

DYNAMICS OF INHIBITORY PULSE-COUPLED OSCILLATORS

YASUMASA NISHIURA
*Research Institute for Electronic Science,
Hokkaido University, Sapporo 060, JAPAN*

JUNKO SHIDAWARA
*Department of Mathematics, Hiroshima University,
Higashi-Hiroshima 739, JAPAN*

and

TAKESHI TAKAISHI
*Faculty of Engineering, Hiroshima-DENKI Institute of Technology,
Hiroshima 739-03, JAPAN*

ABSTRACT

A complete classification of dynamics of a population of a inhibitory pulse-coupled oscillators is presented. The model is based on the work of Mirollo and Strogatz, but our model has an inhibitory coupling between oscillators which makes a sharp contrast with the dynamics of the above authors' model. The main result is that for a large class of initial conditions, the population approaches a periodic state in which all the oscillators keep finite size of phase difference (we call it "*phase locking solution*" here). For the remaining class of initial data except for nongeneric ones, it evolves to a periodic state with a cluster or a synchronous state depending on a size of cluster. The criterion for the classification is explicitly given and can be judged easily only by the initial condition.

1. Introduction

This work was motivated by the study of Mirollo and Strogatz¹ on synchronization of biological oscillators typically displayed by the flashing of fireflies in perfect unison. Their model consists of a population of identical integrate-and-fire oscillators. The coupling between oscillators is all to all and pulsatile: when a given oscillator fires, it pulls the others up by a fixed amount, or brings them to the firing threshold, whichever is

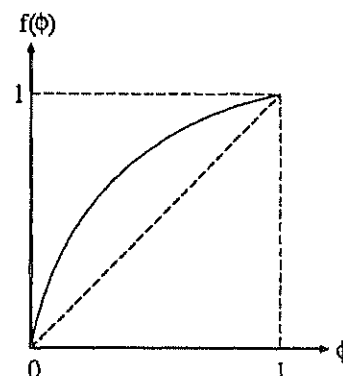


Figure 1: Functional form of $f(\phi)$

less. They showed that for almost all initial conditions, the population evolves to a synchronous state. The main issue of this paper is to study the dynamics of a population of oscillators when they interact in an *inhibitory* way, namely, when a given oscillator fires, it pulls the others *down* by a fixed amount. This type of coupling becomes important especially in models of neural oscillators²

In contrast to activation case, phase locking states become dominant for inhibitory case instead of synchronization. In fact generically there are three basins of attractions; phase locking, phase locking with cluster, and synchronization. The precise meaning of each state will become clear at the end of this section. A complete classification of initial data according to their asymptotic states is done by simple criterions depending only on initial condition. We consider a population of $N + 1$ oscillators and each oscillator is characterized by a state variables x which is assumed to increase monotonically toward a threshold $x = 1$. When x reaches the threshold, the oscillator fires and x jumps back instantly to zero, after which the cycle repeats. Hereafter we assume that x depends only on a phase variable $\phi \in [0, 1]$ and evolves according to $x = f(\phi)$, where $f : [0, 1] \rightarrow [0, 1]$ is a smooth function satisfying $f' > 0$, $f'' < 0$, $f(0) = 0$, and $f(1) = 1$ (see Fig. 1).

The phase variable ϕ is such that $d\phi/dt = 1/T$, where T is the cycle period. The coupling between oscillators is defined as follows. If x_i fires, then $x_j(\phi)(j \neq i)$ is pulled down instantaneously by the amount $|\epsilon|$, or to zero, whichever is more, i.e., $x_j(\phi + 0) = \max(0, x_j(\phi) + \epsilon) \forall j \neq i$. Note that ϵ is always a negative number. Absorption occurs when an oscillator is pulled down below zero level (see Fig. 3 and 4). Namely, when x_i fires, an oscillator $x_j(j \neq i)$ is absorbed by x_i if $\max(0, x_j(\phi) + \epsilon) = 0$ holds. We assume that the absorbed oscillators behave in the same way as x_i thereafter. We call such a group of oscillators a **cluster**. If a cluster of k oscillators fires, it pulls all the other oscillators down by $|k\epsilon|$. When all the oscillators act as one, we call it **synchronization**. Since the interaction among oscillators is pulsatile, and when an oscillator (a cluster) fires, it instantaneously returns to zero phase, it suffices

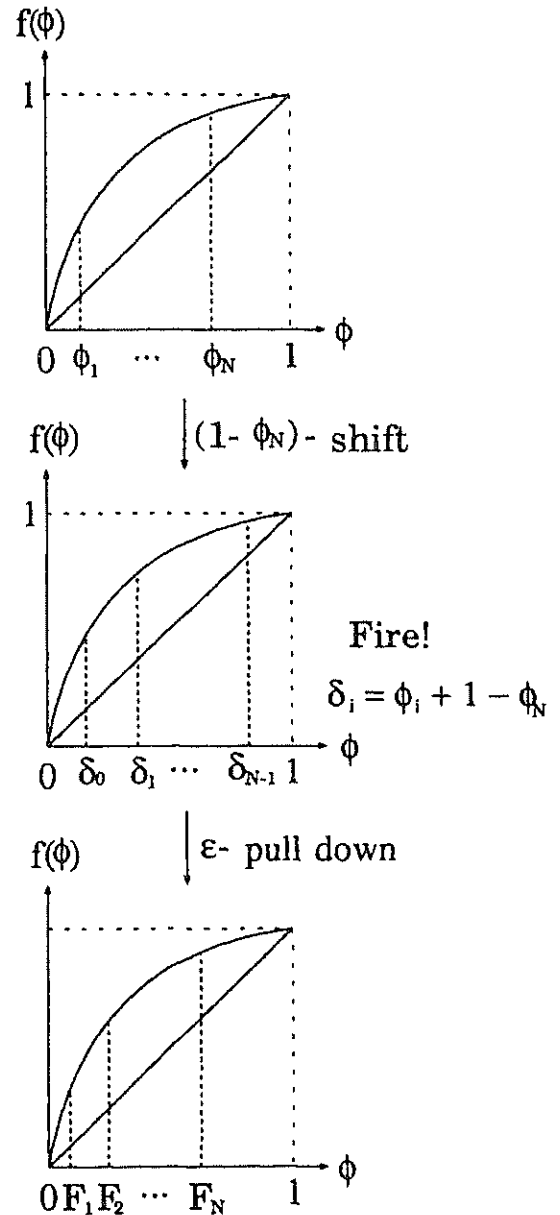


Figure 2: Firing map

Figure 2: Firing map. Three vertically stacked graphs showing the function $f(\phi)$ on the y-axis and ϕ on the x-axis. The top graph shows a smooth curve $f(\phi)$ starting at $(0,0)$ and ending at $(1,1)$, with a diagonal line $y=\phi$. Points ϕ_1, \dots, ϕ_N are marked on the x-axis. The middle graph shows the same curve shifted down by $(1 - \phi_N)$, with points $\delta_0, \delta_1, \dots, \delta_{N-1}$ marked on the x-axis. A vertical arrow labeled $(1 - \phi_N) - \text{shift}$ points from the top graph to the middle one. The text "Fire!" and the equation $\delta_i = \phi_i + 1 - \phi_N$ are shown to the right. The bottom graph shows the curve shifted down by ϵ , with points F_1, F_2, \dots, F_N marked on the x-axis. A vertical arrow labeled $\epsilon - \text{pull down}$ points from the middle graph to the bottom one.

to study the following firing map F to know the asymptotic behavior (see Fig. 2):

$$F : \begin{pmatrix} \phi_1 \\ \phi_2 \\ \vdots \\ \phi_N \end{pmatrix} \mapsto \begin{pmatrix} F_1 \\ F_2 \\ \vdots \\ F_N \end{pmatrix} \quad \Phi = \begin{pmatrix} \phi_1 \\ \phi_2 \\ \vdots \\ \phi_N \end{pmatrix} \in D(0,1)$$

$$F(\Phi) = \begin{pmatrix} F_1 \\ F_2 \\ \vdots \\ F_N \end{pmatrix} = \begin{pmatrix} g(f(1 - \phi_N) + \epsilon) \\ g(f(\phi_1 + 1 - \phi_N) + \epsilon) \\ \vdots \\ g(f(\phi_{N-1} + 1 - \phi_N) + \epsilon) \end{pmatrix} \quad g \equiv f^{-1} \quad (1.1)$$

where $D(0,1)$ is the ordered space in $(0,1)$, i.e., $D(0,1) = \{\Phi \mid 0 < \phi_1 < \phi_2 < \dots < \phi_N < 1\}$. It is clear that F preserves order. Also note that one oscillator always sits at $\phi = 0$, so the firing map F becomes N -dimensional. $F^k(\Phi)$ stands for the k -iterations of firing map F , if it can be defined and $F_i^k = F_i^k(\Phi)$ ($i = 1, \dots, N$) denotes the i -th component. $\Phi^* = (\phi_1^*, \dots, \phi_{k-1}^*)$ is called a k -phase locking solution if it is a fixed point of F^k , i.e., $F^k(\Phi^*) = \Phi^*$. This notion can be easily generalized to the case where there are clusters (see Section 3). Our goal is to show the following theorem.



Figure 3: No absorption

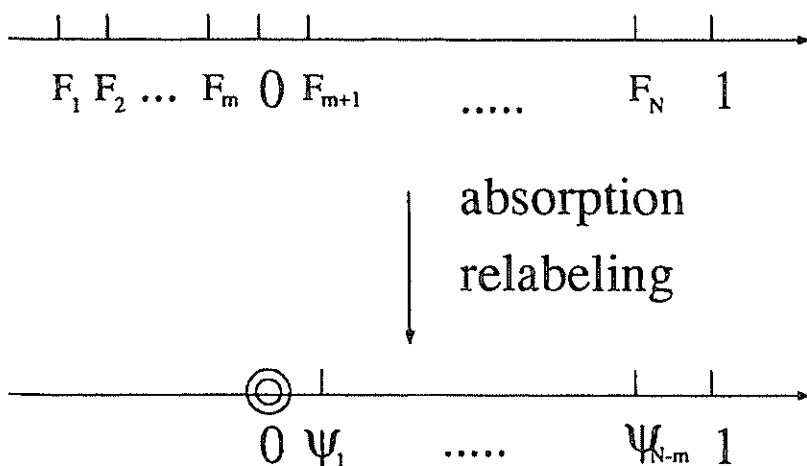


Figure 4: Absorption

Main Theorem

Suppose an initial condition $\Phi = (\phi_1, \phi_2, \dots, \phi_N) \in D(0, 1)$ is given, then the asymptotic state is determined by the following diagram.

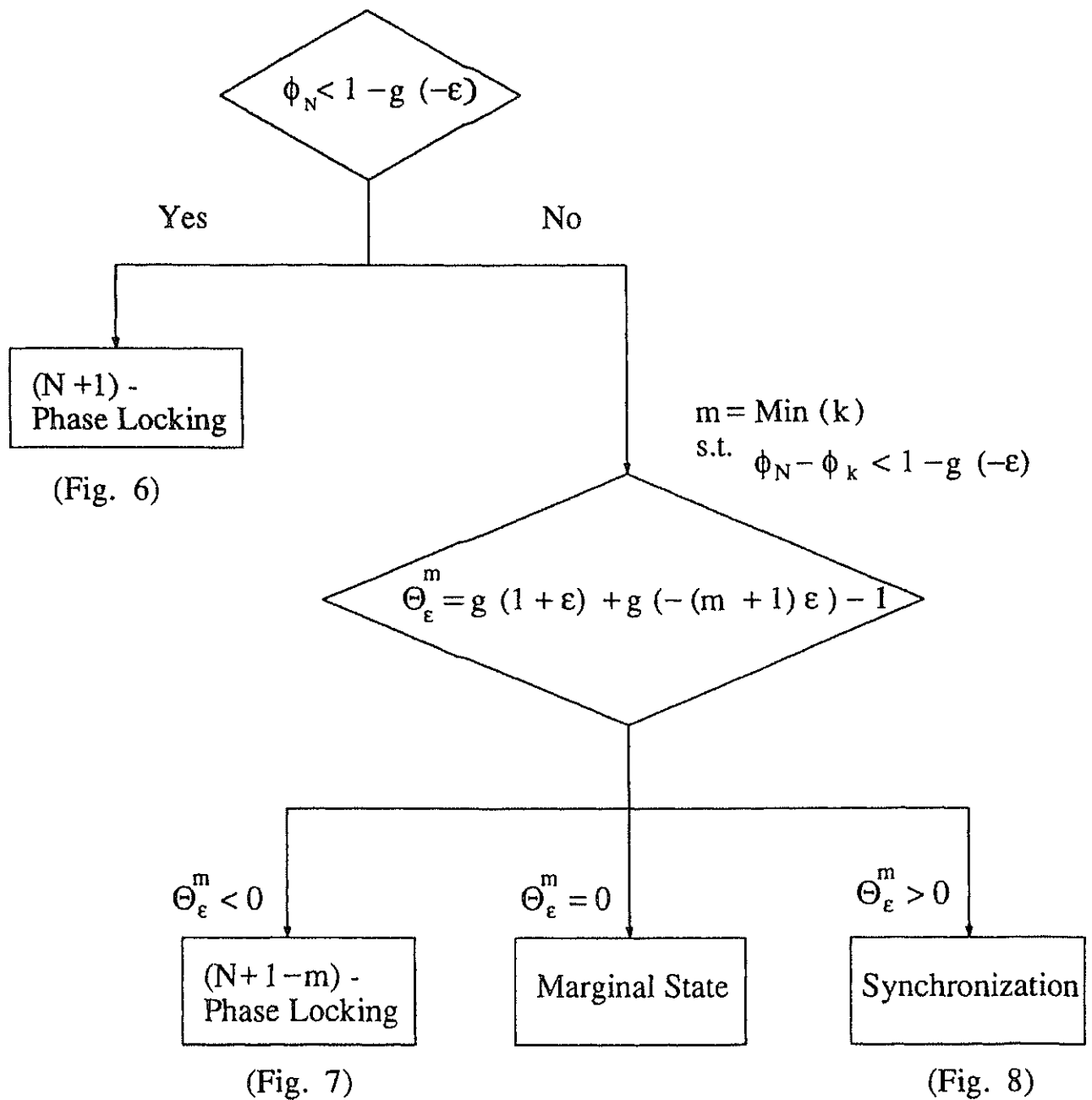
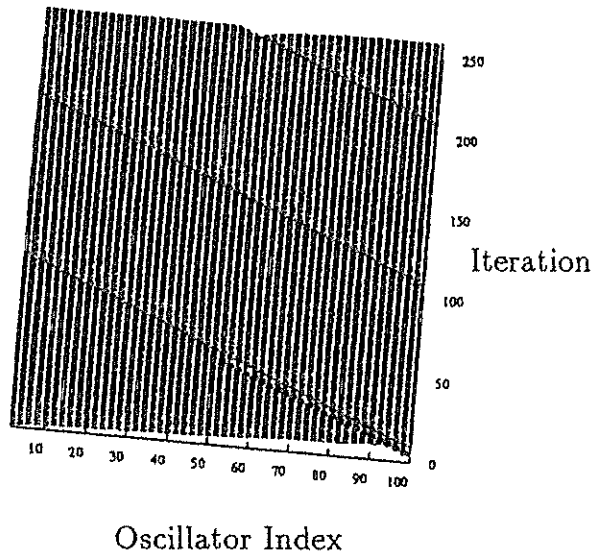
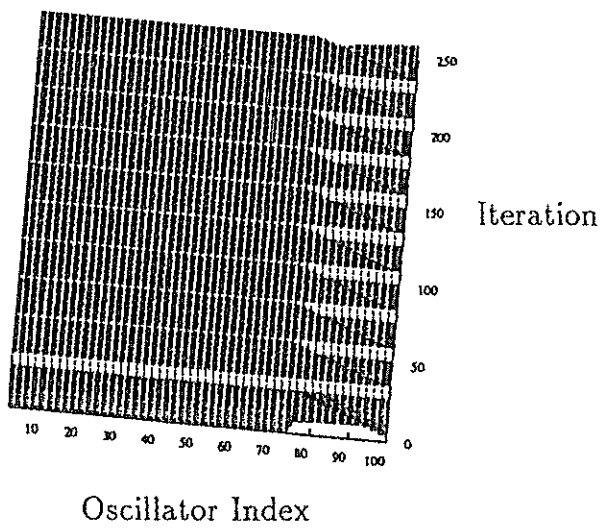


Figure 5: classification of asymptotic dynamics

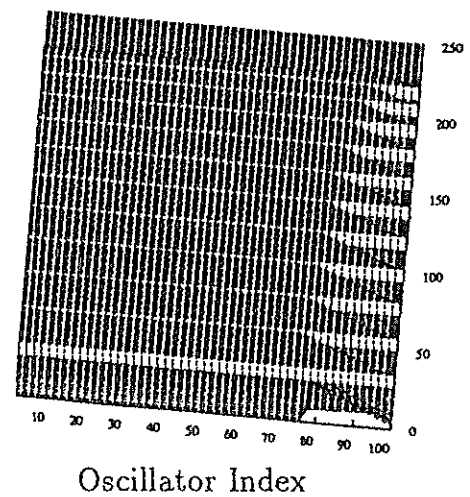


The vertical direction denotes the phase axis.

Figure 6: Phase locking solution



Oscillator Index



Oscillator Index

Figure 7: Phase locking solution with cluster

Figure 8: Synchronization

We shall prove *Main Theorem* in the subsequent sections. In Section 2, $(N + 1)$ -phase locking case (the left-half part of the diagram) is treated and the remaining part is proven in Section 3.

2. Convergence to phase locking state

We shall prove in this section that the oscillators tend to a unique phase locking state (see Fig. 6) if there does not occur absorption at the first firing, i.e., the first left option in the diagram of *Main Theorem*. The following lemma tells us whether an absorption occurs or not at firing, and how many if it does.

Lemma 1

$$(1) \text{ No absorption} \iff \phi_N < 1 - g(-\epsilon)$$

$$(2) m \text{ oscillators in } \Phi \text{ are absorbed by } F$$

$$\iff \exists m \equiv \max\{i\} \quad \text{s.t.} \quad \phi_N - \phi_{i-1} > 1 - g(-\epsilon)$$

Proof of Lemma 1

See the definition (1.1) of the firing map F . ■

We focus on the case (1) of *Lemma 1*. The convergence proof is divided into two parts; first there never occurs absorption for subsequent firing and then show the existence of globally attracting periodic point of the map F . The next lemma shows the first part.

Lemma 2

If $F_1^1 > 0$, then, $F_1^k > 0$ holds for any $k \geq 2$.

Proof of Lemma 2

We prove this by induction.

Suppose that there exists a l such that $F_1^k > 0$ for any $k \leq l$. Then

$$F^{l+1}(\Phi) = F \begin{pmatrix} F_1^l \\ F_2^l \\ \vdots \\ F_N^l \end{pmatrix}.$$

Hence,

$$F_1^{l+1} = g(f(1 - F_N^l) + \epsilon).$$

Using the monotonicity and convexity of g , we have

$$\begin{aligned} F_N^l &= g(f(F_{N-1}^{l-1} + 1 - F_N^{l-1}) + \epsilon) \\ &< g(1 + \epsilon) \\ &< 1 - g(-\epsilon). \end{aligned}$$

Applying f on both sides, the inequality becomes

$$\begin{aligned} 1 - F_N^l &> g(-\epsilon) \\ f(1 - F_N^l) &> -\epsilon \\ f(1 - F_N^l) + \epsilon &> 0 \end{aligned}$$

Thus

$$F_1^{l+1} > g(0) = 0,$$

which completes the proof. \blacksquare

The firing map F turns out to be contracting everywhere as in the following lemma.

Lemma 3

Let $DF|_{\Phi}$ be the Jacobian matrix of F at Φ , and $\sigma_i(\Phi)$ ($i = 1, \dots, N$) be the eigenvalues of $DF|_{\Phi}$. Then,

$$\max_i (|\sigma_i(\Phi)|) < 1$$

for any $\Phi \in D(0, 1)$.

Proof of Lemma 3

In view of Eq.1.1,

$$\frac{\partial F_i}{\partial \phi_N} = -g'(f(\phi_{i-1} + 1 - \phi_N) + \epsilon) \cdot f'(\phi_{i-1} + 1 - \phi_N).$$

Letting $h_i \stackrel{def}{=} g'(f(\phi_{i-1} + 1 - \phi_N) + \epsilon) \cdot f'(\phi_{i-1} + 1 - \phi_N)$. We have

$$\begin{aligned} \frac{\partial F_i}{\partial \phi_{i-1}} &= g'(f(\phi_{i-1} + 1 - \phi_N) + \epsilon) \cdot f'(\phi_{i-1} + 1 - \phi_N) \\ &= h_i \quad (2 \leq i \leq N) \\ \frac{\partial F_i}{\partial \phi_j} &= 0 \quad (j \neq i-1, N) \end{aligned}$$

Hence

$$DF|_{\Phi} = \begin{pmatrix} 0 & \cdots & \cdots & 0 & -h_1 \\ h_2 & \ddots & & \vdots & -h_2 \\ 0 & \ddots & \ddots & \vdots & \vdots \\ \vdots & \ddots & \ddots & 0 & -h_{N-1} \\ 0 & \cdots & 0 & h_N & -h_N \end{pmatrix}$$

The next sublemma is useful to compute the characteristic polynomial of DF .

Sublemma 1

$$\det(DF - \lambda I) = (-1)^i h_N \cdots h_{N-i+1} \cdot \begin{vmatrix} -\lambda & 0 & \cdots & 0 & -h_1 \\ h_2 & \ddots & \ddots & \vdots & -h_2 \\ 0 & h_3 & \ddots & 0 & \vdots \\ \vdots & \ddots & \ddots & -\lambda & -h_{N-i-1} \\ 0 & \cdots & 0 & h_{N-i} & -P_i \end{vmatrix},$$

where

$$P_i = \frac{\lambda^{i+1} + h_N \lambda^i + h_N \cdot h_{N-1} \lambda^{i-1} + \dots + h_N \dots h_{N-i}}{h_N \dots h_{N-i+1}} \quad (1 \leq i \leq N-2)$$

Proof of Sublemma 1 This can be proved by induction, so we leave the details to the reader. \blacksquare

Using *Sublemma 1*, we have

$$\begin{aligned} \det(DF - \lambda I) &= (-1)^{N-2} \cdot h_N \cdot \dots \cdot h_3 \cdot \begin{vmatrix} -\lambda & -h_1 \\ h_2 & -P_{N-2} \end{vmatrix} \\ &= (-1)^{N-2} \cdot h_N \cdot \dots \cdot h_3 \cdot (\lambda P_{N-2} + h_1 \cdot h_2) \\ &= (-1)^N (\lambda^N + h_N \lambda^{N-1} + h_N \cdot h_{N-1} \lambda^{N-2} + \dots + h_N \dots h_1). \end{aligned}$$

Hence the characteristic equation becomes

$$\lambda^N + h_N \lambda^{N-1} + h_N h_{N-1} \lambda^{N-2} + \dots + h_2 \cdot h_3 \dots h_N \lambda + h_1 \cdot h_2 \dots h_N = 0 \quad (2.1)$$

We can estimate the modulus of roots of Eq.2.1 with the aid of the following sublemma.

Sublemma 2 (Kakeya-Eneström's theorem³)

Suppose the coefficients of the equation $f(x) = a_0 x^n + a_1 x^{n-1} + \dots + a_{n-1} x + a_n = 0$ are real and satisfy

$$a_0 > a_1 > \dots > a_n > 0,$$

then the modulus of each root is strictly less than 1.

Since it holds that

$$\begin{aligned} h_i &= g'(f(\phi_{i-1} + 1 - \phi_N) + \epsilon) \cdot f'(\phi_{i-1} + 1 - \phi_N) \\ &= \frac{g'(f(\phi_{i-1} + 1 - \phi_N) + \epsilon)}{g'(f(\phi_{i-1} + 1 - \phi_N))} \\ &< 1, \end{aligned}$$

the coefficients of (2.1) satisfy the hypothesis of Sublemma 2, which completes the proof. \blacksquare

Using the above lemmas, the following goal of this section is an immediate consequence.

Proposition 1

$$\Phi \in D(0, 1 - g(-\epsilon))$$

$$\implies \exists! \Phi^* = \begin{pmatrix} \phi_1^* \\ \phi_2^* \\ \vdots \\ \phi_N^* \end{pmatrix} \in D(0, 1 - g(-\epsilon)), \quad \lim_{k \rightarrow \infty} F^k(\Phi) = \Phi^*$$

Proof of Proposition 1

By *Lemma 1*, the hypothesis of this proposition indicates no absorption. So by *Lemma 2*, we have for any k

$$\Phi \in D(0, 1 - g(-\epsilon)) \implies F^k(\Phi) \in D(0, 1 - g(-\epsilon))$$

Hence by *Lemma 3* and the principle of contraction mapping, there exists a unique fixed point Φ^* which is globally asymptotically stable in $D(0, 1 - g(-\epsilon))$ ■

It should be remarked that the criterion (1) of *Lemma 1* is satisfied for any ϕ_N as $\epsilon \downarrow 0$, which implies that the basin of attraction of $(N + 1)$ -phase locking state covers the whole initial space as $\epsilon \downarrow 0$.

3. Phase locking with cluster and synchronization

When an absorption occurs at first firing (i.e., the right option in the diagram of Main Theorem), the subsequent dynamics is different from that of Section 2 due to the existence of cluster. Suppose that m oscillators are absorbed by firing, we have a $(m + 1)$ -cluster at phase 0 at the next moment. Since the members of the cluster behave in unison, we regard this to be one oscillator with strength $(m + 1)\epsilon$. The number of oscillators is therefore reduced to $N + 1 - m$ with new labelling $\Psi = (\psi_1, \dots, \psi_{N-m})$. It may happen that there occurs another absorption until the next firing of cluster, and another cluster may be formed. However this is not the case, namely

Lemma 4

If m oscillators are absorbed by the first F , then,

$$F_1^k(\Psi) > 0$$

holds for $1 \leq k \leq N - m$

Proof of Lemma 4

This can be done in a parallel way to that of *Lemma 2*, so we omit the details. ■

This lemma implies that if the absorption occurs again, it must be done by the cluster's firing. It is convenient to define a firing map H of cluster:

$$H : \begin{pmatrix} \psi_1 \\ \psi_2 \\ \vdots \\ \psi_{N-m} \end{pmatrix} \mapsto \begin{pmatrix} H_1 \\ H_2 \\ \vdots \\ H_{N-m} \end{pmatrix} \quad H_i = H_i(\Psi), \quad \Psi = \begin{pmatrix} \psi_1 \\ \vdots \\ \psi_{N-m} \end{pmatrix}$$

$$\begin{pmatrix} H_1 \\ H_2 \\ \vdots \\ H_{N-m} \end{pmatrix} = \begin{pmatrix} g(f(1 - \psi_{N-m}) + (m + 1)\epsilon) \\ g(f(\psi_1 + 1 - \psi_{N-m}) + (m + 1)\epsilon) \\ \vdots \\ g(f(\psi_{N-m-1} + 1 - \psi_{N-m}) + (m + 1)\epsilon) \end{pmatrix}.$$

In view of the above observation, it is reasonable to consider a composite mapping R defined by

$$R(\Psi) = \begin{pmatrix} R_1 \\ \vdots \\ R_{N-m} \end{pmatrix} \equiv H \circ F^{N-m}(\Psi).$$

R is a sort of Poincaré Mapping consisting of one round of firings of oscillators. In what follows we study the mapping R . Note that the next absorption, if it happens, can be captured by R owing to Lemma 4. The mapping R is also a contracting one.

Lemma 5

Let $\delta_i(\Psi)$ ($i = 1, \dots, N - m$) be the eigenvalues of $DR|_{\Psi}$, Then,

$$\max_i |\delta_i(\Psi)| < 1$$

for any $\Psi \in D$

Proof of Lemma 5

Noting that H satisfies a similar property as in Lemma 3, and that R is a composite mapping of F and H , we easily see the conclusion. ■

After a cluster is formed by the first firing F , we need to know a criterion on whether the absorption occurs or not. The next result gives a non-absorption condition.

Proposition 2

$$g(1 + \epsilon) + g(-(m + 1)\epsilon) < 1 \tag{3.1}$$

$$\implies \exists \Psi^* = \begin{pmatrix} \psi_1^* \\ \psi_2^* \\ \vdots \\ \psi_{N-m}^* \end{pmatrix} \in D(0, g(1 + \epsilon)), \quad \lim_{k \rightarrow \infty} R^k(\Psi) = \Psi^*$$

Proof of Proposition 2

We prove this by induction. Suppose that there occurs no absorption up to $k - 1$. Then

$$R^k \begin{pmatrix} \psi_1 \\ \psi_2 \\ \vdots \\ \psi_{N-m} \end{pmatrix} = (H \circ F^{N-m}) \circ R^{k-1} \begin{pmatrix} \psi_1 \\ \psi_2 \\ \vdots \\ \psi_{N-m} \end{pmatrix}$$

Thanks to Lemma 2, there are no absorption by applying F^{N-m} .

$$\text{Let } F^{N-m} \circ R^{k-1} \begin{pmatrix} \psi_1 \\ \psi_2 \\ \vdots \\ \psi_{N-m} \end{pmatrix} = \begin{pmatrix} \eta_1^k \\ \eta_2^k \\ \vdots \\ \eta_{N-m}^k \end{pmatrix},$$

Then

$$R^k(\Psi) = H \begin{pmatrix} \eta_1^k \\ \eta_2^k \\ \vdots \\ \eta_{N-m}^k \end{pmatrix}$$

In view of *Lemma 1*, it suffices to show the following for the non-occurrence of absorbing by H :

$$\eta_{N-m}^k < 1 - g(-(m+1)\epsilon).$$

Since the state vector ${}^t(\eta_1^k, \dots, \eta_{N-m}^k)$ is obtained right after F^{N-m} , it holds that

$$\eta_{N-m}^k < g(1 + \epsilon)$$

Using the hypothesis, we obtain

$$\eta_{N-m}^k < 1 - g(-(m+1)\epsilon).$$

Thanks to *Lemma 5* and the principle of contraction mapping, we conclude that there exists a unique fixed point Ψ^* of R which is globally asymptotically stable. ■

Thus if the criterion (3.1) is satisfied, we don't have absorption any more, and all the orbits approach a phase locking solution with cluster (see Fig. 7).

Suppose the inequality (3.1) does not hold, the oscillators, in general, eventually approach synchronization. When we regard the first component $R_1(\Psi)$ as a function of ψ_1 , we denote it by $\tilde{R}(\psi_1)$.

Proposition 3

- (1) $g(1 + \epsilon) + g(-(m+1)\epsilon) > 1 \implies 0 < \tilde{R}'(\psi_1) < 1, \quad \tilde{R}(0) < 0$
- (2) $g(1 + \epsilon) + g(-(m+1)\epsilon) = 1 \implies 0 < \tilde{R}'(\psi_1) < 1, \quad \tilde{R}(0) = 0,$

where $\tilde{R}'(\psi_1)$ is strictly bounded away from 1 and $\tilde{R}(0) \equiv \lim_{\psi_1 \downarrow 0} \tilde{R}(\psi_1)$.

Proposition 3 gives us the remaining part of the proof of Main Theorem as follows.

In case of (1), there exists k such that $\tilde{R}^k(\psi_1) < 0$, which implies that absorption occur again by finite times operating of R . Moreover, it is clear that if $g(1 + \epsilon) + g(-(m+1)\epsilon) > 1$, then $g(1 + \epsilon) + g(-(n+1)\epsilon) > 1$ for $\forall n \geq m$. Therefore synchronization must be reached by finite firing (see Fig. 8).

In case of (2), since $\tilde{R}(0) = 0$, absorption doesn't occur by finite times firing of R . Furthermore, since the distance of phase between the cluster and other oscillators tends to zero as $k \rightarrow +\infty$, so it is not a phase locking solution. We call such a neutral solution a **Marginal solution**.

Proof of Proposition 3

Differentiating each component of $F(\Psi)$ by ψ_1 (denoted by $'$), we obtain for $F(\Psi)$:

$$\begin{cases} F_2' = g'(f(\psi_1 + 1 - \psi_{N-m}) + \epsilon) \cdot f'(\psi_1 + 1 - \psi_{N-m}) \\ F_i' = 0 \quad (i \neq 2) \end{cases}$$

Similarly for $F^2(\Psi)$,

$$\begin{cases} (F_3^2)' = g'(f(F_2 + 1 - F_{N-m}) + \epsilon) \cdot f'(\psi_1 + 1 - \psi_{N-m}) \\ F_i' = 0 \quad (i \neq 2) \end{cases}$$

We have in general the following:

$$\begin{cases} (F_1^0)' = 1 \\ (F_i^0)' = 0 \quad (i \neq 1) \\ (F_{j+1}^j)' = g'(f(F_j^{j-1} + 1 - F_{N-m}^{j-1}) + \epsilon) \cdot f'(F_j^{j-1} + 1 - F_{N-m}^{j-1}) \cdot (F_j^{j-1})' \\ (F_i^j)' = 0 \quad (i \neq j+1, \quad 1 \leq j \leq N-m-2) \end{cases}$$

$$(F_{N-m}^{N-m})' = g'(f(F_{N-m-1}^{N-m-1} + 1 - F_{N-m}^{N-m-1}) + \epsilon) \cdot f'(F_{N-m-1}^{N-m-1} + 1 - F_{N-m}^{N-m-1}) \cdot (-F_{N-m}^{N-m-1})'.$$

From $R_1(\Psi) = g(f(1 - F_{N-m}^{N-m}) + (m+1)\epsilon)$ and the above formulation,

$$\begin{aligned} \tilde{R}'(\psi_1) &= g'(f(1 - F_{N-m}^{N-m}) + (m+1)\epsilon) \cdot f'(1 - F_{N-m}^{N-m}) \cdot (-F_{N-m}^{N-m})' \\ &= g'(f(1 - F_{N-m}^{N-m}) + (m+1)\epsilon) \cdot f'(1 - F_{N-m}^{N-m}) \\ &\quad \cdot g'(f(F_{N-m-1}^{N-m-1} + 1 - F_{N-m}^{N-m-1}) + \epsilon) \cdot f'(F_{N-m-1}^{N-m-1} + 1 - F_{N-m}^{N-m-1}) \cdot (F_{N-m}^{N-m-1})'. \end{aligned}$$

Noting that

$$f'(X(\psi_1)) = \frac{1}{g'(f(X(\psi_1)))}$$

and

$$\begin{aligned} g'(f(X(\psi_1)) + n\epsilon) \cdot f'(X(\psi_1)) &= \frac{g'(f(X(\psi_1)) + n\epsilon)}{g'(f(X(\psi_1)))} \\ &< 1, \end{aligned}$$

we have

$$\begin{aligned} g'(f(1 - F_{N-m}^{N-m}) + (m+1)\epsilon) \cdot f'(1 - F_{N-m}^{N-m}) &< 1 \\ g'(f(F_{N-m-1}^{N-m-1} + 1 - F_{N-m}^{N-m-1}) + \epsilon) \cdot f'(F_{N-m-1}^{N-m-1} + 1 - F_{N-m}^{N-m-1}) &< 1. \end{aligned}$$

Moreover, we can obtain by induction

$$(F_j^{j-1})' < 1 \quad j = 2, \dots, N-m$$

which implies that

$$\tilde{R}'(\psi_1) < 1$$

for both cases (1) and (2). The positivity of $\tilde{R}'(\psi_1)$ is easily seen from the assumption for f and the above discussions.

Next let us find the value of $\tilde{R}'(0)$. Again by induction we can show that when $\psi_1 \downarrow 0$,

$$F_j^j = F_{j+1}^j \quad j = 1, 2, \dots.$$

Hence,

$$\begin{aligned} F_{N-m}^{N-m} &= g(f(F_{N-m-1}^{N-m-1} + 1 - F_{N-m}^{N-m-1}) + \epsilon) \\ &= g(1 + \epsilon). \end{aligned}$$

For the first case (1), we have

$$\begin{aligned}\tilde{R}(0) &= g(f(1 - F_{N-m}^{N-m}) + (m+1)\epsilon) \\ &= g(f(1 - g(1 + \epsilon)) + (m+1)\epsilon) \\ &< g(f(g(-(m+1)\epsilon)) + (m+1)\epsilon) \\ &= 0.\end{aligned}$$

Similarly for the second case (2)

$$\begin{aligned}\tilde{R}(0) &= g(f(1 - g(1 + \epsilon)) + (m+1)\epsilon) \\ &= g(f(g(-(m+1)\epsilon)) + (m+1)\epsilon) \\ &= 0.\end{aligned}$$

Thus we complete the proof. ■

References

1. R. E. Mirollo and S. H. Strogatz, Synchronization of pulse-coupled biological oscillators, *SIAM J. Appl. Math.* **50** (1990), 1645-1662.
2. G. B. Ermentrout and N. Kopell, Inhibition-produced patterning in chains of coupled nonlinear oscillators, *SIAM J. Appl. Math.* **54** (1994), 478-507.
3. E. Landau, *Archiv d. Math.* **21**(3) (1913), 253.

