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Firing Modes in Reciprocal Inhibition Neural Networks and Their Analysis

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1. Introduction

Neural networks of reciprocal inhibition structure are seen in various parts of sensory(1) and motor systems(2),(3), and play an important role in information processing and motor pattern generation. Although those networks have been analyzed from various aspects(4)-(10), few studies have been made on the pulsewise characteristics of the networks consisting of a large number of cells.

Tamura et al.(11) studied the reciprocal inhibition neural network of a linear structure having excitatory periodic input with pulse transmission delay and showed that the network generates rhythmic activity, the period of which is much longer than that of the input pulse train. Such an activity can be a most feasible model of behavioral rhythm generation.

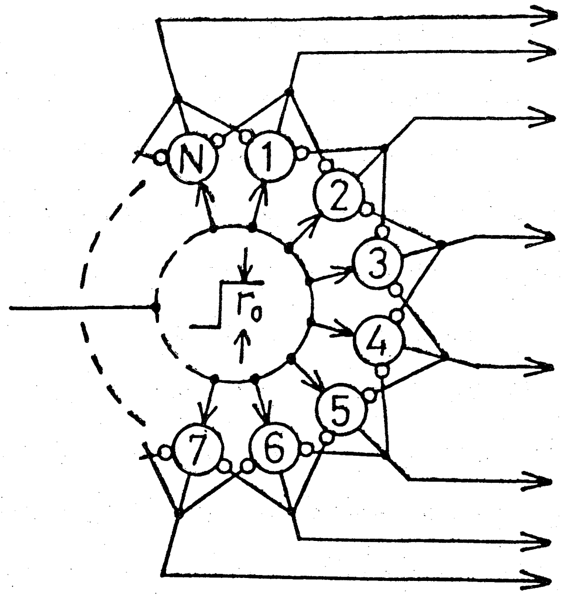
A number of behavioral rhythm generators, however, are shown to be under control of aperiodic level signal instead of periodic input(12)-(14). Yokoyama(15) showed thereafter by computer simulation that the network of a linear structure without periodic input also generates long period rhythm, and suggested that this rhythmic activity is not particular to the input but is specific to the network structure[16].

We have improved the computer simulation and made further analysis of reciprocal inhibition neural networks of a linear and a ring structures with dc input. It has been shown from this study that the long period mode is one of the most dominant firing modes of the reciprocal inhibition networks, and that the region in which the long period mode exists is quite large. Moreover, we ascertained there exists the super long period mode, the period of which is longer than that of the long period mode. The regions of parameters in which the long and the super long period modes occur as well as those of other firing modes were determined analytically.

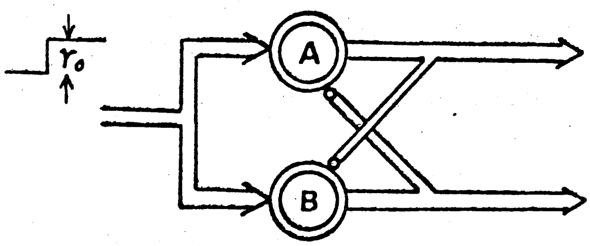
In this paper, the discussion is limited to the reciprocal inhibition network of a ring structure, and we first show three fundamental firing modes which are seen in this network. Further, we derive more complex firing modes, which can be understood as composites of the fundamental firing modes, and typical examples of the firing patterns of the modes are shown by computer simulation. The regions of parameters which satisfy the conditions of the existence of each firing mode are presented by theoretical study.

2. Reciprocal inhibition network

The neural network in the present study has a ring structure of a linear array of N neurons, shown in Fig.1. Every neuron receives an external excitatory input r_o and inhibitory from the adjacent neurons of both sides. This structure can be transformed into two neural nuclei A and B, each of which inhibits the other



(a) a ring structure



(b) a network of neural nuclei

Fig.1 A reciprocal inhibition neural network.

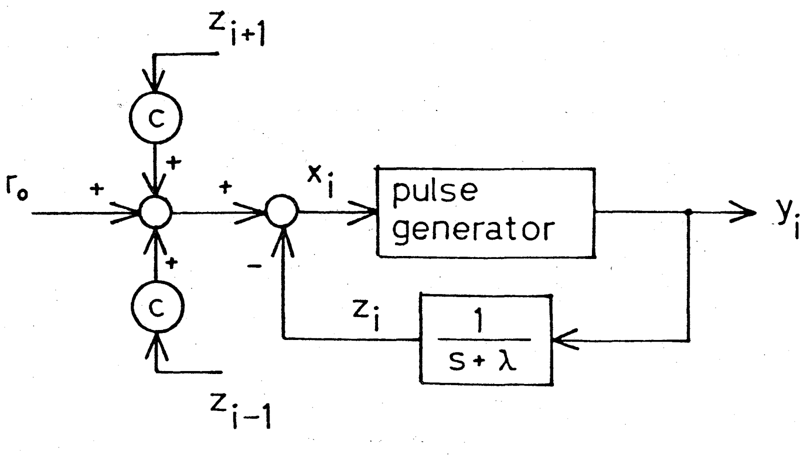


Fig.2 Neuron model.

reciprocally by a neural tract.

Firing characteristics of a neuron are shown by the model in Fig.2. When the cell is in the resting state, the internal activity x_i of i-th cell is negative and the output y_i of i-th cell is zero. At moment x_i changes its sign from negative to positive, a unit impulse is generated in y_i. At the same time the relative threshold z_i of cell i increases by one and hereafter decreases with a decaying constant λ. The synaptic coefficient c is a negative constant, and the synaptic delay is neglected. The decaying constants of the postsynaptic potential and relative threshold are taken equal. Thus synaptic input from cell i±1 to cell i is represented as $cz_{i\pm1}$,respectively.

Firing interval T_o of the single neuron to a constant positive input r_o is determined by the equation

$$T_o = \ln[(1+r_o)/r_o]/\lambda. \qquad (1)$$

3. Characteristics of the network with two neurons

The network with two neurons is the simplest of the networks of a ring structure. It is essential to make the properties of this network clear in order to analyze the characteristics of multineuron networks of a ring structure. In this chapter, we describe the existence region and the stability of the firing modes which occur in the network with two neurons. One of the cells is denoted by cell 1, the other cell 2.

Following three firing modes occur in this network.

(a) Synchronous mode. Firings of two cells are synchronized in phase at a constant interval, which is denoted by T_s. It is assumed that time t=0 is one of the firing instants. Since $x_i(0)=0$, the firing condition is expressed by

$$r_o - z_1(0) + cz_2(0) = 0. \tag{2}$$

Therefore, the relation between input and structure parameters is given by

$$r_o = e^{-\lambda T_s}(1-c)/(1-e^{-\lambda T_s}). \tag{3}$$

From Eq.(3), it can be deduced that the synchronous mode exists in the region; $r_o > 0$ and $c < 0$.

(b) Alternating mode. Each neuron fires alternatingly one after another. Let T_a denote the firing interval of cells, and it is assumed that time t=0 is one of the firing instants of cell 1 and time $t=\theta T_a$ of cell 2 $(0<\theta<1)$. Since $x_1(0)=0$ and $x_2(\theta T_a)=0$, equations,

$$r_o - z_o e^{-\lambda T_a} + cz_o e^{-\lambda T_a(1-\theta)} = 0 \tag{4}$$

and

$$r_o - z_o e^{-\lambda T_a} + cz_o e^{-\lambda T_a \theta} = 0 \tag{5}$$

are obtained, where

$$z_o = 1/(1-e^{-\lambda T_a}). \tag{6}$$

From Eqs.(4) and (5), it follows that

$$\theta = 1/2, \tag{7}$$

which means that two cells fire with a phase difference of half the firing interval. The relation between input and structure parameters is expressed by

$$r_o = z_o e^{-\lambda T_a}(1-ce^{\lambda T_a/2}). \tag{8}$$

In general, in order that a particular firing mode exists, in addition to the firing conditions, it is necessary that cells do not fire except at specified firing instants. We call it exclusion condition of firing. In case of the alternating mode, the following exclusion conditions of firing are necessary;

$$x_1(\theta T_a) < 0 \text{ and } x_2(0) < 0.$$

These conditions are equivalent and rewritten as

$$(1+c)(1-e^{\lambda T_a/2}) < 0. \quad (9)$$

From Eq.(9), the existence region of the alternating mode is expressed by

$$-1 < c < 0 \quad (10)$$

(c) Bistable mode. Only one of two cells fires at a constant interval while the other remains quiescent. The bistable mode is subdivided into c_1 and c_2, depending on which one of two fires. Since the active cell receives no inhibitory input, its firing interval is equal to T_o given by Eq.(1). The existence region of the bistable mode is expressed by

$$c < -1, \quad (11)$$

from the exclusion condition of firing of the quiescent cell.

Stability of these firing modes is examined by local stability analysis[(17)]. The synchronous mode is unstable in the case $c < 0$. The alternating mode is stable in the case $-1 < c < 0$. The bistable mode is stable in the case $c < -1$. Detailed discussion of stability is omitted here. Since the synchronous mode is unstable in the reciprocal inhibition network with two neurons, any firing mode in which adjacent neurons fire synchronously in phase is also unstable in multi-neuron networks.

Comparing above results with the firing modes of the network with two neurons which receives pulse input[11], essential difference in the firing characteristics of the networks with and without pulse input is clear.

4. Firing modes in multi-neuron networks of a ring structure

From the analysis of the network with two neurons, it is suggested that even in multi-neuron networks of a ring structure, a local firing pattern in a short interval of time is either the alternating or the bistable mode, and the total firing mode of the network can be regarded as a composite of various local firing modes. By means of computer simulation, in addition to such modes, various rhythmic activities were obtained.

In computer simulation, determination of firing instants should be made with a high accuracy in order not to lose the characteristics of the neural network as a nonsynchronous pulse system.

The determination was made as follows. At first, based on the input and internal states at the current time, the queue of firings of all the cells are formed with an accuracy of 0.1μs. Then, the first cell of the queue is allowed to fire. Successively,under consideration of change of the internal states due to that firing the queue of firings at the instant imediately after that firing is reformed. This procedure is repeated.

In this chapter, examples of firing modes in multi-neuron networks are illustrated and some features of them are described. In following figures, the short horizontal line represents the firing instant of an odd numbered cell, and the longer vertical line, an even numbered cell. Parameters are chosen as

$$r_o = 0.1,\ \lambda = 0.25\ (/\mathrm{ms}),$$

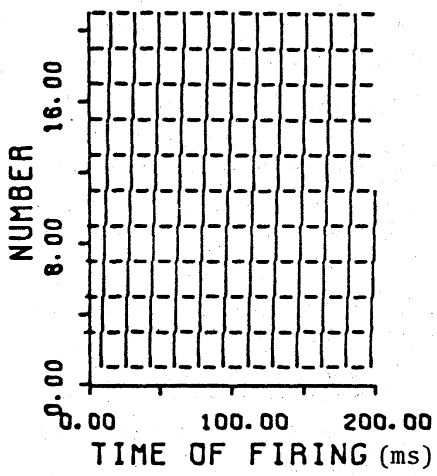
so that the firing interval of a cell without mutual inhibitory interactions (c=0) is approximately 10 ms.

Stationary firing modes in the multi-neuron array are classified as follows.

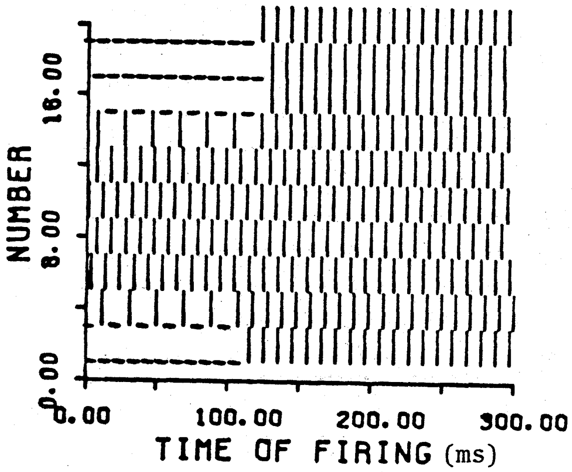
(a) Uniform modes. All neurons fire uniformly in the alternating mode or in the bistable mode. An example of the alternating mode is shown in Fig.3(a). In the example of Fig.3(b), after transient firings are seen at the beginning, firings finally settle in the bistable mode. The bistable mode exists only in the case number of cells is even. Whether odd or even numbered cells are active depends upon the initial values of relative threshold z_i (i=1,2, ..., N).

(b) Compound modes. The firing mode of each neuron is different in location but invariant with time. In the case that the overall firing mode is a composite of the bistable modes, it is called the multi-stable mode. In the case that the overall firing mode is a composite of the alternating mode and the bistable mode, it is called the mixed mode. There are many different firing patterns in compound modes depending on the local combination of the alternating and/or the bistable modes c_1 and/or c_2. Examples of the compound modes are shown in Fig.3(c) and (d).

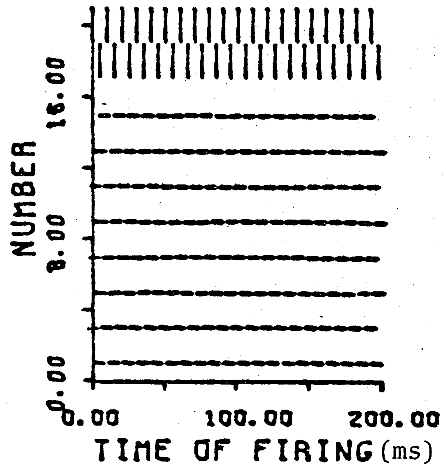
(c) Rhythmic modes. The firing mode differs in location and gradually changes its location with time. If the firing mode of a pair of neighboring neurons changes periodically between two bistable



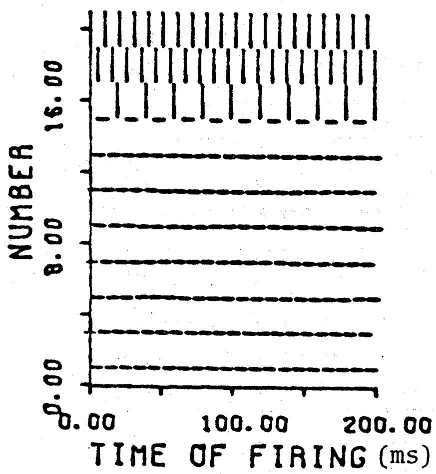
(a) Alternating mode, c= -0.3, N= 21.



(b) Bistable mode, c= -0.85, N= 20.



(c) Multi-stable mode, c= -1.05, N= 21.

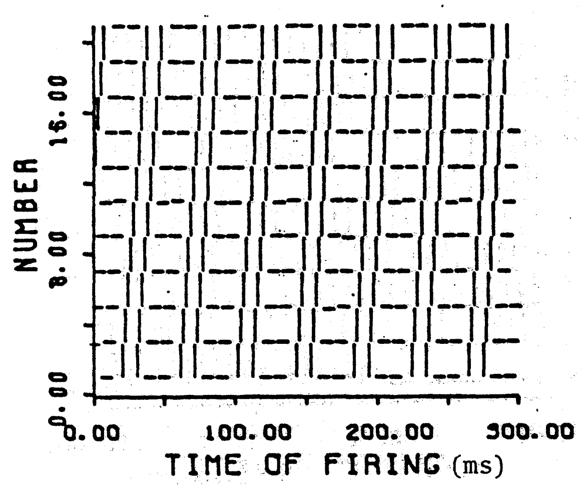


(d) Mixed mode, c= -0.85, N= 21.

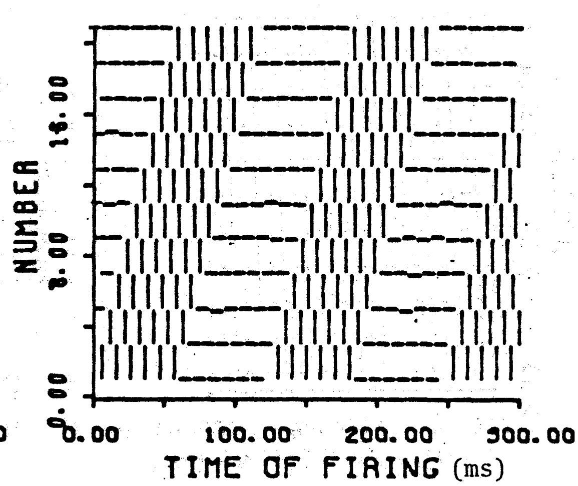
Fig.3 Typical firing modes in a reciprocal inhibition network of a ring structure.

modes ($c_1 \rightleftarrows c_2$), it is called the long period mode (Figs.4 and 5). If a neighboring pair changes its mode from one bistable mode (c_1) to the alternating mode and then to the other bistable mode (c_2), the overall firing mode is called the super long period mode (Fig.5).

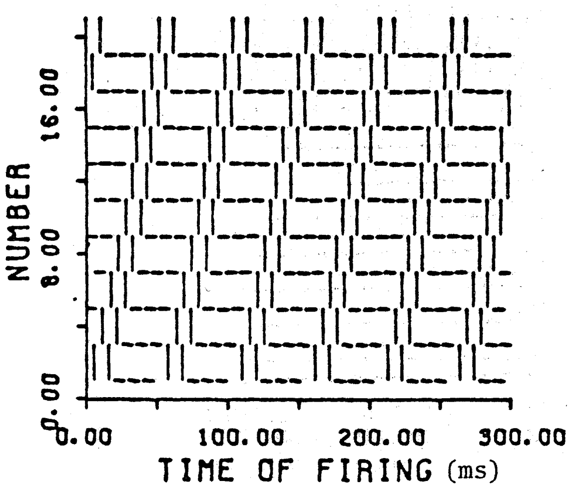
In the long period mode, each cell has the active and the quiescent phases. In the active phase, several firings are seen at



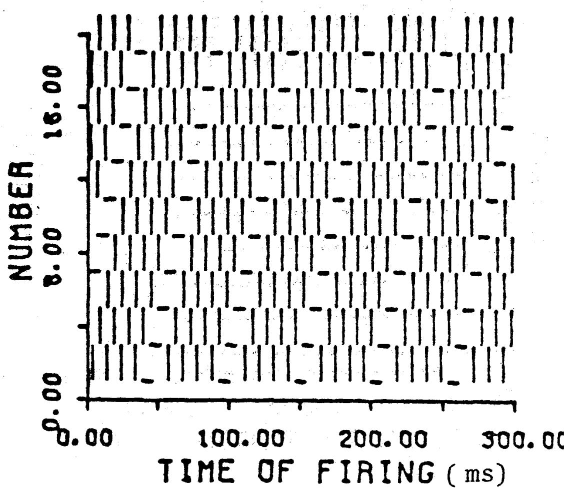
(a) c= -0.5, N= 21.



(b) c= -0.5, N= 21.



(c) c= -0.5, N=20.



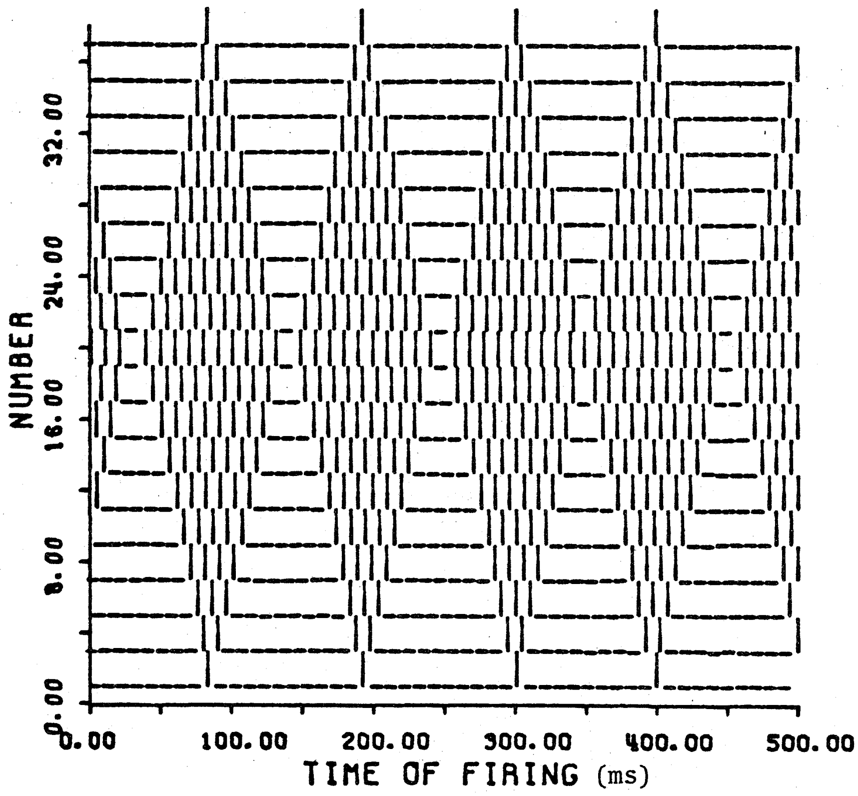
(d) c= -0.5, N=20.

Fig.4 Long period mode.

the constant interval, while the firings are inhibited in the quiescent phase. The long period mode is subdivided into two modes.

In one mode, the phase transition from quiescent to active phase and its inverse proceeds successively in one direction from one cell to the cell next to the nearest neighbor by a constant phase transition delay time (Fig.4). In the other mode, the phase transition

(a)



(b)

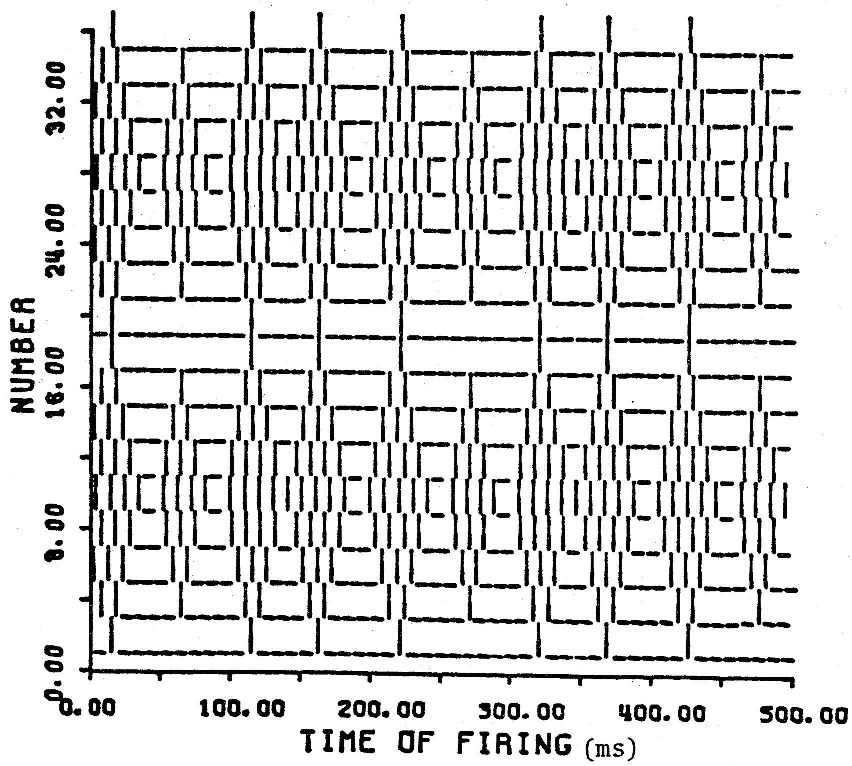
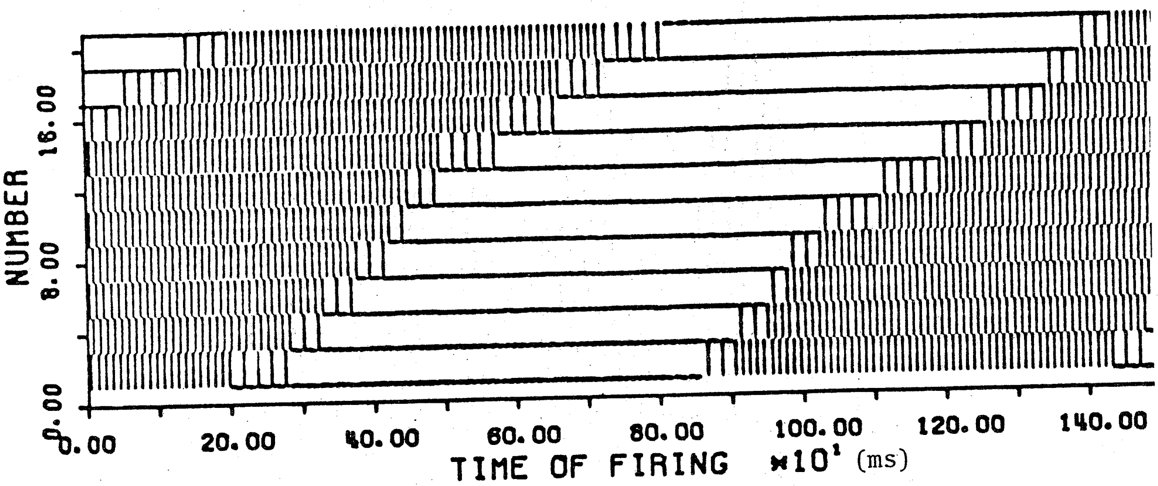
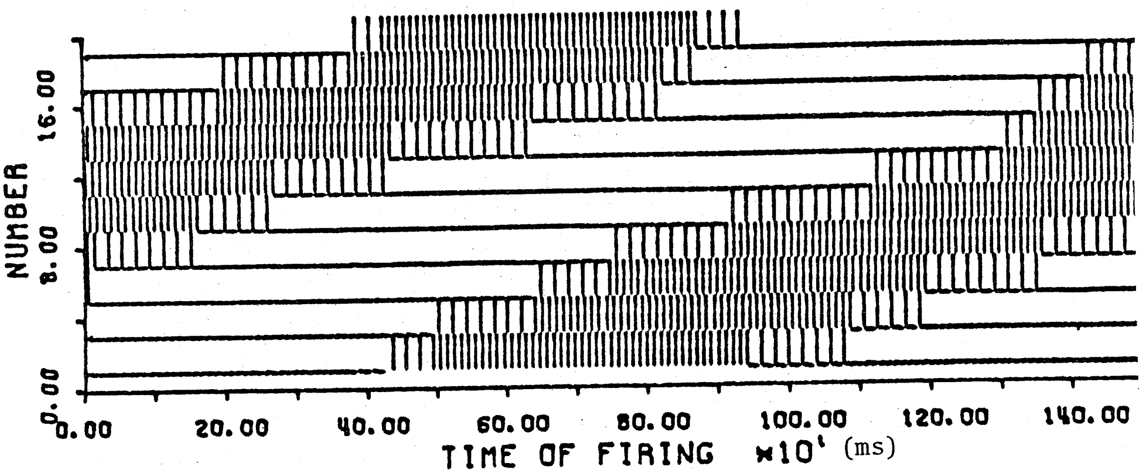


Fig.5 Long period mode, (a) c= -0.45, N=38, (b) c= -0.45, N=36.



(a) c= -0.85, N=21.



(b) c= -0.9, N=20.

Fig.6 Super long period mode.

proceeds in both directions (Fig.5). The latter occurs in the case that the number of cells is even.

Although there is certain difference in existence of firing modes depending on the odd or even of the number of cells N, these modes exist to every N however large it may be.

5. Analysis of multi-neuron networks

The existence regions of the firing modes in multi-neuron networks of a ring structure can be obtained in the following procedure. We define the time variable component Σ_i of internal activity x_i by

$$\Sigma_i(t) = r_o - x_i(t).$$

$\Sigma_i(t)$ are also expressed by

$$\Sigma_i(t) = z_i(t) - c[z_{i-1}(t) + z_{i+1}(t)],$$
$$(i=1,2,\ldots\ldots,N;\ i\pm1=\mathrm{mod}\ N)$$

The firing condition and the exclusion condition of firing at time t_o are expressed by

$$r_o = \Sigma_i(t_o),$$

and

$$r_o < \Sigma_i(t_o),$$

respectively. We determine the time relation of firings in each firing mode. Then by obtaining the firing conditions and the exclusion conditions of firing of each cell using above relationship, we derive the existence region in r_o-c plane.

5.1 Alternating mode

Detailed report of analysis of the alternating mode was made elsewhere(18), so we describe only the firing condition and the exclusion conditions of firing for existence of the fundamental firing pattern which are expressed using input and structure parameters.

Let h_1 denote the phase transition delay time. The firing condition is expressed by

$$c = \frac{e^{-\lambda N h_1} - e^{-\lambda T_o}}{e^{-\lambda (N-1) h_1/2} (1 + e^{-\lambda N h_1})(1 - e^{-\lambda T_o})} \tag{12}$$

and the exclusion conditions of firing by

$$h_1 < 2T_o/(N-1) \tag{13}$$

and

$$c > \frac{-e^{-\lambda (T_o - h_1)} [1 - e^{-\lambda \{(N+1) h_1/2 - T_o\}}]}{1 - e^{-\lambda T_o}} . \tag{14}$$

The minimal synaptic coefficient c which is given by Eq.(12) and satisfies both Eqs.(13) and (14) gives the lower bound of the existence region.

When the number of cells N is even, there exists the alternating mode which is equivalent to that in the case of the network with two neurons. The existence region of this mode is $-1/2<c<0$.

5.2 Bistable mode

The firing interval of active cells in the bistable mode is equal to T_o given by Eq.(1), as is the case with the network with two neurons. The exclusion condition of firing depends upon phase difference in inhibition from two adjacent cells. The inhibition from the adjacent cells is least effective when all the active cells fire simultaneously. From the exclusion condition of firing in this case, the existence region of the bistable mode regardless of the phase difference is given by

$$c < -1/2. \tag{15}$$

The inhibition from the adjacent cells is most effective when active cells fire with the phase difference

$$\left.\begin{array}{ll} d = T_o/2 & (N=4m), \\ d = (N+2)T_o/2 & (N=4m+2), \end{array}\right\} \tag{16}$$

where m is any natural number. Eq.(16) is derived from the requirement that the phase difference of firings between any active cell and the cell next to its neighbor is identical. The existence region in the case Eq.(16) holds is expressed by

$$c < -1/(1+e^{\lambda T_o/2}) \qquad (N=4m), \tag{17}$$

and

$$c < -1/(1+e^{\lambda(N+2)T_o/N}) \quad (N=4m+2). \tag{18}$$

5.3 Multi-stable Mode

The firing interval of active cells in the multi-stable mode is equal to T_o given by Eq.(1). The existence region is derived from the exclusion condition of firing of the quiescent neighbors and expressed by

$$c < -1. \tag{19}$$

The number of pairs of quiescent neighbors can be

$$\left.\begin{array}{lll} 2m, & m=1,2,\ldots\ldots, [N/6] & (N:\text{even}), \\ 2m-1, & m=1,2,\ldots\ldots, [(N+3)/6] & (N:\text{odd}), \end{array}\right\}$$

where [x] means the largest integer that does not exceed x. Consequently, the multi-stable mode exists when the number of cells $N=3$, or $N \geqq 5$.

5.4 Mixed mode

The firing interval of the cells in the bistable mode is equal to T_o given by Eq.(1), and that in the alternating mode to T_a given by Eq.(8). From the exclusion condition of firing of the cells in the alternating mode, it is required that

$$c > -1, \tag{20}$$

as is the case with the network with two neurons. On the other hand, from the exclusion condition of firing of quiescent cells, which is embedded by the cell in the bistable mode and the cell in the alternating mode, it is required that

$$\frac{e^{-\lambda T_o}}{1-e^{-\lambda T_o}} + c\left(\frac{e^{-\lambda T_o}}{1-e^{-\lambda T_o}} + \frac{e^{-\lambda T_a}}{1-e^{-\lambda T_a}}\right) < 0. \qquad (21)$$

The maximal synaptic coefficient c which satisfies Eqs.(1), (8) and (21) gives the upper bound of the existence region. The lower bound is given from Eq.(20) by

$$c = -1.$$

The number of pairs of the cells in the alternating mode can be

$$\left.\begin{array}{ll} 2m,\ m=1,2,\ldots\ldots,\ [N/10] & (N:\text{even}), \\ 2m-1,\ m=1,2,\ldots\ldots,\ [(N+5)/10] & (N:\text{odd}), \end{array}\right\}$$

where [x] means the largest integer that does not exceed x. Consequently, the mixed mode exists when N=5, 7, or $N \geqq 9$.

5.5 Long period mode

Detailed report of analysis of the long period mode was made elsewhere[(18)-(20)].

The long period mode as shown in Fig.4 exists when $N \geqq 7$.

5.6 Super long period mode

The upper bound of the existence region of the super long period mode with respect to the synaptic coefficient c coincides with the lower bound of the long period mode, while the lower bound of the super long period mode coincides with the upper bound of the mixed mode.

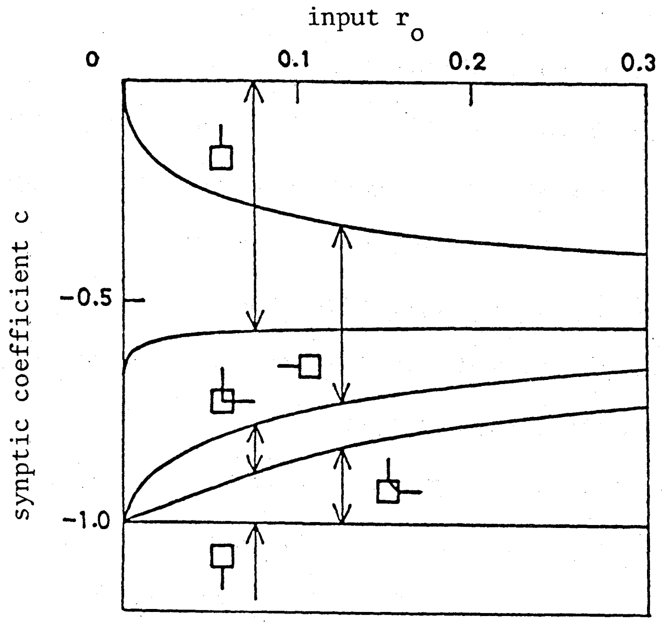
6. Existence regions of firing modes

The existence regions of various firing modes with respect to input parameter r_o and synaptic coefficient c are determined by analytical approach described in chapter 5, and are shown in Fig.7. Fig.7(a) shows a typical example in the case N is odd (N=21), and Fig.7(b) in the case N is even (N=20), where λ is set to 0.25(/ms). There is no great difference in the existence regions due to the difference in N in the case N is larger than some large value. The decaying constant λ has no influence on the existence regions of the firing modes but on time scale of them.

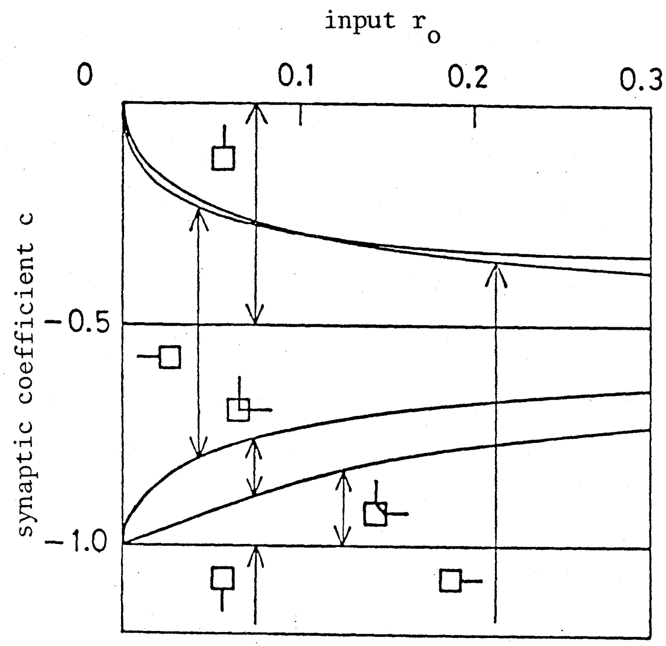
The existence regions of firing modes mostly overlap with each other, that is, to the identical input and structure parameters, several firing modes can occur. Moreover, there are a number of firing patterns in each of the multi-stable, the mixed, the long period and the super long period mode, and the number of the firing patterns increases with the increase of the number of cells N. Occurrence of each firing pattern depends on initial values of relative threshold z_i (i=1,2, ..., N) of each cell. Therefore, many of modes show certain memory features and a firing pattern can be seen by suitable selection of initial conditions.

In the long period mode, there exist a number of firing patterns each different in number of firings k in the active phase and in the direction of the phase propagation. In the case N=21, k can be an integer satisfying $2 \leqq k \leqq 9$. The larger the number of cells N is, the larger is the possible k value, which is approximately proportional to N.

The period of the long period mode is defined as the time interval from a beginning of an active phase to the next. The larger the value of k is, the longer is the period, so the larger the number of cells N is, the wider is the controllable range of the period



(a) N=21



(b) N=20

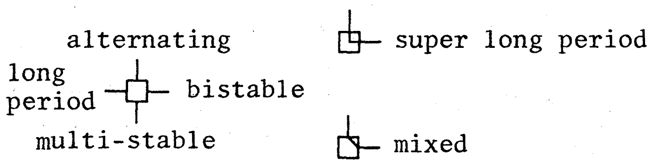


Fig.7 Regions of input and structure parameters in which various firing modes occur.

of the long period mode.

The period of the super long period mode for a constant c value is approximately proportional to N, as well as that of the long period mode. Moreover, it varies with the value of c. The larger c is, it becomes the closer to that of the long period mode, while the smaller, or the closer to the boundary to the mixed mode c is, it becomes the longer to an unlimited extent regardless of N value.

Let us consider the reciprocal inhibition structure of neural nu clei A and B as is shown in Fig.1(b). For the parameters in which the existence regions of the alternating mode, the bistable mode and the long period or the super long period mode overlap, it can show three macroscopic states, that is, the state in which A or B is dominantly active, the state in which A and B is equally active and the state in which A and B alternate in activity with a long period. For the parameters in which the multi-stable mode or the mixed mode exists, activity levels of A and B may show various ratio.

According to computer simulation, all of the firing modes presented here exist even if the number of inhibitory connections to the cells in other neural nucleus increases.

7. Conclusions

Firing modes of reciprocal inhibition neural networks of a ring structure are analyzed. To begin with, the network with two neurons is studied. Then, the analytical study is extended to the network with an arbitrarily large number of cells. It is shown that only two firing modes can occur in the network with two neurons, and the stationary firing patterns in multi-neuron networks are classified into some firing modes, which as we understand are spatial and/or temporal composites of the two modes in the network with two neurons.

The existence regions of the firing modes are determined analytically. These regions mostly overlap with each other. Therefore many of the modes show certain memory features. The relation between the initial conditions of the network and the firing mode to be generated is discussed elsewhere[19].

The stability of the firing modes of the network with two neurons is described briefly. The stability of the long period mode is also discussed elsewhere[20].

In this paper, for the convenience of analysis, the discussion of the firing modes is made separately in the cases N is even and N is odd. However, except the bistable mode, there is no essential difference in the firing modes between two cases. Further, the bistable mode can be generated also in the case N is odd if the input condition is modified slightly.

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