

A Model of Navigation in a Complex Maze Inspired by Hippocampus

M. Bures, M. Jirina, *Czech Technical University in Prague, Czech Republic*

Abstract – A model of navigation inspired by rodent hippocampus stores several navigational maps in a single attractor (Hopfield-like) neural network. Hippocampus is a part of brain involved in spatial orientation. It models such phenomena as place cells, long-term potentiation, long-term depression, path integration, inhibitory interneurons etc. Structure of the model conforms to functional schema of hippocampal formation. In order to validate the model we've developed a spatial task within a complex maze: an animat has to follow a complex trajectory passing gateways between chambers and avoiding barriers. We compare the model to hippocampus and we discuss simplifications we've committed.

I INTRODUCTION

Spatial navigation or rodents is a subject of intensive research. Moreover, artificial models – animats – have been introduced as well. As a result of our preceding research we published a model [4] of navigation within a single environment inspired by Morris water maze [9]. Herein we remain in line with our previous work and we propose a model of navigation within a maze of several chambers. We introduce a biologically inspired method of storing several navigational maps in a single artificial neural network.

II HIPPOCAMPUS – BIOLOGICAL BACKGROUND

Hippocampus plays a central role in navigation, especially in memory formation and recall. An indication that hippocampus maintains a spatial information was described in [12]. Responsibilities of rat hippocampus for spatial memory have been found out on experiments [13], [9], or [3].

Hippocampal place cells [10] fire when a rat appears in a corresponding place of environment, referred to as a place field. Their firing doesn't depend on rat's heading in open arenas, though directional dependency is observable in radial mazes. It is neither dependent on rat's intention [19]. A place field, in some environment, has around 30% of neurons located in the hippocampus proper. In an arbitrary position, around 1% of hippocampal cells are active [17]. Place cells are implemented by extensive network of pyramidal cells and inhibitory interneurons in regions CA3-CA1 of hippocampus. Activity of the place cells persist even in dark [11]. Their

Manuscript received September 4th, 2006. This research has been supported by projects CTU0607513 "Knowledge Mining for Modeling of Cognitive Processes" and IET101210513 "Information Society".

M Bures is with the Gerstner Laboratory, Department of Cybernetics, Czech Technical University in Prague, Karlovo náměstí 13, 121 35, Prague 2, Czech Rep. (phone: +420 224 357 666; fax +420 224 357 666; email: buresm2@fel.cvut.cz; web: <http://gerstner.felk.cvut.cz/>).

M. Jirina is with the Faculty of Biomedical Engineering, Czech Technical University in Prague (email: jirina@fbmi.cvut.cz; web: <http://www.fbmi.cvut.cz/>).

activity is discoverable just after entering a novel environment [17]. Place fields of a place cell in distinct environments aren't correlative [17] – there is no algorithm to predict a place field in a novel environment, even if place fields from other environments are known. Changes such as scaling the environment result in a partial remapping of place cells [10]. Remappings are observed when a barrier is placed onto the floor. Cells near the barrier have their discharging suppressed whereas others remain.

On the other hand, activity of head-direction (HD) cells [20] is tuned by heading of the animal. The HD neuron discharges only when the animal is heading in neuron's preferred direction, regardless of the animal's location. HD cell's activity spans 100° [21].

Recently, grid cells [6] were discovered in 2005. They are posed in medial entorhinal cortex, one synapse upstream of the place cells. A grid cell fires strongly when an animal is in specific locations in an environment. In contrast to a hippocampal place cell, a grid cell has multiple firing fields with regular spacing.

From behavioral studies it is clear that animals involve path integration [8], namely the dead-reckoning method. However, its exact location in the brain is not clear. Animals process signals coming from vestibular system (providing information about both straight-lined and angular acceleration), from receptors in muscles (registering changes of distinct parts of the body) and from brain motor cortex (it is supposed to send copies of motion signals).

Mechanisms that underlay learning in long-term memory are long-term potentiation (LTP) and long-term depression (LTD) in conjunction with theta precession [14]. LTP is believed to contribute to synaptic plasticity in living animals, providing the foundation for an adaptable nervous system.

III MODEL

A Spatial Task

The world our animat has to move through is a maze of several chambers. There are narrow gateways between certain chambers. Each chamber contains several cues distinguishable by symbols. In order to recognize current chamber and its location in it, the animat detects position of all cues in the chamber. Whereas the set of cue symbols is the same in each chamber, animat can distinguish individual chambers by standing (distances, order etc.) or appearance of the cues. Every symbol appears at most once in a chamber.

Animat describes each chamber by a separate chart. All charts are stored in a single attractor neural network. After entering a familiar chamber the animat recalls the corresponding chart and detect position in it. This is based on the sensory inputs and path integration.

B Design

Structure of the model (fig. 1) conforms to functional schema of hippocampal formation. Each subsystem consists of an artificial neural network. Sensory inputs (SI) gather and process allothetic information from the environment. Position recognition (PR) subsystem detects actual animat's position and selects appropriate map. Position of the animat is coded by both head direction (HD) system and place cells (PC). The path integrator (PI) updates supposed location during locomotion. Navigational maps (NM) of chambers are being developed during learning phase. Reading in the current map is role of the locomotion control (LC) subsystem. It sends motor (Mo) signals that are also received by the PI and HD subsystems. NM is the only plastic subsystem modified by the learning process, whereas the others are pre-wired.

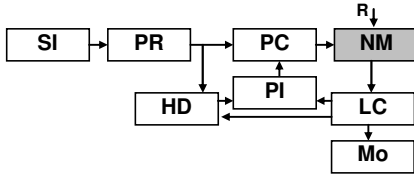


Fig. 1. Structure of the model: sensory inputs (SI), position recognition (PR), head direction (HD), place cells (PC), path integrator (PI), navigational maps (NM), learning signal (R), locomotion control (LC) and motor (Mo).

C Allothetic Inputs

Allothetic sensory inputs (SI) detect position of environmental cues relative to the animat. We pose several point cues [15] inside the maze. Neither chamber boundaries nor any other objects in the environment are detected.

We simulate SI by a pre-wired one-layer RBF neural network. Activity of SI neurons is given by distance of the cue from the animat

$$A_i^R = e^{-\frac{(R_i - R)^2}{2R_\sigma^2}}, \quad (1)$$

where R_i is nominal distance of SI distance-sensitive neurons, R represent current distance of the cue from the animat and R_σ govern dispersion of elements of the RBF network.

For each cue symbol, a separate group of SI neurons exists. All cues in the current chamber are detected by the animat simultaneously, regardless of their position or direction of the animat's heading. Cues in other chambers are invisible for the animat. A similar highly processed signal is supposed to enter the rodent's hippocampus [15].

D Head Direction System

The resulting activity of the HD cells is given by

$$A_i^{HD}(t) = e^{K_{HD}(\cos(\theta - \theta_i) - 1)}, \quad (2)$$

where θ is animat's heading, θ_i is preferred direction of HD cell i and K_{HD} governs amount of active HD cells. It should be chosen with respect to fact that every. We focused on this subsystem in detail in our previous work [4].

E Place Cells

We simulate the hippocampal place cells (PC) as a pre-wired attractor neural network consisting of several charts. In each chart, each place cell has its own place field. The closer place fields of two place cells in a particular chart the stronger linkage between the two cells. Distant cells have no linkage between each other.

Partial weights between PC for each chart c are

$$w_{i,j;c}^{PC} = g(\text{dist}(\mathbf{X}_{i;c}, \mathbf{X}_{j;c})), \quad i \neq j \quad (3)$$

$$w_{i,i;c}^{PC} = 0$$

where $\mathbf{X}_{i;c}$ and $\mathbf{X}_{j;c}$ are place field centers of neurons i and j in chart c and $\text{dist}(\cdot)$ computes Euclidean distance.

The last term in (3) is a distribution weight function $g(\cdot)$. It links two neurons the strongly the place fields are closer. For more distant place fields, we request a nearly zero link. We've chosen a simple Gaussian-like function. However, one could use a linear function with saturations as well.

Place fields of a single place cell in different charts don't correlate. Synaptic weights between two place cells are given as a summary of all partial weights values in each chart (C is the number of charts):

$$w_{i,j}^{PC} = \sum_{c=1}^C w_{i,j;c}^{PC}, \quad (4)$$

The attractor network maintains an activity packet, a set of place cells with close place field that fire altogether, selecting a single chart as being active. Calculations of the maximal number of stored uncorrelated spherical attractor charts in a Hopfield-like network give the number of $0.0042 \times N_{PC}$ [16].

The output of the PC subsystem is given by

$$\mathbf{A}^{PC}(t+1) = \sigma \left(\frac{K_{PC} \cdot (\mathbf{W}^{PC} + \mathbf{W}^{PI}(t)) \cdot (\mathbf{A}^{PC}(t) + \mathbf{V}^{PC}(t))}{\frac{1}{N_{PC} \cdot C} \sum (\mathbf{W}^{PC} + \mathbf{W}^{PI}(t)) \cdot (\mathbf{A}^{PC}(t) + \mathbf{V}^{PC}(t))} \right), \quad (5)$$

where $\sigma(\cdot)$ is a sigmoid function discussed later, \mathbf{W}^{PC} is a synaptic matrix of the PC subsystem, \mathbf{V}^{PC} represents influence of the PR (and is mostly zero) and parameter K_{PC} works similar as a gain in a loop-back system. $\mathbf{W}^{PI}(t)$ is path integrator modulation matrix (10). It's zero when the animat isn't moving. We shall discuss it further.

The equation (5) provides a simple mechanism to control activity of the network: whenever the activity of the network becomes higher, the denominator of (5) becomes high as well and it causes attenuation in the network, and vice versa. It simulates role of inhibitory interneurons.

We have found a value of the parameter K_{PC} as a minimum of quadratic norm of difference between several (n_c) iterations of the network:

$$K_{PC} = \arg \min_{K_{PC}} \left\| \mathbf{A}^{PC}(t) - \mathbf{A}^{PC}(t + n_c) \right\|_2, \quad (6)$$

We use a modified sigmoid function $\sigma(\cdot)$ similar to that presented in [21]:

$$\sigma(x) = \ln\left(1 + \frac{e^{x-b}}{a}\right), \quad (7)$$

This function shows a better accordance of the resulting activity to experimental data than in case when using usual sigmoid or hyperbolic functions.

F Path Integrator

Whereas PC store animat's supposed position, the path integrator (PI) moves animat's supposed position with respect to locomotion signals. The animat updates its supposed position in a chamber without processing any sensory information for a limited time period, because it would be a time-consuming operation. After elapsing a period of time or entering another chamber the animat corrects differences between real and supposed positions. That time the sensory information is being processed.

PI consists of four pre-wired matrices \mathbf{W}^{PI-N} , \mathbf{W}^{PI-S} , \mathbf{W}^{PI-E} and \mathbf{W}^{PI-W} to move the coded location to the four cardinal points. As in case of PC, we have partial weights values for each chart

$$\begin{aligned} w_{i,j;c}^{PI-N,S,E,W} &= g(\text{dist}(\mathbf{X}_{i;c}, \mathbf{X}_{j;c} + \mathbf{B}_c^{N,S,E,W})) - w_{i,j;c}^{PC}, \quad i \neq j; \\ w_{i,i;c}^{PI-N,S,E,W} &= 0 \end{aligned} \quad (8)$$

and the resulting synaptic weights are given by a sum

$$w_{i,j}^{PI-N,S,E,W} = \sum_{c=1}^C w_{i,j;c}^{PI-N,S,E,W}, \quad (9)$$

Symbols $\mathbf{B}_c^{N,S,E,W}$ represent unit vectors in directions of the cardinal points with respect to the particular chart.

In fact, we model PI as a modulation of synapses between place cells. The path integrator modulation matrix $\mathbf{W}^{PI}(t)$ is defined as

$$\mathbf{W}^{PI}(t) = v_S(t)\mathbf{W}^S + v_J(t)\mathbf{W}^J + v_V(t)\mathbf{W}^V + v_Z(t)\mathbf{W}^Z, \quad (10)$$

where $v_{N,S,E,W}(t)$ are animat's velocity components:

$$\begin{aligned} v_N &= \max(0, \sin(\theta)), \quad v_S = \max(0, -\sin(\theta)), \\ v_E &= \max(0, \cos(\theta)), \quad v_W = \max(0, -\cos(\theta)), \end{aligned} \quad (11)$$

where θ is animat's heading. Animat's speed is constant. Synapses between HD and PI select one or two PI groups. This mechanism shifts the supposed position to any direction. Activity of PI cells is triggered by motor (Mo) signals.

G Navigational Map and Locomotion Control

The navigational map (NM) is built upon the PC during the learning phase. Consider two grids of neurons. The first is the formerly presented PC system. The second is a duplicate of the first one where the map will emerge. Initially, the

neurons in the latter grid code actual animat's location, as the PCs do. During the learning phase the position coded by the NM grid shifts in sense of the learned trajectory. Hence, difference between PC and NM determines learned direction.

The learning process is based on the long-term potentiation (LTP) and long-term depression (LTD) [14]. Each step, we compute a potential of every NM cell as

$$\begin{aligned} P_i^{NM}(t) &= \max(A_i^{NM}(t), k_{d-NM} \cdot P_i^{NM}(t-1)), \quad (12) \\ P_i^{NM}(0) &= 0 \end{aligned}$$

where k_{d-NM} is the decay factor in range 0 to 1, and $A^{NM}(t)$ is an activity of the NM-cells.

Whereas the PC-to-PC synapses \mathbf{W}^{PC} remain fixed, the NM-to-NM synapses \mathbf{W}^{NM} change during the learning as

$$\Delta w_{i,j}^{NM} = r(t) \cdot A_i^{NM}(t) \cdot A_j^{NM}(t) \cdot \max(-\beta, \text{sign}(A_i^{NM}(t) - A_j^{NM}(t))), \quad (13)$$

Let i is an index of the postsynaptic cell and j index of the presynaptic one. Change of the synapse between two NM cells is proportional to the potentials of each cell. If the potential of the presynaptic cell is bigger then the potential of the postsynaptic one, the synapse reinforces. It happens as the presynaptic cell fires sooner then the postsynaptic one. In reverse case, the synapse weakens, but this influence is β -times smaller (we choose values of the β parameter in range 0 to 1). This parameter is more comprehensively discussed in [2]. The first term in (13) is a function $r(t)$ – the learning signal. The learning process described above is proceeding only in case of the non-zero $r(t)$. The signal is has a positive value during the learning phase.

Locomotion control (LC) subsystem decodes the NM. Direction of the next animat's step is computed by comparing NM cells activity with PC activity. If NM is learned enough, both activities significantly differ and right movement direction can be determined; animat is exploiting its NM. If both subsystems coincide, the map is not suitable for the navigation and animat's direction remains unchanged so that exploration is performed.

H Place recognition

As with the experiments held on living animals and with respect to our previous model [4], we expect the animat to get around a familiar environment. Hence, we simulate the exploration phase by pre-learning synapses from SI downstream to PC. We iteratively pose the animat to places in chambers and update the synapses as

$$\Delta w_{i,j}^{V-PC} = A_i^{PC} \cdot A_j^{SI} - r_d \cdot w_{i,j}^{V-PC} \cdot A_j^{SI} \cdot (1 - A_i^{PC}), \quad (14)$$

where A^{SI} is output from SI and r_d is decay factor. When animat is familiar with the environment, PR output is

$$\mathbf{V}_{PI} = \sigma \left(K_{V-PC} \frac{\mathbf{W}^{V-PI} \cdot \mathbf{A}^{SI}}{\frac{1}{N_{PC}} \sum (\mathbf{W}^{V-PI} \cdot \mathbf{A}^{SI})} \right). \quad (15)$$

IV EXPERIMENTS AND RESULTS

A Experimental Setup

Our system contained in sum nearly 10.000 neurons. We modeled SI by creating 16 distance-sensitive neurons for each of the 4 different cue symbols. The cues marked as A, B, C and D were posed in the corners of each chamber. The HD system was simulated by $N_{HD}=100$ neurons. PC formed a grid 40×40 neurons ($N_{PC}=1600$) containing $C=4$ charts (even if theoretical capacity should be $C \sim 6$). The largest part, PI, consisted of $4 \times N_{PC} = 6400$ neurons. N_{PC} (1600) neurons were also used for PR. Additional neurons were used for LC, activity control of the network etc.

For function $\sigma(\cdot)$ defined by equation (7) following parameters were chosen: threshold $b=0.3$ and $a = \ln(e^1 - 1) / (1 - b) = 0.7733$ for normalization $\sigma(1)=1$ and $\sigma(0) \approx 0$. We set other parameter values to $K_{HD}=8.1$, $K_{PC}=0.039$, $\beta=0.7$, $k_{d-NM}=0.7$, $K_{V-PC}=0.11$ and $r_d=0.01$.

The place cells were mapped to an area of 120×120 units. Nominal distances of SI cells were $R_i = (0; 2; 4; 8; 12; 20; 30; 40; 50; 60; 70; 80; 90; 100; 110; 120; 140)$ and dispersion $R_\sigma = 10$. Speed of the animat was constant $v=3$ units.

B Place Recognition and Place Cells

An activity packet should emerge after entering a familiar environment in the map corresponding to the chamber it has been mapped to during exploration. In other words, after placing the animat to an arbitrary position in a chamber, it should recognize its position within the chamber as well as the actual chamber it has been placed in.

We arbitrarily placed the animat into a chamber and waited a number of iterations of the (5) till the activity packet remained stable. We discovered that 10 iterations were enough to stabilize the activity packet. During 100 trials, the animat didn't ever miss the chamber and mean square error of estimates of its position was 4.1 units.

Further, we compared shapes of activity packets emerged in networks with one and more maps stored in it. You can look through the results at fig. 2. Although the activity packet emerged in a multi-chart PC subsystem was a bit rustled, its shape was evident.

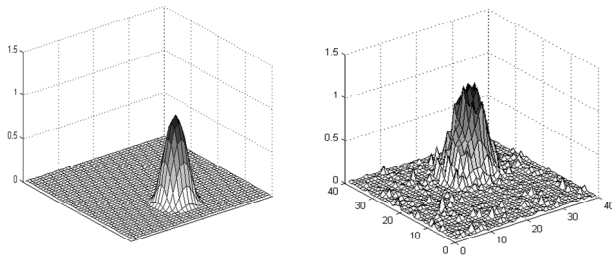


Fig. 2. Activity packets emerged in PC subsystem with a single chart (upper), with $C=4$ charts as in other experiments (bottom).

C Spatial Task

In order to validate our model, we developed a simple spatial task (fig. 3). The animat has followed a trajectory introduced by a teacher during a learning phase and it is supposed to recall the trajectory by its own. The trajectory

goes through several chambers passing the gateways between them and avoiding obstacles in them.

Two of resulting spatial maps are drawn at fig. 4 together with the trajectories passed within the chambers. As you can see the maps don't interfere with each other. Moreover, the map not mapped to any chamber (fig. 5) remained still pure and ready to learn. No consistent trajectory was written there.

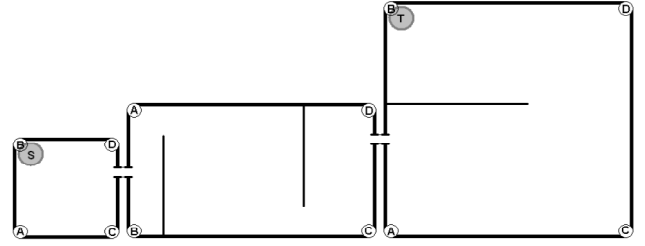


Fig. 3. The maze consisted of 3 chambers interconnected by gateways. The chambers were distinguishable by its size and posing of the cues. Barriers were present in some chambers.

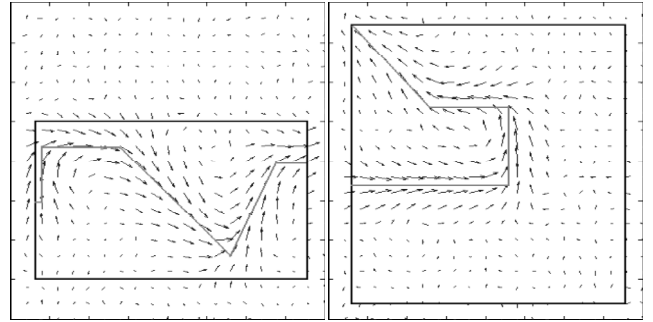


Fig. 4. Trajectories passed with a teacher during learning phase (gray line) within the chambers (black rectangles denote boundaries of the chambers) and resulting spatial maps (arrows): the middle chamber (left map), the last chamber (right map). Arrows point towards coded direction and their size is proportional to relative strength of information within the chart.

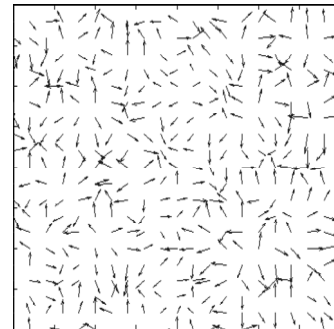


Fig. 5. A pure map not influenced by learning. As in fig. 4, arrows point towards coded direction. No useful information is coded in the map.

V CONCLUSION

We have presented a bio-inspired model of navigation capable to operate in a maze of several chambers. We have shown that our attractor neural network is capable to store a number of independent charts. Moreover, the charts may be interconnected by gateways so that the animat can proceed from one to another.

The algorithm is both robust and efficient: whereas it stores more maps into a single network, the information is coded by an ensemble of neurons so that a failure of a single cell does not cause any vitiation of the stored map.

A Conjunction to Biology

We come out from a biological inspiration of rodents' hippocampus. As our PC subsystem, hippocampus is considered to be a pre-wired neural network with many recurrent synapses. In contrast to our model, place cells in the brain are not posed intentionally to their respective place fields. Instead, the place fields of the place cells in the brain emerge spontaneously after entering a novel environment.

The model implements building blocks expected to be presented in neural circuits of animals' hippocampal formation. It models such phenomena as place cells or the path integrator. Sensory information consisting of distance of the spatial cues is also modeled by biologically plausible way – both animals and humans use egocentric-bearing related information for navigation [18].

The synapses between place cells in our model change neither during the learning phase nor during the recalls. Though they probably do change – remapping of place cells is an argument for it. However, we didn't model phenomenon of place cells remapping, so there is a potential for a further research.

Our regulation mechanism of neural activity in PC subsystem (5) is biologically implausible. Inhibitory interneurons should be modeled rather by a set of inhibitory cells to be likewise to real brain circuits.

Our model consists of 10.000-odd neurons. It is about fifty times less than rodents' hippocampus is suggested to contain. On the other hand, this is a result of computational demands. Note that over three quarters of neurons falls on path integrator, which is the most complex part of our model.

B State-of-the-Art Models

Several models have been designed to study animal's navigation. The model in [17] is a sophisticated and detailed theoretical work, simulating such phenomena as θ rhythm. Whereas it also contains proposals for navigation in multiple environments, it doesn't consider interactions to the environment. RatSLAM [7] extends the classical model of PC and HD by developing a competitive attractor network of "pose cells" that code both position and heading. Although there is no biological justification for it, the system was successfully tested in an indoor environment with landmarks. The mobile robot in [1] has been successfully tested even in a multi-target task in a single environment, but it also doesn't contain PI. Moreover its learning algorithm totally differs. Some models [5] use spiking model of neuron instead of our simple mathematical model.

Our preceding model [4] solved a hidden-target task in a single chamber similar to Morris water maze [9]. The animat moved freely around the chamber being constrained by the walls and an eventual obstacle. It detected standing of all cues in relation to its position. On contrary, the animat described here moves through a maze of several chambers. It doesn't look for a hidden target because it potentially could

be a long-lasting task. Instead, it follows a trajectory introduced by a teacher during learning phase and it then recalls the trajectory by its own. This is enough to demonstrate storing several trajectories in a single network.

REFERENCES

- [1] A. Arleo, W. Gerstner: Spatial cognition and neuro-mimetic navigation: A model of Hippocampal Place Cell Activity. *Biological Cybernetics*, Vol. 83, No. 3, 2000, pp. 287-99
- [2] K. I. Blum, L. F. Abbott: A model of spatial map formation in the hippocampus of the rat. *Neural Computing*, Vol. 8, No. 1, 1996, pp. 85-93
- [3] J. Bures, A. A. Fenton, Y. Kaminsky, L. Zinyuk: Place cells and place navigation. *Proceedings of the National Academy of Sciences USA*, 1997, Vol. 94, pp. 343-350
- [4] M. Bures, M. Jirina: Modeling of Spatial Navigation Inspired by Rodent Hippocampus. *WSEAS Transactions on Systems*. No. 1, 2005, pp. 325–330
- [5] T. Degris, L. Lachèze, C. Boucheny, A. Arleo: A Spiking Neuron Model of Head-Direction Cells for Robot Orientation. In *Proceedings of the Eighth Int. Conf. on the Simulation of Adaptive Behavior, from Animals to Animats*, MIT Press, 2004, pp. 255-263
- [6] T. Hafting, M. Fyhn, S. Molden, M. B. Moser, E. I. Moser: Microstructure of a spatial map in the entorhinal cortex. *Nature*, 436, 2005, pp. 801-806.
- [7] M. J. Milford, G. Wyeth, D. Prasser: RatSLAM: A Hippocampal Model for Simultaneous Localization and Mapping. In proceedings of *International Conference on Robotics and Automation*, New Orleans, United States, 2004
- [8] M. L. Mittelstädt, H. Mittelstädt: Homing by path integration in a mammal. *Naturwissenschaften* No. 67, pp. 566-567, 1980
- [9] R. G. Morris, pp. Garrud, J. N. Rawlins, J. O'Keefe: Place navigation impaired in rats with hippocampal lesions. *Nature* No. 297, 1982, pp. 681-683
- [10] R. U. Muller, J. L. Kubie, E. M. Bostock, J. S. Taube, G. Quirk: Spatial firing correlates of neurons in the hippocampal formation of freely moving rats. In J. Paillard: *Brain and Space*. Chapter 17, pp. 296-333, Oxford University Press, New York, 1991
- [11] O'Keefe J. (1976). Place units in the hippocampus of the freely moving rat. *Experimental Neurology*, 51, 78-109
- [12] J. O'Keefe, J. Dostrovsky: The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, Vol. 34, 1971, pp. 171-5
- [13] J. O'Keefe, L. Nadel: *The Hippocampus as a Cognitive Map*. Clarendon Press, Oxford, 1978
- [14] C. Pavlides, Y. J. Greenstein, M. Grudman, J. Winson: Long-term potentiation in the dentate gyrus is induced preferentially on the positive phase of θ rhythm. *Brain Research*, 1988 Vol. 439, pp. 383-387
- [15] A. D. Redish: *Beyond the cognitive map*. School of Computer Science, Carnegie Mellon University, Pittsburgh, 1997
- [16] A. Samsonovich: *Attractor-map theory of the hippocampal representation of space*. PhD thesis, The University of Arizona, 1997
- [17] A. Samsonovich, B. L. McNaughton: Path integration and cognitive mapping in a continuous attractor neural network model. *Journal of Neuroscience*, Vol. 17, No. 15, 1997 pp. 5900-5920
- [18] H. Schone: *Spatial Orientation: The Spatial Control of Behavior in Animals and Man*. Princeton University Press, 1984
- [19] A. Speakman, J. O'Keefe: Hippocampal complex spike cells do not change their place fields if the goal is moved within a cue-controlled environment. *European Journal of Neuroscience*, Vol. 2, No. 6, 1990, pp.544-555
- [20] J. S. Taube, R. U. Muller, J. B. Ranck Jr.: Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *Journal of Neuroscience*, Vol. 10, No. 2, 1990, pp. 420-435
- [21] K. Zhang: Representation of spatial orientation by the intrinsic dynamics of the head direction cell ensemble: A theory. *Journal of Neuroscience*, Vol. 16, No. 6, 1996, pp. 2112-2126