

Learning spatial localization: from rat studies to computational models of the hippocampus

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#### Author Note

This work is funded by NSF IIS Robust Intelligence research collaboration grant #1117303 at USF and U. Arizona entitled “Investigations of the Role of Dorsal versus Ventral Place and Grid Cells during Multi-Scale Spatial Navigation in Rats and Robots,” and supported in part by the “Agencia Nacional de Investigacion e Innovación (ANII)” and by the “Asociación Mexicana de Cultura, S. A.” Corresponding author: Alejandra Barrera ([abarrera@itam.mx](mailto:abarrera@itam.mx)), Department of Computer Engineering, College of Engineering, Instituto Tecnológico Autónomo de México (ITAM), Río Hondo 1, Progreso Tizapán, CP 01080, Mexico City, Mexico.

### Abstract

In his landmark paper, Richard Morris (1981) introduced a set of rat experiments intended “to demonstrate that rats can rapidly learn to locate an object that they can never see, hear, or smell provided it remains in a fixed spatial location relative to distal room cues.” These experimental studies have greatly impacted our understanding of rat spatial cognition. In this paper, we address a spatial cognition model primarily based on hippocampus place cell computation where we extend the prior Barrera-Weitzenfeld model (2008) intended to allow navigation in mazes containing corridors. The current work extends beyond the limitations of corridors to enable navigation in open arenas where a rat may move in any direction at any time. The extended work reproduces Morris rat experiments through virtual rats that search for a hidden platform using visual cues in a circular open maze analogous to Morris water maze experiments. We show results with virtual rats comparing them to Morris original studies with rats.

*Keywords:* spatial cognition, spatial learning, cognitive map, place cells

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Spatial cognition is an interdisciplinary area of research where studies have demonstrated the close relationship between space localization and neural activity in the brain. It has been hypothesized that there is cognitive map representation responsible for estimating the rat's position within the environment and its relative direction to a goal (Tolman, 1948; O'Keefe and Nadel, 1978). The cognitive map is constructed through exploration of the environment by relating topological and metric information in space (Poucet, 1993), and can be exploited to optimize goal-oriented navigation by use of landmarks and path integration (Mittelstaedt and Mittelstaedt, 1982; Etienne and Jeffery, 2004).

O'Keefe and Dostrovsky (1971) proposes the rat's hippocampus as the neural substrate for the cognitive map, after performing recordings of individual pyramidal cells in hippocampal substructures CA1 and CA3. These neurons were termed place cells due to the high correlation between their firing and the animal's location in the environment (McNaughton, Knierim, and Wilson, 1994; McNaughton et al, 1994). Studies have shown that the response of place cells is derived from combining kinesthetic self-motion and allothetic distal cue information (Jeffery and O'Keefe, 1999). Another important discovery is that place cells continue firing even after some of the visual cues are removed from the environment (O'Keefe and Conway, 1978), and in some cases continue to respond in the dark (Quirk, Muller, and Kubie, 1990).

In his landmark paper, Richard Morris (1981) introduced a set of rat experiments intended "to demonstrate that rats can rapidly learn to locate an object that they can never see, hear, or smell provided it remains in a fixed spatial location relative to distal room cues". These experiments involved a water maze where the rat had to swim to reach a platform to escape from

cold water. The platform could be visible or hidden, placed in a fixed or variable location during training trials.

The biological and behavioral findings previously described have provided a basis for the development of computational models of the rat spatial cognition system, which can be evaluated by solving goal-oriented learning tasks. Over the past years, we have designed a computational model aiming at ultimately developing advanced robot architectures for spatial localization based on continuous spatial learning. Our computational model provides the generation of the cognitive map for a particular environment considering the ensemble of place cell activity as a code for the current location, and learns based on a delayed reward system (O'Keefe and Nadel, 1978). Our model has been validated by reproducing, with simulated and real robots, well-known spatial tasks performed with rats in controlled environments such as the T-maze and the radial maze devised by O'Keefe in 1983 (Barrera and Weitzenfeld, 2008). We also have directly contrasted results from experiments in mazes with cyclic corridors in rats and robots (Barrera et al, 2011). In these experiments, robots navigated through small corridors to reach a goal using either their taxon abilities or relating to a number of distal cues in the environment. In the present work we remove the restriction of corridors, which required extensions to the existing computational model to eventually afford critical challenges on robot navigation. In this paper we describe these extensions by studying open maze navigation based on hidden goals and visual cues as originally described in the water maze experiments by Morris (1981).

We describe our work in the rest of the paper as follows: Section "Related work" discusses related computational models and corresponding experimental studies; Section "A bio-inspired spatial cognition model" summarizes our extended computational model highlighting the challenges on the model imposed by experimentation in open arenas; Section

“MIRO/ASL/NSL simulation system” overviews our simulation environment for the experimental studies; Section “Experimentation protocols” describes the experimentation protocols that we implemented; Section “Experimentation results” provides results from our corresponding experimental studies with virtual rats; and Section “Conclusions and Discussion” provides conclusions and discussions on our current work in progress.

### **Related Work**

The study of behavioral and neurophysiological mechanisms involved in rat spatial cognition has inspired the development of several computational models implementing goal-oriented learning tasks, such as the models by Burgess, Recce, and O’Keefe (1994), Brown and Sharp (1995), Redish and Touretzky (1997), Guazzelli, Corbacho, Bota, and Arbib (1998), Arleo and Gerstner (2000), Gaussier, Revel, Banquet, and Babeau (2002), Filliat and Meyer (2002), Arleo, Smeraldi, and Gerstner (2004), Milford and Wyeth (2007, 2010), Dollé, Sheynikhovich, Girard, Chavarriaga, and Guillot (2010), Alvernhe, Sargolini, and Poucet (2011), and Barrera and Weitzenfeld (2008). In the current paper we contrast with spatial cognition models that consider primarily bounded arenas for robot navigation, in particular Brown and Sharp (1995), Guazzelli et al (1998), Arleo and Gerstner (2000), Gaussier et al (2002), Dollé et al (2010), and Alvernhe et al. (2011).

In Brown and Sharp (1995), spatial behavior is explained in the Morris water maze by modeling the hippocampal projection to the nucleus accumbens, a subcortical structure. The researchers provide a stimulus-response system allowing virtual rats to show rapid learning of efficient routes to the goal after minimal experience from somewhat novel starting positions. In their model, firing patterns of place cells and head direction cells activate motor cells in the nucleus accumbens. Each motor cell causes a particular locomotor movement in a virtual rat.

Connection strengths between cells are initially set randomly, and when the animal encounters the reward location, recently active synapses are strengthened. In contrast to our approach, this work suggests that the novel route generation demonstrated by simulations does not require a cognitive mapping strategy, but only a stimulus-response system based on place cell firing information.

In Guazzelli et al. (1998) the model was validated by simulating with a virtual rat some classical spatial tasks in corridor mazes, not in open arenas. The model allowed a virtual rat to learn goal locations from a fixed departure position within mazes that included just one decision point; however, it was unable to find the target in more complex mazes or reach it from arbitrary starting positions.

In Arleo and Gerstner (2000), the researchers designed ad-hoc spatial tasks, not directly related to experiments formerly devised for real rats, in order to validate their proposed reward-based learning scheme. They employed a Kephra robot in a square arena with walls covered by random sequences of black and white stripes, where combinations of these stripes provided input patterns for the vision system of the robot, and a specific target region was predefined so the robot built up a navigational strategy to reach that region from different locations. In our model, in contrast, we provide an explicit construction of a topological map of places and their metric relations.

In Gaussier et al. (2002), their model was tested with a mobile robot in a delimited open environment, which was randomly explored to progressively develop a cognitive map composed of transition nodes between different places. The experiment was limited to learn a very simple arena consisting of five transitions and one target location. After exploration, the robot was placed back at the initial position. By recognizing its current location from the visual scene, the

robot could predict all possible transitions and select the one leading to the target. Even if the experiment was successful, the authors acknowledged that their model could not distinguish between visually similar places that appear in long hallways or in dark conditions, which does not occur in our model because of the integration of kinesthetic in addition to visual information as input to the system.

In Dollé et al (2010), researchers produced a model that switches between path-planning and cue-guided navigation strategies. Results obtained from simulation were validated by reproducing rat behavior in biological experiments similar to the water maze task, in which both navigation strategies were shown to interact. In a subsequent publication (Caluwaerts, Staffa, N'Guyen, Grand, Dollé, Favre-Felix, Girard, and Khamassi, 2012), the model was tested in robots navigating in a 2m x 2.5m open environment. The robot implementation involved the extension of the model by adding a strategy selection meta-controller, which allows the robot to select among a response strategy to perceived cues or a place strategy building a map of place cells. Experimental results showed the ability of the robot to switch between behavioral strategies. In contrast to Dollé's work, in which the locale expert simulates place cells that represent pre-established locations in the arena, place cells in our model dynamically learn and recall locations in the arena by exploiting kinesthetic information and external visual cues.

In Alvernhe et al (2011), the researchers demonstrate in behavioral rat experiments that it is very likely that topological representations and metric information (angles and distances) are combined so that the animal could be aware of its location in current space, and of the relationship between current and remote space. Furthermore, authors argue that the rat's brain contains the necessary mechanisms not only to process such relationships but also to update them flexibly. In the experiments described in the paper, rats were first exposed during four 5-min

trials to a complex environment divided into several sectors that were separated by doors allowing either unrestricted or restricted access to other sectors. In the fifth test trial, authors measured the behavior of the animals when the initial environment's topological structure was altered. The authors found clear evidence that rats detected those changes in the environment. In our approach, we also tested the virtual rat facing changes in the environment, not in its structure but in the goal location during training trials of Morris experiments, and even though the model is able to adapt the cognitive map correspondingly, our results showed rats are unable to stabilize the escape latency by the end of the training phase of the experiment.

In Barrera and Weitzenfeld (2008) we describe a spatial cognition model for navigation in corridor-based mazes that replicate O'Keefe experiments with T-mazes and 8-arm mazes. One of the challenges faced by this model when experimenting with bounded open environments is the allocation of both topological and metric information in the cognitive map. In the original model, metric relations between different locations considered only rotation angles and forward motions to reach a place. We did not represent physical distances between places in the map, but changes in possible displacement actions. Thus a complete corridor in a maze was represented in the map by three places (nodes) regardless of how long it was, i.e. one node for the beginning of the corridor where the displacement action corresponds to "move forward", one node for the middle of the corridor where displacement actions correspond to "move forward" or "return", and another node for the end of the corridor where the displacement action corresponds to "return". In an open arena, all possible displacement actions are available for the rat in the entire environment except for the boundaries, thus a distance metric between physical locations is required to enable map construction.

### **A bio-inspired spatial cognition model**

The spatial cognition model (Barrera & Weitzenfeld, 2008; Barrera et al., 2011) is composed of several modules implementing specific functions of the rat spatial cognition system (see Figure 1). All modules are described in detail in those publications. Figure 1 highlights the main input and output for each module. As the figure illustrates, input to the model consists of internal rat information, including internal states / incentives and kinesthetic information perceiving body motions, and external environment information including landmarks information and action space (affordances) information. The output of the model corresponds to the next rat direction (DIR), rotation (ROT) and displacement (DIS).

Our prior computational model was intended primarily to replicate experiments devised by O'Keefe for rats. The experimental protocols we implemented required a real robot to navigate through small corridors to reach a goal restricting the taxon and action space mostly to 90° rotations where 0° corresponds to a relative move forward. In the extended model we eliminate the restriction of 90° rotations to allow 45° rotations while also enabling full open space motions (direction, rotation and displacement) which results in additional challenges with respect to the previous corridor-based mazes. In addition to open maze experiments, we also extended the simulation environment to allow for the incorporation of hidden goals that can only be perceived when the virtual rat is next to them. In the rest of this section we provide an overview of the modules that were improved with recent extensions; i.e. Affordances Processing, Landmarks Processing, Place Representation, and Learning.

#### **Affordances Processing**

The model adopts from Gibson (1966) the notion of affordances for movement representing all possible motor actions that a rat can execute through the immediate sensing of its

environment. In the current version of the model, the possible motor actions are represented as turns relative to the rat’s head from  $-180^\circ$  to  $+180^\circ$  in  $45^\circ$  intervals, as opposed to the prior version dealing with  $90^\circ$  intervals.

Our approach employs perceptual schemas as originally conceived by Arbib (2002), modeled as functions from  $\mathbb{R}^n$  to  $\mathbb{R}$ , where the domain corresponds to possible rotation angles ( $x$ ), and the function value  $f(x)$  represents the output of that perceptual schema for that value  $x$ ; i.e. whether or not the virtual rat can navigate towards direction  $x$ . Figure 2 illustrates the resulting affordances perceptual schema when only turns of 90 and 225 degrees can be executed.

The affordances perceptual schema is implemented using a linear array referred to as AF holding in its cells the function values at discrete points in the domain. Specifically, the value stored at cell  $i$  in the array is computed by Eq (1):

$$AF_i = he^{\frac{-(i-a)^2}{2d^2}} \quad (1)$$

where  $a$  and  $d$  are correspondingly the first two moments of a Gaussian function and  $h$  is a scaling factor. We employ the relationship  $a = 4 + 9m$  where  $m$  is an integer with value between 0 and 8 corresponding to an affordance between  $-180^\circ$  and  $+180^\circ$  in  $45^\circ$  intervals.

### Landmarks Processing

Rats exploit spatial information in the environment by relating the location of the goal to a set of visual cues or landmarks. In our experiments, we use cylinders as landmarks that are distinguished by colors. The model estimates relative size, distance and orientation of each visible landmark to the current virtual rat perspective as seen by its local camera.

At every time step, a panoramic image covering a 210-degree field of view is built while navigating the environment. This image is stored as a matrix with 400 columns and 80 rows, and the relative orientation of a landmark is computed by identifying the column with the maximum

amount of pixels corresponding to the color of the landmark being measured, i.e. the mode of an histogram for that color.

Eq. (2) represents the relative distance  $D(L_i)$  to the  $i_{th}$  landmark  $L$  which is estimated by the ratio between the perceived number of pixels colored as the landmark within the current panoramic image ( $maxCL_i$ ) and the maximum number of pixels colored as the landmark within any given panoramic image ( $maxL_i$ ):

$$D(L_i) = (maxL_i - maxCL_i)/maxL_i \quad (2)$$

Relative distance and orientation to each visible landmark are represented within the landmark perceptual schema (LPS) built as the same function described by Eq. (1). LPS has double size relative to AF in order to represent both orientation and distance of the corresponding landmark relative to the rat's perspective. The highest value in the orientation array corresponds to the relative rotation of the rat to the landmark (between  $-180^\circ$  and  $+180^\circ$  in  $45^\circ$  intervals), whereas the highest value in the distance array is determined by the ratio described in Eq. (2).

The model applies Hebbian learning (Hebb, 1949) to update connection weights between layers of neurons within the modules, ensuring in this way that the next time the same or similar input pattern is presented to the virtual rat, the same set of neurons are activated. In the case of Landmarks Processing module, LPS layer is connected to a LFDL layer for each corresponding landmark in the environment, i.e.  $LPS_1-LFDL_1$ ,  $LPS_2-LFDL_2$ , ... ,  $LPS_n-LFDL_n$ . All LFDL layers are combined into a single landmarks layer (LL) following the same connectivity pattern used to define the connections between any couple LPS-LFDL. Hebbian learning updates connection weights between layers  $LFDL_1$ ,  $LFDL_2$ , ... ,  $LFDL_n$  and LL, producing groups of neurons in LL that respond to specific information patterns derived from the integration of all

landmarks present in the environment. In this way, visual information patterns stored in the array, referred to as LP, represent an egocentric view of the environment to the virtual rat.

### Place Representation

The model combines kinesthetic information (PI) and visual information from landmark processing (LP) as input to the place cell layer (PCL) to determine the activity of hippocampal place cells, as shown in Figure 3. The synaptic efficacy between layers is maintained by Hebbian learning using the activation values stored in the place cell (PC) linear array, which stores the ensemble activity registered by the collection of units in PCL encoding kinesthetic and egocentric visual information.

The world graph layer (WGL) implements a topological map inside the place representation module where nodes in the map represent distinctive places, and arcs between nodes are associated with the direction of movement from one node to another. Given that the model assumes eight possible directions of movement from any given place, i.e. from  $0^\circ$  to  $315^\circ$  in  $45^\circ$  intervals, eight activation patterns generated by PCL are stored in the corresponding map node and associated to the eight different directions.

To determine whether or not the rat recognizes a place, WGL searches for the current activation pattern PC produced by PCL within all nodes in the map. This search involves the computation of the Euclidean distance  $d$  between PC and every stored pattern,  $pat$ , associated with the same absolute direction (from  $0^\circ$  to  $315^\circ$ ) as the current rat direction, as described in Eq. (3), where  $N$  is the number of values stored in every activation pattern.

$$d(PC, pat) = \sqrt{\sum_{i=1}^N (PC_i - pat_i)^2} \quad (3)$$

The minimum distance obtained is compared with a threshold value, which is set empirically. Being smaller than this value indicates the recognition of the current pattern as

previously stored within the map. A new pattern is created otherwise. To determine which map node the new pattern should be associated to, the model evaluates if the current absolute direction of the rat is different from the previous one. If this is the case, the virtual rat has not moved so the new pattern corresponds to the current map node if it exists. If the rat did move, a new map node is created. Thus, physical distances between places are represented in the model by virtual rat motor displacements, as opposed to the prior version of the model where a new map node was created only when the affordances perceptual schema had changed.

In the event a node is created, this is linked to the previous one using the navigated direction. Just after the node creation, the virtual rat proceeds to rotate in every possible direction to generate a 360 degree perception, which is stored in the node and later used for comparison with subsequent activation patterns during navigation in any direction, and recognition of the node when returning to it regardless of the direction of the rat's head.

### **Learning**

In our prior model, we implemented an Actor-Critic architecture (Barto, 1995) that processed expected values of future reinforcement through an Adaptive Critic and up to eight Actor units. In the newer model, we have implemented the Q-Learning method (Sutton and Barto, 1998) based on the approximation of value functions estimating how good it is for the virtual rat to execute certain action in a given state. The behavior or policy followed must be such that it allows the virtual rat to select those actions that increase the expected reward.

Off-policy methods such as Q-Learning allow for the virtual rat to learn the policy regardless of the path traveled in a given episode. This is opposed to on-policy methods like Actor-Critic that depend on the rat's future decisions in order to learn the reward for performing a particular action (Sutton and Barto, 1998). In other words, if the virtual rat has learned a

lengthy path to the goal and finds a shortcut at some point in that path, the Q-learning method would learn the new optimal path right away, while the Actor-Critic method would need to have the rat first following the old path from that point to learn the convenience of the shortcut. Given that our goal is to implement the extended model in real robots, this improvement in learning efficiency will help reducing the amount of training trials, which are expensive to perform.

Formally, the learning model consists of a set of states  $S$  where the rat may be in the environment, and a set of actions  $A$  that the rat can execute at any of the states. In the context of our spatial cognition model  $S$  is represented by the nodes of the topological map, whereas  $A$  relates to possible affordances or actions the rat may take at the current location.

The action-value function,  $Q(s, a)$ , is defined as the expected reward value of executing a given action  $a$  in a certain state  $s$  following a specific policy. The objective is to select a policy that results in a unique optimal  $Q$  function, which maximizes the value of any given state-action pair.

Table I describes the Q-Learning algorithm estimating the optimal action-value function  $Q(s, a)$ . The parameter  $\alpha$  defines a value that corresponds to the importance of new updates relative to previous values, and the discount factor  $\gamma$  is a value between 0 and 1 that reduces the influence of reinforcements received in the future. The parameter  $r$  defines the reward given to the rat after it reaches the goal.

In the Q-Learning algorithm employed in the spatial cognition model, the amount of reward  $r$  is set to 1 only if the virtual rat reached the goal, otherwise  $r$  is set to 0, while  $\gamma$  and  $\alpha$  are set to 0.7.

The maximum expectation of reward  $\max Q$  is obtained from the eight arcs adjacent to the active node in the map. The node visited immediately prior to the current one is found in the

map, and reinforcement is applied to the arc linking both nodes in the corresponding travel direction. The computation of the action-value function determines the new expectation of reward  $ER$  within the previously activated node  $pn$  in the specific direction  $d$  leading to the active node  $an$ , as described by Eq. (4):

$$ER(pn, d) = ER(pn, d) + \alpha[r + \gamma (\max Q(an) - ER(pn, d))] \quad (4)$$

Assuming that virtual rat sensors and effectors are naturally noisy, we applied the non-deterministic version of the Q-Learning rule appropriate within stochastic domains, where the execution of an action over the same state may produce different state transitions or reinforcements.

After applying the learning rule, the reward expectation signal is built in order to influence the next virtual rat choice of rotation. To do this, the model evaluates the policy to choose between carrying out an exploration or exploitation process.

Exploitation is selected if the current immediate reward value (as a proportion of  $dmax$ , the maximum immediate reward value) exceeds a random value and the subject is not executing habituation. In an exploitation situation, the vector storing the reward expectation signal in the eight different directions is set to the eight reward expectation values associated to the active map node. In an exploration situation, on the other hand, the vector storing the reward expectation signal in the eight different directions is set to minimum values.

### **Improvements from previous models**

Summarizing, our current model differs with previous ones in that it navigates in open environments and it uses an off-policy learning algorithm (Q-Learning) to learn the best path over the world graph layer, as opposed to the usual on-policy Actor-critic models.

Open field navigation has been challenging in that the use of affordances, as explained above, do not provide great information about the rat's location, whereas they are a great source of certainty in closed corridors.

This imposed a challenge on the computation of the PCL layer. The visual information integration and node initialization and merging processes had to be redesigned to cope with this higher uncertainty scenario.

### **MIRO/ASL/NSL simulation system**

We have developed a rat simulation environment where the spatial cognition model was developed and all experiments have been performed. This system consists of the integrated MIRO/ASL/NSL system:

- Mobile Internet Robotics (MIRO) comprises the rat simulation system that enables simulation of our neural models developed using the ASL/NSL system with additional extensions to physical robots (Weitzenfeld et al., 2003).
- Abstract Schema Language (ASL) is a schema-based modeling system to describe animal and human behavior in a modular fashion (Weitzenfeld et al., 2002a).
- Neural Simulation Language (NSL) is a neural simulation language enabling the mapping of behaviors to computational models of neural regions in the brain (Weitzenfeld et al., 2002b).

The most critical aspects of our simulation environment are to perform (1) visual perception of landmarks, and (2) motor actions and navigation, as explained in the following sections.

## Visual Perception

For the open maze experiments described in this paper we built a circular arena with four differently colored cylinder-shaped landmarks evenly distributed around the maze as shown by the top view of the arena in Figure 4 (right). In this figure the rat is located in the center of the maze looking “north” towards the blue landmark. In a coordinate system relative to the body of the rat, i.e. an egocentric coordinate system, the front view is the  $0^\circ$  angle and the system simulates the rat with a  $210^\circ$  viewing angle. Thus the “north” view for the centrally located rat involves an egocentric perspective angle from  $-105^\circ$  to  $105^\circ$  as shown in Figure 4 (left).

The egocentric coordinate system is shown in Figure 5(a) with  $0^\circ$  always corresponding to the front view of the rat (thick arrow) independent from its current location and orientation in the arena. To determine the rat position and orientation in the arena we use an allocentric coordinate system that never changes and is independent from rat position and orientation. Figure 5(b) shows the allocentric representation with “north” (thick arrow) always corresponding to  $90^\circ$  independent of rat position or orientation.

## Motor Actions and Navigation

As the rat moves and orients itself inside the maze, different views of visual landmarks are computed in terms of distance and angle to each landmark. These computations are the basis for the generation of perception patterns associated with specific location in the maze. The combination of these perception patterns with path integration navigation patterns is the basis for our spatial cognition model. In Figure 6 we show examples of three different rat locations and orientations. Views are from the top of the circular arena having 4 colored cylinders used as external landmarks. Figure 6 shows (a) the rat at the center of the maze looking “north”, (b) the

rat next to the “magenta” landmark after following the trajectory shown by the white line, and (c) the rat next to the “yellow” landmark after following the trajectory shown by the white line.

In order to locate the rat in the arena we define a 9x9 place cell grid represented by the nodes in the world graph layer (WGL), as shown in Figure 7. These nodes specify a discrete set of possible “places” in the circular arena where the rat may be located at any time. These places are defined by the corresponding perceived landmark perceptions patterns and path integration patterns as processed by the model. At each step, the rat processes current perception and trajectory patterns and compare to previously stored patterns in order to recognize matching places already traversed. Figure 7 shows the corresponding locations and motor actions for the rat shown in Figure 6: (a) the rat is located in the center of the arena (darkest node) looking “north” with a relative view corresponding to the 5 adjacent (medium dark) nodes with the option to move in 8 possible directions corresponding to 45° orientations, (b) the rat has traveled the trajectory represented by the connected nodes in black and is currently looking “north west” with a relative view corresponding to the 5 adjacent nodes (medium dark and one dark node since it specified the previous location of the rat), and (c) the rat is now looking “south” with a relative view corresponding to the 5 adjacent nodes (medium dark and one dark node since it specified the previous location of the rat).

### **Experimentation Protocols**

In his landmark paper, Morris (1981) introduced a set of rat experiments in a water maze with visible and hidden platforms (goals) to evaluate the ability of a rat to swim towards the goal and escape from cold water by exploiting sensorial information. Although the experiments were exclusively behavioral without any electrical readings from the rat brain, the ultimate goal was to understand how the cognitive map in the rat hippocampus works. Related work in developing an

understanding of spatial cognition was developed by O'Keefe (1983) where the experiments he carried out involved primarily a T-maze and 8-arm maze as originally studied by Tolman (1948).

In this section we describe the experimentation protocols corresponding to the open-field rat experiments reported by Morris (1981). We designed two experiments for evaluation in correspondence to the hidden platform experiments exploiting visual cues, also referred to as landmarks, around the open field as originally specified by Morris:

- Experiment 1 is intended to demonstrate that rats employed their locale navigation system (as opposed to the taxon navigation system) to find the hidden platform in the arena; that is, rats need to relate the platform position with the location of environmental cues in the environment in order to find it.
- Experiment 2 further studies spatial learning due to the rat locale navigation system using different placement of the hidden platform: (a) *Place*, where the hidden platform is static during the complete experiment and (b) *Place-Random*, where the hidden platform is moved between four different locations.

Morris specified two additional set of experiments: *Cue + Place* and *Cue-Only*, where above-water platforms were positioned at a fixed and at different locations, correspondingly. Those experiments were meant to provide positive and negative controls, assuring the rat was not able to use direct cues to find the platform. Since it is certain that the virtual rat only perceives the platform when it is right over it, these experiments were not performed.

## **Experiment 1**

**Method.** Subjects: Fifteen instances of a virtual rat. Apparatus: A circular arena delimited with a boundary as illustrated by the top view in Figure 8. Four differently colored cylinders, named L1, L2, L3 and L4, surround the arena representing distinctive landmarks located at four

equidistant positions, N, W, E, and S, correspondingly. The apparatus includes a small colored circle representing the target platform or goal corresponding to the hidden white platform below the water surface in the Morris experiment. The virtual rat is only able to see this platform when it is directly over it.

**Procedure.** The procedure followed consisted of one (a) Pretraining trial, (b) Training (Escape Acquisition) trials, and (c) Test trials. A rat completes a trial of the experiment by reaching the goal location. This corresponds to the rats escaping from the cold water by standing over the hidden platform. During the experiment, Morris measured the latencies to reach the platform. However, since rats' swimming speed is not directly comparable with the displacement velocity of the virtual rat, we measured instead the number of actions performed, i.e., rotations executed at the current location and displacements to different locations. The trajectories traveled by the virtual rats were registered as Morris did with the real rats.

**Pretraining.** At the beginning of the experiment, all rats were given one trial in which they were placed into the arena for a while in order to get familiar with it and build a preliminary map as shown in Figure 7. No platform was present.

**Training (Escape Acquisition).** During the training procedure, the rats were organized in three groups performing 15 escape trials distributed in three sessions consisting of 6, 6 and 3 trials respectively, with every trial started at the arbitrarily designated W position and the platform always in position NE, as shown in Figure 9. The groups of rats differed only with respect to what happened in the test trials, which followed immediately after the 15th training trial.

**Test trials.** There were three successive test trials for all rats according to the group they belonged to, as follows:

Group *Same-Place* (6 rats). The platform was still in position NE, but the rat started successively from three novel start locations N, S, and E. The sequences of start location were uniformly distributed across rats within the group. Table II shows the departure positions for each rat in each one of the three testing trials.

Group *New-Place* (6 rats). Each rat was required to reach the platform using the same sequence of novel start locations but with the platform moved on each test trial. Table III shows pairs of “start location - platform location” employed for each trial, which correspond to the angular relationship held constant throughout training. In case the virtual rats had learned the sequence of motor actions required to reach the platform from the starting location, this series of test trials should present no difficulty; but in the opposite case, they would not be able to easily find the platform (showing that they truly employed their locale and not a form of taxon navigation system).

Group *Control* (3 rats). Test trials for this group started from W to reach the platform in NE. Their purpose was to provide a stable measure of the latency to reach the platform against which to assess the test session performance of the other two groups.

## **Experiment 2**

**Method.** Subjects: Sixteen instances of a virtual rat. Apparatus: The same circular arena and hidden platform as in Experiment 1.

**Procedure.** The procedure followed consists of (a) Pretraining trials, (b) Training (Escape Acquisition) trials, and (c) Test trials. We formed two groups of eight subjects. A rat completes a trial of the experiment by reaching the goal location that may vary from experiment to experiment.

***Pretraining.*** At the beginning of the experiment, all rats were given two consecutive trials in which they were placed into the arena for a while with no platform.

***Training (Escape Acquisition).*** During the training procedure, the rats were organized in two groups (8 per group) performing 20 escape trials distributed in three sessions consisting of 8, 8, and 4 trials respectively. The groups of rats were as follows:

***Group Place.*** The arena included the hidden platform placed at a fixed location throughout training for a given rat. The rat could only perceive the platform when directly on top of it. Platform locations were fixed at an arbitrarily designated SW, NW, NE, and SE location (not true magnetic directions, as shown in Figure 8) and uniformly distributed across the group (2 rats per platform location). A training trial began with placing the rat into the arena at position N, E, S, or W (see Figure 8). The number of actions executed by the rat to reach the platform was recorded, and the rat was placed for Trial 2, this time at a different starting location. Table IV shows the locations of the platform and starting points for each virtual rat in each trial of each session labeling the rats to identify them. The intention of this training protocol was to study how variability in the starting location affects learning of the static platform location.

***Group Place-Random.*** Rats in this group were trained with the hidden platform, but its location in the arena was moved from trial to trial. The hidden platform was placed in positions SW, NW, NE, and SE, but in an unpredictable sequence such that it was moved between two different locations across the 8 trials of the training session. The purpose of this training protocol was to study how variability in both the starting and the platform locations affects learning the task. Table V shows the platform locations sequence and departure points for each rat in each training trail.

During the second session of eight trials, only the sequence of start locations (for both groups) and end locations (for Group Place-Random) were changed. Finally, Session 3 included a further series of four training trials by which time performance appeared to have stabilized. In addition to measuring the number of actions to reach the platform, the paths traveled were recorded during these last four training trials.

**Test.** The fourth training trial of Session 3 was immediately followed by one of two test procedures: Test A and Test B. The groups were subdivided, with four rats from each group doing each test. The assignment was such that, for Group Place, a unique rat was trained for each compass position in each test condition.

**Test A.** This test was an assessment of the spatial bias of a trained rat. The platform used during training was removed from the arena and the rat placed in again for a while. The movements of the rat were recorded and analyzed by calculating the amount of time spent in each quadrant (SW, NW, NE, and SE) of the arena. Table VI shows the departure location of each rat (4 from Group Place, 4 from Group Place-Random) performing this one trial in Test A. Within each group, 4 compass departure positions were used, one per rat.

**Test B.** This test was also an assessment of spatial bias, but this time with the platform still in the arena so that the rats could try to learn a new spatial position. After the four training trials of Session 3, the platform was moved to a position diagonally opposite its training location (Group Place) or put in a fixed location for the first time for a sequence of four trials (Group Place-Random). A record was taken on the movements made by the rats to reach the platform, the path lengths were measured, and the paths were drawn. Table VII shows the departure locations and platform positions for each one of the rats (4 from Group Place, 4 from Group Place-Random) in each trial of Test B (for a total of 4 trials).

Table VIII summarizes the experimentation protocols.

### **Experimentation Results**

We used a virtual rat with local camera as described in the simulation environment (Section “MIRO/ASL/NSL simulation system”) to navigate in the arena and recognize objects by color. All the experiments were tested under simulation. We validated the experiments through a comparative behavioral analysis with results reported by Morris (1981) with rats.

#### **Experiment 1**

The results obtained from this experiment coincide with those reported by Morris (1981). All virtual rats learned the target location by the end of the training phase showing a stabilized number of executed actions on Trials 13-15. Figure 10 (left) shows this performance together with the test performance (Trials 16-18). All rats in Group New-Place showed a larger average number of actions over the three test trials than any rat in Groups Same-Place and Control. The numbers of these two groups overlap considerably, and this fact is also evident from Figure 10 (right), where the same data are plotted as a function of the departure location on the test trials. Comparing the performance of rats in Groups Same-Place and Control, it can be observed that it is invariant to starting position; i.e. the number of actions does not vary significantly when the rats are tested to navigate from N, S, E or W to NE, as opposed to the Group New-Place, where the target location has been changed.

Figure 11 illustrates the paths traveled on the first test trial by each virtual rat in each group. The rats in Group Same-Place reached the platform from any novel departure location by following very direct paths, whereas rats in Group New-Place searched first in the old platform location NE. These paths confirm that rats truly learned the platform location NE, which was reached from any starting location, and that they did not learn the sequence of motor actions

required to reach the platform location, since it was searched in its old location even though the same angular relationship between the starting and the platform locations was held constant both in training and testing phases.

## **Experiment 2**

As illustrated in Figure 12, Group Place-Random showed considerably poorer performance than Group Place during escape acquisition. For Group Place, the average number of actions executed to reach the platform location was within one standard deviation of the terminal number of actions by trial 15 of training. This was a slower rate of learning than the one reported by Morris with the rats belonging to this group, who reached mean escape latency within two standard deviations of the terminal acquisition latency by trial 6 of training. On the other hand, as Morris showed with rats, virtual rats of Group Place-Random were unable to stabilize the escape latency by the end of the training phase of the experiment due to variability of platform location. We analyzed the paths traveled by the virtual rats during the final training trial (Trial 20) and found out that the range of heading directions relative to the platform location observed at an arbitrary point of one radius of the arena into their track was  $15^\circ$  to  $165^\circ$ . This fact suggests that even though the rats of Group Place-Random were able to learn something, there wasn't any directionality in their behavior explaining the poorer performance compared to Group Place, where the average deviation from heading directly to the platform was  $0^\circ$ .

After performance had stabilized (Trials 17-20), the steady-state escape behavior of both groups was analyzed. Specifically, Figure 13 shows the average path lengths performed by the rats belonging to each group. As Morris found with rats comparing qualitatively the behavior between both groups, the virtual rats in Group Place-Random traveled very long paths with

considerable trial-to-trial variability, whereas Group Place showed progressively shorter paths by the end of the training phase of the experiment.

Also by analyzing the virtual rats' performance over Trials 17 through 20, we could observe that Group Place showed excellent directionality in its path toward the platform from all four starting locations N, S, E, and W. Figure 14 illustrates the tracks or trajectories followed by the virtual rat in each group that performed just worse than the median (there is an even number of rats in each group). As can be seen, only the rats in Group Place-Random behaved in a non-directional manner, i.e., confused on identifying a direct route to the platform. All paths in the figure are composed of lines oriented to 45 or 90 degrees revealing displacements from node to node within the topological map built during training (also shown in Trail 19 of Figure 14).

Figure 15 illustrates the paths taken during the first test trial by the same two virtual rats whose paths were shown in Figure 14. The rat of Group Place executed Test B showing a strong spatial bias toward the NE quadrant, which had been the rat goal platform's position throughout training. During this test trial, the platform was located in the SW quadrant for the first time, and even though the rat was able to reach the platform, it shows the behavioral strategy of searching for the platform in the quadrant where it used to be located.

On the other hand, the rat of Group Place-Random executed Test A (i.e., without the platform). As observed in Figure 15, the rat searches for the platform all over the arena until it was removed after a while.

While analyzing the performance of the four virtual rats in each group on the condition of removing the platform (Test A), we registered the time they spent in each quadrant and the corresponding number of actions executed. The average results are shown in Figure 16, where it can be observed that the rats in Group Place present a strong bias toward their respective training

quadrant as opposed to rats in Group Place-Random, who show no directional bias because they had not even learnt the variable platform location during training.

The performance of the four virtual rats in each group during Test B consisting of four trials is illustrated by Figure 17. As can be observed, the maximum average number of actions executed by the rats of both groups is reported for the first test trial (see Figure 17, left), as well as the maximum path length (see Figure 17, right). Rats in Group Place traveled to and about the place where the platform used to be located during training until eventually they reached the platform at its new location. For rats in Group Place-Random, this test condition was their first experience with the platform placed in a fixed location for a series of four trials, and the results showed a decrease in their number of actions and the path length traveled across the four test trials. Actually, comparisons between performance of both groups indicate that Group Place reached the new platform location slower than Group Place-Random, which reflects once more the strong spatial bias toward the platform position used throughout training of Group Place.

### **Conclusions and Discussion**

The goal of the research described in this paper is to study rat spatial cognition in circular arenas by exploiting visual cues in the environment. For this purpose we extended the Barrera-Weitzenfeld (2008) model to support rat navigation in open mazes without corridors. Open arenas pose additional challenges to mazes with corridors in that navigation may take place in any direction at any time while space representation requires metric information as opposed to corridor mazes where topology is sufficient to support goal-oriented navigation.

The experiments with virtual rats described in this paper were originally devised for rats by Morris (1981). Experiment 1 accomplished its purpose: demonstrate that rats employed their locale navigation system to find the hidden platform in the arena. The fixed location of the

platform, with no cues spatially concurrent with it available to guide the rat to the goal, was truly learned relative to visual cues. It was clear that rats did not learn the sequence of motor actions required to reach the platform location; if that would be the case, rats would not have searched the platform in its old location but in the new one, since the same angular relationship between the starting and the platform locations was held constant in both training and testing phases.

Another important result from Experiment 1 is the fact that rats in Group Same-Place were able to adapt their behavior to find the fixed platform from novel locations with no significant increase in their number of actions relative to the static starting location.

Once the spatial learning strategy followed by rats was identified, Experiment 2 further analyzes the impact of introducing variability in the hidden platform location. When this variability is present during training, as was the case for Group Place-Random, rats are unable to learn the goal location. They show no directionality to the platform during their path, but a broad range of heading directions relative to the platform location fluctuating from  $15^\circ$  to  $165^\circ$ , as opposed to rats in Group Place, where the average deviation from heading directly to the platform was  $0^\circ$ .

Considering the testing phase Experiment 2, the search strategy showed by virtual rats in Group Place indicates that they learned a lot about the spatial location of the hidden platform, since they spent some time searching for the platform in the quadrant where it used to be located during training. This behavior was shown when the platform was removed from the arena (Test A), and also when it was only moved within the arena (Test B), and in this last case, rats were able to relearn the new platform location rapidly.

The performance of Group Place-Random is another aspect of interest in the test results of Experiment 2. Even though the virtual rats showed no directionality in their platform approach

paths during training, they were able to improve their behavior by decreasing the average number of actions executed in the four trials of Test B from 134 to 107 actions. This improvement was even more evident in the results by Morris, where the rats of Group Place-Random reduced their average escape latency in 70% approximately, whereas virtual rats did it in 20% approximately.

Finally, it is worth to notice how, even though our model emphasizes the use of place cells for navigation, the actual learned policy involves an association between PCL (hippocampus) activation patterns stored in the WGL (cortex) and actions to perform. Since the PCL layer's activity integrates both visual and kinesthetic information, our model is consistent with recent findings that the hippocampus plays a role in path integration navigation strategies (Maaswinkel, Jarrard, Whishaw, 1999). Namely, the deactivation of the PCL layer would prevent self-motion cues to be properly used by the learned action selection policy.

In summary, our work demonstrates the accuracy of our spatial cognition model to the corresponding results reported by Morris: (1) the sudden emergence of a search strategy never seen during training when the hidden platform was moved or removed; (2) the speed with which the virtual rats learned a new platform location; and (3) the ability of the virtual rats to show instantaneous transfer to new starting locations with no evidence that the direction of approach to the platform influence accuracy or latency. The successful performance of the virtual rats in Experiments 1 and 2 depends on effective place recognition and learning capabilities provided by the extended model.

A future objective of this work is to test with physical robots including testing the new model in open and corridor mazes (Barrera and Weitzenfeld 2008; Barrera et al 2011). In the current circular arena experiments, there are important challenges in terms of space

representation that were not present before and require further analysis. The most important challenge is the integration of space representation based on landmarks with the robot odometry (Tejera et al., 2013). The lift of discrete rotation angles constraint and the addition of noise to the self-motion cues another challenge associated with running the system in real robots. Discrete angles combined with the absence of noise simplify the problem in that the rat always visits a finite discrete set of points in the environment.

In order to solve these challenges, we are currently working on a representation of space that integrates place cells with grid cells and head orientation cells. Furthermore, we are considering representation at a multiple scale similar to dorso-ventral organization of grid cells and place cells in the mammalian brain (Jung et al., 1994; Hafting et al., 2005; Barry et al., 2007; Stensola et al., 2012; Erdem and Hasselmo, 2012 & 2014; Milford et al., 2010).

We also believe that additional competing or cooperating behaviors should be incorporated in the model, in order for it to contemplate some of the recent findings about rats' psychology behind water maze solving. Recent findings point out to additional strategies, other than locale, taking control at different stages of a single trial, such as taxon navigation (for cued versions) and directional behaviors (Hamilton, Rosenfelt, Whishaw, 2004; Hamilton DA, Akers KG, Johnson TE, Rice JP, Candelaria FT, Redhead ES, 2009).

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## Tables

Table I

*The Q-Learning algorithm employed in the spatial cognition model.*

Instruction Number	Instruction
1	Set $Q(s, a)$ randomly
2	Repeat (for each trial)
3	Select an action $a$ from state $s$ using a policy derived from $Q$
4	Execute action $a$ observing the immediate reward received $r$ and the next state $s'$
5	Update $Q(s, a)$ using: $Q(s,a)=Q(s,a)+\alpha[r+\gamma\max_{a'}Q(s',a')-Q(s,a)]$
6	Set $s$ to $s'$
7	Until $s$ is a final state

Table II

*Departure locations during 3 test trials of 6 rats composing Group Same-Place.*

Virtual rat ID	Trial starting locations		
	1	2	3
1S	N	S	E
2S	S	E	N
3S	E	N	S
4S	N	E	S
5S	E	S	N
6S	S	N	E

Table III

*Start locations and platform locations employed for each test trial, corresponding to the same angular relationship held constant throughout the training phase of Group New-Place.*

Test Trial	Rat Start Location	Platform Location
1	N	SE
2	E	SW
3	S	NW

Table IV

*Platform locations and rat starting positions during 20 training trials of 8 rats composing Group Place.*

Virtual rat ID	Platform location	Trial starting position																			
		Session 1					Session 2					Session 3									
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1P	NE	W	S	W	S	N	E	N	E	S	W	S	W	E	N	E	N	W	S	N	E
2P	NE	W	S	N	E	W	S	N	E	E	N	S	W	E	N	S	W	W	S	N	E
3P	NW	S	E	S	E	N	W	N	W	E	S	E	S	W	N	W	N	S	E	N	W
4P	NW	S	E	N	W	S	E	N	W	W	N	E	S	W	N	E	S	S	E	N	W
5P	SE	N	W	N	W	E	S	E	S	S	E	S	E	W	N	W	N	N	W	E	S
6P	SE	N	W	E	S	N	W	E	S	S	E	W	N	S	E	W	N	N	W	E	S
7P	SW	E	N	E	N	S	W	S	W	N	E	N	E	W	S	W	S	E	N	S	W
8P	SW	E	N	S	W	E	N	S	W	W	S	N	E	W	S	N	E	E	N	S	W

Table V

*Platform locations sequence and starting positions during 20 training trials of 8 rats integrating Group Place-Random.*

Virtual rat ID	Platform location	Trial starting position																			
		Session 1										Session 2					Session 3				
		1	2	3	4	5	6	7	8	9	10	1	1	1	1	1	1	1	1	1	2
1R	NE-NW- SE-SW	W	S	W	S	N	E	N	E	S	W	S	W	E	N	E	N	W	S	N	E
2R	SW-SE- NW-NE	W	S	N	E	W	S	N	E	E	N	S	W	E	N	S	W	W	S	N	E
3R	NW-SE- SW-NE	S	E	S	E	N	W	N	W	E	S	E	S	W	N	W	N	S	E	N	W
4R	NE-SW- SE-NW	S	E	N	W	S	E	N	W	W	N	E	S	W	N	E	S	S	E	N	W
5R	SE-SW- NE-NW	N	W	N	W	E	S	E	S	S	E	S	E	W	N	W	N	N	W	E	S
6R	NW-NE- SW-SE	N	W	E	S	N	W	E	S	S	E	W	N	S	E	W	N	N	W	E	S
7R	SW-NE- NW-SE	E	N	E	N	S	W	S	W	N	E	N	E	W	S	W	S	E	N	S	W
8R	SE-NW- NE-SW	E	N	S	W	E	N	S	W	W	S	N	E	W	S	N	E	E	N	S	W

Table VI

*Starting positions during Test A of 4 rats integrating Group Place and 4 rats in Group Place-Random.*

Group Place		Group Place-Random	
Virtual rat ID	Starting position	Virtual rat ID	Starting position
1P	SW	1R	SW
3P	SE	3R	SE
5P	NW	5R	NW
7P	NE	7R	NE

Table VII

*Platform locations and rats starting positions during 4 trials of Test B for 4 rats integrating*

*Group Place and 4 rats in Group Place-Random.*

Group Place					Group Place-Random				
Virtual rat ID	Platform location	1	2	3 4	Virtual rat ID	Platform location	1	2	3 4
2P	SW	W	S	N E	2R	NE	W	S	N E
4P	SE	S	E	N W	4R	NW	S	E	N W
6P	NW	N	W	E S	6R	SE	N	W	E S
8P	NE	E	N	S W	8R	SW	E	N	S W

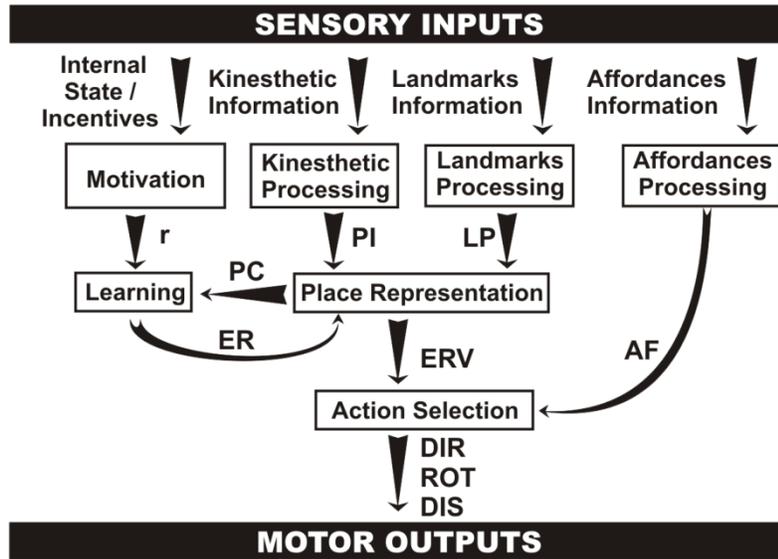
Table VIII

*Experiment Summary.*

<b>Experiment</b>	<b>PreTraining</b>	<b>Training</b>		<b>Test 1 (Test A)</b>		<b>Test 2 (Test B)</b>	
	<b>Starting Position</b>	<b>Starting Position</b>	<b>Platform Location</b>	<b>Starting Position</b>	<b>Platform Location</b>	<b>Starting Position</b>	<b>Platform Location</b>
1 (same-place)	Random	Static	Static	Variable	Static		
1 (new-place)	Random	Static	Static	Rotated	Rotated		
2 (place)	Random	Variable	Static	Variable	None	Variable	Static
2 (place-random)	Random	Variable	Variable	Variable	None	Variable	Static

*Note:* Variable corresponds to cardinal points, whereas Rotated maintains in the test same angular relationship between starting and platform location during training.

Figures



*Figure 1.* The modules of the spatial cognition model and their interaction.  $r$  = immediate reward; PI = kinesthetic information pattern; LP = landmarks information pattern; AF = affordances perceptual schema; PC = place information pattern; ER = expectation of reward corresponding to PC in the active map node and the current rat direction; ERV = array of eight expectations of reward associated to each direction in the active map node; DIR = next rat direction; ROT = rat rotation; DIS = next rat moving displacement.

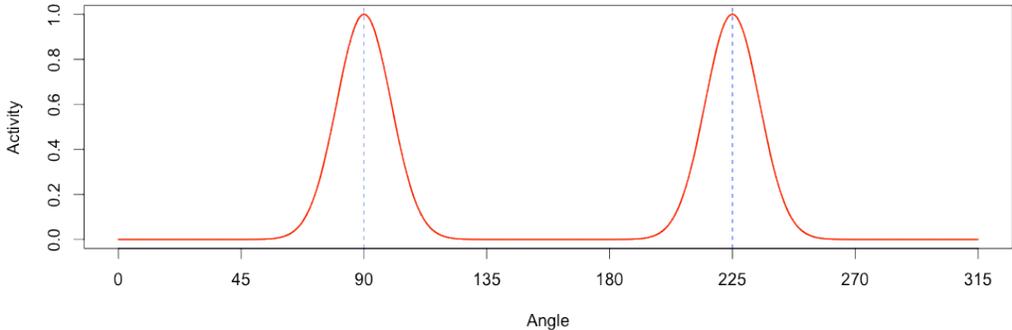
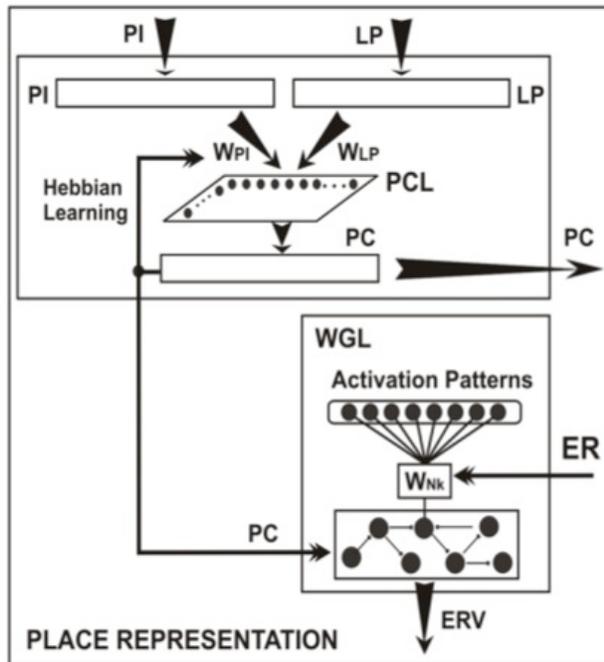
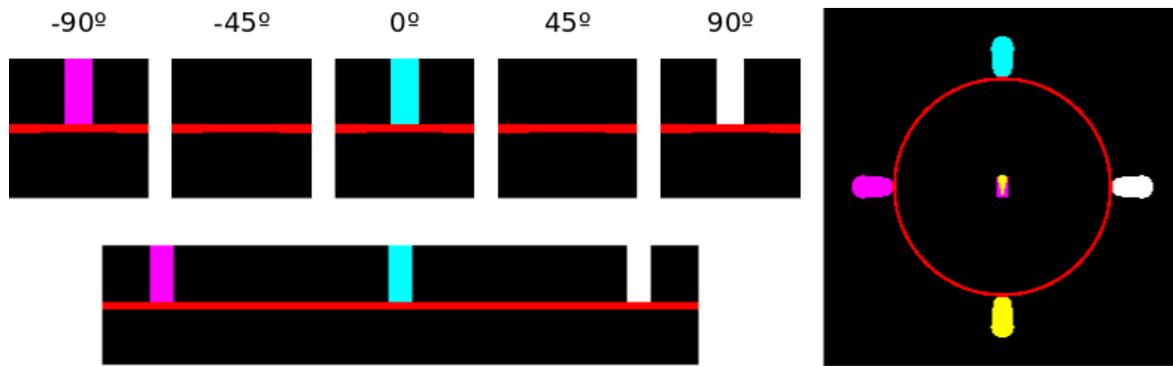


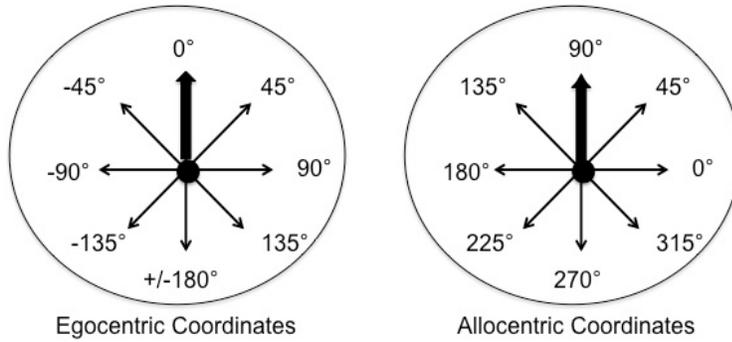
Figure 2. Affordances perceptual schema (AF) when only affordances of 90 and 225 degrees can be executed.



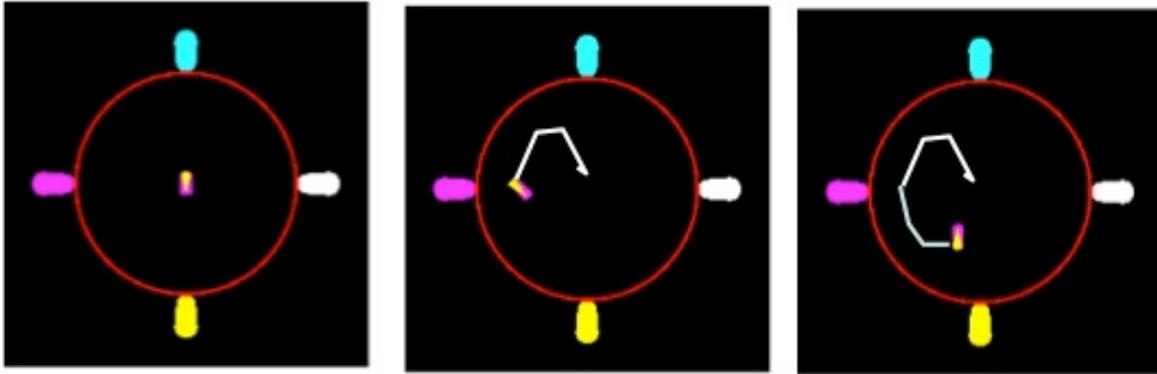
*Figure 3.* The place representation module of the spatial cognition model combines kinesthetic information and landmark processing input. Glossary: PCL= place cell layer; WGL= world graph layer; PI= kinesthetic information pattern; LP= landmarks information pattern;  $W_{PI}$ = connection weights between PIFDL and PCL;  $W_{LP}$ = connection weights between LL and PCL;  $W_{Nk}$ = connection weights between any given map node  $k$  and its corresponding Activation Pattern units; PC= place information pattern; ER = expectation of reward corresponding to PC in the active map node and the current rat direction; ERV = array of eight expectations of reward associated to each direction in the active map node.



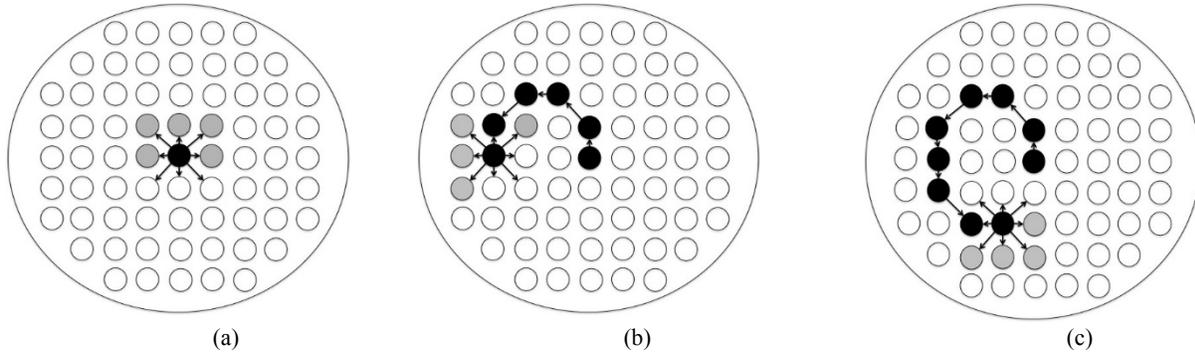
*Figure 4.* Virtual rat looking “north” from the center of a circular arena corresponding to a  $0^\circ$  egocentric view: (left) panoramic image covering a 210-degree field of view, (right) corresponding top view of the arena with the rat in its center.



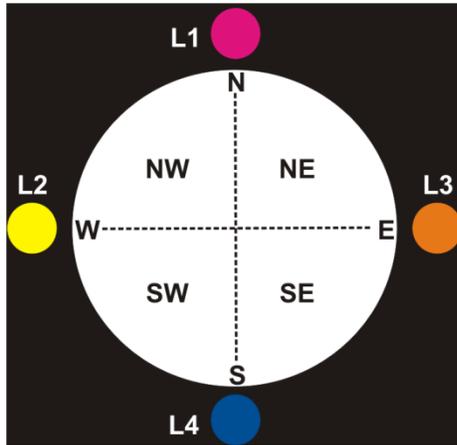
*Figure 5.* (a) Egocentric (local) reference frame representing rat orientation relative to its body with  $0^\circ$  representing front view, and (b) allocentric (global) reference frame representing absolute orientations with respect to the maze independent from rat location or orientation.



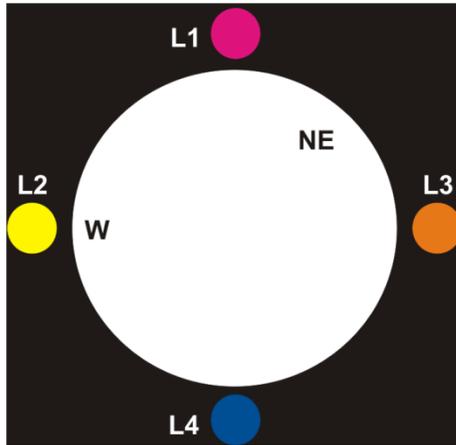
*Figure 6.* The figure shows a virtual rat (a) located in the center of the maze with  $90^\circ$  orientation (looking “north”) in allocentric coordinates, (b) located west next to the magenta landmark after moving for a short time, and (c) located south-west next to the yellow landmark after additional time with  $270^\circ$  orientation (looking “south”) in allocentric coordinates.



*Figure 7.* The diagram corresponds to the rat motions shown in Figure 6 with the open arena represented by approximately 9x9 world graph nodes organized in a grid where a maximum of 8 adjacent nodes can be considered for navigation at any time. In (a), the rat is facing north and its view corresponds to the 5 adjacent (medium dark) nodes with the option to move in 8 possible directions from the center location. In (b), after having traveled all dark nodes, the view looking “north west” is shown (4 adjacent medium dark nodes, plus one dark node above the rat). In (c), the rat is now looking “south”, and its relative view after having traveled the path specified by the connected dark nodes is shown.



*Figure 8.* Circular arena employed during simulated experiments with several instances of virtual rats. Four colored circles surrounding the arena represent distinctive landmarks located at four equidistant positions. A hidden circle representing the platform of the Morris experiment is sometimes put inside the arena at particular locations NW, NE, SW, or SE. The virtual rats initiate from positions N, S, E or W.



*Figure 9.* The circular arena showing the platform location, NE, and the departure position of rats during training, W.

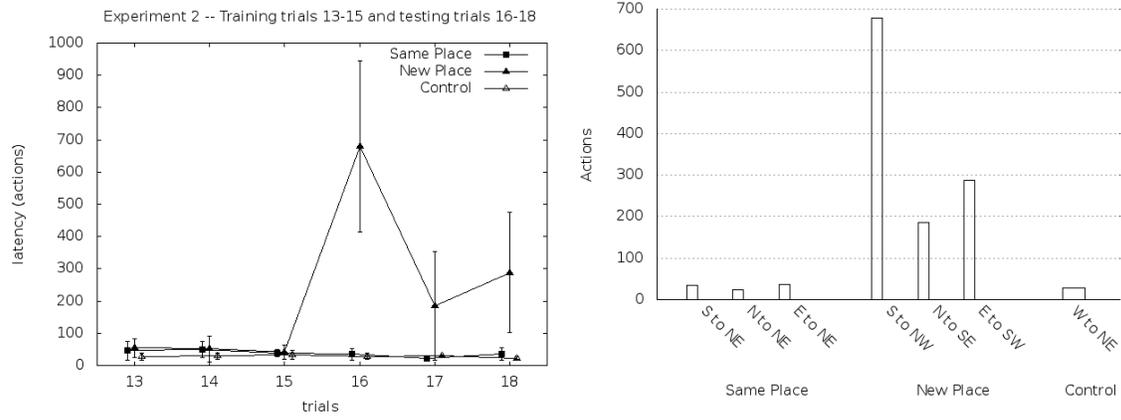
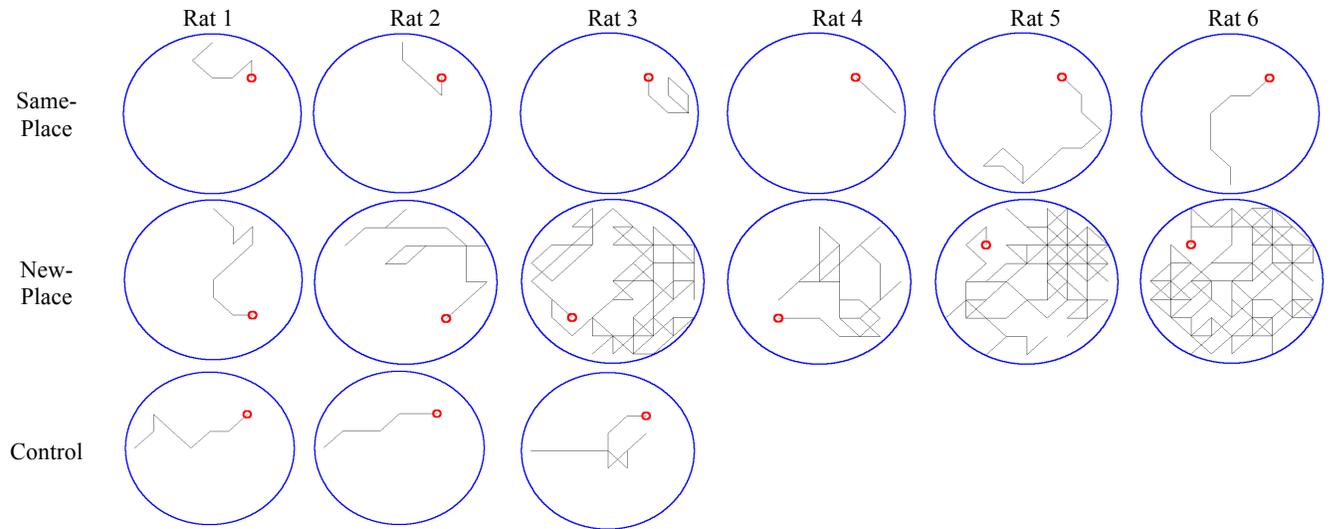


Figure 10. The average number of actions executed by virtual rats over Training Trials 13-15 and Test Trials 16-18 in Experiment 1 (left). Test trials data are plotted again in (right) as a function of the departure and target locations.



*Figure 11.* A top-view of the paths traveled by the 15 virtual rats during the first test trial of Experiment 1. The rats are organized in Groups Same-Place, New-Place, and Control.

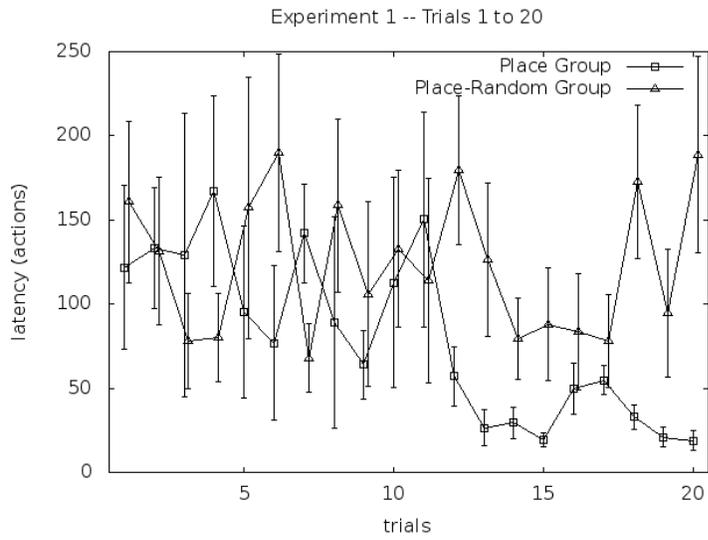
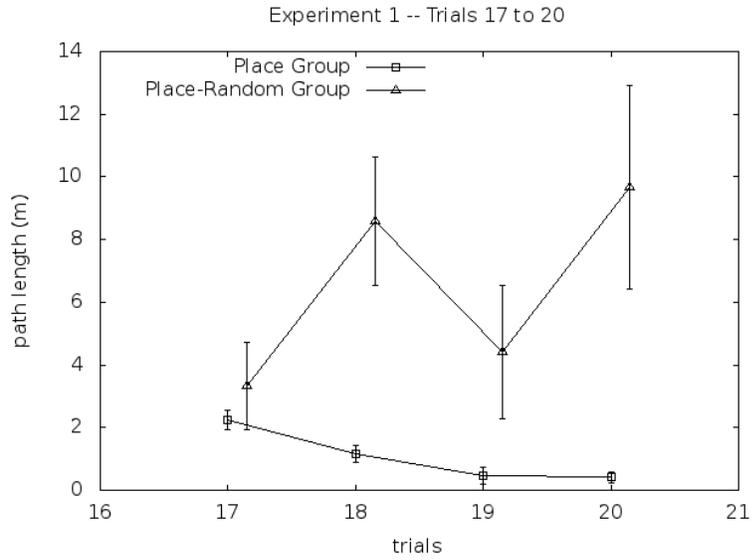
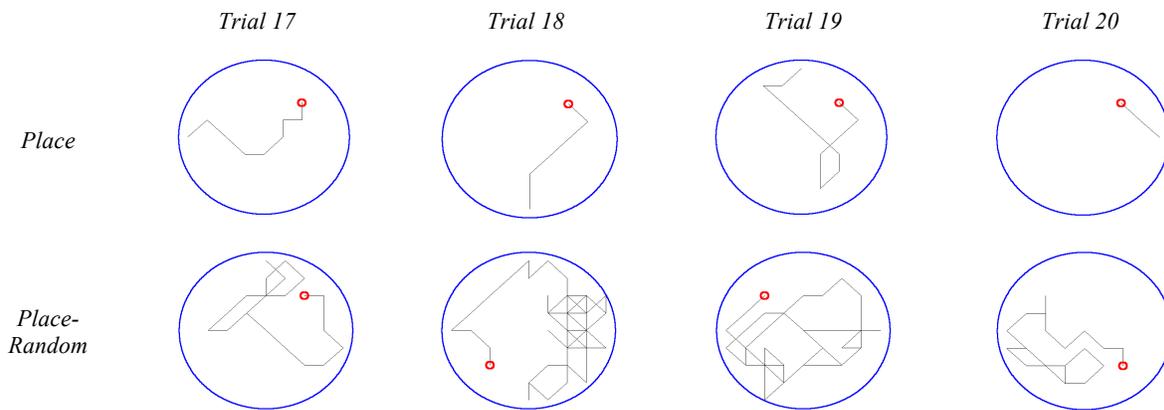


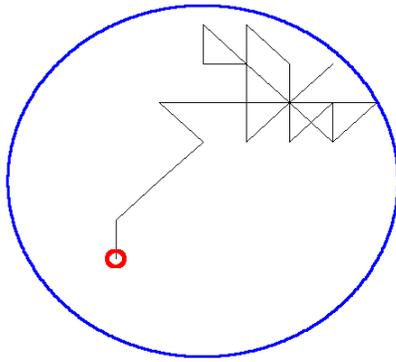
Figure 12. Escape latency expressed in number of actions performed by virtual rats over Trials 1-20 of the training phase of Experiment 2. All data points are plotted +/- 1 SE.



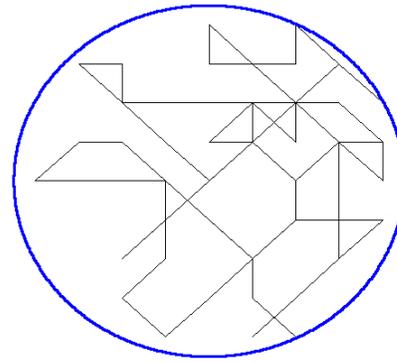
*Figure 13.* Path lengths in meters traveled by virtual rats over Trials 17-20 of the training phase of Experiment 2. All data points are plotted +/- 1 SE.



*Figure 14.* A top-view of the tracks taken by the virtual rat in Group Place and in Group Place-Random that performed just worst than the median (with respect to directionality). The paths are reasonably direct for the rat of Group Place departing from W in Trial 17, S in Trial 18, N in Trial 19, and E in Trial 20, whereas the rat of Group Place-Random traveled all over the arena departing from N in Trial 17, S in Trial 18, E in Trial 19, and W in Trial 20.

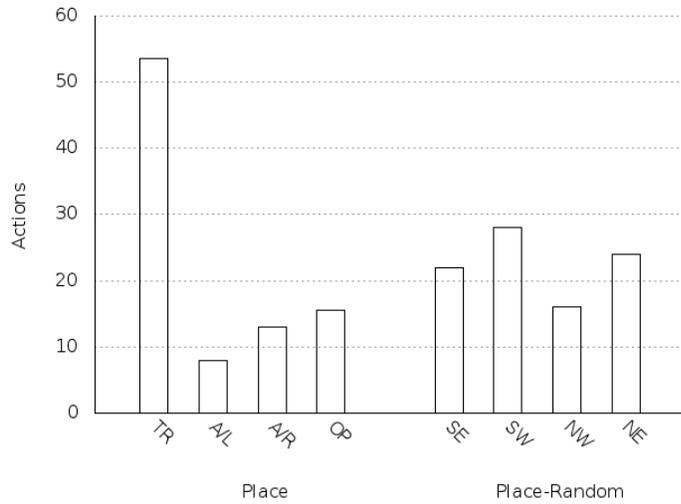


Group Place - Test B



Group Place-Random - Test A

*Figure 15.* A top-view of the tracks taken by the same virtual rat as in Figure 14 during their first test trial. The rat in Group Place (left) executed Test B, whereas the rat in Group Place-Random executed Test A removing the platform (right).



*Figure 16.* The average number of actions executed by the virtual rats in each quadrant during Test A. For Group Place, TR is the training quadrant, A/L and A/R correspond to the adjacent quadrants to the left and to the right respectively, and OP refers to the opposite quadrant.

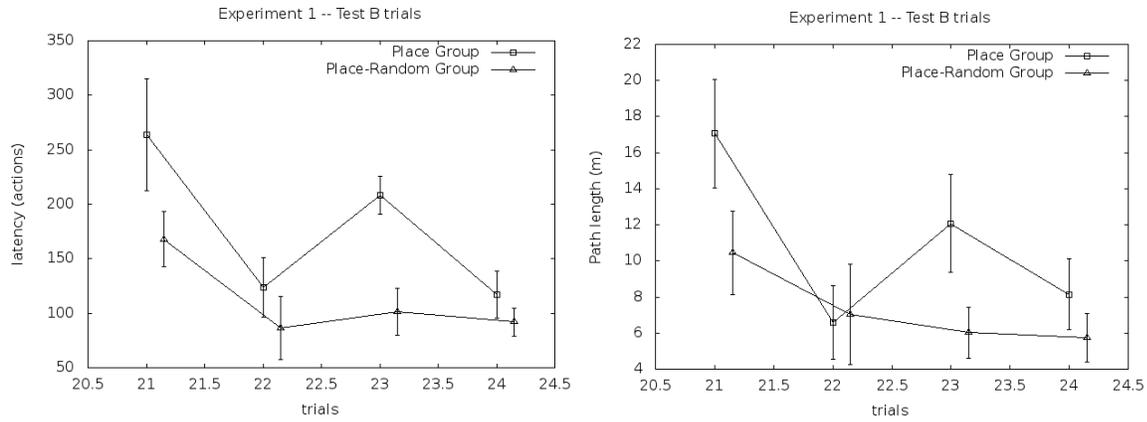


Figure 17. The average number of actions executed by virtual rats of both groups in each one of the four trials of Test B (left), and the corresponding path lengths registered (right).