
A ROBOTIC NAVIGATION MODEL INSPIRED ON THE RAT HIPPOCAMPUS: SIMULATION WITH NSL

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Abstract: This paper presents the specification, design and simulation of a robotic navigation model inspired on the neurophysiology of the rat hippocampus. The paper also discusses the results of the experiments that our research group has performed with the model and describes our future work.

Keywords: affordances for movement, exploration, Hebbian learning, landmarks, mapping, navigation, path integration, rat hippocampus, reinforcement learning, world graph.

1 INTRODUCTION

The navigation of an autonomous mobile robot in an environment includes four interrelated activities: **exploration**, which is the strategy that guides the robot to select the next direction to go; **mapping**, which implies the construction of a spatial representation of the environment; **localization**, which is the strategy for determining the robot's position in the map; and **path planning**, which is the strategy the robot follows to find a path to the goal location, where that path could be optimal or not.

In the 1980's and early 1990's, the field of robotic navigation was divided into metric and topological approaches. Metric navigation is based on the construction of a metric map, which captures the geometric properties of the environment, while the topological approach is based on the construction of a topological map, which describes connectivity between different places with a graph, where nodes correspond to distinct situations, places or landmarks, and the arcs indicate the existence of direct paths between nodes.

A promising alternative to classical robotic navigation is based on the workings of the rat brain. Experimentation has shown that rats are able to solve spatial problems, to navigate by close or distant visual landmarks, and to use spatial information creatively, finding shortcuts to reach a goal. To explain their ability to process the spatial information, Tolman [Tolman 1948] argued in 1948 that the rats should have a **cognitive map** in some part of the brain, and in 1978, O'Keefe and Nadel [O'Keefe 1978] argued that the map was in the **hippocampus**.

According to Hölscher [Hölscher 2003], experimental work has shown that there exist at least two distinct populations of neurons in the rat hippocampus known as **place cells** and **head-direction cells**. Place cells codify information about physical locations of the animal. The areas of the environment to which

the place cells respond are known as **place fields**. Head-direction cells, on the other hand, codify orientations of the animal's head.

There exist many navigation models based on the hippocampus' neurophysiology. Some of them are proposed by Burgess and O'Keefe [Burgess 1994], Touretzky and Redish [Touretzky 1996], Balakrishnan, Bhatt and Hanovar [Balakrishnan 1998], Trullier and Meyer [Trullier 2000], Arleo and Gerstner [Arleo 2000], Gaussier, Revel, Banquet and Babeau [Gaussier 2002], Guazzelli [Guazzelli 1999], and recently Milford and Wyeth [Milford 2003]. In general, these models are based on a topological approach since experimental research on the rat hippocampus has shown that recognizing places implies activity in neurons associated with these places and with particular head orientations.

This paper presents a robotic navigation model based on the Guazzelli's work and its implementation on the Neural Simulation Language (NSL) [Weitzenfeld 2002]. The simulated rat navigates in a T-maze motivated by the presence of food in one of the arms of the "T". The paper also discusses the results of the experiments that our research group has performed with the model and describes the challenges involved in the implementation of the model on a robot.

2 THE ROBOTIC NAVIGATION MODEL

O'Keefe and Nadel [O'Keefe 1978] distinguished between two paradigms of navigation, one based on maps and the other based on routes, and proposed that independent neural systems exist in the brain to support these types of navigation. The systems were called the local system for map-based navigation and the taxon system for route navigation.

The model presented in this paper integrates two sub-models: the **Taxon-Affordances model** (TAM) and the **World Graph model** (WG). The former is used to determine the direction of movement, and the latter is used to build a map-based representation of the environment. Both sub-models are composed of layers of neurons that implement Hebbian and reinforcement learning in order to allow the expression of goal-oriented behavior. The following sections describe these sub-models and their integration.

2.1 The Taxon-Affordances model (TAM)

Guazzelli and his colleagues adopted the term **affordances** from Gibson [Gibson 1966] to refer to the parameters considered for motor interactions signaled by sensory cues without the necessary intervention of object recognition. They

Acknowledgements:

This work is sponsored by UC MEXUS (ITAM – UCSC), LAFMI (ITAM – ISC), NSF CONACYT (ITAM – UCI) under grant 42440 and "Asociación Mexicana de Cultura, S. A."

relate the taxon to the notion of **affordances for movement**. A rat has a wide repertoire of affordances for possible actions associated with the immediate sensing of its environment; e.g., for visual sighting of a corridor – go straight ahead; for sensed branches in a maze – turn; etc.

TAM is based on a model of detour behavior in anurans (frogs and toads). Ingle [Ingle 1980] and Collett [Collett 1982] observed that the approach of a frog/toad to a prey or the avoidance of a threat are influenced by the stationary objects in the animal's surrounding. Collet presented toads with different prey-barrier configurations (figure 1) and analyzed the number of trails in which toads chose to head directly towards the prey versus the number of trails in which they chose to detour around a stationary barrier to get the prey.

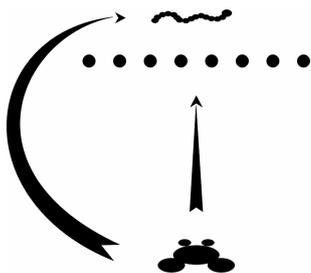


Fig. 1. Toad detour behavior. Arrows show two different trajectories elected by toads while approaching a prey (a worm), which is behind the barrier (the row of dots).

The determination of the direction of movement in the model presented here is based on the detour behavior models of Arbib and House [Arbib 1987], and Corbacho and Arbib [Corbacho 1995]. The frog direction to the prey is replaced by the direction of a rat orientation vector, while the barriers correspond to directions in which no arm of the maze is visible; i.e., the presence of a wall constrains the possible movements of the animal. Visible arms are encoded by the use of excitatory fields, according to the idea of affordances (e.g., go straight if an opening exists).

Affordances for movement are coded in a linear array of cells called **affordances perceptual schema**, which represents turns from -180° to $+180^\circ$. In this way, when the rat is in the center of an eight-arm radial maze, it is able to sense eight different visible arms and consequently eight different affordances (nine if we consider that -180° and $+180^\circ$ are represented separately). Figure 2 shows the information picked up by the affordances perceptual schema when the rat is in the center of a radial maze.

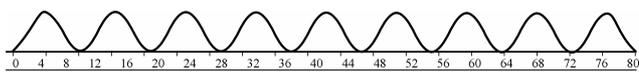


Fig. 2. Available affordances when the rat is in the center of an eight-arm radial maze. Each peak of activity represents a different affordance. The activity is coded by a perceptual schema through an array of 80 cells. The leftmost peak codes for turning 180° to the left and the rightmost peak codes for turning 180° to the right. The remaining peaks of activity code for turns in between -180° and $+180^\circ$ in 45° intervals.

Figure 3 shows the different layers that compose TAM. The affordances perceptual schema is sent to the **affordances feature detector layer**, a layer of neurons whose activation constitutes a pattern that represents the group of affordances available for the rat at the current time.

The activity pattern generated over the affordances feature detector layer is stored within a specific unit in the **affordances state layer**.

TAM is able to associate expectations of future reward to specific affordances states; e.g., the expectation of reward associated with the turning left affordance at the junction of a T-maze is increased if the rat finds food at the end of the left arm. To do this, TAM incorporates an **egocentric motivational schema**, which receives information from the current affordances state and sends its output to the **action selection schema**, the module that computes the choice of the correct affordance; i.e., the one that leads the animal to the goal.

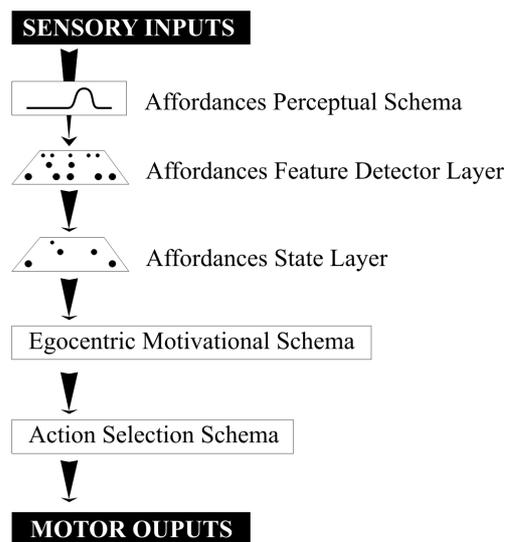


Fig. 3. Assemblage of TAM components.

2.2 The World Graph model (WG)

The WG model is composed mainly of a place cell layer and a world graph layer. Place cell activity is influenced by two kinds of inputs: path integration and visual information.

Path integration, also referred to as dead-reckoning, describes the process in which signals generated during locomotion allow the subject to update the position of its point of departure (an environmental anchor) in relation to its current position each time it moves. In this way, path integration allows the animal to return home. Path integration is initially the dominant influence on the navigation behavior, but visual cues gradually acquire priority as the animal becomes more familiar with the environment. Without the help of external spatial cues, path integration by itself is not precise enough to be used beyond limited excursions.

As can be seen in figure 4, the WG model includes a **path integration module** composed of a **dynamic remapping layer** defined as a two-dimensional perceptual schema which represents the particular environment and the anchor coordinates, and a **path integration feature detector layer** where the activation of its neurons constitutes a pattern of kinesthetic information.

On the other hand, visual information is derived from landmarks and walls represented by perceptual schemas. The walls perceptual schema is projected to a **walls feature detector layer**, and there exist two perceptual schemas for each landmark to codify the bearing and distance to that landmark from the animal. Both schemas serve as input to a feature detector layer (FDL), and there is an FDL for each

landmark. The output of all FDL's is then combined into a single **landmarks layer**.

The process of adding path integration and visual inputs is carried out by the **place cell layer** (PCL). The activation of a set of units in the PCL generates a pattern of activity which represents a single place in the environment.

The world graph is implemented in the WG model by the **world graph layer** (WGL), whose nodes are created on demand. Every unit in the PCL is connected to every node in the WGL. The arcs in a topological graph are represented by links between two WGL nodes. If the animal is at place x and moves to the north, the node x' associated with north is activated and a link is created between nodes x and x' .

The creation of nodes in the WGL is modulated by the activation of distinct affordances states in the TAM. A node will not be created if the activity pattern generated over the PCL is similar to a previously stored one. Each WGL node can store eight different activity patterns, one for each direction, assuming that the animal can orient itself in eight different directions and it can experiment different views of the same place.

If two WGL nodes are activated when the animal is at a certain location, they are merged because they represent the same place. If that is the case, both nodes disappear to form a new node whose output will consist of the outputs of the eliminated nodes and will store the array of activity patterns stored in both nodes for each direction.

The WG model incorporates an **allocentric motivational schema**, which associates the place information to expectations of future reward in order to influence the selection of the next action. Specifically, expectations of future reward are associated to pairs of nodes/arcs and are computed over a sequence of nodes. The expectation of future reward associated with an arc is divided by the number of steps associated to the same arc. In this way, the animal will balance the action selection between sites whose expected reward is low and are located nearby and sites whose expected reward is high and are

located far away. This process will continue until the expectations start to decrease or the goal node is achieved.

2.3 The integrated TAM-WG model

The integrated model, called TAM-WG, combines the TAM and the WG models. Figure 5 shows this integration.

Sensory inputs are used to compute the affordances, to select a node in the world graph, and to update the drive value, which is a primary necessity associated with the goal; e.g., for the hunger drive, the goal is food, and for the thirst drive, the goal is water. These inputs are then used by the allocentric and egocentric motivational schemas to allow the animal to successfully navigate in the maze.

The decision to turn to a certain angle is given by a winner-take-all process performed over the integration of activation fields produced by the available affordances (AF), the drive relevant stimuli (ST), the expectation of reward derived from TAM (RE_TAM), and the expectation of reward derived from the WG model (RE_WG). RE_TAM and RE_WG contain an associated noise factor. In this way, the total input I to the action selection module becomes

$$I(i, t) = AF(i, t) + ST(i, t) + (RE_TAM(i, t) + noise_tam) + (RE_WG(i, t) + noise_wg),$$

where i varies from 1 to N , the length of the population of cells (80) in the linear arrays used to represent the perceptual schemas, and t represents a certain time.

Eventually, the selected motor outputs will enable the animal to reach the goal. When an action is executed, it will produce changes in the animal's internal state and in the way it perceives the world. The internal state will alter the drive levels, which will in turn influence the selection of the next node in the world graph and so on.

The action selection schema is responsible for collecting votes from the egocentric and the allocentric motivational schemas, which are then used to select the most appropriate affordance.

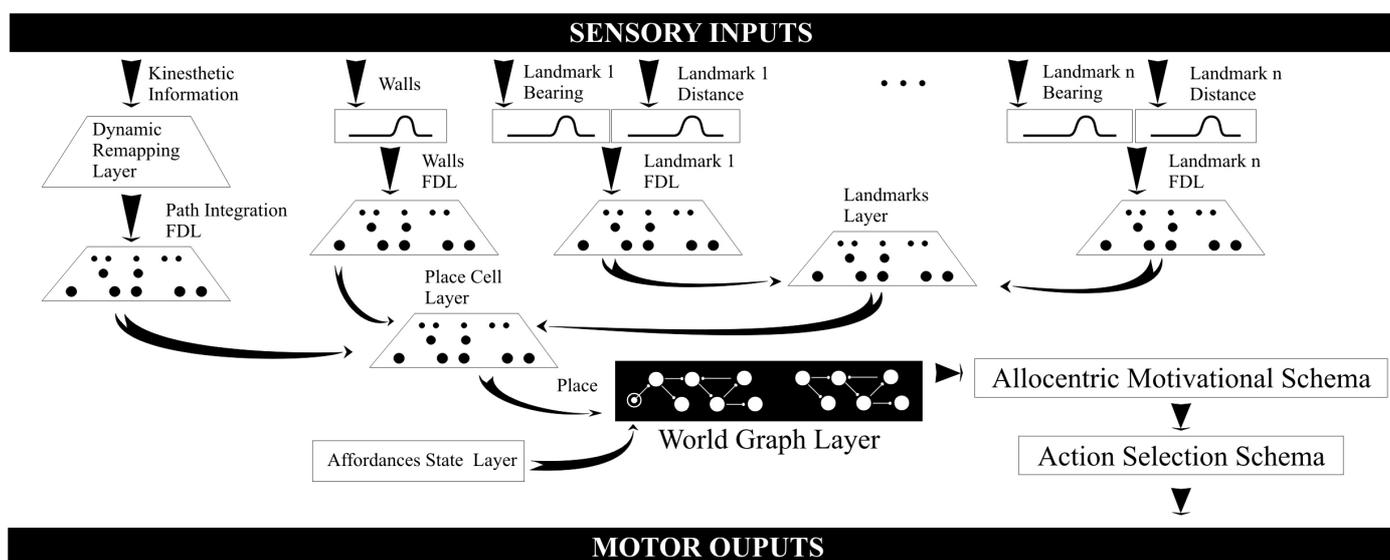


Fig. 4. The WG model. FDL stands for Feature Detector Layer.

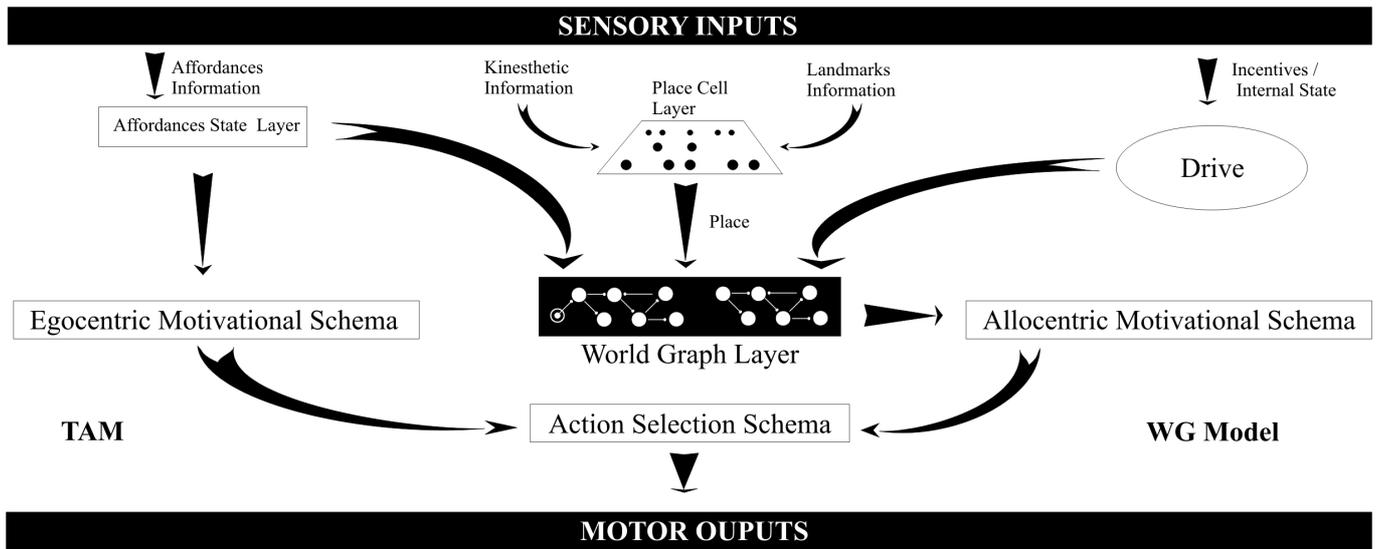


Fig. 5. Integrated TAM-WG model of rat navigation.

3 MODEL DESIGN

The model was implemented using the NSL modeling language. It is composed of 17 modules which are shown in figure 6 and described in the following sections.

3.1 Rat

This module represents the simulated rat and its behavior. When the rat is located at any place inside the maze, it captures the current view, which can include whole corridors, landmarks located outside the open maze, and food. Then, the rat computes the distance and angle to the visible food and landmarks.

Initially the rat receives its original position (xI , yI) and direction (aI). During subsequent iterations, the ActionSelectionS module indicates to the rat the position ($x1$, $y1$) and the direction ($hA1$) to take in the next step.

3.2 Drive

This module represents the rat's internal need to eat. The hunger drive is increased by the presence of food and reduced by the ingestion of it. The module computes the hunger value (hv) at every rat step using the formula

$$hv = ((phv + \alpha * d) - r * phv) + i * d,$$

where phv is the previous hunger value, α is a constant, d is the difference between the maximum value that the drive can take and its previous value, r is a reduction constant registered when the rat eats, and i is an incentive constant registered when the rat perceives the food.

The Drive module also computes the amount of reward or reinforcement (rv) the animal gets by the presence of food using the formula

$$rv = (phv / mhv) * r,$$

where mhv is the maximum hunger value.

In order to determine the possible reduction or increase of the hunger value, the Drive module receives from the Rat module the distance to the food (dF) if it is visible.

3.3 Affordances Perceptual Schema

The AffordancesPS module generates the current affordances perceptual schema described in section 2.1. In order to determine it, this module receives from the Rat module its current position (x , y) and head direction (hA).

3.4 Affordances Feature Detector Layer

The AffordancesFDL module is a feature detector layer composed of 400 neurons organized in a two-dimensional grid. The grid is divided into 5 neighborhoods of neurons, each composed of 80 neurons. AffordancesFDL receives from AffordancesPS the perceptual schema (aPS) and connects randomly each of its 80 neurons to 50% of the neurons of this feature detector layer.

The adjustments to the connection weights between the two layers follow a normalized Hebbian learning algorithm, which increases the connection strength from active units in the perceptual schema to active feature detector units. This ensures that the next time the same or similar pattern of activity is presented, the same set of feature detector units is activated.

3.5 Affordances State Layer

The AffordancesSL module is a layer of nodes created on demand. Each node represents an affordances state that the rat has experimented and stores the current activation pattern of the AffordancesFDL neurons. This pattern is searched for within the existing nodes. If none is similar, a new node will be created storing the new activation pattern. Otherwise, the recognized node is activated storing the most recent activation pattern.

AffordancesSL is involved in the reinforcement learning process. Every node in this layer has an adaptive-critic architecture associated, which is composed of eight actors and an adaptive-critic unit. The adaptive-critic unit tries to predict the total reinforcement, while the actors try to maximize the immediate internal reinforcement signal. The actors are associated to the eight different directions the animal can point to, representing, in this way, the expectation of the rat to find

reward if it moves in the direction that corresponds to the actor. Every node in this layer stores the weight of the adaptive-critic unit, the weights of the eight actor units and the eligibility trace of the actors.

Beginning a model iteration, the reinforcement is initiated by updating the eligibility trace of the current node associated with the last turn that the animal had to make to orient itself to its current direction. That update can be an increase (positive reinforcement), if the last movement allowed the perception of food, or a decrease (negative reinforcement), if it didn't.

After the creation or activation of a node, the reinforcement process is carried out for all the nodes in the layer, updating the weights of the adaptive-critic units, the weights and the eligibility traces of the actor units.

This module receives from AffordancesFDL the activation pattern of its 400 neurons (aFDL); from Rat, the distance to the food (dF); from Drive, the reward value (r); and from ActionSelectionS, the action taken by the rat to orient itself along its current direction (aT).

3.6 Walls Perceptual Schema

The WallsPS module codifies the current presence of walls in a perceptual schema, which is the complement of the affordances perceptual schema. To define the schema, this module receives from Rat its current position (x, y) and its head direction (hA).

3.7 Walls Feature Detector Layer

The WallsFDL module is a feature detector layer like AffordancesFDL and receives from WallsPS the current perceptual schema (wPS).

3.8 Dynamic Remapping Layer

The DynamicRL module builds a two-dimensional perceptual schema for the anchor of the environment, using its absolute position and the dimensions of the environment. The relative position of the anchor is updated, considering the opposite direction and the same magnitude of the rat movement. The module resets the perceptual schema on every new trial of the rat during the exploration of the environment.

3.9 Path Integration Feature Detector Layer

The PathIntFDL module is a generic feature detector layer, which receives from DynamicRL the anchor perceptual schema (piPS).

3.10 Landmarks Perceptual Schema

The LandmarksPS module builds a perceptual schema for each landmark perceived by the rat at the current time. A landmark perceptual schema is implemented as a linear array of 160 neurons, where the first 80 represent the relative angle from the position of the rat's head to the landmark position, and the other 80 neurons codify the distance from the rat to the landmark. In the current experiment three landmarks are used, so there will be at most three perceptual schemas built by this layer. The distances (dL) and angles (aL) to the landmarks are received from Rat.

3.11 Landmarks Feature Detector Layer

The LandmarksFDL module represents three generic feature detector layers, corresponding to the three perceptual schemas (ps1, ps2, ps3) generated by the previous layer.

3.12 Landmarks Layer

The LandmarksL module is also a generic feature detector layer, where the activation of its neurons represents the total influence of the landmarks perceived by the rat at the current time over the definition of a place in the environment. The module receives the activation patterns (fdl1, fdl2, fdl3) generated by LandmarksFDL.

3.13 Input to Place Cell Layer

The module InputPCL combines the visual and kinesthetic information in order to build a linear array of 1200 neurons which will be the input to the place cell layer of the model. InputPCL receives the activation patterns derived from WallsFDL (wFDL), PathIntFDL (piFDL) and LandmarksL (IFDL).

3.14 Place Cell Layer

The PlaceCellL module is a feature detector layer. The activation pattern of its neurons represents the current place visited by the rat. The module receives the combination of inputs (iPCL) generated by InputPCL.

3.15 World Graph Layer

The WorldGraphL module represents the topological map of the environment. Every arc of the map stores the identifier of the node that it points to, the direction that the rat followed to reach the corresponding place and the number of steps that the rat took to do it. As this layer is involved in the reinforcement learning process, the arcs also store the expectation of future reward.

There is a general adaptive-critic architecture for the world graph and a particular adaptive-critic architecture for each of its nodes. The layer initiates the general reinforcement, updating the eligibility traces of the most active neurons of the place cell layer for the last turn the rat made to reach its current direction. If the food is perceived after the turn, the reinforcement is positive, while if no food is perceived after that, the reinforcement is negative. Then, the general reinforcement process is carried out for all the neurons of the place cell layer, updating the weights of the adaptive-critic units, the weights and the eligibility traces of the actor units. After that, the layer initiates the particular reinforcement, increasing the eligibility trace of the current map node in the current rat direction.

The creation or activation of a node in the map is the next activity committed by the world graph layer. The activation pattern that defines the current place is searched for within the existing nodes. If the current affordances state is different from the previous one and there is no similar pattern in the map, a new unit will be created storing the new activation pattern, and if the place is recognized, the corresponding node is activated storing the most recent activation pattern. A node is also activated if the current affordances state is the same as the previous one and there is a similar pattern in the map.

unlearn that the food was in the left arm and learn that it is in the right one now.

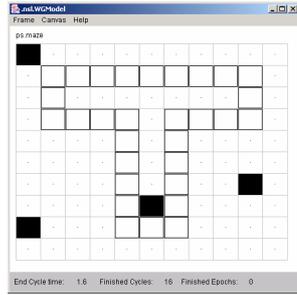


Fig. 7. The experimental maze.

4.2 Results

During the habituation phase, the simulated rat builds the world map. As can be seen in figure 8, the base of the T-maze is represented in the map by three nodes. From south to north, the first node corresponds to the place of departure (figure 9a); the second one represents four locations indicated in figures 9b to 9e. Despite being different places with different distances and angles to the visible landmarks, the affordances state is the same in all of them, so just one node is needed to represent them in the map. Finally, the third node of the graph corresponds to the location at the junction of the “T” (figure 9f), where the rat decides randomly to turn right. Figure 10 shows the representation of this arm in the world map composed of two nodes. The rightmost node corresponds to the location at the end of the corridor, while the previous one corresponds to the two places located between the junction and the end. In a new trial, the rat picks up the left arm, adding two new nodes to the map as can be seen in figure 11.

During the training phase, the food is put in the leftmost place of the maze. When the rat reaches the junction of the “T”, the sight of food makes the rat to decide to turn left (figure 12). Despite of the presence of food, the rat recognizes the leftmost place as the same stored in the graph. After 10 trials the rat has learnt the position of food.

When the testing phase begins, the food is moved to the right arm, but the rat still believes that it will find the food in the opposite arm and turns to the left as shown in figure 13. The unlearning process lasts several trials and, finally, the rat decides to turn right in order to ingest the food, but at the beginning of this relearning process the rat tends to choose the left arm wrongly. It takes the rat 20 trials approximately to pick up the right arm in every testing trail.



Fig. 8. The map of the base of the “T”. The bigger circles represent the nodes and the little half circles between the nodes represent the arc directions. The node marked with an “X” indicates the current node in the map.

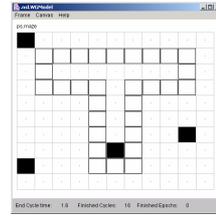


Fig. 9a. Place of departure.

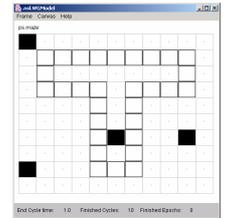


Fig. 9b. First place represented by the second node.

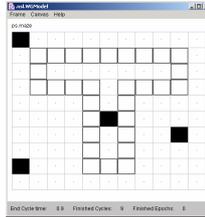


Fig. 9c. Second place represented by the second node.

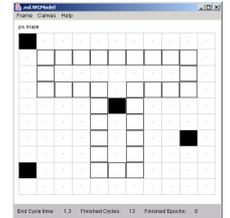


Fig. 9d. Third place represented by the second node.

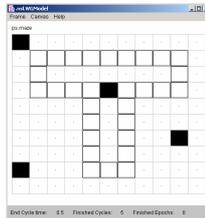


Fig. 9e. Fourth place represented by the second node.

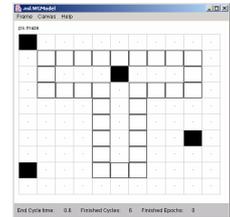


Fig. 9f. Place represented by the third node.

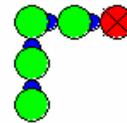


Fig. 10. The map of the right arm of the “T”, showing the rightmost node as the one currently visited by the rat.

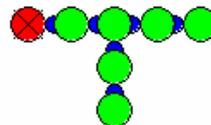
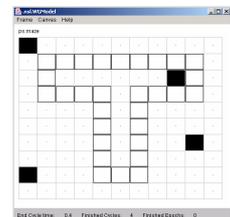


Fig. 11. The map of the left arm of the “T”, showing the leftmost node as the one currently visited by the rat.

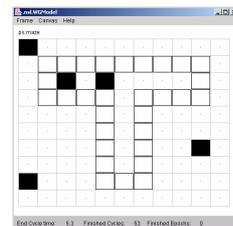
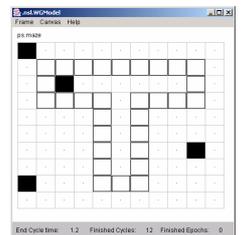


Fig. 12. In the training phase the food is put at the end of the left arm and the rat is approaching it.

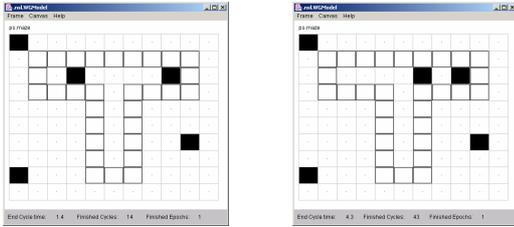


Fig. 13. In the testing phase the food is put at the end of the right arm. It takes the rat several trials to forget that the food is located in the left arm. Finally, as shown in the right figure, the rat turns to the right, demonstrating that it has learnt the new position of the food.

5 CONCLUSIONS AND FUTURE WORK

We believe that the inspiration on neurophysiology of animals that have proved to be able to solve spatial problems efficiently, like rats, must lead to design good models to support the robotic navigation.

In this paper we have presented the specification, design and simulation of one of these models. The simulated rat is able to explore a T-maze motivated by its internal need to eat, to map the environment, and to use it to navigate searching for food. The model allows this by including the neurophysiological mechanisms of real rats: the Hebbian and reinforcement learning, the preprogrammed reactions called affordances that allow the rat to move in a maze, and the definition and recognition of the places of a maze as a combination of visual and kinesthetic information.

The model is based on Guazzelli's theoretical work. We added to this work a complete reinforcement learning process which includes both positive and negative reinforcement in order to allow the rat to learn the goal location effectively. Then we designed the modules that compose the model and simulated it using NSL. We are working now on designing and implementing some extensions that will include the following aspects: to use the model in the exploration and mapping of more complicated mazes and of environments less structured than the mazes; to experiment with the use of path integration in order to allow the rat to return home in the absence of visual information; to use spatial landmarks for actively guiding rat navigation and not only as part of the definition of a location; and to develop a virtual 3D interface which will make the input data towards the rat more realistic, facilitating the migration of the model from the virtual to the real world.

As a future work, our research group will implement the model on individual and multiple robots. We will analyze and test different strategies to explore and map the environment in a distributed manner. We will also study strategies for integrating partial maps obtained by the individual robots into a global map of the environment. Our eventual goal is to be able to use biologically – inspired navigation models in non – biological applications such as urban search and rescue.

REFERENCES

[Arbib 1987] Arbib, M. A., and House, D. Depth and detours: an essay on visually guided behavior. In M. A. Arbib and A. R. Hanson (Eds.), *Vision, Brain, and Cooperative Competition* (pp. 129-163). Cambridge, MA: MIT Press (1987).

- [Arleo 2000] Arleo, A., Gerstner, W. Spatial cognition and neuro-mimetic navigation: a model of hippocampal place cell activity. *Biological Cybernetics* 83, 287-299 (2000).
- [Balakrishnan 1998] Balakrishnan, K., Bhatt, R., Honavar, V. A computational model of rodent spatial learning and some behavioral experiments. In: M. A. Gernsbacher & Sharon J. Derry (Eds.), *Proceedings of the Twentieth Annual Meeting of the Cognitive Science Society*. Mahwah, NJ: Lawrence Erlbaum Assoc. (1998).
- [Burgess 1994] Burgess, N., Recce, M., O'Keefe, J. A model of hippocampal function. *Neural Networks*, Vol. 7, Nos. 6/7, pp. 1065-1081 (1994).
- [Collett 1982] Collett, T. S. Do toads plan routes? A study of detour behavior of *B. viridis*. *Journal of Comparative Physiology*, 146: 261-271 (1982).
- [Corbacho 1995] Corbacho, F. J., and Arbib, M. A. Learning to detour. *Adaptive Behavior*, 3 (4): 419-468 (1995).
- [Gaussier 2002] Gaussier, P., Revel, A., Banquet, J. P., Babeau, V. From view cells and place cells to cognitive map learning: processing stages of the hippocampal system. *Biological Cybernetics* 86, 15-28 (2002).
- [Gibson 1966] Gibson, J. J. *The senses considered as perceptual systems*. Allen and Unwin (1966).
- [Guazzelli 1999] Guazzelli, A. Integrating motivation, spatial knowledge, and response behavior in a model of rodent navigation. *PhD Thesis*, University of Southern California (1999).
- [Hölscher 2003] Hölscher, C. Time, space and hippocampal functions. *Reviews in the Neurosciences* (2003).
- [Ingle 1980] Ingle, D. The frog's detection of stationary objects following lesions of the pretectum. *Behavioral Brain Research*, 3: 151-173 (1980).
- [Milford 2003] Milford, M. and Wyeth, G. Hippocampal Models for Simultaneous Localisation and Mapping on an Autonomous Robot. *Proceedings of the 2003 Australasian Conference on Robotics and Automation*. Brisbane, Australia (2003).
- [O'Keefe 1978] O'Keefe, J., Nadel, L. *The hippocampus as a cognitive map*. Oxford University Press (1978).
- [Tolman 1948] Tolman, E. Cognitive maps in rats and men. *Psychological Review* 55, 189-208 (1948).
- [Touretzky 1996] Touretzky, D., Redish, A. A theory of rodent navigation based on interacting representations of space. *Hippocampus* 6, 247-270 (1996).
- [Trullier 2000] Trullier, O., Meyer, J.A. Animat navigation using a cognitive graph. *Biological Cybernetics* 83, 271-285 (2000).
- [Weitzenfeld 2002] Weitzenfeld, A., Arbib, M., Alexander, A. *The Neural Simulation Language: A System for Brain Modeling*. MIT Press (2002).