Synchronization of neural activity and models of information processing in the brain

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Abstract

The paper considers computational models of neural networks aim to reproduce neurophysiological experimental data on spatio-temporal patterns registered in brain structures and to check hypotheses about the role of synchronization, temporal and phase relations in information processing. Three sections of the paper are devoted, respectively, to the neuronal coding, to the models that are used to study phase relations in oscillatory activity of neural assemblies, and to synchronization based models of attention.

Introduction

The theoretical study of the temporal structure of neural activity is very important. Despite the great complexity and variability of electrical activity in the brain, constantly increasing experimental data reveal consistent temporal relations in the activities of single neurons, neural assemblies and brain structures. Without a proper theoretical background, it is very difficult to guess how these relations can appear and what their role could be in information processing. This is especially important in the situation when detailed knowledge of the mechanisms of neural activity and neural interactions have not led to a significant progress in understanding how the information in the brain is coded, processed, and stored. What are the general principles of information processing in the brain? How can they be discovered through the analyses of electrical activity of neural structures? Which part of available experimental data reflects these general principles and which is related to the peculiarities of biological implementation of these principles in different brain structures? Are the observed temporal relations in neural activity related to information coding or they are the artifacts generated by special experimental conditions? These questions still wait their answer in future theoretical studies.

Computational neuroscience is one of the promising directions in developing the brain theory. The mathematical and computer models provide the possibility: to form general concepts and to apply them to the analysis of experimental data; to extract essential variables and parameters of neural systems which determine their information processing capabilities; to analyze the role of different mechanisms (biophysical, biochemical, etc.) in neural system functioning; to propose new hypotheses and to check their validity by comparing the modeling results with experimental data, to make suggestions about the further progress of neuroscience, to formulate the main ideas of new experiments and possible drawbacks.

In this paper, we consider several hypotheses which have been put forward to explain the role of temporal structure of neural activity for information processing. We describe neural networks that have been developed in support of these hypotheses and whose analysis reveals what kind of model neurons or neuron assemblies are suitable and how their interaction should be organized to implement different types of information coding and processing.

Neuronal Coding

Traditionally, a neuron is considered as a device that transforms a changing sequence of input spikes into discrete action potentials that are transmitted through the axon to the synapses of other neurons. What are the properties of the neural spike train that provide the possibility to carry the information or take part in information processing? Until recently, the most popular hypothesis has stated that this property is the rate of spikes in the train. Rate coding explains how the presentation and intensity of the stimulus can influence neural activity but this coding neglects the temporal organization of spike trains.

Experiments show that temporal patterns of neural activity can be very complex, and it is natural to admit that there should be some information encoded by the moments of spike generation. For example, different stimuli or tasks can elicit different patterns of activity that have the same firing rate. Experimental data obtained in the last years show that in the slowly changing surrounding the rate code might be useful, but its efficiency drops abruptly if stimulation conditions change quickly. In the latter case, the fine temporal structure of spike trains should play a much more important role (Mainen & Sejnowski, 1995).

If we agree that the temporal pattern of activity carries the information about the stimulus, which features of this pattern are important? The popular hypothesis is that the stimulus-driven oscillatory activity in a neuron is a code of a significant stimulus (Borisyuk et al., 1990; more recent discussion of this problem can be found in Singer, 1994). The essence of oscillatory coding can be reduced to two basic ideas: place coding: the stimulus is coded by the location of a neuron that shows the oscillatory activity; and binding: the integration of local stimulus representations is realized through impulsation synchrony.

The other approach takes into account the fine temporal structure of spike trains. The approach is based on the evidence that under some conditions of multiple stimulus presentation a neuron can reply, reproducing the moments of spikes with precision of 1 msec (Mainen & Sejnowski, 1995). Note that the general pattern of activity is far from being regular in these experiments.

Phase Relations of Neural Activity

Here we consider the case when the dynamics of neural activity is of an oscillatory type. This case is important for modeling since many EEG recordings show various rhythms (alpha, beta, gamma, etc.) during background activity (without presentation of an external stimulus) and in some functional states. For example, the importance of oscillatory activity and corresponding phase relations for information processing has been demonstrated by O'Keefe and Recce (1993). They have found specific phase relationships between the activity of hippocampal place cells and the EEG theta-rhythm.

To perform mathematical analyses of oscillatory processes in neural system, the theory of oscillatory neural networks has been developed which concentrates on the dynamical behavior of interacting oscillators. Usually an oscillator is formed by two interacting populations of excitatory and inhibitory neurons. For simplicity, a population can be approximated by a single excitatory or inhibitory element, which represents the average activity of a neural population (the term "neuron" is kept to denote this element as well). A typical example is the Wilson-Cowan oscillator (Wilson & Cowan, 1972), its modifications are most frequently used in oscillatory neural networks. If the input signal is absent or small, the oscillator will keep a low stationary level of activity. If an oscillator receives a strong enough input signal, the activity of its excitatory and inhibitory components starts to oscillate. Being connected to each other in a network, the oscillators are capable of running with the same frequency. Thus, one or several assemblies of in-phase running oscillators are formed with different phase shifts between the assemblies. The values of the shifts mostly depend on the constrains put on the oscillators and their coupling.

We omit papers on weakly coupled neural oscillators because complete presentation of this subject is contained in the recently published book by Hoppensteadt and Izhikevich (1997), where a reader can find all necessary details. In the following text, we address to the case, where connections between oscillators are strong enough.

Usually, if connection strengths are not small, it is impossible to describe phase relations in terms of a mathematical theorem. The main tool kit for such investigations includes computer simulations and numerical methods for bifurcation analysis and parameter continuation.

Complete bifurcation analysis of the system of two coupled neural oscillators of a Wilson-Cowan type is given in (Borisyuk et al., 1995). In these papers, the authors study how the type and the strength of connections affect the dynamics of a neural network. All different connection architectures are investigated separately from each other. In the case of weak connections, the connections from excitatory to inhibitory neurons and from inhibitory to excitatory neurons (synchronizing connections) lead to periodic in-phase oscillations, while the connections between neurons of the same type (from excitatory to excitatory and from inhibitory to inhibitory) lead to periodic anti-phase oscillations (desynchronizing connections). For intermediate connection strengths, the network can enter quasiperiodic or chaotic regimes, and can also exhibit multistability. More generally, the analysis highlights the great diversity of neural network dynamics resulting from the variation of network architecture and connection strengths.

Phase shifts of oscillations in a system of two electrically coupled Fitzhugh's oscillators are studied in (Kawato et al., 1979). A stable regime of anti-phase oscillations and bistability (coexisting in-phase and anti-phase oscillations) are found.

Similar results are obtained by Cymbalyuk et al. (1994) for two electrically coupled model neurons described by Hindmarsh-Rose equations. It is shown that the system demonstrates one of the five possible dynamical regimes, depending on the value of the external polarizing current:

1) in-phase oscillations with zero phase shift;
2) anti-phase oscillations with half-period phase shift;
3) oscillations with an arbitrary fixed phase shift depending on the value of the current;
4) both in-phase and anti-phase oscillations for the same current value, where the oscillation type depends on initial conditions;
5) both in-phase and quasiperiodic oscillations for the same current value.

Ermentrout and Kopell (1994) present a learning algorithm to memorize the phase shift between oscillations in a system of two identical Wilson-Cowan oscillators. The case where the first oscillator influences on the second one through the connection between the excitatory neurons is considered. Some functional is introduced to describe the synchronization of two oscillators. The functional is used to modify the connection strength between the oscillators to increase the synchrony. The learning rule is implemented in the form of a differential equation for the connection strength. The steady state of the equation coincides with the desirable phase shift. It has been shown by Borisyuk et al. (1995) that in the case of excitatory connections the oscillators can run with the same period but some phase shift (out-of-phase oscillations). The phase shift value varies in a broad range depending on the coupling strength and other parameters of oscillators. The learning rule introduced by Ermentrout and Kopell allows step by step adaptation of the connection strength to move the phase shift to an assigned value.

There is no general theory of oscillatory neural networks in the case of more than two interacting oscillators and an arbitrary architecture of connections. Most results are related to the following important types of architectures: all-to-all (global) connections and local connections. In both cases non-trivial relations between oscillation phases can appear. For example, in a network of identical oscillators with global connections, a so-called splay-phase state can exist, when there is a constant time lag in the phase dynamics of oscillators (see, e.g., Swift et al., 1992).

Synchronization based models of attention

According to modern concepts, the information in the brain is processed on two relatively independent levels. A **low level** (associated with preattention processing) is responsible for extracting features from input stimuli and for providing simple combinations of features. At this level, the brain structures operate in parallel without preselection of input components. A **high level** (associated with attention) is responsible for forming complex representations of reality. At this level, the information fragments supplied by sensory modalities, memory, and motor components are bound into meaningful patterns that are recognized and memorized. A characteristic feature of this level is its serial form of processing. At any moment attention is focused on a portion of information that is analyzed more carefully and in greater detail than the other information available (this portion of information is said to be in the focus of attention). The attention focus then moves from one object to another with a preference for new, strong, and important stimuli.

The concept that there should be common principles of grouping the information on both levels of processing led to the application of synchronization hypothesis to explain also how the focus of attention is formed (Crick & Koch, 1990; Kryukov, 1991). The following difference has been assumed to exist between these two levels: on the low level the synchronization appears as a result of interaction between neural assemblies in the primary cortical areas, while on the higher level the synchronization is controlled by some special brain structures (the thalamus, the hippocampus, the prefrontal cortex), which participate in selective synchronization of cortical areas that should be included in the attention focus. Thus, this point of view suggests a plausible and general mechanism of parallel processing on the low level and of sequential processing on the higher level.

A model of attention is formulated in terms of an oscillatory neural network with a central element in (Kryukov, 1991). In Kryukovs model the central element is an oscillator (the so called central oscillator (CO)), which is coupled with other oscillators (the so called peripheral oscillators (PO)) by feedforward and feedback connections. Such network construction facilitates the analysis of network dynamics and interpretation of network elements in terms of brain structures. It is presumed that the septo-hippocampal region plays the role of the CO, while the POs are represented by cortical columns sensible to particular features. This concept is in line with Damasios hypotheses that the hippocampus is the vertex of a convergent zone pyramid (Damasio, 1989) and the ideas of Miller (1991) who formulated the theory of representation of information in the brain based on cortico-hippocampal interplay.

Attention is realized in the network in the form of synchronization of the CO with some POs. Those POs that work synchronously with the CO are supposed to be included in the attention focus (here synchronization implies nearly equal frequencies). The parameters of the network that control attention focus formation are coupling strengths between oscillators and natural frequencies of oscillators (the frequency becomes natural if all connections of an oscillator are cut off).

Let the set of POs be divided into two groups, namely A and B, each being activated by one of two stimuli simultaneously presented to the attention system. The following types of dynamics of the network are interesting for attention modeling:

(a) **global synchronization** of the network (this mode is attributed to the case when the attention focus includes both stimuli);

(b) **partial synchronization** of the CO and a group of POs (this mode is attributed to the case when the attention focus includes one of two competing stimuli);

(c) **no-synchronization** mode (this mode is attributed to the case when the attention focus is not formed).

For mathematical analysis, the model has been specified as a network of phase oscillators (a phase oscillator is described by a single variable, the oscillation phase). The study has been restricted by the case when natural frequencies of oscillators representing the features of a stimulus are similar to each other.

The results of the study give complete information about conditions when each of the above-mentioned types of dynamics takes place and describe possible scenarios of transition from one mode to another under the variation of some parameters (Kazanovich & Borisyuk, 1994; Kazanovich & Borisyuk, 1999; Borisyuk et al., 1999). In particular, the model shows that switching the focus of attention from one stimulus to the other goes through an intermediate state when the focus of attention is absent or when both stimuli are included in the attention focus. Another result of modeling is the formulation of conditions, when decreasing the interaction of the CO with the oscillators representing one of two stimuli that form the attention focus may lead not to focusing attention on the other stimulus but to destruction of the attention focus. For some parameter values it is found that the CO is capable of synchronizing alternately with one or the other of two groups of POs. This can be interpreted as a spontaneous switching of the attention focus which is observed in some psychological experiments.

The model of attention considered above is based on synchronization of regular oscillations. The following example shows that regularity is not an obligatory condition to obtain synchronous oscillations of neural activity, also synchronized chaotic oscillations can be generated by the networks of integrate-and-fire neurons. This gives the possibility to use chaotic oscillations in binding and attention models. An example of a neural network that combines chaotic dynamics with synchronization is presented in (Borisyuk & Borisyuk, 1997). The authors have developed a neural network of excitatory and inhibitory integrate-and-fire neurons with global connections that can show spatially coherent chaotic oscillations. A specific property of this regime is that the periods of neuron bursting activity alternate with irregular periods of silence. Moreover, the number of spikes in burst and interburst intervals varies in a broad range. Despite of the irregular, chaotic dynamics of a single neuron, the global activity of the network looks very coherent. Almost all neurons of the network fire nearly simultaneously in some short time intervals.

Conclusions

The purpose of this paper was twofold. First, we were going to show that temporal structures appearing in dynamical activity of neural network models are rich enough to properly reflect the basic neurophysiological data. Second, we aimed to show that dynamical models are helpful for checking the validity of hypotheses about the principles of information processing in the brain. In particular, the models can be used to elucidate the possible significance of temporal relations in neural activity. We demonstrated that these models are compatible with experimental data and are promising for parallel implementation of information processing.

In comparison with traditional connectionist theories, the theory of oscillatory neural networks has its own advantages and disadvantages. This theory tries to reach a better agreement with neurophysiological evidence, but this results in more complicated analysis of the models. The further progress of the theory may be achieved in the following directions.

1. Oscillatory networks with varying input signals. Most of the models developed until now restrict their consideration to the case when the input signals of oscillators are fixed. It would be much more important to study neural networks which are influenced by a time dependent stimulus (in mathematical terms, this results in the study of non-autonomous dynamical system).

2. Hierarchical oscillatory neural networks. Multilayer oscillatory neural networks with different architectures should be developed and analyzed. It seems reasonable to use for the earlier stages of information processing oscillatory neural networks with local connections which could provide the interaction of small neural assemblies similar to the interaction of pyramidal neurons in cortical columns. Convergent forward and backward connections can be used for parallel transmission of information between the layers. For later stages of information processing the networks with the central element should be used to provide the intensive information exchange between arbitrary parts of the network with a relatively small number of long-range connections. In particular, such networks are relevant to modeling the interaction between the hippocampus or the thalamus and the cortex.

3. Networks with multifrequency oscillations. Envelope (multifrequency) oscillations have not received much attention yet. We believe that envelope oscillations may be very helpful for information encoding. It is known that frequency encoding of stimuli is impeded by insufficiency of information capacity. Indeed, the range of admissible frequencies is not large, and due to relatively low resolution in the frequency domain, it may not be easy to distinguish between different frequencies. Therefore increasing the number of admissible frequencies will be helpful for weakening the limitations of frequency encoding. For example, double-frequency oscillations make it possible to extend frequency encoding, since the second frequency can play the role of a second encoding variable. Therefore, two coordinates could be used for encoding instead of one.

Besides the theory of information processing in the brain, there is another important field of applications of oscillatory neural networks. We mean the theory of artificial neural networks. After a period of intensive development, this theory seems to suffer from the reduction of the flow of new ideas. Neuroscience is a reliable and never exhausted source of such ideas. In the near future we can expect a significant progress in neurocomputing in relation to better understanding the principles of information processing in the brain.

The dream of many researchers involved in neurobiological modeling is that some day their findings will result in development of artificial neural systems with a broad spectrum of intellectual capabilities competitive with those of the living systems. This dream may soon come true. An important step in this direction would be to develop a computer system for a combined solution of the problems of binding, attention, recognition and memorization. This project is quite real now. All necessary components are known already. The current task is just to scan through the set of existing models in order to choose those which are most efficient and most compatible with the modern concepts of neuroscience and then to find a proper interaction of these models in a unified system. Many details of this interaction are known already, others should be discovered by further experimental investigations and relative mathematical and computer modeling.

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