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STUDIES ON STOCHASTIC MODELING OF NEURONS

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ABRISS

Es werden stochastische Formungen der Neuronen und Neuronenbevölkerungen entwickelt. Diese Arbeit hat drei Themen, und zwar Neuronen des spontanen Typs, Neuronen des gezwungenen Typs und wechselseitig hemmende Paare. Das Hauptgewicht wird ihren stochastischen Eigenschaften beigelegt.

Kapitel eins dient zur Verdeutlichung der Stellung dieser Arbeit. Bio-Systeme besitzen viele bemerkenswerte Funktionen. Wenn sie vom technologischen Standpunkt aus erörtert werden, bedient man sich der auf der Kybernetik fußenden Methodik. Diese besagt, daß Bio-Systeme und Maschinensysteme sowie kombinierte Systeme aus beiden zusammen behandelt werden können, so lang Energie und Information im Mittelpunkt stehen. Daher ist die Untersuchung des Informationsflusses von wesentlicher Bedeutung, um lebende Körper als Systeme zu verstehen. Das Nervensystem ist eines der hervorstechendsten informationsverarbeitenden Systeme in den Bio-Systemen. Der erste Schritt zu einer mathematischen Diskussion der Nervenaktivität wurde von W. S. McCulloch und W. H. Pitts unter verwendung des logischen Kalküls unternommen. Seit ihrer Pionierarbeit nahmen die meisten Forscher auf diesem Gebiet unwillkürlich die Meinung an, daß die Informations verarbeitung im Nervensystem mittels deterministischer Methoden voll verstanden werden kann. Dagegen zeigen neuere Versuchsarbeiten eine Vielzahl von Gegenbeispielen. Es gibt Neuronen, die sich spontan ohne Regelmäßigkeit erregen. Und es wird auch vom

Auftreten eines nichtidentischen Feuerschemas bei identischem Reiz berichtet. Es ist nicht unmöglich zu der Auffassung zu kommen, daß diese Regellosigkeit die oberflächliche Erscheinungsform einer äußerst komplexen Verschlüsselung ist, wenngleich es nur spärliches Beweismaterial für diese Idee gibt. Diese Tatsachen dienen als beste Beispiele, um die Notwendigkeit von Methoden der Wahrscheinlichkeitsrechnung zu belegen.

In Kapitel zwei ein kleiner Betrag mathematischer Einleitung gegeben, und das Neuron des spontanen Typs behandelt. Zwei grundlegende Veränderliche in der Neuronendynamik sind das Neuronenpotential und die Schwelle. In dem Augenblick, wenn das Neuronenpotential die Schwelle erreicht, feuert das Neuron. Da das Neuronenpotential als eine Zufallsveränderliche behandelt wird, wird die obige Eigenschaft in das Problem der Kurvenüberschneidung oder das Problem der Erstdurchgangszeit übersetzt. Dieses Problem wird zur Erörterung der Neuronen des spontanen Typs angewandt. Hierbei liegt das Ziel darin, die Dichte der Übergangswahrscheinlichkeit des Neuronenpotentials und die Dichte der Wahrscheinlichkeit der Erstdurchgangszeit zu erhalten. Diese erfüllen die Kolmogorov'schen Gleichungen und die Erhaltung der Wahrscheinlichkeit, die in der Einleitung oben genannt ist. Und die Veränderung der Schwelle wird auf das Problem der beweglichen Grenze zurückgeführt. Die numerische Lösung wird versucht wie auch die analytische, und die erhaltenen Lösungen erklären die spontanen Aktivitäten der Neuronen recht gut.

Kapitel drei behandelt Neuronen mit stochastischen Eingangsimpulsreihen. Poisson-Impulsreihen werden als Eingänge angenommen. Die Angemessenheit dieser Annahme wird durch die Begrenzungssätze bei Überlagerung der Impulsreihen untermauert. In der Folge werden die mathematischen Modelle der Neuronen des erzwungenen Typs mit erregenden und hemmenden Eingangsimpulsreihen, die auf den Poisson-Verfahren beruhen, betrachtet. Es gibt zwei Arten von Hemmungen. Die eine ist die subtraktive Hemmung, die das Neuronenpotential um einen gewissen Betrag verringert, während die zweite es teilt order verzweigt. Beide Fälle werden betrachtet und analysiert unter Verwendung der Dichte der Übergangswahrscheinlichkeit des Neuronenpotentials und der Dichte der Wahrscheinlichkeit der Erstdurchgangszeit, die die Kolmogorov'schen Gleichungen und das Gesetz der Erhaltung der Wahrscheinlichkeit erfüllen. Bei dem Problem der Neuronen der gezwungenen Typs unterscheiden sich folgende Punkte von den Neuronen des spontanen Typs : die Notwendigkeit der Diffusionsnäherung des Differentialgebers für die Sachgemäßheit des Problems der Erstdurchgangszeit ; das Problem des Vergleichs der beiden Typen von Hemmung ; die Probleme der zeitweisen Uneinheitlichkeit infolge der Impulstempomodulation. Bei der Diffusionsnäherung wird die Lösung mit der Digitalsimulation verglichen und eine gute Übereinstimmung erreicht. Beim Vergleich der beiden Typen von Hemmung ist der Unterschied zwischen ihnen abhängig vom Rückstellwert des Neuronenpotentials. Und bei Anwendung der Impulstempomodulation läßt sich berichten, daß die Dichte der Wahrscheinlichkeit der Erstdurchgangszeit je nach Modulation eine multimodale Verteilung zeigt. Wenn die modulation periodisch ist, wird das Problem der Intervalldichte der Ausgangsimpulsspitzen aufgezeigt. Solch eine Situation wird herbeigeführt, um die Informationsprozesse bei Neuronen zu erforschen, unter Verwendung eines periodischen Reizes. Die Relevanz der Intervalldichte der Ausgangsimpulsspitzen zur Dichte der Erstdurchgangszeit wird betrachtet und die Näherungsgleichung dafür gegeben.

Kapitel vier behandelt zwei Arten von wechselseitig hemmenden Paaren. Einmal das System, daß jedes Neuron eine unabhängige Poisson-Eingangsimpulsreihe besitzt, zum anderen das System, daß jedes Neuron eine gemeinsame Poisson-Eingangsimpulsreihe hat, die mit einer Verspätung an ein Neuron des Paares angebracht wird. Diese beiden Systeme zeigen multimodale Intervalldichten der Ausgangsimpulsspitzen trotz zeitweise einheitlicher Poisson-Eingangsimpulsreihen. Diese Tatsache bedeutet, daß die stochastischen Rhythmen von solchen Systemen erzeugt werden. Diese beiden Systeme unterscheiden sich nicht, so lang sie über die Mittelwerte der Ausgangshäufigkeiten verglichen werden, wärend die Querbeziehungen sehr unterschiedlich sind, was die Interferenz der Impulsreihen wiederspiegelt. Weiterhin werden zeitweise uneinheitliche Eingänge behandelt. In diesem Fall, können Eingangsimpulsreihen mit unterschiedlicher Impulstempomodulation für jedes Neuron angewendet werden. Es wird dargelegt, daß der untere Bereich der Impulstempomodulation die Hauptrolle spielt.

In Kapitel fünf werden Zusammenfassung und Schluß gegeben.

Die wesentlichen Ergebnisse sind die Systematisierung der stochastischen Modellformung und Methode für Neuronen und Neuronbevölkerung, und die sinnvolle Interpretation der neuralen Verhaltensweisen, die eine Erklärung nach der deterministischen Methode abweisen.

CHAPTER ONE

INTRODUCTION

1.1 Prologue

Biological systems have many remarkable functions in comparison with artificial tools or machines. And until now, most of them have not been realized artificially. Even if some of them are made, they are not so compact or reliable. However, when they are discussed from the engineering side, the same methodology is adopted. Its main idea is nicely stated in the Cybernetics advocated by N. Wiener in 1947, which tells that machines and animals as well as their combined systems can be discussed unitedly as long as they are considered centering around energy and information. Therefore, it is essential to study aspects of information in order to discuss a living body from a viewpoint of a system.

Nervous system is one of the most skilful systems to treat with information in a living body. It is made up of neurons and the information in it is delivered and received by electrical pulses. In 1943, W. S. McCulloch and W. H. Pitts made a threshold logic model which explains the basic functions of neurons and the logic of a digital computer.

Since the McCulloch-Pitts model was presented, an idea that the information processing in nervous systems can be understood at length by means of deterministic methods had become prevalent among researchers.

But the experimental results revealed noisy properties of neurons. For example, random spontaneous activities of neurons or non-identical responses under an identical stimulus were informed recently. These are good instances that it is not sufficient to consider only deterministic information processing in nervous systems. It is important to make clear the essential point which is brought by the probabilistic nature of nervous systems. Therefore, probabilistic method naturally arises besides deterministic method.

This dissertation tries to discuss stochastic properties of neurons with the aid of probabilistic models.

1.2 Historical Background

In this section, a brief historical review on the studies related to the information processing of nervous systems is presented.

From the viewpoint of Cybernetics, it is possible to look back until R. Decartes. In 17th century, he compared a living body with a machine of clockwork. It is said that the nervous system in his image was made up of pipes of the organ.

It has been known that activities of nervous systems are accomplished by certain electrical potentials. L. Galvani was the first person who found that by observing the activity of the detached leg of the frog (1768). This was the birth of the science of neurophysiology. In 1848, E. H. du Bois-Reimond tried further study and certified the relation between the galvanism and the nervous conduction. In 1850, H. von Helmholtz obtained the velocity of nervous signal by measuring the contraction of muscles.

In 1922, H. S. Gasser and J. Erlanger studied the action currents of the nerve with a cathode ray oscillograph. That was an epoch-making event. This descent leaded to A. L. Hodgkin and A. F. Huxley's studies (1939 and 1952). They measured the pulse transmission along the giant fiber of Loligo and made mathematical models on the membrane activities and the excitation of an axon. The models are called H-H models which explain the generation of a pulse and the wave shaping action.

It was at the end of 19th century that Ramón y Cajal considered on multiple neuron system. He presented an idea that a brain is made up of many independent neurons. After that, his idea was proved with the aid of the electronic microscope. In 1897, C. S. Sherrington discussed the mammalian spinal cord as an organ of reflex action. R. Lorenté de Nó analysed the activity of the chains of internuncial neurons in 1938.

Such steady pile leaded to the next great development. In 1943, W. S. McCulloch and W. H. Pitts made a threshold logic model of neurons. It has both excitatory and inhibitory inputs as well as the threshold, and is described as

$$x_i(t+\tau) = 1[\sum_j a_{ij}x_j(t) - \theta_i] \qquad (1.1)$$

where x_i takes 0 or 1, a_{ij} means the synapse weight coefficient and θ_i is the threshold. By this model, it is possible to make the basic logic of the digital computer.

Several years later, they joined the Wiener's group of Cybernetics. N. Wiener also considered similarity and difference between computing machines and the nervous system in his monograph " Cybernetics " (1948).

Thereafter, many studies were presented under the influence of Cybernetics. In 1956, S. C. Kleene considered events in nerve nets by the usage of the finite automata theory. In 1958, F. Rosenblatt presented the perceptron and explained some aspects of learning processes. In 1961, the M-P model was extended by E. R. Caianiello. The model includes the characteristics of past records, the refractory period and the variation of the coefficients.

$$x_i(t+\tau) = 1[\sum\sum_{jr} a_{ij}{}^{(r)} x_j(t-r\tau) - \theta_i] \tag{1.2}$$

$$a_{ii}{}^{(r)} = \begin{cases} -L & 0 \leqq r < R_1 \\ -f(r) & R_1 \leqq r < R_1 + R_2 \\ 0 & R_1 + R_2 \leqq r \end{cases} \tag{1.3}$$

$$a_{ij}{}^{(r)} = \{ \alpha^{(r)} x_j(t-r\tau) x_i(t) - \beta^{(r)} 1[a_{ij}{}^{(r)}(t) - a_{ij}{}^{(r)}(0)] \} a_{ij}{}^{(r)}(t)$$

$$1[A_{ij}{}^{(r)} - a_{ij}{}^{(r)}(t)]$$

$$\alpha^{(r)} >> \beta^{(r)} > 0 \quad , \quad A_{ij}{}^{(r)} \geqq a_{ij}{}^{(r)} \geqq 0 \tag{1.4}$$

This model shows the reverberation activity and both memorization and oblion. The reverberation was nicely simulated by B. C. Farley and W. A. Clark with the aid of the computer in 1961. And R. F. Reiss made a similar model, however, his model includes the function of the fatigue (1962).

Electronic models also prevailed after the First Symposium on Bionics in 1960 (" Bionics " was named by J. S. Steele in 1958.). L. D. Harmon's neuromime (1961) and H. D. Crane's neurister (1962) are worth noting.

Mutual concessions between physiology and technology is represented by J. Y. Lettvin et. al.'s study on frog's eye. They analysed what the frog's eye tells the frog's brain (1959). The data were used to make an electronic model by H. von Foester (1962). Another example is T. B. Martin and S. S. Talavage's application of the neural logic to the speech analysis and recognition (1963). Although the disposition is a little different, P. R. Westlake's discussion on the possibility of neural holographic processes (1968) is also worthy to note.

Since McCulloch-Pitts' pioneering work, most researchers have believed involuntarily that the information processing in the nervous system can be fully understood by means of deterministic methods. But C. Pecher had already reported fluctuations in excitability of neurons (1939). In 1952, a more detailed work was presented by P. Fatt and B. Katz. They studied spontaneous subthreshold activities at motor nerve endings, which leaded them to find that the discharge of synaptic vesicles has essential random properties and nerve inpulse has an effect to increase the probability of the discharge temporally.

These facts are early steps which suggest the importance of probabilistic nature of the nervous system. And from the engineering side, J. von Neuman pointed out that the nervous system is rather probabilistic in his posthumous manuscript (1958).

G. L. Gerstein and N. Y.-S. Kiang et al.'s works in early sixties made a significant step. Kiang studied the spontaneous firing and the non-identical firing despite an identical stimulus in the cochlea nucleus of cats (published in 1965). In 1964, G. L. Gerstein and B. Mandelbrot made a random walk model for the spike activity of single neurons assuming that the neuron potential is a Wiener process with a positive drift. This was the first trial to use stochastic processes in order to discuss probabilistic activities of neurons.

In 1965, W. M. Siebert considered the stochastic behavior of primary auditory neurons. And T. F. Weiss made a model of the peripheral auditory system by introducing the low pass filtered Gaussian noise to the neuron potential (1966).

A little later, Grestein's model was improved to explain input-output relation by M. Ten Hoopen (1966), B. Gluss (1967), P. I. M. Johannesma (1968) and R. M. Capocelli and L. M. Licciardi (1971).

Another trial is D. H. Perkel et. al.'s study on neural spike trains (1967), and J. P. Segundo et. al.'s study on the effect of multi-input channels (1968). They are related to the coding and information processing in the nervous systems.

Although probabilistic methods have been paid attention, they are not in a satisfactory status. It is necessary to develop the probabilistic method as well as the deterministic one.

In this dissertation, some theoretical considerations are presented for the probabilistic behavior of neurons and several new results are obtained.

1.3 Structure and Activity of Neuron

Neurons are cells usually not more than 0.1 mm in diameter, which have become specially adapted to processing and transmitting electrical signals within the nervous system. Each neuron comprises a soma, together with dendrites, and a single axon. The dendritic complex functions as an antenna, collecting incoming signal and conveying them to the soma, while the axon functions as a tramsmitter, conveying outgoing signals to other neurons and to muscles. Such signals generally have to cross separating gaps between neurons, called synaptic clefts. This is done by the discharge of synaptic vesicles involving chemical transmitter substances. Then the post synaptic potential occurs with a little time delay. Therefore the signal transmission is one-way.

There are two kinds of post synaptic potentials : the excitatory post synaptic potential (EPSP) and the inhibitory post synaptic potential (IPSP).

As neural connections, three kinds of ones are known. They are the excitatory connection, inhibitory connection and the pre-synaptic inhibitory connection. A neuron is connected with many synapses of other neurons (multi-input), however, it generates one output signal.

The output signal generation mechanism is as follows. EPSP's and IPSP's are summed up in a cell body (spatial summation). Meanwhile, there is the temporal summation in a single synapse when input signals are applied one after another. Then, the total neuron potential increases in spite of its tendency of approach to the rest value. And at last, it reaches the threshold. Then the neuron produces a sharp pulse (spike) and it is transmitted to other neurons along the axon with the wave shaping.

After a firing, there is an absolute refractory period in which the neuron can not fire again. Then the threshold decays to the normal value. This period is called an relative refractory period.

Other properties are the adaptation and the accomodation. When a neuron is applied a stimulus continuously, its output pulse frequency drops gradually (adaptation). And if an input stimulus is increased by degrees, the output does not follow the input increase but is fixed (accommodation).

In addition to above properties, the stochastic nature is reported, especially on noise of the neuron potential. One reason for the existence of noise is due to a thermal environment.

1.4 Significance of Pulse Distribution

Signals which carry information from outside are converted by receptors into the form which is acceptable in nervous systems. It is necessary to investigate in what form the information exists in the nervous system in order to understand the information processing of the system. In other words, it is to study what code is used by the nervous system for its internal transmission.

The internal signals are neural pulses, or spikes. They are essentially the same height so that the information transmitted by the neuron must be coded in the pattern of the pulse series. And wide varieties of patterns are found. In neurons which control the strech of muscles, pulse trains are comparatively regular. On the contrary, they are quite random in others, e. g. auditory neurons.

Most of pulse trains have fluctuations in their pulse interval. And it is not impossible to consider that this randomness is the superficial appearance of very complex coding. However, there are rare reasons to support the idea. Counterwise, the essential randomness of the discharge of information transmission substances is reported and it is considered that a neural pulse increases the probability of the release of synaptic vesicles temporally. Therefore, the randomness in pulse distribution owing to the noisy character of the neuron needs to be considered when the neural coding is discussed.

One candidate for the neural code is the frequency of pulse trains.

In other words, pulse frequency modulation is a plausible one. Examples can be seen in motor nerve pulse trains which control muscles and the typical one is reported by G. D. Bittner. He presented the fact that the contraction of muscles due to sparse pulse trains becomes much stronger when dense pulse trains are applied suddenly.

Another candidate is the pulse pattern. D. H. Perkel et. al. measured the output pulse frequencies when a Poisson pulse train or a regular one with the same mean frequency is applied, and recognized that they are very different. C. A. G. Wiersma and R. T. Adams studied the influence of nerve impulse sequence on the contractions of different crustacean muscles. By their report, the contraction is far stronger when the input pulse train has a combination of successive long and short intervals rather than that in the case of uniform intervals.

A special example is reported by D. M. Wilson and R. J. Wyman. According to their report, the motor output pattern of locusts is not affected by that of input pulses but it is regular.

There are many varieties in neural codings. And among them, the frequency code is the one which is widely seen and most general. And this coding is considered after.

1.5 Description of Problems

After due consideration on the preceeding sections, the description of problems in this work is presented here.

The signal unit of nervous system is each pulse, which has almost the same shape. Therefore the information transmission in nervous systems does not take the form of waves or other shapes but pulse trains. And this pulse trains can be regarded as stochastic ones in many cases. For example, some neurons fire spontaneously with fluctuations or non-identically despite an identical stimulus. It may be considered that such stochastic nature is the superficial appearence of very complex information code, however, the evidences to support such an idea are rare. On the contrary, the essential randomness of the discharge of information transmission substances is reported.

Therefore neuron modeling to study stochastic behaviors is of real necessity. For all that, the cultivation is not in a satisfactory status. This work is devoted to improve this situation, and discusses following problems.

The first one is the spontaneous type neuron which produces spikes according to its own fluctuation. The mathematical model has following assumptions. The neuron potential has a fluctuation and obeys the Ornstein-Uhlenbeck process, because the neuron potential is not so perfectly random as that of the Wiener process but has an attraction to the rest value. The threshold varies exponentially and the neuron potential has a constant lower limit. When the neuron potential reaches the threshold, the neuron fires and the neuron potential is reset to a certain position. After a firing, an absolute refractory period exists. In discussing stochastic properties of neurons, the transition probability density function and the first passage time probability density function are the important quantities, which are governed by the Kolmogorov's equations and the law of the probability conservation. Although they can be set up easily, the analytical solutions in time domain are rarely obtainable in general. Hence, the numerical analysis is performed as well as analytical method, and a good deal of fair results are obtained and discussed.

The second one is the forced type neuron which has input pulse trains based on the Poisson processes. This is certified by theorems on the superposition of pulses. Other assumptions and methods are almost the same as above except the diffusion approximation of the stochastic processes. In this case, the temporally inhomogeneous processes due to the pulse frequency modulation arise, whose first passage time density reveals the multimodal distribution. And the comparison of the two kinds of inhibitions, i. e. the subtractive inhibition and the shunting inhibition, is also made. Furthermore, the output spike interval density is discussed in the case of the periodic modulation.

The third discussion is made on two types of reciprocal inhibitory pairs as the problems on neuron populations. The first type has two excitatory driving inputs which are mutually independent. The second type has one common excitatory input but it advances in two ways, one of which has a time lag. The neuron dynamics is the same as that of the forced type with subtractive inhibition and each neuron has an identical structure. The inputs are assumed to be based on the Poisson processes and the inhibition occurs when the companion neuron fires. In this case, the digital simulation is mainly relied upon. Both temporally homogeneous case and inhomogeneous case are considered.

The discussions on the adaptation and the accommodation are left as further attempts.

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CHAPTER TWO

SPONTANEOUS TYPE NEURON

2.1 First Passage Time Problem of Neuron Potential

In chapter one, the necessity to consider stochastic properties of neurons was explained. And in the section 1.3, many properties of the neural activity were pointed out. Among them, the threshold property is the most essential one. In this section, it is seen that the threshold property is related to the first passage time problem of stochastic processes.

A sample path of the neuron potential is denoted by $Y(t,\omega)$ where t means time and ω is a sample point of the sample space Ω . Then the pulse generating mechanism is interpreted as follows. $Y(t,\omega)$ varies by some reasons as time passes, and at last it reaches the threshold. The output pulse is spiked at that moment. That is to say, the curve crossing problem is presented. And the curve crossing time is no other than the first passage time.

When the threshold is denoted by $d(t)$, the first passage time is defined by

$$\mathfrak{T}_d(\omega) = \inf_{u \geqq s} \{ u : Y(u,\omega) \geqq d(u) \mid Y(s,\omega) < d(s) \} \tag{2.1}$$

Afterwards, the transition probability density and the first passage time probability density are used frequently. The transition probability density of the neuron potential $Y(t,\omega)$ is denoted by $f(y,t|x,s)$. It means that the probability that the neuron potential $Y(t,\omega)$ takes a value in dy-neighborhood of y is $f(y,t|x,s)dy$ when $Y(s,\omega)$ is equal to x . Therefore, by using the probability distribution function,

$$f(y,t|x,s) = \frac{d\Pr\{ Y(t,\omega) \leq y \mid Y(s,\omega) = x \}}{dy} \tag{2.2}$$

holds.

The first passage time probability density is denoted by $g(d,t|x,s)$. It means that the probability that the neuron potential reaches the threshold d at the time in dt-neighborhood of t is given as $g(d,t|x,s)$ when $Y(s,\omega)$ is equal to x . Therefore, by using the probability distribution function,

$$g(d,t|x,s) = \frac{d\Pr\{ \mathfrak{T}_d(\omega) \leq t \mid Y(s,\omega) = x \}}{dt} \tag{2.3}$$

holds.

The relations between these probability density functions and the first passage time problem are as follows. On the transition probability density of the neuron potential, $f(d,t|x,s)$ becomes zero, because the neuron potential never takes a value larger than the threshold. And on the first passage time probability density, $g(d,s|x,s)$ is equal to zero if x is unequal to d . On the contrary, $g(d,t|d,s)$ is equal to $\delta(t-s)$, where $\delta(\cdot)$ is the Dirac's delta function. This is because only the state which lay on the threshold originally lies on it unless time does not pass.

These conditions on both probability density functions mean that the curve crossing problem is reduced to the absorbing barrier problem.

Another important relation immanent to the first passage time problem is the law of the probability conservation. That is to say,

$$\int_{r}^{d(t)} f(y,t|x,s)dy + \int_{s}^{t} g(d(u),u|x,s)du = 1 \tag{2.4}$$

holds. The first term is the probability that the neuron potential is subthreshold, and the second one is the probability that the neuron potential has already reached the threshold and the neuron has already fired. Here, r is the lower limit of the neuron potential.

By differentiating with respect to t ,

$$g(d(t),t|x,s) = -\frac{\partial}{\partial t}\int_{r}^{d(t)} f(y,t|x,s)dy \tag{2.5}$$

is obtained.

2.2 Discussion of Spontaneous Type Neuron

The spontaneous type activity of a neuron is discussed in this section using results in the preliminary section 2.1 . To make a model of this type of a neuron, the Wiener integral is introduced to express the fluctuation of the neuron potential. Of course various models of stochastic processes can be made on the fluctuation, but the Ornstein-Uhlenbeck process is adopted because the neuron potential is not so perfectly random as the Wiener process but has an attraction to the rest value. T. F. Weiss treated similar model in discussing the peripheral auditory system, however, he used only the digital simulation and did not make an exact formulation.

2.2.1 Assumptions on the Spontaneous Type Neuron

The assumptions on the model are as follows.

a. The neuron potential has a fluctuation which obeys the Ornstein-Uhlenbeck process.

b. The threshold value is time varying function that

$$d(t) = d_0 \exp(- \frac{t-s}{\tau_d}) \qquad (2.6)$$

where s is the time when the previous spike was generated.

c. The neuron potential has the lower limit r . If the neuron potential reaches $d(t)$, the neuron fires and the neuron potential is reset to x . The threshold is also reset to d_0 .

d. $s \leqq t < s + \delta$ is the absolute refractory period and in this period the neuron potential decays deterministically with a time constant τ_r.

Therefore, a sample path of the neuron potential is expressed as follows by using the Wiener integral.

$$Y(t,\omega) = (x-\eta)\varepsilon^{-\frac{t-s}{\tau_r}} + \eta \qquad (s \leqq t < s+\delta) \qquad (2.7)$$

$$Y(t,\omega) = \int_{s+\delta}^{t} \varepsilon^{-\frac{t-u}{\tau}} dW(u,\omega) + \{Y(s+\delta,\omega) - \eta\}\varepsilon^{-\frac{t-(s+\delta)}{\tau}} + \eta \qquad (t \geqq s+\delta) \qquad (2.8)$$

where $W(t,\omega)$ is $(0,\sigma^2)$-Wiener process, η is the rest value of the neuron potential and τ is the time constant of the neuron potential.

As $Y(s+\delta,\omega)$ and η are deterministic quantities, δ and η may be eliminated by the transformations $s+\delta \rightarrow s$, $Y-\eta \rightarrow Y$. Then

$$Y(t,\omega) = \int_{s}^{t} \varepsilon^{-\frac{t-u}{\tau}} dW(u,\omega) + x\varepsilon^{-\frac{t-s}{\tau}} \qquad (t \geqq s) \qquad (2.9)$$

is obtained. Hereafter, this case will be treated. The statistical quantities about the activities of neurons would be deduced more conveniently through the Kolmogorov's equations governing the transition probability density functions. For a preparation, the equation (2.9) is tramsformed into the equation (2.10).

$$Y(t,\omega) = x - \frac{1}{\tau}\int_{s}^{t} Y(u,\omega)\, du + \int_{s}^{t} dW(u,\omega) \qquad (t \geqq s) \qquad (2.10)$$

2.2.2 Discussion of the Spontaneous Type Neuron using the Kolmogorov's Equation

In this part, the Kolmogorov's equation which governs the neural activity is obtained. From the equation (2.10),

$$\lim_{\Delta t \to +0} \frac{1}{\Delta t} \mathcal{E}\{ \Delta Y \mid Y(t,\omega) = y \}$$

$$= \lim_{\Delta t \to +0} \frac{1}{\Delta t} \mathcal{E}\{ -\frac{y}{\tau}\Delta t + \int_t^{t+\Delta t} dW(u,\omega) + o(\Delta t)\}$$

$$= -\frac{y}{\tau} \tag{2.11}$$

and

$$\lim_{\Delta t \to +0} \frac{1}{\Delta t} \mathcal{E}\{ (\Delta Y)^2 \mid Y(t,\omega) = y \} = \sigma^2 \tag{2.12}$$

holds. $\mathcal{E}$ denotes the expectation operator. Then, the following Kolmogorov's (forward) equation is obtained.

$$\frac{\partial f(y,t|x,s)}{\partial t} = \frac{\partial}{\partial y} \frac{y}{\tau} f(y,t|x,s) + \frac{1}{2} \frac{\partial^2}{\partial y^2} \sigma^2 f(y,t|x,s) \tag{2.13}$$

In this case, the terms higher than the second order are zero because of the nature of the diffusion process. But in the chapter three, this property could be assumed under some conditions because the sample path of the forced type neuron is continuous only in probability.

The initial condition (IC) and the boundary conditions (BC's) are as follows.

IC $\qquad f(y,s|x,s) = \delta(y-x) \qquad (2.14)$

BC $$f(d(t),t|x,s) = 0 \tag{2.15}$$

BC $$\left[\frac{y}{\tau} f(y,t|x,s) + \frac{\sigma^2}{2} \frac{\partial f(y,t|x,s)}{\partial y} \right]_{y=r} = 0 \tag{2.16}$$

The equation (2.14) means that the original state of the neuron potential is x. And the equation (2.15) means that $d(t)$ is the threshold. The equation (2.16) is set because the probability flow equals zero at $y=r$ which is the lower limit of the neuron potential.

The first passage time probability density satisfies

$$g(d(t),t|x,s) = -\frac{\partial}{\partial t} \int_r^{d(t)} f(y,t|x,s)dy \tag{2.17}$$

as was obtained in the section 2.1 .

This problem is equivalent to the following because only the difference in the potential between the threshold and the state, $Z(t,\omega)$, has an effect on the first passage time. $Z(t,\omega)$ satisfies

$$Z(t,\omega) = x - \frac{1}{\tau} \int_s^t Z(u,\omega)du + d_0\left(1 - \varepsilon^{-\frac{t-s}{\tau_d}} \right) + \int_s^t dW(u,\omega) \qquad (t \geqq s) . \tag{2.18}$$

Hence,

$$\frac{\partial f(z,t|x,s)}{\partial t} = \frac{\partial}{\partial z} \left(\frac{z}{\tau} - \frac{d_0}{\tau_d} \varepsilon^{-\frac{t-s}{\tau_d}} \right) f(z,t|x,s) + \frac{1}{2} \frac{\partial^2}{\partial z^2} \sigma^2 f(z,t|x,s) \tag{2.19}$$

IC $$f(z,s|x,s) = \delta(z-x) \tag{2.20}$$

BC $$f(d_0,t|x,s) = 0 \tag{2.21}$$

BC $$\left[\left(\frac{z}{\tau} - \frac{d_0}{\tau_d}\varepsilon^{-\frac{t-s}{\tau_d}}\right)f(z,t|x,s) + \frac{\sigma^2}{2}\frac{\partial f(z,t|x,s)}{\partial z}\right]_{z=r^*(t)} = 0 \tag{2.22}$$

are obtained. Here,

$$r^*(t) = r + d_0\left(1 - \varepsilon^{-\frac{t-s}{\tau_d}}\right) \quad . \tag{2.23}$$

And

$$g(d_0,t|x,s) = -\frac{\partial}{\partial t}\int_{r^*(t)}^{d_0} f(z,t|x,s)dz \tag{2.24}$$

holds.

In the simple case that $\tau_d = \infty$, $f(y,t|x,s)$ can be redescribed by $f(y,t,x)$, and $g(d,t|x,s)$ by $g(d,t,x)$. Then, the Kolmogorov's backward equation which is adjoint to the forward equation is available to discuss the first passage time problem. The equation is

$$\frac{\partial f(y,t,x)}{\partial t} = -\frac{x}{\tau}\frac{\partial f(y,t,x)}{\partial x} + \frac{\sigma^2}{2}\frac{\partial^2 f(y,t,x)}{\partial x^2} \quad . \tag{2.25}$$

In this case the equation (2.17) is redescribed by

$$g(d_0,t,x) = -\frac{\partial}{\partial t}\int_{r}^{d_0} f(y,t,x)dy \quad . \tag{2.26}$$

From the equations (2.25) and (2.26),

$$\frac{\partial g(d_0,t,x)}{\partial t} = -\frac{x}{\tau}\frac{\partial g(d_0,t,x)}{\partial x} + \frac{\sigma^2}{2}\frac{\partial^2 g(d_0,t,x)}{\partial x^2} \tag{2.27}$$

is obtained. The above equation is conditioned by

IC $$g(d_0,0,x) = 0 \qquad (x \neq d_0) \tag{2.28}$$

BC $$g(d_0,t,d_0) = \delta(t) \tag{2.29}$$

BC $$\left[\frac{\partial g(d_0,t,x)}{\partial x} \right]_{x=r} = 0 \quad . \tag{2.30}$$

The expectation of the first passage time is defined by

$$M(x) = \mathcal{E}\{\mathfrak{T}_{d_0}(\omega)\} = \int_0^{\infty} t g(d_0,t,x)dt \quad . \tag{2.31}$$

Then,

$$\frac{\sigma^2}{2}\frac{d^2M(x)}{dx^2} - \frac{x}{\tau}\frac{dM(x)}{dx} = -1 \tag{2.32}$$

BC $$M(d_0) = 0 \tag{2.33}$$

BC $$\left[\frac{dM(x)}{dx} \right]_{x=r} = 0 \tag{2.34}$$

are obtained. And the solution is given as

$$M(x) = \frac{\sqrt{\pi\tau}}{\sigma}\int_x^{d_0} \varepsilon^{\frac{x^2}{\sigma^2\tau}} \{ \operatorname{erf}(\frac{x}{\sigma\sqrt{\tau}}) - \operatorname{erf}(\frac{r}{\sigma\sqrt{\tau}}) \}dx \ . \tag{2.35}$$

The equation (2.27) is only a special case of (2.17), however, its analytical solution in time domain cannot be obtained. Hence, the numerical analysis must be tried.

Remark

If $\tau = \infty$ and $r = -\infty$ furthermore, the analytical solution is given as

$$g(d_0,t,x) = \frac{d_0 - x}{\sqrt{2\pi}\,\sigma} t^{-\frac{3}{2}} \exp\{ -\frac{(d_0 - x)^2}{2\sigma^2 t} \} \quad . \tag{2.36}$$

But this case is rather oversimplifying as a problem of a neuron.

2.2.3 Numerical Analysis and Results

The technique of the numerical analysis is the finite difference method. Both implicit and explicit methods are available. But, on the equation (2.27), a iltte consideration is necessary because it has the singularity that the Dirac's delta function is put on the cross point of the IC and the BC, and the implicit method never converges. Therefore only the explicit one is applicable. Now, the several results by means of the numerical analysis are shown.

Fig. 2.1.a shows the solution of the equation (2.13). The state starts from 6 mv and it diffuses. The threshold varies as time proceeds, which is observed from the movement of the absorbing barrier. The probability that the neuron potential is subthreshold tends to zero as t goes to the infinity and its negative rate of change at every moment is just the first passage time probability density. Fig. 2.1.b is the solution of the equation (2.19) which has the positive drift toward the threshold. Fig. 2.1.c is the first passage time probability density obtained from the equations (2.13) and (2.17). Dots are values from the digital simulation using 5,000 sample paths which satisfy the equation (2.10). Fig. 2.1.a and Fig. 2.1.b are related to the section of x=6 mv in Fig. 2.1.c because the x-axis means the original state.

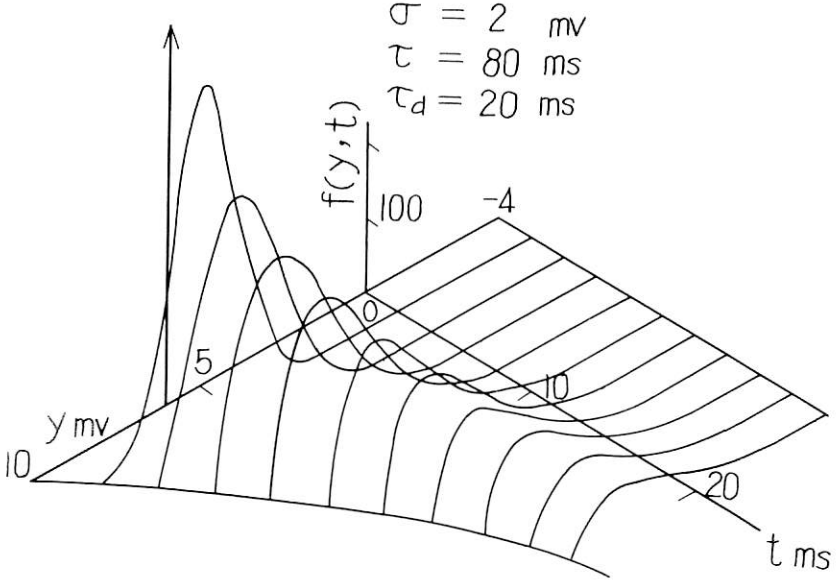

Fig. 2.1.a Transition probability density of the neuron potential

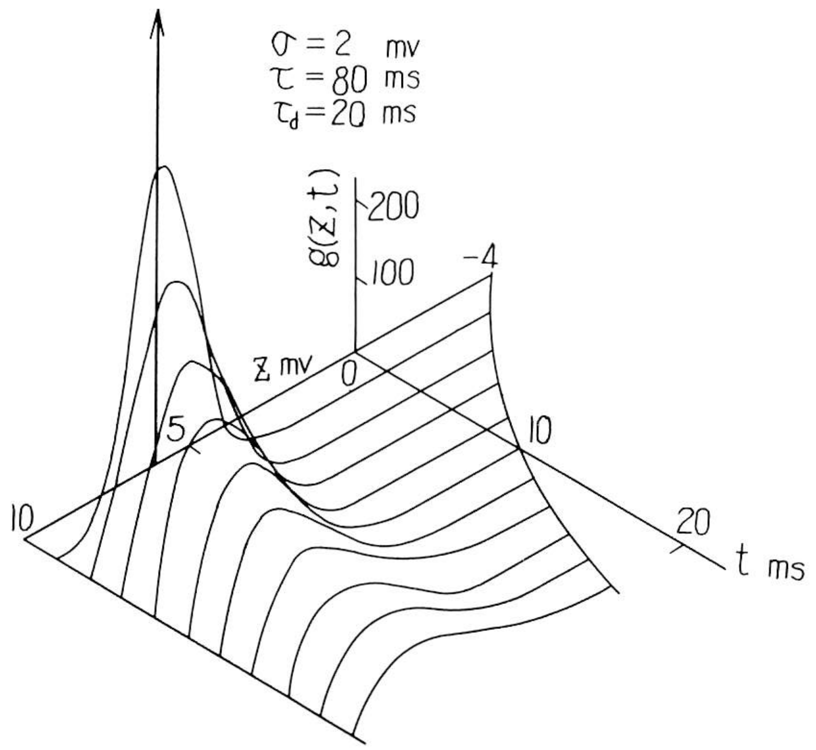

Fig. 2.1.b Transition probability density of the potential difference between the threshold and the neuron potential

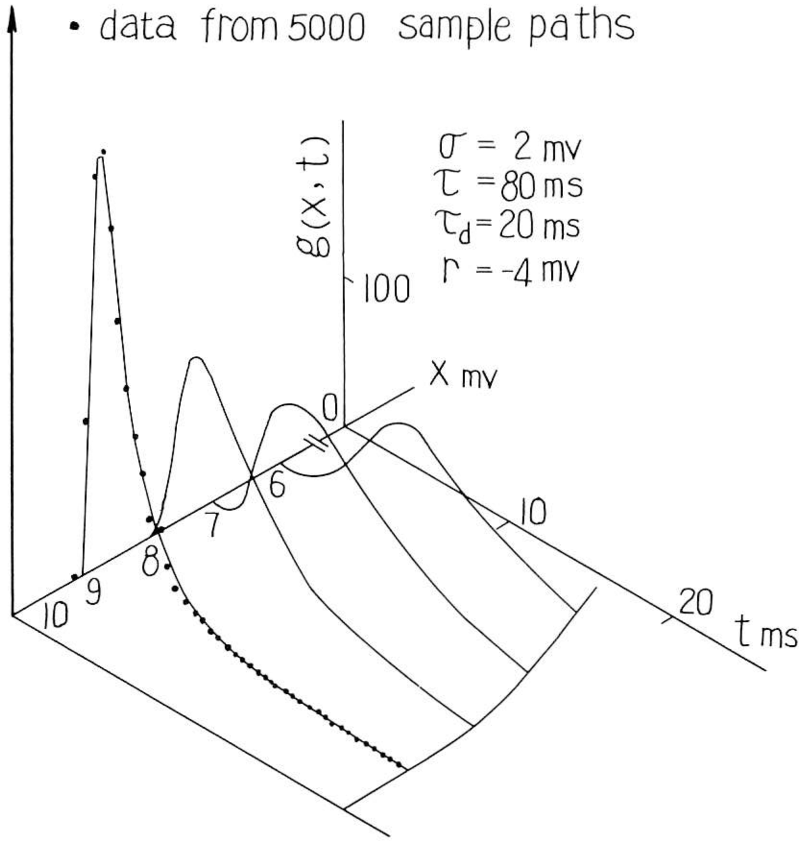

Fig. 2.1.c First passage time probability density

2.3 Concluding Remarks

The equation (2.27) was not treated, because a similar equation will be discussed afterwards for the forced type neuron.

The initial value of the neuron potential was chosen fixed, but if the probability density function of the initial state, p(x), is given, the first passage time probability density is expressed by

$$g^*(d(t),t|x,s) = \int_r^{d_0} g(d(t),t|x,s)p(x)dx \quad . \tag{2.37}$$

Results obtained in this chapter are the transition probability density of the neuron potential and the first passage time probability density in the case of the spontaneous type neuron. At present, it is difficult to measure the former with high accuracy in vivo. But the latter can be obtained by measuring output pulse intervals. Experimental results are obtained by N. Y.-S. Kiang et. al. , and the obtained first passage time probability density shows an agreeable tendency with them. The model presented here is eligible to be that of the spontaneous type neuron.

When the lower limit r takes the value of the negative infinity, the boundary condition corresponding to that is the natural boundary placed at the negative infinity.

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CHAPTER THREE

FORCED TYPE NEURON

3.1 Superposition of Stochastic Point Processes

In this chapter, forced type neurons with excitatory and inhibitory input pulses which are based on Poisson processes are discussed.

The reason why Poisson inputs are adopted is related to the superposition of stochastic point processes. There are many input channels (synaptic knobs of other neurons) in one neuron. As stated in the section 1.3, the effect of input pulse trains through them is added (spatial summation), therefore, input pulse trains can be regarded as one pooled process (D. R. Cox and W. L. Smith, 1953 and 1954 ; B. Grigelionis, 1963). On such problems, following theorems are important.

Theorem 3.1

Let the events on any sources occur at exactly regular intervals so that the sequence S_i is $[\ \theta_i\ ,\ 2\theta_i\ ,\ \cdots]$, where θ_i is the period of i-th source.

If θ_i's ($i = 1, 2, \cdots, N$) are mutually irrational in the sence that there exists no set of positive or negative integers n_i , not all zero, such that

$$\sum_{i=1}^{N} n_i \theta_i = 0 \quad , \tag{3.1}$$

then the distribution of the interval between successive events in the pooled sequence tends to the exponential distribution as N increases. ☒

Proof can be made by using the Weyl's theorem in the theory of numbers.

Theorem 3.2

Let $X_n(t)$ be a random step process such that

$$X_n(t) = \sum_{r=1}^{k_n} X_{nr}(t) \tag{3.2}$$

where $X_{nr}(t)$ is a mutually independent step process with stationary increments. Then, the sequence of the processes $\{ X_n(t) \}$ converges to a Poisson process with parameter Λ,

iff, for fixed t,

$$\lim_{n\to\infty} \sum_{r=1}^{k_n} \lambda_{nr} \int_0^t \phi_{nr}(0,u)du = \Lambda t \tag{3.3}$$

and

$$\lim_{n\to\infty} \sum_{r=1}^{k_n} \lambda_{nr} \int_0^t \phi_{nr}(1,u)du = 0 \quad , \tag{3.4}$$

where

$$\lambda_{nr} = \lim_{t\to+0} \frac{\Pr\{ X_{nr}(t) > 0 \}}{t} \tag{3.5}$$

and

$$\phi_{nr}(k,t) = \lim_{\tau\to+0} \frac{\Pr\{ X_{nr}(t+\tau) - X_{nr}(\tau) = k \ , \ X_{nr}(\tau) > 0 \}}{\Pr\{ X_{nr}(\tau) > 0 \}} \ . \tag{3.6}$$

☒

A more general version of Theorem 3.2 is as follows.

Theorem 3.3

The sum of infinitesinal independent step processes

$$X_n(t) = \sum_{r=1}^{k_n} X_{nr}(t) \tag{3.7}$$

converges to a Poisson process with a leading function $\Lambda(t)$,

iff

$$\lim_{n\to\infty} \Lambda(t,s) = \Lambda(t) - \Lambda(s) \tag{3.8}$$

and

$$\lim_{n\to\infty} B_n(t,0) = 0 \tag{3.9}$$

hold, where

$$\Lambda_n(t,s) = \sum_{r=1}^{k_n} p_{nr}(1;t,s) \ , \tag{3.10}$$

$$p_{nr}(k;t,s) = \Pr\{ X_{nr}(t) - X_{nr}(s) = k \} \tag{3.11}$$

and

$$B_n(t,s) = \sum_{r=1}^{k_n} \{ 1 - p_{nr}(0;t,s) - p_{nr}(1;t,s) \} \ . \tag{3.12}$$

$\boxtimes$

Remark

" infinitesimal " means

$$\lim_{n\to\infty} \max_{1\leq r\leq k_n} \{ 1 - p_{nr}(0;t,0) \} = 0 \ . \tag{3.13}$$

Theorem 3.1 means that the superposition of regular processes leads to the exponential distribution of intervals. One might think that the pooled process is close to a Poisson process, however, its variance-time curve oscillates, which is far from that of a Poisson process. The variance-time curve of a Poisson process is a straight line.

The variance-time curve obtained from a neural pulse train is close to a line, therefore, the superposition of input pulse trains in neural systems can be regarded as that of stochastic pulse trains. Hence, Theorem 3.2 or Theorem 3.3 is applied to the superposition of input stochastic pulse trains due to the probabilistic activities of neurons, and then the pooled process in one neuron can be regarded as a Poisson process.

It is difficult at present to check up the conditions of Theorem 3.2 or Theorem 3.3 in vivo. But even the superposition of two independent stochastic point processes makes an process which is extremely resemble to a Poisson process. As there are many input channels in one neuron, it may not be contradictory to approximate the pooled process by a Poisson process.

3.2 Discussion of Forced Type Neuron with Subtractive Inhibition

In this chapter, the discussion is made on the forced type neuron with excitatory and inhibitory input pulse trains which are based on the Poisson processes, and the inhibition is the subtractive type.

The method is similar to that of the chapter 2, however, it differs in the following respects.

a. The procedure to get the Kolmogorov's equations is somewhat different.

b. The diffusion approximation is necessary.

c. The temporally inhomogeneous problems occur when the input pulse frequency is modulated.

3.2.1 Assumptions on the Forced Type Neuron with Subtractive Inhibition

A neuron treated here has following properties.

a. The excitatory input pulse train $dE(t,\omega_1)$ and the inhibitory input pulse train $dI(t,\omega_2)$ are independent. Here, ω_1 and ω_2 denote sample points. $E(t,\omega_1)$ is a sample path of the Poisson process which causes excitatory pulse application with probability $Ne(t)\Delta t + o(\Delta t)$ in the interval $[t,t+\Delta t)$. $I(t,\omega_2)$ is the same with probability $Ni(t)\Delta t + o(\Delta t)$.

b. The neuron potential $Y(t,\overline{\omega})$ is right continuous, and varies e by every excitatory pulse application and i by every inhibitory pulse application, where e is a positive constant and i is a negative one. And $\overline{\omega} = (\omega_1,\omega_2)$.

c. In the period during which no input pulse is applied, the neuron potential approaches the rest value η asymptotically with a time constant τ .

d. The neuron potential has the lower limit r . When the neuron potential reaches the threshold d , the neuron fires and the neuron potential is reset to x .

e. After a firing, $s \leqq t < t+\delta$ is the absolute refractory period and the neuron potential is never influenced by inputs but decays deterministically with a time constant τ_r .

f. e and $-i$ are sufficiently small in comparison with $d-x$.

Discussions can be developed even when the threshold is time varying as in the chapter 2. But the threshold is fixed here, because the forced type neuron has the positive drift and it brings almost the same properties as the decaying threshold.

Then a sample path of the neuron potential is expressed by the equations (3.14) and (3.15).

$$Y(t,\overline{\omega}) = (x-\eta)\varepsilon^{-\frac{t-s}{\tau_r}} + \eta \qquad (s \leqq t < s+\delta) \qquad (3.14)$$

$$Y(t,\overline{\omega}) = \int_{s+\delta}^{t} \varepsilon^{-\frac{t-u}{\tau}} d\{ E(u,\omega_1) + I(u,\omega_2) \} + \{ Y(s+\delta,\overline{\omega}) - \eta \}\varepsilon^{-\frac{t-(s+\delta)}{\tau}} + \eta$$

$$(t \leqq s+\delta) \qquad (3.15)$$

Since $Y(s+\delta,\overline{\omega})$ and η are deterministic quantities, they can be omitted by transformations $s+\delta \to s$, $Y-\eta \to Y$, and

$$Y(t,\overline{\omega}) = \int_s^t \varepsilon^{-\frac{t-u}{\tau}} d\{ E(u,\omega_1) + I(u,\omega_2) \} + x\varepsilon^{-\frac{t-s}{\tau}} \qquad (t \geqq s) \tag{3.16}$$

is obtained. Hereafter, this case is treated. As the equation (3.16) is an expression of a sample path, it is necessary to derive the equations which govern the transition probability density of the neuron potential and the first passage time probability density.

3.2.2 Discussion of the Forced Type Neuron with Subtractive Inhibition using Kolmogorov's Equation

The forward equation is deduced in a following manner which is different from that of the chapter 2.

There may be three transitions in a very short period $[t,t+\Delta t)$.

$(y-e+y\frac{\Delta t}{\tau}, t) \to (y, t+\Delta t)$ (if E-pulse is applied)

$(y-i+y\frac{\Delta t}{\tau}, t) \to (y, t+\Delta t)$ (if I-pulse is applied)

$(y+y\frac{\Delta t}{\tau}, t) \to (y, t+\Delta t)$ (if no pulse is applied)

Above three kinds of transitions occur with probabilities $Ne(t)\Delta t+o(\Delta t)$, $Ni(t)\Delta t+o(\Delta t)$ and $1-\{Ne(t)+Ni(t)\}\Delta t+o(\Delta t)$ respectively.

Therefore, the equation (3.17) is obtained when Δt is small.

$$\begin{aligned} f(y,t+\Delta t\,|\,x,s) &= Ne(t)\Delta t f(y-e+y\tfrac{\Delta t}{\tau},t\,|\,x,s) \\ &+ Ni(t)\Delta t f(y-i+y\tfrac{\Delta t}{\tau},t\,|\,x,s) \\ &+ [\, 1 - \{ Ne(t) + Ni(t) \}\Delta t \,] f(y+y\tfrac{\Delta t}{\tau},t\,|\,x,s) \end{aligned} \tag{3.17}$$

The stochastic process $Y(t,\bar{\omega})$ is a Markov process, therefore, the Chapman-Kolmogorov's equation holds.

$$f(y,t+\Delta t|x,s) = \int_{\mathcal{D}} f(y,t+\Delta t|z,t)f(z,t|x,s)dz \qquad (3.18)$$

Here, $\mathcal{D}$ is the range of the random variable. From the equation (3.18), the forward equation is obtained.

$$\frac{\partial f(y,t|x,s)}{\partial t} = \sum_{n=1}^{\infty} \frac{(-1)^n}{n!} \left(\frac{\partial}{\partial y}\right)^n A_n(y,t)f(y,t|x,s) \qquad (3.19)$$

where

$$A_n(y,t) = \lim_{\Delta t \to +0} \frac{1}{\Delta t} \int_{\mathcal{D}} dz z^n f(y+z,t+\Delta t|y,t) \quad . \qquad (3.20)$$

Then, the equations (3.17) and (3.20) produce

$$A_1(y,t) = Ne(t)e + Ni(t)i - \frac{y}{\tau} \qquad (3.21)$$

$$A_n(y,t) = Ne(t)e^n + Ni(t)i^n \qquad (n \geqq 2) \quad . \qquad (3.22)$$

Since it is assumed that e and -i are sufficiently small in comparison with d-x , the following diffusion-approximated equation is obtained.

$$\frac{\partial f(y,t|x,s)}{\partial t} = -\frac{\partial}{\partial y}\{ m_1(t) - \frac{y}{\tau} \}f(y,t|x,s) + \frac{1}{2}\frac{\partial^2}{\partial y^2} m_2^2(t)f(y,t|x,s) \qquad (3.23)$$

where

$$m_1(t) = Ne(t)e + Ni(t)i \qquad (3.24)$$

$$m_2^2(t) = Ne(t)e^2 + Ni(t)i^2 \quad . \qquad (3.25)$$

By a similar procedure, the backward equation is obtained.

$$-\frac{\partial f(y,t|x,s)}{\partial s} = \{ m_1(s) - \frac{x}{\tau} \} \frac{\partial f(y,t|x,s)}{\partial x} + \frac{1}{2} m_2^2(s) \frac{\partial f(y,t|x,s)}{\partial x^2} \qquad (3.26)$$

The diffusion approximation makes the first passage time problem a well-posed one. Then, the first passage time probability density is obtained from the law of the probability conservation.

$$g(d,t|x,s) = -\frac{\partial}{\partial t} \int_r^d f(y,t|x,s)dy \qquad (3.27)$$

But the subsequent methods differ depending on whether input pulse trains are temporally homogeneous or not. Therefore the discussions are separated.

a . Temporally Homogeneous Case

This is the case that $Ne(t)=Ne$ and $Ni(t)=Ni$. The stochastic process $Y(t,\bar{\omega})$ becomes temporally homogeneous and $f(y,t|x,s)$ can be denoted by $f(y,t,x)$, and $g(d,t|x,s)$ by $g(d,t,x)$. Then the equation (3.23) becomes

$$\frac{\partial f(y,t,x)}{\partial t} = -\frac{\partial}{\partial y} (m_1 - \frac{y}{\tau}) f(y,t,x) + \frac{m_2^2}{2} \frac{\partial^2 f(y,t,x)}{\partial y^2} \qquad (3.28)$$

and the equation (3.26) becomes

$$\frac{\partial f(y,t,x)}{\partial t} = (m_1 - \frac{x}{\tau}) \frac{\partial f(y,t,x)}{\partial x} + \frac{m_2^2}{2} \frac{\partial^2 f(y,t,x)}{\partial x^2} \qquad (3.29)$$

From the equation (3.27), the first passage time probability density becomes

$$g(d,t,x) = -\frac{\partial}{\partial t}\int_r^d f(y,t,x)dy \quad . \tag{3.30}$$

From the equations (3.29) and (3.30), it can be seen that the first passage time probability density satisfies

$$\frac{\partial g(d,t,x)}{\partial t} = \left(m_1 - \frac{x}{\tau} \right) \frac{\partial g(d,t,x)}{\partial x} + \frac{m_2^2}{2} \frac{\partial^2 g(d,t,x)}{\partial x^2} \quad . \tag{3.31}$$

The initial condition and the boundary conditions are as follows.

For the equation (3.28),

IC $$f(y,0,x) = \delta(y-x) \tag{2.32}$$

BC $$f(d,t,x) = 0 \tag{3.33}$$

BC $$\left[- \left(m_1 - \frac{y}{\tau} \right) f(y,t,x) + \frac{m_2^2}{2} \frac{\partial f(y,t,x)}{\partial y} \right]_{y=r} = 0 \quad . \tag{3.34}$$

The equation (3.32) means that $y=x$ at $t=0$. And the equation (3.33) describes an absorbing barrier which means that $y=d$ is the threshold. And the equation (3.34) means that the probability flow equals zero as $y=r$ is the lower limit of the neuron potential.

For the equation (3.31),

IC $$g(d,0,x) = 0 \qquad (x \neq d) \tag{3.35}$$

BC $$g(d,t,d) = \delta(t) \tag{3.36}$$

BC $$\left[\frac{\partial g(d,t,x)}{\partial x} \right]_{x=r} = 0 \quad . \tag{3.37}$$

The equations (3.35) and (3.36) mean that only the state which lay on the threshold lies on it if time does not pass. And the equation (3.37) implies that the first passage time probability densities starting from the neighborhood of the lower limit r are equivalent.

The mean value of the first passage time is derived from (3.31), (3.35) $\sim$ (3.37) and

$$M(x) = \mathcal{E}\{ \mathfrak{T}_d(\overline{\omega}) \} = \int_0^\infty t g(d,t,x) dt \quad . \tag{3.38}$$

Then, it satisfies

$$\frac{m_2^2}{2} \frac{d^2 M(x)}{dx^2} + (m_1 - \frac{x}{\tau}) \frac{dM(x)}{dx} = - 1 \tag{3.39}$$

BC $$M(d) = 0 \tag{3.40}$$

BC $$[\frac{dM(x)}{dx}]_{x=r} = 0 \quad . \tag{3.41}$$

The solution is given as

$$M(x) = \frac{\pi\tau}{\sqrt{m_2^2}} \int_x^d \varepsilon^{\frac{(x - m_1\tau)^2}{m_2^2\tau}} \{ \mathrm{erf}(\frac{x - m_1\tau}{\sqrt{m_2^2\tau}}) - \mathrm{erf}(\frac{r - m_1\tau}{\sqrt{m_2^2\tau}}) \}dx \quad . \tag{3.42}$$

Remark

The analytical solution of the equation (3.31) conditioned by the equations (3.35) $\sim$ (3.37) is not obtained in time domain. However, the solution of the special case that $\tau = \infty$ and $r = -\infty$ is obtained in time domain, and is described as

$$g(d,t,x) = \frac{d-x}{\sqrt{2\pi m_2^2}} t^{-\frac{3}{2}} \varepsilon^{-\frac{(d - x + m_1 t)^2}{2m_2^2 t}} \quad . \tag{3.43}$$

But this case is rather oversimplifying as the solution of the neural process.

b. Temporally Inhomogeneous Case

In this case, Ne(t) and Ni(t) are time varying functions and the pulse frequency modulation exists, therefore, it is impossible to consider the first passage time problem through the backward equation. Hence, it becomes necessary to discuss the equation (3.27) with the aid of the equation (3.23). The initial condition and the boundary conditions are as follows.

IC $$f(y,s|x,s) = \delta(y-x) \tag{3.44}$$

BC $$f(d,t|x,s) = 0 \tag{3.45}$$

BC $$\left[\left\{ m_1(t) - \frac{y}{\tau} \right\} f(y,t|x,s) + \frac{1}{2}\frac{\partial}{\partial y} m_2^2(t) f(y,t|x,s)\right]_{y=r} = 0 \tag{3.46}$$

The equation (3.44) corresponds to that the value of the neuron potential at time s is x. And the equation (3.45) means that $y=d$ is the threshold. The equation (3.46) implies that r is the lower limit of the neuron potential.

When the pulse frequency modulation is periodic, the problem of the phase between the period of the pulse frequency modulation and the first passage time occurrs. This problem will be treated in the section 3.4 in relation to the output spike interval.

3.2.3 Results

Here are shown the results by means of the numerical analysis. The technique of the analysis is the finite difference method, which is the same as that of the section 2.2.3 . And the explicit difference is mainly used because the minute difference of the time direction is easy to obtain. It is necessary in the temporally inhomogeneous problem.

a. Temporally Homogeneous Case

Fig. 3.1.a is the transition probability density of the neuron potential, the original state of which is y=x=0 mv . This is obtained as the solution of the equation (3.28). It can be understood by observing the neighborhood of the threshold d that the neuron potential begins to reach it from about 9 ms and completes at about 20 ms. Fig. 3.1.b is the first passage time probability density with identical parameters, which is the solution of the equation (3.31). Fig. 3.1.a corresponds to the section x=0 mv of Fig. 3.1.b , from which it can be also observed that the neuron fires almost in the duration of t=9 ms ∿ t=20 ms . The transition probability density of the neuron potential shows when the neuron potential reaches the threshold, and the first passage time probability density shows when the neuron fires.

A curve on x-t plane of Fig. 3.1.b is the mean value of the first passage time which is the solution of the equation (3.39), i. e. (3.42).

Fig. 3.1.c and Fig. 3.1.d show the comparison between the solutions of the equations (3.28) and (3.31), and the values from the digital

simulation using 10,000 sample paths which satisfy the equation (3.16). And they are in good agreement. This implies that the diffusion approximation is reasonable.

Fig. 3.2.a and Fig. 3.2.b are the case of τ=20 ms. As the neuron potential decays more rapidly, the first passage time becomes tardier. Fig. 3.3.a and Fig. 3.3.b are the case of Ne=6 1/ms. In this case, the first passage time becomes also tardier because the excitatory pulse application is less frequent.

b. Temporally Inhomogeneous Case

The sinusoidal pulse frequency modulation is adopted here because it is used in practice. Fig. 3.4.a is the transition probability density of the neuron potential which is the solution of the equation (3.23) conditioned by (3.44) and (3.45) as well as (3.46). Dots express the values from the digital simulation using 5,000 sample paths. Fig. 3.4.b is the first passage time probability density which is the solution of the equation (3.27). In these cases, the pulse frequency modulation is sinusoidal with the frequency 0.25 kHz. And it is observed that the pulse-frequency-modulated information lies in the shape of the first passage time probability density which shows the multimodal distribution.

Remark

In order to generate sample paths which satisfy the equation (3.16), exponential random numbers are used in the temporally homogeneous case and modulated exponential random numbers are used in the temporally inhomogeneous case. On the contrary, normal random numbers were used to generate sample paths which satisfy the equation (2.10) in the problem of the chapter 2.

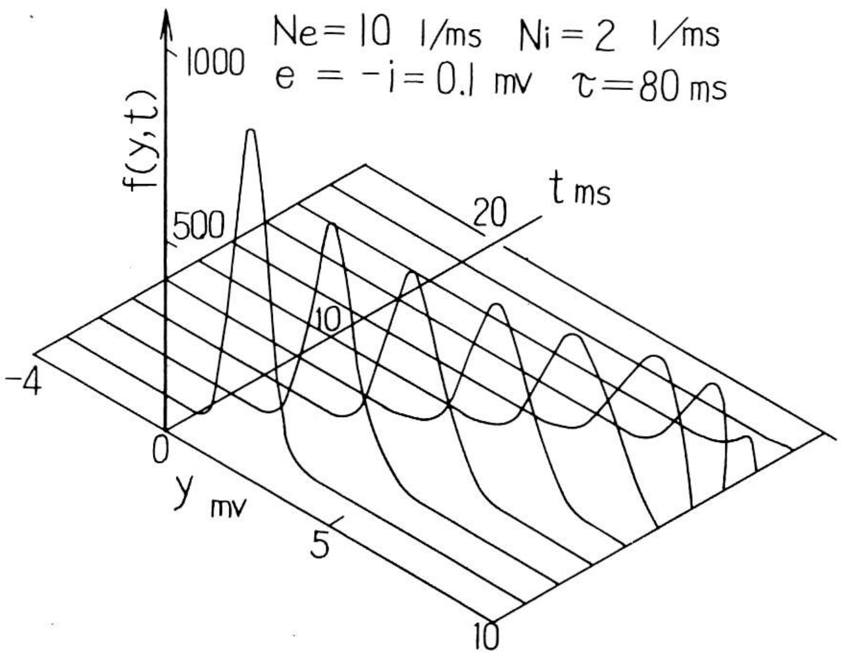

Fig. 3.1.a Transition probability density of the neuron potential

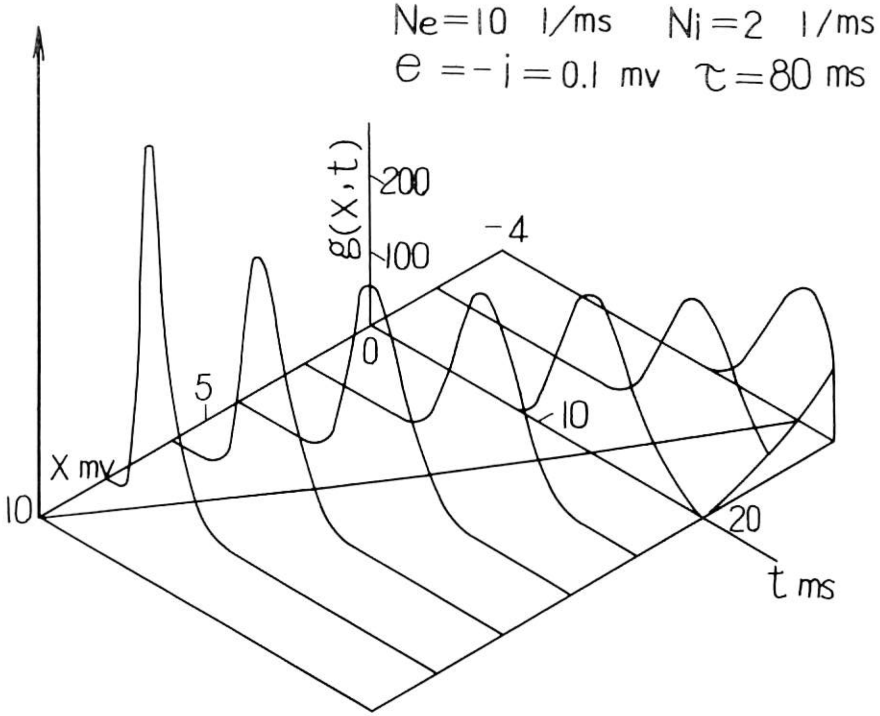

Fig. 3.1.b First passage time probability density

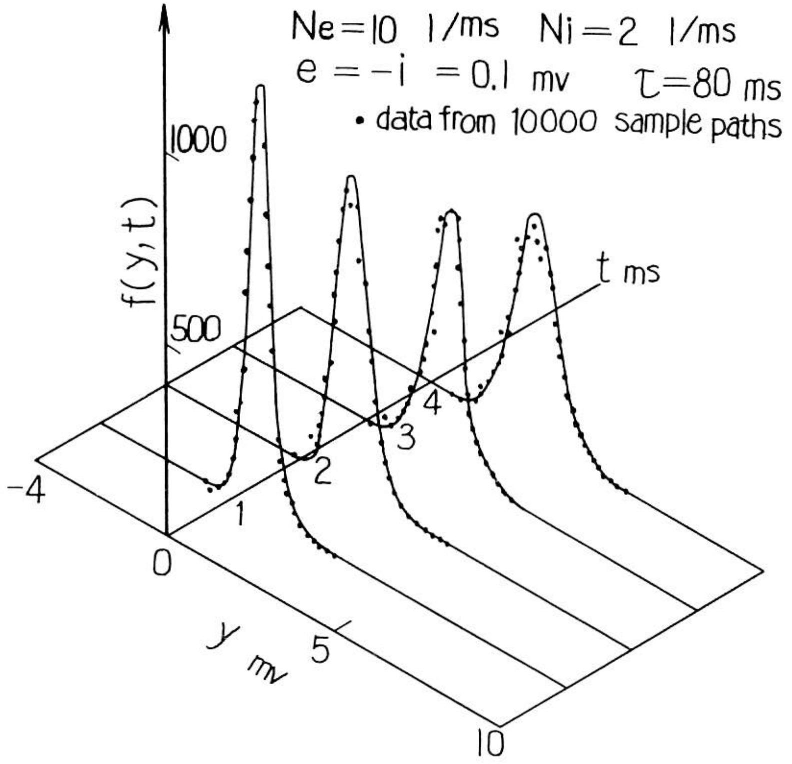

Fig. 3.1.c Transition probability density of neuron potential, numerical solution and digital simulation

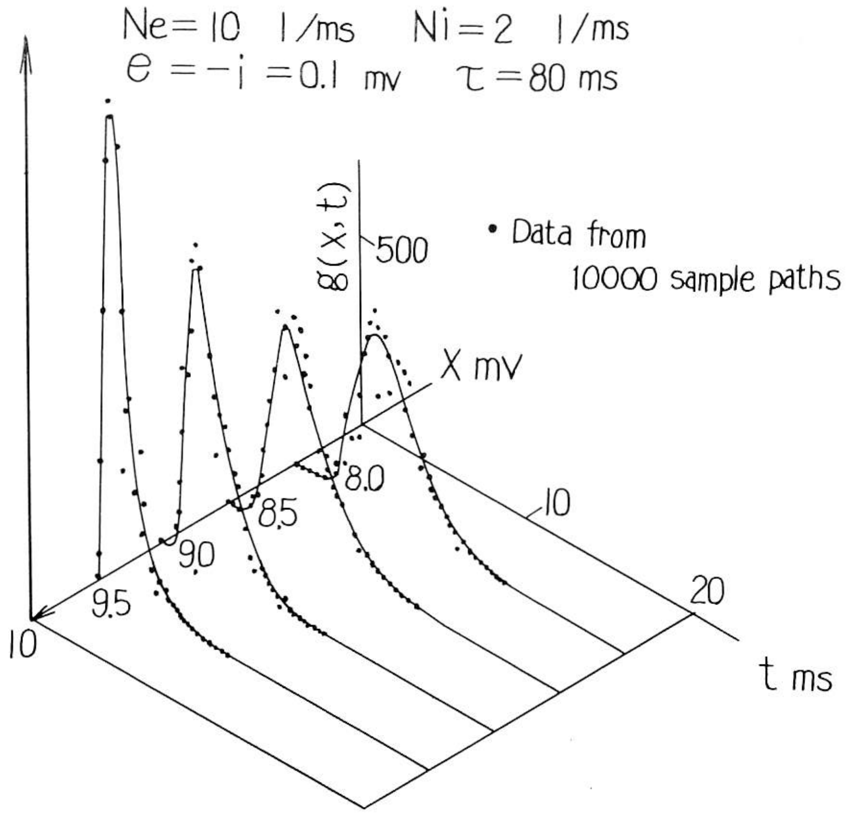

Fig. 3.1.d First passage time probability density, numerical solution and digital simulation

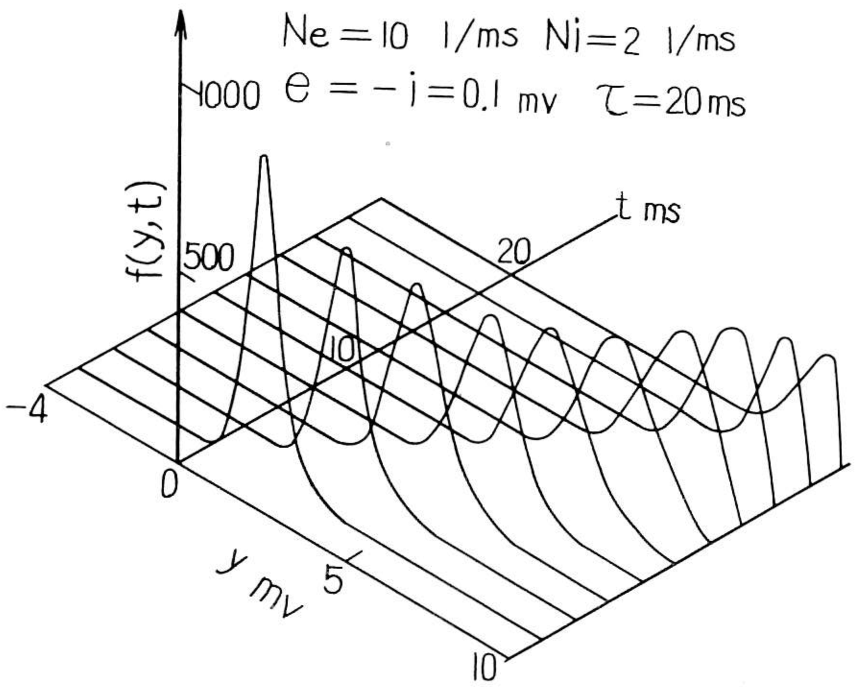

Fig. 3.2.a Transition probability density of the neuron potential, τ=20 ms

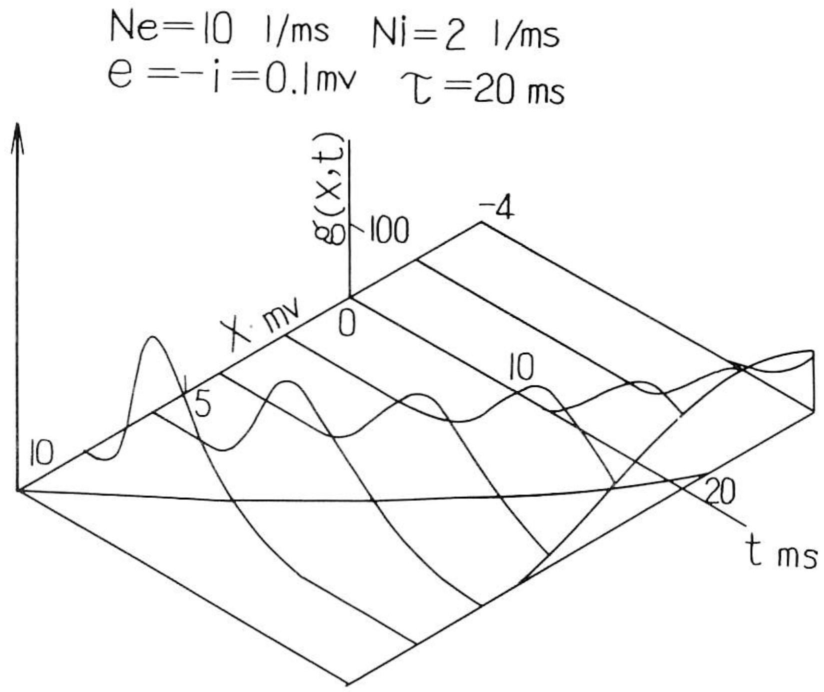

Fig. 3.2.b First passage time probability density, τ=20 ms

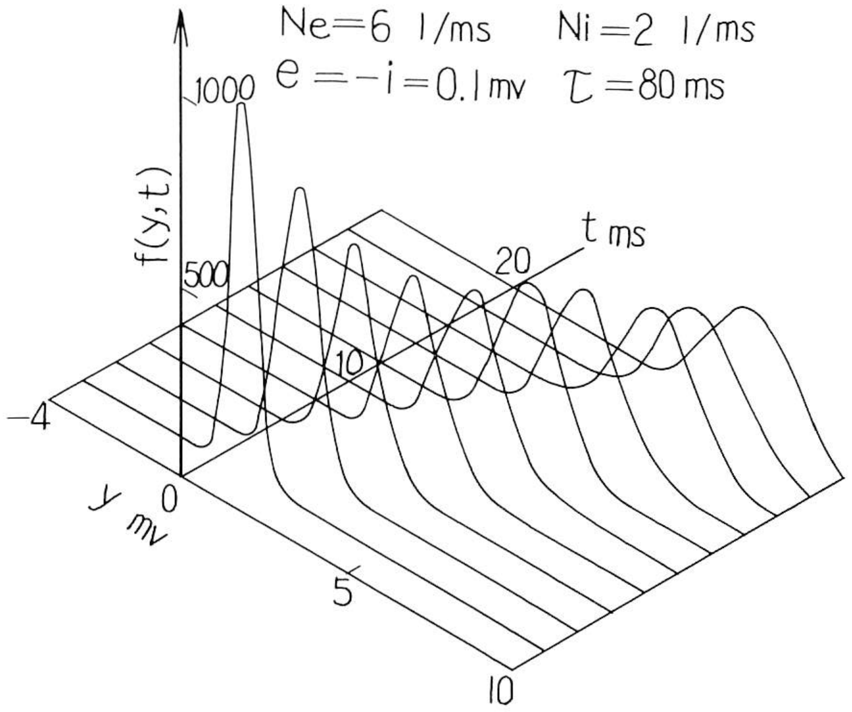

Fig. 3.3.a Transition probability density of the neuron potential, Ne=6 1/ms

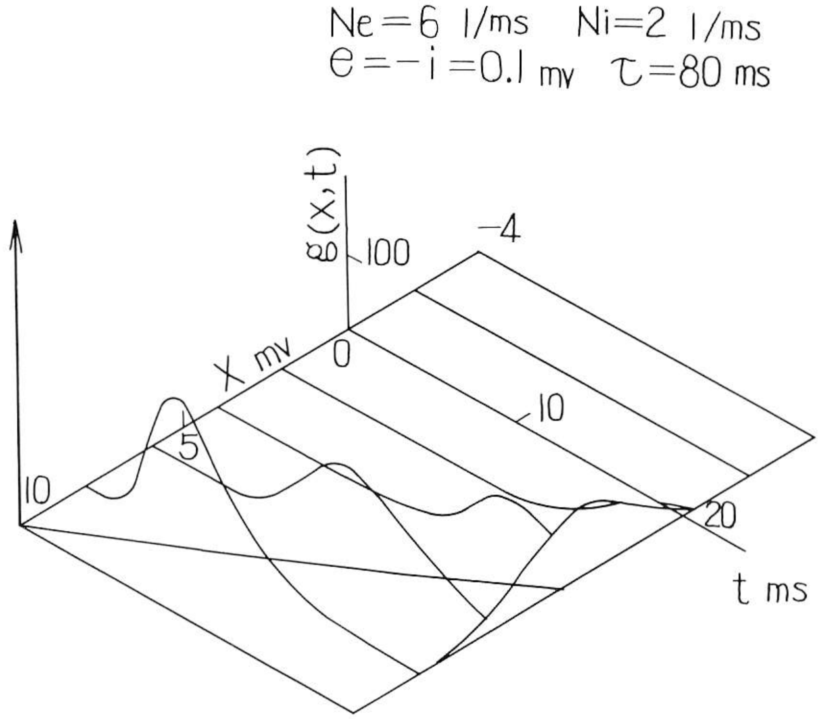

Fig. 3.3.b First passage time probability density, Ne=6 1/ms

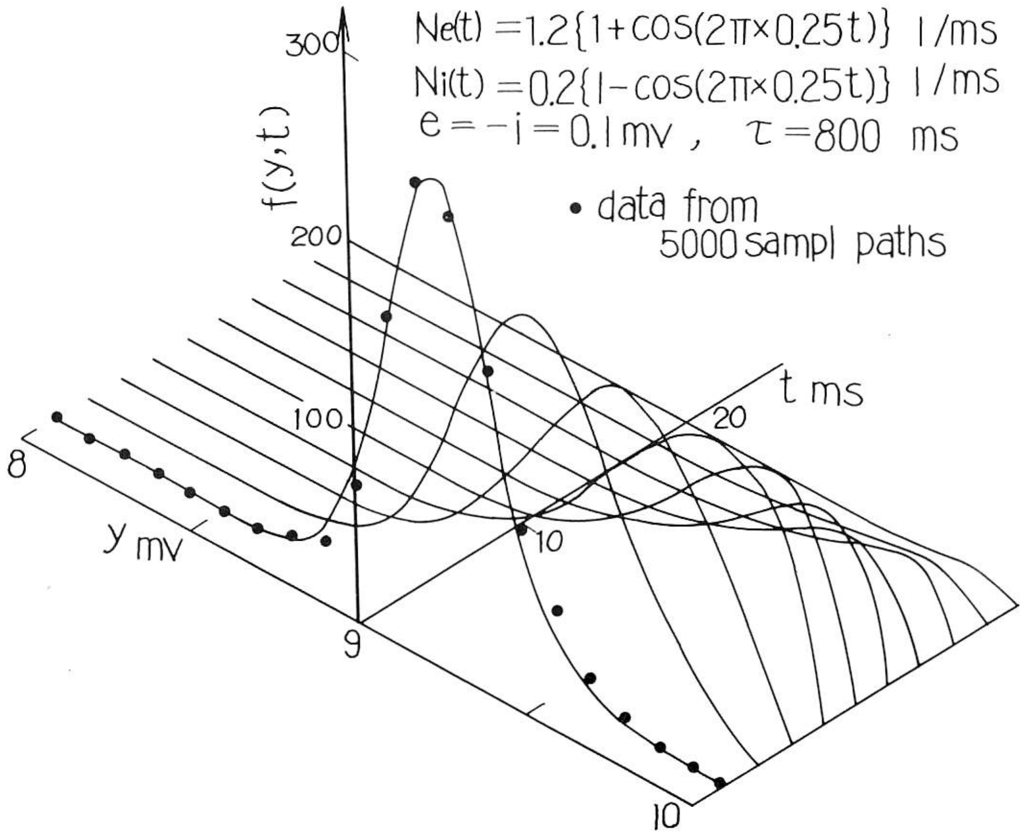

Fig. 3.4.a Transition probability density of the neuron potential, temporally inhomogeneous case

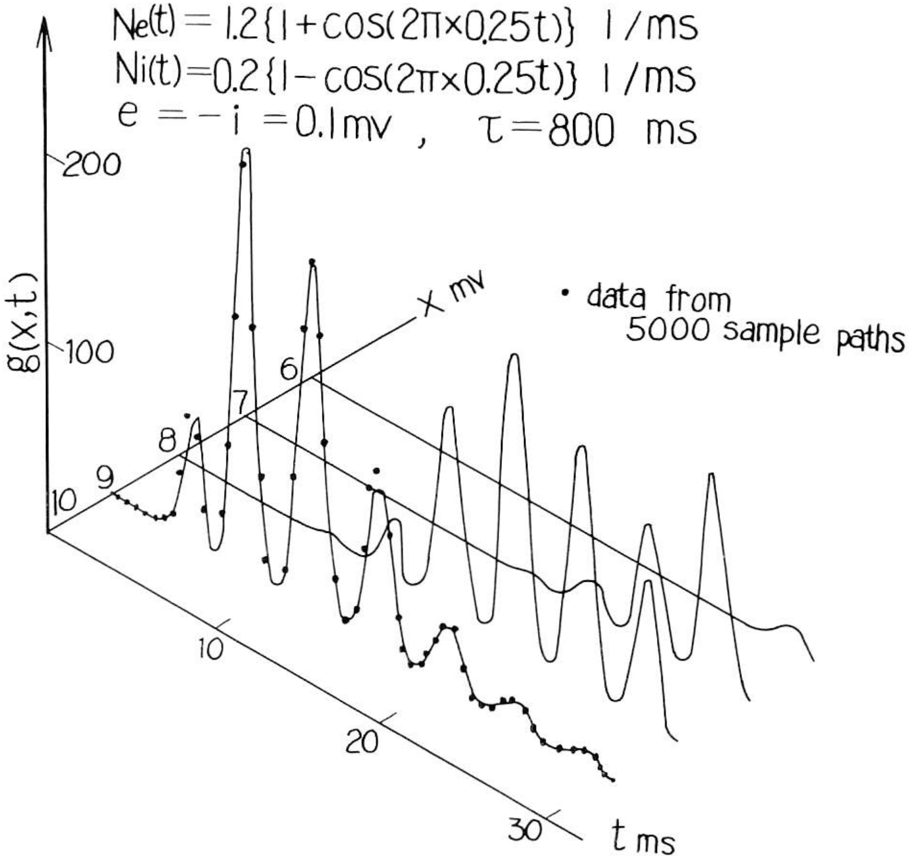

Fig. 3.4.b First passage time probability density, temporally inhomogeneous case

3.3 Discussion of Forced Type Neuron with Shunting Inhibition

In the preceeding section, the subtractive inhibition which lowers the neuron potential with a certain quantity was dealed with.

On the contrary, the shunting inhibition which divides or shunts the neuron potential is recognized by J. Y. Lettvin (1962), then G. G. Furman and U. Büttner et. al. discussed this type of inhibition through analog models (1968). But signals and informations are carried by the pulse frequency modulation mainly, therefore, discussions containing the pulse characteristics are necessary. Moreover, it has a significant meaning to investigate the case that the pulse trains have fluctuations as one of random properties in the nervous system.

This section treats how input pulse trains which are based on Poisson processes are influenced by the shunting inhibition. This case has not been reported because a state-dependent noise exists. And also the comparison with the subtractive inhibition is presented.

3.3.1 Assumptions on the Forced Type Neuron with Shunting Inhibition

A neuron treated here has following properties.

a. The excitatory input pulse train $dE(t,\omega_1)$ and the inhibitory input pulse train $dI(t,\omega_2)$ are independent. Here, ω_1 and ω_2 denote sample points of a sample space Ω. $E(t,\omega_1)$ is a sample path of the Poisson process which causes the excitatory pulse application with probability $Ne(t)\Delta t + o(\Delta t)$ in the interval $[t,t+\Delta t)$. $I(t,\omega_2)$

is the same with probability $Ni(t)\Delta t + o(\Delta t)$.

b. The neuron potential $Y(t,\bar{\omega})$ is right continuous, and an excitatory input pulse adds e to the neuron potential and an inhibitory input pulse lowers it so that the difference against r becomes $1/\alpha$ $(\alpha > 1)$, where e is a positive constant, r is the lower limit of the neuron potential and $\bar{\omega} = (\omega_1,\omega_2)$. This type of inhibition is called the shunting inhibition. On the contrary, the subtractive inhibition lowers the neuron potential by a certain quantity i (<0).

c. In the period during which no input is applied, the neuron potential approaches the rest value η with a time constant τ.

d. When the neuron potential reaches the threshold d, the neuron fires and the neuron potential is reset to x.

e. After a firing, $s \leqq t < s+\delta$ is the absolute refractory period and the neuron potential is never influenced by inputs but decays deterministically with a time constant τ_r.

f. The varying quantities of the neuron potential by an excitatory or an inhibitory input pulse are sufficiently small in comparison with $d-x$.

Then a sample path of the neuron potential is expressed as follows.

$$Y(t,\bar{\omega}) = (x-\eta)\varepsilon^{-\frac{t-s}{\tau_r}} + \eta \qquad (s \leqq t < s+\delta) \qquad (3.47)$$

$$Y(t,\bar{\omega}) = \int_{s+\delta}^{t} \varepsilon^{-\frac{t-u}{\tau}} \left[dE(u,\omega_1) + \frac{\alpha-1}{\alpha}\{ Y(u-0,\bar{\omega}) - r \} dI(u,\omega_2) \right]$$

$$+ \{ Y(s+\delta,\overline{\omega}) - \eta \}\varepsilon^{-\frac{t-(s+\delta)}{\tau}} + \eta \qquad (t \geqq s+\delta) \qquad (3.48)$$

This shows that the neuron potential is a state-dependent stochastic process. As $Y(s+\delta,\overline{\omega})$ and η are deterministic quantities, they can be omitted by transformations $s+\delta \to s$, $Y-\eta \to Y$, then

$$Y(t,\overline{\omega}) = \int_s^t \varepsilon^{-\frac{t-u}{\tau}} [\, dE(u,\omega_1) + \frac{\alpha-1}{\alpha}\{ Y(u-0,\overline{\omega}) - r \}dI(u,\omega_2) \,] + x\varepsilon^{-\frac{t-s}{\tau}} \qquad (t \geqq s) \qquad (3.49)$$

is obtained. Hereafter, this case is treated.

3.3.2 Discussion of the Forced Type Neuron with Shunting Inhibition using Kolmogorov's Equation

The forward equation is deduced in a following manner which is similar to that of the section 3.3.2 .

There may be three transitions in a very short period $[t,t+\Delta t)$. If an excitatory pulse is applied, the transition is

$$(y-e+y\frac{\Delta t}{\tau} , t) \quad \to \quad (y , t+\Delta t).$$

If an inhibitory pulse is applied, the transition is

$$[\{(y-r)\alpha+r\}(1+\frac{\Delta t}{\tau}) , t] \quad \to \quad (y , t+\Delta t).$$

If no pulse is applied, the transition is

$$(y+y\frac{\Delta t}{\tau} , t) \quad \to \quad (y , t+\Delta t).$$

The state transition when an inhibitory pulse is applied is explained as follows. If an inhibitory pulse is applied in $[t,t+\Delta t)$ and

$Y(t+\Delta t,\overline{\omega}) = y$, $Y(t,\overline{\omega})$ must have taken the value neither inhibited nor relaxed. Therefore, the state at time t is a product of $\{(y-r)\alpha+r\}$ and $(1+\frac{\Delta t}{\tau})$.

These three transitions occur with probability $Ne(t)\Delta t + o(\Delta t)$, $Ni(t)\Delta t + o(\Delta t)$ and $1-\{Ne(t)+Ni(t)\}\Delta t + o(\Delta t)$ respectively, therefore,

$$\begin{aligned} f(y,t+\Delta t\,|\,x,s) &= Ne(t)\Delta t f(y-e+y\frac{\Delta t}{\tau},t\,|\,x,s) \\ &\quad + Ni(t)\Delta t f[\{(y-r)\alpha+r\}(1+\frac{\Delta t}{\tau}),t\,|\,x,s] \\ &\quad + [1-\{Ne(t)+Ni(t)\}\Delta t]f(y+y\frac{\Delta t}{\tau},t\,|\,x,s) \end{aligned} \tag{3.50}$$

holds.

As the stochastic process $Y(t,\overline{\omega})$ is a Markov process, the Chapman-Kolmogorov equation holds. And the transition probability density of the neuron potential is obtained from

$$\frac{\partial f(y,t\,|\,x,s)}{\partial t} = \sum_{n=1}^{\infty} \frac{(-1)^n}{n!} \left(\frac{\partial}{\partial y}\right)^n A_n(y,t) f(y,t\,|\,x,s) \tag{3.51}$$

where

$$A_n(y,t) = \lim_{\Delta t\to+0} \frac{1}{\Delta t} \int_{\mathcal{D}} dz z^n f(y+z,t+\Delta t\,|\,y,t) \quad . \tag{3.52}$$

Then, the equations (3.50) and (3.52) produce

$$A_1(y,t) = Ne(t)e + Ni(t)\left(\frac{1-\alpha}{\alpha}\right)(y-r) - \frac{y}{\tau} \tag{3.53}$$

$$A_n(y,t) = Ne(t)e^n + Ni(t)\left(\frac{1-\alpha}{\alpha}\right)^n (y-r)^n \quad (n \geqq 2) \ . \tag{3.54}$$

Since it is assumed that the varying quantities of the neuron potential, e and $(1-\alpha)(y-r)/\alpha$, are sufficiently small in comparison with $d-x$, $A_n(y,t)$ $(n \geqq 3)$ can be neglected and the following equation is obtained.

$$\frac{\partial f(y,t|x,s)}{\partial t} = -\frac{\partial}{\partial y}\{Ne(t)e + Ni(t)\left(\frac{1-\alpha}{\alpha}\right)(y-r) - \frac{y}{\tau}\}f(y,t|x,s) + \frac{1}{2}\frac{\partial^2}{\partial y^2}\{Ne(t)e^2 + Ni(t)\left(\frac{1-\alpha}{\alpha}\right)^2(y-r)^2\}f(y,t|x,s) \tag{3.55}$$

The adjoint equation against the above is obtained as

$$-\frac{\partial f(y,t|x,s)}{\partial s} = \{Ne(s)e + Ni(s)\left(\frac{1-\alpha}{\alpha}\right)(x-r) - \frac{x}{\tau}\}\frac{\partial f(y,t|x,s)}{\partial x} + \frac{1}{2}\{Ne(s)e^2 + Ni(s)\left(\frac{1-\alpha}{\alpha}\right)^2(x-r)^2\}\frac{\partial^2 f(y,t|x,s)}{\partial x^2} \tag{3.56}$$

by a similar procedure. And the first passage time probability density is obtained from the law of the probability conservation.

$$g(d,t|x,s) = -\frac{\partial}{\partial t}\int_r^d f(y,t|x,s)dy \tag{3.57}$$

And the subsequent methods differ depending on whether input pulse trains are temporally homogeneous or not. Hence the separate discussions are made.

a. Temporally Homogeneous Case

This is the case that $Ne(t)=Ne$ and $Ni(t)=Ni$. And the stochastic process $Y(t,\overline{\omega})$ becomes temporally homogeneous and $f(y,t|x,s)$ can be denoted by $f(y,t,x)$, and $g(d,t|x,s)$ by $g(d,t,x)$. In this case, the equations (3.55), (3.56) and (3.57) become as follows.

$$\frac{\partial f(y,t,x)}{\partial t} = -\frac{\partial}{\partial y}\{Ne\varepsilon + Ni\left(\frac{1-\alpha}{\alpha}\right)(y-r) - \frac{y}{\tau}\}f(y,t,x) + \frac{1}{2}\frac{\partial^2}{\partial y^2}\{Ne\varepsilon^2 + Ni\left(\frac{1-\alpha}{\alpha}\right)^2(\cancel{x}y-r)^2\}f(y,t,x) \quad (3.58)$$

$$\frac{\partial f(y,t,x)}{\partial t} = \{Ne\varepsilon + Ni\left(\frac{1-\alpha}{\alpha}\right)(x-r) - \frac{x}{\tau}\}\frac{\partial f(y,t,x)}{\partial x} + \frac{1}{2}\{Ne\varepsilon^2 + Ni\left(\frac{1-\alpha}{\alpha}\right)^2(x-r)^2\}\frac{\partial^2 f(y,t,x)}{\partial x^2} \quad (3.59)$$

$$g(d,t,x) = -\frac{\partial}{\partial t}\int_r^d f(y,t,x)dy \quad (3.60)$$

From the equations (3.59) and (3.60),

$$\frac{\partial g(d,t,x)}{\partial t} = \{Ne\varepsilon + Ni\left(\frac{1-\alpha}{\alpha}\right)(x-r) - \frac{x}{\tau}\}\frac{\partial g(d,t,x)}{\partial x} + \frac{1}{2}\{Ne\varepsilon^2 + Ni\left(\frac{1-\alpha}{\alpha}\right)^2(x-r)^2\}\frac{\partial^2 g(d,t,x)}{\partial x^2} \quad (3.61)$$

is derived. The initial condition and the boundary conditions for the equation (3.58) are

IC $\quad f(y,0,x) = \delta(y-x) \quad (3.62)$

BC $\quad f(d,t,x) = 0 \quad (3.63)$

BC $\quad [-\{Ne\varepsilon + Ni\left(\frac{1-\alpha}{\alpha}\right)(y-r) - \frac{y}{\tau}\}f(y,t,x) + \frac{1}{2}\frac{\partial}{\partial y}\{Ne\varepsilon^2 + Ni\left(\frac{1-\alpha}{\alpha}\right)^2(y-r)^2\}f(y,t,x)]_{y=r} = 0 \, . \quad (3.64)$

The equation (3.62) means that $y=x$ at $t=0$. The equation (3.63) means that $y=d$ is the threshold. And the equation (3.64) implies that $y=r$ is the lower limit of the neuron potential. The initial condition and the boundary conditions for the equation (3.61) are given as

IC $$g(d,0,x) = 0 \qquad (x \neq d) \tag{3.65}$$

BC $$g(d,t,d) = \delta(t) \tag{3.66}$$

BC $$\left[\frac{\partial g(d,t,x)}{\partial x}\right]_{x=r} = 0 \ . \tag{3.67}$$

The equations (3.65) and (3.66) mean that only the state which lay on the threshold lies on it unless time passes. And the equation (3.67) implies that r is the lower limit and the first passage time probability densities starting from the neighborhood of r are equivalent.

The mean value of the first passage time is defined by

$$M(x) = \mathcal{E}\{\mathfrak{T}_d(\bar{\omega})\} = \int_0^{\infty} t g(d,t,x)dt \quad . \tag{3.68}$$

From the equations (3.61), (3.65), (3.66) and (3.67) as well as (3.68),

$$\frac{1}{2}\{\mathrm{Ne}e^2 + \mathrm{Ni}\left(\frac{1-\alpha}{\alpha}\right)^2 (x-r)^2\}\frac{d^2M(x)}{dx^2} + \{\mathrm{Ne}e + \mathrm{Ni}\left(\frac{1-\alpha}{\alpha}\right)(x-r) - \frac{x}{\tau}\}\frac{dM(x)}{dx} = -1 \tag{3.69}$$

BC $$M(d) = 0 \tag{3.70}$$

BC $$\left[\frac{dM(x)}{dx}\right]_{x=r} = 0 \tag{3.71}$$

are obtained. The solution is given as

$$M(x) = \Xi(d) - \Xi(x) \tag{3.72}$$

where

$$\Xi(x) = \int \varepsilon^{-\int \frac{2\Psi(x)}{\Phi(x)} dx} \{\chi(x) - \chi(r)\} dx \tag{3.73}$$

$$\Phi(x) = Ne\theta^2 + Ni\left(\frac{1-\alpha}{\alpha}\right)^2 (x-r)^2 \tag{3.74}$$

$$\Psi(x) = Ne\theta + Ni\left(\frac{1-\alpha}{\alpha}\right)(x-r) - \frac{x}{\tau} \tag{3.75}$$

$$\chi(x) = \int \frac{2\varepsilon^{\int \frac{2\Psi(x)}{\Phi(x)} dx}}{\Phi(x)} dx \quad . \tag{3.76}$$

b. Temporally Inhomogeneous Case

In this case, the backward equation is not available. Therefore, the equation (3.55) is solved under the conditions

IC $$f(y,s|x,s) = \delta(y-x) \tag{3.77}$$

BC $$f(d,t|x,s) = 0 \tag{3.78}$$

BC $$[-\{Ne(t)\theta + Ni(t)\left(\frac{1-\alpha}{\alpha}\right)(y-r) - \frac{y}{\tau}\} f(y,t|x,s) + \frac{1}{2}\frac{\partial}{\partial y}\{Ne(t)\theta^2 + Ni(t)\left(\frac{1-\alpha}{\alpha}\right)^2 (y-r)^2\} f(y,t|x,s)]_{y=r} = 0 \quad . \tag{3.79}$$

Then, the equation (3.57) is used to obtain the first passage time probability density.

3.3.3 Results

Here are shown results on neurons with shunting inhibition by means of the numerical analysis, and the comparison with subtractive inhibition is made.

a. Temporally Homogeneous Case

Fig. 3.5.a shows the transition probability density of the neuron potential which lay on $y=x=0$ mv at time 0 ms. This is the solution of the equation (3.58) conditioned by the equations (3.62), (3.63) and (3.64). Dots are the values from the digital simulation by 5,000 sample paths which satisfy the equation (3.49). Fig. 3.5.b is the first passage time probability density with common parameters to Fig. 3.5.a and is the solution of the equation (3.61) conditioned by the equations (3.65), (3.66) and (3.67). Fig.3.5.a corresponds to the section of $x=0$ mv in Fig. 3.5.b. For example, the neuron potential begins to reach the threshold $d=10$ mv from about $t=5$ ms and completes to reach it at about $t=18$ ms. This can be observed from the section of $x=0$ mv in Fig. 3.5.b. A curve on the x-t plane is the mean value of the first passage time which is the solution of the equation (3.69), i.e. (3.72).

Fig. 3.6.a and Fig. 3.6.b are the transition probability density of the neuron potential and the first passage time probability density respectively, in which case $\alpha=1.012$ and the shunting inhibition is stronger, therefore, the time when the neuron potential reaches the threshold becomes tardier.

b. Temporally Inhomogeneous Case

Here is treated the case that the input pulse trains are modulated sinusoidally. Fig. 3.7.a shows the transition probability density of the neuron potential which lay on $y=x=0$ mv at time $t=s=0$ ms , which is the solution of the equation (3.55) with conditions (3.77), (3.78) and (3.79). Dots are the values from 5,000 sample paths. Fig. 3.7.b is the first passage time probability density. It is obtained in the same manner as Fig. 3.7.a . In this figure, an important property, the multimodality, is appeared in the first passage time probability density according to the pulse frequency modulation of inputs.

c. Comparison of Shunting Inhibition with Subtractive Inhibition

Fig. 3.8 shows the comparison of both inhibitions with the common parameters except α and i in the temporally homogeneous case. A continuous curve is the case of the shunting inhibition which satisfies the equation (3.58) and a dotted line is that of the subtractive inhibition which satisfies the equation (3.28). The difference between both types of inhibitions depends on x which is the reset value of the neuron potential. And this is due to the fact that the inhibition value of each inhibitory pulse is large when the neuron potential is close to the threshold, and small when it is close to the lower limit. Therefore, in Fig. 3.8 , the first passage time of the shunting inhibition is tardier than that of the subtractive inhibition when x is close to d , and the property is reversed when x is close to r . And the mean value of the first passage time of the shunting inhibition shows stronger nonlinearity than that of the subtactive inhibition.

In the next place, the temporally inhomogeneous case is compared. Fig.3.9 is the first passage time probability density in the case of the subtractive inhibition, which is the solution of the equation (3.27) using the equation (3.23). And this has the common parameters to those of Fig. 3.7.b except α and i . The difference between both also depends on x , and in these figures when x is close to d , the first passage time probability density of the subtractive inhibition (Fig. 3.7.b) is sharper than that of the shunting inhibition (Fig. 3.9) because the inhibition effect of the subtractive one is smaller than that of the shunting one. And this property is reversed when x is close to r .

Remark

In this section, the problem of the state-dependent process was presented and discussed. In that problem, the correction term in the differential generator is required generally. But it was not introduced in this section, because the method of obtaining the differential generator is based on the state transition and it contains the correction procedure.

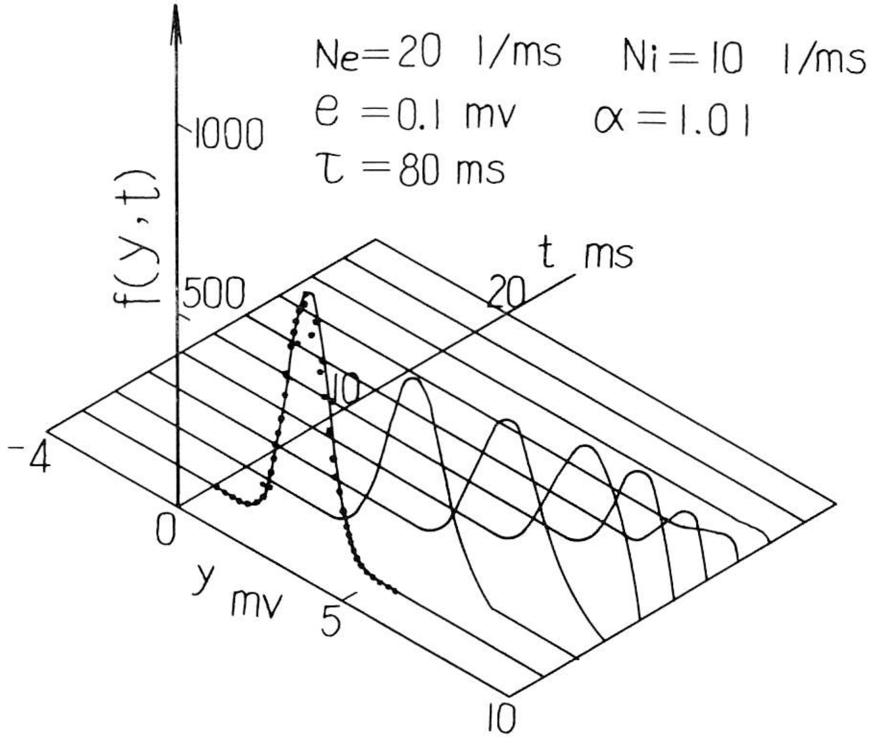

Fig. 3.5.a Transition probability density of the neuron potential, shunting inhibition

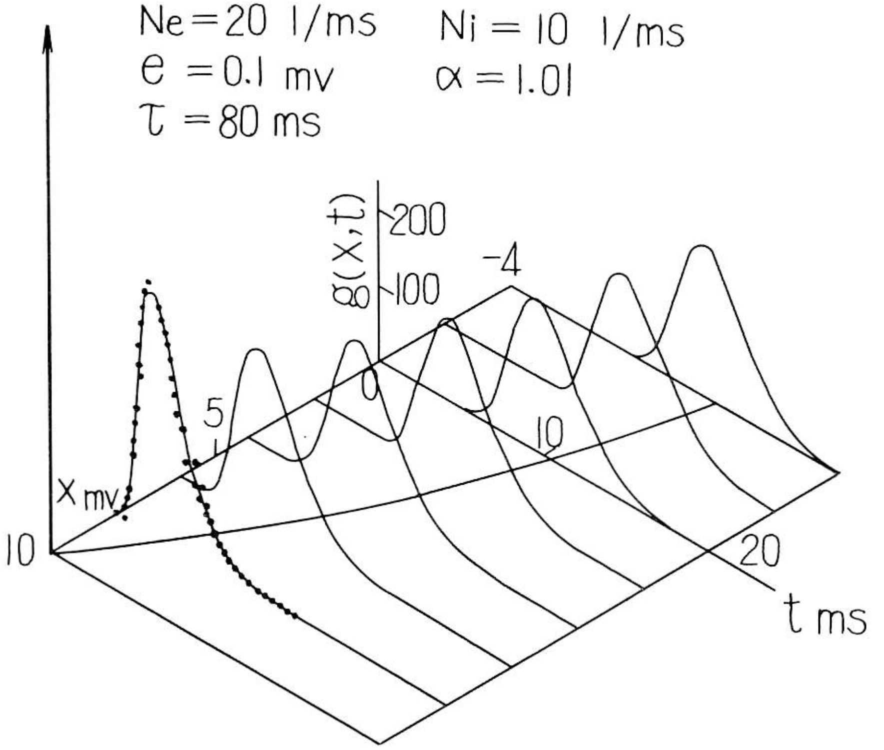

Fig. 3.5.b First passage time probability density, shunting inhibition

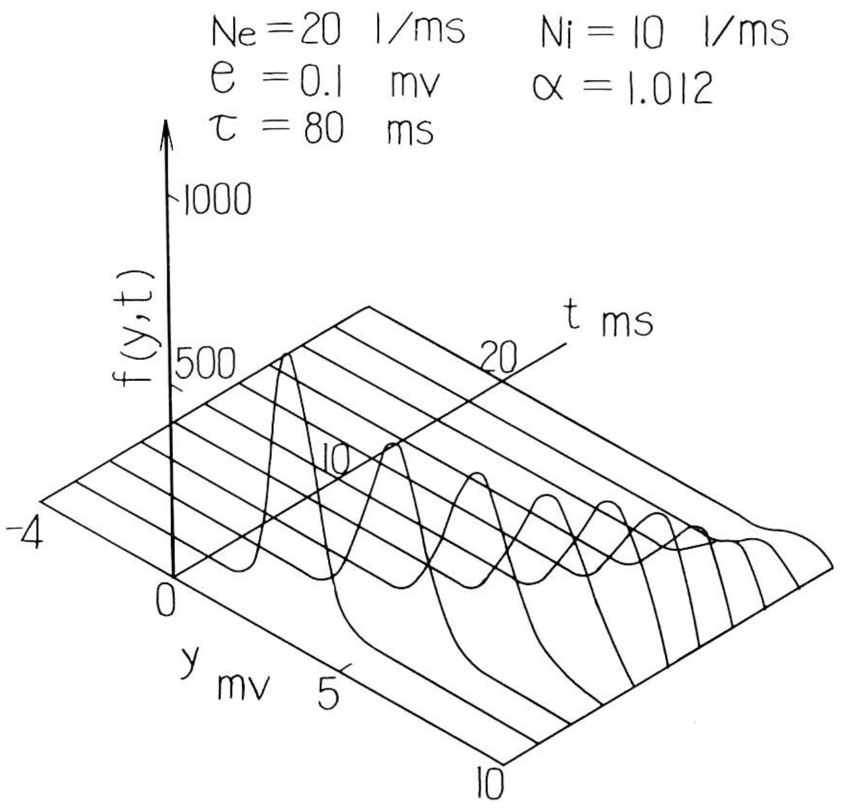

Fig. 3.6.a Transition probability density of the neuron potential, shunting inhibition, $\alpha=1.012$

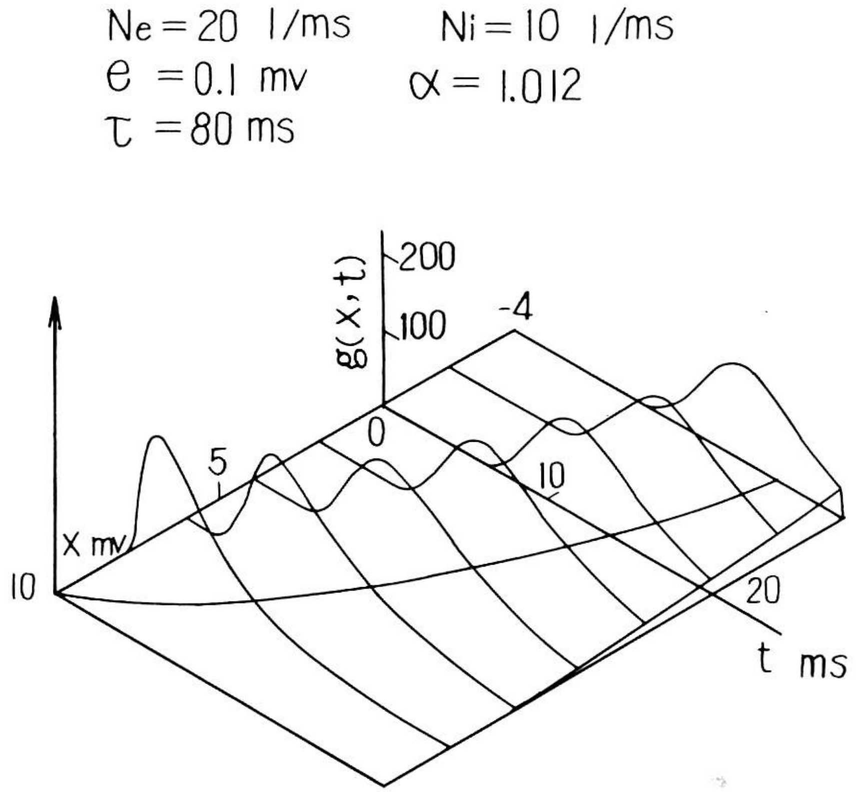

Fig. 3.6.b First passage time probability density,
shunting inhibition, $\alpha=1.012$

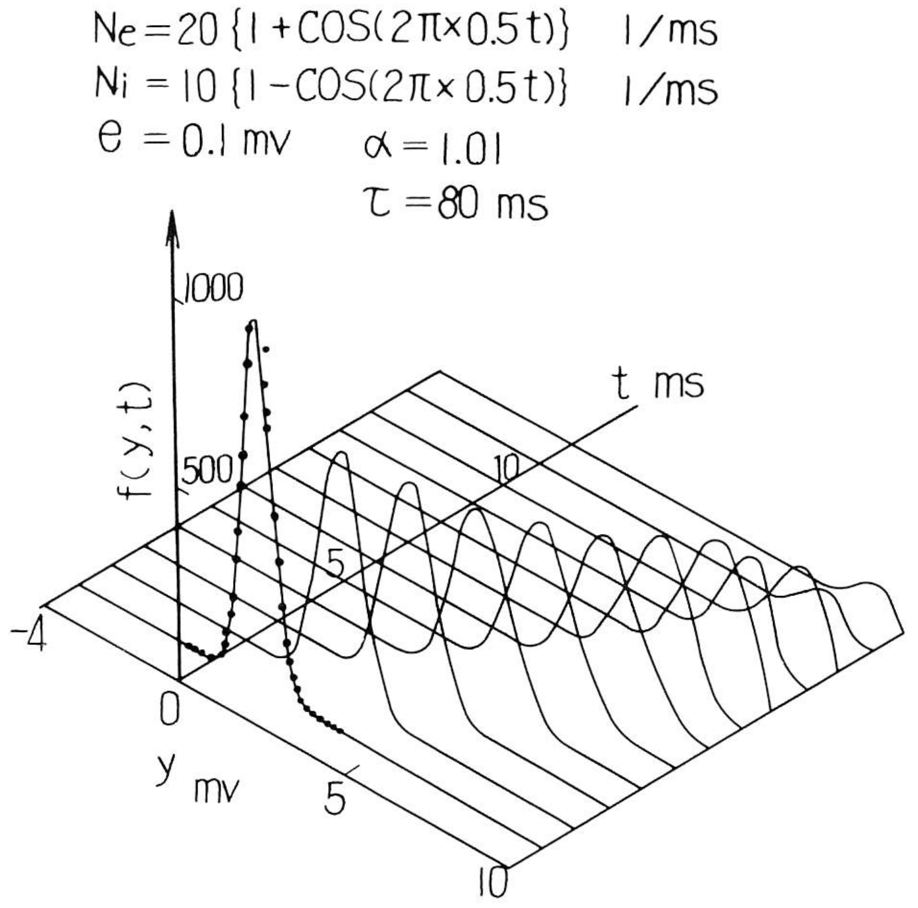

Fig. 3.7.a Transition probability density of the neuron potential, shunting inhibition, temporally inhomogeneous case

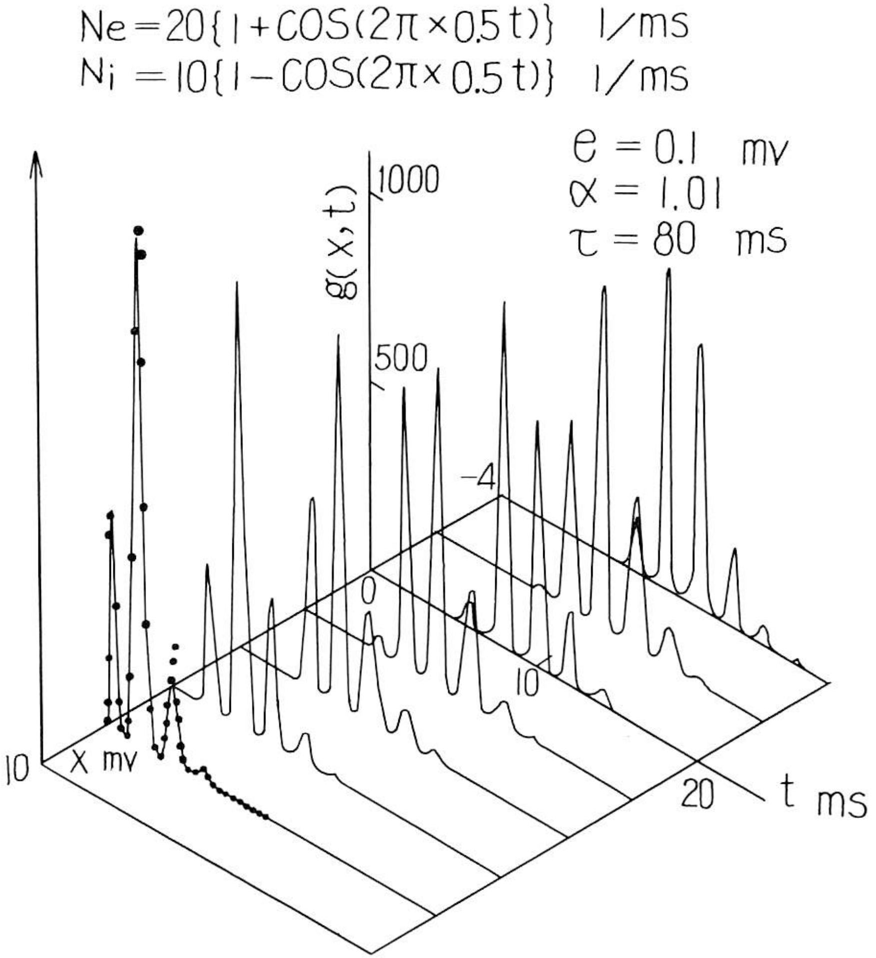

Fig. 3.7.b First passage time probability density, shunting inhibition, temporally inhomogeneous case

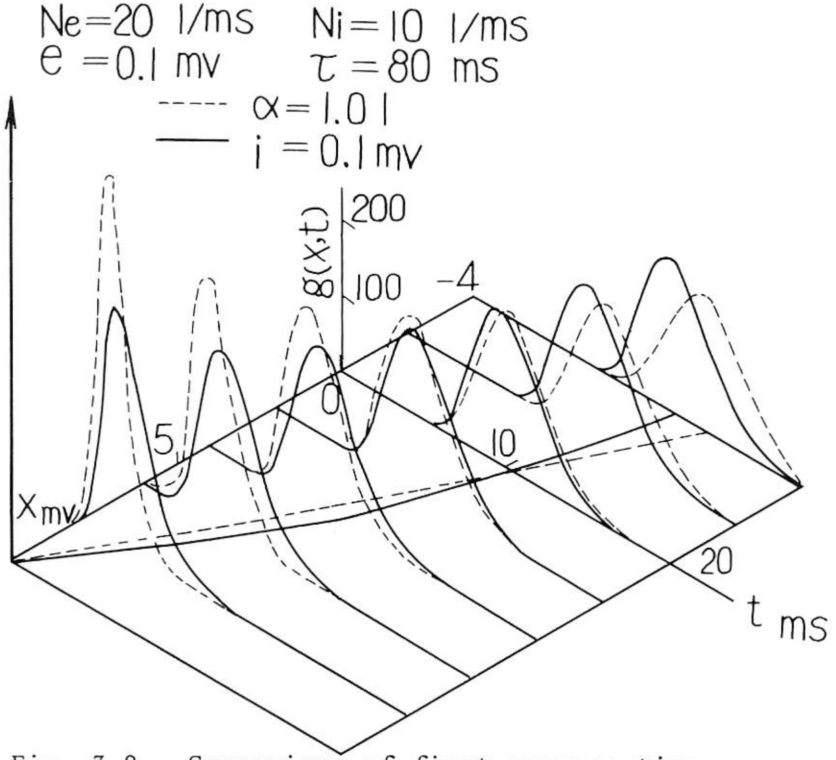

Fig. 3.8 Comparison of first passage time probability densities, subtractive inhibition and shunting inhibition, temporally homogeneous case

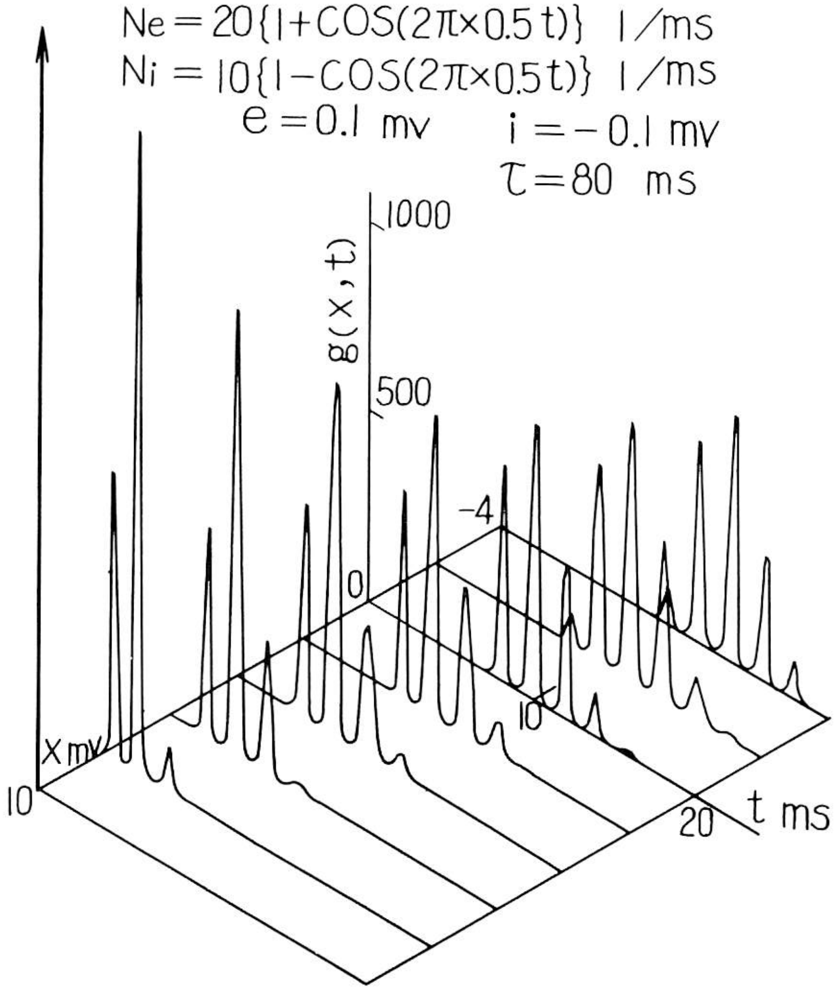

Fig. 3.9 First passage time probability density,
subtractive inhibition,
temporally inhomogeneous case,
This figure is compared with Fig. 3.7.b .

3.4 Output Spike Interval Density

There is a case that the stochastic input pulse trains are modulated periodically. Such a situation is made in order to study the information processes in nervous systems by applying a periodical stimulus. In this case, it is of great importance to calculate the output spike interval density because it is the quantity which characterizes the periodic pulse frequency modulation and can be measured easily in an in vivo experiment.

3.4.1 Representation of Output Spike Interval Density

The first passage time probability density and the output spike interval density are equivalent to each other in the temporally homogeneous case, however, they differ in the inhomogeneous case. In the periodic inhomogeneous case, their difference is concentrated to the fact that the input phase is always fixed in the first passage time problem but it is regarded as a random variable in the output spike interval problem. Namely, the input phase differs for every spike and it distributes statistically.

Then, it becomes necessary to consider the method to approximate the output spike interval density using the first passage time probability densities with various phases. The first passage time probability density depends on the initial phase of the input signal which is denoted by ϕ_s at time s . The phase dependent first passage time probability density is denoted by

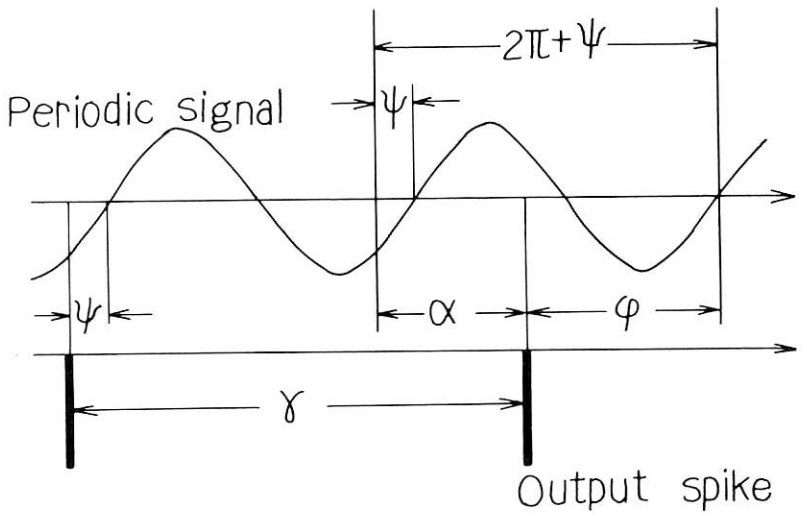

Fig. 3.10 Relation between two contiguous input phases

$$g_{\phi_s=\phi}(d,t|x,s) \quad .$$

Clearly,

$$g_{\phi_s=\phi}(d,t+s|x,s) = g_{\phi_0=\phi}(d,t|x,s) \quad . \tag{3.80}$$

For brevity, the right side of the equation (3.80) is redenoted by $h_\phi(d,t,x)$, which is the probability density with respect to t that the initial phase of the inputs and the state are ϕ and x respectively and the neuron potential reaches d after time t. Then the output spike interval density is defined by

$$h(d,t,x) = \int_0^{2\pi} h_\phi(d,t,x)q(\phi)d\phi \tag{3.81}$$

where $q(\phi)$ is the probability density of the input phase. And it is obtained by the following procedure. The conditional probability density of two contiguous input phase ψ and ϕ is introduced and denoted by $q(\phi|\psi)$. The relation of ψ and ϕ is illustrated in Fig. 3.10. Then clearly

$$q(\psi|\phi)q(\phi) = q(\phi|\psi)q(\psi) \quad . \tag{3.82}$$

Hence,

$$\frac{q(\psi|\phi)}{q(\phi|\psi)}q(\phi) = q(\psi) \quad . \tag{3.83}$$

By integrating with ψ,

$$q(\phi) = \frac{1}{\displaystyle\int_0^{2\pi} \frac{q(\phi|\psi)}{q(\psi|\phi)}\,d\psi} \tag{3.84}$$

is obtained.

Then the problem of $q(\phi)$ becomes that of $q(\phi|\psi)$ and $q(\psi|\phi)$. And $q(\phi|\psi)$ can be obtained from $h_\psi(d,t,x)$ by overlaying itself with modulo T which is the period of the pulse frequency modulation. It is necessary to calculate the phase angle γ which corresponds to the first passage time.

$$h_\psi(d,t,x) \quad \rightarrow \quad \frac{T}{2\pi} h_\psi(d,\gamma,x) \qquad (3.85)$$

And $\mathfrak{h}_\psi(\alpha)$ is defined by

$$\mathfrak{h}_\psi(\alpha) = \sum_{k=0}^{\infty} \mathfrak{S}^k \left[\frac{T}{2\pi} h_\psi(d,2k\pi+\alpha,x)u(2k\pi+\alpha)\right] \qquad (3.86)$$

where $\mathfrak{S}$ is the operator which shifts a function of α to the left by 2π, and

$$u(2k\pi+\alpha) = \begin{cases} 1 & 0 \leqq \alpha < 2\pi \\ 0 & \text{otherwise} \end{cases} . \qquad (3.87)$$

The equation (3.86) is the probability density of α that the output is spiked when the angle gains $\gamma=\alpha+2k\pi$ $(k=0,1,2,\cdots)$ under the condition that the input phase is ψ.

Then between two contiguous input phases ψ and ϕ, the following relation holds.

$$\phi = \begin{cases} \psi - \alpha & 0 \leqq \alpha \leqq \psi \\ 2\pi + \psi - \alpha & \psi < \alpha < \pi \end{cases} \qquad (3.88)$$

Therefore,

$$q(\phi|\psi) = \begin{cases} \mathfrak{h}_\psi(\psi - \phi) & 0 \leqq \phi \leqq \psi \\ \mathfrak{h}_\psi(2\pi + \psi - \phi) & \psi < \phi < 2\pi \end{cases} . \qquad (3.89)$$

Using the equations (3.81) and (3.84) as well as (3.89), the output spike interval density is obtained. For the numerical calculations, it is necessary to approximate an integration by a summation and also truncate k' in the equation (3.86). Then, the output spike interval density can be expressed by

$$h(d,t,x) = \int_0^{2\pi} \frac{h_\phi(d,t,x)}{\int_0^{2\pi} \frac{q(\phi|\psi)}{q(\psi|\phi)} d\psi} d\phi \tag{3.90}$$

and approximated by

$$\sum_{i=1}^{n} \frac{h_{\phi_i}(d,t,x)}{\sum_{j=1}^{n} \frac{\Pr(\phi_i|\psi_j)}{\Pr(\psi_j|\phi_i)}} \tag{3.91}$$

where $\Pr(\phi_i|\psi_j)$ is defined by $\Pr(\phi_i - \frac{\Delta\phi}{2} \leqq \phi < \phi_i + \frac{\Delta\phi}{2} \mid \psi_j)$, and $\Delta\phi = \Delta\psi = \frac{2\pi}{n}$. The accuracy of this approximation depends on k in the equation (3.86) and n in the expression (3.91). But it is not necessary to require so large k or n , because the expression (3.85) takes very small value when γ is large, and $q(\phi|\psi)$ is smooth enough (see the section 3.4.2) .

3.4.2 Results

Here is shown an examples of the output spike interval density according to the procedure in the section 3.4.1 . And the method is applied to the forced type neuron with the subtractive inhibition. The approximation is performed with $k=8$ and $n=5$. Fig. 3.11.a shows that the first passage time probability density differs depending on the input phase of the sinusoidal pulse frequency modulation. From these $h_\phi(d,t,x)$'s , the approximated value of the input phase probability density is obtained. Fig. 3.11.b shows this. Bold poles are the approximated values which are constructed from $h_\phi(d,t,x)$'s of Fig. 3.11.a , and slender poles are the simulated values from 4,000 sample paths which satisfy the equation (3.16). The bold ones are used because it has a significant meaning that the output spike interval density can be obtained from the first passage time probability densities without using any values of the digital simulation. Then from the expression (3.91), the output spike interval density is obtained and it is shown in Fig. 3.11.c . Slender poles show the values from the digital simulation using 4,000 sample paths and a continuous curve is the approximated value. They are in good agreement.

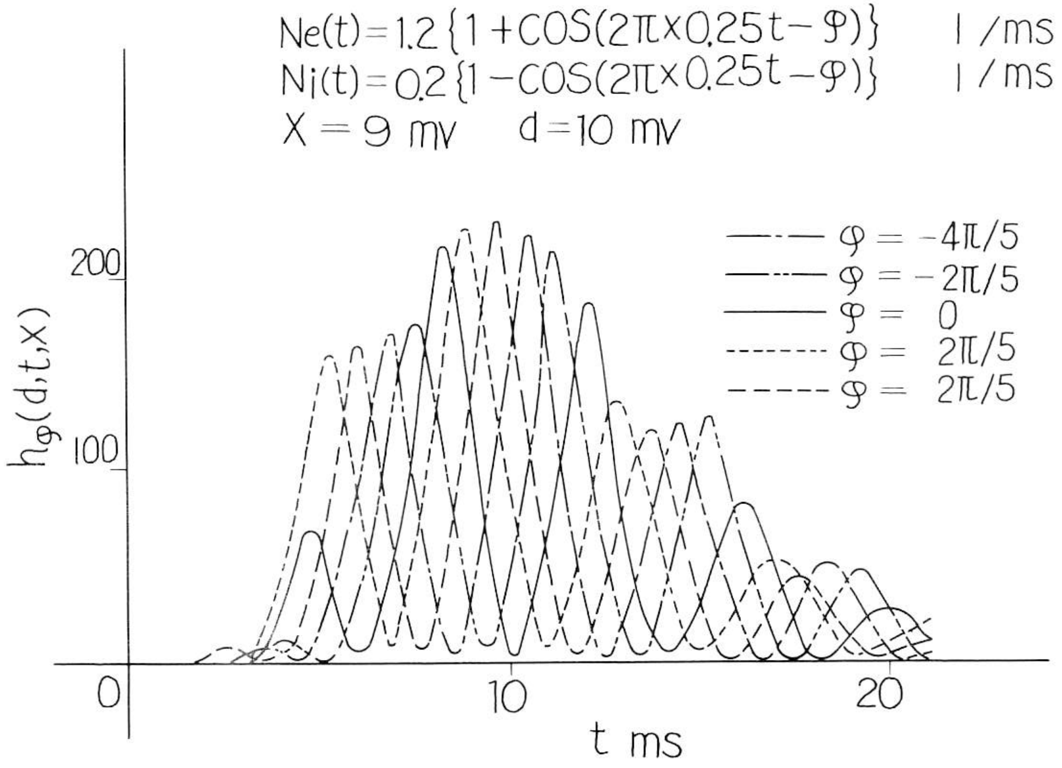

Fig. 3.11.a First passage time probability densities with various phases

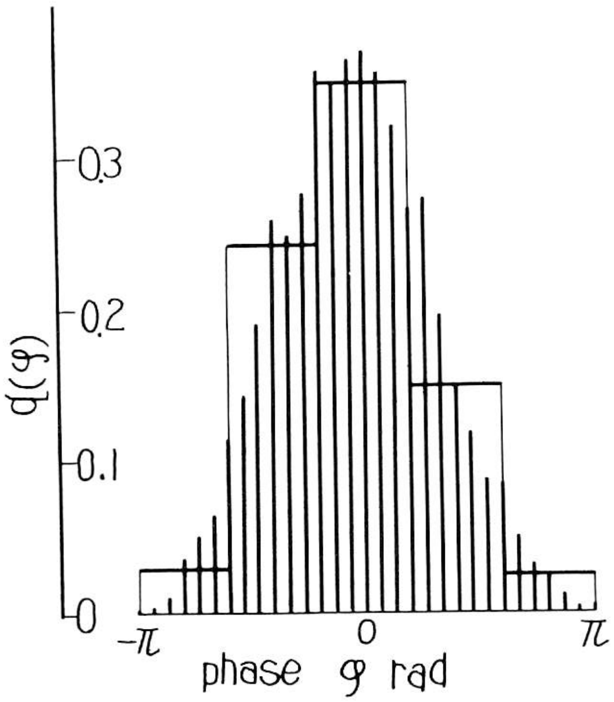

Fig. 3.11.b Density of input phase.
Slender poles are the values from the digital simulation using 4,000 sample paths and the bold ones are the values approximated from the first passage time probability densities.

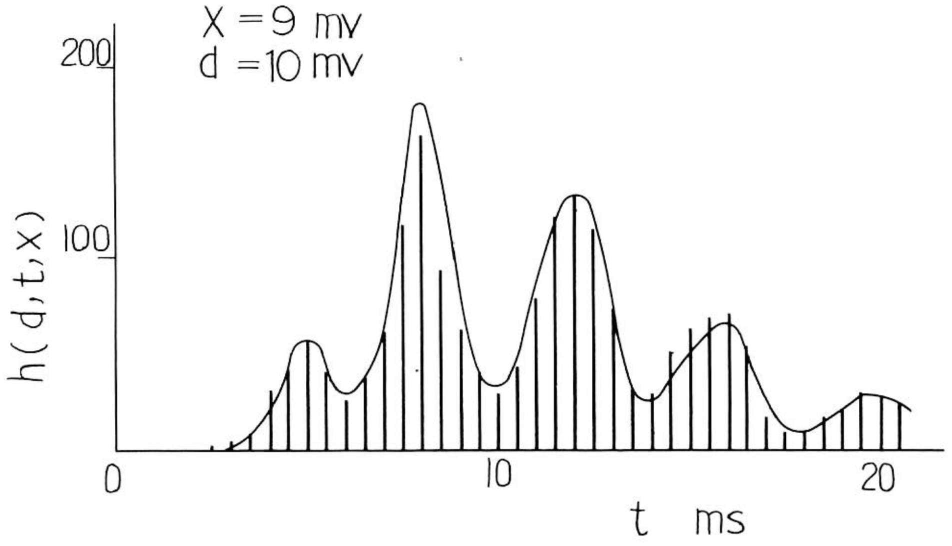

Fig. 3.11.c Output spike interval density.
A curve is the value from the first passage time densities and slender poles show the values of the digital simulation using 4,000 sample paths.

3.5 Concluding Remarks

In this section, several problems on forced type neurons were discussed. The superposition of pulse trains were presented in the section 3.1 . The first case was that of deterministic pulse trains and the second case was that of stochastic pulse trains. The second one should be applied to the problem of neurons because there is an irregularity in neural pulse trains which is not a superficial appearance of complex information codes.

In the section 3.2 and 3.3 , the multimodality of the first passage time probability density was presented when the pulse frequency modulation existed. This property corresponds well to the data reported by N. Y.-S. Kiang et. al. and obtained for the first time by the author of this dissertation as the solution of the first passage time problem.

Several authors treated the shunting inhibition, however, their discussions did not involve the time characteristics. In the section 3.3 , the shunting inhibition was discussed with dynamics of the neuron potential. In such a case, the problem of the state dependent noise arose. The neuron potential with the state dependent noise was formulated and analysed for the first time by the author of this dissertation. And also the comparison between the subtractive inhibition and the shunting inhibition was tried and it was reported that the difference between them depends on the reset value of the neuron potential.

In the section 3.4 , the output spike interval density was discussed.

K. Dietz had considered Markov chains which generate multimodal interval densities. But the problem establishment is not feasible as that of neurons. On the contrary, the problem in the section 3.3 was fully combined with neurodynamics. And the relation to the first passage time probability density was mentioned. This is a new trial.

In addition to the spike interval density, the joint interval density is used to examine the information in neural pulse trains. The equation which governs this quantity is not obtained at present because of the complexity.

It is possible to construct a model which contains both natures of the spontaneous type and the forced type. In this case, the neuron potential is described by a generalized stochastic process and the probability density functions are governed by the Kolmogorov-Feller's equations. But the diffusion approximation is also necessary because of the wellposedness of the first passage time problem, and little changes in the level of the probability density shape appear except the vanishment of the sharpness.

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CHAPTER FOUR

RECIPROCAL INHIBITORY PAIRS

4.1 Neuron Populations

The preceeding chapters treated the behaviors of single neurons and considerable amount of properties were presented. But, it is still necessary to investigate how input pulse trains are converted by multiple neurons, i. e. the dynamics of the signal processing by neuron populations. (The term " neuron population " was used to represent a session of 1973-IFAC SYMPOSIUM.)

The motivation for this work originates from the belief that senior functions in nervous systems depend on cooperations by neural connections. And the researches in this field are made to clarify the relevance between the structure and phenomena at present. This direction of researches should be exceedingly developed in the near future too.

Principal treatments of neuron populations are as follows. W. Reichardt et. al. discussed lateral inhibitions using analog models without time characteristics (1962). R. F. Reiss treated reciprocal inhibitory pairs and he considered the effect of noise a little. But it does not make use of stochastic theory, therefore, the results on irregular properties are insufficient (1962). D. M. Wilson et. al. also considered reciprocal inhibitory pairs by means of electronic circuits (1965). But the discussion is confined to observe the firing patterns. U. Kling et. al. proposed the problem on neuron rings (1968) and later R. Suzuki et. al. compared such a structure with that of a starfish (1971). He introduced a noisy neuron, however, the discussion of companion neurons drived by it still lies in the deterministic methods. Another trial is R. J. MacGregor's work on ladder nets as the models for reticular-like networks (1971). His discussion is made on the sensitivity of the nets to the input patterns. An important contribution to the statistical analysis of neuron populations was made by D. H. Perkel et. al. (1967). They used pulse cross correlation (1968). But the backward connection was not treated. Seeing above, one can notice that the stochastic approaches of neuron populations are very few neverthless stochastic properties have roles in the signals of the nervous systems.

Here are considered two types of reciprocal inhibitory pairs because they are fundamental ones in the multiple systems which have the backward connections. And the stochastic properties are investigated, which have the fundamental importance in the information processing in the nervous systems.

4.2 Cross Correlation of Pulse Sequences

In the discussions of single neurons, the first passage time probability density and the output spike interval density are effective measures and describe the neural behavior completely. But in the multiple systems, other statistical quantities are necessary.

A cross correlation function of pulse sequences is convenient to see the mutual relation between two neurons. It was introduced by D. R. Cox and P. A. W. Lewis (1966) and discussed by D. H. Perkel et. al. (1967). The pulse cross correlation $\zeta_{AB}(\lambda)$ is defined by

$$\zeta_{AB}(\lambda) = \lim_{\Delta t \to +0} \Pr\{ \text{ an event of B in } [t_0+\lambda, t_0+\lambda+\Delta t) \mid \text{an event of A at } t_0 \}/\Delta t \quad . \qquad (4.1)$$

The right side of the definition (4.1) can be expressed by cross interval densities and the equation (4.2) is obtained.

$$\zeta_{AB}(\lambda) = \sum_{i=-\infty}^{\infty} \xi_i(\lambda) \qquad (i \neq 0) \qquad (4.2)$$

where $\xi_i(\lambda)$ is the cross interval density of order i . The cross interval of order $i > 0$ means the interval from a certain pulse to i-th preceeding pulse in another pulse train. When i is a negative integer, it is the interval to i-th preceeding pulse.

The cross correlation has a useful symmetry relationship.

$$\frac{\zeta_{AB}(\lambda)}{\mu_B} = \frac{\zeta_{BA}(-\lambda)}{\mu_A} \qquad (4.3)$$

where μ_A and μ_B are the mean interspike intervals of the train A and the train B respectively. Therefore, it is sufficient if one side is obtained.

Remark

If train A is perfectly random and there is no cross correlation, the right side of the definition (4.1) is described by

$$\lim_{\Delta t \to +0} \Pr\{ \text{ an event of B in } [t_0+\lambda, t_0+\lambda+\Delta t) \mid \text{random instant } t_0 \}/\Delta t$$

$$= \mu_B \quad . \tag{4.4}$$

And as a special case, if two trains are homogeneous Poisson trains $\zeta_{AB}(\lambda)$ is equal to μ_B which is a constant.

4.3 Discussion of Reciprocal Inhibitory Pairs

4.3.1 Description of Reciprocal Inhibitory Pairs

Two kinds of systems are shown in Fig. 4.1 . Their driving input forms are different. The system 1 has two excitatory driving inputs which are statistically independent. They are denoted by $dE_A(t,\omega_A)$ and $dE_B(t,\omega_B)$. The system 2 has one common excitatory input and it advances in two ways, one of which includes a time delay. It is denoted by $dE(t,\omega)$. $E_A(t,\omega_A)$, $E_B(t,\omega_B)$ and $E(t,\omega)$ are sample paths of Poisson processes whose excitatory pulse applications occur with probability $Ne_A(t)\Delta t + o(\Delta t)$, $Ne_B(t)\Delta t + o(\Delta t)$ and $Ne(t)\Delta t + o(\Delta t)$ respectively in the interval $[t,t+\Delta t)$. When the neuron A fires the inhibition occurs in B and vice versa.

In the system 1, sample paths of the neuron potentials of the neuron A and the neuron B are expressed as

$$Y_A(t,\overline{\omega}) = \int_{s_A}^{t} \varepsilon^{-\frac{t-u}{\tau}} d\{ E_A(u,\omega_A) + I_B(u,\overline{\omega}) \} + x\varepsilon^{-\frac{t-s_A}{\tau}} \qquad (t \geqq s_A) \qquad (4.5)$$

$$Y_B(t,\overline{\omega}) = \int_{s_B}^{t} \varepsilon^{-\frac{t-u}{\tau}} d\{ E_B(u,\omega_B) + I_A(u,\overline{\omega}) \} + x\varepsilon^{-\frac{t-s_B}{\tau}} \qquad (t \geqq s_B) \qquad (4.6)$$

where $\overline{\omega} = (\omega_A,\omega_B)$. s_A and s_B are the times when the spikes

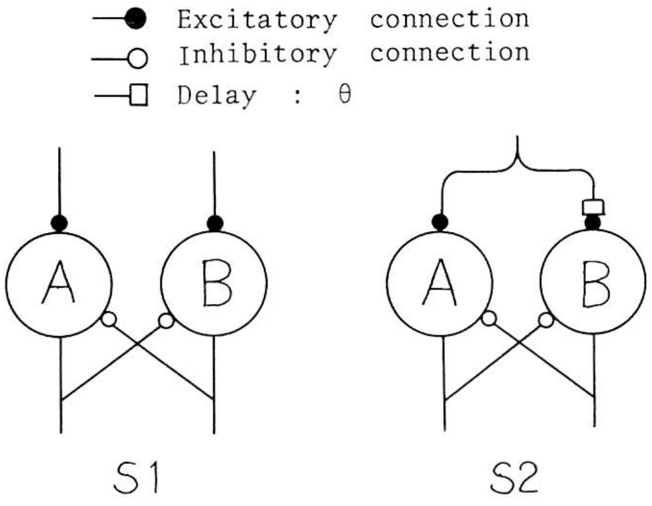

Fig. 4.1 Reciprocal inhibitory pairs

of the neuron A and B occured previously. $I_A(t,\overline{\omega})$ is the step process which is lowered by a certain quantity i , when the neuron A fires. $I_B(t,\overline{\omega})$ is also understood in the same manner.

In the system 2, sample paths of the neuron potentials of the neuron A and the neuron B are expressed as

$$Y_A(t,\omega) = \int_{s_A}^{t} \varepsilon^{-\frac{t-u}{\tau}} d\{ E(u,\omega) + I_B(u,\omega) \} + x\varepsilon^{-\frac{t-s_A}{\tau}} \qquad (t \geqq s_A) \qquad (4.7)$$

$$Y_B(t,\omega) = \int_{s_A}^{t} \varepsilon^{-\frac{t-u}{\tau}} d\{ E(u-\theta,\omega) + I_A(u,\omega) \} + x\varepsilon^{-\frac{t-s_B}{\tau}} \qquad (t \geqq s_B) \qquad (4.8)$$

where θ is the value of time lag.

In the cases such as the system 1 and the system 2, it is not possible to make a parallel discussion to the chapter 2 or the chapter 3. This is because the differential generators which govern the probability density functions can not be obtained as the neuron potentials of these cases are more complicated than those of preceeding chapters. This difficulty originates from the backward connections.

But the digital simulation is available even in such cases because the dynamics of the sample paths of the neuron potentials are described by the equations (4.5) ~ (4.8).

4.3.2 Results

Here are shown the results by means of the digital simulation. Each result used just 10,000 spikes of the neuron A and the neuron B, i. e. about 5,000 spikes for each neuron. And the equation (4.2) was used in order to obtain the cross correlation because probability density functions of output spike intervals are easy to obtain. The results are presented separately depending on whether the input pulse trains are temporally homogeneous or not.

a. Temporally Homogeneous Input

There are two kinds of data, the output spike interval density and the cross correlation. The cross correlation is obtained by summing up the cross interval densities of all orders except zero.

In this case, the input pulse trains are based on the homogeneous Poisson processes. Therefore, their spike interval densities show exponential distributions. That is to say, the distributions are unimodal. And the matter of interest in this section is to investigate how the characteristics of inputs are converted by the system 1 and the system 2.

Then, the results are shown and the discussion of each system and the comparison of both systems are made. In this case, the parameters of the inputs of both systems are chosen identically.

Fig. 4.2 is the output spike interval density of the system 1 of the neuron A. This is almost the same as that of the neuron B because two neurons have a homogeneous structure.

Fig. 4.3.a is the output spike interval density of the neuron A of the system 2 whose time lag is 8 ms . Fig. 4.3.b is that of the neuron B in the same case. In the system 2, the output spike interval densities of the neurons A and B differ. The difference is observed from the envelopes of the output spike interval density too. In the system 1, it has a longer tail than that in the system 2. This difference can be observed more clearly by using the cross correlation. This is reported later.

It is a quite important nature that above output spike interval densities show the multimodal distributions neverthless the inputs are temporally homogeneous Poisson type. That is to say, stochastic rhythms emerge by the reciprocal inhibitions. And the period of this rhythm depends mainly on the relaxation time constant of the neuron potential. Fig. 4.4 shows such a property.

Then the group behavior is investigated using the pulse cross correlation. Fig. 4.5 is the cross correlation of two output pulse trains in the system 1. And Fig. 4.6.a ~ Fig. 4.6.d are the cross correlations of two output pulse trains in the system 2 whose time lags are 1 ms , 4 ms , 8 ms and 25 ms respectively. The cross correlation of these systems is very weak near $\lambda=0$ ms . This means that the neuron A and the neuron B seldom fire simultaneously because of the reciprocal inhibitions. In Fig. 4.6, a conspicuous peak is appeared. The location of this sharp peak almost corresponds to the time lag and this is natural, however, the correspondence is not held when the time lag θ is small. The reciprocal inhibitions show such a property. When θ is proper, the peak becomes very sharp (Fig. 4.6.c) . This means that two output pulse trains are more co-phasic than than other cases. And when θ becomes larger, the system 2 becomes equivalent to the system 1 (Fig. 4.6.d) .

b. Temporally Inhomogeneous Inputs

Here are shown the results when the inputs are modulated sinusoidally. Fig. 4.7 is the output spike interval density of the neuron A of the system 1. This is also almost the same as that of the neuron B. The pulse frequency modulation is 80 Hz. Fig. 4.8.a is the output spike interval density of the neuron A of the system 2 whose time lag is 6.25 ms , i. e. π rad . Fig. 4.8.b is that of the neuron B in the same case. In these cases, all structures and input natures are the same as those of the temporally homogeneous case except the pulse frequency modulation. The output spike interval densities show the multimodality according to the pulse frequency modulation. And another multimodality can be also seen. That is due to the rhythm generated by the reciprocal inhibitions.

Then, the group behavior is discussed through the cross correlation. Fig. 4.9.a is the cross correlation of two output pulse trains in the system 1. And Fig. 4.9.b is that of the system 2 whose time lag is 6.25 ms , i. e. π rad . In these cases, the effect of the pulse frequency modulation can be observed. The oscillating trend of the cross correlation means that the output of the companoin neuron is spiked with high probability according to the pulse frequency modulation. Other properties are the same as those of the temporally homogeneous inputs.

In the temporally inhomogeneous case of the system 1, two input signals may be modulated differently. Fig. 4.10.a and Fig. 4.10.b are the output spike interval densities of the neuron A and the neuron B respectively. In this case, the pulse frequency modulations of excitatory inputs are 80 Hz and 20 Hz . Each output spike interval density reflects the pulse frequency modulation. Fig. 4.11.a is the cross correlation of the system 1 whose excitatory pulse frequency modulations occur with frequencies 80 Hz and 40 Hz . Fig. 4.11.b is the case with frequencies 80 Hz and 20 Hz . These figures show that the lower frequency of the pulse frequency modulation plays main role in the pulse cross correlation of the reciprocal inhibitory pair.

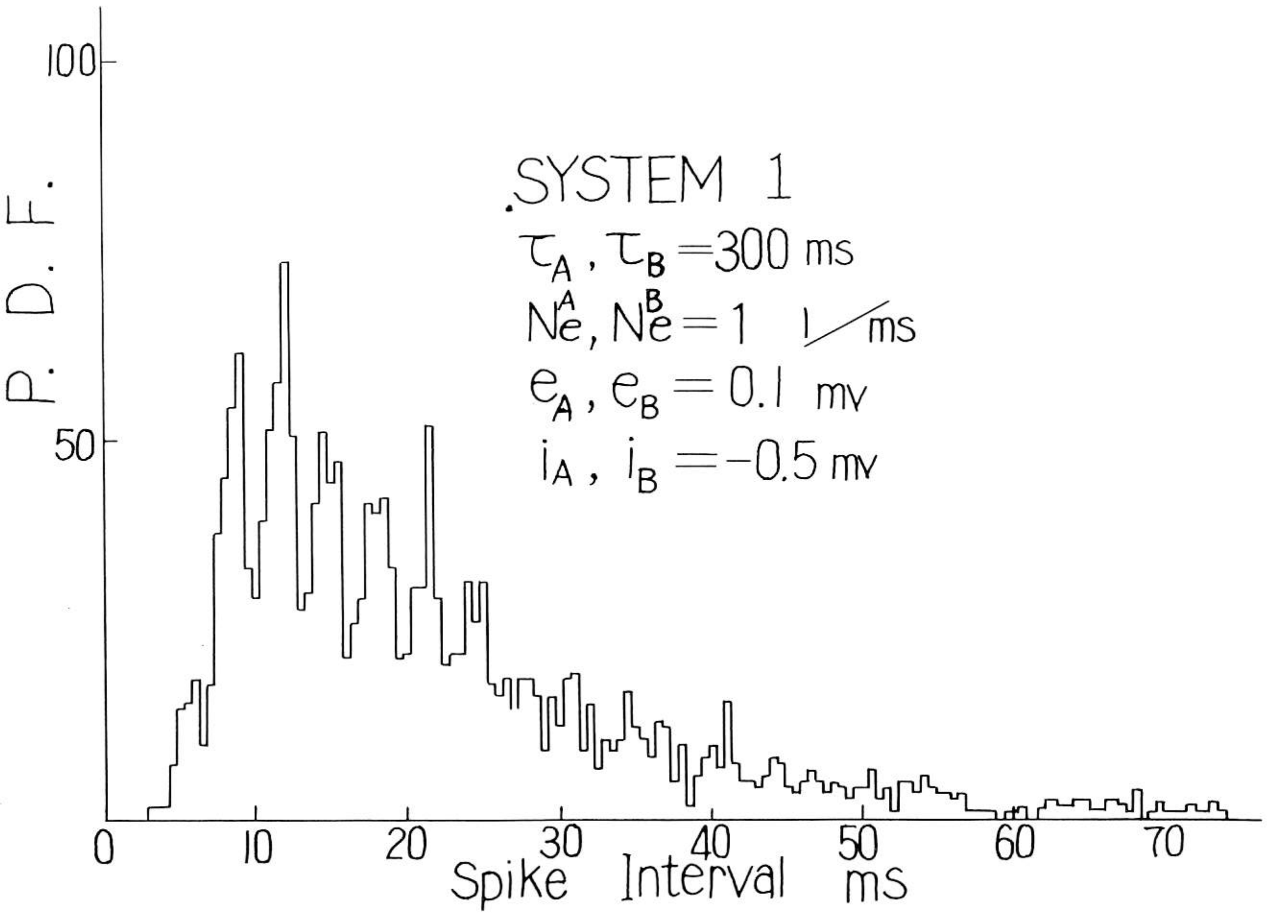

Fig. 4.2 Output spike interval density of Neuron A in the System 1

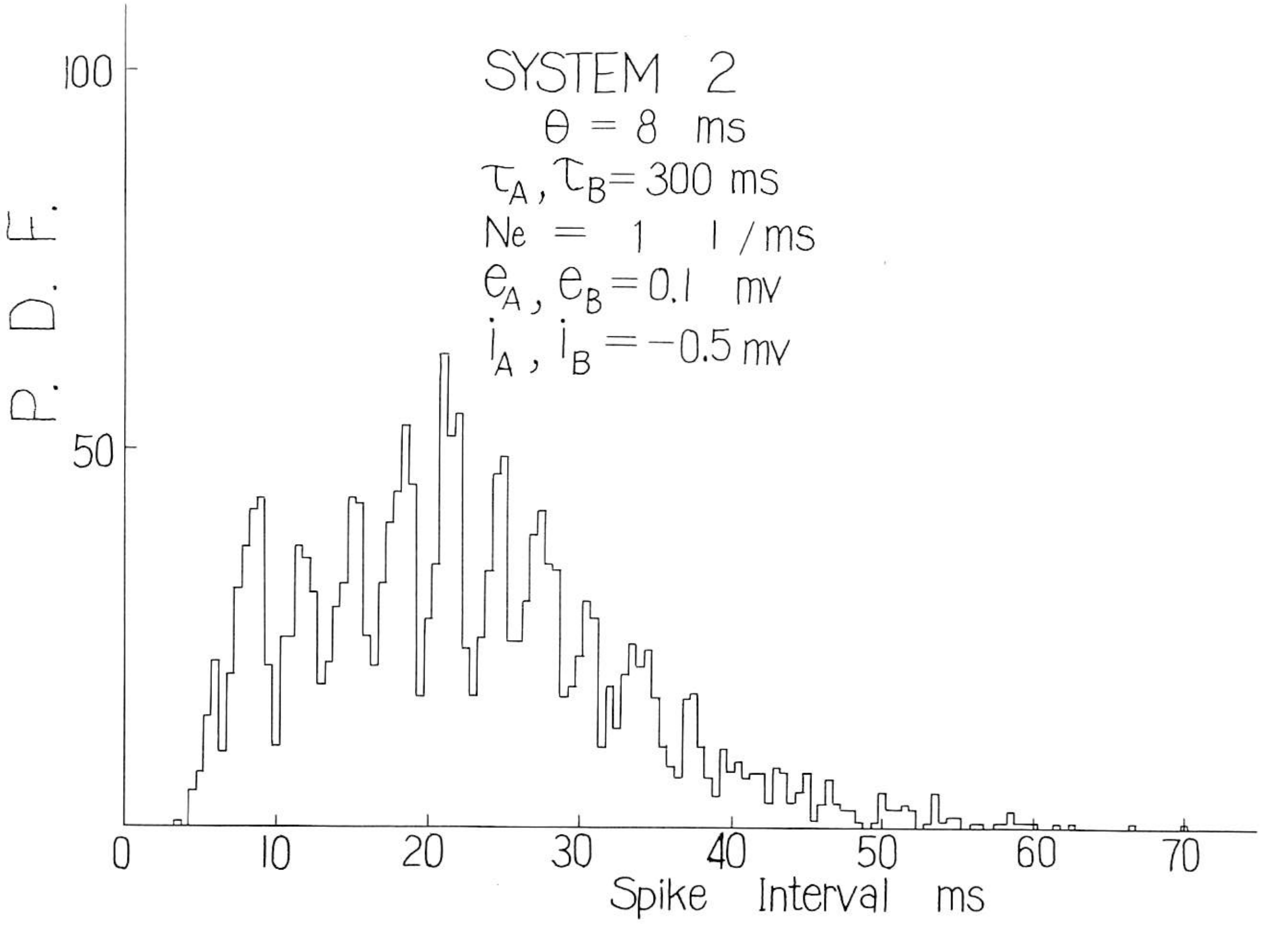

Fig. 4.3.a Output spike interval density of Neuron A in the System 2

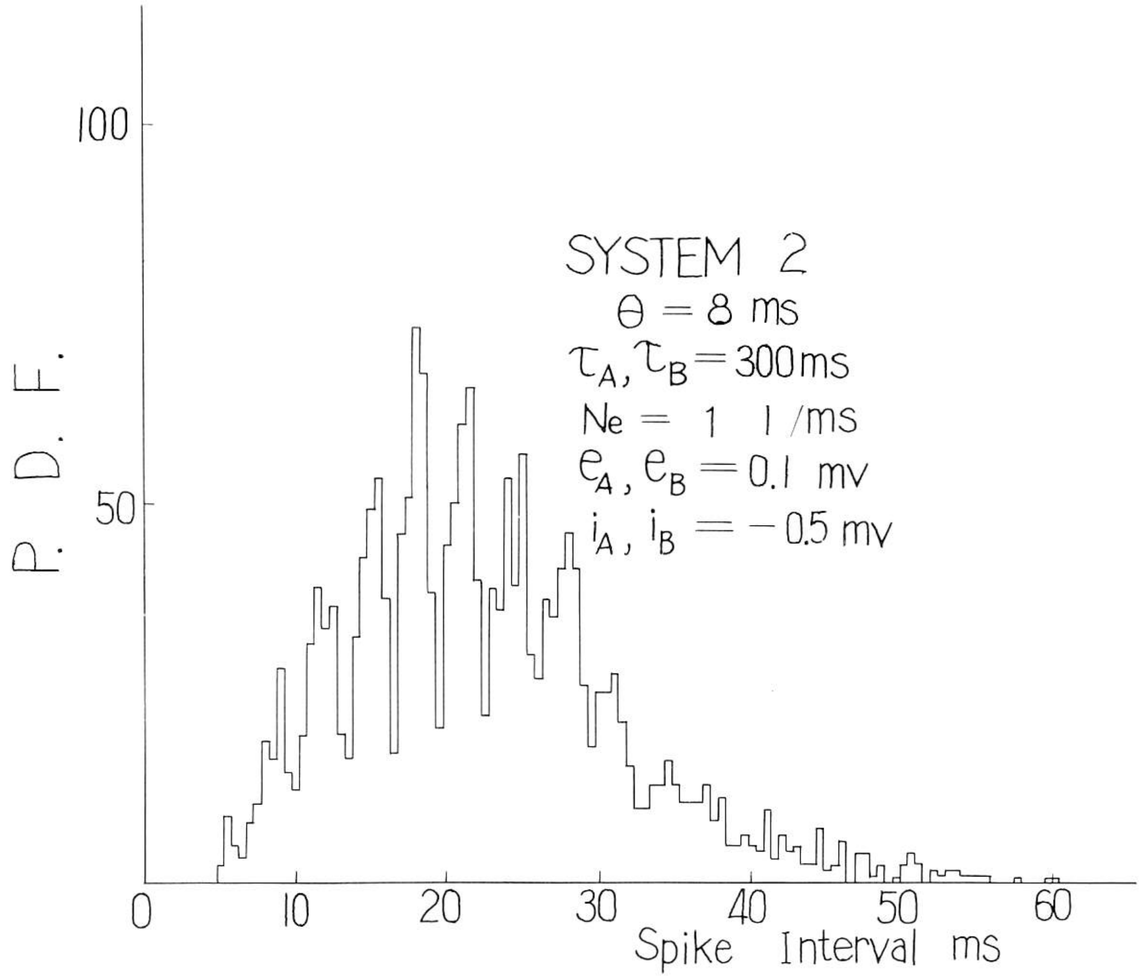

Fig. 4.3.b Output spike interval density of Neuron B in the System 2

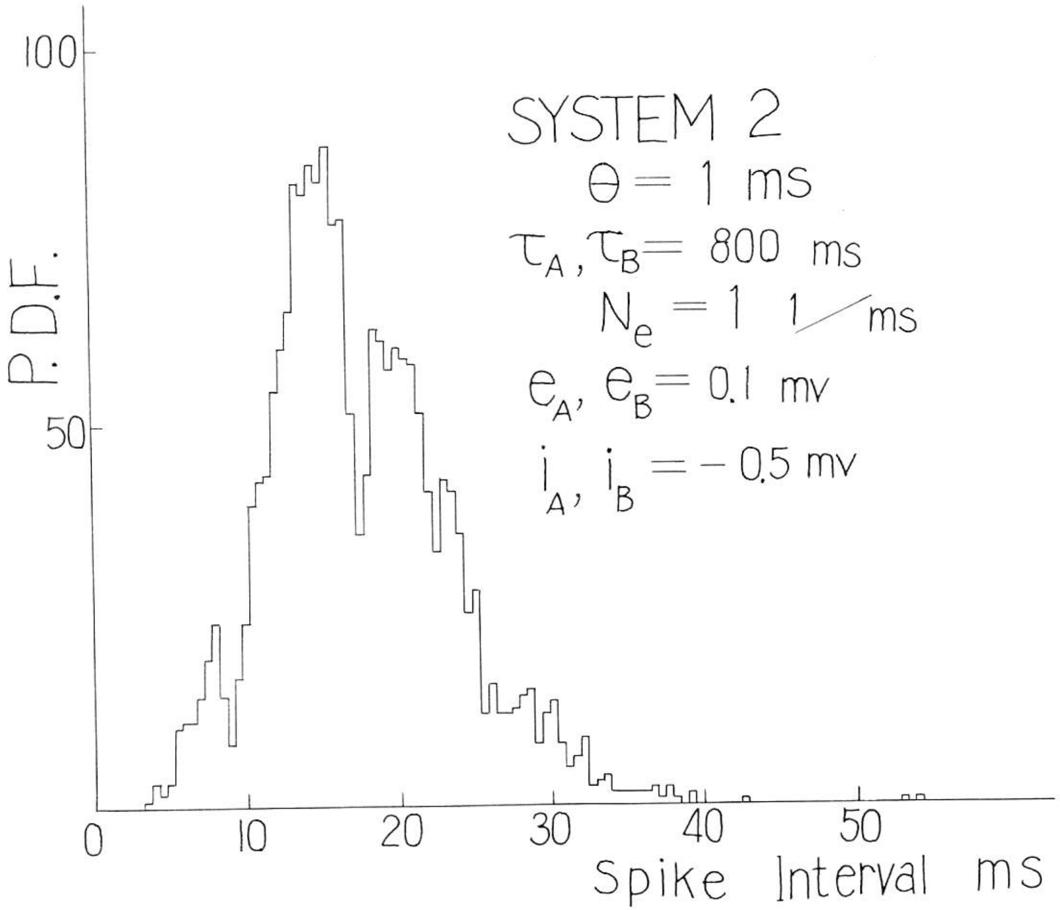

Fig. 4.4 Output spike interval density of Neuron A in the System 2

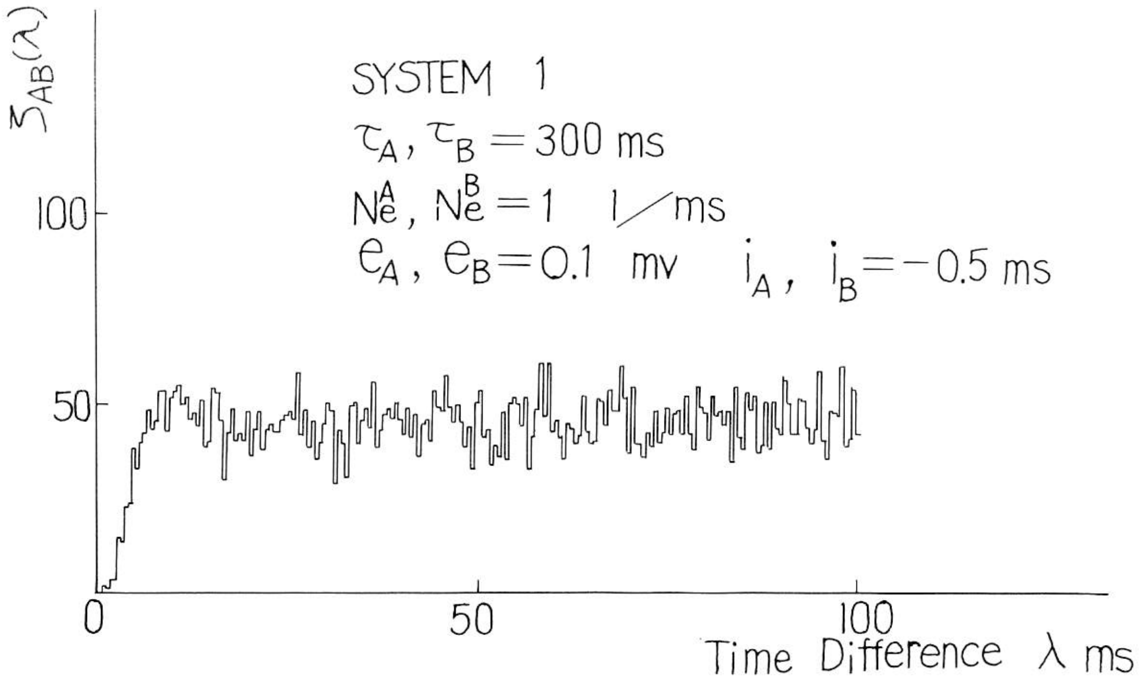

Fig 4.5 Corss correlation of two output pulse trains in the System 1

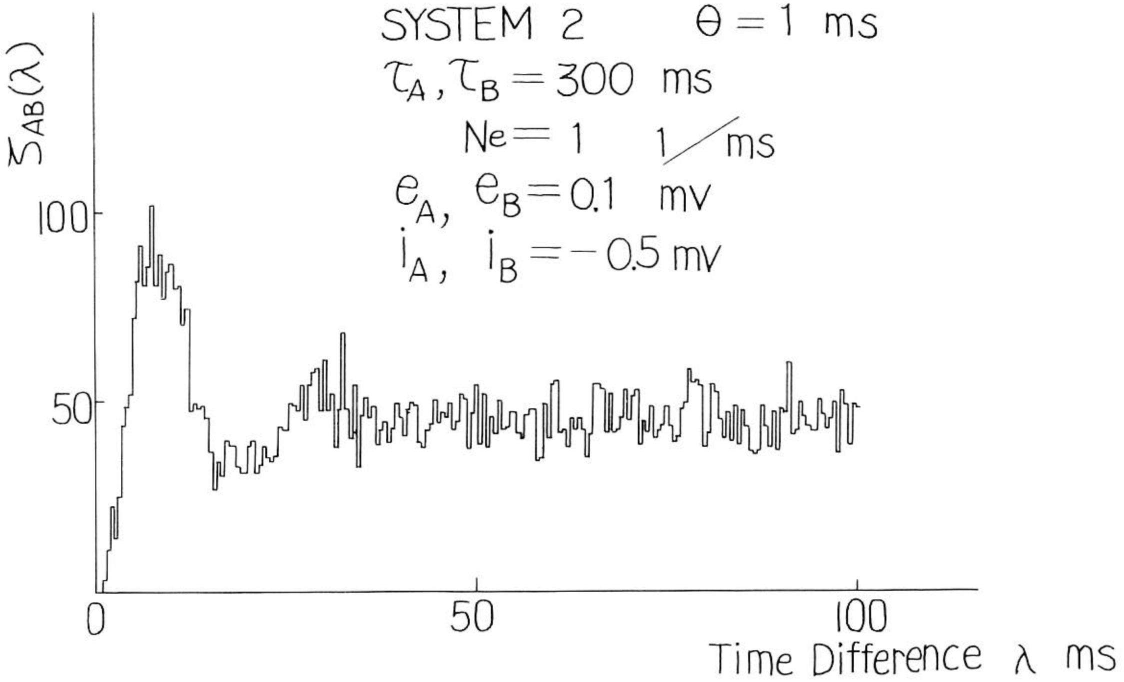

Fig. 4.6.a Cross correlation of two output pulse trains in the System 2, θ=1 ms

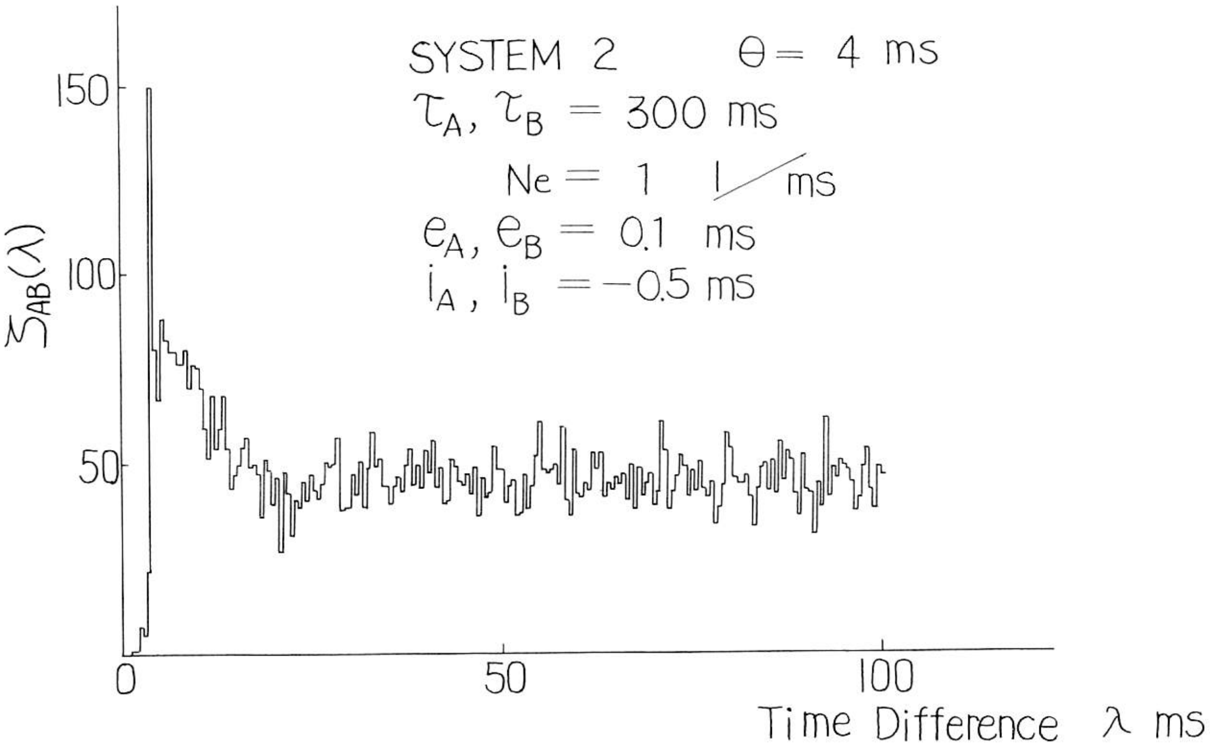

Fig. 4.6.b Cross correlation of two output pulse trains in the System 2, θ=4 ms

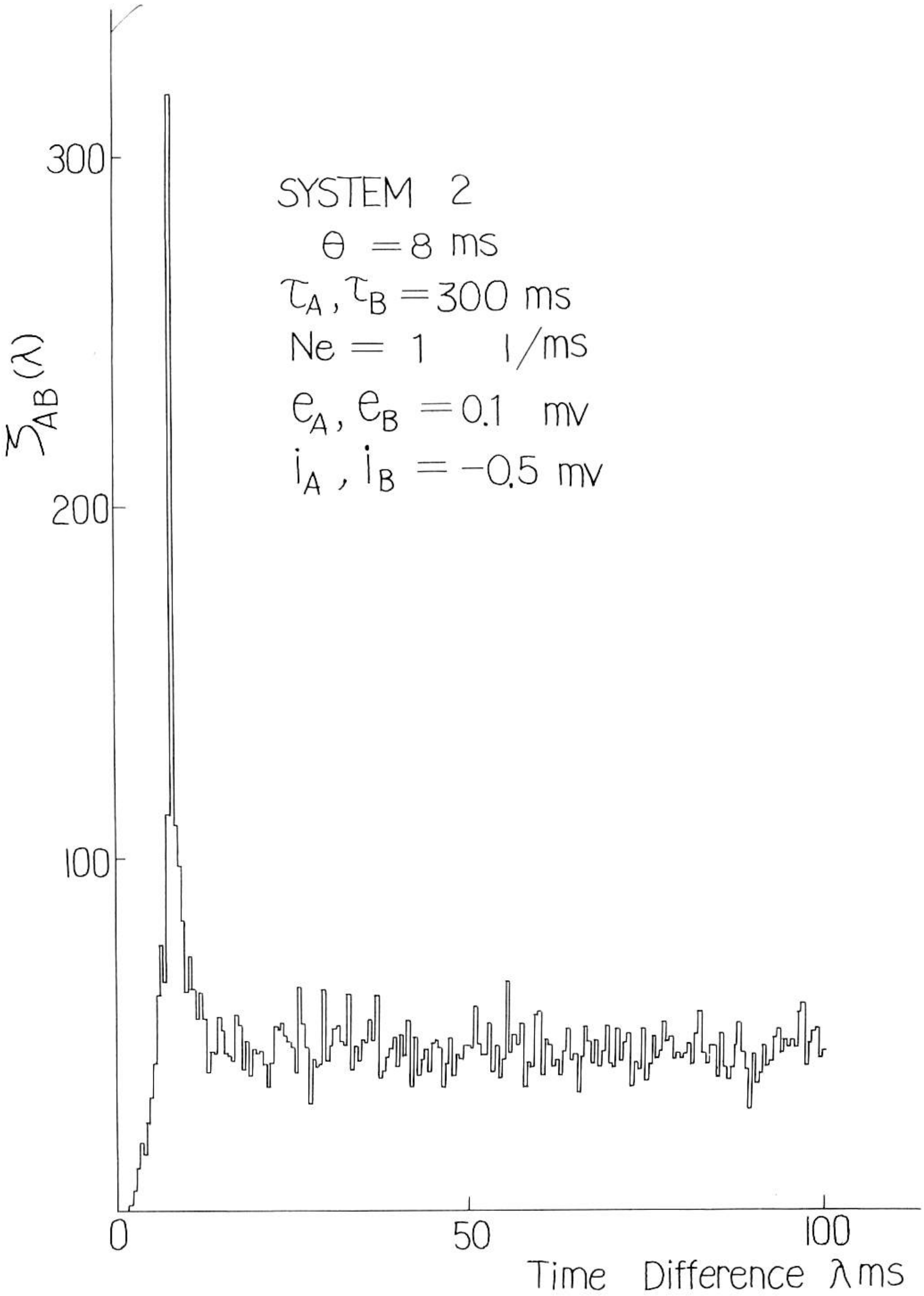

Fig. 4.6.c Cross correlation of two output pulse trains in the System 2, θ=8 ms

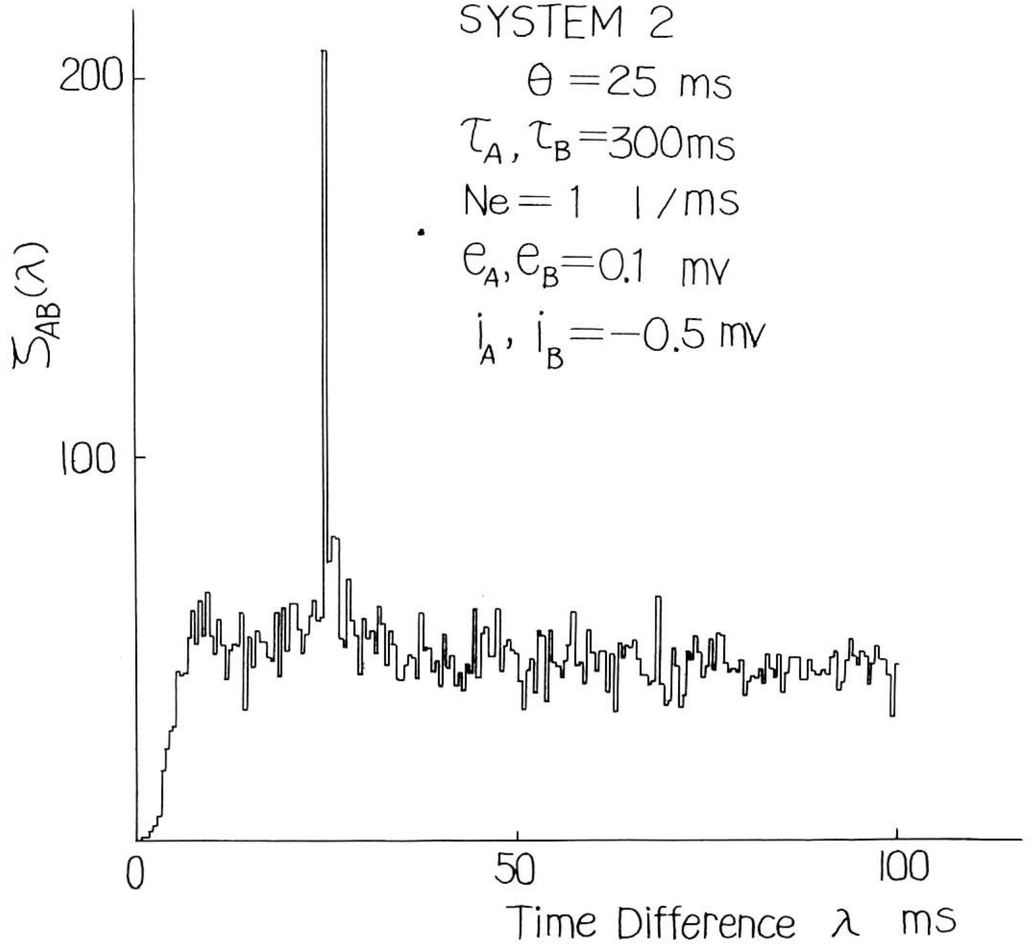

Fig. 4.6.d Cross correlation of two output pulse trains in the System 2, θ=25 ms

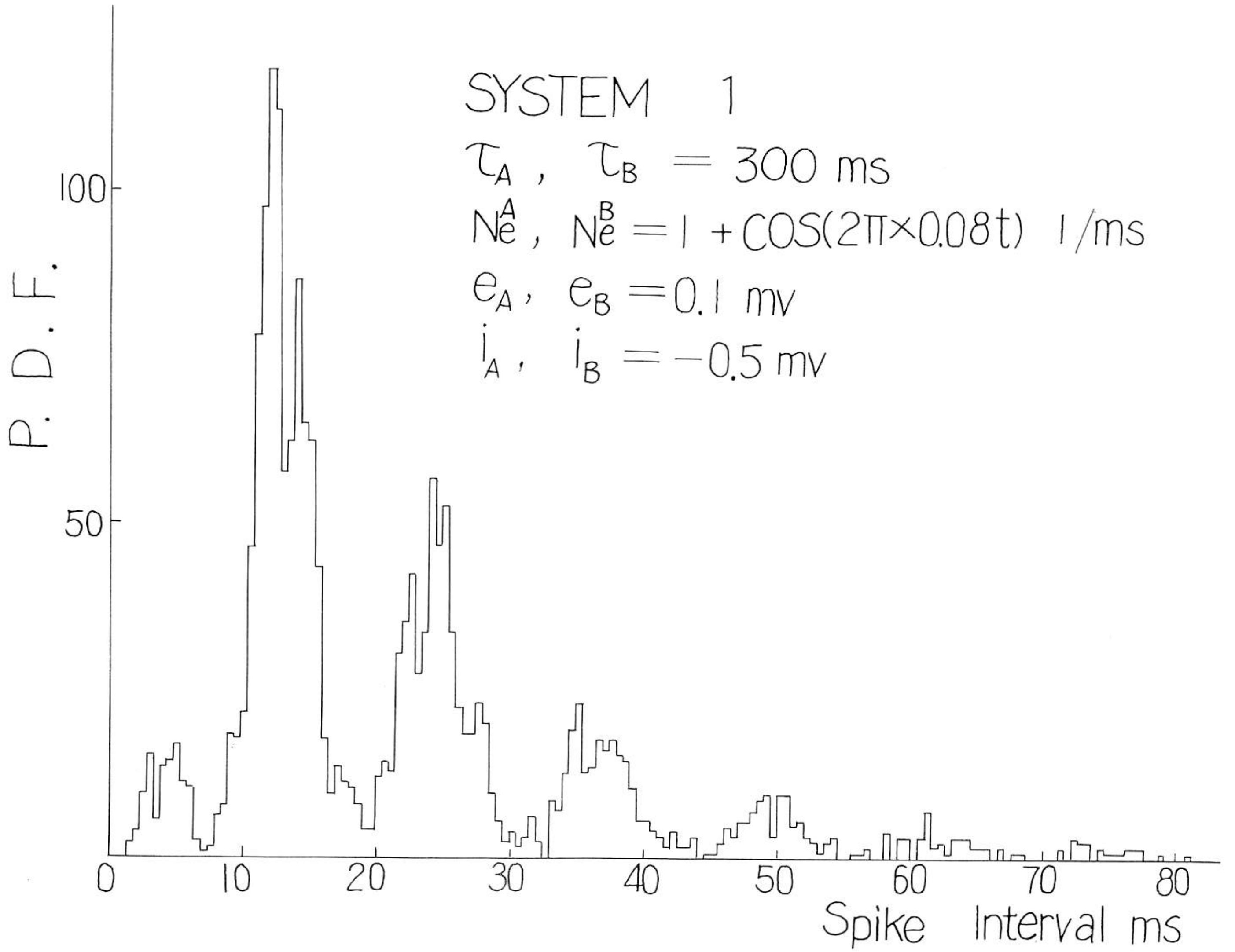

Fig. 4.7 Output spike interval density of Neuron A in the System 1, temporally inhomogeneous inputs

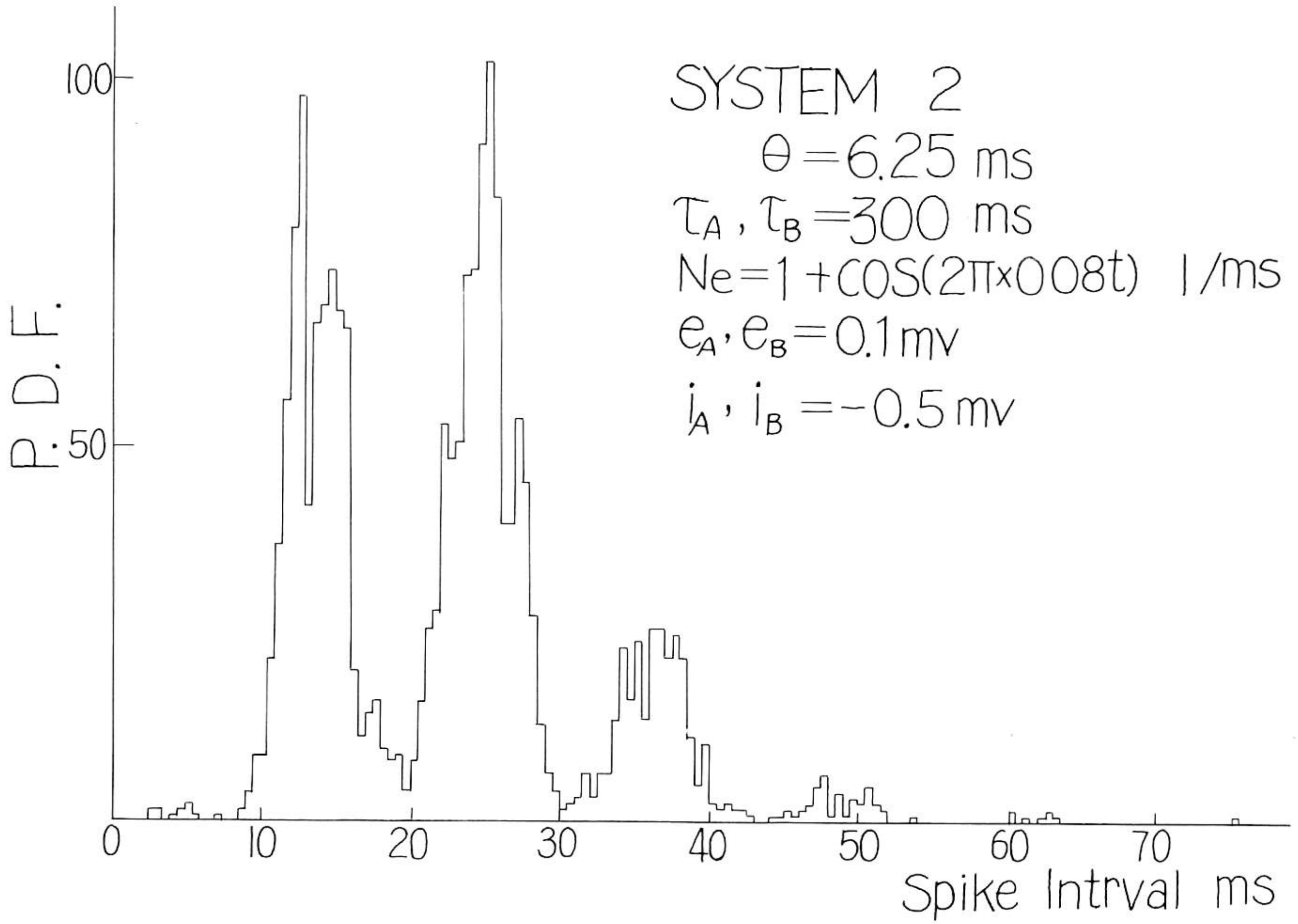

Fig. 4.8.a Output spike interval density of Neuron A in the System 2, temporally inhomogeneous inputs

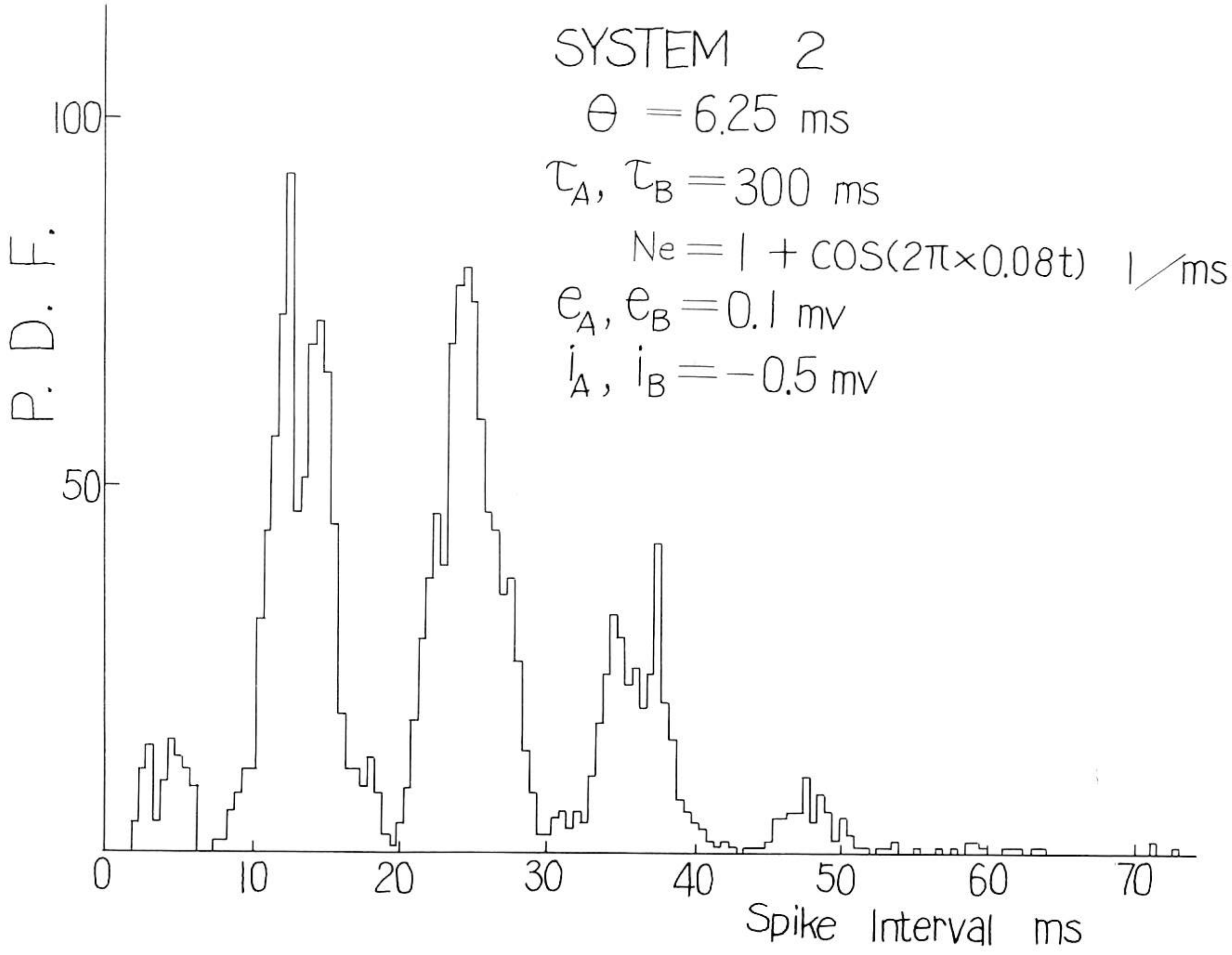

Fig.4.8.b Output spike interval density of Neuron B in the System 2, temporally inhomogeneous inputs

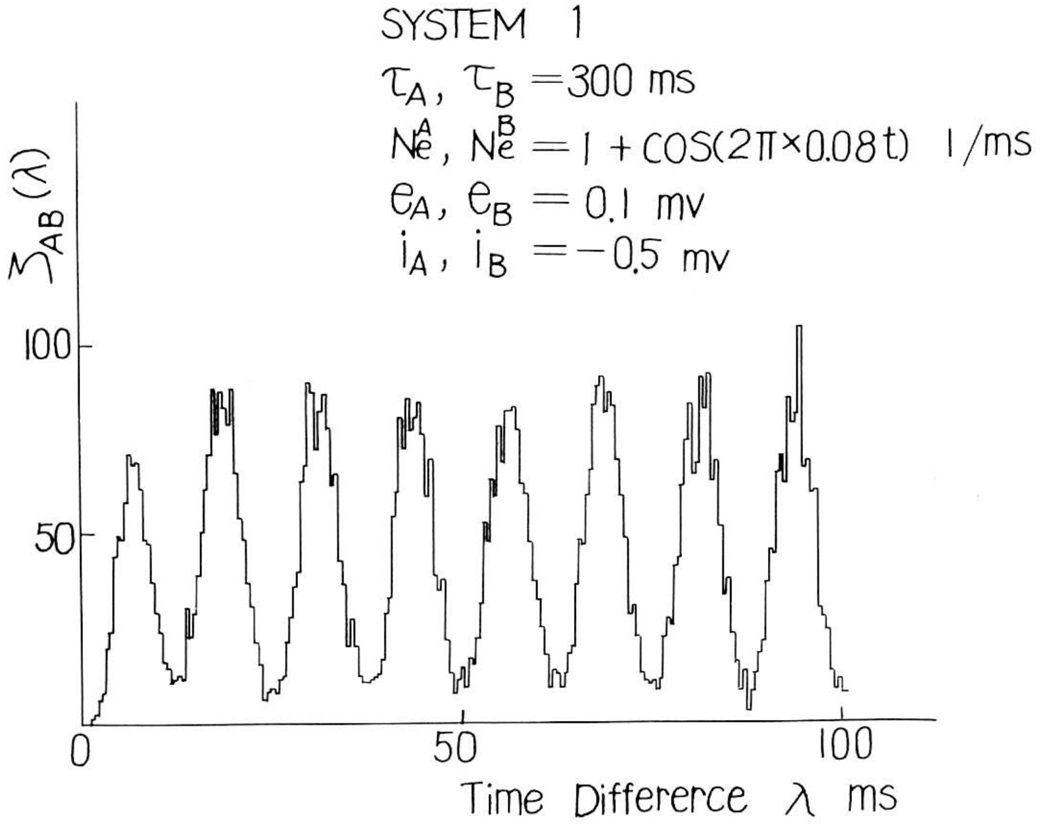

Fig. 4.9.a Cross correlation of two output pulse trains in the System 1, temporally inhomogeneous inputs

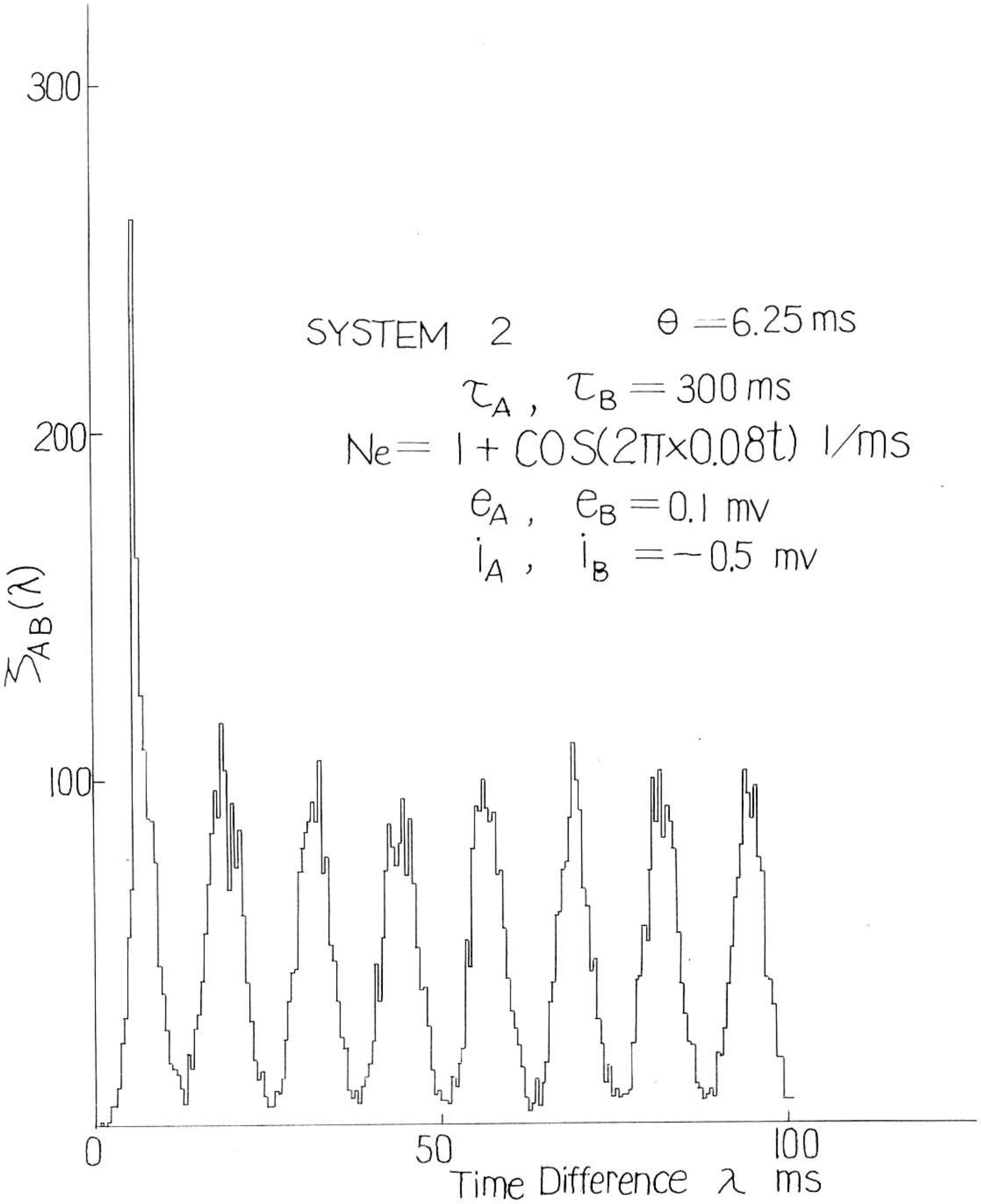

Fig. 4.9.b Cross correlation of two output pulse trains in the System 2, temporally inhomogeneous inputs

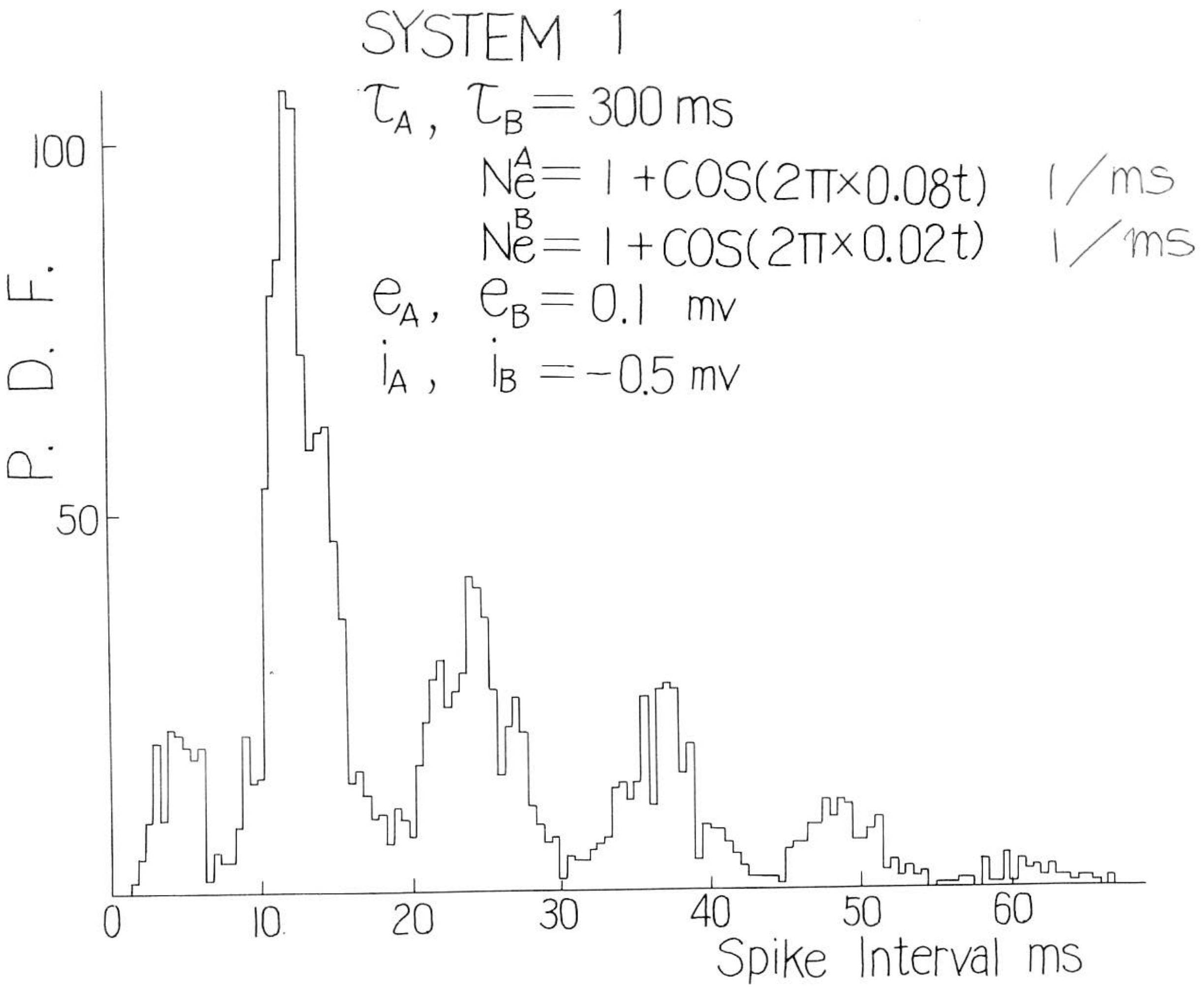

Fig. 4.10.a Output spike interval density of Neuron A in the System 1, the case of different pulse frequency modulations

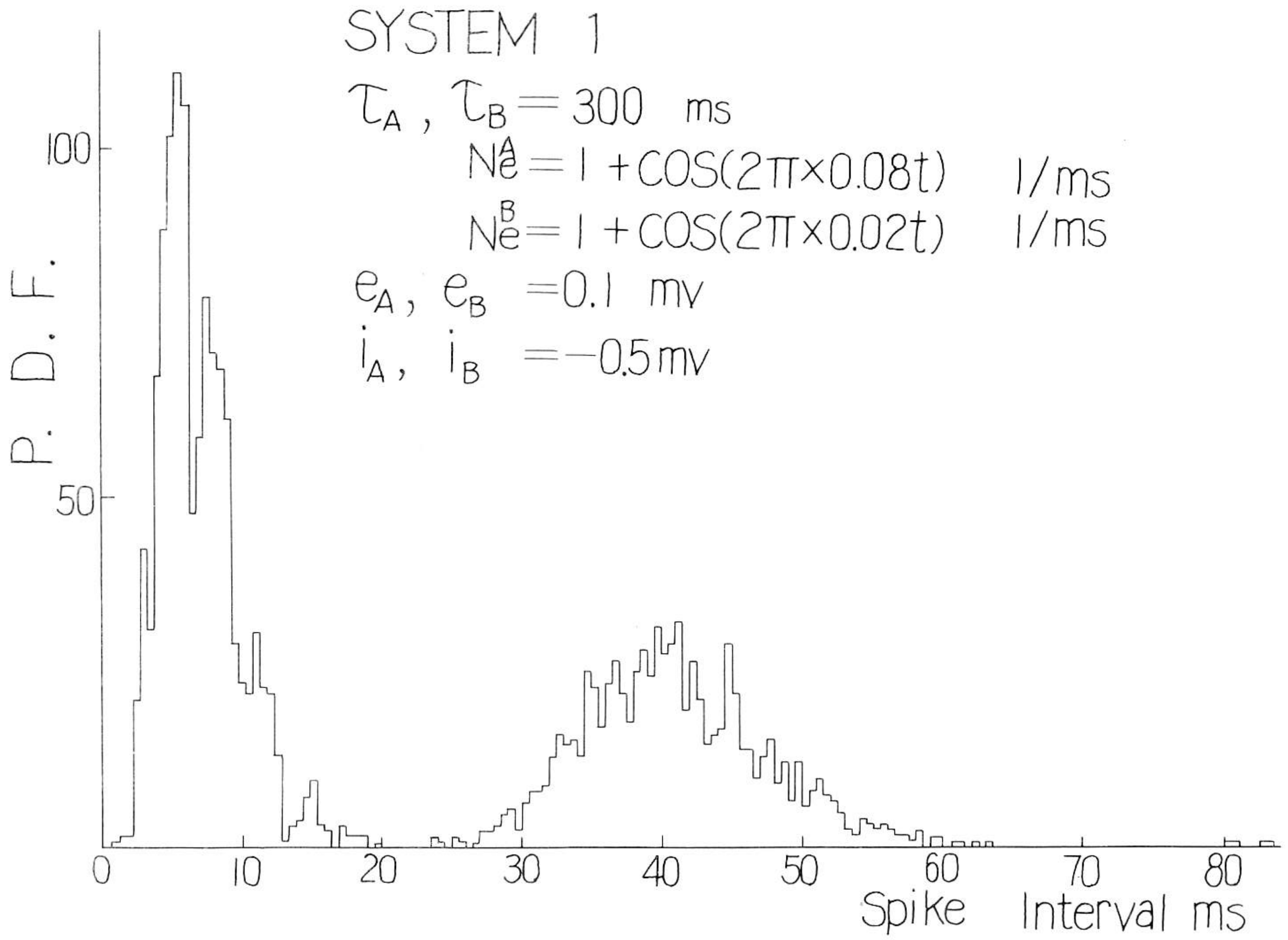

Fig. 4.10.b Output spike interval density of Neuron B in the System 1, the case of different pulse frequency modulations

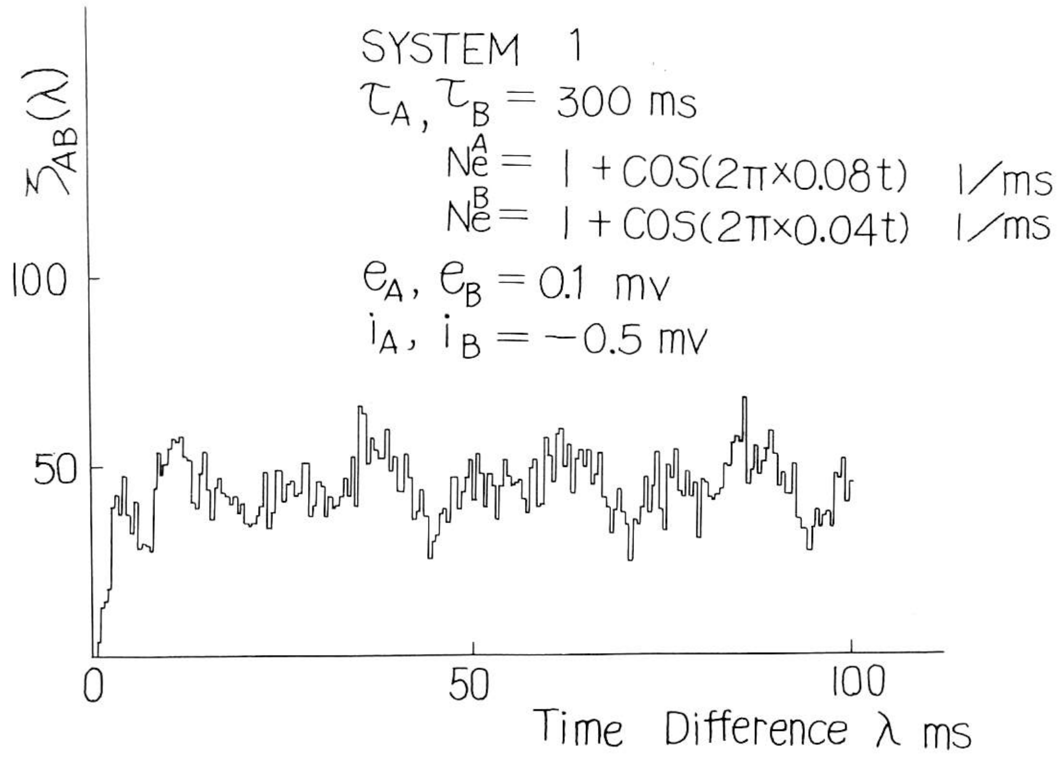

Fig. 4.11.a Cross correlation of two output pulse trains in the System 1, the case of different pulse frequency modulations, 40 Hz and 80 Hz

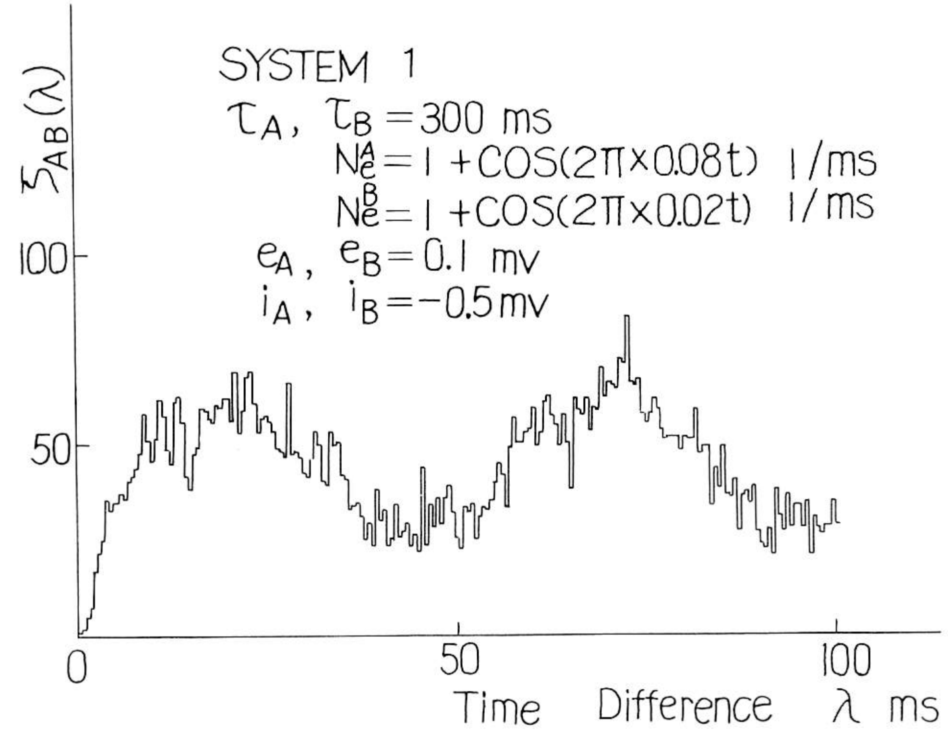

Fig. 4.11.b Cross correlation of two output pulse trains in the System 1, the case of different pulse frequency modulations, 20 Hz and 80 Hz

4.4 Concluding Remarks

Reciprocal inhibitory pairs were discussed as one of the problems of neuron populations. The discussion was made with a desire to realize the property of the interference of pulse trains and the role of pulse distributions.

There were two kinds of reciprocal inhibitory pairs. One is the system that each neuron has an independent Poisson input pulse train, and the other is the system that each neuron has a common Poisson input pulse train, which is applied with a time lag to one neuron of the pair. And it was confirmed that these reciprocal inhibitory pairs show multimodal output spike interval densities in spite of temporally homogeneous Poisson input pulse trains. This means that the stochastic rhythms emerge by these systems because of the interference of pulse trains. And the rhythms in this case have the smoothness which can not be appeared in the deterministic case. The smoothness is one of the important natures of the systems in the living body, therefore, the stochastic modeling and discussions are necassary. Two systems in this chapter do not differ as long as they are compared through the mean values of output frequencies, however, the cross correlations are very distinctive reflecting the interference of pulse trains. This property do not appear in the deterministic case.

Furthermore, temporally inhomogeneous inputs were treated. In this case, the problem of two different pulse frequency modulations was presented in the first system. And it was reported that the lower frequency of the pulse frequency modulation plays the main role.

Perhaps it may not be refused to express the output spike interval density of the first system by obtaining the probability density of the state at the moment when the companion neuron fires. Further discussion is a prospective problem and worthy to try.

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CHAPTER FIVE

SUMMARY AND CONCLUSION

The stochastic modeling of neurons and neuron populations were discussed. Three subjects, i. e. the spontaneous type neuron, the forced type neuron and the reciprocal inhibitory pairs were considered. And the numerical techniques were used as well as the analytical ones.

In this work, the attention was focused on the stochastic properties. The necessity of the stochastic treatment arises from essential irregularity which is discussed briefly in the chapter one. " What is the prime of the fluctuation ? " remains a matter of discussion, however, the irregularity in the nervous system is not the superficial appearance of complex coding of the information.

Since the M-P model explained the logical nature of neurons, an idea that the nervous system can be understood thoroughly by the deterministic method was fixed in many researchers involuntarily. But the stochastic method provides more complete understanding of the properties of the neural systems.

The new trials and results presented in this work are as follows. In chapter two, the problem of the spontaneous type neuron was formulated exactly and discussed. Since the neuron potential is treated as a random variable, the problem of firing is translated into the first passage time problem. The discussion was made on the transition probability density of the neuron potential and the first passage time probability density. They were obtained from the Kolmogorov's equation and the law of the probability conservation. In this case, the variation of the threshold was reduced to the moving boundary problem. Examples of both probability densities were presented and they explained the stochastic property of the irregular spontaneous activity.

In chapter three, neurons with stochastic input pulse trains were discussed. Poisson input pulse trains were adopted as inputs and the appropriateness of this assumption was considered. It is assured by the limitting theorems on the superposition of pulse trains. Subsequently, the mathematical models of the forced type neurons with excitatory and inhibitory input pulse trains which were based on the Poisson processes were considered. Two kinds of inhibitions were discussed. One is the subtractive inhibition which lowers the neuron potential by a certain quantity, and the other divides or shunts it. Both cases were considered and analysed using the transition probability density of the neuron potential and the first passage time probability density which satisfy the Kolmogorov's equations and the law of the probability conservation. In the problems of the forced type neurons, the following matters are distinct from those of the spontaneous type neurons. They are the necessity of the diffusion approximation of the differential generator for the wellposedness as the first passage time problem, the comparison problem of two types of inhibitions and the temporally inhomogeneous problems due to the pulse frequency modulation. On the diffusion approximation, the solution was compared with the digital simulation and a good agreement was obtained. On the comparison of two types of inhibitions, the difference between them depends on the reset value of the neuron potential. And it was reported that the first passage time probability density shows the multimodal distribution when the pulse frequency modulation exists in the input pulse trains. This multimodality corresponds to the input signal. In the case of the periodic pulse frequency modulation, the output spike interval density was considered. Such a situation is set in order to study the information processes in neurons by applying a periodical stimulus. The output spike interval density was constructed from the first passage time probability densities for various input phases. This value shows the multimodal distribution too. Such a property is agreed with the tendency obtained in vivo.

In chapter four, two kinds of reciprocal inhibitory pairs were considered as the problems of neuron populations. In the first system, each neuron has two independent Poisson input pulse trains. And in the second system, each neuron has a common Poisson pulse train, which is applied with a time delay to one neuron of the pair. These two systems showed multimodal output spike interval densities in spite of the temporally homogeneous Poisson input pulse trains. This fact means that the stochastic rhythms are generated by such systems. Then the comparison between these systems was tried. They do not differ as long as they are compared through the mean values of output frequencies, however, the cross correlations are very distinctive reflecting the interference of pulse trains. Furthermore, temporally inhomogeneous inputs were treated. In this case, the input pulse train with different pulse frequency modulation may be applied to each neuron. It was reported that the lower frequency of the pulse frequency modulation plays the main role.

By this work, the stochastic methods to discuss the neural activities were considerably developed. Of course deterministic methods do not lose their footing, however, the introduction of stochastic methods is very helpful when the neural coding is discussed. That is because it is impossible to express an intermediate value or a continuous signal by deterministic pulse trains.

It is remarkable that the nervous system holds high functions as a whole in spite of the local irregularity. The study on this subject is the core problem of further works. One of the clues is to investigate the minimal structure which corresponds to a peculiar function.

APPENDIX A

A SUFFICIENT CONDITION FOR MARKOV PROPERTY

In the capter two or three, it is necessary to check up the Markov property. The following theorem is useful.

Theorem

Let $X(t)$, $a \leqq t < b$ be a stochastic process which moves in a second countable, locally compact space S. If there exists a random variable Y which is independent of $X(\tau)$, $a \leqq \tau \leqq t$ for every $(a \leqq)\ t < s\ (< b)$, and $X(s)$ can be written as a B-measurable function of $X(t)$ and Y, then, $X(t)$, $a < t < b$ is a Markov process. ⧖

Proof is presented in K. Ito, "Probability Theory", Iwanami (1952).

APPENDIX B

INTERVAL DENSITY OF PERIODIC POISSON PROCESS

In the chapter three, the periodic Poisson input pulse train was adopted. Its interval density is described as follows.

A pulse occurs with probability $\lambda_0 (1 + a\sin\omega t)$ in the interval $[t, t + \Delta t)$. Then, the distribution of the intervals between two successive pulses is given by

$$\varepsilon^{-\lambda_0 t}\left\{ I_0\left(\frac{2\lambda_0 a}{\omega} \sin\frac{\omega t}{2} \right) - a\cos\frac{\omega t}{2}\, I_1\left(\frac{2\lambda_0 a}{\omega} \sin\frac{\omega t}{2} \right) \right\}$$

where I_0 and I_1 are modified Bessel functions.

Details are found in D. M. Willis, Biometrika 51, 399 (1964).

APPENDIX C

GENERATION OF MODULATED EXPONENTIAL RANDOM NUMBERS

In the chapter three, modulated exponential random numbers were used in order to generate sample paths of neuron potentials. They are obtained as follows.

a. Let u_i be a uniform random number over $[0, 1]$.

b. Then an exponential random number with a parameter λ_0 is made by

$$\xi_i = -\frac{1}{\lambda_0} \log_e u_i$$

c. Let the pulse frequency modulation occur with $\lambda_0(1 + a\sin\omega t)$. Then, t_i which satisfies

$$\xi_i = \int_{t_{i-1}}^{t_i} (1 + a\sin\omega t)dt$$

or

$$\xi_i = \left[t - \frac{a}{\omega}\cos\omega t \right]_{t_{i-1}}^{t_i}$$

is the modulated exponential random number.

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