Physiol. Res. 45: 413–420, 1996

A Model of Stochastic Activity of Neurone in Some Types of Gaussian Input Processes

V. NOVÁK[1], J. SCHMIDT[2]

[1]Department of Biocybernetics, Institute of Physiology, First Faculty of Medicine, Charles University and [2]Logica, Prague, Czech Republic

Received October 30, 1995
Accepted April 26, 1996

Summary

A new approach to computer modelling of neuronal stochastic activity is described. The output dynamic activity which depends on the types and the number of input synapses, weights of the synaptic efficacy, the absolute refractory phase duration and threshold level is evaluated on this model in some types of Gaussian input processes. The behaviour of this model for one excitatory and one inhibitory synapse is described in dependence on the changes of excitation weight. The neuronal behaviour presented depends on the number of interspike intervals and the excitation weight and interspike interval density distribution. A novel concept of the e-curve is being introduced, which shows the dependence of the number of output interspike intervals on the weight of excitation on a stable inhibition level, the absolute refractory phase value and the threshold level. The properties of e-curves are discussed. Furthermore, examples of transformations of input stochastic processes are mentioned from the aspect of density distribution changes of interspike intervals.

Key words

Model of neuronal stochastic activity – E-curves – Interspike interval density distribution – Stochastic transformations

Introduction

Current approaches to modelling of the dynamic properties of neurones often concentrate on the mathematical formulation of the problem. Its aim is to identify the transmission of information by a neuronal cell. Different approaches followed Stein's description of neuronal stochastic activity (Stein 1965). His model has its shortcomings and therefore a number of authors have modified it (Tuckwell 1979, Lánský and Lánská 1987, Lánský and Musila 1992). In the above mentioned modifications, in order to solve this problem, input point processes with Poisson's distribution are always presumed. Although based on Palm-Chinchin's theorem (Sampath and Srinivasan 1977) the influence of many input synapses is well modelled by such type of process, for the study of informative-transmitting qualities of a neurone is just one of the possible input variables. When analyzing the output action in a living neuronal cell, there appear processes that have other than a Poisson's distribution of interspike intervals (Sampath and Srinivasan 1977).

On the basis of these facts, we mainly concentrated on the relations between input and output processes. These are influenced by the dynamic on the neuronal membrane and depend on a number of physiological processes. Some of them are modelled by the adjustable parameters of our model. The neurone is considered to be a dynamic system with discrete stochastic variables (point processes are led to the input synapse), continuous internal dynamics (processes on the membrane) and one discrete output variable (output point process in the axon). The realized model enables a simulation of actions corresponding to influences of a different number of synapses, with one synapse on the beginning up to multisynaptic inputs. In our work we observe dynamical actions caused by two input synapses, where stochastic point processes with Gaussian distribution of interspike intervals are loaded. The aim of this paper is a description of some phenomena, which are in relation to the activity of two synapses, just opposite type. Due to the changes of physiologically interpreted parameters, the input stochastic point processes ares

markedly transformed into an output process. These transformations have also relation to the changes of other statistic parameters of the output process, including changes of an inner time structure. In many experimental situations we tried to do justice to an influence of changes of some, physiologically interpreted parameters to the space-temporal summation. This summation has been realized by the one excitatory and one inhibitory synapse. The obtained results are able to supplement already known facts, which are related to the description of the space-temporal summation. At the same time there mean also an inspiration for the simulation of actions corresponding to multisynaptic inputs. To the dynamics of multisynaptic inputs and corresponding Poisson's processes we pay attention in our next papers.

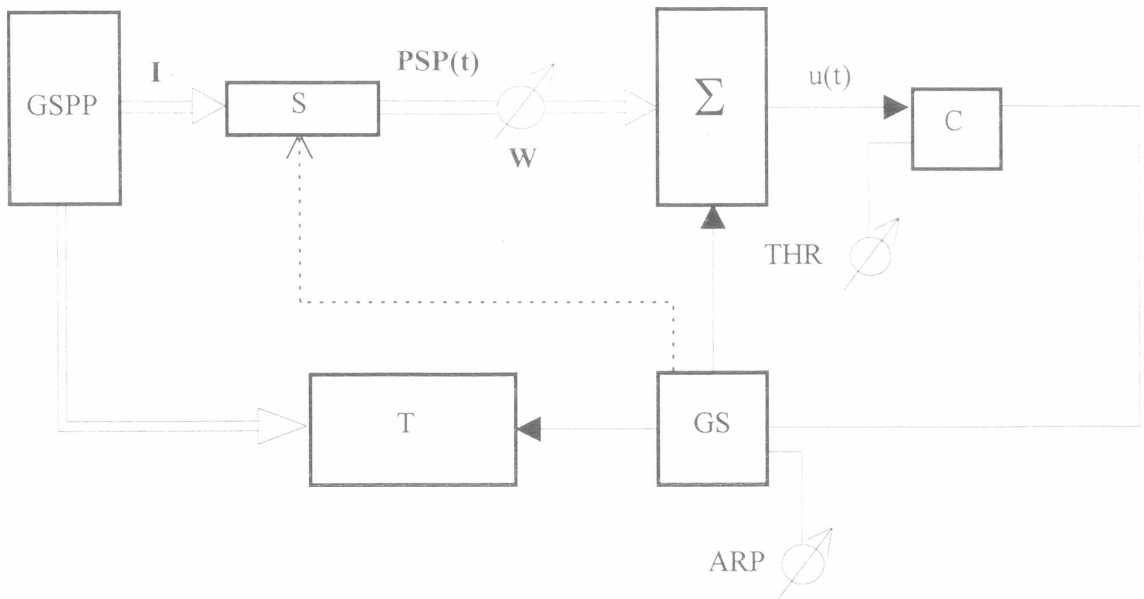


Fig. 1
A model of neuronal stochastic activity. GSPP - the generator of the n-dimensional vector I of input stochastic point processes. S – models of input synapses. PSP(t) – the n-dimensional vector of post-synaptic potentials. W – the n-dimensional vector of weights of efficiencies of input synapses. The eventual potential u(t) is compared in the comparator C with the adjustable threshold level (THR). By the result, system GS generates an output spike with an adjustable absolute refractory phase duration (ARP). The tester T provides testing of input (output) stochastic processes.

Methods

The block diagram of the proposed computer model is shown in Fig. 1. The model has a number of input synapses, where stochastic point processes of known properties can be loaded. The modelling of the space-temporal summation is proceeding from electrophysiological actions, which are presented on the membrane of a neurone. The time course of spikes and continuous changes of the post-synaptic membrane potential and changes of the threshold level were approximated by polynoms or spline functions. We selected samples from the work of Schmidt and Thews (1977). The insensitivity of the model to input stochastic processes during the absolute refractory phase is modelled by changes of the threshold level to infinity. Its recovery, which includes the relative refractory phase, is approximated by spline functions. The corresponding course of the threshold was also taken from the work of Schmidt and Thews (1977). By the space-temporal summation the variable, which is modelling the membrane potential of a neurone is obtained. Its value is compared with the threshold level and on the basis of this comparison there is or is not generated the time course, modelling the output spike (Fig. 2). Individual synapses are either excitatory (E) or inhibitory (I) in character. When modelling the summation processes, each axo-somatic excitatory and inhibitory synapse is given the weight of its efficacy (WE, WI). This weight can, to a certain extent, imply the distance of the synapse from the axon hillock (Schmidt *et al.* 1978, Lánský *et al.* 1992). In accordance with transmission in the CNS, the weight of synaptic efficacy can be considered as one of the phenomena connected with neuronal plasticity (Kohonen 1984, Nakamura and Ichikawa 1990, Clothiaux *et al.* 1991). The model does not concern any of the known optimalisation algorithms that change the value of

synaptic weight (Marko 1988, Wünsch 1994). In our model, this weight is an external influence, when experimenting with a convertible parameter, which influences the dynamics of the testing processes. Further adjustable and physiologically interpreted parameters of the model include the threshold level, absolute refractory phase (ARP), the type and number of input synapses. The included feedback expresses the influence of afterhyperpolarization and facilitation that must be additionally treated in classical models of the Stein's type (Lánský and Musila 1991, Lánský *et al.* 1992). Our model has a high number of degrees of freedom and ensures a large spectrum of realizable experiments, such as the consequences of dynamic processes and also the dynamic performance of multisynaptic inputs. This model makes it possible to generate input stochastic point processes with a Gaussian (G), log-norm (LN), exponential (E), Weibull's (W) and gamma (G) density distribution of interspike intervals. These distributions of ISIs were found in the output of living neuronal cells (Bishop *et al.* 1964). The multisynaptic input is modelled by a Poisson's input process. The model enables the testing the statistical properties of output point processes.

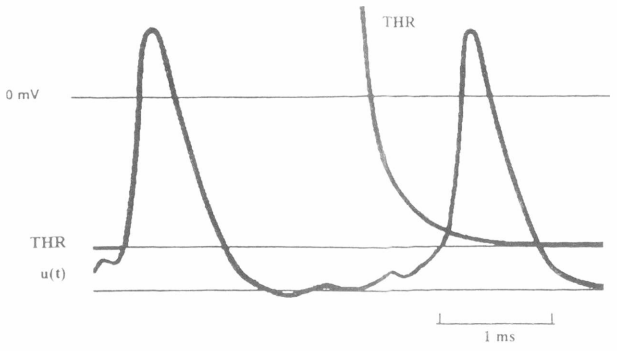


Fig. 2
An example of time course of stochastically changeable membrane potential u(t) and corresponding two spikes of the output stochastic process. The potential u(t) is a result of space-temporal summation of modelled post-synaptic potentials, which are generated in dependence on excitatory I_E or inhibitory I_I events of an input stochastic point process. When threshold (THR) is reached, the spike time course and the time course of a threshold during absolute and relative refractory phase is simulated.

The described experiments are corresponding to two input synapses, one excitatory and the other inhibitory. An excitatory synapse of computer model generates the excitatory post-synaptic potential EPSP(t) and an inhibitory synapse generates the inhibitory post-synaptic potential IPSP(t). Both post synaptic potentials are meant as time-dependent functions. The adjusted excitatory and inhibitory weight (WE and WI) is applicable in the space-temporal summation of these potentials. At every input synapse, we loaded the realization of input stochastic point processes with Gaussian distributions of ISIs (mean value E = 0.6 ms, variance s = 0.01 ms, the number of input ISIs equals 8000). Except the time of the lasting of a refractory phase, the threshold level was same for all experiments (THR = −60 mV) and the level of resting membrane potential was −80 mV. The extreme values of post-synaptic potentials in unitary values of the weights were 3 mV for excitation and 2 mV for inhibition (Schmidt and Thews 1977). In this case, the model showed three degrees of freedom which corresponded to the change of excitatory weight WE, inhibitory weight WI and the duration of the absolute refractory phase (ARP). Every experiment was repeated five times with a different realisation of input processes.

Results

E-curves

The e-curve is designed as the graphical dependence of the number N of ISIs of the output stochastic process on the excitatory weight WE, in the presence of the constant inhibitory weight WI. The threshold level is the same during all the experiments (THR = −60 mV).

Fig. 3a shows the e-curve for the inhibition weight WI = 1 and the absolute refractory phase duration ARP = 2.4 ms. The e-curve shows the existence of a saturated state in which, for an increasing WE value, the number N of ISIs of the output stochastic process arrests its increase. For mutual comparing of the following experiments, we introduce a reference number of interspike intervals N(WE = 3000), for value of the excitatory weight WE = 3000. Around this value of excitatory weight, e-curves are flat in character and the chosen reference number of interspike intervals N(3000) allows to have an approximate estimation of the asymptotic character of the e-curve in every series of experiments. In Table 1, a series of experiments are shown which were carried out for the value of an absolute refractory phase ARP = 2.4 ms. E-curves shown in Fig. 3b correspond with these values. This proves that the e-curves, differing in their value of inhibitory weight WI, converge to the same limiting number of ISIs of the output point process. The speed of convergence is in a reverse proportion with the value of the weight of inhibition.

The above mentioned phenomenon also depends on the duration of the absolute refractory phase ARP. A review of experiments for obtaining the value of the absolute refractory phase ARP = 4.8 ms is shown in Table 1. Even in this case, we can find e-curves converging onto the same limiting number of ISIs in the output process (Fig. 4a). A twofold duration

of the absolute refractory phase was demonstrated here by a marked decrease of the reference number N(3000). The relation between the value of the absolute refractory phase and the reference number N(3000) is shown in Fig. 4b. As the course of e-curves shows, the dependence is almost invariable to the value of inhibitory weight WI.

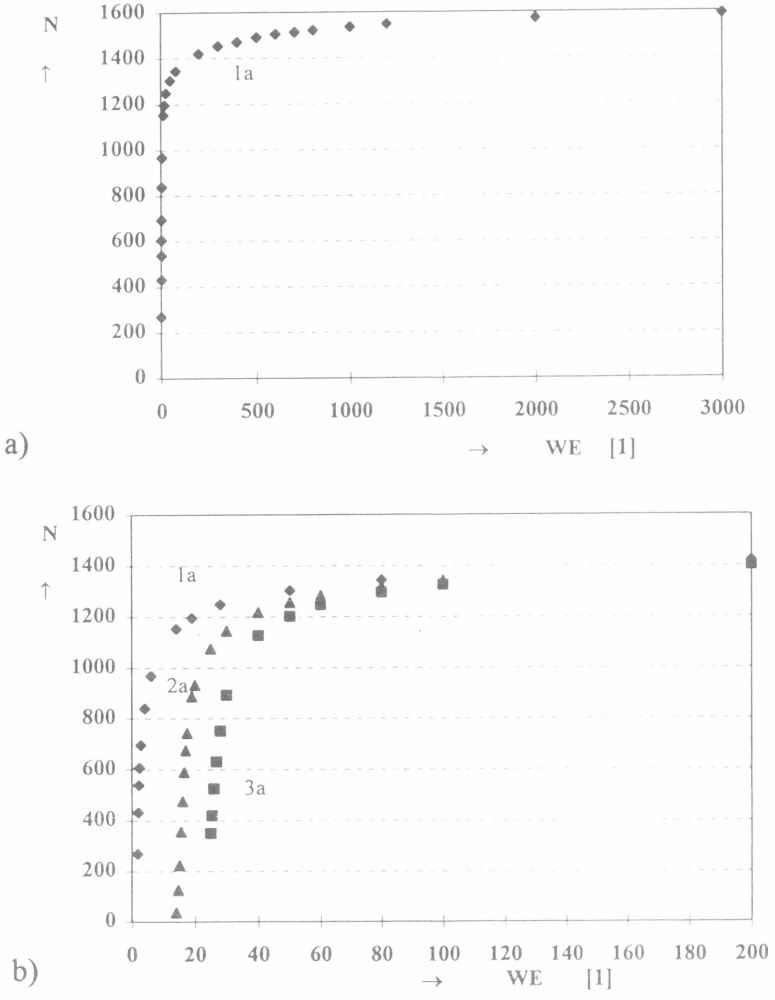


Fig. 3

a) The course of e-curve for series of experiments 1a (WI = 1, ARP = 2.4 ms, TRH = −60 mV). On this curve, the value of excitatory weight WE = 3000 corresponds with the reference number of ISIs N(3000) = 1588.

b) Detail of the increasing parts of e-curves in the area of values of excitatory weight WE ∈ <0;200>. The curve 1a corresponds with the series of experiments with the value of inhibitory weight WI = 1. The curve 2a analogously accords with the series of experiments with WI = 15 and the curve 3a corresponds with the series of experiments with WI = 25 (Tab. 1). These curves converge for the values of excitatory weight WE to the same limiting number of ISIs.

Table 1

Survey of the presented parameters in the individual series of experiments

Series of experiments	WI [1]	ARP [ms]	N(3000)
1a	1	2.4	1588
2a	15	2.4	1586
3a	25	2.4	1587
1b	1	4.8	883
2b	15	4.8	883
3b	25	4.8	883

WI – weight of the efficiency of an inhibitory synapse; ARP – duration of absolute refractory phase; N(3000) – reference number of ISIs of output point processes for the value of excitatory weight WE = 3000

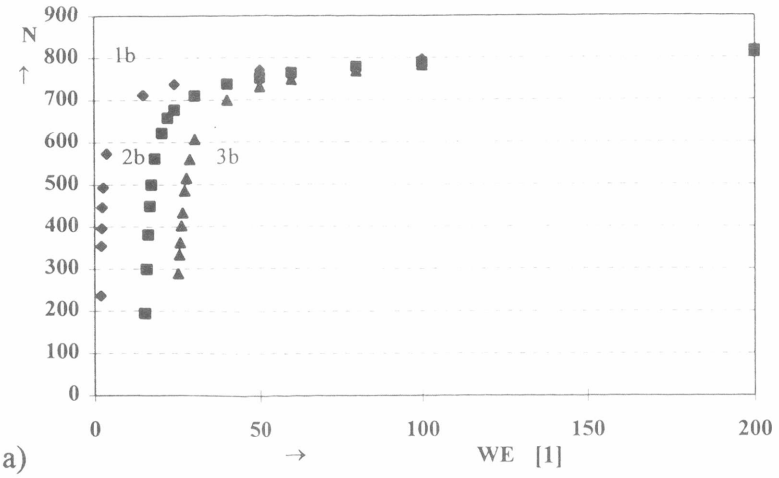
Mean values of interspike intervals

Figs 5a,b show the course of changes of the mean value E of ISIs, according to the series of experiments **a** (ARP = 2.4 ms) and **b** (ARP = 4.8 ms). In both cases, together with the growing value of excitatory weight WE, the mean value of ISI converges to the magnitude of the absolute refractory phase ARP.

Density distributions of ISIs of output stochastic processes

A neurone has the ability to transform the density distribution of ISIs. All the above described experiments assumed Gaussian processes at the input of the model. In dependence of the changes of excitatory weight WE and at a constant level of other physiological parameters (WI, ARP, THR) different distributions of ISIs of output stochastic process were found.

For example, in the series of experiments 1a (WI = 1, ARP = 2.4 ms) in the range of values WE ϵ <0; 2.0> the output process did not show any of the characteristic distributions of ISIs, which have been observed at the output of a living neuronal cell (i.e. Gaussian, log-norm, exponential, the Weibull's and gamma distribution). In the range of values of excitatory weight WE ϵ <2.1; 5.0> a log-norm distribution of ISIs was found (Fig. 6a). Its significance reaches a maximum approximately in the middle of this interval and decreases in the direction to either side. When the excitatory weight WE (i.e. WE>5.0) is increasing, then in certain cases we find differently modified multimodal distributions of ISIs that have been observed at the output of a living neuronal cell (Bishop *et al.* 1964). Their high occurrence is increasing together with the rate of decrease of changes of the number of ISIs of the output point process.



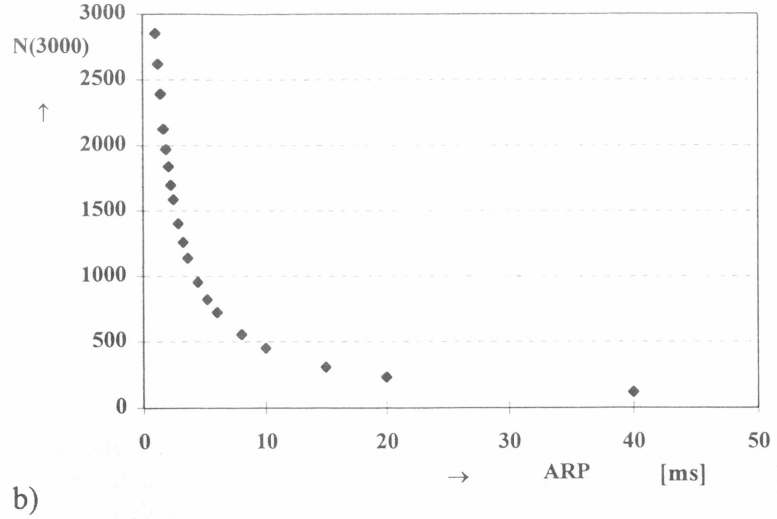


Fig. 4
a) Detail of the increasing parts of e-curves for the value ARP = 4.8 ms. They correspond with the series of experiments 1b (WI = 1), 2b (WI = 15) and 3b (WI = 25) (see Table 1). b) Dependence of the number of ISIs on the duration of the value of excitatory weight WE = 3000. This value WE corresponds with the reference number of ISIs N(3000).

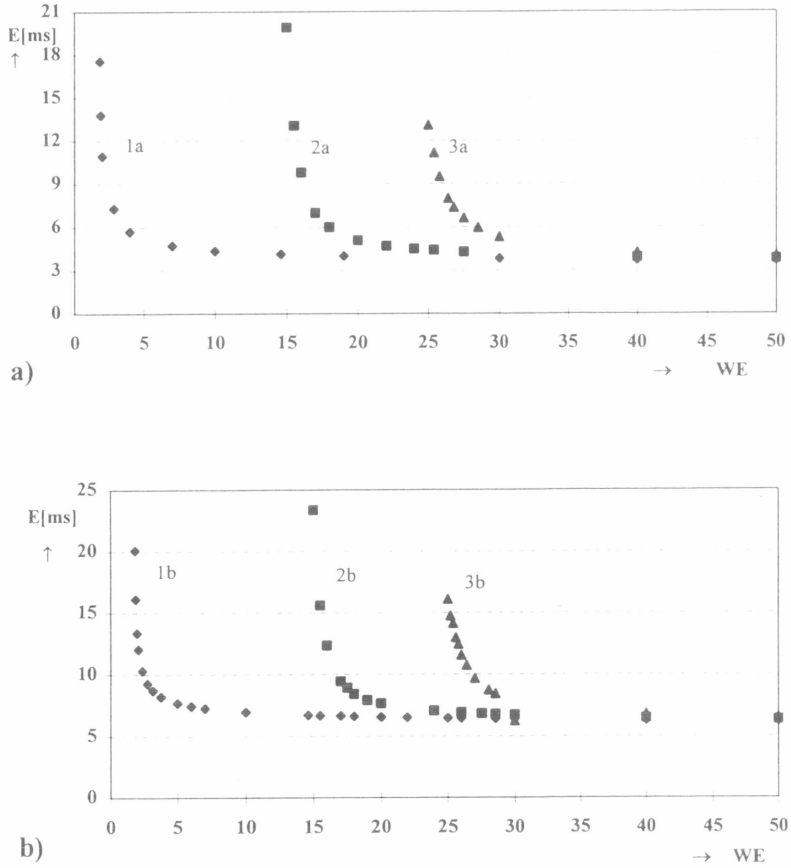


Fig. 5

a) Dependence of the mean value E of ISIs for the series of experiments 1a, 2a, 3a in the area of the excitatory weight WE ϵ <1;50>. For the values WE>>50, the course of the mean value of E converges to the value ARP = 2.4 ms.

b) Dependence of the mean value E of ISIs for the series of experiments 1b, 2b, 3b in the area of the excitatory weight WE ϵ <1;50>. For the values WE>>50, the course of the mean value of E converges to the value ARP = 4.8 ms.

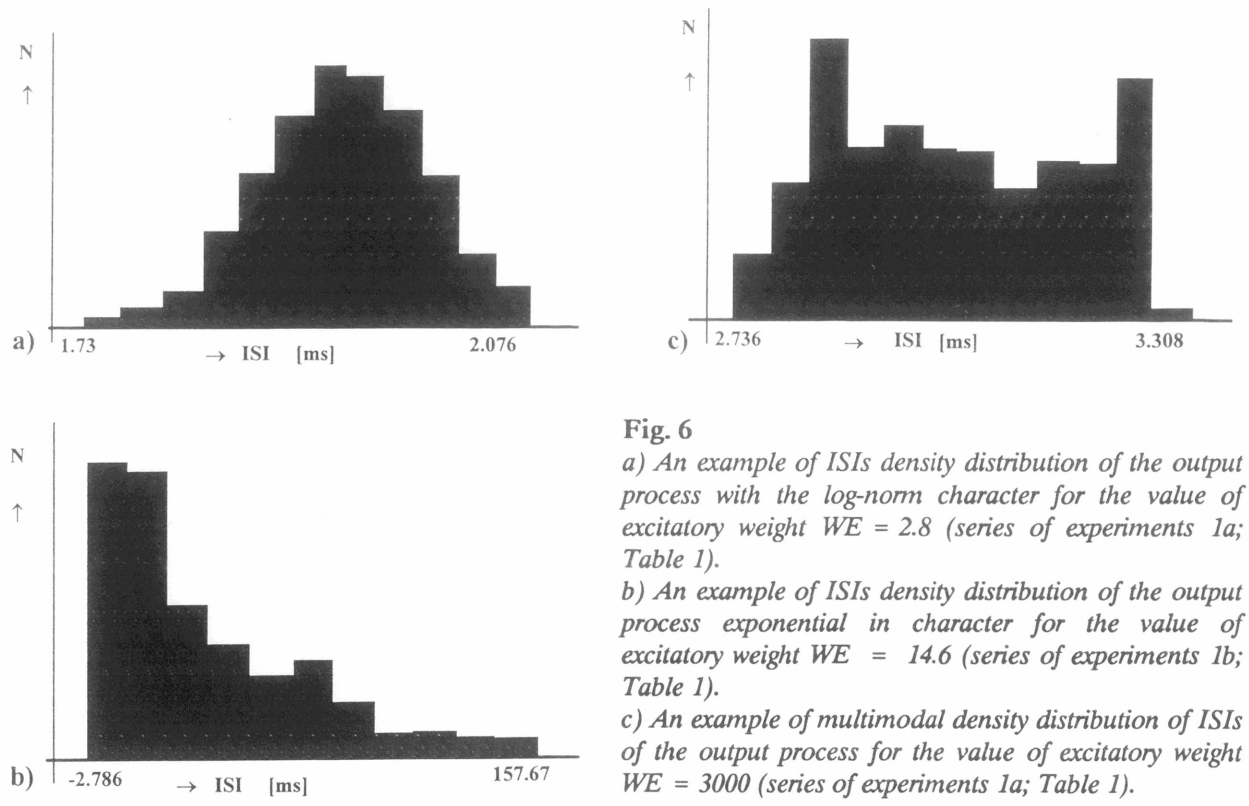


Fig. 6

a) An example of ISIs density distribution of the output process with the log-norm character for the value of excitatory weight WE = 2.8 (series of experiments 1a; Table 1).

b) An example of ISIs density distribution of the output process exponential in character for the value of excitatory weight WE = 14.6 (series of experiments 1b; Table 1).

c) An example of multimodal density distribution of ISIs of the output process for the value of excitatory weight WE = 3000 (series of experiments 1a; Table 1).

With increasing values of WI as a constant parameter, the above mentioned phenomenon becomes less marked. In the 2a experimental series (WI = 15, ARP = 2.4 ms), the exponential distribution of ISIs appeared in the range of values of the excitation weight WE ϵ <14.0; 15.0> (Fig. 6b). The maximum of significance again corresponds roughly to the middle of this interval. With a further increase (WE>15.0) we mainly found a multimodal density distribution. In the series 3a (WI = 25, ARP = 2.4 ms) none of the above mentioned density distributions were observed. The occurrence of the multimodal distribution corresponds with the results mentioned in the previous paragraph (Fig. 6c).

The same phenomena were found in experiments with a twofold value of the absolute refractory phase. In the series of experiments 1b (WI = 1, ARP = 4.8 ms) the log-norm distribution of ISIs appeared in the range of values WE ϵ <2.0; 7.0>. In series 2b (WI = 15, ARP = 4.8 ms), the exponential distribution appeared in the range of values WE ϵ <14.0; 14.6>. Finally, in the series of experiments 3b (WI = 25, ARP = 4.8 ms), in accordance with our previous results, only areas of the multimodal distribution of ISIs were found.

It can thus be concluded that typical distributions of ISIs (log-norm or exponential) are to be found in the experiments the parameters of which correspond to the steep increasing areas of e-curves, and do not exhibit high values of inhibitory weight. In other cases only multimodal distributions of ISIs of the output point process are to be observed.

Conclusions

The presented simulation experiments have provided results which may serve as the starting point to the study of problems encountered with the described model. They have shown some typical phenomena, which accompany the dynamics of two input synapses one excitatory and the other inhibitory. In Gaussian input point processes we measured the so-called e-curves, indicating the number of ISIs of the output process that depend on the variable values of the excitatory weight WE in the constant value of the inhibitory weight WI ($N = N_{WI}(WE)$). Some experiments corresponding with the steep increasing areas of e-curves, showed a transformation of input processes with the Gaussian distribution of ISIs to the output process with a typical log-norm or exponential distribution. Distribution of ISIs of the output process with further grow of excitatory weight WE were often transformed into a multimodal distribution. The above mentioned phenomena can be modified by the duration of the absolute refractory phase ARP. For the high values of excitatory weight WE, the e-curves come closer and asymptotically converge to the same limiting number of ISIs, which depends on the size of the absolute refractory phase. In this respect, only multimodal distributions of ISIs are observed. It can be expected, that the output point process, corresponding to the same value of excitatory weight WE and various values of inhibitory weight WI (i.e, represented by individual e-curves), will disclose some common intrinsic time correlations. The above mentioned facts, as will be shown in our future work, can be confirmed by calculation of cross-correlation coefficients and especially by application of the so-called method of recurrence plot (Kaluzny and Tarnecki 1993). Using these methods we can identify a rapid, several milliseconds lasting processes appearing in the activity of the model of a neurone and which are reflected in the presence of non-typical groups of ISIs. The mentioned experiments correspond to modelled situations, simulating the space-temporal summation of post-synaptic potentials of two input synapses. With increasing number of synapses we come up to multisynaptic inputs. The description of their influences is a next step in using of the presented models.

Acknowledgment

This work was supported by grant Grant Agency of the Czech Republic No. 106/94/1503.

References

BISHOP P.O., LEWICK W.R., WILLIAMS W.O.: Statistical analysis of the dark discharge of lateral geniculate neurones. *J. Physiol. London* **170**: 598–612, 1964.

CLOTHIAUX E.E., BEAR M.F., COOPER L.N.: Synaptic plasticity in visual cortex: Comparison of theory with experiment. *J. Neurophysiol.* **66**: 1785–1804, 1991.

HOLDEN A.V.: *Models of the Stochastic Activity of Neurons.* Springer, Berlin, 1976.

KALUZNY P., TARNECKI R.: Recurrence plots of neuronal spike trains. *Biol. Cybern.* **68**: 527–534, 1993.

KOHONEN T.: *Self-Organisation and Associative Memory.* Springer, New York, 1984.

LÁNSKÝ P., LÁNSKÁ V.: Diffusion approximation of the neuronal model with synaptic reversal potentials. *Biol. Cybern.* **56**: 19–26, 1987.

LÁNSKÝ P., MUSILA M.: Variable initial depolarization in Stein's neuronal model with synaptic reversal potentials. *Biol. Cybern.* **64**: 285–291, 1991.

LÁNSKÝ P., MUSILA M.: A neuronal model with variable synaptic input effect. *Cybern. Systems* **23**: 29–40, 1992.

LÁNSKÝ P., MUSILA M., SMITH C.E.: Effects of afterhyperpolarization on neuronal firing. *BioSystems* **27:** 25–38, 1992.

MARKO H.: Pattern recognition with homogeneous and space variant neuronal layers. In: *Processing Structures for Perception and Action*, Weitheim, 1988.

MUSILA M., LÁNSKÝ P.: Generalized Stein's model for anatomically complex neurons. *BioSystems* **25:** 1991.

NAKAMURA K., ICHIKAWA A.: Cerebral mechanism for reward-mediated learning: A mathematical model of neuropopulational network plasticity. *Biol. Cybern.* **63:** 1–13, 1990.

SAMPATH G., SRINIVASAN S.K.: *Stochastic Models for Spike Trains of Single Neurons.* Springer, Berlin, 1977.

SCHMIDT R.F., THEWS G.: *Physiologie des Menschen.* Springer, Berlin, 1977.

SCHMIDT R.F., DUDEL J., JANIG V., ZIMMERMANN M.: *Fundamentals of Neurophysiology.* Springer, Berlin, 1978.

STEIN R.B.: A theoretical analysis of neuronal variability. *Biophys. J.* **5:** 173–193, 1965.

TUCKWELL H.C.: Synaptic transmission in a model for stochastic neuronal activity. *J. Theor. Biol.* **77:** 65–81, 1979.

WÜNSCH Z.: Modelling in contemporary neurophysiology (in Czech) *Cs. fyziol.* **43:** 143–154, 1994.

Reprint Requests

Doc. Ing. V. Novák, CSc. Department of Biocybernetics, Institute of Physiology, Albertov 5, 128 00 Prague 2, Czech Republic.