

## **Sustained Oscillations Generated by Mutually Inhibiting Neurons with Adaptation**

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**Abstract.** Autonomic oscillatory activities exist in almost every living thing and most of them are produced by rhythmic activities of the corresponding neural systems (locomotion, respiration, heart beat, etc.). This paper mathematically discusses sustained oscillations generated by mutual inhibition of the neurons which are represented by a continuous-variable model with a kind of fatigue or adaptation effect. If the neural network has no stable stationary state for constant input stimuli, it will generate and sustain some oscillation for any initial state and for any disturbance. Some sufficient conditions for that are given to three types of neural networks: lateral inhibition networks of linearly arrayed neurons, symmetric inhibition networks and cyclic inhibition networks. The result suggests that the adaptation of the neurons plays a very important role for the appearance of the oscillations. Some computer simulations of rhythmic activities are also presented for cyclic inhibition networks consisting of a few neurons.

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### **1 Introduction**

Various oscillatory or rhythmic activities exist in almost every animal and most of them are produced without receiving any particular extrinsic oscillatory stimulus. Locomotive motions such as locomotion of quadrupeds, flapping of bird wings, swimming of fish, etc. are typical examples of oscillatory activities. Respiration and heart beat are other familiar examples of rhythmic activities occurring inside the body. Oscillation can also be observed in sensory systems. When the compound eye of the horseshoe crab is subjected to uniform illumination, periodic oscillation appears in the optic nerve (Barlow and Fraioli, 1978). It is also observed in the lateral geniculate nucleus of the cat's

vision system (Wall et al., 1979). Binocular rivalry might be a psychological example observed in the human vision system (Matsuoka, 1984).

To explain the mechanism of such autonomic oscillatory activities, various models of neural networks have been suggested. In all the models, neurons are connected such that one neuron's excitation suppresses the other neurons' excitations. Reiss (1962) showed that a pair of reciprocally inhibiting neurons with fatigue can produce alternate bursts of firing. Kling and Székely (1968) investigated rhythmic activities of circular networks with cyclic inhibitions. Suzuki et al. (1971) also investigated the dynamics of a circular network of five neurons to explain the movements of starfish. Friesen and Stent (1977) explained the locomotory rhythms by neural network with current cyclic inhibition. Nagashino et al. (1981) showed that a circular network with lateral inhibition can generate various types of rhythm patterns.

Although these models successfully demonstrated the oscillation, it was generally difficult to obtain specific conditions in which the oscillations occur. It is because their neuron models have more or less "digital" features. On the other hand, Morishita and Yajima (1972) analysed networks represented by a continuous-variable neuron model and gave mathematical conditions in which the networks have stable stationary states and sustain oscillations. As for the oscillation, however, they only analysed a very special type of networks.

This paper also gives mathematical conditions for mutual inhibition networks represented by a continuous-variable neuron model to generate oscillation. It deals with three general classes of networks which are important from practical point of view: lateral inhibition networks of linearly arrayed neurons, symmetric inhibition networks, and cyclic inhibition networks. Morishita and Yajima's (1972) model is a special case of the last class of networks. These models

are more general in two respects than the previous models mentioned above.

First, in our models each neuron received a different magnitude of external input (stimulus) in general, and the synaptic weights between the neurons are not necessarily equal. Meanwhile, in almost every previous models, each neuron receives the same external input and the synaptic weights are all equal. Secondly, adaptation is incorporated into them (as a special case, it includes the case of no adaptation). That is, the neuron has a property such that the firing rate decreases when given a constant stimulus energy. Our analysis will show that adaptation has an important role on the appearance of the oscillation.

## 2 Analyses of Mutually Inhibiting Neurons

### 2.1 Model of the Mutual Inhibition Network

Among many models representing a single neuron's activity (Harmon and Lewis, 1966) we shall adopt a continuous-variable neuron model. Since the model represents the firing rate of a neuron by a continuous variable with time, it is suitable to describe the behaviour of the neuron whose impulse frequency changes slowly in comparison with the impulse intervals.

Although various continuous-variable models are conceivable, the following model are widely used for its mathematical simplicity (Morishita and Yajima, 1972; Hadel, 1974), with slight modifications by some authors (Sugawara et al., 1983):

$$\left. \begin{aligned} \tau \dot{x} + x &= \sum_{j=1}^n c_j s_j & (\dot{\phantom{x}} \triangleq d/dt) \\ y &= g(x - \theta) & (g(x) \triangleq \max(0, x)). \end{aligned} \right\} \quad (1)$$

Here  $x$  is a membrane potential of the neuron,  $s_j$  impulse rate of the input stimuli,  $\theta$  the threshold value below which the neuron does not fire,  $\tau$  a time constant,  $c_j$  weights of synaptic conjunctions ( $>0$  for excitatory synapses and  $<0$  for inhibitory synapses), and  $y$  is an output or a firing rate of the neuron.

Although this model has been used by many authors, its behaviour does not resemble real neurons' one in one respect. When the neuron receives a step input, the output (firing rate) will increase monotonically with time and approach to a stationary state ( $x = \sum_j a_j c_j$ ). Actual neurons, however, commonly do not exhibit such a time course; the output increases rapidly at first and then gradually decreases to a lower level. This decrease of the firing rate is called adaptation (Luciano et al., 1978). It was shown by Reiss (1962) and Suzuki et al. (1971) that the adaptation of neurons has an essential role in the generation of the oscillation on computer simulation or by analog models without mathematical analysis.

Instead of (1), therefore, we shall consider the following neuron model which takes into account the adaptation:

$$\left. \begin{aligned} \tau \dot{x} + x &= \sum_{j=1}^n c_j s_j - b x' \\ T \dot{x}' + x' &= y \\ y &= g(x - \theta), \end{aligned} \right\} \quad (2)$$

where  $x'$  is the variable that represents the degree of the adaptation, and  $T (>0)$  and  $b (\geq 0)$  are the parameters that specify the time course of the adaptation. Values of these parameters should be determined such that the step response will not be a (damped) oscillation in consideration of the behaviour of the actual neurons. The condition for that is

$$(T - \tau)^2 \geq 4T\tau b. \quad (3)$$

It should be noted that the previous model without adaptation, (1), is a special case of the present model ( $b=0$ ). Oppositely when  $b$  is very large ( $b \rightarrow \infty$  with  $b/T = \text{constant}$ ) it will become a kind of differentiator, which responds only to changing input but not to constant input. The neuron with small  $b$  is the so-called "sustained-type" or "tonic" neuron; on the other hand, that of large  $b$  corresponds to a "transient-type" or "phasic" neuron. Step responses of three cases,  $b=0$ ,  $0 < b < \infty$ , and  $b = \infty$ , are shown in Fig. 1.

Throughout this paper we discuss oscillations generated by mutual inhibition between  $n$  neurons with adaptation:

$$\left. \begin{aligned} \dot{x}_i + x_i &= - \sum_{j=1}^n a_{ij} y_j + s_i - b x'_i \\ T \dot{x}'_i + x'_i &= y_i \\ y_i &= g(x_i) \quad (i=1, \dots, n). \end{aligned} \right\} \quad (4)$$

Here  $a_{ij}$  indicates the strength of the inhibitory connection between the neurons;  $a_{ij} \geq 0$  for  $i \neq j$  and  $=0$  for  $i=j$  (we consider neither excitatory connection nor self-inhibition).  $\sum a_{ij} y_j$  represents the total input from the neurons inside a neural network and  $s_i$  the total input from the outside of the network.  $\tau$  and  $\theta$  are omitted in this equation, for we can let  $\tau=1$  and  $\theta=0$  in (2) by replacing  $x_i - \theta$ ,  $t/\tau$ ,  $T/\tau$ , and  $s_i - \theta$  by  $x_i$ ,  $t$ ,  $T$ , and  $s_i$ , respectively. Henceforth we assume that inputs  $s_i$  are positive and constant with time.

Morishita and Yajima (1972) investigated the case of  $b=0$  and gave a sufficient condition for the absence of stable stationary states in a special type of networks. The present paper gives some conditions to the case of  $b \geq 0$  and more general types of networks. When the conditions are satisfied, the networks will produce and sustain oscillation (not necessarily periodic) for any initial state and for any temporary disturbance.

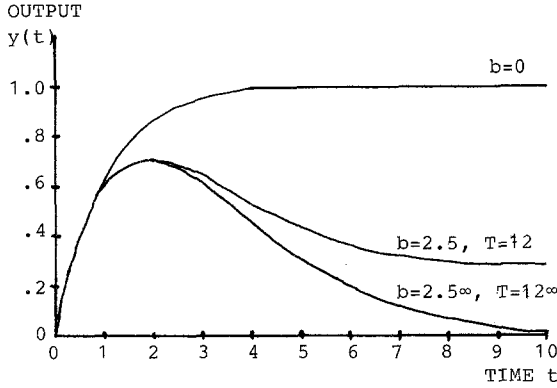


Fig. 1. Step responses of the neuron model for three typical cases;  $b=0, 2.5,$  and  $\infty$  with constant  $\tau(=1)$  and  $b/T(=2.5/12)$

Before analysing the stability of stationary states we describe a basic theorem on the existence, uniqueness and boundedness of the solution of (4).

**Theorem 1.** *A solution of Eq. (4) exists uniquely for any initial state and is bounded for  $t \geq 0$ .*

*Proof.* The existence and the uniqueness of the solution can be easily proved by checking Lipschitz's condition.

To prove the boundedness, solve the second equation of (4) with respect to  $x'_i$ ;

$$x'_i(t) = x'_i(0)e^{-t/T} + \frac{1}{T} e^{-t/T} \int_0^t g(x_i(u))e^{u/T} du. \tag{a}$$

Since  $g(x_i(u))$  is nonnegative,

$$x'_i(t) \geq -|x'_i(0)| \quad (t \geq 0). \tag{b}$$

Solving the first equation in (4) with respect to  $x_i$ , we obtain

$$x_i(t) = x_i(0)e^{-t} + s_i(1 - e^{-t}) - \sum_j a_{ij} e^{-t} \int_0^t g(x_j(u))e^u du - b e^{-t} \int_0^t x'_i(u)e^u du. \tag{c}$$

Applying (b) to (c), we get

$$\begin{aligned} x_i(t) &\leq |x_i(0)| + s_i + b e^{-t} \int_0^t |x'_i(0)|e^u du \\ &= |x_i(0)| + s_i + b|x'_i(0)|(1 - e^{-t}) \\ &\leq |x_i(0)| + s_i + b|x'_i(0)|. \end{aligned} \tag{d}$$

Applying (d) to (a) gives similarly

$$x'_i(t) \leq |x'_i(0)| + |x_i(0)| + s_i + b|x'_i(0)|. \tag{e}$$

Applying (d) and (e) once again to (c), we obtain

$$\begin{aligned} x_i(t) &\geq -|x_i(0)| - \sum_j a_{ij}(|x_j(0)| + s_j + b|x'_j(0)|) \\ &\quad - b(|x'_i(0)| + |x_i(0)| + s_i + b|x'_i(0)|). \end{aligned} \tag{f}$$

From (b), (d), (e), and (f) we can conclude that any solution is bounded for  $t \geq 0$ . Q.E.D.

### 2.2 Stationary Solutions

Let  $y^0(=[y_1^0, \dots, y_n^0]^T)$  be an output in a stationary state, then it must satisfy the following equation

$$y^0 = F[y^0] \triangleq [f_1(y^0), \dots, f_n(y^0)]^T, \tag{5}$$

where

$$f_i(y^0) \triangleq g\left(-\sum_j a_{ij}y_j^0 + s_i - by_i^0\right) \quad (i=1, \dots, n).$$

Conversely, if  $y^0$  satisfies (5), then  $x_i = -\sum_j a_{ij}y_j^0 + s_i - by_i^0, x'_i = y_i^0 (i=1, \dots, n)$  is a stationary solution of (4). As for the existence of stationary states, the following theorem holds.

**Theorem 2.** *Equation (4) has at least one stationary solution.*

*Proof.* Define a bounded, convex region  $D$  in the  $n$ -dimensional Euclidean space  $R^n$  by  $D \triangleq \{0 \leq y_i \leq s_i; i=1, \dots, n\}$ . Since  $0 \leq g\left(-\sum_j a_{ij}y_j^0 + s_i - by_i^0\right) \leq s_i$  for arbitrary  $y_i^0, F$  is a continuous, contractive mapping from  $D$  into  $D$ . According to Brouwer's fixed point theorem there must be a fixed point of  $F$  and it is a stationary solution of (4). Q.E.D.

Let  $S$  be a subset of  $N \triangleq \{1, \dots, n\}$ . It is obvious that  $x = x^0(=[x_1^0, \dots, x_n^0]^T)$  is a stationary solution of (4) if  $x^0$  satisfies the following equalities and inequalities:

$$\left. \begin{aligned} x_i^0 &= \left\{ -\sum_{j \in S} a_{ij}x_j^0 + s_i \right\} / (1+b) > 0 && \text{for } i \in S \\ x_i^0 &= -\sum_{j \in S} a_{ij}x_j^0 + s_i < 0 && \text{for } i \notin S \end{aligned} \right\} \tag{6}$$

(we shall not consider the case where the inequalities become equalities to avoid too delicate discussion).  $S$  implies a set of neurons which are more or less firing in a stationary state. In general there are more than one subset that satisfy (6) and we denote the family of such  $S$  by  $\bar{S}$ . It is not easy to find all solutions of (6), but we shall only use the following simple lemmas which assure the positivity of the  $i^{\text{th}}$  neuron's output  $y_i^0$  in every stationary state.

**Lemma 3.** *If  $s_i > \sum_j a_{ij}s_j$ , then  $x_i^0 > 0$  for every  $S \in \bar{S}$ .*

Here  $a'_{ij} \triangleq a_{ij}/(1+b)$  (this denotation' will be frequently used).

*Proof.* If  $x_i^0 > 0$ , then  $x_i^0 = y_i^0 = x_i^0$ . Therefore  $x_i^0 = -\sum_j a_{ij}y_j^0 + s_i - bx_i^0 \leq s_i - bx_i^0$ , giving  $y_i^0 \leq s_i/(1+b)$ . If  $x_i^0 \leq 0$ , of course,  $y_i^0 \leq s_i/(1+b)$ . Thus  $y_i^0 \leq s_i/(1+b)$  in every case. Hence

$$x_i^0 \geq -\sum_j a'_{ij}s_j + s_i - bx_i^0. \tag{a}$$

We here suppose  $x_i^0 \leq 0$  or  $y_i^0 = 0$ . Then, since  $x_i^0 = y_i^0$ , (a) becomes

$$0 \geq x_i^0 \geq -\sum_j a'_{ij}s_j + s_i. \tag{b}$$

Since it is contradictive to the assumption of the lemma,  $x_i^0$  must be positive. Q.E.D.

A less strict condition for the positivity of  $x_i^0$  can be obtained as follows. Suppose that  $x_i^0 \leq 0$ , and find certain lower bounds of the outputs of the neurons other than  $i$ ;  $x_j^0 \geq \bar{u}_j^i/(1+b)$ . Then we can find certain upper bounds of the outputs;  $x_j^0 \leq \bar{v}_j^i/(1+b)$ . If  $\sum a_{ij}\bar{v}_j^i/(1+b)$  is less than  $s_i$ , there will never exist a stationary solution such that  $x_i^0 \leq 0$ . Therefore, if  $x_i^0 \leq 0$ , then  $\sum a_{ij}\bar{v}_j^i/(1+b) \geq s_i$ . Thus we have

**Lemma 4.** For  $i \in N$ , define  $u_k^i \triangleq s_k - \sum_{l \neq i} a'_{kl}s_l$ ,  $\bar{u}_k^i \triangleq g(u_k^i)$ ,  $v_j^i \triangleq s_j - \sum_{k \neq i} a'_{jk}\bar{u}_k^i$  and  $\bar{v}_j^i \triangleq g(v_j^i)$ ,  $k, j \in N$ . Then if  $s_i > \sum_j a'_{ij}\bar{v}_j^i$ ,  $x_i^0 > 0$  for every  $S \in \bar{S}$ .

*Proof.* Suppose that  $x_i^0 \leq 0$  or  $y_i^0 = 0$ , then inputs to the  $k^{\text{th}}$  neuron are  $s_k$  and  $-a_{kl}y_l^0$  ( $l \in N, l \neq i$ ). Since  $y_l^0 \leq s_l/(1+b)$  (see the proof of Lemma 3), the total input to the  $k^{\text{th}}$  neuron is not less than  $u_k^i \triangleq s_k - \sum_{l \neq i} a'_{kl}s_l$ . If  $u_k^i$  is positive,  $y_k^0 = x_k^0 \geq u_k^i/(1+b)$ . Since  $y_k^0$  is always nonnegative,

$$\begin{aligned} y_k^0 &\geq u_k^i/(1+b) && \text{for } k \text{ such that } u_k^i \geq 0 \\ &\geq 0 && \text{for } k \text{ such that } u_k^i < 0. \end{aligned}$$

That is,  $y_k^0 \geq \bar{u}_k^i/(1+b)$ . Using this result we obtain  $y_j^0 \leq \bar{v}_j^i/(1+b)$  in the same way.

Since we supposed  $x_i^0 \leq 0$ , the total input to the  $i^{\text{th}}$  neuron must be nonpositive, which gives

$$s_i - \sum_j a'_{ij}\bar{v}_j^i \leq 0.$$

However it contradicts the assumption in the lemma. Therefore,  $x_i^0$  must be positive on the assumption. Q.E.D.

Since  $\bar{v}_j^i \leq s_j$ , the condition in Lemma 4 is a less strict condition than that in Lemma 3.

Stability of a stationary solution will be found by investigating the differential equation which is obtained by linearizing (4) in the vicinity of the stationary solution:

$$\left. \begin{aligned} \dot{x}_i + x_i &= - \sum_{j \in S} a_{ij}x_j - bx'_i \\ Tx'_i + x'_i &= x_i \quad (i \in S). \end{aligned} \right\} \quad (7)$$

If the origin of (7) is unstable for every  $S \in \bar{S}$  or (4) has no stable stationary state, then every solution (other than the unstable stationary states) must be oscillatory (not necessarily periodic) due to the boundedness of the solution (Theorem 1).

Without losing generality, we assume that  $S = \{1, \dots, m\}$  ( $m \leq n$ ). Expressing (7) in a matrix form

gives

$$\begin{bmatrix} \dot{x}_S + x_S \\ T\dot{x}'_S + x'_S \end{bmatrix} = \begin{bmatrix} -A_S & -bI \\ I & 0 \end{bmatrix} \begin{bmatrix} x_S \\ x'_S \end{bmatrix}, \quad (8)$$

where

$$x_S = [x_1, \dots, x_m]^T, \quad x'_S = [x'_1, \dots, x'_m]^T,$$

$$A_S = \begin{bmatrix} 0 & a_{1,2} & \dots & -a_{1,m} \\ a_{2,1} & 0 & \dots & \vdots \\ \vdots & \vdots & \ddots & \vdots \\ a_{m,1} & \dots & -a_{m,m-1} & 0 \end{bmatrix}$$

and  $I$  is the  $m^{\text{th}}$  order unit matrix. The characteristic equation of (8) becomes

$$\begin{vmatrix} (\lambda + 1)I + A_S & bI \\ -I & (T\lambda + 1)I \end{vmatrix} = 0. \quad (9)$$

It can be modified to

$$\left. \begin{aligned} |\lambda I + A_S| &= 0 \\ \lambda &= (\lambda + 1) + b/(T\lambda + 1) \\ &\text{(i.e., } T\lambda^2 + (1 + T - T\lambda)\lambda + (1 + b - \lambda) = 0). \end{aligned} \right\} \quad (10)$$

If a root of the equation,  $\lambda$ , has a positive real part, the stationary solution is unstable.

In the sequel we shall only discuss the following three important cases from a practical point of view:

I) lateral inhibition between neighbouring neurons in a linear network;  $a_{i,i-1} = a_1$ ,  $a_{i-1,i} = a_2$  ( $i = 2, \dots, n$ ) and other  $a_{ij}$  are zero.

II) symmetric inhibition;  $a_{ij} = a_{ji}$  ( $i, j = 1, \dots, n$ ).

III) cyclic inhibition in a circular network;  $a_{ij} = a_{i-1,j-1}$  ( $i, j = 2, \dots, n$ ),  $a_{1j} = a_{n,j-1}$  ( $j = 2, \dots, n$ ),  $a_{i1} = a_{i-1,n}$  ( $i = 2, \dots, n$ ).

### 2.3 Case I: Lateral Inhibition in a Linear Network

The most simple mutual inhibition network will be one consisting of a pair of neurons ( $n=2$ ) reciprocally inhibiting each other's excitation. Reiss (1962) investigated the rhythmic behavior of such a network of digital neurons by computer simulation. Matsuoka (1984) gave a mathematical condition in which the present continuous-variable model has no stable stationary solution. He investigated the case of  $a_{12} = a_{21}$ , and a similar result can be derived in the case of  $a_{12} \neq a_{21}$  in the same way:

**Theorem 5.** Equation (4) in the case of  $n=2$  has no stable stationary solution if and only if

$$a'_{12} < s_1/s_2, \quad a'_{21} < s_2/s_1, \quad \text{and} \quad \sqrt{a_{12}a_{21}} > 1 + 1/T.$$

The theorem can be generalized to a tri-diagonal matrix with equal diagonal elements:

$$A = \begin{bmatrix} 0 & a_2 & 0 & \dots & 0 \\ a_1 & 0 & a_2 & \dots & 0 \\ 0 & \dots & \dots & \dots & a_2 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & \dots & 0 & a_1 & 0 \end{bmatrix}. \quad (11)$$

This matrix can be interpreted as a lateral inhibition between neighbouring neurons in a network consisting of linearly arrayed neurons.

**Theorem 6.** *If there exist  $i_1$  and  $i_2$  ( $\in N$ ,  $i_1 < i_2$ ) that satisfy the following inequalities*

$$s_i > (a_1 s_{i-1} + a_2 s_{i+1}) / (1+b) \quad (i = i_1, \dots, i_2) \quad (12)$$

and

$$2\sqrt{a_1 a_2} \cos(\pi/(M+1)) > 1 + 1/T \quad \text{or} \quad 1+b \\ (M \triangleq i_2 - i_1) \quad (13)$$

then Eq. (4) has no stable stationary solution. Here  $s_0$  and  $s_{n+1}$  are regarded to be zero when  $i_1 = 1$  or  $i_2 = n$ .

*Proof.* From (12) and Lemma 3, there exist  $k_1$  ( $\leq i_1$ ) and  $k_2$  ( $\geq i_2$ ) for each  $S \in \bar{S}$  such that  $x_{k_1-1}^0 < 0$ ,  $x_{k_2+1}^0 < 0$ , and  $x_i^0 > 0$  ( $k_1 \leq i \leq k_2$ ); that is, the  $k_1$ -th to  $k_2$ -th neurons are not influenced at all by the other neurons' activities in the neighbourhood of the stationary state. Therefore, if the linearized differential equation (7) for the small set of neurons ( $k_1 \leq i \leq k_2$ ) is unstable for each  $S \in \bar{S}$ , all the stationary states of the original system will be unstable. The characteristic equation of the linear differential equation (10) becomes (Appendix A)

$$\prod_{i=1}^K \{A - 2\sqrt{a_1 a_2} \cos(\pi i / (K+1))\} = 0 \quad (K \triangleq k_2 - k_1)$$

i.e.,

$$T\lambda^2 + \{1 + T - 2\sqrt{a_1 a_2} T \cos(\pi i / (K+1))\} \lambda \\ + \{1 + b - 2\sqrt{a_1 a_2} \cos(\pi i / (K+1))\} = 0 \\ (i = 1, \dots, K). \quad (a)$$

Meanwhile, from  $K \geq M$  and (13) we have

$$2\sqrt{a_1 a_2} \cos(\pi/(K+1)) > 1 + 1/T \quad \text{or} \quad 1+b.$$

Thus, the coefficient of the second or third term of (a) for  $i = 1$  becomes negative, which implies that a root of (a) has positive real part. Q.E.D.

Roughly speaking, oscillation will occur when the following conditions are satisfied:

(i) A part of neurons receive equal degrees of inputs; one can see that (12), i.e.  $1 > (a_1 s_{i-1} / s_i$

$+ a_2 s_{i+1} / s_i) / (1+b)$ , will not be satisfied if  $s_{i-1} / s_i$  or  $s_{i+1} / s_i$  is very large for all  $i = 2, \dots, N-1$ .

(ii) The inhibitory synaptic weights,  $a_1$  and  $a_2$ , are around one; if they are too great or too small, (12) or (13) will not suffice, respectively.

(iii) The neurons have a strong adaptation effect, or large  $b$  and  $T$ .

These three conditions will also apply to the other classes of networks.

Almost all vision systems (the retina for example) are basically two-dimensional networks. However, they can often be described by one-dimensional models without losing their essential functions. Oscillations in the optic nerve of the horseshoe crab (Barlow and Fraioli, 1978) and in the lateral geniculate nucleus of the cat (Wall et al., 1979) might be explained by the present model.

#### 2.4 Case II: Symmetric Mutual Inhibition

We now assume that the matrix  $A$  is symmetric;  $a_{ij} = a_{ji}$  ( $i, j \in N$ ). Then the following theorem holds.

**Theorem 7.** *Assume that for some  $i$  and  $k$  ( $i \neq k$ )*

$$(i) \quad s_i - \sum_j a'_{ij} s_j > 0 \quad \text{and} \quad s_k - \sum_j a'_{kj} s_j > 0$$

$$(ii) \quad a_{ik} > 1 + 1/T \quad \text{or} \quad a_{ik} > 1 + b,$$

then Eq. (4) does not have any stable stationary solution.

*Proof.* Since we have assumed that  $A$  is a symmetric matrix,  $A_s$  is also symmetric for every  $S \in \bar{S}$ . So,  $\lambda$  that satisfies (10) is a real number. Therefore, a necessary and sufficient condition for real part of some  $\lambda$  to be positive is

$$1 + 1/T - A < 0 \quad \text{or} \quad 1 + b - A < 0.$$

Since (10) can be modified to

$$|-A'I + \{A_s + (1 + 1/T)I\}| = 0$$

$$A' = 1 + 1/T - A$$

or

$$|-A''I + \{A_s + (1 + b)I\}| = 0,$$

$$A'' = 1 + b - A,$$

the condition for a root of Eq. (9) to have a positive real part is that matrices  $A_s + (1 + 1/T)I$  or  $A_s + (1 + b)I$  has at least one negative eigenvalue.

From assumption (i) and Lemma 3 every  $S \in \bar{S}$  includes  $i$  and  $k$ , and according to assumption (ii)  $A_s + (1 + 1/T)I$  or  $A_s + (1 + b)I$  has a negative principal minor of the following form:

$$\begin{vmatrix} 1 + 1/T & a_{ik} \\ a_{ki} & 1 + 1/T \end{vmatrix} \quad \text{or} \quad \begin{vmatrix} 1 + b & a_{ik} \\ a_{ki} & 1 + b \end{vmatrix}.$$

Thus  $A + (1 + 1/T)I$  or  $A + (1 + b)I$  must have a negative eigenvalue (a condition that all eigenvalues of a matrix have nonnegative real parts is that every principal minor of  $A$  is nonnegative). Q.E.D.

This theorem suggests that, also in symmetric networks, if at least one pair of neurons satisfy three conditions in the last section, (i), (ii), and (iii), some oscillation will appear.

When the weights of the inhibitions between the neurons are all equal ( $a_{ij} = a$  for every  $i$  and  $j$ ), we can get a stronger result than Theorem 7. Since the network has a completely symmetric structure, we can suppose that  $s_1 \geq s_2 \geq \dots \geq s_n$  without losing generality. Then,

**Theorem 8.** *If and only if  $a/(1 + b) \leq s_2/s_1$  and  $a > 1 + 1/T$ , Eq. (4) has no stable stationary solution.*

*Proof (Necessity).* It is obvious that if  $as_1/(1 + b) > s_2$  (accordingly,  $\geq s_3 \geq s_4 \dots$ ), there exists a stable stationary solution;  $x_1^0 = s_1/(1 + b) > 0$  and  $x_i^0 < s_i - as_1/(1 + b) < 0$  ( $i = 2, \dots, n$ ). Therefore,  $a/(1 + b) \leq s_2/s_1$  must hold for the absence of stable stationary solutions. Then the number of elements of  $S$ , denoted by  $m$ , is greater than one and the characteristic Eq. (10) becomes (Appendix A):

$$\{T\lambda^2 + (1 + T - Ta)\lambda + (1 + b - a)\}^{m-1} \{(T\lambda + 1)(\lambda + 1) + b + (m - 1)(T\lambda + 1)a\} = 0 \quad (m \geq 2). \quad (a)$$

The condition for a root of the equation to have positive real part is  $a > 1 + 1/T$  [note that  $a \leq 1 + b$  from  $a/(1 + b) \leq s_2/s_1 \leq 1$ ].

(Sufficiency) If  $a/(1 + b) \leq s_2/s_1$ , then every  $S(\in \bar{S})$  includes more than two elements and the corresponding characteristic equation becomes (a). From  $a > 1 + 1/T$ , a root of (a) must have positive real part. Q.E.D.

2.5 Case III: Cyclic Inhibition in a Circular Network

Let us consider the matrix that has a cyclic structure as

$$A = \begin{bmatrix} 0 & a_1 & \dots & a_{n-1} \\ a_{n-1} & 0 & & a_{n-2} \\ \vdots & \vdots & \ddots & \vdots \\ a_2 & & & a_1 \\ a_1 & \dots & a_{n-1} & 0 \end{bmatrix}. \quad (14)$$

This type of mutual inhibition were investigated by many authors with various neuron models (Kling and Székely, 1968; Suzuki et al., 1971; Morishita and Yajima, 1972; Nagashino et al., 1981). As for the present neuron model, the following theorem holds:

**Theorem 9.** *If*

- (i)  $s_i - \sum_j a'_{ij}s_j > 0$  for all  $i \in N$ , and

- (ii)  $a_1 \cos(2\pi k/n) + \dots + a_{n-1} \cos(2\pi k(n-1)/n) < -(1 + 1/T)$  for some  $k (= 1, \dots, n-1)$ , then Eq. (4) has no stable stationary solution.

*Proof.* From Lemma 3 the only element of  $\bar{S}$  is  $N$ . The characteristic equation (10) is (Appendix A)

$$\prod_{k=0}^{n-1} \{(\lambda + 1) + b/(T\lambda + 1) + a_1\omega^k + a_2\omega^{2k} + \dots + a_{n-1}\omega^{(n-1)k}\} = 0, \quad (15)$$

where  $\omega$  is a primitive root of  $\omega^n = 1$ . Let

$$p_k \triangleq a_1 \cos(2\pi k/n) + \dots + a_{n-1} \cos(2\pi k(n-1)/n)$$

$$q_k \triangleq a_1 \sin(2\pi k/n) + \dots + a_{n-1} \sin(2\pi k(n-1)/n)$$

$$\lambda = iz \quad (i \text{ is an imaginary unit})$$

then (15) becomes

$$\prod_{k=0}^{n-1} \{\phi_0(z) + i\phi_1(z)\} = 0,$$

where

$$\phi_0(z) = Tz^2 + Tq_kz - (1 + b + p_k),$$

$$\phi_1(z) = -(1 + T + Tp_k)z - q_k.$$

Constructing Sturm sequence from  $\phi_0(z)$  and  $\phi_1(z)$  (see Appendix B), we obtain a series of algebraic functions:

$$\phi_0(z), \quad \phi_1(z),$$

$$\phi_2(z) = 1 + b + p_k - T^2q_k^2(1 + p_k)/(1 + T + Tp_k)^2.$$

Thus

$$\phi_0(\infty) = \phi_0(-\infty) = \infty,$$

$$\phi_1(\infty) = -(1 + T + Tp_k)\infty,$$

$$\phi_1(-\infty) = (1 + T + Tp_k)\infty,$$

$$\phi_2(\infty) = \phi_2(-\infty) = 1 + b + p_k$$

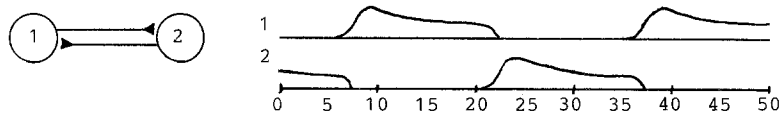
$$- T^2q_k^2(1 + p_k)/(1 + T + Tp_k)^2.$$

If  $1 + T + Tp_k < 0$  (the second assumption in the theorem), then  $\phi_1(\infty) = \infty$  and  $\phi_1(-\infty) = -\infty$ . Thus  $V(\infty) - V(-\infty)$ , defined in Appendix B, is less than 2 regardless of the sign of  $\phi_2(\infty) = \phi_2(-\infty)$ , which implies that a root of (15) has positive real part. Q.E.D.

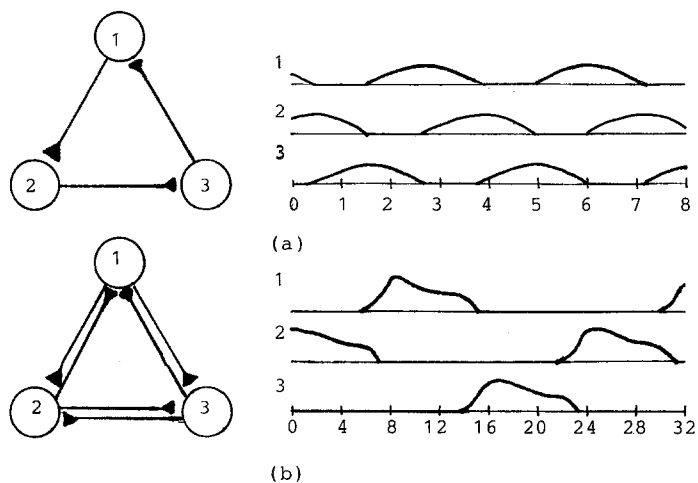
2.6 Examples

This section presents some examples of oscillations generated by cyclic inhibition networks consisting of two to five neurons.

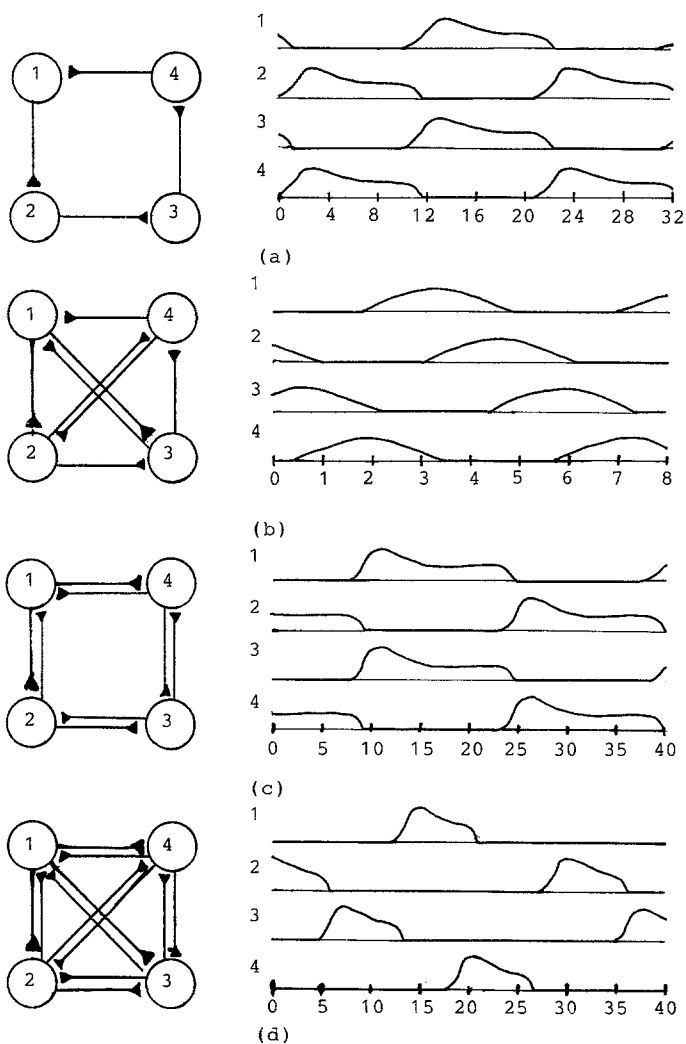
All neurons of a network receive the same input ( $s_i = 1, i \in N$ ). Parameters  $T$  and  $b$  are given the values that satisfy (3);  $T = 12$  and  $b = 2.5$ . Parameters  $a_i$  are all equal for every inhibition if it works from a neuron to another neuron and are zero if not. They are determined such that they satisfy Theorems 8 or 9 (the parameters  $a_i$  in Fig. 5b does not satisfy the first



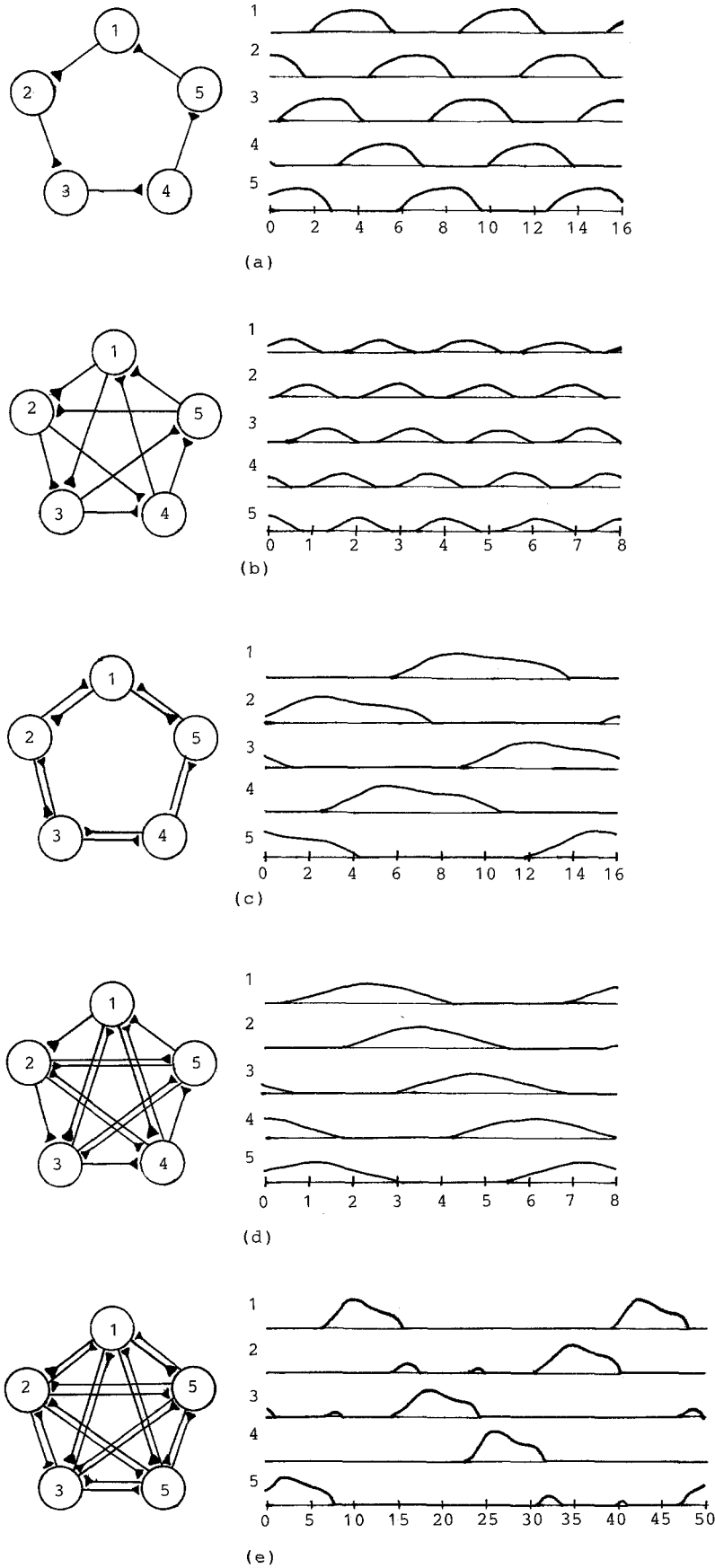
**Fig. 2.** A neuron ring consisting of two neurons and its rhythmic activity. The neurons receive the same magnitude of excitatory stimuli from the outside of the network, and inhibitory stimuli from the inside neurons.  $a_1 = 2.5$



**Fig. 3a and b.** Neuron rings consisting of three neurons and their rhythmic activities. The neurons receive the same magnitude of excitatory stimuli from the outside of the network, and inhibitory stimuli from the inside neurons. **a**  $a_1 = 2.5$  and  $a_2 = 0$ ; **b**  $a_1 = a_2 = 2.5$



**Fig. 4a-d.** Neuron rings consisting of four neurons and their rhythmic activities. The neurons receive the same magnitude of excitatory stimuli from the outside of the network, and inhibitory stimuli from the inside neurons. **a**  $a_1 = 2.5$ ,  $a_2 = a_3 = 0$ ; **b**  $a_1 = a_2 = 1.5$  and  $a_3 = 0$ ; **c**  $a_1 = a_3 = 1.5$  and  $a_2 = 0$ ; **d**  $a_1 = a_2 = a_3 = 2.5$



**Fig. 5a-e.** Neuron rings consisting of five neurons and their rhythmic activities. The neurons receive the same magnitude of excitatory stimuli from the outside of the network, and inhibitory stimuli from the inside neurons. **a**  $a_1=2.5$  and  $a_2=a_3=a_4=0$ ; **b**  $a_1=a_2=2.27$ ,  $a_3=a_4=0$ ; **c**  $a_1=a_4=1.5$  and  $a_2=a_3=0$ ; **d**  $a_1=a_2=a_3=1$  and  $a_4=0$ ; **e**  $a_1=a_2=a_3=a_4=2.5$



condition of Theorem 9 or Lemma 3, but it satisfies Lemma 4).

The results by computer simulation (Runge-Kutta-Gill method) are presented in Figs. 2–5. They all exhibit oscillation and most of them are periodic. The oscillation of Fig. 2 could be considered as a (figurative) model for central activities in respiration, heart beat, bipedal locomotion, flapping of bird wings, etc. Figure 4b and d might suggest locomotion of quadrupeds. (Figure 4a and c are essentially the same as Fig. 2.) Figure 5 could explain the mechanism of the movements of starfish. Only the case of Fig. 5e does not show periodic oscillation, but it is not clear whether it is a periodic oscillation with a very long period or is really a nonperiodic oscillation.

It should be noted that Kling and Székely investigated networks of the same structures but their models did not produce rhythms in the case of Fig. 2, Fig. 3b, Fig. 4a, c, d, and Fig. 5c and e. This might correspond to the fact that if there is not the adaptation effect ( $b=0$ ), any value of  $a_i$  does not satisfy Theorem 8 nor 9 in these cases.

Indeed, we can prove that, if  $b=0$  and  $s_i=s$  for all  $i$ , the following cases give at least one stable stationary solution for any value of  $a_i$ :

(i)  $a_1=a_2=\dots=a_{n-1}=a$  (Fig. 2, Fig. 3b, Fig. 4d, Fig. 5e);

(ii)  $n$  is an even number and  $a_2=a_3=\dots=a_{n-1}=0$  (Fig. 4a);

(iii)  $n$  is an even number and  $a_1=a_{n-1}=a$  and  $a_2=\dots=a_{n-2}=0$  (Fig. 4c);

(iv)  $n=5$ ,  $a_1=a_4=a$ , and  $a_2=a_3=0$  (Fig. 5c).

It is evident from Theorem 8 that the first case (i) has a stable stationary solution for any  $a$ .

In the second case, if  $a_1 < 1$ , then a stationary solution  $x_i^0 = s/(1+a_1)$  ( $i=1, \dots, n$ ) is stable because its characteristic equation  $\prod_{k=0}^{n-1} (\lambda + 1 + a_1 \omega^k) = 0$  [see (15)] does not have a root with positive real part. If  $a_1 \geq 1$ , then  $x_1^0 = x_3^0 = \dots = x_{n-1}^0 = s$  and  $x_2^0 = x_4^0 = \dots = x_n^0 = 1 - a_1 s \leq 0$  is obviously a stable stationary solution. Therefore the case (ii) also has a stable stationary solution for any  $a_1$ .

In the third case, if  $a < 1/2$ , then a stationary solution  $x_i^0 = s/(1+2a)$  ( $i=1, \dots, n$ ) is stable, because its characteristic equation,  $\prod_{k=0}^{n-1} (\lambda + 1 + 2a \cos(2\pi k/n)) = 0$ , does not have a root with positive real part. If  $a \geq 1/2$  there exists a stable stationary solution  $x_1^0 = x_3^0 = \dots = x_{n-1}^0 = s$ ,  $a_2^0 = x_4^0 = \dots = x_n^0 = (1-2a)s \leq 0$ .

In the last case, if  $a < 1/(2 \cos(\pi/5))$ , then a stationary solution  $x_i^0 = s/(1+2a)$  ( $i=1, \dots, 5$ ) is stable, because the characteristic equation,  $\prod_{k=0}^4 (\lambda + 1$

$+ 2a \cos(2\pi k/5)) = 0$ , does not have a root with positive real part. If  $a \geq 1/(2 \cos(\pi/5))$ ,  $x_1^0 = s$ ,  $x_3^0 = x_4^0 = s/(1+a) > 0$ ,  $x_2^0 = x_5^0 = (1/(1+a) - a)s < 0$  is a stable stationary solution.

### 3 Concluding Remarks

From Theorems 5 to 9 we can in general conclude that the mutual inhibition network generates and sustains oscillation when it has the following properties:

(i) part of (or the whole) neurons receive the same degrees of inputs;

(ii) those neurons mutually inhibit their excitations with a medium strength;

(iii) the neurons have a strong adaptation effect.

The most important result is that the adaptation plays a very important role on the generation of the oscillation. If there were not the adaptation, oscillation could only occur in networks of special structures; as for the examples in 2.6 only half of those oscillation would be “stable” in the sense that the state of the network does not fall into some stable stationary state for any disturbance. On the other hand, if a network has a strong adaptation, it can easily generate stable oscillation.

In this paper we have only derived some conditions in which there is no stable stationary solution, but some important and difficult problems remain unsolved; for example,

(i) In what condition does a periodic or non-periodic oscillation appear?

(ii) Are there more than one patterns of stable periodic oscillation for a network?

### Appendix A

Some formula on determinants

$$\begin{vmatrix} p & r & 0 & \dots & 0 \\ & q & & & | \\ 0 & & & & | \\ | & & & & | \\ | & & & & | \\ 0 & \dots & 0 & q & p \end{vmatrix} = \prod_{i=1}^n \{p - 2\sqrt{qr} \cos(\pi i/(n+1))\},$$

$$\begin{vmatrix} p & q & \dots & q \\ q & p & & | \\ | & & & | \\ | & & & | \\ | & & & | \\ q & \dots & q & p \end{vmatrix} = (p-q)^{n-1} \{p + (n-1)q\},$$

$$\begin{vmatrix} a_0 & a_1 & \dots & a_{n-1} \\ a_{n-1} & a_0 & \dots & a_{n-2} \\ | & & & | \\ | & & & | \\ a_1 & a_2 & \dots & a_0 \end{vmatrix} = \prod_{k=0}^{n-1} \{a_0 + a_1 \omega^k + \dots + a_{n-1} \omega^{(n-1)k}\},$$

where  $n$  is the order of the determinants and  $\omega$  is a primitive root of  $\omega^n = 1$ .

## Appendix B

A condition for a root of an algebraic equation with complex coefficients to have positive real part (Marden, 1966).

Let  $f(\lambda)$  be an algebraic function of degree  $m$  and divide  $f(iz)$  ( $i$  is the imaginary unit) to two parts according to real and imaginary parts of the coefficients:

$$f(iz) = \phi_0(z) + i\phi_1(z).$$

Applying the Euclidean algorithm to  $\phi_0(z)$  and  $\phi_1(z)$ ,

$$\phi_{h-1}(z) = \psi_h(z)\phi_h(z) - \phi_{h+1},$$

we obtain a series of algebraic functions (Strum sequence)

$$\phi_0(z), \phi_1(z), \dots, \phi_k(z).$$

Further we define  $V(x)$  as the total number of neighbouring pairs of  $\phi_{h-1}(x)$  and  $\phi_h(x)$  whose signs are different to each other's, where  $x$  is a real number. Then, if

$$V(\infty) - V(-\infty) < m,$$

at least one root of  $f(\lambda)$  exists on the right half of the complex plane.

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