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NEURODYNAMIC OSCILLATORS

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Abstract

Oscillation of electrical activity has been found in many nervous systems, from invertebrates to vertebrates including man. There exists experimental evidence of very simple circuits with the capability of oscillation. Neurons with intrinsic oscillation have been found and also neural circuits where oscillation is a property of the network. These two types of oscillations coexist in many instances. It is nowadays hypothesized that behind synchronization and oscillation there is a system of coupled oscillators responsible for activities that range from locomotion and feature binding in vision to control of sleep and circadian rhythms.

The huge knowledge that has been acquired on oscillators from the times of Lord Rayleigh has made the simulation of neural oscillators a very active endeavor. This has been enhanced with more recent physiological findings about small neural circuits by means of intracellular and extracellular recordings as well as imaging methods. The future of this interdisciplinary field looks very promising; some researchers are going into quantum mechanics with the idea of trying to provide a quantum description of the brain.

In this work we describe some simulations using neuron models by means of which we form simple neural networks that have the capability of oscillation. We analyze the oscillatory activity with root locus method, cross- correlation histograms, and phase planes. In the more complicated neural network models there is the possibility of chaotic oscillatory activity and we study that by means of Lyapunov exponents. The companion paper shows an example of that kind.

1 Introduction

Recent advances in nonlinear dynamics, chaos and fractals have been of great benefit not only in Physics and Mathematics but as well as in the study of the dynamic activity of the brain. These tools allow to characterize neural phenomena that are usually described by means of graphical methods as it is the case of electroencephalography (EEG) and some other similar recordings.

A topic that has pervaded neurophysiology along decades of this century has been the observation of oscillations in external (scalp) EEG. Likewise, oscillations of neuronal activity have been found in extracellular and intracellular electrical recordings in cortical and subcortical areas of the brain of man and animals. These observations of oscillating electrical activity have been described since the works of Mayer, Carlson, and Sherrington in 1906, as well as in the studies of Gray and Lissman in 1950 and in the work of Wilson in 1961 [1]. From then to the eighties there exist many other descriptions in the literature about oscillatory behavior. The common feature of these observations is the lack of a theoretical framework where to place them and the ignorance about the mechanisms and function of oscillatory activity.

In recent years the study of neural oscillation has been renewed applying analytical and computational tools. Among them the more notorious are nonlinear dynamics, spectral analysis, signal processing methods, chaos, and artificial neural networks. On the one hand, these tools allow to characterize neural oscillation in a manner not possible before and, on the other hand, they also allow to model and simulate oscillating phenomena in such a way that it is possible to make inferences about the mechanisms that at the level of neuronal circuits could be responsible of producing, modulating and using the oscillatory capabilities of neurons, neural networks, and neural systems.

It has been said that we do not know what could be the use of oscillations and chaos in the brain [2], but we have the tools to detect and quantify them in such a way that could lead us towards new knowledge and new tools.

2 Biological Oscillation

It is well known that oscillatory activity can be detected in the EEG. According to the brain state different oscillatory bands can be defined, namely: delta(1-4 Hz), theta(5-8 Hz), alpha(10 Hz), beta(20-30 Hz) and gamma(30-50 Hz). Beta and gamma bands are related to very active states. If at the same time the activity of neurons is recorded, it is possible to find rhythmic firing that is coherent with the beta or gamma oscillations. The most prominent example of this fact is the discovery by Singer, Gray and others [3] of oscillations of 40 Hz in the cat visual cortex. They recorded the EEG in two different places and found strong coherence between them. At the same time, the firing of neurons recorded in the same locations is rhythmically synchronized with the EEG. Since there is evidence that the features of an object are processed in parallel channels along the visual pathway they think that response synchronization of cortical neurons is a possible mechanism for feature binding in the visual system. This is probably the most important role that has been given to neural oscillation. However, it has to be realized that feature binding is not equivalent to perception.

The hippocampus is another example of oscillation where three different components can be discriminated in the hippocampal EEG: A rhythmic slow activity (RSA) or theta rhythm (with harmonics), an irregular slow activity (ISA) that may be high-amplitude (large irregular activity, LIA) or small-amplitude (small irregular activity, SIA), and fast waves or beta rhythms. It is not known what role, if any, these components play in the hippocampal functioning.

One important question is what neuronal circuits underlie both the generation of rhythmic firing and the oscillations in the EEG. There are single neurons that have the machinery for rhythmic firing and others fire rhythmically due to the properties of the network which they belong to. According to Getting [4] some simple biological circuits employ one of the following arrangements: mutual excitation, recurrent inhibition, reciprocal inhibition, and feedback inhibition. It has been shown that in biological neural systems both ways of producing rhythmic firing are used, even in combination.

3 Models of Oscillation

Modeling is an important tool for understanding biological phenomena. There are several approaches to simulate oscillatory activity. Here we show several examples. In one of them oscillation is produced by the intrinsic properties of a dynamic linear system and in the other two examples the firing pattern depends on the connectivity properties of a simple neural network where single neurons have increasing complexity in their mathematical modeling.

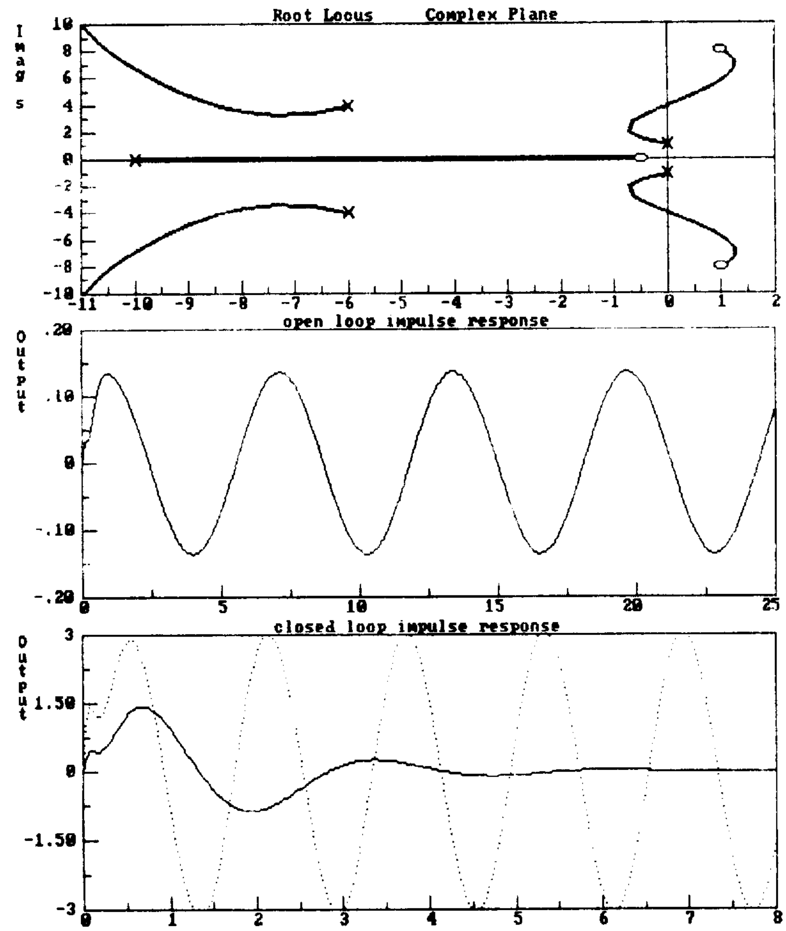

FIG. 1. Model of linear oscillator with complex dynamics. The behavior is dependent on the gain.

For the model in FIG. 1, the upper plot shows the root locus for a fifth order linear model of a dynamic system which in open loop practically behaves as a linear harmonic oscillator due to the dominance of the imaginary poles. Due to its intrinsic characteristics, the open loop response of the model produces a periodic oscillation as shown in the middle plot in FIG. 1. When negative feedback is added to the model, new properties appear, for one, the possibility of two different types of oscillation. One transient oscillation (continuous curve in lower plot of FIG. 1) when a given gain produces complex poles in the left-hand side of the complex plane, and periodic oscillation (dotted curve in lower plot of FIG. 1) when another gain produces imaginary poles. Notice that the frequency of periodic oscillation is different between the open loop and the closed loop responses. The complexity of responses of a simple model like this can be enriched by adding a nonlinear element in the forward path and a delay in the feedback path. A system like this has been proposed to model the fast rhythm generation in the hippocampus [5].

For the first case of the second example, Net 1, Net 2, and Net 3 shown in FIG. 2 are simple neural networks in which we study the conditions to achieve periodic firing patterns. The neuron models (circles) are not endogenous units: to initiate their activity it is necessary one activating element (fiber).

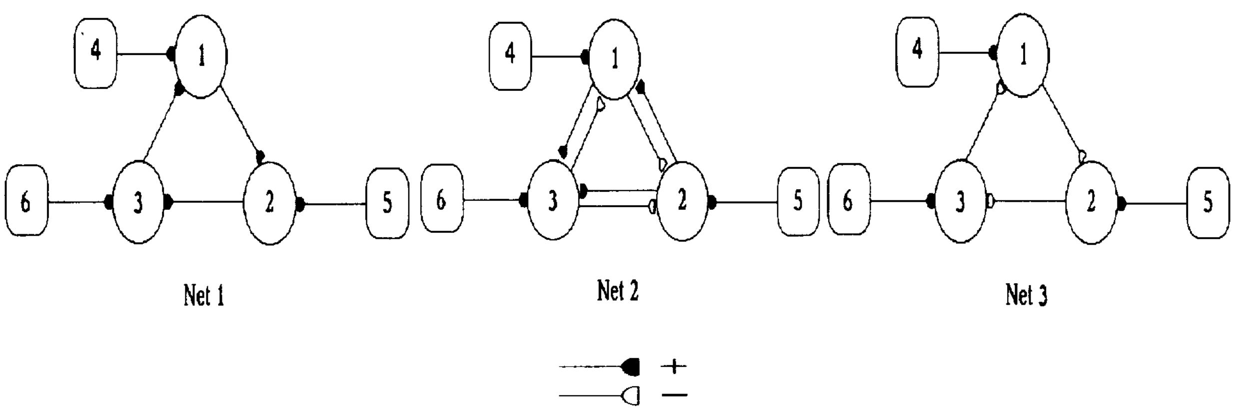

FIG. 2. Neural networks with periodic firing patterns.

The firing patterns shown in FIG. 3 were obtained by varying the synaptic intensity (weight) in each connection of the network and keeping unaltered other biological parameters. The cross-correlation histograms are useful for inferring functional connectivity and for assessing temporal relations between the firing patterns. In the histograms shown we see an increasing degree of synchronous activity in the firing patterns from Net 1 to Net 3. Actually, in Net 3 we observe a rhythmic oscillation.

For the second case of the second example, the electrical properties of individual neurons are described with Hodgkin- Huxley type voltage and time-dependent ionic currents. Neurotransmitter fluxes are additional state variables in such networks and the action of chemical synapses is modeled by additional kinetic equations. In FIG. 4 and FIG. 5 we show in the left column the firing activity of the neurons and in the right column the phase planes. A single neuron model can fire rhythmically, as exhibited by type 1 neuron in the upper part of FIG. 4, or it can display the apparently chaotic activity seen at the bottom of the figure. The difference between the two models is simply the value of a time-dependent sodium current variable.

We formed a network with recurrent inhibition like the one in Net 3 (see FIG. 2). In FIG. 5 we show the activity of the neurons in the ring-network. When type 1 neurons are used, the individual activities remain rhythmic. By contrast, when type 2 neurons are used in the network the activity becomes rhythmic in all three neurons, which is madè more evident in the corresponding phase plane plots. The overall behavior of the second network is different from the behavior of the single components.

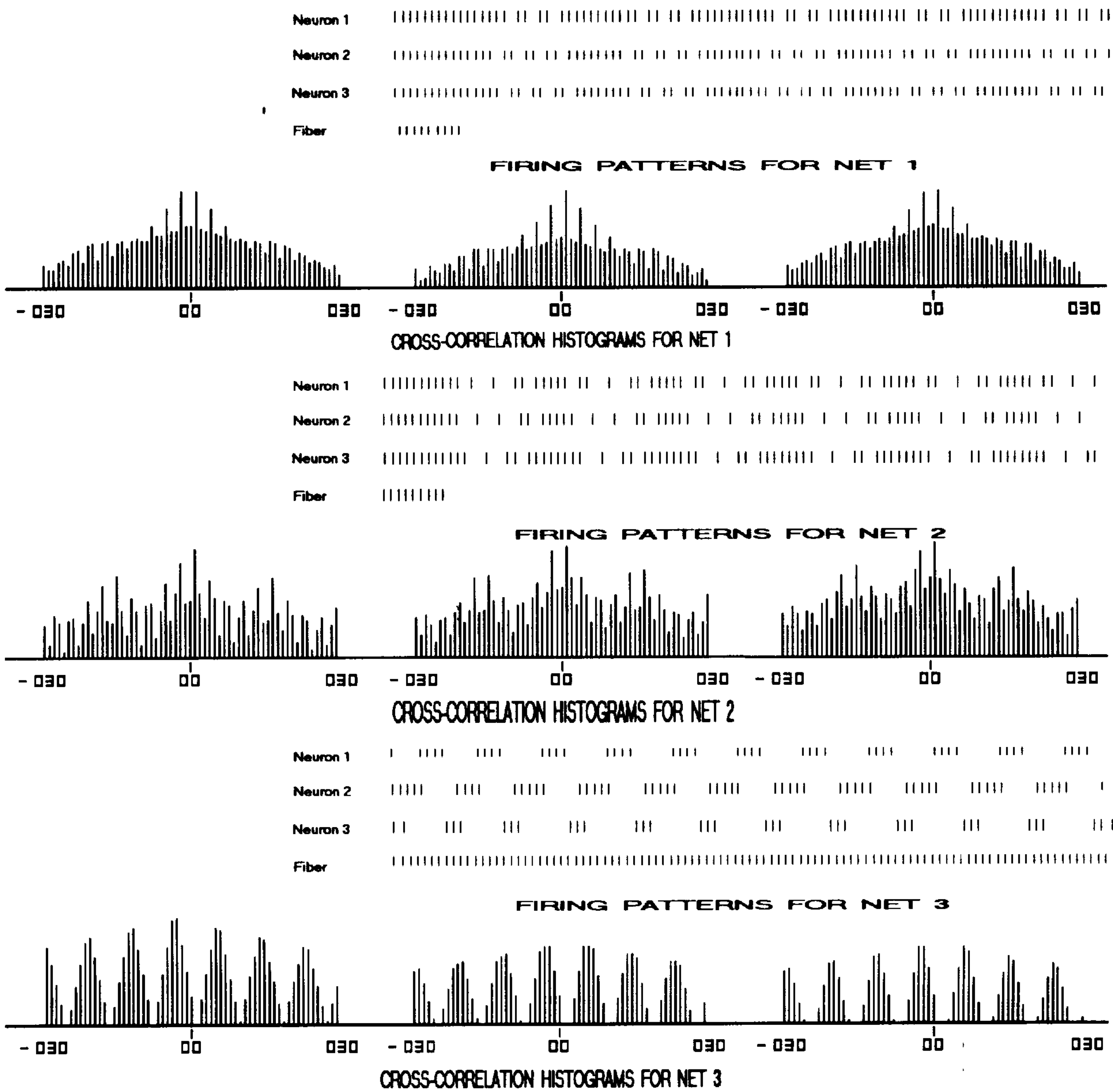

FIG. 3. Firing patterns and cross-correlation histograms for nets of Fig.2. From left to right, the histograms show the cross-correlation between neurons 1-2, 2-3, and 3-1, respectively. The weights between neurons 1-2, 2-3, and 3-1 are: 10, 4, 5 for Net 1; 5/-6, 12/-6, 5/-6 for Net 2; and -12, -16, -24 for Net 3. Negative weights indicate inhibitory connections.

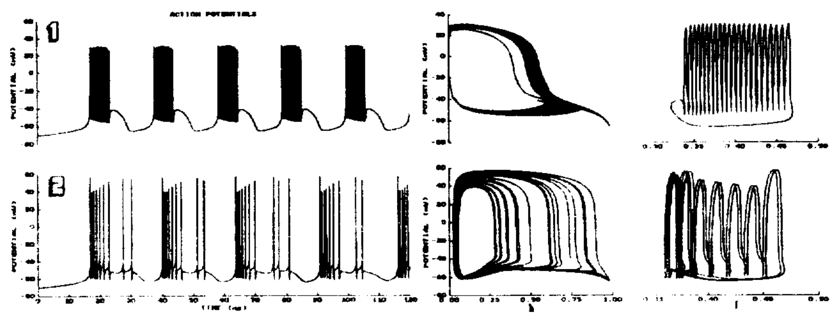

FIG 4. Examples of activity in single neurons. Type 1 neuron shows a periodic attractor while type 2 neuron exhibits an apparently chaotic attractor.

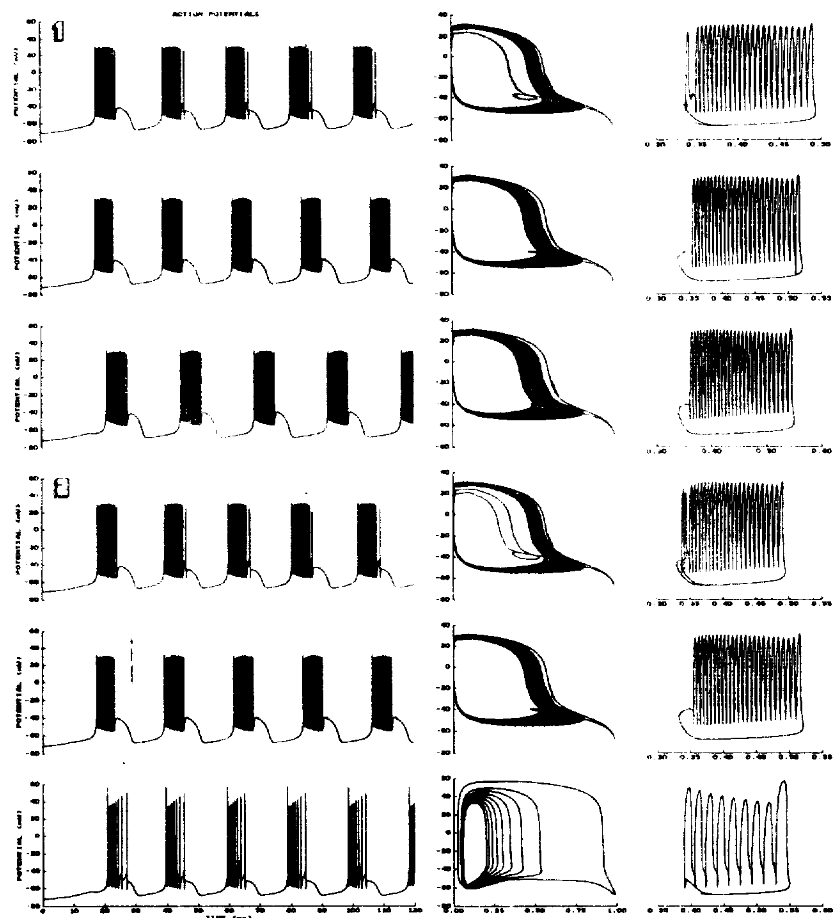

FIG. 5. Neuron activity in a ring-net similar to Net 3 of FIG. 2. Type 1 neurons were used for the first net and type 2 for the second one. Type of neuron notwithstanding all neurons display a rhythmic activity in the net.

4 Concluding Remarks

As it happens in High-Energy Physics where powerful colliders allow to look for new elementary particles, in Neuroscience, instruments like Magnetic Resonance Imaging (MRI) and Positron-Emitted Tomography (PET), allow to look for unknown mechanisms involved in normal brain functioning. However, unlike Physics, Neuroscience does not possess theoretical frameworks with the power of Quantum Theory and Classical Mechanics, that is, there is not a brain theory which could embrace the evidence provided by experiments at the molecular level as well as at the system level.

Many neuroscientists think that understanding of the mechanisms underlying perception, memory, learning and consciousness will require a quantum theory framework which would include nonlinear dynamics and chaos [6].

For example, brain waves and neuromuscular systems have attracted the use of harmonic analysis and feedback control theory since the times of Wiener [7] and Ashby [8]. In the same line but in a different field was Hebb with his reberveratory circuits [9]. They were using these tools as a mathematical characterization of macro-events in physiological systems. More recently, in trying to understand special mechanisms in the organization of biological neural networks, the theory of feedback has been brought to light again, namely by Humphrey [10] and by Edelman [11] with his idea of reentrant loops. In including negative or positive feedback in a system the conditions for oscillation are highly likely.

On the other hand, Penrose [12] has argumented that consciousness will not be understood on a computational basis, but it will require a fuller understanding of quantum mechanics, specifically the application of micro quantum mechanics to macro events [13]. However, Crick remarks that Penrose considers physics incomplete because there is as yet no theory of quantum gravity and hopes that an adequate theory of it might explain consciousness but he is very vague as to how it might do so [14]. On the side of perception, Pribram describes works which propose a quantum neurodynamics based on the Schröedinger equation and also a neural wave equation akin to Schröedinger's. He also mentions that Heisenberg matrices have been identified as instruments for the evolution of group structures, a process shown capable of accounting for the neural processes entailed in the perception of objects [6]. It is agreed at this time that all the hypotheses on consciousness are very vague as to exactly what is crucial for it and the same can be said about perception.

It is important to notice that a single neuron has a great molecular complexity [15]. However, it is in neural nets and systems of nets where higher brain functions are supposed to take place [14]. Moreover, advances in molecular neurobiology point to the place where two neurons communicate -called the synapse- as very important for higher brain functions, mainly the events that occur at the dendritic tree and the dendritic spines which are the sites that have the molecular machinery (receptors and channels) for receiving the molecules of neurotransmitter coming from the sending neuron. These phenomena could be studied by means of coupled harmonic oscillators as it has been done for finding soluble models in molecular physics [16]. After all, it was the great quantum theorist Schröedinger whose lectures in Dublin, when published in 1944 with the title "What Is Life?", had a major influence on the development of molecular biology [13]. In that book Schröedinger had one question and one answer: "How can the events in space and time which take place within the spatial boundary of a living organism be accounted for by physics and chemistry? The obvious inability of present-day physics and chemistry to account for such events is no reason at all for doubting that they can be accounted for by those sciences." [17].

Acknowledgments

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