

Models of neural dynamics in brain information processing — the developments of ‘the decade’

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DOI: 10.1070/PU2002v045n10ABEH001143

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Abstract. Neural network models are discussed that have been developed during the last decade with the purpose of reproducing spatio-temporal patterns of neural activity in different brain structures. The main goal of the modeling was to test hypotheses of synchronization, temporal and phase relations in brain information processing. The models being considered are those of temporal structure of spike sequences, of neural activity dynamics, and oscillatory models of attention and feature integration.

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Received 13 November 2001, revised 25 January 2002
Uspekhi Fizicheskikh Nauk 172 (10) 1189–1214 (2002)
Translated by Yu V Morozov; edited by M S Aksent'eva

1. Introduction

1.1 The ‘Decade of the Brain’

In modern biology, neurosciences hold a leading position in that they attract as many physicists and mathematicians as molecular genetics and biotechnologies do; but on the other hand they are probably more than a match for these disciplines in terms of complexity of mathematical problems posed by their subject matter. In the past years, *Uspekhi Fizicheskikh Nauk* [*Physics – Uspekhi*] has published several reviews on physical and mathematical aspects of neural activity [1–3]. This article continues this series.

The rapid accumulation of experimental data during the last quarter of the 20th century laid down the foundations for the accomplishment of no less a task than the creation (based upon recent progress in physics, biophysics, and computer technologies) of a concept of brain work consistent with the available findings, even if it does not give a definitive answer to the question ‘*How does man think?*’. There are more motives for the priority development of neurosciences, such as meeting practical needs of medicine and the search for non-traditional approaches to the construction of ‘intellectual’ technologies.

By way of example, a session of the US Congress, by the joint Resolution of the Senate and the House of Representatives of July 25, 1989, proclaimed the ‘Decade of the Brain’. The Resolution, covering various fields of neuroscience is represented in full in [4]. Here are its opening and closing paragraphs.

“Whereas it is estimated that fifty million Americans are affected each year by disorders and disabilities that involve the brain, including the major mental illnesses; inherited and degenerative diseases; stroke; epilepsy; addictive disorders; injury resulting from prenatal events, environmental neurotoxins and trauma, and speech, language, hearing and other cognitive disorders;

— Whereas it is estimated that treatment, rehabilitation and related costs of disorders and disabilities that affect the brain represent a total economic burden of 305,000,000 US dollars annually;

— Whereas the people of the Nation should be aware of the exciting advances in research on the brain and of the availability of effective treatment of disorders and disabilities that affect the brain;

— Whereas a technological revolution occurring in the brain sciences, resulting in such procedures as positron emission tomography and magnetic resonance imaging, permits clinical researchers to observe the living brain noninvasively and in exquisite detail, to identify brain systems that are implicated in specific disorders and disabilities, to study complex neuropeptides and behavior as well as to begin to learn about the complex structures underlying memory;

— Whereas scientific information on the brain is amassing at an enormous rate, and the field of computer and information sciences has reached a level of sophistication sufficient to handle neuroscience data in a manner that would be greatly useful to both basic researchers and clinicians dealing with brain function and dysfunction;

— Whereas advances in mathematics, physics, computational science, and brain imaging technologies have made possible the initiation of significant work in imaging brain function and pathology, modeling neural networks and simulating their dynamic interactions;

— Whereas comprehending the reality of the nervous system is still on the frontier of technological innovation requiring a comprehensive effort to decipher how individual neurons, by their collective action, give rise to human intelligence ...”, etc.

In the context of this paper, key phrases of the Resolution are those given in boldface. The Resolution concluded as follows:

“... whereas the people of the Nation should be concerned with research into disorders and disabilities that affect the brain, and should recognize the prevention and treatment of such disorders and disabilities as a health priority and whereas the declaration of the Decade of the Brain will focus needed government attention on research, treatment, and rehabilitation in this area: Now, therefore, be it Resolved by the Senate and House of Representatives of the United States of America in Congress assembled, That the decade beginning January 1st, 1990, hereby is designated the ‘Decade of the Brain,’ and the President of the United States is authorized and requested to issue a proclamation calling upon all public officials and the people of the United States to observe said decade with appropriate programs and activities.”

In 1989, American colleagues invited Russian research institutions to take part in the ‘Decade of the Brain’, the reason being such comprehensive studies require large funds that place a heavy burden on the budget of any country, even such a rich one as the United States. In February 1990, one of the authors (jointly with professor O S Vinogradova to whose memory this paper is dedicated) proposed a national neurological research program. However, the dissolution of

the USSR followed by the collapse of the country’s economic system, inflation, and practical cessation of state funding for scientific research in the early 1990s buried the program. What remains are two monographs by a panel of expert scientists [5, 6] assembled to review the then most topical issues of the problem and a booklet [4] expounding the program and giving reasons for its necessity. Many participants of the program joined universities in the USA and Europe to continue their studies in the framework of the ‘Decade of the Brain’ even though some work is still underway at the institutions of the Russian Academy of Sciences.

The present review is concerned with those lines of research that are printed in boldface in the citation of the Resolution proclaiming the ‘Decade of the Brain’ in preceding paragraphs. Main attention is given to the studies on modeling neuron activity dynamics carried out during the last decade.

1.2 Technical tools for brain research.

Classification of neural networks

Studies of neuron activity dynamics raise great interest amongst both neurobiologists and specialists in mathematical modeling. Notwithstanding the utmost complexity and variability of brain electrical activity, there is a wealth of experimental data suggesting persistent spatio-temporal relations between activities of individual neurons, neural ensembles, and brain structures. Theoretical interpretation of these findings is indispensable for the success of further purpose-oriented studies.

The available data on neural activity and principles of neuron interactions appear insufficient for understanding the mechanisms of information processing in the brain, such as coding, memorizing, recalling, recognizing, decision making, thinking, etc. Mechanisms of attention, discrimination of conscious and unconscious psychic processes, emotional effects are equally obscure.

Are there general principles of brain information processing? If any, what are their specific manifestations in electrical activity of different brain structures? Are the known patterns of neural activity consistent with these general principles or are they merely experimental artefacts? Answers to these questions depend, to a large extent, on the theoretical interpretation of the experimental findings.

The theory of neural networks (terms ‘computational neuroscience’ and ‘neural computations’ are used to the same effect in the literature) is a promising line of theoretical brain research. Mathematical and computer models, developed in the framework of this theory, may be helpful in the solution of the following problems:

- development of general concepts and hypotheses, verification of their practicability and consistency with the available experimental data;

- identification of main (essential) variables and parameters of neural systems responsible for their informational characteristics;

- analysis of the role of various mechanisms (biochemical and biophysical) in the functioning of neural structures;

- designing new targeted experiments and prediction of difficulties likely to be encountered during their performance.

A neural network is a system of dynamically interacting elements that emit and receive signals. The simplest variant of a discrete element is presented in Fig. 1a, where φ_i are input

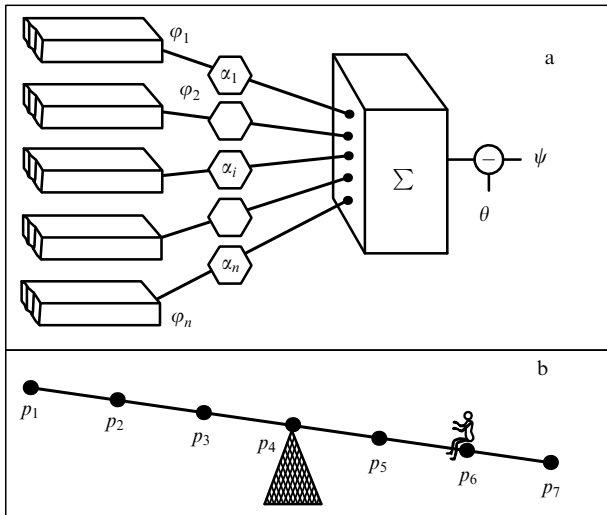


Figure 1. The simplest model of an integrate-and-fire neuron: (a) schematic representation, (b) mechanical analog illustrating the principle of work.

functions, $\Phi(\varphi_1, \varphi_2, \varphi_3, \dots, \varphi_n)$ — family of input functions, $\{\alpha_{\varphi_1}, \alpha_{\varphi_2}, \alpha_{\varphi_3}, \dots, \alpha_{\varphi_n}\}$ — set of numbers (weight coefficients), θ — threshold function, ψ — output function. Let X be a set of characteristics of external stimuli that come to receptors generating input functions φ_i . Therefore, in a discrete threshold variant, $\psi(X) = 1$ if only $\sum \alpha_{\varphi_i} \varphi_i(X) > \theta$. Intuitively, it is clear that each φ_i contains information of whether an output function ψ is true or false for each external situation X . If $\psi(X)$ is on the whole positively correlated with family $\varphi(X)$, it may be expected that weights will be positive too. Conversely, in case of negative correlation, weights α_{φ_i} will be negative. However, the idea of a correlation should be regarded here as an analogy rather than literally. It will be shown below that networks of neurons give rise to more complicated relationships than mere correlations. Depending on the problem to be resolved, elements of a neural network may, with a different degree of detalization, simulate the principles of functioning of individual neurons, their populations (e.g. inhibitory or excitatory) or neural structures (see Conclusion for a more detailed consideration). In classical neurophysiological experiments, these levels of detalization are represented by the spike-generating activity of individual neurons, local field potential of neural ensembles, and whole brain electroencephalogram (EEG) patterns produced by the multielectrode technique.

The simplest mechanical analog of computation in neural networks is ‘a swing with a distributed weight’ in a one-dimensional case or ‘a ball rolling down an inclined surface cut by ravines’ in a two-dimensional one. Figure 1b shows ‘a swing’. Assume that an external situation X is depicted as weight location in certain zones $\{p_1, p_2, \dots, p_n\}$. Let $\varphi_i(X) = 1$ when the weight is at the i -th point. In the case shown in Fig. 1b, $\alpha_i = (i - 4)$, $\theta = 0$, and the result of computation is $\sum (i - 4) \varphi_i(X) > 0$. The logical conclusion is that ‘the board descends to the right’, i.e. only one decision is chosen of the two at hand.

Modern approaches to the analysis of neural structure activity include, besides EGG, such methods as positron emission tomography (PET), magnetic resonance imaging (MRI), and functional magnetic resonance imaging

(fMRI)¹. These methods provide good spatial resolution but relatively low temporal resolution (of the order of 1 s). This restricts their application to the analysis of rapid processes in the brain.

By way of example, a relatively new technique, magnetic encephalography (MEG), is described below. The discovery of low-temperature superconductivity was used to construct transducers with which to record weak magnetic fields. It opened the possibility for observation of electromagnetic processes in excitable and contractile organs, such as heart, stomach, muscles, and (first and foremost) the brain. This method is advantageous in that it produces a ‘magnetic image’ of an organ noninvasively, that is, without introducing a probe into the organ (Fig. 2). Records of varying magnetic field contours over the head surface are used to locate cerebral foci of electrical activity with relatively good accuracy. This technique is possessed of a high spatial and

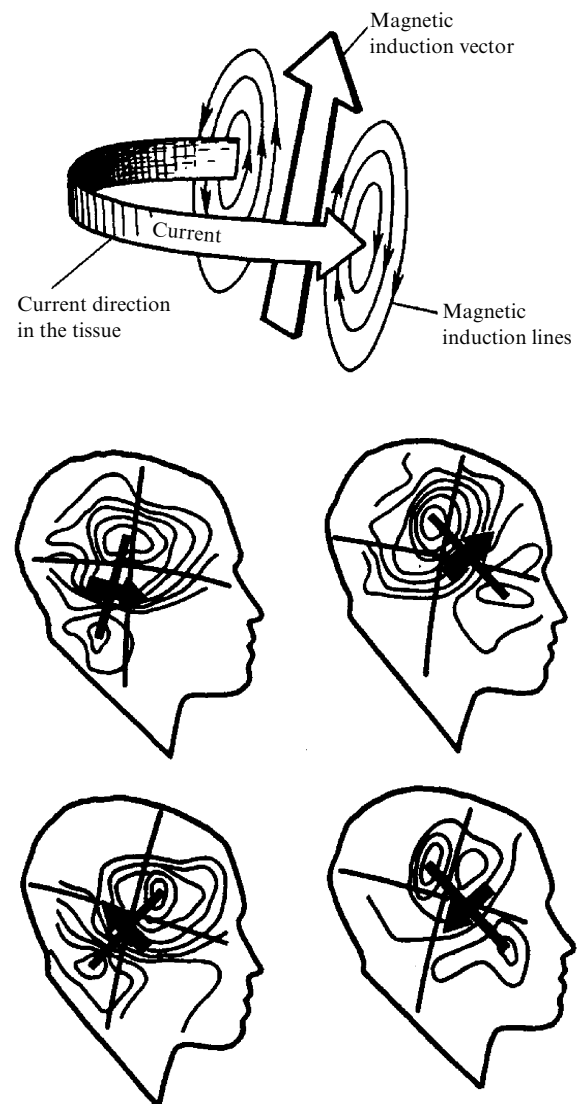


Figure 2. Magnetic encephalography (MEG), an example of one relatively new method for brain research. Records of magnetic field contours over the head surface allow foci of enhanced electrical activity of the brain to be located.

¹ Positron emission tomography is based on recording sugar distribution in brain structures while magnetic resonance imaging records oxygen distribution in the same structures.

temporal resolving power, but its practical application encounters serious difficulties as it comes to the interpretation of the results being obtained.

Input signals (stimuli) for neural networks are constant or varying continuous signals as well as random or deterministic spike sequences. These signals can be delivered either to the entire network or to its selected elements; also, the elements may receive either identical or different signals. Spike trains, averaged activity dynamics of the elements or phase relations between oscillations in different parts of the network, may serve as its output signals. In the first case, multidimensional stochastic processes offer an adequate mathematical tools for the description of network dynamics. In the second and third cases, deterministic processes in dynamic systems may be used to the same effect. One of the characteristic features of a neural network is a learning ability manifested as the modification of element properties and connection weights in response to external stimulation. Such a modification may result in altered dynamics of the network after presentation of input stimuli.

There are four classes of neural networks differing in the type of constituent elements [2, 7]:

1. *Neural networks in which the dynamics of each element are described by a system of differential equations.* These may be equations for transmembrane ion transport as in the Hodgkin–Huxley model [8], or compartment models in which the equations describing current dynamics in neuron structures (dendrites, soma, axones) are combined accordingly to Kirchhoff's laws [9]. This class also includes simplified phenomenological models designed to represent essential features of Hodgkin–Huxley neuron dynamics described by simpler equations. These are the Hindmarsh–Rose [10], FitzHugh–Nagumo [11, 12], Morris–Lecar [13] models and the like. Networks of such neurons allow many peculiarities of real cell functioning to be fully taken into account, but the analysis of their dynamics entails great difficulties.

2. *Networks of integrate-and-fire neurons.* The integrate-and-fire model is a relatively simple system that accumulates incoming signals and generates an impulse (spike) as soon as a certain threshold is reached. Figure 1a gives an example of such a model where function ψ is a spike. The model accounts for such aspects of functioning of a real neuron as absolute and relative refractoriness, synaptic delay of signal transmission, postsynaptic potential dynamics, noise component (e.g. imitating remote dendrites or synaptic noise), etc. Up to now, these networks remain the most popular object of both theoretical and simulation studies.

3. *Networks of interacting neural oscillators.* An oscillator usually includes interacting populations of excitatory and inhibitory neurons. Oscillator dynamics are described by average population activity. A typical example is the Wilson–Cowan oscillator [14, 15]. Networks of neural oscillators are explored by bifurcation theory methods which allow for analytical and numerical descriptions of parameter regions in which one or another network dynamic pattern occurs. The results of investigations may be compared with experimental findings of local and evoked potentials, EGG, and behavioral reactions. The introduction of delays in signal transmission between network elements complicates both network dynamics and its investigation because a system with the delayed argument describing such a network requires that the infinite-dimensional space of the initial conditions be considered.

4. *Phase oscillator networks.* When a neural ensemble exhibits oscillatory activity, it may be conveniently described in terms of phase oscillator [16] dynamics which are characterized by a single variable, oscillation phase. Networks of phase oscillators are useful for analytical and numerical studies of synchronization conditions in a system of oscillators. The main problem is to describe parameter space regions corresponding to different synchronization regimes (complete or partial synchronization).

The following subtypes of neural networks are distinguished, taking into consideration the architecture of neural connections:

1. *Networks with local connections, 'all-to-all' connections, random and sparse connections.* The uniform structure of connections between identical elements provides a basis for analytical characterization of such networks by methods of statistical mechanics. The best-known example is the Hopfield model of associative memory with symmetric 'all-to-all' connections [17, 18] (see also the second part of Ref. [3]).

2. *Multilayer networks with forward, backward, and recurrent connections between layers.* Specifically, such architecture of connections is characteristic of multilayer perceptrons extensively used in various learning tasks. Learning is formulated as a task of minimizing an error function. In many cases, this task is accomplished by the so-called back propagation of errors [5, 19]. The architecture under consideration is especially popular in applications of neural networks to pattern recognition, time series prediction, signals encoding and filtering, memorization of temporal sequences, etc.

3. *Networks with a central element.* These networks avoid a large number of connections due to the fact that a special central element coupled to all the remaining ones. Such architecture was proposed for the models of attention [20]. Dynamics and synchronization regimes in such networks are described in Refs [21, 22].

4. *Networks with complicated architecture.* This type includes networks with a hierarchical structure made up of simpler networks of various types. This kind of network is needed for multistage data processing and simulation of complex behavior [23, 24].

1.3 Statement of the task

In the last decade, the theory of neural networks gave rise to a separate line of research concerned with the dynamic aspects of neural activity. Russian-language publications include, besides an article in *Uspekhi Fizicheskikh Nauk* [2], an overview [25] covering a period until 1992, that for the first time, emphasized the role of synchronization in dynamic models of neural networks. The foreign literature contains many reviews amongst which monographs [26, 27] and journal papers [7, 28] are worth mentioning. During the past decade, a large number of new works on the subject have been published which gives an incentive to resume the discussion on dynamic models with a view of summarizing the available data, reveal new trends, and map out future research.

The present paper considers a few hypotheses suggested to explain the role of the spatio-temporal structure of neural activity in brain information processing and describes neural networks developed to test these hypotheses. Analysis of these models shows which variants of the choice of neural network elements (model neurons or neural assemblies), neural connection architecture, and interaction algorithms are most suitable for the solution of problems related to

mathematical modeling. In accordance with the main types of models, the paper is divided into parts highlighting the different aspects of neuron network dynamics as follows:

- 1) time structure of spike sequences;
- 2) dynamic activity of neural ensembles, synchronization and phase relations in neuron and neural ensemble activity;
- 3) synchronization of neural activity in models of preattention and attention.

In Section 2, we consider information coding by spike sequences. To-day, this issue is addressed in two different ways. One is coding by the averaged spike frequency in a sequence, the other is coding by the temporal structure of spike trains generated by individual neurons. For brevity, we refer to these two approaches as frequency and temporal (or spatio-temporal) coding, respectively.

In Section 3, we describe typical aspects of neural network dynamics with special reference to neuron activity synchronization and phase relations which may arise depending on the interaction between neural populations and the type of external stimulation.

Section 4 is devoted to the application of the synchronization principle to modeling preattention (feature integration) and attention. We give examples of the approaches to the simulation of feature integration that differ in the ways of problem formalization and the structure of synchronizing and desynchronizing connections. Also, we describe results obtained with a model of attention in which the idea of synchronization in a phase oscillator network is combined with the idea of central executive element. It will be shown how the attention focusing problem can be formulated and analysed in terms of a special synchronous dynamics, the so-called partial synchronization regime in which the central element runs in phase with a certain number of network oscillators.

In Section 5, we discuss how recent progress in neural network modeling contributed to the understanding of brain processes and propose some promising lines of future research.

2. Coding by spike sequences

2.1 The neuron and characteristics of spike sequences

In this Section, we consider, in the context of information coding and transmission, models of individual neurons and neural networks used to study time-related characteristics of neuron-generated spike sequences. We shall try to demonstrate the possibility of such encoding and the conditions for its optimization.

In line with an established tradition, the neuron is considered to be a device that converts an input sequence of spikes into discrete output action potentials transmitted along axones to the synapses of other neurons. The question is, which characteristics of spike trains may be of informational value?

Until recently, the prevailing opinion was that such a characteristic is the mean spike frequency in a train. This hypothesis was based on the fact that neurons are able to modulate the frequency of spike generation upon a change in stimulation. Moreover, it has been shown that spike generation frequency correlates with input stimulation intensity (see, for instance, [29]).

Doubts about the efficiency and universality of frequency encoding arise from the fact that different modes of stimula-

tion may produce identical frequencies of spikes. Moreover, it is obvious (and is confirmed by experiment) that frequency encoding may be efficient under conditions of slow-changing stimulation but is of little use in case of rapid rate variations. An alternative to frequency coding is a hypothesis of information coding by the temporal structure of a spike train. The potential diversity and complexity of temporal structures guarantees the possibility to code information regardless of its amount and content [30–32]. The available experimental data indicates that, under certain conditions, a temporal pattern of neural activity arising in response to identical stimuli, is reproducible to less than 1 ms [30]. It should be emphasized that the neuron activity pattern in these experiments is far from being regular.

Because the informational value of temporal patterns has never been directly confirmed in an experiment, it is interesting to examine the theoretical basis for such an approach using biologically plausible neural models. There is a variety of temporal patterns of neural activity [33]. For example, in an animal performing a given task, cortical cell activity may give rise to interspike intervals with a coefficient of variation (CV) close to 1. This means that such an activity is random and can be described only by a statistically probabilistic process with the Poisson distribution. On the other hand, the activity of a motor neuron may be regular, with CV in a range from 0.05 to 0.1. This raises a question as to the kind of a model of an individual neuron capable of reproducing such forms of activity. Specifically, what are the conditions for the generation of a spike train whose irregularity is not reduced to an effect of a noise component present in the input signal? Theoretical analysis indicates that integrate-and-fire elements with potential leakage (usually employed as components of neural networks) are not suitable for the purpose because they can generate only very regular trains of spikes in response to a random sequence of input signals. How, then, can irregular temporal patterns of activity appear? To answer this question, Softky and Koch consider active dendrites that rapidly transport Na^+ and K^+ ions. Accelerated decay of synaptic potential in such neurons leads to the suppression of the time-averaging of input signals. In addition, the authors postulate concurrent activation of a large number of synaptic inputs, such that a spike is generated due to the rapid crossing of the firing threshold. The feasibility of such rapid conductance remains to be confirmed experimentally.

An alternative way of obtaining irregular spike trains is proposed in Ref. [34]. Here, the desired effect of irregularity is achieved by means of a specially selected balance between excitatory and inhibitory components of neural activity.

It has been demonstrated in [35] that under certain conditions, even standard leaky integrate-and-fire neurons can produce highly irregular firing. The authors arrived at this conclusion after introducing into the model a partial reset of membrane potential by an output spike fired by a neuron: the membrane potential U takes the value of βU_{th} , where U_{th} is the threshold and β is the reset parameter ($0 \leq \beta \leq 1$). Also, they showed that spike trains with different CV can be elicited by changing β . It should be noted that Softky and Koch considered a case of total reset of potential corresponding to $\beta = 0$. In their study, a model neuron generated a near-regular spike train in response to a stochastic sequence of input signals. This explains why CV was close to zero in their model. CV increases with increasing β (e.g. $\beta = 0.91$ gives $\text{CV} \cong 1$ while $\beta = 0.98$ gives $\text{CV} \cong 1.6$).

In principle, there is one more possibility to obtain an irregular spike train using integrate-and-fire neurons with the time-dependent threshold. However, it has been shown in [35] that this model is equivalent to a model with a partial reset of membrane potential.

2.2 Stochastic neuron and neuron as a coincidence detector

Ref. [36] reports the evaluation of the accuracy of neural signal representation in time. Specifically, the authors studied the transformation of information in a neuron, taking into account that the input signal is noisy and different subcellular structures (synapse, dendrite, soma, axone) are also sources of noise. Two cases are considered.

1. *Signal evaluation.* In this case, it is assumed that the signal is encoded in the mean firing rate of a presynaptic neuron. The objective of estimation is to find the continuous input signal from the membrane potential of the postsynaptic neuron.

2. *Signal detection.* In this case, the input signal is assumed to be a binary one, and presynaptic spike, if any, is to be detected from the postsynaptic membrane potential.

Comparison of the results of these two approaches allows for a conclusion about the efficiency of the synaptic transmission and the discussion of its optimality. Parameter values derived from experimental data on the neocortex are used to demonstrate that a single cortical synapse can not transmit information reliably, but redundancy obtained using multiple synapses leads to a significant improvement in the information capacity of synaptic transmission. Evidently, averaging in case of temporal or spatial redundancy may be used to create informatively reliable systems from unreliable elements.

Ref. [37] compares the behavior of deterministic and stochastic variants of the Hodgkin–Huxley model. The starting point for this work were the results of an experimental study [30] and a subsequent publication [38] in which it was shown that, for a constant input, spike timing in repeated experiments is highly unreliable although reliability and precision are significantly increased (to nearly 1 ms) for fluctuating current inputs. The authors demonstrated that the deterministic model fails to reproduce experimental findings whilst the stochastic model is in excellent agreement with the experiment. Such an advantage of the stochastic model is due to the fact that the behavior of membrane potential near the threshold and the generation of action potential are critically determined by a relatively small number of excitable ion channels that are opened near threshold for spike firing rather than by the total number of channels that exist in the membrane patch. The following neuron properties under discussion are of interest: subthreshold oscillations in the membrane potential in response to a constant input, spontaneous spikes for a subthreshold input, and ‘missing’ spikes for a suprathreshold input. Slowly varying uncorrelated inputs are coded with low reliability and accuracy; hence, the information about such inputs is encoded almost exclusively by the mean spike rate. On the other hand, correlated presynaptic activity produces sharp fluctuations in the input to the postsynaptic cell which is then encoded with high reliability and accuracy. In this case, information about the input is coded by the exact timing of spikes.

Ref. [39] considers coincidence-detector properties of an integrate-and-fire neuron transforming a time-coded input

signal (temporal pattern) into a rate-coded one (firing rate pattern). A stochastic non-homogeneous Poisson process was used as the input. The authors derived a formula to describe the dependence of the coincidence detector on model neuron properties and parameters.

2.3 Adaptation of neural activity

A series of studies carried out in the past decade were designed to investigate adaptive formation of activity dynamics in individual neurons. Ref. [40] reports a study of burst generation and spike frequency adaptation in a variant of the Hodgkin–Huxley neuron model, based on the theory of bifurcation of singularly perturbed (rapid-slow, with a small parameter at some derivatives) systems. The paper presents a detailed analysis of two bifurcations leading to the breakdown of oscillatory bursting activity, namely mergence of the limit cycle with the homoclinic orbit (a loop of saddle separatrix) and bifurcation of the appearance of a saddle-node in the limit cycle. Either bifurcation leads to the elimination of the limit cycle (oscillations) by a highly specific mechanism. The difference between the two bifurcations arises from the peculiar asymptotic behavior of rhythmic activity frequency near the critical point. In both cases, the frequency of oscillations tends to zero, even though the rate of approximation is different. In case of the homoclinic bifurcation, the cycle period grows slowly as the logarithm of deviation from the parameter’s critical value. For the saddle-node bifurcation, the period grows rapidly as $\varepsilon^{1/3}$. Basing on the bifurcation analysis, the authors proposed a model of neuron spike frequency adaptation to a stimulating current observed experimentally in neurons of lobster stomatogastric ganglion.

The authors of Refs [41, 42] studied firing adaptation in a model neuron of the Hodgkin–Huxley type, where the mean value and the dispersion of an input signal were possible to reproduce. In [42], it was shown that the dispersion of intervals between spikes increased in case of slow dynamics of the current induced by postspike hyperpolarization; conversely, variability of interspike intervals decreased if postspike hyperpolarization dynamics were rapid. In [41], the adaptation algorithm controls membrane potential by estimating the intercellular somatic calcium concentration. This neural model was realized in the form of a chip containing a silicon neuron.

3. Neuron activity dynamics

3.1 Oscillatory activity of neural ensembles

Neuron-mediated information coding can be realized not only at the level of individual cells, but also at the level of neural ensembles. The principles of encoding used for the purpose are categorized into two types:

- 1) temporal coding and
- 2) spatio-temporal coding.

The former principle implies evolution of activity of a neural ensemble, where activity is understood as the number of spikes generated by the ensemble for a given time (t , $t + \Delta t$) or a mean membrane potential of neurons that make up the ensemble.

In the latter case, the emphasis is laid on characteristics of the spatio-temporal pattern of activity distribution in the ensemble. It is important that in either case coding is performed in terms of dynamic regimes developing in a

coding network under the effect of certain stimuli rather than in terms of the final state of the network [43].

Many researchers pay special attention to the oscillatory activity of neural ensembles for the following reasons. Whole brain EEG reveals rhythmic activity in different frequency ranges (alpha rhythm between 8 and 13 Hz, low beta rhythm between 14 and 20 Hz, high beta rhythm between 20 and 30 Hz, gamma rhythm over 30 Hz, delta-rhythm between 1 and 3 Hz, theta rhythm between 4 and 7 Hz [44]). The oscillations show good correlation with the psychological state of the subject under examination. Different brain structures exhibit different forms of rhythmic activity at the level of individual neurons and their populations. The relevant data is obtained for primary zones of visual and olfactory cortex, motor cortex, thalamus, hippocampus, etc. [45–50].

Because oscillatory activity is intrinsic in many neuron structures, it may be supposed that information about a stimulus is coded on the one hand by oscillation frequency and phase relations (with special role being ascribed to in-phase oscillations) and on the other hand by spatial distribution of oscillating neurons [51–53]. It is believed that the comprehensive examination of the coding problem would be helpful in search of ways for the integration of stimulus features in the neural representation of the stimulus.

In the case of neural activity registration performed with a single electrode, spectral analysis is preferred to other methods for data processing. With the advent of the multi-electrode technique, elucidation of phase relations between signals from different brain regions acquires an increasingly greater importance. An example is provided by the data showing the relationship between the activity of a given hippocampal ‘place cell’ and the phase of the theta rhythm. The ‘place cell’ is a hippocampal neuron that helps an animal (e.g. the rat) to find its way in a maze. The cell is activated when the rat appears in a certain place of the maze. As the rat moves across the ‘receptive field of the place cell’², the cell generates spikes prior to the onset of the next theta rhythm period. This phenomenon is known as phase advance. Thus, there is every reason to believe that the phase relation between theta rhythm and place cell activity provides clues for the animal on its position in the maze.

An oscillatory neural network has one of the following dynamic regimes: regular oscillations, quasiperiodic (multi-frequency) oscillations, and chaotic oscillations. Coding information in such a network is usually described in terms of synchronization between network elements and concomitant phase relations. Numerous studies have demonstrated that the conditions for the development of various dynamic regimes are essentially dependent on the network element model being employed. Unfortunately, a detailed description of an element in terms of multicompartment models [54–56] makes theoretical analysis very difficult and requires laborious computer-assisted calculations. A supercomputer has to be used to simulate even relatively simple networks [57]. Moreover, serious problems arise from the lack of experimental data about parameters of the model. For this reason, mathematical and computer models are usually constructed with the use of integrate-and-fire neurons, neural and phase oscillators [2, 7]. In this way, a compromise is achieved between the accuracy of the description and the simplicity of the mathematical analysis.

² In this context, the receptive field is a maze segment in which a place cell is activated.

3.2 Small oscillatory networks. Bifurcation analysis

The case of two coupled oscillators is most thoroughly studied because it allows analytical results to be relatively easily obtained. Suppose that each of the two identical oscillators are described by a system of differential equations and their parameters are selected so that the trajectory of a stable limit cycle is generated in the phase space. Then, dynamics of a single oscillator can be described by one variable, the current phase of motion over the limit cycle. Dynamics of a system of two weakly coupled oscillators is described by phase difference $\Delta\phi$:

- $\Delta\phi = 0$ (coherent oscillations);
- $\Delta\phi = T/2$, where T is the period of oscillations (anti-phase oscillations);
- $\Delta\phi$ equals neither 0 nor $T/2$ (oscillations with a phase shift).

A study of stability of stationary states for $\Delta\phi$ is based on the construction of the so-called H -function [58, 59]. A situation when H -function tends to zero at a certain point corresponds to a stationary state, the stability of which depends on the sign of H -function derivative at this point. A typical example of a study of the dynamics of weakly connected oscillators composed of Hodgkin–Huxley neurons can be found in [60]. The main result of this work is the discovery of bistability in a system with excitatory connections between neurons at certain parameter values. In other words, the system produces either in-phase or anti-phase oscillations depending on the starting point.

Consideration of models with weakly coupled neural oscillators is beyond the scope of the present communication (see [61] for information about such models). The review is confined to the discussion of strongly connected oscillators.

In the case of strong coupling, it is usually difficult to describe the network dynamics with the help of a mathematical theorem. Therefore, bifurcation analysis and computer modeling become the main research tools. Ref. [62] proposes classification of various rhythmic activity generation mechanisms based on the bifurcation theory. It is noted that neuron activity models are characterized by qualitatively different dynamic behavior in the vicinity of different bifurcations. For example, the disappearance of rhythmic activity near the Andronov–Hopf bifurcation is accompanied by a decrease in the rhythmic activity amplitude at a constant oscillation frequency (the frequency is determined by the imaginary part of critical eigenvalues). In contrast, the appearance of saddle-node bifurcation in the limit cycle is characterized by a tendency of the oscillation frequency to vanish while the frequency amplitude remains unaltered. The difference between dynamic behaviors is exploited, for example, for the induction of different types of bursting activity by means of a combination of different bifurcations leading spikes. Specifically, a burst of pulses may result from the Andronov–Hopf bifurcation and vanish through the same bifurcation. In an alternative case, a burst is fired in association with the Andronov–Hopf bifurcation and vanishes as a result of the saddle-node appearance on the limit cycle. Ref. [62] considers generation of as many as 120 types of bursts.

A comprehensive bifurcation analysis of a system of two coupled Wilson–Cowan neural oscillators is reported in Ref. [63], in which effects of the type and strength of connections between the oscillators on neural network dynamics are examined. Four types of connections are considered including those between (a) excitatory neural populations,

(b) excitatory population of one oscillator and inhibitory population of another, (c) inhibitory population of one oscillator and excitatory population of another, and (d) between inhibitory neural populations. It is shown that weak connections of the (b) and (c) types give rise to correlated oscillations (synchronizing connections) whereas weak connections of the (a) and (d) types produce anti-phase oscillations (desynchronizing connections). A network with intermediate-strength connections is likely to generate quasi-periodic and chaotic oscillations. Also, different dynamic regimes may coexist. A simulation study [64], resulted in a similar diversity of dynamic regimes.

A system of two identical Hindmarsh – Rose neurons with electrical connections was explored in [59]. It was shown that the system had five different dynamic regimes depending on the strength of polarizing current:

- in-phase oscillations;
- anti-phase oscillations;
- oscillations with an arbitrary phase shift (depending on current strength);
- coexisting coherent and incoherent oscillations;
- coexisting coherent and quasiperiodic oscillations.

In the two latter cases, the oscillation regime depended on the initial conditions.

Similar results for the FitzHugh oscillators were obtained in [65] and for relaxation oscillators with excitatory connections in [66]. Both studies revealed anti-phase oscillations and bistability (i.e. coexisting in-phase and anti-phase oscillations) at a number of parameter values.

Ref. [67] reports a system of two electrically coupled pacemaker oscillators. The so-called spike-response technique [68 – 70], was used in this study to explicitly calculate the neuron membrane potential with the help of two functions depending on membrane parameters (parameters of spike generation and reset of membrane potential) and parameters of electrical coupling respectively. This allowed for the description of conditions for synchronization regimes with different phase relations. In particular, the establishment of a given synchronization regime was shown to depend on the spike shape.

Ref. [71] describes a model of two integrate-and-fire neurons with active dendrites. It is shown that, unlike the case of passive dendrites where only phase synchronization of two neural activities is possible, active dendrites admit of resonant synchronization (at a frequency corresponding to the neuron membrane frequency); a rise in bursting activity is equally possible. Positive (excitatory) interaction of neurons leads to synchronous bursting activity whereas a negative (inhibitory) one produces incoherent oscillations.

A system of two excitatory neurons described by a two-compartment model of the Hodgkin – Huxley type was analysed in [72]. This system operates in two oscillatory regimes depending on calcium conductance g_{Ca} . Low g_{Ca} may be associated with rapid oscillations of practically constant frequency. Conversely, oscillations with a decreasing frequency (dying oscillations) are likely to develop at high g_{Ca} . It is shown by reducing the system to phase equations and their bifurcation analysis that only anti-phase oscillations are stable in the former case and only in-phase oscillations in the latter. At intermediate g_{Ca} values, oscillations may have arbitrarily shifted phases between neurons.

Ref. [73] presents a bifurcation study of a small oscillator network of Hodgkin – Huxley type neurons. The system was composed of four neurons making up two coupled oscillators,

each containing an excitatory and inhibitory element. Connections between the oscillators extended from excitatory neurons to inhibitory ones, with delays in signal propagation being taken into account. The study was designed to demonstrate the possibility to generate a synchronous rhythm by changing time-lags in signal propagation from one oscillator to the other. It was shown that the oscillators are synchronous at long delays and asynchronous at short propagation times. The result was obtained using an interesting and simple technique. The authors found numerically a one-dimensional representation corresponding to the difference between spike generation times in the two oscillators and determined the condition at which the zero stationary point lost stability. This example is a specific case of the two-parametric bifurcation picture, when two parameters, the strength of connection between two oscillators and the time-lag are varied. Other studies have demonstrated that the two-parametric bifurcation diagram has a very complicated structure in which regions of synchronous and asynchronous oscillations alternate [74, 75].

3.3 Large oscillatory networks.

‘Games’ with coupling characteristics

There is no theory describing possible dynamic regimes in case of an arbitrary architecture of connections in oscillator neural networks with more than two oscillators. Most of the available results were obtained in studies of neural networks with a large number of elements and uniform structure of connections (of ‘all-to-all’ or ‘local’ types).

A case of local coupling was most thoroughly explored using a chain of oscillators in which each component interacted with its nearest neighbors [76]. It was shown that such a network can produce traveling waves with a constant time shift (this result is especially important for the simulation of lamprey’s swimming).

Local connections on a plane make it possible to observe (in neural networks and other systems) different forms of dynamics of excitable media, such as stripes of synchronous activity, rotating waves, and expanding concentric rings [1, 6, 77, 78]. Moreover, the latter paper describes *excitons*, a variant of solitary waves that occur in neural networks (unlike solitons, they do not merge during collision and destroy one another like classical autowaves).

Local connections on a plane may result in complex spatial dynamics of oscillators even in networks composed of identical elements. A study reported in [79] has demonstrated the possibility for wavelike propagation of activity patterns in networks of inhibitory elements. At first sight, such a mode of propagation seems impossible. Because inhibitory connections reduce the initially activated group of elements, the activity should be expected to rapidly decay rather than propagate. The authors consider neurons showing a special property termed post-inhibitory rebound (membrane depolarization within 30–50 ms after strong inhibition). Networks of such neurons with local connections and connection weights organized as a Gaussian function are able to spread wave activity. The study demonstrates two types of such activity, continuous wave and interrupted, pulse wave. Theoretical analysis of mechanisms of emergence and propagation of an interrupted wave in a simplified neural network model is reported in [80].

A series of analytical results have been obtained for networks of integrate-and-fire neurons. Ref. [81] proves a locking theorem that formulates a simple condition of

stability of synchronous (coherent) regime in such networks. The work concerns nerve cells with a refractory period (decreasing threshold) a unimodal function describing the variation of postsynaptic potential and time delay in connections. It is shown that the synchronization regime is stable once the increasing membrane potential reaches a threshold; it is, however, bound to be unstable if the threshold is reached as the potential decreases.

Networks of integrate-and-fire neurons with rare connections were investigated in [82] using a Fokker–Planck–Kolmogorov equation that describes dynamics of a probabilistic neuron membrane potential distribution function. Different network states are conceivable depending on parameter values, e.g. a synchronous state in which neurons exhibit regular firing patterns and an asynchronous state with stationary global activity and very irregular discharges by individual neurons. Bifurcation diagrams have been constructed that show boundaries of the corresponding regions on the plane of two parameters. The possibility for oscillatory activity is considered and the period of slow oscillations is shown to be dependent in the first place on time-specific characteristics of the membrane. In case of rapid oscillations, the period is largely determined by synapse characteristics.

An interesting approach to the analysis of neuron rhythmic activity in oscillator networks of excitatory and inhibitory neural populations with different types of connections is proposed in [83]. The authors consider a system with rapid and slow variables and use a demonstrative geometric method to analyse transition of a point depicting neural activity from one branch of slow movements to another. Also considered, is the possibility to control this process by inhibitory impacts accelerating or delaying the transition. Specifically, it is shown that, in a certain coupling architecture, rapid inhibitory connections can synchronize oscillations. These findings are used to simulate complex oscillations (spindles) in the thalamus.

Oscillatory dynamics in neural network models usually results from the interaction of excitatory and inhibitory neurons or from the use of pacemaker neurons setting an endogenous rhythm. Oscillatory behavior of neural ensembles made up of identical excitatory cells can be observed in experiment. A putative mechanism of oscillations in such assemblies, considered in [84] is based on the use of a synaptic depression. The authors discuss a time-discrete mean-field model describing the average activity and synaptic depression of two populations of integrate-and-fire neurons symmetrically coupled by a small number of excitatory connections. There are μ connections onto a specific cell. The populations interact via random weak symmetric connections. It is supposed that only part of the physically available connections are active at each moment. The total number of active connections originating in a population is proportional to $s_t \in [0, 1]$, the so-called average synaptic reliability at time t . Dynamics s_t is described in the following way:

$$s_{t+1} = d(\alpha_t) d(1 - s_t),$$

where α_t is mean population activity and $d(x) = 1 - x \exp(-1/\tau)$. In other words, s_t should be small, if it was small during the previous time step or if at this very moment the mean population activity was high. Parameter τ is interpreted as the time constant of recovery from synaptic depression and is referred to as the synaptic depression time. The work under discussion is concerned with the dependence

of network dynamics on parameters μ and τ . By using the averaging theory, bifurcation analysis, and numerical experiments, conditions have been obtained for the existence of in-phase and anti-phase activity of populations, phase-trapped oscillations, and quasiperiodic oscillations.

In recent years, conditions for the appearance of oscillations and their synchronization in networks of inhibitory interneurons, have been considered in [85–92].

Refs [93, 94] deal with synchronization in large networks of identical neurons (both excitatory and inhibitory) and identical connections of the ‘all-to-all’ type, with the external input values randomly distributed between the elements. In Ref. [93], the synchronous state is identified from the critical order parameter value at which the asynchronous regime becomes linearly unstable. It is shown that, in the case of low network activity, synchronization is more stable in the presence of excitatory connections than in systems with inhibitory connections. Synchronization is impossible at high activity in a network with excitatory connections. Ref. [94] considers synchronization in networks with rare connections. It is shown that synchronization is unattainable in a network with a small average number of synapses (smaller than a characteristic threshold value); therefore, the network always remains in a state of asynchronous activity. The network operates in a synchronous mode if the number of synapses exceeds the threshold. Also, theoretical estimates are obtained for the critical number of synapses (in the weak coupling limit with the transition to phase oscillators). For example, the threshold number of synapses per neuron is 364 if the period of refractoriness is zero. The theoretical estimates are in agreement with the results of numerical experiments. The authors also studied synchronization regimes in networks with inhibitory connections. Numerical experiments demonstrated that the degree of synchronous neural activity decreased with increasing strength of inhibitory connections.

3.4 Learning in neural networks

The problem of adaptive formation of system dynamics and necessary phase relations between elements is of interest for a neural network as it is for an individual nerve cell. Such adaptation is usually achieved by an appropriate change of coupling parameters. Ref. [95] proposes a learning algorithm that enables a system of two identical Wilson–Cowan oscillators to memorize a phase shift between the oscillators. The paper considers a case of unidirectional impact of the first oscillator on the second one via a connection between excitatory populations. Synchronization is described by introducing a functional that modifies the coupling strength of oscillators, so as to improve synchrony between the oscillators. The learning rule is formulated as a differential equation for the coupling strength whose stationary state coincides with a desired phase shift. The learning rule being used, ensures gradual adaptation of the coupling strength to such a value at which the desired phase shift is achieved.

Another learning algorithm, based upon the given phase relation in a chain of phase oscillators with different intrinsic frequencies, is described in [96, 97]. The chain is assumed to be maintained by unidirectional connections (not necessarily between immediate neighbors). Each connection is characterized by a specific time-lag. Two oscillators may be connected by several couplings. The learning frequency (common for all oscillators) and phases for each oscillator comes from an external source (teacher). The learning rule leads to a change (adaptation) of both coupling weights and intrinsic frequen-

cies of the oscillators. According to the learning rule, the intrinsic frequency is modulated to be in line with the current oscillator frequency, and the coupling strengths change as

$$w_{ij}^l = h F_i R_{ij}^l,$$

where w_{ij}^l is the weight of the l -th connection between oscillator j and oscillator i , F_i is the input teacher signal for oscillator i , R_{ij}^l is the signal fed into oscillator i from oscillator j via connection l (it depends on the phase difference between oscillators i and j and phase delay of the l -th connection between them), h is a parameter that governs learning velocity. Ref. [97] reports an analytical study of stability conditions for the process of adaptation. It presents results of computer experiments that confirm the possibility for the learning of a given frequency and phase relations in a neural network. It is worthwhile to note that these results can not be extrapolated to a chain of oscillators with bidirectional (forward and backward) signal propagation.

Ref. [98] uses phase-frequency encoding of input signals and adaptation of natural frequencies of oscillators to demonstrate the possibility of memory formation in an oscillator neural network with constant connection weights between elements. The incoming stimuli are coded by groups of oscillators whose natural frequencies are similar to the frequency of the input signal. The ‘retrieval’ of a memorized stimulus is mediated through the resonance of activity of the corresponding ensemble of oscillators in response to an external input. The paper presents evidence of high efficacy of such memory in novelty detection.

3.5 Synchronization and phase relations in respiration and locomotion models

The problems of synchronization and phase relations are traditionally in the focus of attention of researchers interested in modeling respiration, locomotion, and a variety of different gaits.

Neurophysiological breath studies have revealed a conflict of two major concepts, the ‘neural network’ concept and ‘pacemaker’ concept (or the modern form of the latter the ‘hybrid’/‘pacemaker-network’ concept). According to the neural network concept (largely based on *in vivo* findings), the breathing rhythm results from synaptic (mainly inhibitory) interactions between different types of respiratory neurons (‘inspiratory’, ‘post-inspiratory’, ‘expiratory’, etc.). Importantly, the rhythm is generated in the absence of specific pacemaker neurons known to induce endogenous rhythmic bursting firing by virtue of their intrinsic properties. Modeling a respiratory center in the context of the neural network concept is considered in [99–106]. A few such models were developed and subjected to comparative analysis. Finally, the authors used neurons of the Hodgkin–Huxley type to construct a realistic model of the respiratory center, consistent with experimental data at several levels, from cellular (patterns of activity of individual respiratory neurons) to systemic (respiratory reflexes etc.).

The hybrid concept is based on *in vitro* findings. It was shown that spinal cord slices and isolated tissue generate oscillations of neural activity when synaptic inhibition is blocked, (i.e. in a situation which can not be explained in the framework of the neural network concept, and is even wholly at variance with it). The hybrid concept holds that a neural breath generator contains a population of pacemaker neurons (‘kernel’) that produces a ‘basic’ rhythm and a

neural network driven by this rhythm and forming, in its turn, output activity patterns. Smith and co-workers developed a pacemaker neuron model [107, 108] and a complex hybrid model of respiratory center [109, 110]. A main disadvantage of the hybrid model is its inability to account for a number of systemic phenomena, such as the autonomous regulation of the length of different respiratory cycle phases, respiratory reflexes, etc. Moreover, the output activity pattern (recorded *in vitro* and realistically reproduced in pacemaker models) differs from the normal breathing pattern (recorded *in vivo*) and resembles a respiratory pattern under hypoxic conditions.

Rybak et al. [111] have recently undertaken to combine the two conflicting hypotheses based on the ‘switch-over’ concept. In accordance with this concept, the respiratory rhythm is generated either by a purely neural network or hybrid mechanism depending on the state of the system. The authors developed and examined a model of ‘conditional’ pacemaker neurons capable of switching from the continuous firing regime to the pacemaker regime of collective bursting due to disequilibrium in ion currents through non-inactivated sodium channels participating in the generation of pacemaker activity and potassium channels that block it. In the context of this model, ‘conditional’ pacemakers support continuous ‘background’ excitation of respiratory neural networks *in vivo* and thus enables them to generate the respiratory rhythm by the purely neural network mechanism. An elevation of extracellular potassium ions usually practiced *in vitro* to induce rhythmic oscillations (and naturally taking place *in vivo* under hypoxic conditions), leads to a decrease of potassium currents and drives ‘conditional’ pacemakers into a pacemaker regime. In this case, the respiratory network receives an input of rhythmic bursting excitation and begins to operate in the forced oscillation regime, i.e. undergoes switching to the hybrid mechanism. The model described in this paragraph allows for a number of interesting predictions that await experimental verification.

The relationship between the properties of a system of interacting oscillators that control limb movements and observable locomotor patterns has been studied in [112–119]. Each gait is characterized by peculiar phase relations between the extremities. For example, as a horse trots, a diagonal pair of its legs hit the ground in phase, whereas the legs on either side of the body are out of phase. The said studies have demonstrated that switching between gaits can be described by symmetry-breaking bifurcation in a system of coupled oscillators. Elucidation of dynamics of neural networks simulating bipedal, tetrapodal, and hexapodal locomotion made it possible to propose a comprehensive classification of gaits and natural hierarchy of their known forms and bifurcations responsible for a change from one gait to another.

The study reported in [120] models a system of the coordination of human arm movements. It considers a network of two Ellias–Grossberg oscillators [121], each under fast, self-exciting feedback control. The oscillators interact via slow inhibitory connections between an inhibitory neuron of one oscillator and an excitatory neuron of the other. The oscillation frequency is controlled by a constant input signal reaching the oscillators. As shown by bifurcation and numerical analysis, in-phase and anti-phase oscillations may coexist at low frequency values. At higher frequencies, anti-phase oscillations are replaced by in-phase ones, in agreement with the experimental data [122]. When the

frequency is sufficiently high, oscillations with a phase shift other than 0 and π become unstable.

Models of the central pattern generator that governs lamprey swimming are described in [123–128] and reviewed in [129]. The main objective of modeling is to obtain an experimentally observed phase difference between adjacent oscillators, regardless of oscillation frequency (lamprey swimming velocity) and without distortion of the specific chain architecture of connections between the oscillators. One model differs from another by the degree of detalization of the description of functioning of an individual neuron (the scope of detalization ranges from compartment models of the Hodgkin–Huxley type to phase oscillators), structural organization of neuron-to-neuron interplay within one oscillator, and architecture of connections between oscillators (unidirectional and bidirectional interactions with the immediate and remote neighbors).

3.6 Oscillatory models of information processing in the hippocampus

Mathematical studies of phase relations at different dynamic regimes in neural networks provided a basis for the development of several models of information processing in the hippocampus. A series of works were devoted to modeling phase advance mentioned in a previous Section [130–138]. We describe here, by way of example, the last of these models. It is actually a system of two Morris–Lecar neurons, one inhibitory (interneuron) the other excitatory (pyramidal ‘place cell’). A pacemaker signal (theta rhythm) comes to the input of the inhibitory neuron. An information-bearing signal enters the ‘place cell’ from fascia dentata when the external stimulus reaches its receptive field and for some time changes dynamics of the network so that the pyramidal cell makes the interneuron generate oscillations with a frequency higher than that of the theta rhythm. This accounts for phase advance. This dynamic disappears when a rise in phase advance to 2π coincides with the delivery of the pacemaker signal to the interneuron. As a result, the system returns to the initial dynamic regime. Therefore, phase advance may be regarded as a process that develops automatically in time after an initial stimulus. This distinguishes the model being considered, from many others in which phase advance is accounted for by the animal’s spatial position.

It is worthwhile to note that the hippocampus, along with the neocortex and central pattern generator in the spinal cord, is a most popular object of modeling in terms of dynamic systems by virtue of its marked oscillatory activity in a broad range of rhythmic regimes, and a variety of functions performed by the hippocampus in brain information processing.

Ref. [139] describes a simulation of hippocampal theta rhythm. Mechanisms of the development of this slow rhythm (with the frequency in a range from 5 to 9 Hz) having interesting behavioral correlates remain unclear. One difficulty arises from the fact that hippocampal neurons normally function with a frequency one order of magnitude higher than that of the theta rhythm. Hence, an important task is to obtain a slow rhythm with rapid elements. The paper in question puts forward a hypothesis that theta rhythm is generated as the activity passes through a long loop made up of one excitatory population (region CA1 pyramids) and a few GABA-ergic inhibitory populations (interneurons of region CA1, medial septum, and region CA3). The model produces a stable theta rhythm in a wide range of parameters

consistent with experimentally found values. The rhythmic activity arises in the model through the Andronov–Hopf bifurcation. Remarkably, the frequency of oscillations, thus induced, is practically constant (with a small variation in the theta range) both at the boundary of the region of its generation and inside the region of its further existence. The authors also discuss the problem of modulation of theta rhythm frequency by signals coming from brain stem structures. The results obtained are in excellent agreement with experimental findings and theoretical concepts of O S Vinogradova [48].

One of the functions ascribed to the hippocampus is the formation of memory. In Ref. [140], relations between input signals are used as a basis for the simulation of information storage in the hippocampus. The model describes the hippocampus as an oscillator neural network making up a three-dimensional structure, the opposite ends of which receive two input signals to imitate stimuli that in vivo come to the hippocampus from the entorhinal cortex and septum. Both signals are periodic oscillations in a theta range having identical frequency and reaching hippocampal oscillators with a certain phase shift which depends on the applied stimuli and spatial location of the oscillator. It follows from the results of the work, that the phase shift is a critical parameter responsible for the formation of the spatio-temporal activity pattern in the neural network and, accordingly, for memory localization.

This fact can be illustrated by the behavior of an oscillatory network of integrate-and-fire neurons. A mathematical description of neural activity is presented in Section 6.1. The network architecture is shown in Fig. 3. Each oscillator is formed by two neurons, an excitatory pyramidal neuron and inhibitory interneuron (Fig. 3b). The oscillators are located in the nodes of a three-dimensional lattice sized $N \times M \times M$

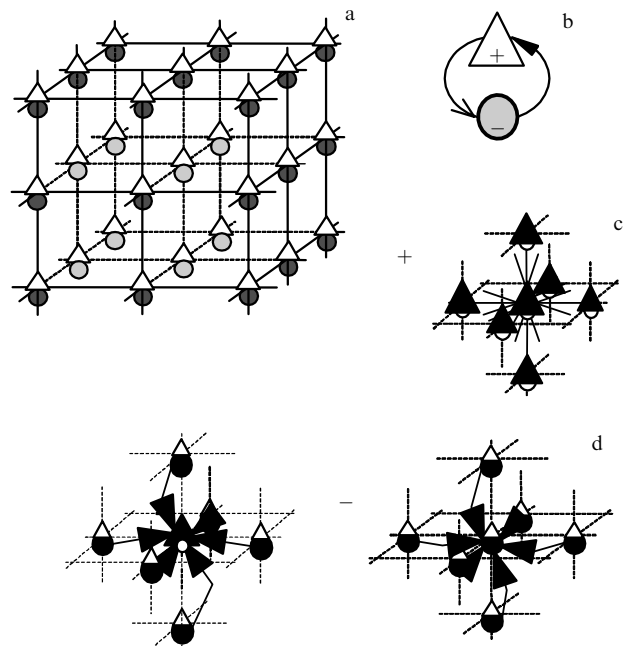


Figure 3. Coupling architecture in a model of hippocampus: (a) three-dimensional coupling structure; (b) construction of oscillator (interacting inhibitory and excitatory neurons); (c) excitatory connections to a pyramidal neuron; (d) inhibitory connections to a pyramidal neuron and interneuron. Open and solid arrows show the direction of negative (inhibition) and positive (activation) connections respectively.

(Fig. 3a). The first coordinate corresponds to the position of the oscillator relative (along) to the septo-temporal axis of the hippocampus. Two other coordinates describe the plane (orthogonal to the said axis) in which a square of $M \times M$ oscillators is located. Each square is characterized by a specific phase shift between inputs from the entorhinal cortex and septum and is interpreted as a segment of the hippocampus (lamella). In other words, this model of the hippocampus is a chain of N interacting segments. Each pyramidal neuron is linked by 6 excitatory connections with adjacent pyramidal neurons (Fig. 3c) and by 7 inhibitory connections with interneurons from the immediate vicinity (including the interneuron located in the same node of the lattice) (Fig. 3d). In addition, there is one excitatory connection between each interneuron and a pyramidal neuron and 6 inhibitory connections linking an interneuron to other interneurons in its immediate vicinity (Fig. 3d). Input signals reach only pyramidal neurons and become distributed along the septo-temporal axis so that the pyramidal neurons of one segment receive identical input signals. Input signal I_C from the entorhinal cortex has the form

$$I_C(n) = a_C \sin(\omega_0 t + (n-1)\Delta t + \phi_C),$$

where n is the segment number ($n = 1, \dots, N$). Input signal I_S from the septum travels over the network in the opposite direction. Therefore, it has the following form for oscillators of segment n :

$$I_S(n) = a_S \sin(\omega_0 t + (N-n)\Delta t + \phi_S).$$

Besides the spike-generating activity of individual neurons, the dynamics of the network are convenient to describe by the N -dimensional pattern of average neural activity in the segment. The main objective of the study is to find the dependence of this pattern on $\Delta\phi = \phi_C - \phi_S$.

Figure 4 illustrates the dynamics at two $\Delta\phi$ values (30 ms in Fig. 4a and 130 ms in Fig. 4b). Each frame in Fig. 4 (the frames are numbered from 1 to 10) corresponds to one segment and shows moments of spike generation in each of the 100 pyramidal neurons (bottom of the frame) and 100 interneurons (top of the frame). Also, each frame demonstrates averaged neural activity in the segment.

It can be seen from Fig. 4a that all 10 segments exhibit theta activity at the level of both individual neuron spikes and mean segment activity oscillating with rather a large amplitude. A phase shift between activities in different segments is worth noting. The shift between the adjacent segments is close to 120 ms.

Figure 4b illustrates different network dynamics. Segments on the right and left ends of the network (three on either side) show regular oscillations in the theta range. In contrast, oscillatory activity in the four segments in the middle of the chain is weak and has a small amplitude. It may be concluded that a phase shift between the oncoming input signals is responsible for radical restructuring of the spatio-temporal pattern of neural activity.

4. Models of attention and feature integration

4.1 Preserving the information about feature association

Modern concepts [141, 142] hold that information processing in the brain occurs at two relatively independent levels. The *lower one* (called preattention) is responsible for extracting

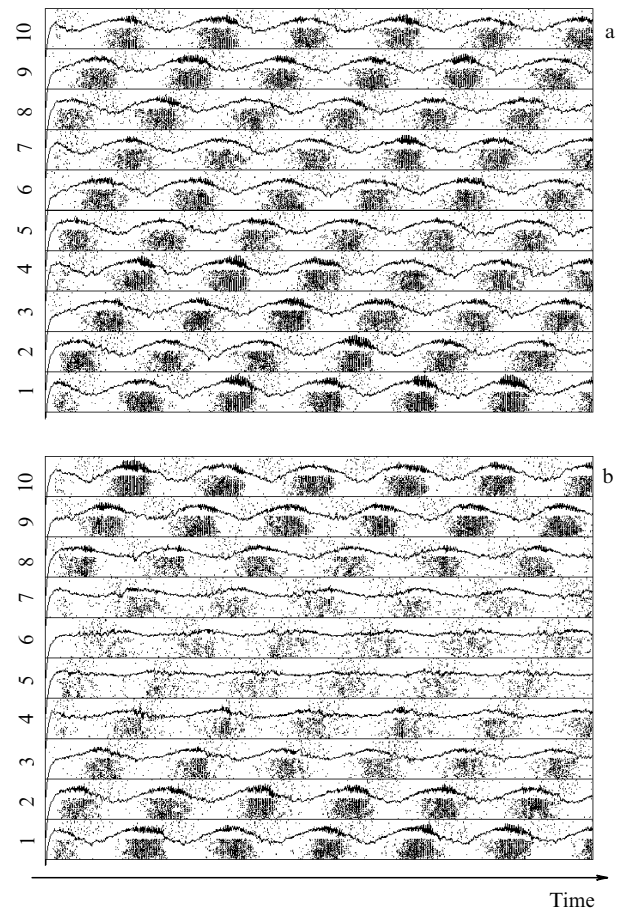


Figure 4. Activity dynamics in a 10-segment oscillatory model of hippocampus ($N = 10$) depending on the phase difference between signals coming from the entorhinal cortex and septum: (a) $\Delta\phi = 30$ ms, (b) $\Delta\phi = 130$ ms. Neuronal activity in a segment is shown in a frame indicated by the segment number. Each segment contains 100 excitatory (frame bottom) and 100 inhibitory (frame top) neurons. Rhythmic activity with a period of about 200 ms takes place in all segments of example (a) and in segments 1–3 and 8–10 in example (b), being low in segments 4, 7 and virtually absent in segments 5, 6 of (b).

features from input stimuli and for providing simple combinations of features. Characteristic of this level is a series of pathways for information processing that run in parallel (without special treatment of a selected part of information). The *higher level* requires attention and is used to perceive reality as a unified whole. At this level, fragments of information originating from sensory modalities, memory, and locomotor structures are assembled by convergence into coherent percepts, detected, analysed for novelty, and memorized, if appropriate in short and long-term memory. A characteristic feature of this level is consecutive processing of information. At each moment, that part of the available information is preferentially processed which is in the focus of attention. In fact, this portion undergoes much more detailed and thorough processing than the remaining one. Attention is shifted successively from one object to another to be eventually concentrated on new, ‘strong’ or essential stimuli.

Features used in coding information about signals in primary regions of the cortex are of a different nature. For example, they can be related to spectral, geometric or dynamic characteristics of an image. Also, features may differ in terms of modality depending on a source of sensory

information (e.g. optical or acoustical). It is known that primary processing of features of different nature or modality occurs in specialized neural structures of the cortex. Coherent percepts of objects are only obtained at the level of associative regions of the cortex [143, 144]. This poses a problem of neural mechanisms necessary to preserve information about association of the features of interest with individual objects and integrate these features into the whole representation of a given object. This issue, known as the binding problem, is reviewed in [145].

The problem is addressed in two ways based on the localized (grandmother cells) or distributed representation of an object, respectively. Difficulties encountered in the former mode of representation, for example, when the visual scene contains closely located or intersecting objects on a complex background, have been extensively discussed in the literature [52, 145, 146]. The use of distributed representation for feature integration was proposed in [146] and found further support in theoretical [147] and experimental [45, 46] studies. According to this hypothesis, the object’s features are encoded by coherent activity of neurons in different cortical regions. Such coherence serves as a ‘mark’, that labels information about a given object. Experimental studies of primary regions of the animals’ visual cortex [45, 46] revealed stimulus-specific oscillatory activity of neurons and neural ensembles and its coherence under certain stimulating conditions.

A view that principles of information grouping must be the same at both processing levels prompted use of synchronization of neural activity for the elucidation of mechanisms of formation and switching of the focus of attention [147, 20]. It is supposed that realization of this general approach, at the two levels, differs in that the lower level of synchronization reflects direct interactions between neural ensembles in primary cortical regions, probably with the participation of the pulvinar nucleus of the thalamus and mesencephalic reticular formation [148, 149]. At the higher level, synchronization is under control of specialized brain structures (such as the septo-hippocampal system and frontal lobes of the cortex) that play the role of ‘terminals’ during the transmission of information over the cortex. At the lower level, synchronization is used to form simple features (e.g. the presence of a linear segment with a definite slope). At the higher level, it is used to integrate all information concentrated in the focus of attention. As the focus of attention shifts, synchronization encompasses new cortical zones. This accounts for the successive information processing at this level.

In what follows, we shall describe models in which the principle of synchronization is employed to resolve problems pertaining to feature integration and formation of the focus of attention.

4.2 Feature integration models: parallel procedures

Let us assume that the sensor input of a neural network is exposed to activation by a few objects at a time. The oscillatory neural model of feature integration usually satisfies the following condition. *Features of one object are represented by an ensemble of synchronously operating oscillators. Synchronization between ensembles of oscillators encoding features of different objects must be excluded.* Neural assemblies functioning in synchrony are formed either in parallel (synchronous ensembles are formed simultaneously for all objects) or consecutively (synchronous ensembles coding different objects arise in a certain sequence). Simula-

tion of integration of elementary features of one type, in agreement with the experimental data obtained in the laboratories of Singer and Eckhorn, is discussed at length in [2]. Therefore, we shall focus on a case in which objects are represented by a few different features.

When developing a model of synchronization-based feature integration, it must be clearly understood that synchronization of neural network elements is achieved by means of adequately combined local connections. Unfortunately, realization of this approach encounters difficulty. On the one hand, the connections between elements being weak, the synchronizing forces prove insufficient to ensure rapid and reliable synchronization of all oscillators encoding the features of one object. On the other hand, strong connections may lead to the synchronization of the groups of oscillators encoding different objects.

Two approaches to surmounting this difficulty were suggested. One proposes the use of adaptive connections [150] on the assumption that the coupling force between oscillators working in synchrony must increase, and that between asynchronous oscillators decrease. The other suggestion was to use synchronizing local connections between adjacent oscillators and desynchronizing connections between oscillators farther apart or those encoding for qualitatively different features [151]. Both approaches lead to the same effect, that is, synchronization between assemblies of oscillators can not be achieved if they form isolated clusters.

Realization of these ideas in neural network models differs in the degree of approximation to experimental results. The feature integration model described in [150, 23, 152] shows an apparent tendency to agree with experimental conditions. Model [150] has been designed to work with moving objects whose contours are approximated by straight lines. Modification of the model, as in [23], allows color images to be considered. This network is composed of integrate-and-fire neurons sensible to the presence of such features of the object as color, shape, and motion in their receptive fields. Oscillators of this network are constructed based on the interaction between ensembles of excitatory and inhibitory neurons. The architecture of this model is rather complicated and reproduces in many known details the structure of connections between different brain regions involved in visual information processing, including the frontal cortical zone that controls eye movements.

The model of Schillen and Konig [151] may be considered in the context of the development of earlier studies on the so-called ‘holonic computer’³ (see, for instance, [153]). The objective of modeling is to demonstrate realizability, in principle, of feature integration in a neural network (and feasibility of its subsequent technical applications). The network consists of a few interacting modules, each coding one of the features (e.g. brightness, orientation, color, speed, etc.). A module is a three-dimensional network, the component elements of which are oscillators of the Wilson–Cowan type. Two-dimensional horizontal planes correspond to visual area topography whilst planes located at different levels correspond to different gradations of a given feature. The adjacent and remote oscillators within a module are coupled by synchronizing and desynchronizing connections, respectively. The modules are kept in touch by synchronizing

³ Holonic computer (from Greek *holos*, ‘total, whole’) means connections of the ‘all-to-all’ type.

connections between oscillators corresponding to one and the same pixel of the visual area. Such architecture of the network makes it possible to work with objects the images of which are superimposed in the visual area. Specifically, if intersecting images of objects differ in brightness, correct integration of their features is possible because these objects are represented in the brightness-coding module by non-intersecting clusters of oscillators with synchronizing connections inside the clusters and desynchronizing ones between them.

Ref. [154] published a few years after [151] differs from it by only a few non-essential details. It is oriented towards the work with inputs that contain contours and is closer to the holonic computer in this respect. Its main results include the demonstration that the extent of contour enhancement and neural synchrony increases with the smoothing, lengthening and closure of the contours.

In 1999, Verschure and Konig [155] proposed a markedly improved variant of the earlier Schillen – Konig model. The main difference of the new model from the previous one consisted in the use of integrate-and-fire neurons instead of neural oscillators as network elements. As before, the network consists of modules, but each module is composed of four serially connected layers of neurons, including one of excitatory neurons, two layers of inhibitory GABA-A and GABA-B neurons, and a layer of modulatory glutamate-ergic neurons. Input signals are fed into the latter layer. A central feature of the model is the presence of a layer of modulatory neurons. These neurons do not directly influence the membrane potential of other neurons but have an effect on their synaptic contacts and therefore can rapidly change effective connectivity between the units. The network is designed to experiment with arbitrarily graded color images.

The work under consideration demonstrates at least two new options of image processing, besides the ability to synchronize activity of neurons encoding different objects that is inherent in a feature integration model. One is the possibility to work with moving objects using no special detectors of motion. In this case, activity is synchronized as soon as an object enters the receptive fields of the corresponding neurons, in agreement with experimental data. The second option ensues from model responsiveness to the context that presents objects contained in an image. This capacity is illustrated by two examples below.

The first is an image consisting of two spaced objects each represented by 4 stripes of two alternating colors. One object is light-colored (L1 – L2 – L1 – L2), the other is dark-colored (D1 – D2 – D1 – D2). The network is capable of discriminating between the two objects. In the second example, the image consists of 8 light stripes alternating as follows: L1 – L2 – L1 – L2 – L1 – L2 – L1 – L2. In this case, the network responds to the image (in terms of activity synchronization) as the one containing two unrelated objects made up of L1 and L2 stripes respectively. This mode of network functioning is consistent with the results of psychological experiments. It is worthy of note that the network has a special system that governs decoding one or other context.

It is important that feature integration in the aforementioned work was achieved by synchronization in a range of gamma rhythm frequencies regardless of image processing procedure, either one-step or hierarchical. Hierarchical systems more adequately reflect the real information treatment process in the brain because primary visual areas of the cortex integrate only similar simple features, such as the presence of a moving short bar with a definite tilt angle.

More complicated combinations of features are distinguished in secondary and associative areas. Because the brain uses a wide frequency spectrum including several oscillation ranges (delta, theta, alpha, beta, gamma), it may be supposed that hierarchical feature integration can be accomplished using multifrequency quasiperiodic oscillations. The idea of the realization of such a hierarchical system has been suggested in [156, 157]. For the simplest case of a two-level system, the authors put forward a hypothesis that synchronization of high-frequency oscillations is used to integrate simple features whilst complex features are integrated by means of additional synchronization at lower frequency.

This idea was realized in the framework of a neural network model as described below. The model consists of two layers, each being a chain of Wilson – Cowan oscillators. Oscillators inside both layers are linked by synchronizing local connections. In addition, there are feedforward and feedback synchronizing convergent connections between the layers through which an oscillator in one layer receives signals from a segment of a few locally coupled oscillators of the other layer. Stimulation is simulated by the transmission of constant input signals to some excitatory neurons of the first layer. As a result, the oscillators undergo transition into an oscillatory activity regime. It is supposed that features of a simple stimulus evoke activity in a segment of first layer oscillators whereas complex features induce activity in several segments spaced by inactive oscillators.

An important feature of the network under consideration is the ability to generate quasiperiodic oscillations (high-frequency oscillations modulated by low-frequency ones; frequencies of these oscillations differ by an order of magnitude).

An example of networks functioning in response to a complex stimulus is presented in Fig. 5. It can be seen from

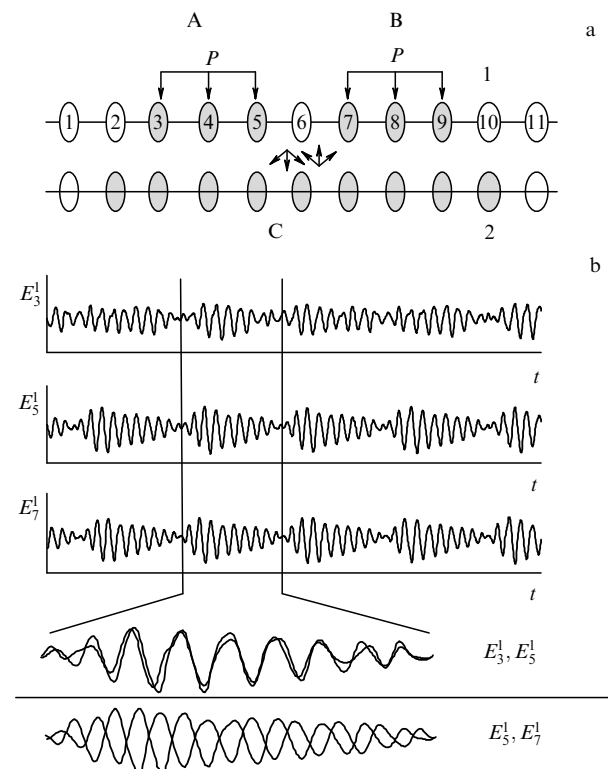


Figure 5. Functioning of an hierarchical feature integration model showing quasiperiodic oscillations in response to a complex stimulus.

Fig. 5a that stimulus P activates number 3, 4, and 5 oscillators (group A) and number 7, 8, and 9 oscillators (group B) in the first layer. The activity of number j excitatory neuron in the same layer is denoted by $E_j(t)$. Figure 5b shows activity dynamics of neurons 3, 5, and 7 in the first layer. Evidently, there is coherence between $E_3(t)$ and $E_5(t)$ (because these oscillators correspond to the same segment) whereas $E_7(t)$ shows anti-phase oscillations, corresponding to a different segment. At the same time, all these oscillators are synchronized at a low frequency. In-phase oscillations within one segment are related to intralayer connections, whereas synchronization of low-frequency oscillations in different segments of the first layer is due to effect of a segment of the second layer (group C) containing locally connected oscillators. Such synchronization of complex stimulus features may be interpreted as hierarchical.

4.3 Feature integration models: consecutive procedures

This Section is devoted to a different class of models in which integration of features of simultaneously presented objects is performed sequentially, one after another. The sequence of objects can be either deterministic or random. As shown in [158], the deterministic search in an image may have an advantage of automatically providing information about the number of connected objects and distinguishing objects with different types of connectivity.

Examples of models using a consecutive procedure are given in [159, 160]. These models can be regarded as a translation of the Hopfield model of associative memory [17, 18] into the language of oscillator neural networks. As usual, the network elements are oscillators made up of a pair of integrate-and-fire neurons coupled by one excitatory and one inhibitory connection. Connections between the oscillators are of the ‘all-to-all’ type. They are fixed and chosen from an available set of objects (patterns) using the Hebbian learning rule analogous to that used in Hopfield’s networks [17, 18] (the connections can be either synchronizing or desynchronizing). Such a choice ensures that synchronizing couplings connect oscillators belonging to one and the same pattern whilst desynchronizing couplings connect oscillators belonging to different patterns.

If patterns of certain objects used to form connections arrive simultaneously at the input of such a network then synchronous activity of oscillators representing one object will be, after some time, superseded by that of oscillators representing another object, etc. (the sequence of object selection being random). The matter is that a pattern active at one time suppresses oscillator activity in other patterns; however, it is in turn suppressed by the growing activity of its constituent inhibitory neurons. It should be noted that in addition to feature integration, the model is capable of associative reproduction of the patterns stored in memory. If an object is represented with some distortions, the network will restore its correct pattern in the form that came to be stored in memory when the connections were built up in the network.

A similar feature integration model is described in [161]. The authors also used a network of oscillators with ‘all-to-all’ connections but chose to avoid learning (making connections) in accordance with the Hebb rule. Instead, they exploited an optimization criterion for the learning quality that implies maximal discrimination of input patterns in a minimal learning time. The criterion is peculiar in that it was obtained for a given small pool of neurons instead of its

laborious calculation for the whole network. Corresponding optimization was achieved by annealing [162]. It was shown that the use of this criterion ensured synchronous firing of oscillators encoding each pattern. When a few patterns were presented simultaneously, periodic changes of activity were observed in oscillators encoding different patterns. Also, it was demonstrated that the results of learning were consistent with those obtained using the Hebb rule (correlation between coupling weights in the two learning modalities was of the order of 0.9).

Desynchronizing connections are used in one or another form in many feature integration models. The model of Ritz and co-workers [160], discussed in preceding paragraphs, contains numerous long-range desynchronizing connections which, in principle, can couple any pair of oscillators in a network. Such a complicated (and biologically irrelevant) system of connections can be avoided by using as, a source of desynchronization, a small number of inhibitory neurons (sometimes only one of them), each linked to the corresponding group of excitatory neurons by forward and backward couplings. This approach has been realized in the models developed by Horn and co-workers, Malsburg and Buhmann, Wang and Terman [163–165].

Ref. [163] was one of the first studies performed with the use of this approach. The principle of feature integration as employed in this work is convenient to illustrate with an example of a network of four excitatory ($e_1^1, e_2^1, e_1^2, e_2^2$) and two inhibitory (i^1, i^2) neurons. The neurons are combined into two groups labeled 1 and 2 by superscripts. Inside each group, there are feedforward and feedback couplings between excitatory and inhibitory neurons. Interactions between the groups are maintained by virtue of connections linking inhibitory neurons. There are no connections between excitatory neurons.

Excitatory neurons of groups 1 and 2 encode characteristics of the object’s shape (e.g. triangle or square) and color (e.g. red or green) respectively. The situation with two objects simultaneously presented to the network input (e.g. a red triangle and green square) is simulated by signals of the following form incoming the excitatory neurons:

$$inp_j^k = I_j^k + R_j, \quad j = 1, 2; \quad k = 1, 2,$$

where I_j^k is the signal coding the k -th feature of the j -th object and R_j is the noise with the parameters identical for the features of one object.

Elements of the network show oscillatory activity which is organized so that neurons e_1^1, e_2^1 responding to the red triangle work as coherent similar to neurons e_2^1, e_2^2 responding to the green square. At the same time, pairs of neurons e_1^1, e_2^1 and e_1^2, e_2^2 are out of phase. Coherent functioning is maintained due to identical noise parameters for each object whilst alternation of the activity of the neurons encoding different objects is ensured by inhibitory neurons.

A similar mechanism of asynchronous activity of oscillators coding different objects is described in [168]. The authors examine dynamics of a network of two Wilson–Cowan oscillators coupled by excitatory connections and interacting with a common inhibitory neuron. It is shown that such a network is subject to anti-phase oscillations, if the action of the inhibitory neuron is sufficiently strong. This finding is extrapolated to a large three-dimensional network in which different horizontal layers encode different features. Input objects are represented by the activity of non-intersecting populations of oscillators. It is demonstrated that in a two-

object system, the inhibitory neuron supports anti-phase population activity whereas synchronization within a population is achieved through the agency of horizontal and vertical excitatory connections between oscillators.

This model was improved in [165] that considers a two-dimensional network called LEGION (Locally Excitable, Globally Inhibitory Oscillator Network). The network consists of relaxation oscillators with local connections and a common inhibitory neuron interacting with all oscillators of the network and having a desynchronizing effect on the activity of locally uncoupled oscillator ensembles. The network is peculiar in that the strength of excitatory connections depends on oscillator activity. Given sufficiently high activity of an oscillator, it has a strong effect on the surrounding oscillators. Due to this, reliable synchronization of oscillators representing one and the same object is maintained.

Let us consider how the LEGION network functions in case of a binary image in which objects are represented as connected sets of pixels. Oscillators coding an object in the network synchronize their activity through local excitatory connections. Ensembles of oscillators coding different objects compete with one another via a common inhibitory neuron. Network parameters are chosen in such a way as to ensure ‘survival’ of an oscillator ensemble, the activity of which grows faster than that of other assemblies in which it rapidly declines. The survival is short-term, however, because after a time the activity of the entire network is suppressed by the inhibitory neuron. In this way, the network is made ready for activation of another oscillator ensemble. The time-sequence of activation of oscillator ensembles is conditioned by a noise component of incoming signals. Therefore, different ensembles are activated in a random sequence.

In [166, 167], the LEGION network was used to segment objects in real medical images with promising results.

It should be noted that a network in which a consecutive examination of the objects is realized, may be considered as a model of both feature integration and attention. The possibility of such dual interpretation is emphasized in one of the early works concerned with models of attention [168]. The choice of a fraction of sensory information, corresponding to one object of the presented set of objects, is regarded as a principal task to be solved with the help of an attention model [169]. This aspect of attention proves identical with integration of the features of an object in the focus of attention. The inhibitory element interacting with all oscillators and determining synchronization regime actually serves as a central executive structure for the system of attention. However, it is difficult to explain the presence of such central inhibitory elements in the system of attention from the biological standpoint.

4.4 Models of attention

A model of attention based on the use of a network with one central element was proposed by Kryukov [20]. It differs from the Wang–Terman model in that its central element is not an inhibitory neuron but an oscillator (the so-called central oscillator, CO), interacting with other oscillators of the network (the so-called peripheral oscillators, PO), through the agency of synchronizing forward and backward connections. In terms of brain neuron structures, the model is interpreted in the following way: the central oscillator simulates the septo-hippocampal system whilst peripheral oscillators represent cortical columns corresponding to some definite features of the object.

The focus of attention is formed in a network as synchronization of the CO and a certain PO ensemble (here, under synchronization is meant the work of the CO and a PO at roughly identical frequencies). In [20], network elements are phase oscillators whose dynamics are described by a single variable (oscillation phase), and interaction between oscillators is realized following a phase-locking scheme (see Eqns 1–2 in Section 6.2). Such oscillations have been extensively used to construct models in recent neurophysiological studies [58, 61, 72, 96, 97, 170, 171]. For simplicity, connections between POs are assumed to be absent, so that all interactions occur via the CO. The network parameters determining which oscillators are involved in the focus of attention are the coupling strengths and natural frequencies of oscillators (natural or intrinsic frequency is the frequency at which an oscillator works when the connections are switched off).

Conditions under which synchronization regimes develop in the models of attention as well as scenarios of transition from one regime to another were investigated in [22, 157]. Let us consider a case in which a set of oscillators are divided into two groups so that oscillators of group k are activated by stimulus S_k and have intrinsic frequencies distributed over interval Δ_k ($k = 1, 2$). It is assumed that intervals Δ_1 and Δ_2 do not intersect. Both stimuli, S_1 and S_2 , are simultaneously delivered to the input of the system of attention. In the context of attention modeling, the following synchronization regimes are of interest:

- **global synchronization** of all oscillators in the network (corresponding to the case when both stimuli are included in the focus of attention);
- **partial synchronization** of the CO and one group of POs (corresponding to the involvement of a single stimulus in the focus of attention);
- lack of CO synchronization with any PO group (corresponding to the absence of the focus of attention).

It has been shown in [22, 157] that switching of attention between two stimuli implies an intermediate state in which the focus of attention is either absent or encompasses both stimuli. Moreover, it has been demonstrated that the exclusion of one stimulus from a focus of attention containing two stimuli may lead to the destruction of the focus instead of concentration of attention on the remaining stimulus.

An important operational regime of the system of attention under natural and experimental conditions consists of spontaneous switching of the focus of attention between several stimuli that simultaneously reach the input. It has been shown that spontaneous deployment of attention from one complex stimulus to another may serve as a mechanism of their successive sorting in pop-out experiments [172]. Under complex stimulus it is meant a stimulus conveying information about more than one feature, e.g. shape and color. The term pop-out is used to describe identification of an object characterized by a given set of features in a visual scene containing several objects. In what follows, we show how a model of spontaneous deployment of attention can be formulated for an oscillator network with the central element.

To begin with, it should be noted that the above model of attention is assumed to have parameters (coupling strengths and intrinsic frequencies of oscillators) that remain unaltered during formation of the focus of attention. The current frequency of the CO in the course of partial synchronization depends on these parameters and, in its turn, determines the ensemble of oscillators recruited to participate in partial

synchronization. Given fixed parameters, the possible outcome of the formation of the focus of attention may be an empty ensemble or an ensemble containing only a part of the oscillators encoding a certain stimulus or even an ensemble of some oscillators that encode for two different stimuli (in the latter case, the focus of attention contains a ‘chimera’, i.e. a combination of incomplete sets of features of different stimuli). Such defects in the formation of the focus of attention can be accounted for by the ‘unfortunate’ localization of CO intrinsic frequency on the frequency axis and can be corrected if the CO intrinsic frequency is not constant but varies (adapts) somehow during the formation of the focus of attention.

We describe here a biologically motivated algorithm of adaptation of CO intrinsic frequency leading automatically to its shift, such that it excludes the aforementioned defects in the formation of the focus of attention.

The possibility of adaptation of the frequency of a biological neural oscillator to the frequency of input stimulus was demonstrated by Ukhtomsky and co-workers [173]. Ukhtomsky regarded frequency adaptation (oscillator lability) as one of the general mechanisms of information processing in the brain. Specifically, this mechanism was believed to be instrumental in the formation of stable excitation in a neural ensemble. It was called ‘Ukhtomsky dominant’. Similar experimental results concerning frequency adaptation were obtained in [174].

Frequency adaptation of network oscillators to enable them to memorize a set of stimuli of different frequencies was realized in [175]. The principles of adaptation of neural activity to an input have been considered in Section 2. That a central oscillator can modify intrinsic frequency during formation of the focus of attention was also postulated in [20].

A mathematical formulation of the model of spontaneous deployment of attention [176] is presented in Section 6.2. Eqns (1), (2), and (3) describe dynamics of CO, PO, and CO intrinsic frequencies respectively. It follows from the latter equation that CO intrinsic frequency varies, tending to match the current CO frequency value (in other words, the oscillator undergoes gradual ‘habituation’ to its current frequency and thus makes it its intrinsic frequency).

It is assumed that a set of r stimuli S_k ($k = 1, \dots, r$) is simultaneously fed into the input of the system of attention. Each S_k is encoded in the activity of a group of POs containing q oscillators, whose intrinsic frequencies are uniformly distributed in a Δ_k interval on the frequency axis. For simplicity, all intervals are taken to have length 1 and be spaced by empty intervals of length 1,

$$\Delta_k = (2k - 1, 2k), \quad k = 1, 2, \dots, r.$$

Therefore, the entire interval over which PO frequencies ($\omega_{\min}, \omega_{\max}$) are distributed is as large as $2r - 1$. (It is worthwhile to note that the shift of all intrinsic frequencies of oscillators in Eqns (1)–(2) is equivalent to the change of phase variables; hence, the possibility to choose arbitrary values for ω_{\min} without the loss of generality).

Let us break up the entire stimulation time $(0, T)$ into equal intervals t_1, t_2, \dots, t_s . The procedure of spontaneous switching of attention is as follows: at the outset, all oscillators start with phases randomly and uniformly distributed over the interval $(0, 2\pi)$. The initial CO intrinsic frequency is $\omega_{\min} - 1$. At the starting point of each time interval t_j ($j = 1, \dots, s$), CO intrinsic frequency ω_0 abruptly

changes to acquire an arbitrarily selected value within the interval $(\omega_{\min} - 1, \omega_{\max} + 1)$. In other moments, the network evolves as described by Eqns (1)–(3) in Section 6.2.

Let us now fix the value of oscillator-to-oscillator connection ($w = 0.5$). This value is chosen to be sufficiently large to ensure synchronization of group k at an appropriate ω_0 (close to the middle of interval Δ_k). However, it is too small to synchronize oscillators of other groups (because the spectrum of PO intrinsic frequencies which can be synchronized by the central oscillator with intrinsic frequency ω_0 is given as $|\omega_0 - \omega_i| \leq w$). Results of numerical simulation indicate that the CO is synchronized with oscillators of one of the PO groups during a time interval t_j . Which group of PO oscillators is involved depends on ω_0 values at the starting point of interval t_j . From this moment onward, the CO intrinsic frequency evolves towards PO intrinsic frequencies in the nearest (in terms of distance on the frequency axis) group. The final position of CO intrinsic frequency is close to the center of a group of oscillators with which CO works in synchrony during time t_j .

The results of the simulation are presented in Fig. 6. The graphs illustrate evolution of current PO frequencies and CO intrinsic frequency. Throughout the entire simulation period,

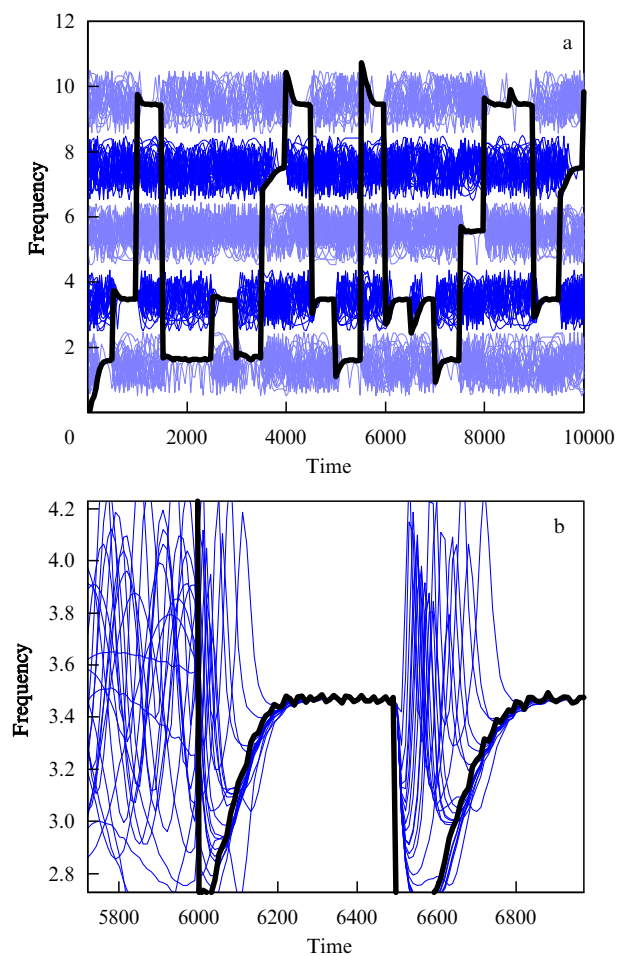


Figure 6. Current PO frequencies (thin lines) and CO intrinsic frequency (thick line) as functions of time. The number of groups $r = 5$, number of oscillators in each group $q = 20$, time interval length $t_j = 500$ units of time. (a) Dynamics during the entire stimulation period $T = 1000$. (b) Magnified fragment showing synchronization of group 2 oscillators (the spectrum of oscillator intrinsic frequencies in this group ranges from 3 to 4).

groups of oscillators underwent synchronization with the CO in the following order: group 1, group 2, group 5, group 1, group 2, etc. It follows from the figure that during time intervals t_j the CO intrinsic frequency varies so as to be optimal for the synchronization of oscillators of one of the PO groups. Current frequencies of these PO oscillators tend to be synchronized with the CO frequency. As a result, after a transitional period, almost all oscillators of the group begin to operate in synchrony with CO.

5. Conclusion

5.1 A 40 year dispute still incomplete

Dynamic models of neural activity, used to verify hypotheses principles of information processing in the brain, are very important for the elucidation of the role of the time structure of activity of individual neurons and temporal relations between activities of different neurons and neural ensembles. This review considers basic ideas underlying the models of brain oscillatory activity that have been developed during the past decade. Also, it shows that many problems can be resolved in the framework of a unified approach based upon synchronization of neural activity. It may be expected that this approach will lead to an optimal combination of parallel and successive information processing consistent with natural mechanisms of brain activity.

Oscillator neural networks have advantages and disadvantages as compared with the traditional paradigm connectionism. The theory of neural networks has emerged from attempts to describe, in formal-mathematical and computational terms, the ability of the brain to resolve complicated intellectual problems. Working principles of artificial neural structures and algorithms developed by the late 1980s provide only a rough approximation to real processes in the brain. They fail to adequately reflect its structural organization, nor do they take into account many important physiological functions of natural neurons. Not infrequently, they operate with nothing else but averaged dynamic characteristics of activity of neural structures and assemblies. In these frameworks, it is equally impossible to model metastable states and phase transitions and to study spatio-temporal relations of neural behavior. This markedly restricts the possibility for information coding and processing. As a rule, such models are designed to accomplish one concrete task (pattern recognition, formation of associative memory and conditioning, etc.), but they are incapable of imitating universal activity, including automatic choice and interaction of different intellectual functions depending on external conditions. No wonder their development has brought no substantial progress in understanding principal brain functions, such as memory, attention, consciousness, motion control, formation of goal-oriented behavior, coordination of ascending and descending information flows, intuitive and logical thinking, emotional support of neurophysiological processes, etc.. The systemic approach to the theory of neural networks and related neurocomputing problems, the development of which was given a powerful boost in the 1980s, suffers by now from the lack of new ideas. The center of gravity in these studies shifted to the improvement of the known approaches and broadening the sphere of their application. Significant progress has been achieved in applied neurocomputing (especially in detecting optical and acoustical images, automatic classification, forecasting and synthesis of time series,

optimization of technological processes) during the last decade. But it is clear that further progress, in both the theory of neural networks and the broadening of their applications, will depend on new breakthroughs in brain research. The brain is by far superior to all modern systems of artificial intelligence in terms of universality, adaptive and learning abilities, optimal behavior under real-life conditions, accuracy and reliability of functioning in uncertain situations or when receiving a noisy message.

Studies on dynamic aspects of brain work may be a source of new approaches and ideas for neurocomputing. In connection with this, a question arises whether oscillations are a crucial attribute of brain activity or only a form of information processing that developed in the course of evolution. It is hardly possible to give a definitive answer to this question now.

Scientists are nearly unanimous in that oscillations naturally arise by processes controlling periodic motion. As regards other brain functions, opinions of neurophysiologists and model designers vary widely from the extreme of total neglect of oscillatory activity (some consider it to be a purely experimental epiphenomenon of no informational value) to attaching great importance to its role in the work of practically all brain structures. To-day, there are numerous experimental materials [44, 48, 50, 145, 177, 178] giving good reason to believe that oscillations are associated with a variety of thought processes. True, it would be premature to conclude definitively that the relationship between synchronization of oscillations on the one hand, and feature integration and attention on the other hand, is an indisputable fact. At present, there is only a promising hypothesis supported by ever increasing experimental evidence.

The present review shows that recent studies have given a deep insight into conditions under which oscillations are produced and their possible role in information processing in the brain. Specifically, substantial progress has been achieved in understanding the synchronization of oscillations and its role in attention and feature integration. At the same time, much more remains to be done to promote practical application of the theory of oscillator neural networks. There are very few applied fields in which oscillator networks can successfully compete with traditional neural networks and other systems of artificial intelligence. This can be accounted for by both the complex nature of the object of research (the description of dynamic behavior is, as a rule, much more complicated than that of stationary states) and the poor understanding of many neurophysiological mechanisms underlying brain work.

In addition, it should be noted that the dispute between representatives of physico-mathematical and neurophysiological sciences over the role of mathematical modeling in the development of brain sciences has a history of more than 40 years (see the Table). Arguments of opposing sides are cited here from Refs [179, 180]. The subject of discrepancy is of crucial importance because there is, thus far, no definite answer to the question ‘How does man think?’ posed in the beginning of this review. The answer to this question is closely connected with the answer to another question: ‘Will computer modeling of intellectual brain activity allow us in the future to understand ‘How man thinks’ or is it simply a tool for the development of intellectual technologies, being of little value for neurophysiology?’

Such discussions amongst representatives of different disciplines are very common in young sciences, such as

Table. Arguments of opposing sides in the 40 year dispute on the role of mathematical modeling in neurosciences

Thesis	Antithesis
Whereas physical components of a computer system have nothing to do with the functions being computed (the computational procedure is directed only by software), a model-program can, in principle, reproduce information processing by the brain to any desired degree of accuracy specified by the programmer. All limitations and defects of the existing programs ensue from the lack of knowledge and so far inevitable simplifications; they are sure to be eliminated in the course of time.	Computer programs manipulate symbols, whereas the brain works with semantic entities. Elements of conscious mind have semantic content indispensable for the survival of an organism. For example, the brain detects contours of a predator in a noisy environment and instantly and adequately responds to its appearance. Similarly, the brain discriminates between edible and inedible items, between a sexual partner and the remaining animals, etc. In a word, it chooses a proper form of semantic behavior in a complex environment. A machine manipulates symbols moving them from one cell to another in accordance with a given set of rules. This is syntax without semantics.
The assertion that systems of ‘artificial intelligence’ must necessarily possess all properties of human brain is essentially absurd. The requirement that such systems should have exactly the same parameters as the brain is akin to the desire to have an aircraft that lays eggs (just because it must fly). Thus far, we know very little about the thought process and semantics. Therefore, one can not be quite sure about concrete properties underlying brain work.	The brain is a ‘biochemical machine’ par excellence for manipulating molecules. It is peculiar properties of biochemical molecules that underlies effects of consciousness described in specific terms of hormone-receptor interplay. Brain activity takes place in the context of such notions as pain, thirst, joy, agitation. etc. This activity develops in a hierarchical system upward from the molecular level to the whole brain (Fig.7). For example, a sensation of thirst is sometimes attributable to the work of certain hypothalamic neurons which are in turn activated by a specific peptide (angiotensin II).
‘ <i>Biochemical brain</i> ’ is not necessarily the sole physical system capable of thinking. Computer software that simulates brain processes must reflect only the informational aspect of these processes. Modeling should not be identified with exact reproduction. A plane flies not because it imitates the bird’s flight. At the same time, one can think (if appropriate) of a model of peptide actions in hypothalamus that would reliably describe them to the level of each individual synapse.	Computer simulation can be just as well employed to model hydrocarbon oxidation in a car engine or digestive process in the stomach. A model of brain processes is as real as a model describing fuel combustion or digestion. A car can not be set in motion by modeling petrol combustion with a computer, nor will food breakdown in the stomach be promoted by computer-simulated digestion. For exactly the same reason, models of thought fail to produce neurophysiological effects of this process.
‘ <i>Artificial brain</i> ’ can work to the same effect without using biological molecules. For example, microprocessors are conceivable (and already available) that can imitate retinal or cochlear function in terms of input and output activity patterns, due to their ability to respond to external signals (light or sound) in real time. Such schemes are constructed based on the known anatomical and physiological characteristics of the cat’s retina and cochlea of the barn owl. Selected parameters of their outputs are very similar to those of the signals produced by the organs they simulate. No neuromediators are used in microprocessors; therefore, neuromediators are not indispensable for obtaining a desired result.	It is impossible to reproduce concrete (versus abstract) properties of the brain only with the help of a formal program for symbol manipulation. This purpose can be achieved if the structure of logical elements originates in biologically important molecules. Such molecules may have developed incidentally in the course of evolution. Once formed, they now underlie the thought process in living systems which depends on structural changes in these molecules. Any system of other nature can probably think too but in a quite different way than biological systems. The thing is modern programs are not simply immature, they take a different route.

biological physics. Indeed, looking back into the history of biophysics, one can see numerous examples of disputes at the dawn of many research fields (e.g. debates between I W Goethe and I Newton concerning physical aspects of color vision, between L Galvani and A Volta on ‘animal electricity’, between K A Timiryazev and P P Lazarev on photochemistry and mechanisms of photosynthesis, etc.). In the majority of cases, subsequent studies by the followers and disciples demonstrated that both opponents proved to be right.

We believe that investigations into brain activity dynamics will further develop through close cooperation between neurophysiologists providing experimental data and model designers using the data. Notwithstanding the aforementioned arguments, new discoveries should be anticipated that will promote the creation of more sophisticated systems of artificial intelligence.

It is worthwhile to note that the late 20th century witnessed a change of paradigms in brain neurophysiology. Many universally accepted basic principles of this science

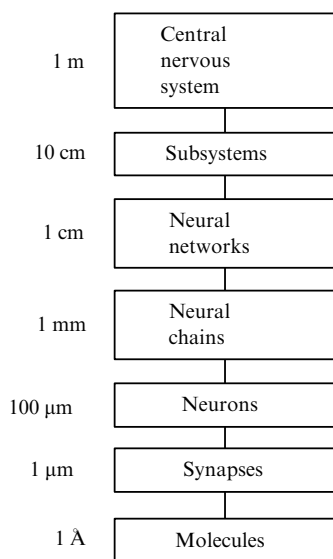


Figure 7. Structural organization of the nervous system shown on different hierarchical scales.

were revised. One of the latest reviews by O S Vinogradova was entitled “Neurosciences in the end of the second millennium: Change of paradigms” [183].

Further productive development of neurosciences is impossible without neural network modeling even though many difficulties will have to be surmounted as shown in this review.

5.2 Prospects of further research

The theory of oscillatory neural networks has advantages and disadvantages compared with the traditional approach based on the concept of threshold elements [PDP 1986]. This theory is in better agreement with experimental findings, but mathematical analysis of oscillatory models is difficult. We believe that further progress in the theory of oscillatory neural networks will depend of the success of the following lines of research.

1. *Dynamic studies of neural networks with a variable input signal.* In mathematical terms, the task can be reduced to the examination of non-autonomous dynamic systems. An example of this approach is presented in [61], where the authors found that certain aspects of information processing in the brain are reminiscent of the work of an ultrashort-wave receiver (FM-radio) in which frequency modulation is employed to encode input signals. Another example is FitzHugh–Nagumo neuron dynamics, in response to a periodic input as described in [184].

Variability of input signals makes it difficult to analyse dynamic regimes of neural networks. Additional difficulties are posed by the necessity to consider these dynamics taking into account that inherent characteristics of the network (such as connection strengths, signal delays, threshold of neurons) also vary during learning and memory formation. The following steps may prove useful for the development of this line of research:

- a study of dynamics and phase relations of possible inputs;
- a study of networks receiving input signals of small amplitude;
- a study of networks dynamics following a short period of stimulation by a constant external signal.

2. *Multilayer oscillator neural networks with different coupling architecture.* Of special importance are neural networks with local connections inside the layers and forward and backward convergent couplings between the layers. Such organization corresponds to the structure of connections between cortical columns. The presence of a central element in such networks facilitates general control of information processing through a moderate amount of connections. In particular, networks with a central element may be used to simulate interactions between the hippocampus and the neocortex.

3. *Oscillator neural networks with multifrequency oscillations.* Neurophysiological considerations dictate that neural networks must function in a relatively narrow frequency range. Moreover, the efficiency of signal coding by different frequencies is poor because of low signal resolution in this frequency range.

There are two options available to enhance coding efficiency. One is to employ spatial frequency coding which consists of the distribution of signals coded in similar frequencies over different parts of the network. This approach is used in [176] for the construction of a novelty detection model. The other option is to use several frequencies at a time to encode information and thus increase coding space dimension.

As noted earlier in this Section, the theory of oscillatory neural networks has an important implication, besides its neurophysiological applications, for the development of artificial neural networks with which to resolve technical problems. To-day, there is a possibility, in principle, to construct artificial neural systems with a broad spectrum of intellectual capabilities. An important breakthrough in this area would be creation of a system of interacting oscillators arranged as a neural network capable of feature integration, attention, recognition and memorization of new information. All necessary components for such a system are at hand. An immediate task is to select those models from the existing ones that could be most effectively used for the purpose and to work out principles of interactions of the available components within the system. Many aspects of such interactions are already known, others will come to be understood in the course of further joint studies of neurophysiologists, psychologists, mathematicians, and computer model designers.

The authors are grateful to I A Rybak and G S Cymbalyuk for the help in the preparation of a part of Section 3 concerning the models of respiration and locomotion. The work of G N Borisyuk, R M Borisyuk, and Ya B Kazanovich was supported in part by the Russian Foundation for Basic Research (grant 99-04-49112). R M Borisyuk and Ya B Kazanovich also received support from EPSRC (GR/N63888/01). The work was supported in part by a RFBS grant for leading scientific schools (G R Ivanitskiĭ, 00-15-97985).

6. Appendices

6.1 Integrate-and-fire neuron dynamics

Dynamics of an integrate-and-fire neuron is given by the following relations.

1. Threshold:

$$r(t+1) = (r_{\max} - r_{\infty}) \exp[-\alpha_{\text{th}}(t - t_{\text{sp}})] + r_{\infty},$$

where r_{\max} is the maximum threshold value, r_{∞} is the asymptotic threshold value at $t \rightarrow \infty$; α_{th} is the rate of threshold decrease, and t_{sp} is the moment of generation of the last spike till moment t .

2. Postsynaptic potential for the input to a neuron:

$$PSP^j(t+1) = PSP^j(t) \exp(-\alpha_{\text{PSP}}^j) + a,$$

$$a = \begin{cases} w^j, & \text{if } t_{\text{sp}}^j + \tau^j = t + 1, \\ 0, & \text{otherwise,} \end{cases}$$

where w^j is the coupling strength (positive for excitatory coupling and negative for inhibitory one), τ^j is time delay, α_{PSP}^j is the rate of decrease of postsynaptic potential of the j -th neuron, t_{sp}^j is the moment of generation of the last spike till moment t for the j -th neuron.

3. Noise:

$$N(t+1) = N(t) \exp(-\alpha_N) + \xi,$$

$$\xi \in \mathbf{N}(0, \sigma),$$

where α_N is the rate of noise attenuation and ξ is the normally distributed random value.

4. Somatic membrane potential:

$$V(t+1) = V_{\text{AHP}} \exp[-\alpha_V(t - t_{\text{sp}})],$$

where V_{AHP} is postspike hyperpolarization, α_V is the rate of decrease of somatic membrane potential, and t_{sp} is the moment of generation of the last spike till moment t .

5. Total potential:

$$P(t+1) = \sum_j PSP^j(t+1) + N(t+1) + V(t+1) + I_{\text{ext}}(t+1),$$

where I_{ext} is the external signal.

6. Spike generation:

if $P(t+1) > r(t+1)$, then $t_{\text{sp}} = t + 1$.

6.2 Oscillatory model of attention

Attention model is formulated in terms of a phase oscillator network. It is described by the following equations:

$$\frac{d\theta_0}{dt} = \omega_0 + \frac{w}{n} \sum_{i=1}^n \sin(\theta_i - \theta_0), \quad (1)$$

$$\frac{d\theta_i}{dt} = \omega_i + w \sin(\theta_0 - \theta_i), \quad i = 1, 2, \dots, n, \quad (2)$$

where θ_0 is CO phase, θ_i — PO phases, ω_0 — CO intrinsic frequency, ω_i — PO intrinsic frequencies, n — the number of peripheral oscillators, w coupling strength between oscillators, $d\theta_0/dt$ — CO current frequency, $d\theta_i/dt$ — PO current frequencies.

Modification of the CO intrinsic frequency is described by equation

$$\frac{d\omega_0}{dt} = -\gamma \left(\omega_0 - \frac{d\theta_0}{dt} \right), \quad (3)$$

where parameter γ gives the rate of adaptation of CO intrinsic frequency to its current frequency.

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