1. Introduction

Recently, decentralized control system has received considerable attention in the field of control engineering for the control of large-scale and complex systems. The decentralized control system has a multiple number of control centers. Each of them controls its own subsystem with specific goal and need to coordinate its activity to satisfy the overall goal.

On the other hand, animal has a high degree of ability to organize autonomous activities of individual organs into one ordered behavior of corrective motion. For example, when starfish is placed upside down, it turns itself over by coordinating the motions of five arms. It should be noted that coordination is preceded by individual random motion of each arm during which the leading arm for coordination is selected from the five arms. Thereafter the individual random motions are inhibited and a systematic turn-over motion starts. (1)

In the author's opinion, animal system can be conceived as a typical example of the decentralized control system.

What mechanism controls this organized process? Answer to this question might be interesting for system engineer as well as for neurophysiologist.

We have taken rhythmic behaviors such as locomotion, swimming as the first step to be studied.

It was found that these rhythmic behaviors are controlled by mutually coupled endogeneous neural oscillators. For example, the coordinated movement of swimmerets in the crayfish is controlled by the distributed neural oscillators in abdomen interacting each other. (2)

The problems are now reduced to the investigation of the behaviors of coupled oscillator neurons and to find how to control them.
of electrotonically coupled neurons. (7) Studying our model according to the theory of Hopf bifurcation, we found the conditions over the diffusion constants of the electrical junctions which give two kinds of periodic solutions. One is the solution where two neurons oscillate in phase synchrony. The other is the solution of 180 degree out of phase oscillation.

Furthermore, the general two-oscillator system was used to explain the splitting phenomena which were first found by Pittendrigh in circadian rhythms. By the theory of Hopf bifurcation, we could show two stable periodic solutions. One is the in-phase and the other is the anti phase solution. The latter corresponds to a splitting pattern. (8)

3. Control of coordinated rhythmical behavior of crayfish swimmeret System

It has been suggested that the rhythmical behavior of invertebrate such as locomotion, swimming or flying are controlled by the neural networks which receive control signals from the command fibers. The crayfish swimmeret system is a good example to find the control mechanism of such rhythmical behaviors. Wiersma and Ikeda (9) showed that rhythmical motor activity can be released in crayfish swimmeret system by stimulating command fibers with constant frequency pulse trains. They found that the period of the rhythm and the latency depend on the stimulus frequency of command fiber. Stein (10) studied intersegmental coordination in swimmeret and proposed the existence of coordinating neuron of interappendage phases.

In this paper, we will show the relationship between the stimulus frequency of command fiber and the burst period more quantitatively and the interappendage phase constancy. The phase is kept constant even when the burst period changes more than twofold. These results are analyzed in terms of a neural model consisting of Wilson Cowan type oscillator.

3.1 Physiological Experiment

The preparation for recording the burst periods was as follows: The abdomen detached from thorax was dissected in the way described by Kennedy and Takeda (11), except that the sternal ribs of the segments were cut along their long axis in the saline solution (Van Harreveld’s
2. Phase entrainment of two coupled neural oscillators

The entrainment behavior of stable oscillators interacting each other can be investigated by phase response curves (PRCs). This method was developed by Perkel and coworkers and applied by Pittendrigh et al. extensively to circadian rhythms. After Winfree’s excellent works, we studied topological properties of PRCs by the theory of a dynamical system and the homotopy theory. (3)

We applied PRC method to the study of human finger tapping. Assuming that 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. (4)

We also investigated the phase entrainment between finger tapping of left hand and that of right hand. 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. It was shown that the performance is better at the phase difference 0.0 and 0.5 than at other phase difference, which means that we can achieve synchronous or alternate rhythm by both hands more easily than other rhythms. This result was analyzed by using of the same method of Daan and Berde. (5)

PRCs were measured for left and right hand finger tappings and steady phase differences were obtained from the intersections of the following two graphs.

\[
\phi_2 = 1 - (\phi_1 + f(\phi_1)) \\
\phi_1 = 1 - (\phi_2 + g(\phi_2))
\]

where \(f(\phi), g(\phi)\) are PRCs for left and right hand finger tapping respectively. This analysis showed a good agreement with the results of experiments. (6)

Oscillator neuron can be described mathematically using nonlinear oscillator model. Thus the theory of coupled nonlinear oscillators, in particular, the theory of Hopf bifurcation is useful to study the phase entrainment between two interacting oscillators and the stability of solutions.

We studied two BVP model neurons coupled by diffusion as a model
solution) kept in the range of 14°C-20°C. This made the first root of each segment free for recording. The rami of the swimmerets were removed so that their movements did not affect the electrodes. The recording was performed with silver-wire suction electrodes and the position of each suction electrode was adjusted along the posterior side of the main first root so as to record the discharges of powerstroke motorneurons. Male animals were used mainly because of their relatively few connective tissue. Recordings were made only from the roots of the third and fifth ganglia and the signals were amplified by conventional means and recorded on FM tape for later analysis.

Command fibers located along the lateral edges of the interganglionic connectives between the second and the third ganglion were stimulated to induce rhythmic activity. This was accomplished with two platinum wire electrodes on which the small nerve bundles from the lateral edges of the connective were lifted in a bath of paraffin oil, reference electrode is placed in the bath. Square wave pulses with the duration of 100 μsec were used for stimulation. The frequency of the pulse trains was varied between 2 and 100 pulses per second.

Increasing the stimulus frequency to the command fibers were usually accompanied by monotonic decreasing of the burst period. The stable interappendage coordinated rhythms were obtained for up to 50 pulses per second of the stimulation. At the same time, the interappendage phases during locomotion were measured. They were almost constant even when the frequency of the motor activity changes more than twofold. (Fig.1)

![Fig.1](image_url)

Relation between burst period and stimulus frequency

Phase delay between the fifth and fourth swimmeret motor discharge
We also could change the oscillating period of swimmeret by increasing stimulating voltage while stimulus frequency fixed. The monotonic decreasing of the period was also obtained. This result can be interpreted as follows. There exist several command fibers in the stimulated portion and each fiber has different threshold to be activated. The increase of stimulating voltage recruits them. In this case the interappendage phase also is kept constant, even though the burst period changes more than twofold.

3.2 Model

In order to analyze such a rhythmical behavior as mentioned above, a neural oscillator model whose oscillating period can be controlled externally must be used. Wilson-Cowan type model (12) has such a property. The model shows the autonomous oscillation within a range of parameter values and the period decreases with increasing the excitatory input to the excitatory population.

We adopted the simplified version of their model as follows:

\[
\tau_e \frac{dE}{dt} = -E + (K_e - rE) S_e (C_1 E - C_2 I + P)
\]

\[
\tau_i \frac{dI}{dt} = -I + (K_i - rI) S_i (C_3 E - C_4 I + Q)
\]

E(t) and I(t) denote respectively the time coarse-grained activities of excitatory and inhibitory neural population at time t. S_e(x) and S_i(x) are called the response function because they give the expected proportion of cells in each subpopulation which can respond to a given level of the input. The form we chose for S(x) is

\[
S(x) = \frac{1}{2} \left\{ 1 + \tanh (a x - a \Theta) \right\}
\]

here a gives average sensitivity and \( \Theta \) gives threshold. \( \tau \) denotes the neural membrane time constant. \( r \) represents the absolute refractory period. \( C_1, C_2, C_3 \) and \( C_4 \) are the interaction coefficients amongst the excitatory and inhibitory populations, \( K_e \) and \( K_i \) are the maximum value of the response function, \( P \) and \( Q \) are the external input to the excitatory and inhibitory population respectively.

Fig.2 (A) shows typical limit cycles in E-I plane for various values of \( P \) and (C) shows waveforms of oscillations. As shown in Fig.2 (B), with increasing \( P \), the amplitude and the period decrease until oscillation stops.
Fig. 2

(A) Phase plane showing limit cycles in response to constant stimulation. $P=0.1$, $0.3$, $0.5$. Points A, B, C, D are equilibrium points for $P=0.1$, $0.5$, $1.0$ and $2.0$

(B) Dependencies of the period and the amplitude on the stimulus strength $P$

(C) Waveforms of oscillation of $E(t)$

For numerical calculation, $r=1$, $a_e=0.75$, $a_1=1.25$, $\theta_e=2.8$, $\theta_i=4.0$ are used.

3.3 Phase response curve of Wilson-Cowan model

Imposing short time increment of $P$ as disturbance, PRCs of Wilson Cowan model were calculated. Fig. 3 shows PRCs for different values of disturbance $\Delta P$. All of the PRCs intersect with negative slope at the same point of phase axis. And that the slope is less than two in the
case of small perturbation, which means that the oscillator can be entrained at this phase, if it receives pulse type input with the same period of the oscillator. PRCs were also obtained by changing the period of oscillation while the magnitude of disturbance fixed. As shown in Fig. 4, the entrainmental phase varies only 0.15, even when the period changes about twofold.

PRCs described above are the steady PRCs. In experiments with real system, it is difficult to obtain the steady PRC. The PRC with swimmeret of crayfish was reported only by Stein which is the first transient PRC. He plotted the first phase delay of the powerstroke motor neuron discharge in the third abdominal ganglion correlated with the discharge of medial ascending coordinating neurons in the 4-3 connective.
The period of oscillator is 44msec at $P=0.1$
28msec at $P=0.2$
21msec at $P=0.3$

$P = 0.2$ and $AP = 0.6$

$P = 0.1$

$P = 0.2$

$P = 0.3$
Fig. 5 is the transient PRC by Stein on which our calculation is superimposed. The good agreement suggests that Wilson-Cowan type oscillator is suitable for the model of the swimmeret system in crayfish.

3.4 Phase entrainment of master-slave model

In this section, we consider the master-slave oscillator model. Each oscillator is Wilson-Cowan type and the interaction between them is uni-directional and continuous. The slave oscillator receives input proportional to the average activity $E(t)$ of excitatory subset of master oscillator.

If the threshold of the response function of the excitatory subset in the master oscillator is higher than in the slave oscillator, which means the period of the slave oscillator is shorter than that of the master, the two oscillators synchronize each other with an almost constant phase difference over a wide range of the oscillating period as shown in Fig.6.

In real system, there might exist threshold in interaction. We assumed that control signal from master to slave is active only when the average activity $E(t)$ of the master exceeds some threshold $E_t$. Fig. 7 shows the dependence of phase difference on the period of oscillation. When two oscillators are identical, phase difference decreases monotonically as their periods become longer. If the threshold of the response function in master oscillator is higher than in slave, then the phase difference decreases at first then increases. So the range of the phase difference becomes narrower than that of coupling of identical oscillator.

3.5 A model of intersegmental coordination of swimmeret in crayfish

Considering the studies by Stein et al, control mechanism of swimmeret system can be modeled as follows.

As suggested by Stein, this system involves four neural processes. First, the command fibers provide excitation to local oscillator by sending impulses continuously. Secondly, the oscillator neurons translate the unpatterned command input into patterned output. In mathematical sense, it corresponds to the bifurcation phenomenon. Third, the coordinating neurons send to each oscillator the temporal information from the other neurons. Fourth, the motorneurons receive oscillator input and drive the swimmeret movements. Stein is saying that the goal
Fig. 6
The relationship between the phase difference and their period. Continuous interaction without threshold. A=0.5

Fig. 7
The relationship between the phase difference and their period. Continuous interaction with threshold. A=0.5, \(E_t=0.25\)
of the more advance model will be to account for the entire intersegmental timing sequence of swimmeret motor output from the known properties of a coupled oscillator system. We will show such a model by using of Wilson-Cowan type oscillator. The command fibers provide excitation to the oscillator in each ganglion. Assuming that the impulses running along the command fiber are integrated before entering each oscillator, the frequency is equivalent to the external input \( P \) of the model. The motorneuron receives the signal from the oscillator in abdominal ganglion and drives the swimmeret movement when the activity of excitatory neuron \( E(t) \) exceeds the threshold \( E_t \). We have two possibilities of the type of coordination. One is that each excitatory neuron in caudal oscillator directly sends impulses to the oscillator in the next ganglion. The other is that the output of the oscillator is integrated in some interneuron and the impulses are carried to the next oscillator only when this activity is higher than some threshold. Results in the previous section show that the variation of phase difference with increasing of oscillating period is small in the former type of coordination. So we adopted the former type of coordination in our modeling.

Fig.8 shows the periods of the oscillator and the phase difference between two oscillators in 3rd ganglion and 4th ganglion, and also between 4th and 5th ganglion with changing external input \( P \). The result resembles to the experimental result shown in Fig.1. We also assume that the sensitivity of the neuron in the caudal ganglion is higher so that the activity begins first in 5th ganglion when the command fiber is stimulated as in our experimental result. The fact that the delay of the first bursting depends on the stimulus frequency which was found by Wiersma and Ikeda can be also simulated in our model.

We have shown the possibility that the phase constancy can be explained by assuming one-directional interaction between oscillators in each ganglion.

4. Concluding remarks

The mutually coupled oscillators have been applied as a mathematical model to explain several biological phenomena such as circadian rhythms. However there have been few attempts to explain rhythmical behavior whose frequency is changed. We showed that the one directionally coupled oscillator are entrained at the frequency of the caudal oscillator and the phase difference is almost independent of the frequency by using Wilson-Cowan type model.
Fig. 8
The model of the crayfish swimmeret
upper: the relationship between the period and stimulation P
middle: phase difference and P
- - 3rd and 4th
- o- 4th and 5th
threshold of response function θ
3rd ganglion: 2.83, 4th: 2.825
5th: 2.8
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