CHAOS AND NEURAL DYNAMICS

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Small neural networks (central pattern generators), which control rhythmic behavior of animals, are considered. The mechanisms responsible for regularity, reliability, and plasticity of such behavior (swimming, running, walking, etc.) are analyzed. New data on the origin of regular cooperative behavior of neurons are obtained by using methods of nonlinear dynamics.

1. INTRODUCTION

Exactly fifteen years ago, we had a talk with A. V. Gaponov and A. A. Andronov in Gaponov's room. We discussed the paper on "Using fractal dimension to analyze systems with chaotic behavior" written by me together with A. Ugodchikov, a graduate student, and F. Izrailev, a physicist from Novosibirsk [1]. In our talk, Andronov proposed to use fractal dimension in analysis of electroencephalograms. Should the dimension appear finite, or, more precisely, moderate, it could be assumed that apparent noisy encephalograms can be produced by a low-dimensional dynamic system. That idea seemed to be very attractive. I mentioned that such an idea was implemented at that time in connection with the analysis of electrocardiograms, and we also began studies in that field. Simultaneously, the paper by L. Glass and coauthors about chaotic dynamics of cardiac cells appeared in Science [4]. We also recollected R. May's papers dealing with chaotic dynamics of populations [5]. There, Gaponov asked a question which none of us could answer at that time: "What is chaos for living beings?"

Years passed. Fate and Perestroika brought me and A. Selverston, an outstanding neurophysiologist, together at the University of California in San Diego. Our interest is not brain activity; we deal with much simpler objects, such as small nerve systems which are responsible for the motor rhythmic activity of organisms (the so-called "central rhythm generators.") And only now can I formulate the question that Andrey Victorovich asked then.

I recollect that the question was "What for...?" rather than "Where from...?", that is, "What is the nature of dynamic chaos in biological systems?". The latter question, and the answer, might even seem too simple at present. Indeed, when we speak about the dynamic behavior of complex (having a large number of degrees of freedom) nonlinear nonequilibrium systems such as nerve systems or even one neuron, it is only a matter of technique to extract chaos generation mechanisms.

Evidently, the question "Why...?" is associated with biological expediency, i.e., the question is about the reason why evolution retained dynamic chaos as a typical mode of behavior in large and small nerve systems. This question is much more difficult and ambiguous. Possibly, the obvious answer to this question is absent at present.

*Such investigations are still performed at present in various research centers (see, e.g., [2, 3]).
2. POINT OF VIEW

In my opinion, the answer to the question "Why...?" can be formulated as follows: Possibly, dynamic chaos in itself is not requisite to living systems. However, the wealth of regular modes in dynamic systems that are potentially able to generate chaos is obviously one of the main features which Nature realizes at the different levels of organization of nerve ensembles.

In other words, it is not chaos itself that is critical to the normal operation of nerve structures but the fact that those structures work at the boundary (and, rather often, beyond the boundary) of instability. This gives them exclusively high adaptive possibilities, ensures rapid mode switching, and, of course, the variety itself of modes of behavior.

To put it differently, dynamic chaos is the inevitable payment for the high adaptivity and versatile activity of nerve systems.

Evolution developed a variety of methods to ensure self-control and self-monitoring of nerve ensembles composed of chaotic elements. On the one hand, these methods have all the advantages of unstable systems and of systems with complex dynamics (short time of transient processes, multiplicity of periodic and nonperiodic modes) and, on the other hand, they make the behavior of the systems predictable.

In what follows, we will show how the above principles are implemented in small nerve systems, using central rhythm generators as an example.

3. EXPERIMENT

Let us discuss at first what progress has been achieved in this area for the last fifteen years and what key experiments can be used for the analysis.

The main results in this avenue are associated with the analysis of the behavior of individual neurons and neural ensembles, which confirms that the dynamics of a collection of neurons is more regular than their individual dynamics. This is true also for small nerve systems such as central rhythm generators [6, 7] and cerebral cortex neurons [8, 9] where the role of separate elements of an ensemble is played by structures consisting of a large number of neurons connected by an "all with each" feature.

Another important result, which follows from the recent (laboratory and model) experiments, consists in the following. Chaotic neurons in the ensemble not only order the behavior of each other but also change easily the mode of behavior (adaptivity) under the action of control parameters. Among such control parameters, we should include, for example, the coupling between neurons (which is determined by the concentration of neural mediators), temperature, etc. [10].

We now discuss some experiments. First of all, we illustrate the fact that indeed irregular pulsations of an individual neuron can be described by a low-dimensional dynamic system [11].

Figure 1 shows oscillograms of an LP neuron in a pyloric lobster rhythm generator. As the parameter $I$, we use an external current fed through a microelectrode to a living nerve cell.

Fairly long neuron activity records were processed to calculate Lyapunov exponents, determine the minimum dimension of a dynamic system which is able to generate a similar signal (embedding dimension), etc. Figure 2 shows the phase portraits of a limiting set which were reconstructed by a temporal shift method (see [12]). For $I = 0$ nA, $I = -1$ nA, and $I = -2$ nA, the reconstructed limiting set is a strange attractor. Calculations show that the embedding dimension is equal to three, while the Lyapunov dimension $D_\lambda = 2.75$. It is clearly seen from Fig. 3 that only one Lyapunov exponent is positive: $\lambda_+ \approx 0.8$.

It follows from the above data that indeed the individual dynamics of an LP neuron is chaotic and low-dimensional. To simulate such dynamics, we need only a three-dimensional dynamic system. An adequate model relating to this case is the model proposed by Hindmarsh and Rose in 1984 [13] and its various generalizations [14, 15]. In a simple version, the model equations are given by

$$\begin{align*}
\dot{x} &= y + az^2 - bz^3 - z + I, \\
\dot{y} &= c - dz^2 - y, \\
\dot{z} &= r(s(z - z_0) - z), \quad r \ll 1,
\end{align*}$$

(1)
Fig. 1. Chaotic pulsation of the membrane potential of an LP lobster neuron as a function of external current.

Here, $z(t)$ is the membrane potential of a nerve cell, $y(t)$ is a variable describing the reconstruction of fast ion densities (usually they are Na$^+$ and K$^+$), and $z(t)$ is a slow variable determined by the ion density Ca$^{++}$. For the parameter values $a = 3$, $b = 5$, $I = 3.281$, $z_0 = -1.6$, $s = 4.0$, and $r = 0.0021$ this system generates the same chaotic sequences as a living neuron (Fig. 4), and a typical attractor in the phase space of system (1) (Fig. 5) has the same topology as the attractors reconstructed from the observed data from a living neuron (Fig. 2).

The domain of dynamic chaos is not so large in the parameter space of system (1). However, the main information which is important in our further analysis is that the regular motions that are potentially possible in this model are extremely varied. How will chaotic neurons (living or simulated) behave when they are combined into a neural network? All depends on the form of coupling. It should be specified that the coupling between chaotic generators, which is considered by tradition in analysis of electron chains, chemical turbulence, etc., is usually dissipative or diffusional. This coupling is proportional to the mismatch of variables in coupled generators, $\epsilon (z_1(t) - z_2(t))$ ($\epsilon$ is the coupling), and, of course, tends to decrease the error signal down to zero. If dissipative coupling is strong enough (compared to the divergence growth rate of chaotic trajectories), then chaotic generators are synchronized completely and operate as one chaotic generator [16, 17]. If coupling is weak, the chaotic synchronization mode $z_1(t) \equiv z_2(t)$ is unstable, and the dynamics of the couple still increases in complexity: the number of positive Lyapunov exponents doubles, the dimension of the limiting chaotic set increases, and so on.

Such electrical (dissipative) coupling is met also in neural networks (see review [18]). However, coupling via a chemical synapse is more typical. It is seen from the data presented in Figs. 6 [18] and 7 [11] that
Fig. 2. Phase portraits of a strange attractor reconstructed from a long temporal realization (~2 min) similar to Fig. 1.

Fig. 3. Behavior of the Lyapunov exponents reconstructed from an oscillogram of a living LP neuron pharmacologically isolated from other neurons ($I = 0$).

the dynamics of an individual neuron is considerably more irregular than in a synaptically coupled pair in both actual and simulated neuron pairs. It can be said that synaptic coupling suppresses chaos. This
phenomenon makes the dynamics of neuron ensembles radically different from, for example, the dynamics of the conventional networks of electron generators [19].

Synaptic coupling is nonlinear coupling which is characterized by the presence of threshold and saturation (a simple model of a chemical synapse can be expressed by a stepwise function in the "input–output" variables plane.) Such coupling (both exciting, which depolarizes the membrane of the nerve cell and suppressing, which hyperpolarizes that membrane) averages the irregular dynamics of spikes. It is exactly this averaging that results in chaos suppression in the case of mutual synaptic coupling between neurons.

To illustrate the idea of adaptivity and variety of the behavior of neuron ensembles consisting of synaptic coupled chaotic elements, we give the results of one experiment with model neurons.*

*Similar experiments with living neurons are conducted at present in A. Silverstone’s laboratory. The preliminary results are encouraging.
Fig. 6. Irregular activity modes of model neurons in a system of two chaotic neurons coupled by mutual suppressing coupling: (1) oscillations with small phase shift; (2) in-phase oscillations (complete synchronization); (3) counterphase synchronization; (4) "almost" counterphase synchronization.

Fig. 7. Regular activity modes of model neurons in a system of two chaotic neurons coupled by mutual suppressing coupling: (1) oscillations with a small phase shift; (2) in-phase oscillations (complete synchronization); (3) counterphase synchronization; (4) "almost" counterphase synchronization.

Consider the operation of a central cardiac rhythm generator in a medicinal leech. The block diagram of that central generator is shown in Fig. 8 [28]. We use the familiar model (1) to simulate the dynamics of an individual neuron. This model imitates well an actual neuron which produces a series of fast spikes against the background of slow and intense pulsations of the membrane potential (cf. Fig. 1). The basic result of the computer experiment is shown in Fig. 9 [21]. It is seen that the period of the central cardiac
Fig. 8. Block diagram of the central cardiac rhythm generator of a medicinal leech. Suppressing synaptic coupling is shown by black circles.

Fig. 9. Variation of the cardiac rhythm period in a model central generator consisting of chaotic neurons (Fig. 4) combined into chains as in Fig. 8. The synchronization is absent when the synaptic coupling \( \epsilon < 0.5 \).

rhythm generator of a medicinal leech is very sensitive to the magnitude of synaptic coupling. The increase in coupling (which is possibly due to the change in neural mediator density) results in a stepwise increase of spikes in each oscillation period and the corresponding decrease of the cardiac pulsation rhythm.

It is significant that in the neuron chain in question, the bifurcations inside the synchronization mode of chaotic neurons, which are observed when synaptic coupling is changed, resemble the bifurcations which are detected in the behavior of one neuron when its parameters are changed [22]. Thus, the potentialities of complex individual dynamics of a neuron do not go to waste but are used purposefully to ensure adaptation and control in the neuron ensemble.

It has recently been shown in [23] that the results which we obtained are also valid when the form of the model is changed and even when the dimension of the model is increased. What matters is only that the model must show correctly the qualitative features of nerve cell activity, such as spike bursts and the dependence of a characteristic pulse period on external current (cf. Fig. 1).
4. ROLE OF NOISE

Clearly, it is extremely difficult to obtain long records of steady-state neuron activity, for example in the cerebrum, and process them carefully as was done for a lobster's LP neuron. Therefore, the nature of the irregular behavior of many species of neurons still remains unclear. In such a situation, it is no easy problem to find out the role of noise in the behavior of small and large neuron ensembles.

By the noise effect, we can also explain the irregular pulsation of neuron generators, especially if they operate in a mode close to generation threshold [24]. In connection with this, the question arises whether noise plays an efficiency role in the operation of neuron ensembles or it is simply “a launching trigger” which ensures the variety of instability mechanisms.

Of course, the noise effect depends on a particular situation. However, it is difficult to conceive that combining noise generators into ensembles can result in ordering of their behavior as is the case with model chaotic neurons in the experiment. At the same time, if we assume that neurons are generators with complex dynamics, then we can predict two important effects due to noise.

The point is that systems which are able to generate dynamic chaos possess a very complicated structure of the phase space. Besides the various attractors (periodic or strange), the nonattracting trajectories too play an important role in the variability of the dynamics of such systems. Among the latter, we should mention saddle-type limit cycles outside the attraction basins of attractors. Our experiments with a Hindmarsh–Rose system [11] (weak Gaussian noise was added to the right-hand side of Eqs. (1)) showed that the noise effect increases the dimension of a chaotic set and the Kolmogorov–Sinai entropy, which in turn enriches the spectrum of individual neuron behavior. When such neurons are combined into an ensemble with synaptic coupling, noise is to a considerable degree suppressed by the synchronization effect. However, the variability of the neuron behavior is retained.

Another factor of the noise effect, which also seems to be obvious, is that noise kills, by averaging, a variety of “pathological” attractors which are characterized by small attraction basins in the phase space and are therefore “unrealiable in service” [11].

5. CONCLUSION

The question about the dynamic behavior of large neuron ensembles is especially interesting and complicated. Obviously, the dynamics of such ensembles is low-dimensional (except the cases of pathological synchronization observed in epilepsy). Such ensembles can produce both regular spatio-temporal patterns and spatio-temporal chaos. Of course, the cerebrum is not a low-dimensional dynamic system, and a different-dimensional analysis of electroencephalograms is of no radical importance from today's position. However, the approach to nerve ensembles from the position of nonlinear dynamics has already brought many challenging results and seems very promising today.

Returning to the initial question, we stress once again that neither nature nor society need developed chaos. The diversity of forms of behavior of complex systems is the basis for existence of living creatures.

REFERENCES