



## COMMENTARY

## THE ROLE OF CHAOS IN NEURAL SYSTEMS

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**Abstract**—The ideas of dynamical chaos have altered our understanding of the origin of random appearing behavior in many fields of physics and engineering. In the 1980s and 1990s these new viewpoints about apparent random oscillations arising in deterministic systems were investigated in neurophysiology and have led to quite successful reports of chaos in experimental and theoretical investigations. This paper is a “view” paper addressing the role of chaos in living systems, not just reviewing the evidence for its existence, and in particular we ask about the utility of chaotic behavior in nervous systems. From our point of view chaotic oscillations of individual neurons may not be essential for the observed activity of neuronal assemblies but may, instead, be responsible for the multitude of regular regimes of operation that can be accomplished by elements which are chaotic.

The organization of chaotic elements in assemblies where their synchronization can result in organized adaptive and reliable activities may lead to general principles used by nature in accomplishing critical functional goals. © 1998 IBRO. Published by Elsevier Science Ltd.

*Key words:* chaos, self-regularization, coupled neurons, variability.

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## 1. INTRODUCTION

In light of the results over the past decade and a half's intensive experimental study of nonlinear dynamical systems, especially in the physical sciences and engineering, it would have been a most remarkable result to discover that neurons, individually or in assemblies, always oscillate in a regular, predictable fashion and choose not to show chaotic motion at all. The numerous ion channels which are the determinants of intracellular voltage for a neuron lead to well-studied nonlinear equations among many dynamical variables, and the appearance of chaos in such a rich dynamical system should hardly be a surprise by now.

Over the past decade there have been many reports of the observation of chaos in the analysis of various

time-courses of data from a variety of neural systems ranging from the simple to the complex.<sup>9</sup> The tools for the analysis of these time-series<sup>1</sup> have been developed and improved over the years, and one now has efficient, user-friendly software which makes the identification of chaotic motions a straightforward, almost routine task. Perhaps the outstanding feature of these various analyses of time-courses from neural observations is not the presence of chaos itself but the appearance of low dimensional dynamical systems as the origin of the spectrally broadband, non-periodic signals observed in many instances. It is hard to imagine that the dynamics of a neuron as observed through the measurement of intracellular voltages could be captured in three or four degrees of freedom, and it is frankly difficult to accept without the clear evidence we now have that this is the case.<sup>2</sup> This feature of the data may actually be more interesting in the long run for detailed investigation of neural assemblies than the full panoply of chaotic motions possible for such systems.

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*Abbreviations:* AB, anterior burster interneuron; CPG, central pattern generators, LP, lateral pyloric; PD, piloric dilator.

The goal of this “point-of-view” paper is to carry the discussion beyond whether chaos appears in this or that neural system, for it makes its appearance widely. We wish to address in a somewhat speculative, perhaps even opinionated fashion, the broader, more qualitative issue how chaos is employed by neural systems to accomplish biologically important goals. We want to focus attention on useful features of neural systems which cannot be understood without taking into account the chaotic nature of neurons. This is a quite different class of question than that associated with the usual inquiry about where in the structure of a neural or other system lies the origin of dynamical chaos. We are not looking at the identification of a mechanism in ion channel activation or other activity or at a mathematical aspect of model equations which lends itself to the generation of chaotic orbits. We will illustrate our views by drawing on specific examples which support those views, but we realize from the outset that the questions we raise go beyond the purely technical, that they are more controversial and difficult to answer, and that it is plausible they have no proper answer whatsoever. None the less, we tackle the general class of question falling into the framework of why evolution has selected chaos as an apparently typical pattern of behavior for neural systems. What might be accomplished by this choice, and perhaps slightly elusively, what could not have been accomplished by the choice of regular, predictable behavior—these too we touch on.

Part of our answer somewhat begs the question or is purely self-consistent. Chaos seems to be almost unavoidable in natural systems comprised of numerous simple or slightly complex subsystems. As long as there are three or more degrees of freedom, chaotic motions are generic in the broad mathematical sense, which translates to unavoidable in the practical sense. So neurons are dealt a chaotic hand by nature and may have little choice but to work with it. Accepting that chaos is more or less the only choice, we can ask what benefits are accrued by this to the robustness and adaptability of neural activity. We may also ask what extreme measures would have to be taken to avoid chaos, if there were to be strong biological benefit by that. In other words, if chaos is generic, neurons would have had to struggle to avoid it, and would only have done so if much were to be accomplished by that effort. So we turn first to the benefits of chaos. There we begin our inquiry about why neural systems are chaotic and how chaos is used by these systems. We adopt the point of view that neurons exhibit chaos because they really have no other choice: that is the way dynamical systems are built. What they do with this chaos is the issue at hand.

## 2. POINT OF VIEW

The first noncircular answer we give to the question of why chaos is found in neural systems

starts with accepting that chaos itself may not be essential for living systems. Such systems, we imagine, could be built out of nonchaotic elements, though we do not propose how this could be accomplished. However, we argue that the multitude of regular regimes of operation that can be accomplished in dynamical systems composed of elements which themselves can be chaotic gives rise to a basic principle used by nature for the organization of neural assemblies. In other words, chaos itself is not responsible for the work of various neural structures, but rather for the fact that those structures function at the edge of instability, and often beyond it. Recognizing chaotic motions in a system state space as unstable, but bounded, this geometric notion gives a sense to the otherwise unappealing idea of system instability.

The instability inherent in chaotic motions, or more precisely in the nonlinear dynamics of systems with chaos, facilitates the extraordinary ability of neural systems to adapt, make transitions from one pattern of behavior to another when the environment is altered, and consequently to create a rich variety of patterns. Chaotic motions explore a broad sector of the system state space albeit sparsely as the dimension of a chaotic attractor is smaller than that of the phase space. Its volume in the state space is zero. In so exploring a large piece of the allowed state space they differ from regular motions which lie on integer subspaces and “see” only a small part of the possible behaviors available to the system. Chaos gives a means to explore the opportunities available to the system when the environment changes, and thus acts as a precursor to adaptive, reliable, and robust behavior for living systems.

Throughout evolution neural systems have developed different methods of self-control or self-organization. On the one hand such methods preserve all the advantages of complex behavior of individual neurons, such as allowing regulation of the time period of transitions between operating regimes, as well as the regulation of the frequency of operation in any given regime. They also preserve the possibility of a rich variety of periodic and non-periodic regimes of behavior. On the other hand these control or organizational techniques provide the needed predictability of behavioral patterns in neural assemblies. Organizing chaotic neurons through appropriate “wiring” associated with electrical, inhibitory, and excitatory connections appears to allow for essentially regular operation of such an assembly. The individual neurons retain their reliability and adaptability while remaining part of a functional network.

To place some flesh on these bones of viewpoint, we will discuss how these principles are manifested in some small neural systems focusing on central pattern generators (CPGs) of some invertebrates. It is, we readily admit, a large leap from the performance of tens of neurons to tens of billions of neurons

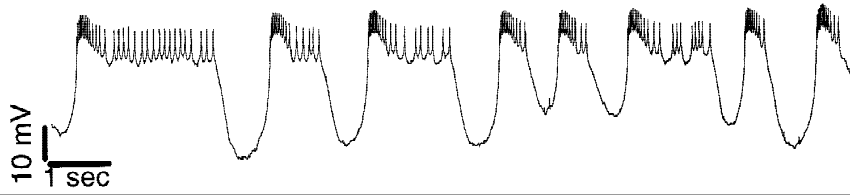


Fig. 1. Membrane potential of a synaptically isolated LP neuron from the pyloric CPG of lobster. Sampling time was 0.5 ms.

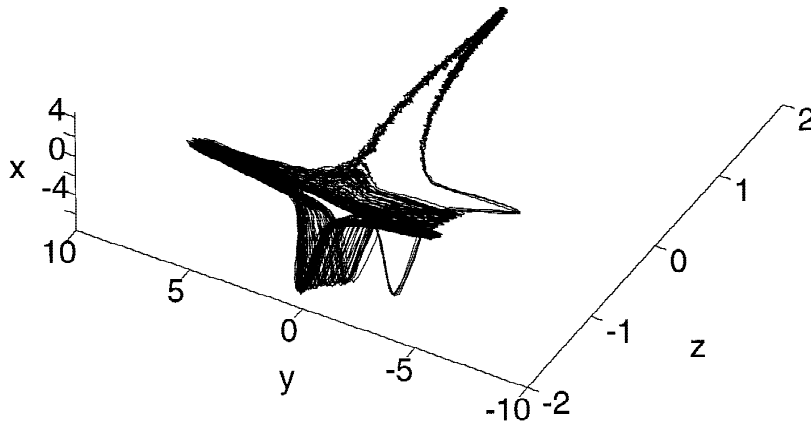


Fig. 2. State-space attractor reconstructed from voltage measurements and their time delays using the isolated LP neuron data seen in Fig. 1. In this figure we have plotted the three-dimensional vectors  $[V(t), V(t-T), V(t-2T)]$  where  $t=t_0+n\tau_s$  and  $T=K\tau_s$ ,  $k$  is an integer which, based on our analysis of the data, we have chosen to be  $k=15$ .  $\tau_s=0.5$  ms.

in human brain functions. Our concentration on CPGs started from the availability of long, clean time-courses of intracellular voltages and from the possibility to carry out extensive experiments to address the phenomena seen in isolated neurons and in a few coupled neurons. These experiments allowed modification of the environment by electrical and chemical means while preserving the ability to collect clean and useful data. We are certainly presuming in the promulgation of our viewpoint that lessons learned in these simple systems have both a direct application to more complex neural systems and underpin the analysis of additional complexities of those larger assemblies.

### 3. CENTRAL PATTERN GENERATOR EXPERIMENTS AND MODELS

Recent work shows that the behavior of neurons inside a network is more regular than that of the individual neurons in isolation. This is true for small neural systems such as CPGs<sup>11</sup> and for neurons in the cortex.<sup>6,12</sup> In the latter the role of an "individual" neuron in an assembly is played by a relatively large collection of neurons connected to one another in an "all-to-all" manner. Another important result of recent laboratory experiments and neural modeling efforts is this: chaotic neurons not only regulate each other's behavior, but easily adapt to extracellular

parameters such as the coupling strengths among the neurons which is determined by the concentration of neuromodulators, the ambient temperature, and other factors.

Turning to experiments on CPGs, we first need to illustrate the fact that the irregular pulsations of an individual neuron can be described by a low dimensional dynamical system both in chaotic and in regular motions. Figure 1 shows the oscillations, spiking and bursting-spiking behavior here, of a synaptically isolated lateral piloric (LP) neuron in the pyloric CPG of the lobster.<sup>2</sup> This time series was used to reconstruct a state space for the neuron using time delay coordinates in the systematic manner noted earlier. The data requires three coordinates to unambiguously unfold the motions of the system from their projection on the voltage axis. In three-dimensional reconstructed phase space the time series produce the phase portrait seen in Fig. 2. We also evaluated the three Lyapunov exponents for this dynamics directly from the data, and find there is a positive Lyapunov exponent characteristic of chaos. In all cases there is a zero Lyapunov exponent and one negative exponent indicating that three ordinary differential equations will produce the voltage-time sequence (for details see Ref. 2).

An adequate three-dimensional model which captures the features of this behavior was suggested some years ago by Hindmarsh and Rose<sup>13</sup> and

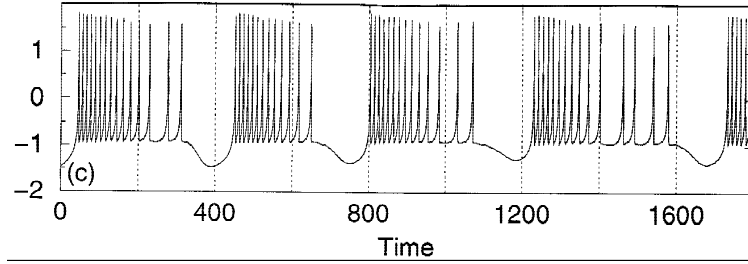


Fig. 3. Time-series of membrane potential from a Hindmarsh-Rose model neuron.

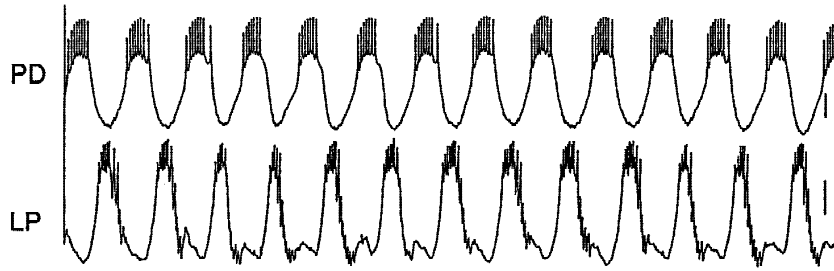


Fig. 4. Simultaneous intracellular recordings of the LP and pyloric dilator (PD) neurons during rhythm generation; central inputs to the STG are intact<sup>8</sup> (voltage traces provided by Robert Elson).

investigated in detail by Wang<sup>19</sup> and by ourselves.<sup>5,14</sup> In the simplest variant the Rose and Hindmarsh model reads

$$\begin{aligned}\frac{dx(t)}{dt} &= y(t) + ax(t)^2 - bx(t)^3 - z(t) + I \\ \frac{dy(t)}{dt} &= c - dx(t)^2 - y(t), \\ \frac{dz(t)}{dt} &= -rz(t) + rS(x(t) - x^0),\end{aligned}\quad (1)$$

with  $r < 1$ .  $x(t)$  is the membrane potential of the neuron,  $y(t)$  is a recovery variable and  $z(t)$  is a slow adaptation current. This set of equations reproduces the phase space and time-course structure of the membrane current as seen in the measurements. Figure 3 shows for example a typical time-course for  $x(t)$  from this simple model. It happens that this particular model has a small region of parameter space where chaos is realized in its solutions. The main important quality for future analysis that this model does exhibit the wide variety of patterns of regular motions which may be performed.

The simplicity of this model coupled with its reliability in reproducing the membrane voltage data and its nonlinear characteristics allows us to ask detailed questions about how this kind of neuron responds when placed into a neuronal web with connections modeling observed couplings in CPGs or other settings. Of course, other models may replace this one, but if they have fewer degrees of freedom, they will miss the chaotic structure found in obser-

vations, and if they have many more, they may represent an inefficient way to capture the dynamics encompassed by membrane voltage measurements.

The behavior one may expect when nonlinear oscillators are coupled together depends on the detailed nature and the strength of the coupling. A simple electrical coupling of the form  $g(x_1(t) - x_2(t))$  between membrane potentials  $x_1$  and  $x_2$ , will certainly lead to complete synchronization for large enough coupling  $g$ , and the cells will act as a single chaotic generator.<sup>3</sup> If the coupling is very weak, then there are two general modes of behavior known to us:

- the phase space of the system attractor is just the product of the spaces of the individual systems, so little has occurred beyond enlarging the effective dynamical system of the oscillators. No synchronization or reduction in the effective phase space occurs. This is not an attractive possibility for coordinated action of the neurons.
- if the chaotic oscillators have both slow and fast motions within their dynamics, as is the case for real and model neurons, even weak electrical-like coupling is able to bring order to the potentially larger chaotic regime and lead to out-of-phase oscillations of the neurons. This regime seems to occur only in a very small domain of the coupling parameters<sup>2</sup>.

Electrical couplings rarely occur alone in neural networks. They are often accompanied by chemical couplings or totally displaced by them. Experimental data shown in Fig. 4 and computations shown in Fig. 5 indicate clearly that the behavior of individual neurons is much less regular than those of chemically

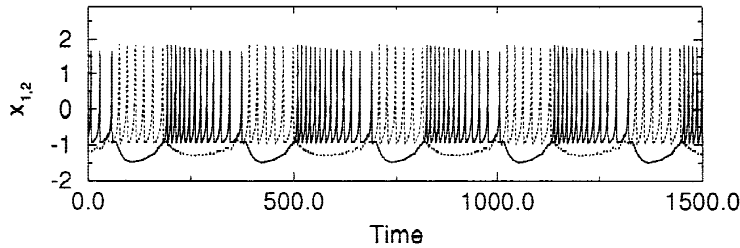


Fig. 5. Periodic out-of-phase oscillations of two chaotic Hindmarsh-Rose neurons connected by inhibitory coupling. Compare these oscillations with those of the isolated Hindmarsh-Rose neuron shown in Fig. 3. When coupled the oscillations are much more regular.

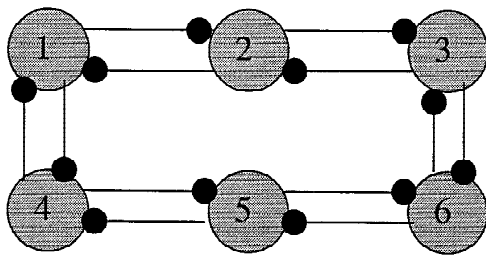


Fig. 6. Chains of neurons forming the heart beat CPG of a leech. The black circles mean inhibitory coupling.

coupled neurons suggesting that chemical coupling actually suppresses chaos. Chemical couplings differ from electrical in having thresholds, saturation levels, and time delays. These are critical features for the regularization of chaotic behavior of the individual elements in neural assemblies.

An example in this regard is illustrative. We consider the heart beat of the leech governed by the CPG shown in Fig. 6.<sup>7</sup> If we model the individual neurons by Hindmarsh-Rose oscillators, we find the behavior seen in Fig. 7 where the period of the oscillation of the leech CPG with model neurons is shown as a function of the common inhibitory coupling strength  $\varepsilon$  among the six neurons. The period is quite sensitive to the value of  $\varepsilon$  for small  $\varepsilon$ . For  $\varepsilon \approx 0.7$  and larger, we see that the frequency stabilizes and occurs in steps of a “staircase”. In each step of this staircase we have a nearly constant frequency for a range of  $\varepsilon$ . This frequency regulation represents a collective regularization of the oscillations of the individual neurons in the CPG. Left to themselves the individual neurons would be chaotic. Even more interesting is the fact, as displayed in Fig. 8, that nearest neighbor neurons oscillate completely regularly and out-of-phase.<sup>4</sup> This permits the pumping of blood for the leech by alternating voltage signals to the appropriate motor functions from alternate neurons. The leech CPG is able to regulate blood flow to the heart with this assembly of neurons in a robust fashion since the same frequency of pumping is achieved for a range of coupling values among the CPG members. If the synaptic coupling strengths, which we assume are altered by neuromodulators, are not precisely on target, the leech is still able to pump at a selected rate.

By varying the coupling the leech is able to change the pumping rate to meet the need for increased or decreased blood flow presumably in response to sensory signals from external conditions.

What is the role of chaos here? Does it matter that the neurons in this CPG are able to achieve chaos? It appears that the ability of the individual neurons to become chaotic is not important for the synchronized, but out-of-phase, rhythmic pattern required for the job of this CPG. In a qualitative sense as shown by Mal'kov *et al.*<sup>16</sup> the same result arises when we alter the model of individual spiking-bursting neurons in the CPG. This includes more complex, higher dimensional models of the member neurons of this CPG. The only requirement on the individual neurons is that they properly capture the main features of spiking and bursting in the time-course of their membrane potential. Models which do not have spiking and bursting in appropriate regimes of external current will not, we presume, lead to the synchronization we require for this function in leech. Chaos would seem to have been lost as a critical aspect of the dynamical function of the CPG.

However, we must remember that were the neuron not to show the correct bursting/spiking action, the fast (spiking) and slow (bursting) motions would not coexist in the orbits of the neuron, and we could not achieve the regulation needed here. How can we achieve the correct spiking/bursting behavior for a wide range of cellular parameters in any neuron? We suggest as central to our point of view that the robust spiking/bursting behavior cannot be achieved without chaotic individual neurons. The fact that real neurons which show spiking/bursting are chaotic supports this view.

The robustness of the spiking/bursting as seen in phase space as fast and slow regions of an attractor which vary smoothly as parameters change is also support for this. In other words, the chaos is required to maintain the robustness of the elements of the CPG while they are “wired up” to produce a regular firing pattern which admirably achieves the desired function. Chaos is there so the overall system through the response of its members is robust and reliable; it is suppressed in the collective action when a particular function is required of the assembly.

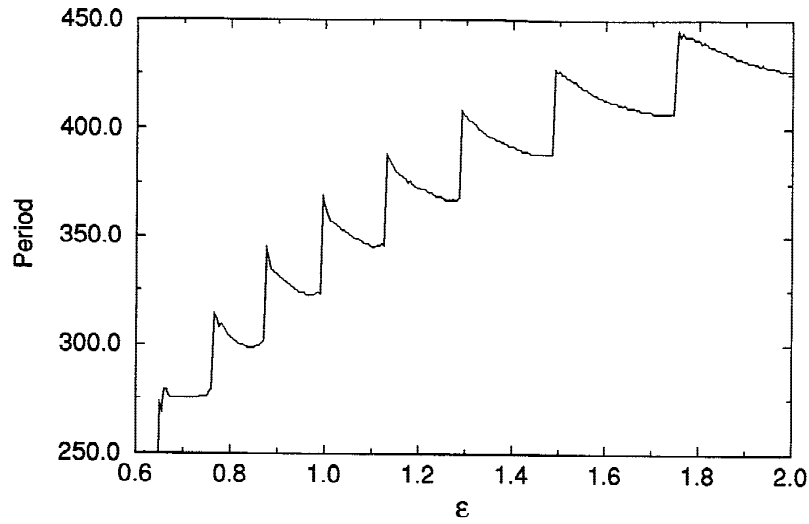


Fig. 7. Average period of heart beat CPG of the leech as a function of the inhibitory coupling  $\varepsilon$ .

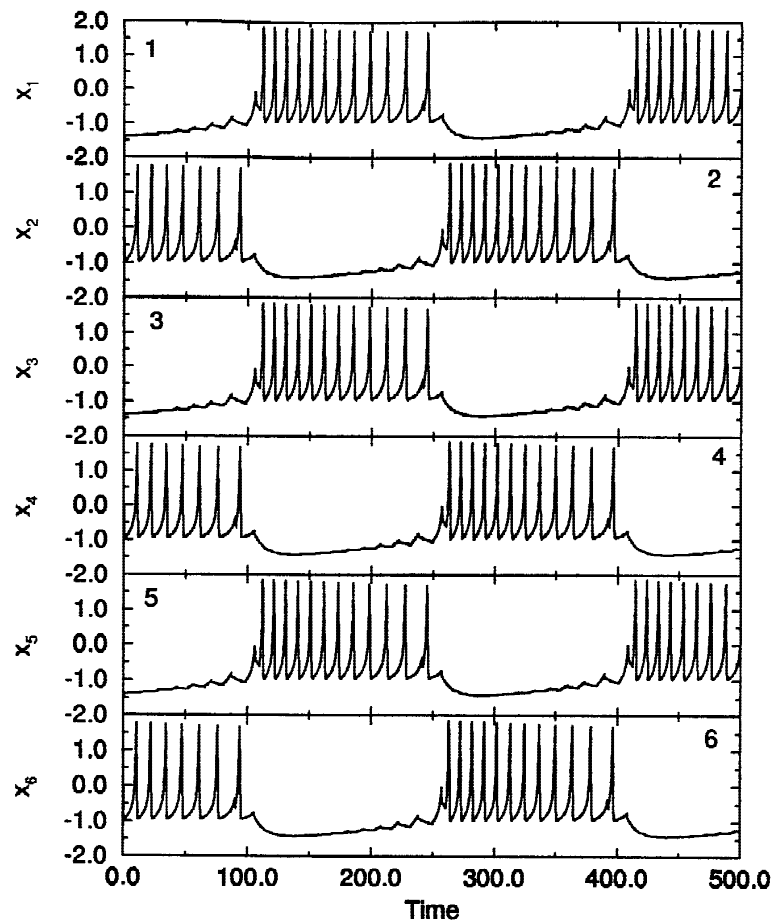


Fig. 8. Membrane potentials  $x_1(t)$ ,  $x_2(t)$ ,  $x_3(t)$ ,  $x_4(t)$ ,  $x_5(t)$ , and  $x_6(t)$  from model leech CPG neurons. The behavior of each individual neuron is chaotic.

#### 4. REGULARIZATION OF CHAOS BY INHIBITION

We have emphasized that the occurrence of chaos in neural activity comes as no surprise after so many years of seeing chaos in so many different dynamical

systems. There is a surprise, however, in the nearly regular activity of neurons as they go about producing effective behavior when coupled in assemblies. This is contrary to the expectation one

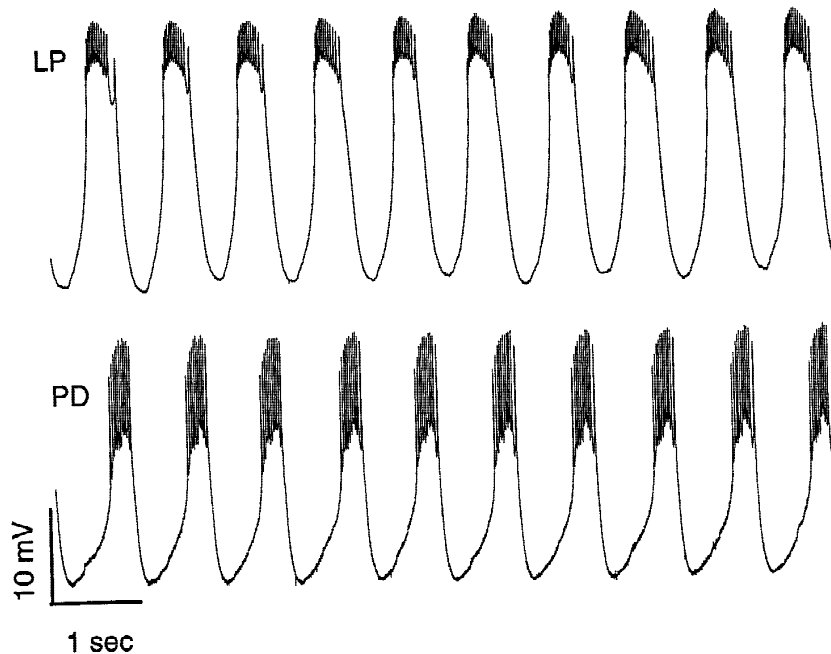


Fig. 9. Membrane potential of an LP neuron (upper trace) driven by one directional inhibitory synaptic action from the anterior burster interneuron/pyloric dilator neuron (AB/PD) unit of the stomatogastric CPG of lobster. In the lower trace is the membrane potential recorded simultaneously from one of the PD neurons in the strongly gap junction coupled AB/PD unit.

may have had from the study of physical systems. For example, in fluid flow as it enters the regime of turbulence, increasing the number of chaotic elements gives rise to a steady increase in the number of positive Lyapunov exponents, the number of active degrees of freedom, and the complexity of the oscillations.

Perhaps the simple answer is that inhibition alone is sufficient to assure this regularization phenomenon. Everyone knows that inhibitory synaptic firing is able to turn off neuronal activity for a short time, and if such a "red light" behavior is produced by the rhythmic activity of a pacemaker group of neurons, the inhibition will stop the chaotic pulsations periodically, and we will see regular oscillations in neuronal assemblies.

This view is not complete, however. Realistic neural assemblies are richer than this. Not all such assemblies have a periodic pacemaker which acts as a "red light" generator. This means we have to look for a cooperative mechanism that may regularize the chaotic oscillations without a source of periodicity. In addition we need to address the fact that regularization of the chaotic oscillations occurs without pause in its activity.

We have already discussed the cooperative action of reciprocal inhibition which may lead to periodic behavior in coupled neurons. Now we turn to the effects of unidirectional inhibitory coupling in regularizing chaos. These results throw new light on

the cellular basis of adaptivity and probably on the methods of information processing in neural assemblies.

All chaotic oscillations occur in a bounded region of the state space of the system. This state space is captured by the multivariate time-course of the vector of dynamical degrees of freedom associated with action potential generation. These degrees of freedom are comprised by membrane voltage and the characteristics of the various ion currents in the cell. We can systematically and rigorously reconstruct a mathematically faithful proxy state space for the neuron by using the membrane voltage and its time delayed values as coordinates for the state space. We can see this in Fig. 2 which is the reconstructed attractor associated with the time series of membrane voltage seen in Fig. 1. Within each such strange attractor is a set (infinite, in principle) of unstable periodic orbits of the system. There are standard methods for extracting these unstable periodic, closed orbits from which the attractor,<sup>1</sup> and using them we have isolated numerous such unstable periodic structures in the orbit in Fig. 2.

To see the role of these unstable orbits let us return to the chaotic time series in Fig. 1. It is very important that at the beginning of each burst the spikes behave quite regularly and the instability we call chaos is developing slowly. This observation leads to the suggestion that in the state space neighborhood of the chaotic trajectory lies an unstable periodic

orbit of the neuronal dynamics. It seems clear that if we apply inhibition regularly in time to return the neuron to the slowly varying burst, the behavior of the system will remain close to one of the unstable periodic orbits and the overall mode of oscillation will become more regular. This is precisely what occurs when the anterior burster and pyloric dilator neurons (AB/PD) “pacemaker” group in the stomatogastric CPG inhibits the LP neuron. As one can see in Fig. 9 the LP oscillations when driven by the AB/PD units behaves much more regularly than in isolation. The same result—regularization of chaotic oscillations—was observed in a variety of different preparations both with direct forcing by the AB/PD unit and with injected current spike trains of the appropriate frequency and very small amplitude acting as hyperpolarizing influences on the LP oscillations.<sup>18</sup>

Quantitatively we established the regularization of the chaotic oscillations by evaluating the Lyapunov exponent spectrum for each experimental setting. The positive exponent seen in isolated LP oscillations decreased by a factor of three to five and became nearly zero when the LP was driven with inhibitory synaptic activity in a frequency range near 0.5 Hz. For lower frequencies, the inhibition had little effect, and over all ranges of frequency excitatory or depolarizing inputs changed little about the neuronal oscillations. It is very important that the effect is restricted to a limited frequency band, or one could otherwise not associate it with the dynamical response of the neural system and the unstable periodic orbits within its strange attractor. If the quantitative regularization of chaotic behavior occurred at all frequencies, the “it is just inhibition” response would be adequate. If the frequency of the inhibitory input is too low, the chaotic oscillations develop too fully between inhibitory actions, and there is no regularization.

### 5. CHAOS AND NOISE

While discussing chaos at length we have avoided the mention of “noise”. In the study of dynamical systems where chaotic behavior is possible and in recognizing that chaotic signals have many of the traditional characteristics attributed to noise, there has developed a view of noise as high dimensional unpredictable dynamics not different from low dimensional chaos except by the dimension itself. More to the point is the view that associated with noise are the large Lyapunov exponents leading to the inability to predict in any practical sense. In the present context we recognize that both chaos and noise are able to organize the irregular behavior of individual neurons or neural assemblies, but the principal difference is that dynamical chaos is a controllable irregularity for it possesses structure in state space, while noise is an uncontrollable action of

dynamical systems. It is extremely important for information processing.

Our point of view is that information has a temporal coding given by the time intervals between action potentials.<sup>15</sup> Cortical neurons, for example, have several thousand inputs through synapses and dendrites. If we imagine that the incoming signals are irregular, we speculate that for chaotic signals the neuron is able to recognize the message using synchronization, but it is impossible to do this with inputs from truly noisy neurons.

The experimental results and modeling results both indicate the relevance of synchronization to global operations, for example, in vision processing, such as object segmentation and binding phenomena.<sup>10,17</sup> For chaotic neurons rapid synchronization or desynchronization is possible and seems to be quite typical. However, assemblies of “noisy neurons” are incapable of generating such large scale rapid and reversible synchronization and desynchronization.

There is a possible function of noise, seen even as high dimensional essentially unpredictable chaotic motion, in neural network studies. In high dimensional systems composed here of many coupled nonlinear oscillators, there may be small basins of attraction where, in principle, the system could become trapped. Noise will blur the basin boundaries and remove the possibility that the main attractors could accidentally be missed and the highly functional synchronized states lost to neuronal activity. Some noise may persist in the dynamics of neurons to smooth out the actions of the chaotic dynamics active in creating the robust, adaptable networks. The chaos itself should not be mistaken for noise, as the former has phase space structure which can be utilized for synchronization, transmission of information, and regularization of the network for performance of critical functions.

### 6. CONCLUSION

Strictly speaking a paper such as this has no “conclusion” *per se*, just an end. Before reaching that, we want to speculate on how the ideas we have discussed which are rooted firmly in the analysis of temporal chaos and the identification of low dimensional dynamical systems in measured time-courses for neurons may alter when we go up numerous orders of magnitude in the number of neurons.

For neural oscillations in the cortex, for example, it is almost certainly inadequate to describe it in detail by low dimensional dynamics. It may be that certain highly filtered measurements as typically found in electroencephalogram data remove enough degrees of freedom to appear low dimensional, but the raw, unfiltered view is certain not to be so simple. We instead imagine that the cortex acts in much the same way as nonequilibrium, excitable media where the chaos is spatio-temporal and has high dimension. This spatio-temporal chaos can be distinguished from



spatial distributed noise using certain universal scaling rules for its phase space structures, but more detail than this we cannot even speculatively suggest now.

We can guess, however, that this spatio-temporal chaos is only a waiting state for the nonequilibrium medium called the cortex. In this "waiting" state one sees the highly irregular spiking activity we might associate with spatio-temporal chaos. In effect, the medium has connections among the chaotic neurons "turned off" while waiting for external signaling with information to act on. When particular sensory stimuli are applied, this state smoothly and easily transforms into one of the many organized states such a medium can support. The organized states can be characterized by more or less precise spatial patterns or structures, and these will become visible with appropriate sensors. It may even be possible to utilize low dimensional dynamics for the description of these patterns and their interaction. In some sense the spatio-temporal chaos resolves itself into "non-linear modes" of the system which themselves can interact with each other—probably weakly. When the environment changes again, either other patterns emerge or the background spatio-temporal chaos returns. Here we do not try to really characterize this background or to suggest appropriate experiments to direct the proper characterization of it or the elusive "patterns" we consider.

In approaching the end here, we can restate our "view" by suggesting that nature uses complex dynamics of neural assemblies in promoting the principles of adaptability and reliability as well as in providing rapid response to changing external stimuli for information processing and response. The latter

idea focuses on instability in the phase space of a chaotic complex system. Our notion is that the use of this instability to control the system toward a selected target state is rapid because of the instability itself. Chaos itself is a necessary companion of complex dynamical systems with many varied patterns of behavior.

In this framework one may conclude that it is not necessary to make a special account of the chaotic dynamics of individual neurons or neural "groups" and to mold it into regularity. We argue that in the attempt to understand the behavior of assemblies of neurons, this would be a serious error. Chaos exists in the time-course of real neurons, and we cannot expect to predict *a priori* the correct regular cooperative behavior of even a few coupled neurons if the individual members are incorrectly modeled. So we are drawn back to chaos as a reality of member neurons in assemblies, and this "view" paper has attempted to extract out of some observations and some computations a broader view of the role of that chaos even when it is reorganized in collective regular motions.

*Acknowledgements*—The work of M. I. Rabinovich was supported by the U.S. Department of Energy, under grant DE-FG03-96ER14592. H. D. I. Abarbanel was supported in part by the U.S. Department of Energy, Office of Basic Energy Sciences, Division of Engineering and Geosciences, under grant DE-FG03-90ER14138, and in part by National Science Foundation grants NCR-9612250 and IBN-96334405. We are most appreciative to Allen Selverston, Ramon Huerta and Robert Elson for numerous productive conversations which lead to the present "viewpoint" and for collaboration on the collection and interpretation of all the data.

## REFERENCES

1. Abarbanel H. D. I. (1996) *Analysis of Observed Chaotic Data*. Springer-Verlag, New York.
2. Abarbanel H. D. I., Huerta R., Rabinovich M. I., Rowat P. F., Rul'kov N. F. and Selverston A. I. (1996) Synchronized action of synaptically coupled chaotic single neurons: I. Simulations using realistic model neurons. *Neural Comput.* **8**, 1567–1602.
3. Afraimovich V. S., Verichev N. N. and Rabinovich M. I. (1986) Stochastic synchronization of oscillations in dissipative systems. *Radiophysics Quantum Electronics* **29**, 795–803.
4. Bazhenov M., Huerta R. and Rabinovich M. I. (1996) Bifurcation inside synchronization regime of coupled chaotic neurons in CPG. *Proc. 3rd Symp. neural Comput.* **6**, 172–179.
5. Bazhenov M., Huerta R., Rabinovich M. I. and Sejnowski T. (1998) *Physica D* (in press).
6. Buzsaki G., Llinas R., Singer W. and Berthoz A. (1994) *Temporal Coding in the Brain: Research and Perspectives in Neurosciences*. Springer-Verlag, Berlin.
7. Calabrese R. L., Nadim F. and Olsen O. H. (1995) Heartbeat control in the medicinal leech: a model system for understanding the origin, coordination, and modulation of rhythmic motor patterns. *J. Neurobiol.* **27**, 390–402.
8. Elson R. and Selverston A. I. (1995) Slow and fast synaptic inhibition evoked by pattern-generating neurons of the gastric mill network in spiny lobsters. *J. Neurophysiol.* **74**, 1996–2011.
9. Glass L. (1995). Chaos in neural systems. *The Handbook of Brain Theory and Neural Networks* (ed. Arbib M.). pp. 186–189. MIT, Cambridge.
10. Gray C. M., König P., Engel A. K. and Singer W. (1989) Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization with reflects global stimulus properties. *Nature* **338**, 334–337.
11. Harris-Warrick R. M., Marder E., Selverston A. I. and Moulins M. (1992). *Dynamic Biological Networks: The Stomatogastric Nervous System*. MIT, Cambridge.
12. Hansel D. and Sompolinsky H. (1996) Synchrony in a model of a hypercolumn in visual cortex. *J. comput. Neurosci.* **3**, 7–34.
13. Hindmarsh J. L. and Rose R. M. (1994) A model of neuronal bursting using tree coupled first order differential equation. *Proc. R. Soc. Lond. B* **221**, 87–102.
14. Huerta R., Rabinovich M. I., Abarbanel H. D. I. and Bazhenov M. (1997) Spike-train bifurcation scaling in two coupled chaotic neurons. *Phys. Rev. E* **55**, R2108–R2110.

15. Mainen Z. F. and Sejnowski T. (1995) Reliability of spike timing in neocortical neurons. *Science* **268**, 1503–1506.
16. Mal'kov V. A., Rabinovich M. I. and Sushchik M. M. (1996). The universal bifurcations of inhibitory coupled spiking-bursting chaotic neurons. *Proc. of Nizhny Novgorod University* (ed. Shalfeev V. D.), pp. 72–80.
17. Murthy V. N. and Fetz E. E. (1992) Coherent 25- to 35-Hz oscillations in the sensorimotor cortex of awake behaving monkeys. *Proc. natn. Acad. Sci. U.S.A.* **89**, 5670–5674.
18. Rabinovich M. I., Huerta R., Abarbanel H. D. I. and Selverston A. I. (1996) Self-regularization of chaos in neural systems: experimental and theoretical results. *IEEE Trans. Circuits Systems I* **44**, 997–1005.
19. Wang X.-J. (1993) Genesis of bursting oscillations in the Hindmarsh–Rose model and homoclinicity to a chaotic saddle. *Physica D* **62**, 263–274.

(Accepted 10 February 1998)