

A Temporal Ratio Model of the Episodic Memory Organization in the ECI-Networks

V.D. Tsukerman

Academy of Biology and Biotechnology
Southern Federal University
194/1, Stachka ave., Rostov-on-Don, 344090, Russia

S.V. Kulakov

Academy of Biology and Biotechnology
Southern Federal University
194/1, Stachka ave., Rostov-on-Don, 344090, Russia

Copyright © 2015 V.D. Tsukerman and S.V. Kulakov. This article is distributed under the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Abstract

Episodic memory – multistage dynamic process with participation various types spatially active cells were found in a hippocampal-entorhinal brain system. In this paper hypothesis of possible participation in this system of the "mirror" neurons which are a neurophysiological basis of learning by imitation. Computing experiments on even cyclic inhibitory networks (ECI-networks) we show: (i) a leading role for the specific temporary patterns organization of entrance influences, as obligatory attribute formation of a response of model of execution of system of mirror neurons in an entorhinal-hippocampal network; (ii) opportunity to keep orthogonal, i.e. untied representations of patterns of entrance signals in numerous temporary scales; (iii) coding and record of episodes in memory is carried out on the ascending phase a theta wave and happens to a reverse of initial temporary sequence; (iv) a call and restoration of an initial temporary order of events in an episode comes from memory thanks to large-scale invariance near minimum a theta wave.

Keywords: Episodic memory, Entorhinal-hippocampal system, ECI-networks, Mirror neurons, Phase coding, Pattern completion, Memory storage and retrieval

1 Introduction

How and where memory is stored in the brain network is one of the fundamental questions in brain and cognitive sciences. Two widely recognized points of view connect entorhinal-hippocampal system with the solution of problems of spatial navigation and episodic memory – at first sight two various fundamental cognitive functions of a brain. However, the recent data indicate the possibility of maintaining the same neural mechanisms not only calculations of distances, positions and trajectories, but also episodic happening of events and planning the sequences of actions and aims of episodic memory [2,3]. Clear parallels between the integration of the way and episodic memory on the one hand, and allocentric navigation and semantic memory, on the other hand, indicate the possibility of maintaining them in the same networks and similar mechanisms in the physical and mental forms of travelling [11]. The recent experiments on rodents demonstrate that the sequence of the cells of a space of a new spatial experience is partially determined by a selection of a set of cellular firing sequences from a repertoire of existing temporal firing sequences in the hippocampal network [4]. It allows to consider the mental challenge of the sequential activation of neural ensembles as a hidden navigation in the existing set of episodes of the subjective experience of an individual. According to Buzsaki, the changes in the power of the synaptic connection between neurons can simply define the direction of the temporal flow of neuronal activity to activate numerous episodic memories or prediction of many possible consequences of the actions [4].

The main characteristic feature of the episodic memory is the ability to store multiple orthogonal, i.e., unlinked presentations. In the current article we have used such presentations by an example of a virtual locomotion using the navigator turns "counter" CCW and "clockwise" CW signal sequences found in any navigation behavior. Episodic memory is a multi-step dynamic process. The coding sequence of event-trigger signals, compression, pattern completion (filling the working memory), consolidation (recording into the long-term memory), storing and retrieving episodes from memory are realized in the complex interaction of neural network, cellular and subcellular mechanisms (in this article a neural network level is observed). At the same time, one of the most complex and least certain processes is connected with the organization of imitative learning (imitation). Imitation is one of the basic forms of learning, the neurophysiological basis of which is the system of "mirror" neurons, linking sensory and motor segments of the cerebral cortex that encode information about the same acts of behaviour [12]. The researches demonstrate that even the specialized system of action perception of 12-month-old children conducts preventive action aimed at the target of eye movements, providing direct support to this representation. Activation of this system requires observation of the interaction between the hand and the object of the agent [6]. The problem of studying the mirror system is more significant as those individuals suffering from autism, as it is known, display the imitation disorder, that many authors connect it with the violation of the mirror neurons work. Whether and how is the system of mirror neurons involved in

processing spatial information in the entorhinal-hippocampal system? We expect their participation in this system, as in many other researched brain systems [7]. Here we demonstrate in calculating experiments that the specific temporal organization of the patterns of input actions in ECI-networks [1, 8, 13] allows to regard them as a mandatory attribute of the formation of the response of the model execution system of mirror neurons in the entorhinal-hippocampal network, even without using in the current version models of plastic synapses.

Episodic memory traces (engrams) will be considered as the phase response curves, located and individualized, along the lines of the time continuum, retreating from the present to the past. This corresponds to the recording and the storage of information. On the contrary, retrieving the episodic sequences of event-trigger signals from memory should be implemented in reverse order to fit the original temporal sequence of the events in the episode. The line of the temporal continuum can be represented as logarithmically compressed one, in consequence of which the location of new events (objects) is easier to distinguish from each other than those in more distant past "merging" the temporary positions of the "old" events. The brain as a complex dynamic system operates in a very wide range of temporal scales from milliseconds to years. Scaling invariance is a central aspect of many models of memory and the timing tasks [10, 15, 16]. The article represents some results of our calculating experiments obtained by means of the hypothesis of free-scalable episodic memory as an adaptive response of the brain to the world around us with the structure in multiple time scales, which implies that it should not necessarily be accurate; at sacrificing accuracy in freely scalable manner it is possible to obtain predictive information from exponentially longer time scales.

2 Methods

Mathematical model for the ECI-network. Mathematical model, all of its parameters, phase and spatial representations algorithms of episodic sequences of signals in the ECI-networks are described in detail in our previous studies [10, 15, 16]. Here we observe the neurodynamic correlates of phase and spatial transformations of the following types of episodes: $\{A_1 \uparrow \text{CCW} [t_1], A_2 \downarrow \text{CCW} [T], B_1 \downarrow \text{CW} [t_2], B_2 \uparrow \text{CW}\}$, where A_1, A_2, B_1, B_2 are gradient signals input to the cell clusters network with a preferred directional setting to turn counter (CCW) and clockwise (CW); the arrows show the direction of the respective gradients; t_1 and t_2 are temporal intervals between unimodal, T is the temporal interval between signal sequences of different modalities. The new methodical approach of the current research is to establish a "mirror" representation of the directional patterns of the input signals in the neural network. Now each gradient signal of certain direction gets its mirror reflection in the network by a signal with an opposite gradient distributed among the neurons of the same preferred direction but in the following theta cycle.

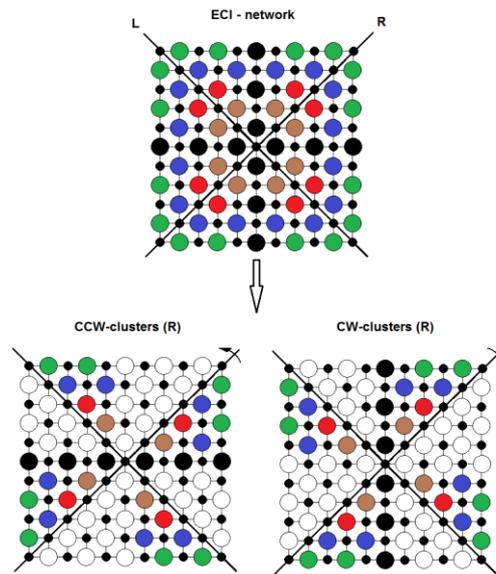


Fig. 1. Participants (structural and functional unit) of the episodic memory code:

- Freely scalable neural network (ECI-network) (at the top)
- Ensembles that combine cells with opposite directional preferences CW- and CCW- and those forming multiple rings (marked with the same colour)
- Clusters of the network cells with the opposite predominant sensitivity to rotate counter- CCW (marked with the colour, bottom left row) and in the clockwise direction CW (bottom right row)
- Groups of orthogonal boundary cells (shown as large black circles)
- Reference subnet of time cells (shown as small black circles)

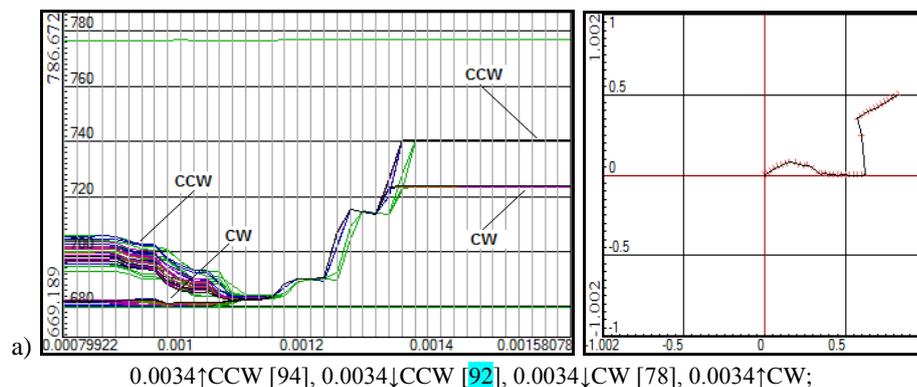
All manipulations and results in the current article are shown by the example of $CCW \rightarrow CW$ episodes where the CCW-sequence signals are the leading. Due to the symmetry of the neural organization of ECI-networks, similar conclusions work for the reverse order. We will separate the impact of external and internal factors on the formation of the episodic memory code. The external factors include: the amplitude and temporal characteristics of the patterns of the input signal sequences; the internal factors include: the context, i.e. the network status, defined by the initial conditions, the translational moving speed and the angular velocity of the virtual navigator turns. The Amplitude-phase encoding in ECI-networks implements linear (proportional) representation of signals. This means that the simultaneous arrival of the gradient signal to the ensemble cells causes a corresponding gradient phase representation of the signal amplitudes in the reference theta-cycle. In other words, the ensemble cells are represented by phase tracks shifted apart to an amount proportional to a step of the gradient.

3 Results

3.1 Dependence of the neural ensemble encoding of an episode on the temporal range between the events of the opposite direction.

Previously we have shown the frequency of the phase and spatial representations of episodes with different temporal ranges between event-trigger sequences in the ECI-network [10, 16]. Here we are going to demonstrate the multiplicity of the phase and spatial representations which depend on different temporal ranges in the input signal sequences. For clarity we are going to consider the episodes represented by the sequences of CCW \rightarrow CW-signals. This choice of the order of signals is quite arbitrary, due to the symmetry of the structural organization of neural networks.

Fig. 2a) - c) show the influence of the temporal range between the input gradient signals of the opposite direction on the ensembles of the CCW- CW-cells. Firstly, due to the independence of the representations the phase response curves of two cell populations with the opposite spatial preferences (CW and CCW) can occupy different relative positions in the reference theta-cycle. The first sequence of signals in the CCW-episode takes a certain time window in the reference theta-cycle (indicated by green horizontal lines) and a further phase encoding of the CW- signals is determined by the temporal range between both directional signal sequences. In particular, at certain values of the temporal range between them, phase representations of both ensemble types can overlap, i.e. show a strong phase synchronization and thus straighten spatial trajectory (marked in Fig. 2b). Deviation from some optimum value (marked with the turquoise-coloured caption below the figure) to one or a different direction leads to a relative phase shift of the CW-sensitive cell ensembles (Fig. 2a, 2c, on the left) and, correspondingly, to a change of the direction of the initial part of the spatial trajectory (Fig. 2a, 2c, on the right). It is also clear that the final part of the trajectory does not depend on the temporal range between the input signals of the opposite direction and is defined only by the first CCW-sequences of signals. Thus, an imbalance in one or a different direction by the temporal range between signal sequences of the opposite direction determines the initial segments of egocentric spatial trajectory (Fig. 2, on the right).



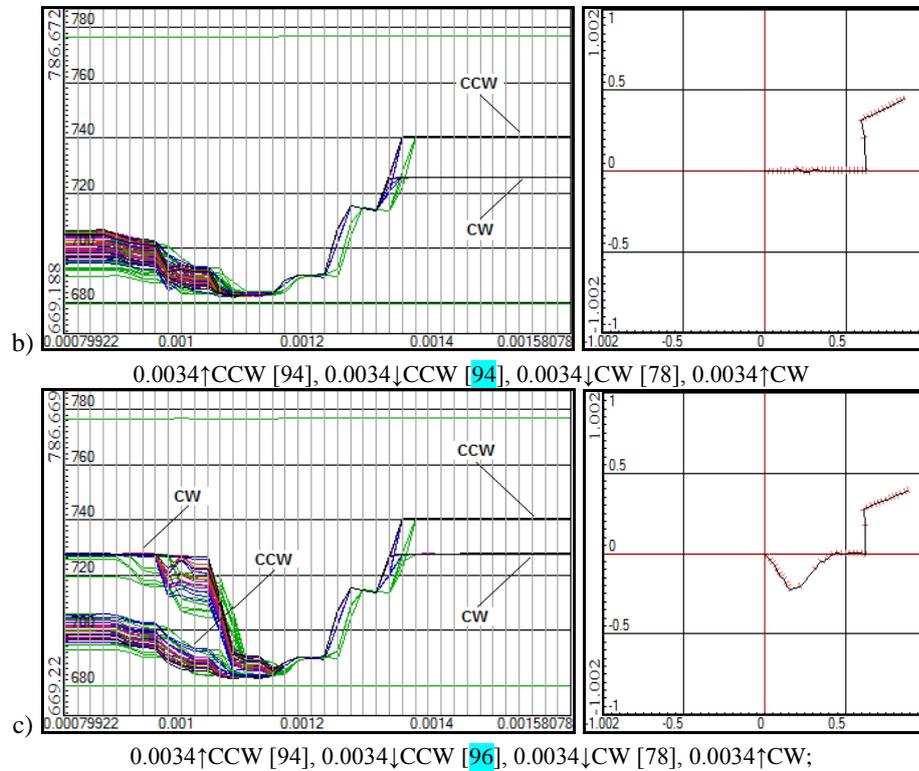


Fig.2. The influence of the temporal range between the gradient input signals of the opposite direction on the phase ensemble encoding (the left column) and the corresponding egocentric representation of the spatial trajectory (the right column) in the ECI-network. The balance between ensembles with the opposite directional preferences is determined by some optimal value of the temporal range between them, in which there is a strong overlap of the phase track neural ensembles of both directions (Fig. 2b, on the left). It is clearly seen that the initial conditions of the egocentric spatial trajectory integration (its initial part) are determined by population phase ensemble shifts of the opposite direction (Fig. 2, the right column).

This suggests that the target direction of the spatial trajectory is strongly influenced by the initial signal sequence in the episode (in the current case, CCW-signal).

3.2 Dependency of the neural ensemble encoding of an episode on the last temporal range.

Here we are going to demonstrate that the change of the last temporal range in the episode also has a strong influence on the target direction of the final part of the spatial trajectory. In order to do this, we fix the temporal range between signal pattern sequences of the opposite direction and will change the last temporal range in the episode. In Fig. 3 it can be seen that the variation of the last intermediate event-trigger temporal range leads to two extremes: from the strong relative phase ensemble deviation of the opposite direction (Fig. 3a, on the left) to their strong phase synchronization (Fig. 3c, on the left).

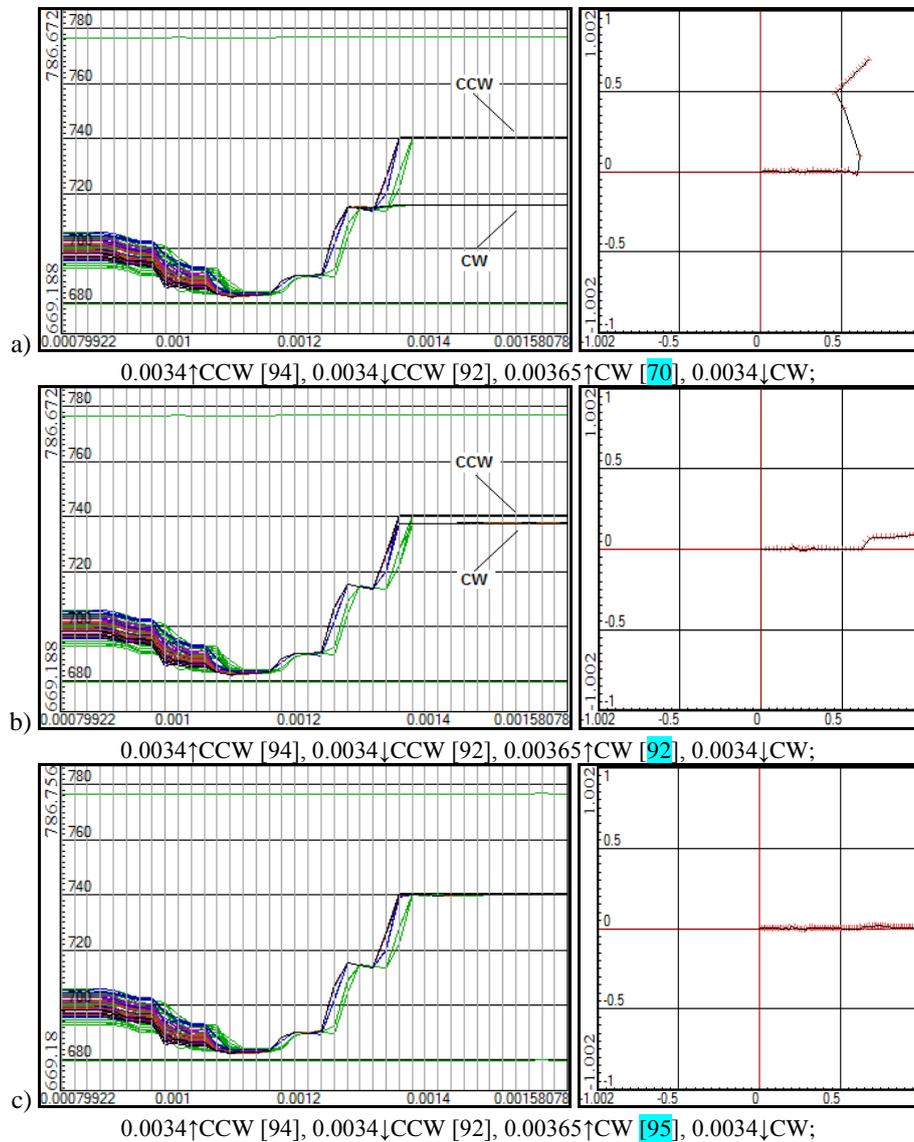


Fig. 3. Experiments with varying of the last intermediate event-trigger temporal range in the episode (variable values are marked with the turquoise-coloured caption below the figures). In this case, there is the previous "optimal" value of the temporal range recorded between the input signals of the opposite direction in which the phase tracks of both ensemble types are showing a strong overlap. In the right part of the same graphs it is seen that there is a strong phase shift of the differently directed CCW and CW cell ensembles.

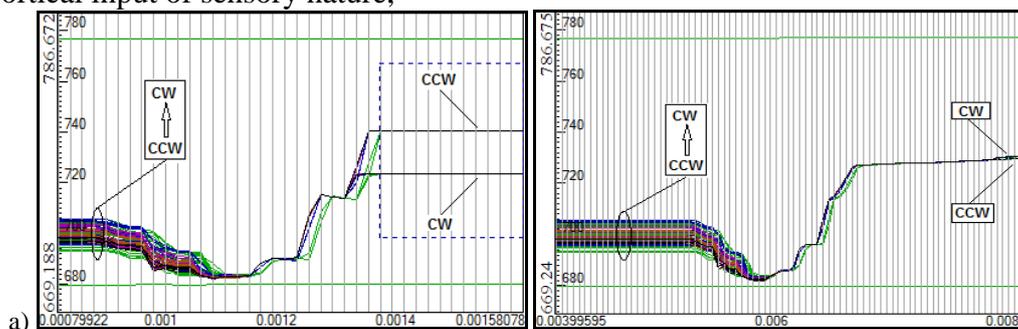
The results of this series of experiments clearly show the characteristic features of the observed process of the event encoding: a) high compression of the ensemble phase representations of the CW- and CCW-signals in the phase code represented in the reference theta-cycle, and b) a strong dependence of the target final part of the egocentric spatial trajectory on the last temporal range in the original episodic

sequence (Fig. 3, the right column). Increasing of the internal temporal range in a certain value range leads to a dense phase synchronization of the neuron ensembles with opposite sensitivity (Fig. 3c).

3.3 Encoding, recording into the working memory and retrieving of neural representations of the episode in a freely-scalable manner.

For several years we have been developing the idea of the schematic organization of neurons as freely-scalable oscillatory networks with the even cyclical deceleration (ECI-networks). In the computer numerical simulation of these networks of small dimension (up to 300 units), we demonstrated many famous phenomena found in studies of spatial navigation under the control of the entorhinal-hippocampal brain systems [9, 13, 14]. On the other hand, as it has been mentioned in the introduction, the other function of this system consists of forming the working memory, the encoding and recording as well as the memory retrieving of a subject. Here we are going to demonstrate the implementation of these processes in the neural network by an example of a particular episode (Fig. 4). The left column in Figure 4 represents the phase encoding and recording tracks of the current episode with one of the main features – recording into the memory, namely, with a reverse of phase tracks. In other words, at the recording into the memory the temporal order of signal sequence changes into reversed, i.e., as a result of reverse, CW-signal sequences become the leading in the sequential phase memory code. Accordingly, CCW-sequences take places later in the reference theta-cycle (Fig. 4, the left column). As it can be seen in the given figure, this temporal order is stored in a wide range of values of the context input, and consequently in many spatial and temporal scales. What is the idea of encoding and recording episodes in oscillatory networks?

Earlier studies of rodent navigation suggest that the two processes are preferably incorporated into the individual phases of the theta-wave: the recording on the rising phase of the wave is close to the wave maximum, and the reading from the memory is at a descending phase, close to the minimum of the theta-wave. Signals are transmitted from the neocortex to the hippocampus, to return back to the neocortex after processing. Theta-rhythm is probably the timer of this process with the "reset" and the relative silence at the peak of each theta-wave, which allows a new cycle of encoding and retrieving to occur [8, 9, 14]. The activity at the beginning of the theta-cycle at the descending phase reflects the cortical input of sensory nature,



Recording: [268-273], amplitude range [0.0008-0.0016]. Retrieving: [240-245], amplitude (0.004-0.008).

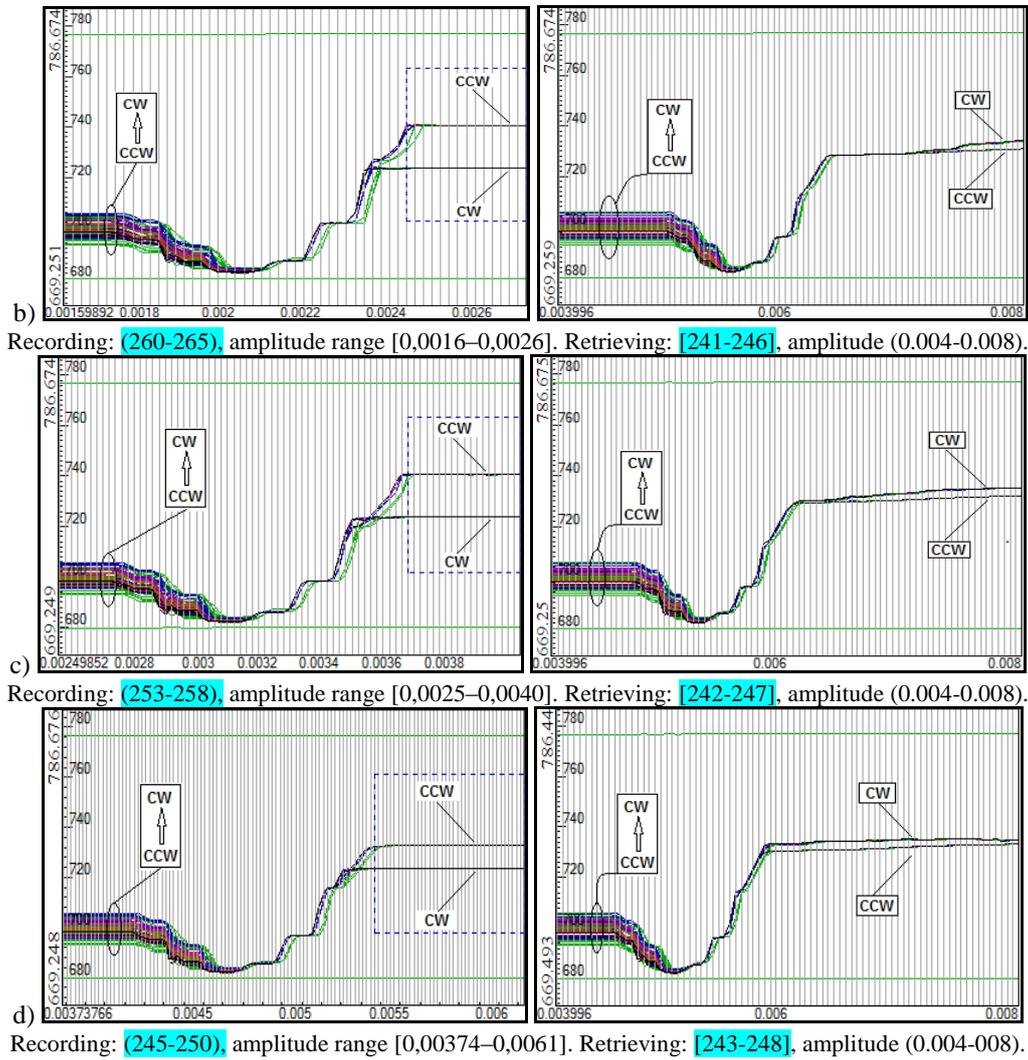


Fig. 4. The encoding and recording into the working memory of multiscale episode representations $\{0.0034\uparrow\text{CCW}$ [94], $0.0034\downarrow\text{CCW}$ [92], $0.00365\uparrow\text{CW}$ [78], $0.0034\downarrow\text{CW}$ (Fig. 4, the left column) and retrieving it from memory (Fig. 4, the right column). The encoding and recording of the episode in the working memory are implemented continuously in a wide range of time scales. Furthermore, on recording into the memory there is a reverse of signal sequence of different orientation taking place (marked with dotted line in the left column). The retrieving of phase tracks from memory (Fig. 4, right column) is characterized by two features: i) the original sequence of event sequences is recovering in the time scale of the reference theta-cycle, namely, CCW and then CW; ii) the retrieving from memory is implemented in a time window at the descending of the theta-wave close to its minimum. The settings of the recording of signal sequences into the memory and retrieving them from memory stated under the figures mean the following: The time window of the recording (268-273), the range of amplitudes [0,0008-0,0016]. The retrieving from the memory was implemented with a signal in the time window [240-245] in the range of amplitudes (0,004-0,008). Similarly, all the other graphs are represented. The step of the context input of the translational speed in all charts is marked with vertical lines and is 2×10^{-5} .

which depends on the location of the navigator, but due to delays associated with the transmission of signals through multiple areas of the brain, it is correlated better with the position of the animal that has recently been in the past. By the end of the theta-cycle (at the increasing phase), the output activity of the hippocampal area CA1 predicts the position, which is going to be in the near future, i.e., it is predicting [9]. This allows to fill in the working memory with subsequent arrivals of environmental signals until the absolute pattern-completion of the working memory, which has a limited volume.

Due to the scale invariance of the system, encoding and recording into the episodic memory can be carried out in *multiple temporal scales*, which is evidenced by a shifting window along the time axis of the system and the reverse in the order of events in the episode (Fig. 4, the left column). The implementation in a neural network of a scale-invariant representation of the temporal history is not a trivial calculating problem. This problem is related to the task of creating a sequential time representation, having a property of *self-similarity in the short and long time scales*. To retrieve an episode from memory it requires a continuous temporal extension, accompanied with the integration of contextual input signals in the network (energy accumulation in the system) and, as a consequence, *restoring of the original time sequence* of events in the intermediate time scales (Fig. 4, the right column).

4 Discussion of results and conclusions

The main property of the episodic memory consists in linking disparate and often independent events together into a coherent sequence and a recollection of self-centered past experiences of the individual in the context of time and space in which the events occurred. [17] Here, by simple examples of two independent sequences of event-trigger CCW- and CW-signals in the context of specific spatio-temporal relations, we have demonstrated the formation and storage of episodes in working spatial memory. It was based on the hypothesis of scaled invariance of the spatio-temporal memory context. There have been shown the evidences of the possible coding and recording of multiscale episode representations, as well as retrieving of this episode from memory (Fig. 4).

It has been demonstrated that the crucial factor mediating all operations in the neural network is a temporal organization of input signal patterns where each input gradient signal has its mirror reflection in the next theta-cycle with a reverse gradient. The episode formation in the working memory happens due to the sequential binding of orthogonal CW- and CCW-signal sequences undergoing multiple temporal compression in the reference theta-cycle. The extended tracks of episodic memory are formed as they are have been filled (pattern completion) due to segmented sets of theta-cycles in different neural network ensembles. Summing up the simulation, it is possible to draw the following conclusions:

- 1) The two processes are integrated into separate phases of the theta-wave and define: recording in the ascending phase close to the wave maximum and reading

from memory in the descending phase close to the minimum of the theta-wave. This structuring of the theta-cycle makes it possible to avoid the interference of the encoded and retrieved information from the working memory.

2) The traces of the phase memory representations of the directional ensembles get reversed temporal order in theta-cycle. Reading the code makes it possible to restore the temporal order of sequences of events.

3) Target egocentric spatial representation of the trajectory is determined by a combination of the temporal ranges between the signals of the opposite direction and the last temporal range in the initial episode.

4) Schematic neuronal organization shown by the example of the ECI-networks, allows to implement multiple time sequences of cell ensembles which are the basis of the mental travelling of the neural system involved in navigation.

In the following experiments it is necessary to explore the formation of tracks of the memory episodes consisting of longer signal sequences of different directions and retrieving of specific episodes from the long-term memory.

References

- [1] G.D. Brown, I. Neath, N. Chater, A temporal ratio model of memory, *Psych. Review*, **114** (2007), 539 - 576. <http://dx.doi.org/10.1037/0033-295x.114.3.539>
- [2] G. Buzsáki, E.I. Moser, Memory, navigation and theta rhythm in the hippocampal-entorhinal system, *Nature Neuroscience*, **16** (2013), 130 - 138. <http://dx.doi.org/10.1038/nn.3304>
- [3] G. Buzsáki, Cognitive neuroscience: Time, space and memory, *Nature*, **497** (2013), 568 - 569. <http://dx.doi.org/10.1038/497568a>
- [4] G. Dragoi, S. Tonegawa, Selection of preconfigured cell assemblies for representation of novel spatial experiences, *Philosophical Transactions of the Royal Society B: Biological Sciences*, **369** (2014), 20120522. <http://dx.doi.org/10.1098/rstb.2012.0522>
- [5] T. Falck-Ytter, G. Gredebäck, C. von Hofsten, Infants predict other people's action goals, *Nature Neuroscience*, **9** (2006), 878 - 879. <http://dx.doi.org/10.1038/nn1729>
- [6] M. Fabbri-Destro, G. Rizzolatti, Mirror neurons and mirror systems in monkeys and humans, *Physiology*, **23** (2008), 171 - 179. <http://dx.doi.org/10.1152/physiol.00004.2008>
- [7] C.R. Gallistel, J. Gibbon, Time, rate, and conditioning, *Psych. Review*, **107** (2000), 289 - 344. <http://dx.doi.org/10.1037//0033-295x.107.2.289>

- [8] M.E. Hasselmo, What is the function of hippocampal theta rhythm?—Linking behavioral data to phasic properties of field potential and unit recording data, *Hippocampus*, **15** (2005), 936 - 949. <http://dx.doi.org/10.1002/hipo.20116>
- [9] V. Itskov, E. Pastalkova, K. Mizuseki, G. Buzsáki, K.D. Harris, Theta-mediated dynamics of spatial information in hippocampus, *Journal of Neuroscience*, **28** (2008), 5959 - 5964. <http://dx.doi.org/10.1523/jneurosci.5262-07.2008>
- [10] Z.S. Kharybina, V.D. Tsukerman, S.V. Kulakov, Mathematical model of the microcircuit organization of freely scalable ECI-network as a former of spatial processing in hippocampal-entorhinal brain system, *Applied Mathematical Sciences*, **8** (2014), 549 - 572. <http://dx.doi.org/10.12988/ams.2014.312681>
- [11] E. Pastalkova, V. Itskov, A. Amarasingham, G. Buzsaki, Internally generated cell assembly sequences in the rat hippocampus, *Science*, **321** (2008), 1322 - 1327. <http://dx.doi.org/10.1126/science.1159775>
- [12] G. Rizzolatti, L. Craighero, The mirror-neuron system, *Annu. Rev. Neurosci.*, **27** (2004), 169 - 192. <http://dx.doi.org/10.1146/annurev.neuro.27.070203.144230>
- [13] K.H. Shankar, M.W. Howard, A scale-invariant internal representation of time, *Neural Computation*, **24** (2012), 134 - 193. http://dx.doi.org/10.1162/neco_a_00212
- [14] J.H. Siegle, M.A. Wilson, Enhancement of encoding and retrieval functions through theta phase-specific manipulation of hippocampus, *eLife*, **3** (2014), e03061, 1 - 18. <http://dx.doi.org/10.7554/elife.03061>
- [15] V.D. Tsukerman, Z.S. Jeremenko, O.V. Karimova, S.V. Kulakov, A.A. Sazikin, Mathematical model of spatial encoding in hippocampal formation. I. Grid cells neurodynamics, *Mathematical biology and bioinformatics*, **7** (2012), 206 - 243. (in Russian) <http://dx.doi.org/10.17537/2012.7.206>
- [16] V.D. Tsukerman, Z.S. Kharybina, S.V. Kulakov, Mathematical model of spatial encoding in hippocampal formation. II. Neurodynamic correlates for mental trajectories and decision-making problem, *Mathematical biology and bioinformatics*, **9** (2014), 216 - 256. (in Russ.). <http://dx.doi.org/10.17537/2014.9.216>
- [17] E. Tulving, Chronesthesia: conscious awareness of subjective time, In: *Principles of Frontal Lobe Function*, (eds. D.T. Stuss, R.C. Knight), 311 - 325, Oxford Univ. Press, New York, 2002. <http://dx.doi.org/10.1093/acprof:oso/9780195134971.003.0020>

Received: August 4, 2015; Published: September 9, 2015