



národní
úložiště
šedé
literatury

Chaotic Dynamics in Simple Neuronal Systems - Theory and Applications

Andrey, Ladislav
2005

Dostupný z <http://www.nusl.cz/ntk/nusl-37198>

Dílo je chráněno podle autorského zákona č. 121/2000 Sb.

Tento dokument byl stažen z Národního úložiště šedé literatury (NUŠL).

Datum stažení: 29.05.2024

Další dokumenty můžete najít prostřednictvím vyhledávacího rozhraní nusl.cz .



Institute of Computer Science
Academy of Sciences of the Czech Republic

Chaotic Dynamics in Simple Neuronal Systems - Theory and Applications

Ladislav Andrey

Technical report No. 933

March 2005



Institute of Computer Science
Academy of Sciences of the Czech Republic

Chaotic Dynamics in Simple Neuronal Systems - Theory and Applications¹

Ladislav Andrey

Technical report No. 933

March 2005

Abstract:

The ubiquitous feature of the nervous system of wide spread occurrence of complex dynamics behaviour is treated. The cardinal question concerning the nature of generators of such complex behaviour, namely if it is ad hoc random or deterministic but strongly non-linear, is analyzed. It is proved analytically that the discrete dynamics of single neurons with the sigmoidal transfer function is potentially chaotic. As the by-product the functional gain-threshold mechanism in neurons is derived. This allows for the new interpretations of famous experiments by Miyashita on squirrel monkeys. Then it is shown that the continuous dynamics of the neural circuits of two-three neurons are endowed with the potentiality of chaotic firing, too. Finally, it will be argued that the classical dogma of stochastic, or the ad hoc random neural coding can be taken as the limiting case of presenting new approach of deterministic or chaotic paradigm.

Keywords:

Chaotic dynamics, single neurons, neuronal circuits, gain-threshold mechanism, neural coding applications

¹This research was partly supported by the Grant Agency of the Czech Republic under GACR 305/02/1487.

Chaotic Dynamics in Simple Neuronal Systems – Theory and Applications

L. Andrey, *Academy of Sciences, Prague*

Running Head: Chaotic Dynamics ...

Correspondence should be addressed to: Ladislav Andrey, UI AV CR, Pod Vodárenskou věží 2, 182 07 Prague 8, Czech Republic, andre@cs.cas.cz. Tel: 00420266052085, Fax 00420286585789

Abstract: The ubiquitous feature of the nervous system of wide spread occurrence of complex dynamics behaviour is treated. The cardinal question concerning the nature of generators of such complex behaviour, namely if it is ad hoc random or deterministic but strongly non-linear, is analyzed. It is proved analytically that the discrete dynamics of single neurons with the sigmoidal transfer function is potentially chaotic. As the by-product the functional gain-threshold mechanism in neurons is derived. This allows for the new interpretations of famous experiments by Miyashita on squirrel monkeys. Then it is shown that the continuous dynamics of the neural circuits of two-three neurons are endowed with the potentiality of chaotic firing, too. Finally, it will be argued that the classical dogma of stochastic, or the ad hoc random neural coding can be taken as the limiting case of presenting new approach of deterministic or chaotic paradigm.

Keywords: Chaotic dynamics, single neurons, neuronal circuits, gain-threshold mechanism, neural coding applications

INTRODUCTION

Chaodynamics, as far as the authors' knowledge in this direction extends was introduced by himself (Andrey, 1986) (See, e.g., Nunez Yepez, 1989 for the citation of Andrey, 1986.) in analogy to other branches of science like thermodynamics, et cetera. It presents a paradigm of modern nonlinear science in general. Let us mention that one of the most famous proponents of theory of deterministic chaos, David Ruelle, has coined a name of chaology. But it seems this is going more to philosophy as to the adequate branch of nonlinear science. It is well accepted now that for a dynamic system to be chaotic a non-linearity is required to guarantee a sensitive dependence upon initial conditions and a dissipativity to guarantee a boundedness of trajectories on the attractor. It is called here the chaotic strange attractor in the appropriate phase space of the treated system. This makes solutions very complicated allowing for a description of this complexity of behavior of the real system under the treatment.

A human brain seems to be the most complex functional structure in the known universe. It is not surprising it fulfills the above mentioned conditions, namely the nonlinearity and dissipativity. It is rather natural as the human brain possesses necessary conditions for a realization of human mind. A part of this complexity lies in the diversity of nerve cells, which Santiago Ramón y Cajal, the father of modern brain science, described as “the mysterious butterflies of the poul, the beating of whose wings may some day – who knows? – clarify the secret of mental life”. This has been very prophetic statement which can be put into an analogy to the celebrating “butterfly effect” by the Ed. Lorenz, the father of modern chaodynamics.

There have been intensive attempts to study and understand more deeply some basic problems in neural systems on different levels during the last years (Arbib, 2003; Kandel, 2000; Koch, 1999; Guastello, 2004; Freeman, 2000). Specifically, concerning the main branches of neurodynamics and chaos one should mention the work on the integrate & fire model, synchronization and chaos (Hopfield, 1994; Kuramoto, 1991; Mirollo & Strogatz, 1990), seminal papers on calcium oscillations, stochastic resonance, bifurcations (Hindmarsh & Rose, 1984; Nikolov, 2004; Dhimala, et al., 2004; Falke, et al., 2000) and finally the attempts to apply chaos to the EEG rhythms (Basar, 1990; Kantz & Schreiber, 1995; Nunez, 1995; Lehnertz, et al., 2002). Alas, a progress seems to be rather slow and not adequate to the energy and interests put in. So far in the field of neuroscience one has not been able to formulate rigorously some fundamental universal laws like in physics. The main ideas and their formulations are rather of phenomenological origin and character. But as Galileo said the “book of Nature is written in the language of mathematics”. To proceed along these lines one needs to look for some general ideas connected to the dynamics of basic processes in such neural systems. By other words, to solve basic problems, so to speak, from the first principles. One will find such a novel approach can be very successful and even surprisingly proliferative.

In the paper, the ubiquitous feature of nervous system namely that of wide spread occurrence of complex dynamics behaviour will be treated from the point of view of theoretical as well as experimental descriptions. Here the cardinal question remains open concerning the nature of generators of such complex behavioural patterns of firing neurons, single ones or in populations. One speaks about a neuronal computing (Koch, 1999) or neural coding problem (Rieke, et al., 1997). Then the cardinal question is as mentioned above if a nature of generators behind neural coding problem is of ad hoc random or deterministic but highly nonlinear dynamics origination.

In this context, it has been believed and accepted till now the idea that a neural firing should depend mostly on the averaged frequencies of long train of incoming pulses (simple presynaptic Action Potentials_s) not on their exact timing. This is called also the firing rates model or the stochastic parading of neural coding. It assumes the ad hoc random dynamics with a Poissonian statistical distribution (Rieke et al., 1997). It has been called also the dogma of neural coding.

But with an advent of paradigm of new nonlinear science, namely the deterministic chaos, it has been natural to ask about a potentiality of chaotic dynamics in neuronal systems in general. This important point will be discussed in more details later. The question has been answered in a very positive and promising way. Namely, it will be shown for the first time analytically here that the biologically originated sigmoidal transfer function form of neurons is sufficient to generate chaotic firings of such single neurons. Then from a shape of firing spikes one can deduce to encode neural information not amplitudes of spikes but their timing should play the fundamental role. One speaks about time – encoding information (Hopfield, 1995). So instead of before mentioned stochastic paradigm of neural coding one has the dynamic (timing) paradigm. This new paradigm of neural coding is rather recent and brings no problems into the game of neural coding, at all. Just opposite – it allows to exploit intensively methods of chaodynamics. Explicitly speaking it means that one applies method of chaodynamics to the time mappings constructed of famous inter-spike-intervals (ISIs).

Besides the discrete dynamics of single neurons with the potentiality of chaotic behaviour and some by-products, we will address the answer to the question concerning a potentiality of chaotic behaviour in the case of continuous dynamics, too. Namely our effort will be concentrated on the minimal possible number of neurons to generate such chaotic dynamics.

POTENTIALITY OF COMPLEX BEHAVIOUR IN SINGLE NEURONS

The ubiquitous feature of the nervous system is the widespread occurrence of complex dynamic behaviours, as mentioned above. Examples range from the spike trains of single neurons to the fluctuating potentials of thousands of neurons measured from the surface of the scalp by the electroencephalogram (EEG) (Amit, 1999; Elbert et al., 1994; McKenna et al., 1992; Milton, 1996; Barbi and Chillemi, 1998).

To begin with it is natural to start at the level of single neurons. Chaotic behavior has been identified experimentally in single neurons at different situations. It was observed that the repetitive firing of action potentials (APs) in sinusoidal current stimulated squid giant axons can be chaotic (Matsumoto, et al., 1982). Later on it was shown that the spontaneous activity of some simian cortical neurons in the precentral gyri of anesthetized squirrel monkeys (Rapp, et al., 1985) is chaotic. And finally, by the inter-spike-intervals (ISIs) measurements on the sciatic nerve of adult male SD and using methods of chaodynamics the chaotic dynamics in the neural information process was discovered (Gong, et al., 1999).

On the other side it has been shown in many numerical simulations that there is chaos in the neuron models, too. Namely, responses of model neurons as simple as Caianello (1961), and Nagumo and Sato (1972) possess chaotic behaviour. The refractory function model, due to a past firing that decreases exponentially with time, can also be chaotic (Aihara, et al., 1990). It has been shown numerically that solutions of the Hodgkin-Huxley equations (Hodgkin and Huxley, 1952) with the periodic stimulation are not always periodic and can be understood as deterministic chaos (Aihara et al., 1990; Matsumoto et al., 1987).

The neurodynamics based on a non-monotone response function for single neurons has been described (Morita, 1993; Yoshizawa, et al., 1993). Such neurons also can behave

chaotically (Shuai, et al., 1996). There are other models of single neurons possessing the chaotic dynamics (Pasemann, 1997; Shilnikov & Rulkov, 2004).

The dynamics of single neurons plays a very important role in recent approaches to artificial neural networks. Model neurons with complicated dynamics are the composer elements of artificial neural networks. Such neural networks are called chaotic neural networks (Aihara, et al., 1990; Bondarenko, 1994).

As mentioned above there is the numerical evidence for chaotic behavior in biologically motivated neuron models. But such models are often rather artificially constructed in a sense just to possess appropriate solutions. To escape from a tautology of the known self-contained contradictory paradigm in biology in general, one needs an analogy to physics to describe and to attack the problem from the first principles. To proceed in this spirit a generalized McCulloch-Pitts like neuron model (McCulloch and Pitts, 1943) with biologically derived sigmoidal response function (Eeckman and Freeman, 1986) will be introduced. Then it will be shown for the first time analytically that such biologically based sigmoidal transfer function is sufficient for single neuron to generate chaotic dynamics in the rather natural manner. But this is principally in agreement with above presented experimental and numerical findings. Let us mention in advance that as a by-product of our analytical treatment the novel functional dependence between two cardinal parameters of sigmoidal transfer function native to every neuron in the brain, namely the threshold and steepness, is earned. When translating from pure technical matters to the adequate biological meaning of these parameters, one can speak about the gain-threshold mechanism in neurons. This surprising and in fact an astonishing result will be discussed in more details later on. And as it would be, the treatment from the first principles allows one to shed new light on some good, and old open problems of biology.

Chaotic Dynamics in a Single Neurons with the Sigmoidal Transfer Function – Analytical Proof

A standard neuron model is a simple threshold element transforming a weighted summation of the inputs into the output through a nonlinear transfer function with a threshold. In what follows, we will use a generalization of classical McCulloch-Pitts neuron model (McCulloch & Pitts, 1943), in which instead of the unit step function the sigmoidal transfer function will be exploited. Then for the i -th neuron dynamics,

$$y_i = g(\xi_i(t_n)) = \frac{1}{1 + e^{-\lambda \xi_i}}, \quad (1)$$

holds, where

$$\xi_i(t_n) = h_i - \theta_i = \sum_j w_{ij} x_j(t_n) - \theta_i. \quad (2)$$

Here $y_i(t_{n+1})$ is the output of the i -th neuron at the discrete time t_{n+1} ; g is the sigmoidal transfer function with a slope λ ; θ is the threshold of the i -th neuron; w_{ij} (for $i \neq j$) is the connection weight with which the firing of the j -th neuron affects the i -th neuron and $h_i(t_n)$ is the local field of i -th neuron at the discrete time t_n . Here $i, j = 1, 2, \dots, N$ is the number of neurons. One can speak about the input dynamics - Eq. (2) and the output dynamics - Eq. (1).

Now a transition from the discrete time dynamics Eq. (1) and Eq. (2) to a continuous time dynamics can be easily made (Andrey, 1991). Denote $\Delta t = t_n - t_{n-1}$ and suppose $\Delta t \ll 1$. Then from (Eq. 2) we have $\frac{1}{\Delta t}(\xi_i(t_n) - \xi_i(t_{n-1})) = -\frac{1}{\Delta t}(\xi_i(t_{n-1}) - \xi_i(t_n))$ and in the limit, where $\Delta t \rightarrow 0$, we get for the input dynamics

$$\frac{d\xi_i}{dt} = -\alpha \left(\xi_i(t_{n-1}) - \frac{\partial E}{\partial y_i} \right) \quad (3)$$

where $\alpha = \frac{1}{\Delta t}$ is a parameter and E is the Hopfield-like energy function

$$E = -\frac{1}{2} \sum_{ij} (w_{ij} x_j y_i - \theta_i y_i). \quad (4)$$

Analogously, from Eq. (1) the time continuous output dynamics Eq. (5),

$$\frac{dy_i}{dt} = -\alpha (y_i - g(\xi_i)). \quad (5)$$

Here we are especially interested in the output dynamics as we are looking for the potentiality of chaotic responses in such neurons. To this end we exploit properties of the sigmoidal transfer function. Namely, from Eq. (1) one gets directly

$$\frac{dy_i}{d\xi_i} = \lambda y_i (1 - y_i), \quad (6)$$

which is a Riccati-like equation.

To analyse the output dynamics of the i -th neuron take the Taylor expansion of the output variable y_i in time,

$$y_i(t_{n+1}) = y_i(t_n) + \frac{dy_i}{d\xi_i} d\xi_i + \dots = y_i(t_n) + \frac{dy_i}{d\xi_i} \frac{d\xi_i}{dt} \Delta t + \dots, \quad (7)$$

where again we assume $\Delta t = t_{n+1} - t_n \ll 1$. After substituting from Eq. (3) and Eq. (6) into

Eq. (7), neglecting terms with $(\Delta t)^k$, $k \geq 2$, one gets after some elementary calculations, suprisingly

$$y(t_{n+1}) = y(t_n) + 4ay(t_n)(1 - y(t_n)), \quad (8)$$

where the parameter

$$a = \frac{\lambda}{4} (\xi(t_{n+1}) - \xi(t_n)). \quad (9)$$

depends upon the steepness of the sigmoidal transfer function and also upon the dynamics of gradient of local fields. That makes the dynamics very complex.

For the sake of simplicity we have omitted the index i , as the analysis is performed for the i -th neuron. For the same reason we can put $y(t_n) \equiv y_n$ and $\xi(t_n) \equiv \xi_n$. Then Eq. (8) can be written in the form

$$y_{n+1} = y_n + 4ay_n(1 - y_n), \quad (10)$$

where

$$a = \frac{\lambda}{4}(\xi_{n+1} - \xi_n). \quad (11)$$

Introducing the substitution

$$z_n = 4ay_n - \frac{1 + 4a}{2}, \quad (12)$$

into Eq. (10) one gets an equivalent form of logistic equation for z 's, namely

$$z_{n+1} = c - z_n^2, \quad (13)$$

where $c = 4a^2 - \frac{1}{4}$ is the parameter and the α is determined by Eq. (11).

Note that the logistic map Eq. (13), on the interval $(-1; 1)$, where c varies in the interval $[0; 2)$, coincides with the more accustomed logistic map Eq. (14)

$$x_{n+1} = bx_n(1 - x_n), \quad (14)$$

mapping the interval $\left(1 - \frac{b}{4}, \frac{b}{4}\right)$ into itself when $2 < b \leq 4$. Under the coordinate change

$$x = \left(\left(\frac{b}{4} - \frac{1}{2} \right) z + \frac{1}{2} \right) \quad \text{with the parameter identification } c = \frac{b^2}{4} - \frac{b}{2}, \quad \text{both families Eq. (13)}$$

and Eq. (14) coincide (Collet and Eckmann, 1980).

It is well known that the quadratic maps Eq. (13) and Eq. (14) can exhibit chaotic behavior. It means there exists some critical value of parameter c_{crit} in Eq. (13) or b_{crit} in Eq. (14) such that for $c \geq c_{crit}$ or $b \geq b_{crit}$ solutions of Eq. (13) or Eq. (14) can be chaotic. For Eq. (13) then one has $c_{crit} = 1.8284$, or for Eq. (14) then $b_{crit} = 3.8284$ (Collet and Eckmann,

1980). From this it immediately follows for the neurons to fire chaotically some restrictions are laid upon the stability conditions through the steepness of sigmoid as well as dynamics of local fields, as mentioned above. This may have naturally interesting biological consequences.

So far we have been able to show for the first time analytically that the output dynamics, or firing patterns, of the generalized McCulloch-Pitts like model of single neuron with the sigmoidal transfer function contains inherently deterministic chaos. In other words, chaotic behavior is natural in such neuronal dynamics.

Some Consequences of Single Neuron Complex Dynamics

The output dynamics described at the first approximation by the logistic equation- Eq. (13) is much more complex as it may appear at the first sight. Namely the parameter c , from Eq. (2) and Eq. (9), is in general the function

$$c = c(\lambda, \theta, n). \quad (15)$$

That means the firing pattern of the neuron depends crucially upon the basic characteristics of the sigmoidal transfer function, namely the threshold Θ and the slope λ . As already mentioned Θ represents the threshold (bias) and from the biological point of view is a measure of sensitivity. So if Θ increases then the sensitivity decreases and vice versa. On the other hand the parameter λ presents the steepness of sigmoidal transfer function and from the biological point of view this is connected with the excitability (Andrey, 1997). We will not go to details here but only mention case of onset of chaos in Eq. (13). For this special case it follows immediately from Eq. (2) and Eq. (9)

$$\lambda_{crit} = \frac{4\alpha_{crit}}{h_{crit} - \theta_{crit}}, \quad (16)$$

where $a_{crit} = \frac{1}{2} \sqrt{c_{crit} + \frac{1}{4}}$ and $c_{crit} = 1.8284$ (Collet and Eckmann, 1980). Surprisingly enough at the onset of potential chaotic behavior we have a functional dependence between basic characteristics of neuronal dynamics, namely $\lambda = \lambda(\Theta)$ (Andrey, 1997). Put it in the biological language the Eq. (16) can be translated as the gain-threshold mechanism working on an onset of chaotic firings of such neurons. The discrete dynamics result of Eq. (16) prescribed in the continuous form simply describes that there should exist an exponential dependence between the steepness (biologically the excitation or irritation) and the threshold-bias (the sensitivity) of the sigmoidal transfer function.

Now, it is well known (Khodorov, 1974) that the threshold Θ can vary as the strength of the stimulating current is changed. Besides, it is observed that the minimum slope λ_{min} is needed to increase the current stimulation in time (Scott, 1977). Below this minimal slope no action potential is observed at any level of stimulating current. But it seems the biological reality is even more sophisticated. On the one hand, with increasing a threshold Θ the sensitivity naturally decreases. On the other hand, with increasing arousal the gain λ of neurons rises as well. This input-dependent increase in gain seems essential for the formation of bursts, as indicated by Freeman (1991). This is understandable if one realizes that the λ determines the stability conditions of the firing process. Indeed, the first derivation of transfer function g is proportional to the λ as it is seen from eqs. (1) and (6). Technically speaking, the λ plays the important role in the Lyapunov stability analysis of the whole process. Biologically, the meaning of λ will be discussed later on.

Let us mention that the logistic equation (13) is different from standard one, exploited, e.g., commonly in physics or in population dynamics. In fact one has the very complex logistic equation with the other complicated nonlinear dynamic equation nested in it through the dynamic parameter c of the form (15) and (16) (Andrey, 2000; 2001; 2002).

The existence of the above mentioned gain-threshold mechanism in single neurons in the equation (16) is a great challenge for the experimental neuroscience. Surprisingly, there are some at least indirect evidences for such a mechanism in the physiology of perception. Namely, the relation between input (wave density) and output (pulse density) at trigger zones in populations of neurons are sigmoid curves with the slope increasing with an arousal (Freeman, 1991; Wright & Liley, 1996; Liljeström, 1991). There is one hot candidate even on a single neuron level. This is a series of remarkable experiments by Miyashita and his coworkers (1988, 1991). Spiking rates emitted by a given neuron in the anterior ventral temporal cortex of a monkey (*macaca fuscata*) as a function of time were recorded. The enhanced activity correlated with abstract feature recognition was observed sustaining for some finite time following the removal of the stimulus. In analyzing these experimental results one can deduce at least qualitatively from the graph of the firing rates dependence upon input currents for different conditions (values of thresholds, in fact) there should exist a functional gain-threshold dependence in this case. (Andrey, 1993; Amit, 1993). (As the lambda-theta mechanism is not the main ingredient of the paper more recent findings will be published elsewhere.)

It is worth mentioning about the implementation of the gain-threshold mechanism into the natural sigmoidal transfer function leads immediately already at the first approximation to the non-monotone transfer function with a typical cubic non-linearity (Andrey & Erzan, 2002). So one gets rather naturally here what many people have been constructing ad hoc in the rather dubious manner in the attempt to increase the capacity of adequate associative memories (Morita, 1993).

Another positive message is that one can build up novel type neural networks of neurons with such gain-threshold mechanism. The natural way is to call them the λ - Θ neural networks. Such networks have been tested on many numerical simulations and it was shown

that such networks possess the fascinating behavior and properties (Andrey, 2000a). (It has been an effort to make patents of them.)

The Minimal Neuronal System with Continuous Dynamics Possessing Chaotic Behaviour

One can summarize that single neurons have the strong potentiality of complex chaotic behavior. But the dynamics of single neurons plays a very important role in recent approaches to artificial neural networks. Model neurons possessing complicated dynamics can be composing elements of artificial neural networks. Such neural networks are then called the chaotic neural networks (Aihara, 1990). In such case it was shown numerically that chaotic behavior in biologically motivated neuron models and neural networks built of such neurons can be caused also by a time delay due to a refractoriness.

Now an open question remains what are sufficient conditions for a potentiality of chaotic behavior in a continuous dynamics case. Surprisingly, this question natural in its technical setting also has an adequate biological counterpart. Well, there is a wealth of anatomical, histochemical and physiological observations which indicate that neurons are incorporated into functional circuits, or modular units. Neural circuits composed of two-three neurons form the basic feedback mechanism involved in the regulation of neural activity. Examples of three neurons circuits are the basic rhythm generating circuits of, for example, central pattern generators and the recently proposed canonical circuit (Milton, 1996).

Two-Three Neurons Chaotic Systems

In looking for a minimal continuous dynamics neural system, or better a neural circuit possessing a chaotic behavior, it is reasonable as mentioned above to take into consideration two or three neurons circuits. On the other hand, it is well known from the theory of deterministic chaos, or shortly from the chaodynamics (Andrey, 1986) that in the continuous dynamics case one needs at least three degrees of freedom for the system to behave chaotically, i.e., to possess a chaotic strange attractor.

Let us have a neural circuit of three neurons interconnected via synapses. (The term neural network will be reserved for systems of more than three neurons.) Then dynamical variables are membrane potentials and one can express the rate of change of membrane potential of the neuron i ; $i = 1; 2; 3$ by the current balance equation in the form

$$\dot{x}_i = -\alpha_i x_i + g_i \left[\sum_{j \neq i}^3 w_{ij} x_j (t - \tau_i) - \theta_i \right] \quad (17)$$

where (17) describes the activation or output dynamics for all three neurons in the circuit (Andrey, 1991).

Here, $\dot{x} = \frac{dx_i}{dt}$ is a time derivative of the activity variable x_i , $i = 1, 2, 3$. The second term on the r.h.s. of (17) represents currents induced by the activity of pre-synaptic neurons and the first term describes a leakage via the finite resistivity of the membrane with a threshold like mechanism. For a sake of simplicity one can introduce

$$\xi_i = \sum_{j \neq i}^3 w_{ij} x_j (t - \tau_i) - \theta_i = h_i - \theta_i \quad (18)$$

$$h_i = \sum_{j \neq i}^3 w_{ij} x_j (t - \tau_i) \quad (19)$$

where h_i is the value of local field (a postsynaptic potential PSP) of the i^{th} neuron, θ_i is a bias (threshold), τ_i - time delays expressing a refractoriness, w_{ij} are fixed (here) weights

between neurons i and j and as already mentioned x_i , $i = 1; 2; 3$ represent presynaptic action potentials or activations of the given neuron by surrounding ones.

To be complete one must specify functions g_i , $i = 1; 2; 3$: Well, g_i are sigmoidal transfer (input-output) functions characterized by two parameters, a steepness λ and already mentioned threshold θ , playing a role of shifting the sigmoid. So functions g_i can be written explicitly in the form

$$g_i(\xi_i) = \frac{1}{1 + e^{-\lambda_i \xi_i}}; \quad i=1,2,3 \quad (20)$$

Let us mention that for a potentiality of chaotic behavior of (17), as it will be seen later, parameters α_i (we suppose $\alpha_i > 0$) and mentioned main characteristics of any transfer function, namely the steepnesses λ_i and threshold θ_i will play a crucial role. It is worthwhile to mention that biologically λ_i play the role of excitability and θ_i that of sensitivity of neurons.

The goal is to bring a proof of possibility of chaotic dynamics of neuronal circuit described by (17). To achieve this it is sufficient to take into account the simplest form of (17) as possible. For a sake of simplicity suppose

$$\alpha_1 = \alpha_2 = \alpha_3 = \alpha > 0 \quad (21)$$

$$g_1 = g_2 = g_3 = g \quad (22)$$

$$\tau_1 = \tau_2 = \tau_3 = 0 \quad (23)$$

i.e., the leakage is constant in all neurons (21), one does not take into account the refractoriness (23) and as it is biologically relevant that one takes the same transfer function for all three neurons in the circuit. Then (17) has a form

$$\dot{x}_i = -\alpha_i x_i + g(\xi_i); \quad i=1,2,3 \quad (24)$$

where

$$\xi_i = \sum_{j \neq i}^3 w_{ij} x_j - \theta_i \quad (25)$$

$$g(\xi_i) = \frac{1}{1 + e^{\lambda_i \xi_i}} \quad (26)$$

Let us now mention that in a case of $\tau_i \neq 0$ it was already shown (Aihara, et al., 1990) that even a single neuron can behave chaotically.

Now a question is if the dynamical system (24) possesses a chaotic dynamics. Well, one has the system of three strongly nonlinear ordinary differential equations, as the function g describing the sigmoidal transfer function is strongly nonlinear. The divergence of the flow of (24), can be easily calculated as follow:

$$\text{div}X = \sum_{x_i=1}^3 \frac{\partial \dot{x}_i}{\partial x_i} = -3\alpha < 0 \quad (27)$$

It is a negative constant so the dynamical system (24) is dissipative. Now it is enough to show that the lowest order approximation of g , i.e., the quadratic nonlinearity approximation will possess a chaotic dynamics. To realize this, one can subtract the Taylor series expansion till the quadratic nonlinearity of the function g in (26). In doing so, one gets the following equality

$$g(\xi_i) = 1 - \frac{1}{4} \left[1 - \lambda_i \xi_i + \frac{1}{2} \lambda_i^2 \xi_i^2 \pm \dots \right] + \frac{1}{8} \left(1 - \lambda_i \xi_i + \frac{1}{2} \lambda_i^2 \xi_i^2 \pm \right)^2 \pm \doteq \frac{7}{8} + \frac{7}{8} \lambda_i^2 \xi_i^2 \quad (28)$$

so the dynamical system (24) has a form

$$\dot{x}_i = -\alpha x_i + \frac{7}{8} + \frac{1}{8} \lambda_i^2 \left(\sum_{j \neq i}^3 w_{ij} x_j - \theta_i \right)^2 \quad (29)$$

To simplify the reasoning, one can put on pure biological basis

$$\lambda_1 = \lambda_2 = \lambda_3 = \lambda \quad (30)$$

$$\theta_1 = \theta_2 = \theta_3 = \theta \quad (31)$$

Besides, we do not consider a learning process here, i.e., we do suppose that weights w_{ij} are fixed. Without loosing of generality one can suppose that the weights are symmetrical

$$w_{ij} = w_{ji}; \quad i = 1, 2, 3 \quad (32)$$

This is done, e.g., for Hopfield like networks to guarantee a stability of memories.

The dynamical system (29) can be written in the following explicit form:

$$\begin{aligned} \dot{x}_1 &= -\alpha x_1 + \frac{7}{8} + \frac{1}{8} \lambda^2 (w_{12} x_2 + w_{13} x_3 - \theta)^2 \\ \dot{x}_2 &= -\alpha x_2 + \frac{7}{8} + \frac{1}{8} \lambda^2 (w_{12} x_1 + w_{23} x_3 - \theta)^2 \\ \dot{x}_3 &= -\alpha x_3 + \frac{7}{8} + \frac{1}{8} \lambda^2 (w_{13} x_1 + w_{23} x_2 - \theta)^2 \end{aligned} \quad (33)$$

So the simplest continuous in time nonlinear dynamics for a neuronal circuit of three neurons can be described by the dynamical system (33). Such system consists of three ordinary differential equations of quadratic nonlinearity and the constant negative divergence of the flow. It can be easily shown that (33) is dynamically equivalent to the famous Lorenz system (Sparrow, 1982) describing a deterministic nonperiodic flow of the homogenous layer of liquid heated from below. But it is well known that the Lorenz system is the prototype of the system possessing a chaotic strange attractor. So one could apply all the machinery of chaos theory to perform the stability analysis of the dynamical system (33).

Now, let us mention some important features of (33). Commonly, in modeling neural networks, the value of parameter α is considered equal to one. Then it is clear that the dynamics of (33) is fully characterized by the values of two main parameters of sigmoidal transfer function, namely a value of threshold θ , playing biologically the role of sensitivity and a value of steepness λ playing the role of excitability. It is also interesting to note that for a quality of dynamical behavior the role of λ is in a sense more important as θ . One can

make some kind of scaling and to put $\theta = 0$, and still (33) can possess a chaotic dynamics. So for $\alpha = 1$; $\theta = 0$ we get of (33)

$$\begin{aligned}\dot{x}_1 &= -x_1 + \frac{7}{8} + \frac{1}{8}\lambda^2 (w_1 x_2 + w_3 x_3)^2 \\ \dot{x}_2 &= -x_2 + \frac{7}{8} + \frac{1}{8}\lambda^2 (w_1 x_1 + w_2 x_3)^2 \\ \dot{x}_3 &= -x_3 + \frac{7}{8} + \frac{1}{8}\lambda^2 (w_3 x_1 + w_2 x_2)^2\end{aligned}\tag{34}$$

where we put for a simplicity

$$\begin{aligned}w_{12} &= w_{21} = w_1 \\ w_{23} &= w_{32} = w_2 \\ w_{13} &= w_{31} = w_3\end{aligned}\tag{35}$$

in accordance with (32). This result is not surprising as it is known from the theory of neural networks that the parameter λ or steepness of sigmoidal transfer function determines in fact a shape of the first derivative of transfer function playing an important role in a learning process and the stability analysis (Andrey, 1991). Let us note that it has not been specified so far if the value of symmetrical weights (35) are positive or negative. In dependence upon a sign of the appropriate weight then the adequate part of the circuit can be excitatory or inhibitory. That finishes our analysis showing that above mentioned examples of three neuronal circuits, namely central patterns generators or the canonical circuit can be simulated by the dynamical systems of form (33) resp. (34) possessing a chaotic activation or output dynamics.

Potential Applications of Chaotic Neural Circuits

It has been shown here that the minimal continuous dynamics neuronal network possessing the chaotic behavior can be realized by the three neurons circuit simulated by the three dimensional dynamical system (34) analogical to the famous Lorenz model of

hydrodynamics (Sparrow, 1982). This partially answers a cardinal question about the origination of the complex behavior in our brain. The answer is that the neural circuits composed of three neurons can generate an observed complicated behavior by means of chaotic dynamics. But as was mentioned before neural circuits can be composed of two neurons, too.

From neurobiology, one knows that such small two-three neurons circuits, in turn, are the basic building blocks to construct larger modular units, e.g., vertically oriented cortical columns in the neocortex (Milton, 1996). Thus, the study of the properties of neural circuits composed of two-three neurons is a first rational step towards the development of an understanding of the behavior of the neurons system upon the adequate level of hierarchy.

On the other hand, one of the consequences of results presented here is a strong suspicion that one cannot apply the methods of chaos to phenomenological EEG signal directly, as the behavior of thousands of interacting neurons recorded by EEG can have a very wide spectrum of complex, qualitatively and quantitatively different dynamical patterns of behavior.

CONCLUSIONS AND FUTURE OUTLOOKS

The human brain seems to be the most complex structure in the known Universe. Remarkably precise connections among more than one hundred billions of neurons in our brain account for all properties of human mind. This is of course connected to the classical mind-body problem. But this is closely related to one of the most exciting problems of today's science, namely that of consciousness. As F. G. Crick says in the Foreword to the new book on consciousness by Ch. Koch (2004): "Consciousness is the major unsolved problem in Biology."

In fact, there is even no present consensus on the general nature of the solution. How do philosophers call “qualia“ arise from the concerted actions of nerve cells, glial cells and their associated molecules? Can qualia be explained by what we now know of modern science, or is some quite different kind of explanation needed? And how to approach this seemingly intractable problem?

In the past few years there has been an enormous interest in the study of consciousness with an enormous flood of books and papers about consciousness, and neuroscience in general (Koch, 2004; Dyan & Abbot, 2001; Wilson & Keil, 1999). One of the novel approaches is to try first to find the neuronal correlates of consciousness, often called the NCC (Koch, 2004). But this seems to be a very hard task, too. The more specific problem is a problem of awareness the subset of which is a problem of selective attention. Here the threshold of neuronal transfer function plays the important role. Namely, there have been attempts to exploit the variable threshold as a model for selective attention in associative neural networks (Wang & Ross, 1991). In such the case the network can achieve the analogy of selective attention by purposefully changing its neuronal threshold in a prescribed manner. By other words one can improve recall in associative memories by dynamic thresholds (Wang, 1994). But neurophysiological aspects related to a variable neuronal threshold remain still open.

In the paper presented here the approach belongs to this direction. One starts, so to speak, from the first principles. And obtained results not only cover well known descriptions of neuronal systems in our case, but go further allowing for new qualities, mechanisms and laws. E.g., before the paradigm of chaos was known it had been commonly used to consider the brain as a noisy processor in which statistical phenomena or stochastic mechanisms lead to generate the organized behaviour. In this context the answer to the cardinal question on the possible origination of very complex spiking patterns of firing neurons has been found. It has

been shown for the first time analytically that the sigmoidal transfer function of neurons is sufficient for neurons to fire chaotically. But one knows from the chaodynamics that such behaviour is in a statistical sense equivalent to the ad hoc random generating processes. Even more, such stochastic process can be viewed as asymptotics to adequate deterministic chaos.

This finding brings automatically a new sight upon the cardinal problem of neural coding, too. There are two extreme views on this problem. One espouses a systematic organization when a simple stimulus features and complex events are encoded by the activity of single neurons. A contrasting view exposes a fully distributed representation that encodes each item by distinct spatio-temporal activity patterns of homogenous arrays of neurons. These opposing views may in fact be reconcilable in our brain. In our case the proved potentiality of very complex dynamics of single neurons sheds a new light on the mentioned problem of neural coding. The classical dogma of stochastic, or ad hoc random coding can be taken as the limiting case to the new, complementary deterministic, or chaotic paradigm.

This view is then supported and strengthened by the construction of continuous minimal two-three neuronal circuits possessing the chaotic dynamics, too. This can have some physiological applications as mentioned above.

As the by-product of our derivation the novel functional dependence between main characteristics of every biological sigmoidal transfer function has been earned. In biological language, it means there should exist the gain-threshold (or λ - θ in our notation) mechanism in neurons. This mechanism presents rather new quality of potential complex behaviour of single neurons, too. It could be a good candidate for above mentioned new approach “to try first to find the neuronal correlates of consciousness” (Koch, 2004).

ACKNOWLEDGEMENT

This research was partly supported by the Grant Agency of Czech Republic under GACR 305/02/1487.

REFERENCES

- Aihara, K. & Matsumoto, G. (1987). Forced oscillations and route to chaos in the Hodgkin-Huxley axons and squid giant axons. In: Chaos in biological systems. H. Degn, A.V. Holden and L. F. Olsen, eds., New York: Plenum Press.
- Aihara, K., et al. (1990). Chaotic neural networks. *Phys. Lett. A*, 144, 6/7, 333-340.
- Amit, D. (1989). *Modeling Brain Function*. Cambridge: Cambridge UP.
- Amit, D. (1993). Dynamic learning in attractor neural networks. INFN- Sezione di Roma, Preprint N. 933.
- Andrey, L. (1986). The Relationship between entropy production and K-entropy. *Prog. Theor. Phys.*, 75, 1258-1260.
- Andrey, L. (1991). Simple biological neural networks and stability criteria for equilibrium memories. *Neurocomputing*, 3, 221-230.
- Andrey, L. & Kufudaki., O. (1993). Threshold-gain mechanism: Theory and simulation. NEURONET '93 conference, Prague, September 1993.
- Andrey, L. (1997). Biological findings supporting a functional dependence λ upon θ as well as a rigorous theoretical derivation - see Techn. Rep. V-711, ICS, Prague.
- Andrey, L. (1998). Complex behavior in single neurons. In: *Chaos and noise in biology and medicine*. Eds. M. Barbi and S. Chillemi. Singapore: World Scientific.
- Andrey, L. (2000a). Analytical proof of chaos in single neurons and consequences. In: *Chaos in Brain?* (Ed.: Lehnertz, K., Arnhold, J., Grassberger, P., Elger, C.E.), Singapore: World Sci., 247-250.
- Andrey, L. (2000b). Gain-threshold mechanism neural networks. *European J. Neurosci.*, 12, No. 11, Suppl., 243.
- Andrey, L. (2001). Perspectives on chaos in neural systems. In: *Nonlinear dynamics and chaos: Where should we go from where?* Bristol, University of Bristol.

- Andrey, L. (2002). Chaotic dynamics in simple neuronal systems. In: Dynamics Days Asia-Pacific. Eds.: Sun, Y.S., He, X.T. Hangzhou, China, p. 14.
- Andrey, L. & Erzan, R. (2002). The sigmoidal transfer function and the gain-threshold exponential dependence for neurons from statistical mechanics treatment. Czechoslov. J. Phys., 52, 12, 1349- 1356.
- Arbib, M.A. (2003). The handbook of brain theory and neural networks. (2nd edition). Cambridge: The MIT Press.
- Barbi, M. & Chillemi, S. (1998). Chaos and noise in biology and medicine. Singapore: World scientific.
- Basar, E. (1990). Chaos in brain function. Berlin: Springer-Verlag.
- Bondarenko, V.E. (1994). A simple neural network model produces chaos similar to the human EEG, Phys. Lett. A 196, 195-200.
- Caianello, E.R. (1961). Outline of a theory of thought-processes and thinking machines, J. Theor. Biol., 2, 204-235.
- Collet, P. & Eckmann, J.P. (1980). Iterated maps on the interval as dynamical systems. Basel: Birkhauser.
- Dayan, P. & Abbott, L.F. (2001). Theoretical neuroscience. Cambridge: The MIT Press.
- Dhamala, M., Jirsa, V.K., Ding, M. (2004). Transition to synchrony in coupled bursting neurons. Phys. Rev. Lett. 92, 0281011- 0281014.
- Eckman, F.H. & Freeman, W.J. (1991). Asymmetric sigmoid nonlinearity in the rat olfactory system, Brain Research, 557, 13-21.
- Elbert, T., Ray, W.J., Kowalik, Z.J., Skinner, J.E., Graf, K.E., Birbaumer, N. (1994). Chaos and Physiology: Deterministic chaos in excitable cell assemblies. Physiol. Rev., 74, 1-40.

- Falke, M., Huerta, R., Rabinovich, M.I., Abarbanel, H.D.I., Elson, R.C., Severston, A.I. (2000). Modeling observed chaotic oscillations in bursting neurons. *Biol. Cybernetics*, 82, 517-527.
- Freeman, W.J. (1991). The physiology of perception. *Scientific American*, 264, 78-87.
- Freeman, W.J. (2000). *Neurodynamics*. Berlin: Springer.
- Gong, Y.F., et al. (1999). Recovering strange attractors from noisy interspike intervals of neuronal firings. *Phys. Lett. A*, 258, 253-262.
- Guastello, S.J. (2004). Progress in applied nonlinear dynamics: Welcome to NDPLS Volume 8. *NDPLS*, 8, 1, 1-15.
- Hindmarsh, J.L. & Rose, R.M. (1984). A model of neuronal bursting using three coupled first order differential equations. *Proc. R. Soc. London, Ser. B* 221, 87-102.
- Hopfield, J.J. (1994). Neurons, dynamics and computation. *Physics Today*, 47, 40-46.
- Kandel, E.R., Schwartz, J.H., Jessel, T.M. (2000). *Principles of neural science* (4th edition). New York: McGraw- Hill.
- Kantz, H. & Schreiber, T. (1995). Dimension estimates and physiological data. *Chaos*, 5, 143 - 154.
- Khodorov, B.I. (1974). *The problem of excitability*. London: Plenum Press.
- Koch, Ch. (1999). *Biophysics of computation: Information processing in single neurons*. New York: Oxford UP.
- Koch, Ch. (2004). *The quest for consciousness: A neurobiological approach*. Englewood, Colorado: Roberts and Co. Publishers.
- Kuramoto, Y. (1991). Collective Synchronization of Pulse Coupled Oscillators. *Physica*, D50, 15-30.
- Liljeström, H. (1991). Modeling the dynamics of olfactory cortex. *International Journal of Neural Systems*, 2, 1-15.

- Matsumoto, G., Aihara, K., Utsunomiya, T. (1982). A spatially-ordered pacemaker observed in squid giant axons. *J. Phys. Soc. Japan*, 51, 3, 942-950.
- Mc-Kenna, T., Davis, J. & Zornetzer, S.F., eds. (1992). *Single neuron computation*, Boston: Academic Press.
- Milton, J. (1996). *Dynamics of small neural populations*. Providence: AMS USA.
- Mirollo, R.E. & Strogatz, S.H. (1990). Synchronization of pulse coupled oscillators, *SIAM Journal of Applied Mathematics*, 50, 1645-1662.
- Miyashita, Y. & Chang, H.S. (1988). Neuronal correlate of pictorial short-term memory in the primate temporal cortex. *Nature*, 331, 68-70.
- Morita, M. (1993). Associative memory with non-monotone dynamics, *Neural Networks* 6, 115-126.
- Nagumo, J. & Sato, S. (1972). On a response characteristic of a mathematical neuron model, *Kybernetik* 10, 155-164.
- Nikolov, S. (2005). An alternative bifurcation analysis of the Rose-Hindmarsh model. *Chaos, Solitons & Fractals*, 23, 1643-1649.
- Nunez Yopez, H.N., et al. (1989). Chaos in a dripping faucet. *Eur. J. Phys.*, 10, 99-105.
- Nunez, P.L. (1995). *Neocortical Dynamics and Human EEG Rhythms*, Chapt. 10. New York. Oxford University Press.
- Pasemann, F. (1997). A simple chaotic neuron. *Physica D*, 104, 205-211.
- Rapp, P.E., Zimmerman, D., Albano, A.M., Deguzman, G.C., Greenbaun, N.N. (1985). Dynamics of spontaneous neural activity in the Simian motor cortex: The dimension of chaotic neurons, *Phys. Lett. A* 110(6), 335-338.
- Rieke, F., et al. (1997). *Spikes*. Cambridge: The MIT Press.
- Sakai, K. & Miyashita, Y. (1991). Neural organization for the long-term memory of paired associates. *Nature*, 354, 152-155.

- Scott, A.C. (1977). *Neurophysics*. New York: A Wiley – Interscience Publ.
- Shilnikov, A.L. & Rulkov, N.F. (2004). Subthreshold oscillations in a map-based neuron model. *Phys. Lett A*, 328, 177-184.
- Shuai, J.W., et al. (1996). A chaotic neural network model, *Chin. Phys. Lett.* 13, 185-187.
- Sparrow, C. (1982): *The Lorenz equations: Bifurcations, chaos and strange attractors*. New York:Springer-Verlag.
- The MIT encyclopedia of the cognitive sciences (1999). Wilson, R. A. & Keil, F. C., Eds. Cambridge: The MIT Press.
- Wang, L. & Ross, J. (1991). Variable threshold as a model for selective attention, (de) sensitization, and anesthesia in associative neural networks. *Biol. Cybern.*, 64, 231-241.
- Wang, T. (1994). Improving recall in associative memories by dynamic threshold. *Neural Networks*, 7, 9, 1379-1385.
- Wright, J.J. & Liley, D.T.J. (1996). Dynamics of the brain at global and microscopic scales: neural networks and the EEG. *Behavioral and Brain Sciences*, 19, 285-320.
- Yoshizawa, S., Morita, M., Amari, S.I. (1993). Capacity of associative memory using a nonmonotonic neural model, *Neural Networks* 6, 167-176.