and procedures of learning of a tapping interval are described in detail in the preceding paper (see Fig. 1). Subjects were instructed to tap the key in synchrony with pacing signals by the right or the left hand and requested to learn a tapping interval. The tapping interval amounted to 1000 ms. Experiments of finger tapping by both hands were carried out under the condition that subjects could continue regular one hand tapping. Two pacing signals with a constant phase difference were displayed for duration of 20 ms with a 1000 ms interval on the monitorscope periodically. The right signal was presented for a tap by the right hand and the left signal was presented for the left hand tap. The delay between the left signal and the right signal was chosen out of 10 steps such as 0, 100, 200 ... 900 ms, that is, the phase difference of the left signal to the right signal was 0.0, 0.1, 0.2 ... 0.9. We call these phase differences standard phase differences. Subjects were instructed to learn the finger tapping by both hands with various phase differences, synchronizing their tappings with pacing signals. During training, if the phase difference of the left hand tap to the right hand tap was fairly different from the indicated standard phase difference, warning signal ("Shorter!" or "Longer!") was displayed on the monitorscope. Allowable deviation from the standard phase difference was ± 0.05. In this way, subjects were trained to perform the coordinated finger tapping for various phase differences. After the training was completed, the pacing signals with the standard phase difference, which was one of 10 steps, were displayed on the monitorscope and subjects were instructed to tap by both hands synchronizing their taps with these signals. The pacing signals were presented only 10 times but subjects were asked to continue the tapping without pacing signals (selfpaced both hands finger tapping) until the stop signal was presented. A series of selfpaced tapping consisted of 20 tappings. 20 phase differences of the left hand tap to the right hand during selfpaced tapping, (i.e., $\phi_1, \phi_2, \ldots, \phi_{20}$), were measured and processed by a PDP-12 minicomputer. The pacing signals for each of 10 standard phase differences were presented four times at random sequence. One set of the experiment was composed of these 40 trials (10 standard phase differences × 4 times) and the four sets of experiments were carried out in all. To estimate the accuracy of selfpaced finger tapping, an average (systematic error) and a standard deviation of the differences between measured delay and standard delay were calculated from 320 data (20 taps × 4 times × 4 sets) for each of 10 standard phase differences. Two groups of subjects were used. The first group was an unskilled group and composed of 4 students who have normal motor functions (T.I., Y.O., H.N., and T.M.). The second group was a skilled group and composed of 5 students of a piano course in a music college (K.M., T.T., E.M., Y.T., and Y.M.). All subjects were right handed.

2.2. Results

Figure 2 shows systematic errors and their standard deviations during selfpaced finger tapping. The systematic error is an average of the difference between measured delay and standard delay. The abscissa is the standard phase difference, where phase difference 0.0 is same as phase difference 1.0. As shown in Fig. 2, when the phase difference is 0.0 and 0.5, the standard deviation is smaller in both groups of subjects in comparison to that of other phases. So, the perfor-

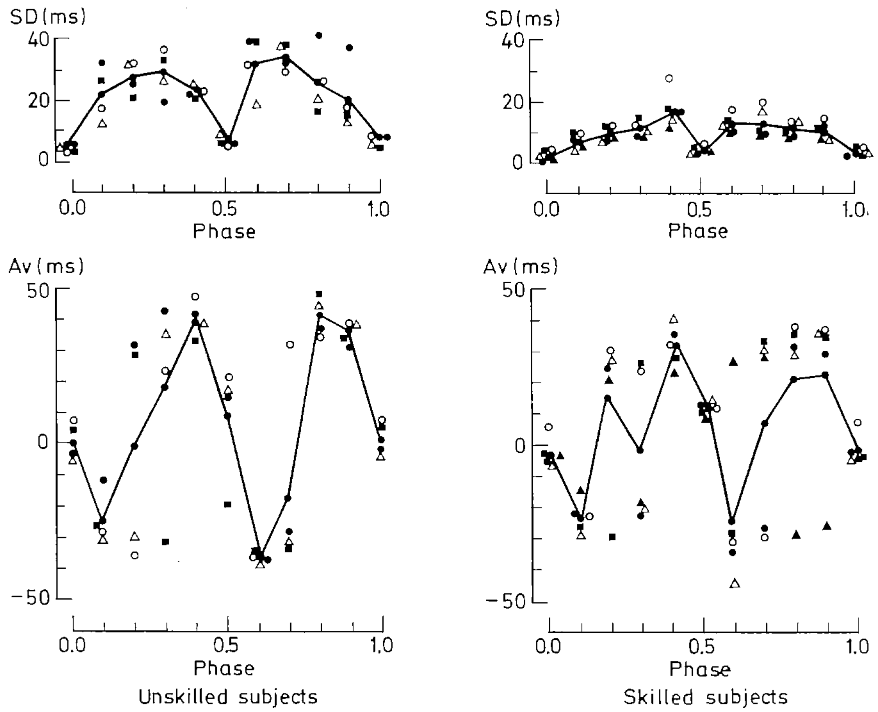

Fig. 2. Systematic error (Av) and their standard deviation (SD)

$$\mathrm{Av}=1/320\sum_{i=1}^{320}(\phi_i-\phi_s),\qquad \mathrm{SD}=\sqrt{1/320\sum_{i=1}^{320}(\phi_i-\bar{\phi}_i)^2}\,.$$

ϕ_s is standard phase difference. Left is unskilled subjects (○ sub. Y.O., ● sub. T.I., ■ sub. T.M., △ sub. H.N.). Right is skilled subjects (○ sub. E.M., ● sub. T.T., △ sub. Y.M., ▲ sub. K.M., ■ sub. Y.T.). Solid line shows the average of each data

mance of both hands finger tapping is better at the phase difference 0.0 and 0.5 than that at other phase differences. Hereafter, we call the finger tapping by both hands with phase difference 0.0 the synchronous rhythm pattern and with phase difference 0.5 the alternate rhythm pattern. The skilled subjects showed smaller standard deviations than the unskilled ones as we had expected. Good performance for the synchronous and the alternate rhythm patterns is noted also from the graph of systematic errors. Let us explain this characteristics on the graph of the unskilled subjects. For example, when the subject tries to tap by both hands with the standard phase difference 0.1, that is, the delay of 100 ms, as the systematic error is −30 ms, the phase difference decreases to 70 ms and the tapping pattern shows a tendency to resemble the synchronous rhythm pattern. Moreover, when the finger tapping by both hands with the phase difference 0.9 is performed, as the systematic error is 40 ms, an average of delay elongates to 940 ms. This tapping pattern also shows a tendency to resemble the synchronous rhythm pattern. On the whole, when the subject tries to tap with the standard phase differences which are close to 0.0 or 1.0 (i.e., 0.1, 0.8, and 0.9), the phase difference shows a tendency to approach to 0.0. Hence the tapping pattern inclines to the synchronous rhythm pattern. Similarly, when the finger tapping is done at the standard phase differences close to 0.5 (i.e., 0.3, 0.4, 0.6, and 0.7), the phase difference shows a tendency to approach to 0.5. Hence the tapping pattern inclines to the alternate pattern. These tendencies are found in the skilled subjects as well.

Mathematically speaking, the phase differences 0.0 and 0.5 are stable steady states because the slope of the curve of the systematic error is negative at 0.0 and 0.5. For the unskilled subjects, phase differences 0.2 and 0.75 are also steady states. But these are unstable as the slope of the curve is positive there. If one carefully observes the data of the systematic error of each subject, one may notice a curious distribution of the data. The data points of four (or five) subjects for phase 0.0 and 0.5 gather around the average. But for several phase differences (especially 0.2, 0.3, 0.7 for the unskilled subjects and 0.2, 0.3, 0.6, 0.7, 0.8, 0.9 for the skilled subjects), the data points split into two groups. For example, ■, △, ▲ are positive systematic errors and ●, ○ are negative errors in the case of the phase 0.7 of the skilled subjects. These distributions of data points are quite different from the normal distribution. These are rather bimodal distributions. We suppose that the bimodal distribution derives from the bistability of the synchronous and the alternate patterns. That is, there

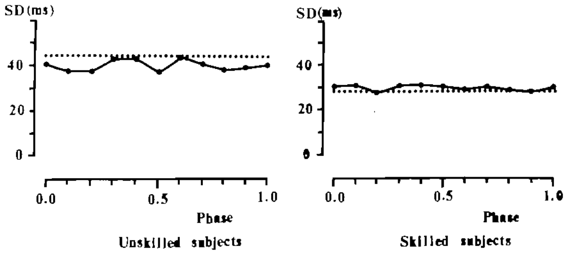

Fig. 3. Standard deviation of the interval of tapping with coordinated both hands. Dotted line shows the data which were measured on right hand tapping

are two possibilities about the both hands tapping with, for example, 0.7 phase difference. One possibility is that the phase difference is drawn toward 0.5. In this case the systematic error is negative (●, ○). Another one is that the phase difference is drawn toward 1.0, and the systematic error becomes positive (■, △, ▲).

Standard deviations of tapping intervals (ca. 1000 ms) during the selfpaced finger tapping for various standard phase differences are shown in Fig. 3. A dotted line is the standard deviation which was measured from the right hand tapping in the previous experiment (Yamanishi et al., 1979). Data were averaged among the subjects in each group. For the skilled subjects there is no difference between the variance of tapping interval of the both hands tapping and that of one hand tapping. For the unskilled subjects, however, tapping interval is reproduced more precisely in the both hands tapping. In either case, the standard deviation of tapping intervals does not depend on the standard phase difference crucially.

3. A Model of Two Coupled Oscillators

Neural mechanism which controls finger tapping is not clarified physiologically but we suppose that there is a neural circuit which produces periodic outputs endogenously. Characteristics of a neural oscillator which controls one hand finger tapping was investigated by measurement of phase transition curves (Yamanishi et al., 1979). We examined the degree of functional interaction between the network which controls the finger tapping and neural networks which control three kind of tasks (key-pushing, voicing and pattern discrimination). As a result of these experiments, it was shown that the neural network which controls the right hand finger tapping had the same characteristics as the neural network of the left hand finger tapping.

Now, we will briefly explain phase response curves and phase transition curves. The phase of regular oscillation is advanced or delayed by perturbation. A phase response curve, $\Delta\phi(\phi)$ is the curve where the phase advance ($\Delta\phi > 0$) and delay ($\Delta\phi < 0$) are plotted as a function of phase ϕ at which the perturbation is applied. In the previous resetting experiment for key-pushing, we presented a signal at various phases of a regular finger tapping by one hand and made a subject perform key-pushing by other hand in response to the signal. Execution of this task is regarded as a perturbation of phase resetting experiments. A phase transition curve, $\phi'(\phi)$ is defined as follows from a phase response curve

$$\phi'(\phi) = \phi + \Delta\phi(\phi).$$

ϕ' is the phase which is transited from the phase ϕ by perturbation. We call ϕ' a new phase (Winfree, 1970, 1977; Kawato and Suzuki, 1978).

Is there any relation between the neural network which controls finger tapping by both hands and the network which controls one hand finger tapping? We assume that the neural network which controls both hands finger tapping is composed of two coupled neural oscillators, each of which controls the right and the left hand finger tapping respectively. Based on this assumption we will analyze the system of two coupled oscillators by phase transition curves measured on one hand finger tapping in the previous experiment. Investigations of interactions between oscillators by phase response curves or phase transition curves was developed about twenty years ago. Perkel (1964) predicted that the firing rate of pacemaker neurons can be modified by regularly spaced synaptic input by using phase response curves. By measurement of phase response curves, Stein (1974) found that the coordinated movements of the swimmerets of the crayfish are controlled by the interaction of neural oscillators which are located in the abdominal ganglion. These are analysis of two coupled oscillators in the case of unilateral interaction. On the other hand, Daan and Berde (1978) studied the behavior of two coupled oscillators in the case of bilateral interaction, simulating the circadian pacemaker in mammalian activity rhythms.

In this section, we consider two coupled oscillators as a model of the neural network which controls the coordinated finger tapping by both hands. Especially the phase entrainment between these two oscillators is discussed by using of the same method of Daan and Berde. Consider a neural oscillator R which controls the right hand finger tapping and a neural oscillator L which controls the left hand finger tapping. It is assumed that the coordinated finger tapping by both hands is performed when both oscillators R and L oscillate at the same time as shown in Fig. 4. Oscillators R and L oscillate with the same periods. $f(\phi)$ denotes the phase response curve of the oscillator R to one tap by the left hand which is imposed as a perturbation. $g(\phi)$ denotes that of the oscillator L to the right hand tap. Bilateral interactions between R and L change phase relation of two oscillators. We define ϕ_1 as a phase difference between the left hand tap and the right hand tap and ϕ_2 as that between the right and the left (see Fig. 4). ϕ_1 and ϕ_2 change according to the following recurrence formula.

$$\phi_2 = 1 - f(\phi_1) - \phi_1 = 1 - (\phi_1 + f(\phi_1)) = F(\phi_1), \tag{1}$$

$$\phi'_1 = 1 - g(\phi_2) - \phi_2 = 1 - (\phi_2 + g(\phi_2)) = G(\phi_2). \tag{2}$$

ϕ'_1 is the phase difference of the next tap. $(\phi_1 + f(\phi_1))$ and $(\phi_2 + g(\phi_2))$ are the phase transition curves of R and L respectively. In the previous paper, we measured $f(\phi)$ or $g(\phi)$ for only one tap by other hand. Here, we use $f(\phi)$ or $g(\phi)$ to study the synchronization of the tapping by both hands. In this case, both the right and the left hands tap the keys many times, so application of $f(\phi)$ and $g(\phi)$ is not always valid. We assume that the state points of both R and L oscillators return to their limit cycles immediately from the perturbation by other oscillator (Kawato and Suzuki, 1978). In order to verify the assumption experimentally, we must do something like the two pulse-experiment in drosophila (Winfree, 1973; Pittendrigh, 1974) although we have not yet done such experiment.

When the both hands tapping is in steady state, phase difference is constant, that is, $\phi'_1 = \phi_1$, $\phi'_2 = \phi_2$. If we substitute these relations into (1) and (2), steady phase difference (ϕ_{1e}, ϕ_{2e}) is obtained from the intersection of the following two graphs

$$\phi_2 = 1 - (\phi_1 + f(\phi_1)) = F(\phi_1), \tag{3}$$

$$\phi_1 = 1 - (\phi_2 + g(\phi_2)) = G(\phi_2). \tag{4}$$

Some of the equilibria are stable and others are unstable. Stable and unstable equilibria can easily be distinguished by comparing the slopes of the two curves at the intersection. The stability criterion is

$$|G'(\phi_{2e}) \cdot F'(\phi_{1e})| < 1, \tag{5}$$

as a result of perturbation analysis applied to ϕ_{1e} and ϕ_{2e}. The slopes of the curves in the point (ϕ_{1e}, ϕ_{2e}) are $F'(\phi_{1e})$ and $1/[G'(\phi_{2e})]$, respectively. Hence in a stable equilibrium the curve $F(\phi_1)$ is closer to horizontal than $G(\phi_2)$. This criterion is of course easily detected graphically.

4. Analysis of Two Coupled Oscillators Model

Figure 5a shows an example of two phase transition curves measured on the right and the left hand tapping of one subject. Figure 5b shows graphs of Eqs. (3) and (4) obtained from phase transition curves shown in Fig. 5a. In this case, there are four equilibrium points, and the stability of these equilibrium points is decided by the criterion (5). It can be easily known that both

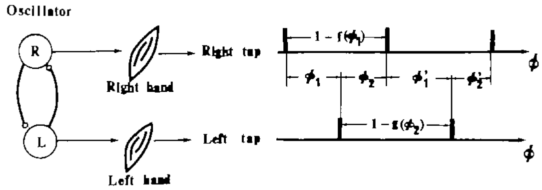

Fig. 4. Two coupled oscillators model

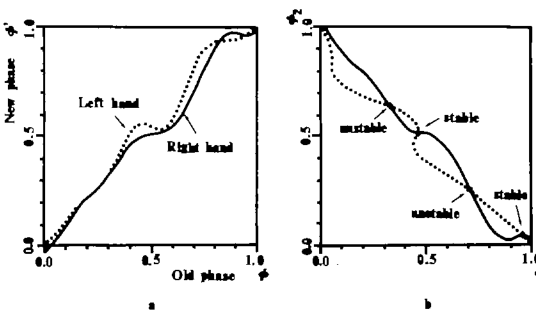

Fig. 5a and b. Graphic solutions of equilibrium from the right hand PTC and the left hand PTC

hands tapping is stable at phase difference $\phi_1 = 0.45$ and 0.95 and unstable at phase difference $\phi_1 = 0.32$ and 0.70. We want to know at what phase difference the model system has stable steady oscillation and at what phase it has unstable steady oscillation. In the previous experiment we measured five phase transition curves for each subject. Five figures such as Fig. 5b are drawn by using these five phase transition curves of the right and the left hand. In order to investigate the distribution of the stable and the unstable equilibrium points, we measured the value of abscissas of all equilibrium points by the graphical method described above. The range of phase difference ϕ_1, i.e., [0, 1] is divided into 10 sections, i.e., [0.95, 0.05), [0.05, 0.15), [0.15, 0.25) ... [0.85, 0.95). 10 sections are denoted by $0, 1, 2, \ldots, 9$ respectively. For the i-th subject, $m_i(j)$ and $n_i(j)$ are defined as follows. $m_i(j)$ is the number of stable equilibrium points whose abscissa ϕ_1 is in the j-th section, i.e., $[j/10 - 0.05, j/10 + 0.05)$ where $j = 0, 1, 2, \ldots, 9$. $n_i(j)$ is the number of unstable equilibrium points whose abscissa is in the j-th section. In order to average the data among the unskilled subjects and among the skilled ones respectively, we define the distribution of the stable and the unstable equilibrium points for the unskilled group $(m_u(j), n_u(j))$ and that for the skilled one $(m_s(j), n_s(j))$ as follows

$$m_u(j) = 1/4 \sum_{i=1}^{4} m_i(j), \qquad n_u(j) = 1/4 \sum_{i=1}^{4} n_i(j)$$

$$m_s(j) = 1/5 \sum_{i=1}^{5} m_i(j), \qquad n_s(j) = 1/5 \sum_{i=1}^{5} n_i(j).$$

These results are shown in Fig. 6. The solid line shows the distribution of the stable equilibrium points and

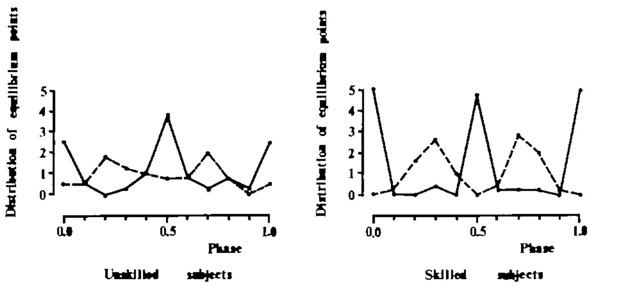

Fig. 6. Distribution of equilibrium points. Solid line shows stable equilibrium points and broken line shows unstable ones

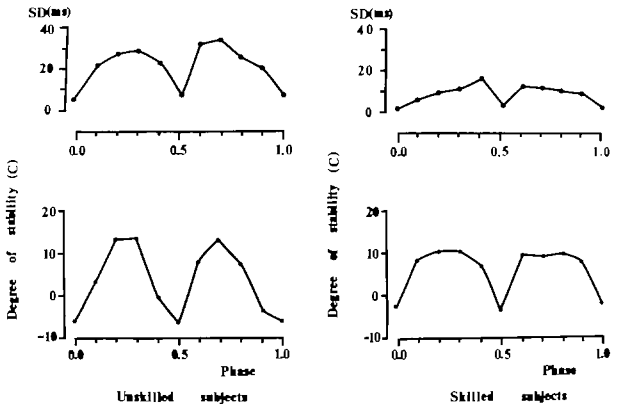

Fig. 7. Comparison of the standard deviation of phase difference (upper) with the degree of stability (lower)

the broken line shows that of the unstable ones. From the results of both groups of subjects, it is shown that there are more stable equilibrium points at phase differences, 0.0 and 0.5 than at any other phase differences and there are more unstable equilibrium points at phase differences, 0.2, 0.3, 0.7, and 0.8 than at any other phase differences. However, there is a little difference between the distribution pattern of two groups. For the skilled subjects, almost all stable equilibrium points concentrate at phase differences, 0.0 and 0.5. On the contrary, for the unskilled subjects, the distribution pattern of the stable equilibrium points is diverse. The distribution pattern of the unstable equilibrium points for two groups also shows a same tendency. These results reflect that the symmetry between the right and the left phase transition curves of the skilled subjects is better than that of the unskilled ones. Many stable equilibrium points are observed at phase differences, 0.0 and 0.5, so it can be considered that the coordinated finger tapping with such a phase difference (synchronous rhythm and alternate rhythm) is easier than that with any other phase differences. However, these results show only the distribution of the equilibrium points and they don't indicate the degree of stability of the equilibrium points.

We can study the degree of stability and unstability of an equilibrium point by using an eigen value of linear approximation of (1) and (2) around the equilibrium point. If the state point (i.e., ϕ_1) is perturbed from the equilibrium point by a small amount of δ, that is

$$\phi_1 = \phi_{1e} + \delta$$

then, by the interaction of two oscillators, next ϕ_1 is obtained as follows

$$\phi_1 = \phi_{1e} + (G' \cdot F')\delta\,,$$

in a linear approximation.

Therefore, $|G' \cdot F'|$ indicates the amplification factor of the small perturbation of δ. If $|G' \cdot F'|$ is smaller than 1, the equilibrium point is stable. If it is close to zero, the degree of stability of the stable equilibrium point is high. On the contrary, if $|G' \cdot F'|$ is larger than 1, the equilibrium point is unstable. Moreover, if it is very large, the degree of unstability of the unstable equilibrium point is high. If $|G' \cdot F'|$ equals 1, this equilibrium point is neutrally stable. Taking account of these results, we define the criterion which indicates the degree of stability and unstability of the equilibrium point as follows

$$c_i = 10(|G'(\phi_{2e}) \cdot F'(\phi_{1e})| - 1)\,,$$

where, suffix i indicates the i-th equilibrium point. c_i is negative for a stable equilibrium point and is positive for an unstable equilibrium point. The smaller c_i is, the stronger the stability is and the larger it is, the weaker the stability is.

Furthermore, we define the degree of stability of phase ϕ, $C(\phi)$ as

$$C(\phi) = 1/n \sum_{i=1}^{n} c_i\,,$$

where n is the number of equilibrium points whose abscissas are in $[\phi - 0.05, \phi + 0.05)$. For example, in the case of the unskilled subjects, the number of the stable equilibrium points is 15 and that of the unstable ones is 3 at the phase 0.5, so the degree of stability of phase 0.5, $C(0.5)$ is calculated as follows

$$C(0.5) = 1/18 \sum_{i=1}^{18} c_i\,.$$

These results for the unskilled group and the skilled one are shown in the lower part of Fig. 7. For comparison, the standard deviations of the systematic errors of the coordinated finger tapping which was indicated in Fig. 2 are shown in the upper part of Fig. 7. We assume that the coordinated finger tapping is controlled by two coupled oscillators. So, we expect that the finger tapping with the phase difference of high stability can be performed easier and more accurately than that with the phase difference of low stability.

From these results, it is also suggested that the synchronous rhythm pattern and the alternate rhythm pattern are stable.

5. Discussion

We proposed two coupled oscillator model for the coordinated finger tapping. One can easily notice from the data shown in Fig. 7 that the variation of SD corresponds with the variation of the degree of stability in both groups of subjects. Prediction of two coupled oscillator model is in good agreement with experimental data. Comparing figures of two groups in detail one can notice that the maximum value of the degree of stability of the unskilled group is higher than that of the skilled group and the minimum value of the former is lower than that of the latter. In other word, at almost all of phase, the displacement from the zero line of the degree of stability of the unskilled group is larger than that of the skilled one. Because the absolute value of c_i is an increasing function of the strength of interaction between the two oscillators, these results imply that the interaction between two oscillators of the unskilled subject is stronger than that of the skilled subject. In the previous paper (Yamanishi et al., 1979), it was suggested that the interaction between two neural networks is weakened by the learning and according to this change, phase transition curves change from type 0 to type 1. Two coupled oscillator model also shows this tendency. Thus, from these results, it may be considered that the coordinated finger tapping is controlled by two coupled neural oscillators and the interaction between these neural oscillators is weakened by the learning. Of course we must take account of higher motor centers which control the coupled system of two neural oscillators. The reason is that subjects can perform the coordinated finger tapping by both hands for any phase difference at least 20 times after they are trained over and over again. If their neural networks which control both hands finger tapping are composed only of two oscillators, they cannot tap with any phase difference other than a few stable phase differences.

6. Conclusion

When the subjects tried to tap by both hands with a constant phase difference, the performance of synchronous rhythm pattern and of alternate rhythm pattern were much better than that of others. Two coupled neural oscillators were proposed as a model of control mechanism of these coordinated finger tapping by both hands. The behavior of the model system at steady state was analyzed by phase transition curves measured on one hand finger tapping. From these analyses, it was shown that synchronous rhythm and alternate rhythm were stable rhythm patterns. These results coincided with the experimental data. It was suggested, therefore, that the neural mechanism which controls the coordinated finger tapping might be composed of the coupled system of two neural oscillators, each of which controls the right and the left finger tapping respectively.

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