Animat Navigation Using a Cognitive Graph

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abstract

This paper describes a computational model of the hippocampus that makes it possible for a simulated rat to navigate in a continuous environment containing obstacles. This model views the hippocampus as a “cognitive graph”, i.e., an hetero-associative network that learns temporal sequences of visited places and stores a topological representation of the environment. Calling upon place cells, head direction cells and “goal cells”, it suggests a biologically plausible way of exploiting such a spatial representation for navigation, which does not require complicated graph-search algorithms. Moreover, it permits “latent learning” during exploration, i.e., the building of a spatial representation without the need of any reinforcement. When the rat occasionally discovers some rewarding place it may wish to rejoin subsequently, it simply records within its cognitive graph, through a series of goal and sub-goal cells, the direction where to move from any given start place. Accordingly, the model implements a simple “place recognition-triggered response” navigation strategy. Two implementations of place cells management are studied in parallel. The first one associates place cells to place fields that are given a priori and that are uniformly distributed in the environment. The second one dynamically recruits place cells as exploration proceeds and adjusts the density of such cells to the local complexity of the environment. Both implementations lead to identical results. The paper ends with a few predictions about results to be expected in experiments involving simultaneous recordings of multiple cells in the rat hippocampus.

1 Introduction

The discovery of *place cells* in areas CA3 and CA1 of the rat hippocampus (O'Keefe and Dostrovsky, 1971) – cells that discharge selectively when the rat is in restricted regions of the environment (their *place fields*) – led to the idea that the hippocampus functions as a *cognitive map* of space (O'Keefe and Nadel, 1978). Cells that fire as a function of the animal's orientation in space, *head-direction cells*, have also been evidenced in various other regions of the rat brain (e.g. postsubiculum [Taube et al., 1990]). Thus, representations of position and orientation, necessary for any navigation system, are present in the rat brain. Here we propose a computational model of rat navigation that calls upon such representations.

The hippocampus is usually considered as an auto-associative network that learns, stores and recalls specific *episodes*, i.e. individual events or configurations of stimuli. According to such a view, the hippocampus learns the relationships between different stimuli that all characterize the same situation or event. At the time of recall, partial cues can be completed and the whole episode can be retrieved (Rolls, 1991). However, there is another view, which is increasingly popular, according to which the hippocampus rather functions as an hetero-associative network, that learns, stores and recalls the relationships between neighboring places (spatial relationships, e.g. [Schmajuk and Thieme, 1992], [Muller et al., 1996]) or between successive events (temporal relationships, e.g. [Jensen et al., 1996], [Wallenstein and Hasselmo, 1997]). At the time of recall, the representation of a place (respectively of an event), associated with the intention of some action, leads to the *prediction* of the next place (respectively of the next event).

The spatial and the temporal domains are quite similar from a navigation point of view. Indeed, we can consider the fact of going from place A to place B and then to place C as the temporal sequence of being at A, at B and then at C. If each of these places are represented by place cells within the rat hippocampus, the movement of the rat through these 3 places is represented by the successive activations of the corresponding place cells.[1] Conversely, predicting that a certain movement from place A will lead to place B and then place C is equivalent to "planning" a trajectory from A to C.

The computational model that we propose in this paper capitalizes on such considerations. It is evaluated within the context of the navigation task of a simulated rat – i.e., a variety of animat (Meyer and Wilson, 1991) – that lives in a continuous environment populated with various obstacles. Basically, it considers that the rat hippocampus stores sequences that can be used to predict the consequences of a considered action and it calls upon the following principles:

- Exploration is a process by which the rat experiences sequences of places.
- The hippocampus learns these temporal sequences as a topological graph by transforming a temporal relationship into a spatial relationship.

[1] Space is continuous, and so is time. The delays between the activations of the 3 place cells depend on how much the corresponding place fields overlap and how far they are from one another.

- This topological graph can be used to learn all the trajectories leading to a specific goal.
- The rat navigates according to what we called a “place recognition-triggered response” strategy (Trullier et al., 1997; Trullier and Meyer, 1997a).

As we will show, this model is based on biologically plausible mechanisms. In particular, because it implements a low-level strategy, it avoids using the unnatural planning algorithms that characterize most hippocampal models of navigation.

In the following, we will first describe the experimental and the theoretical evidence supporting the idea that the rat hippocampus functions as a memory for sequences. Then, we will present the architecture and the mechanisms of our computational model. We will show that the model can cope with continuous environments and can be used to avoid obstacles.

2 The hippocampus as a memory for sequences

One specific property of hippocampal place cells is the specific temporal relationship between the discharge of place cells and the overall theta rhythm, a sinusoidal EEG oscillation between 4 Hz and 10 Hz observed in the rat hippocampus when the animal is engaged in locomotor behaviors (O'Keefe and Recce, 1993; Skaggs et al., 1996). As the rat runs through a place field, the corresponding place cell discharges first at a late phase and progressively at earlier phases of the theta cycle (Fig. 1). Thus, the discharge of a place cell indicates that the rat is within the corresponding place field, while the phase of the discharge indicates whether the rat is entering the place field (the place field is in front of the animal) or leaving the place field (the place field is behind the animal). This property is referred to as “phase precession” or “phase coding”.

Include Figure 1 around here

Include Figure 2 around here

Several computational models were proposed to account for this phenomenon (Tsodyks et al., 1996; Jensen and Lisman, 1996; Samsonovich and McNaughton, 1997; Wallenstein and Hasselmo, 1997). All of them are based upon similar principles : within each oscillation of the theta rhythm (a theta cycle), activities from place cells corresponding to the current position of the rat would propagate, through the recurrent connections of the CA3 region, to other place cells whose place fields would be located in front of the rat. The farther from the current position a place field is, the later in the theta cycle the corresponding place cell would be activated by this propagation. As the rat moves forward, this place field gets nearer and the place cell would fire earlier and earlier.

The connections that enable this propagation of activities have to account for the layout of the place fields. In most models, this is achieved through learning, that is, connections corresponding to neighboring cells get strenghtened while the other connections get weakened. As mentioned above, such a learning can be thought of as the learning of sequences (of places).

Learning of sequences is what is thought to occur in the hippocampus. Indeed, phase coding compresses temporal sequences by storing events that can be hundreds of msec apart into successive gamma sub-cycles that are 10 to 20 msec apart. This latter time separation seems to be the ideal timing for learning to occur (Skaggs et al., 1996). Moreover, phase coding maintains the correct ordering of place cell firing and thus enables asymmetric learning of the connections that can take into account the orientation of the animat and how it moved from one place to the other.

For instance, Jensen et al. (1996) proposed a neural network model of short-term memory and of sequence learning based on a biophysically plausible mechanism. It exploits the superposition of high-frequency gamma oscillations (20-60 Hz) on top of a low-frequency theta oscillation (5-8 Hz) to segment time into cycles that are divided into discrete sub-cycles. Such a network is able to learn sequences of up to 7 ± 2 items. Neurons of this network, each representing a new event, maintain their activity through an intrinsic mechanism (a specific activity-dependent depolarizing current) and discharge within one gamma sub-cycle at each theta cycle. Subsequent events are represented by other neurons that discharge at *subsequent* gamma sub-cycles. Thus, within each theta cycle, successive gamma sub-cycles code for successive events and the whole sequence is stored in the correct temporal order. Thus, neurons that fire within a sub-cycle all correspond to the same particular event and ensembles of neurons that fire within successive sub-cycles correspond to two successive events. A simple Hebbian learning rule, applied to the connections from the first ensemble to the second one, enables the association of one event with the next in the sequence.

As an evidence that the hippocampus might actually function as a memory for sequences, Jensen and Lisman (1996) subsequently showed that their model could account for the *phase precession* of hippocampal place cells. Their model learns sequences of places and subsequently recalls them within a theta cycle. In other words, it predicts future positions from the current one. When the rat is at a certain position, the corresponding place cell discharges at the beginning of a theta cycle and, during the rest of the theta cycle, the hippocampus predicts the 7 places ahead of the animal that it will traverse if it keeps on moving. A step later, the animat is one place further and thus the places it predicted at the previous step are closer and the corresponding place cells fire earlier in the theta cycle (Fig. 2).

3 The Model

The global architecture of our model (Fig. 3, top) is a simplified version of a previous model (Trullier and Meyer, 1997b) that closely emulated the architecture of the rat hippocampus. Each of its 4 layers has a specific and distinct function but only the last two are simulated here.

Include Figure 3 around here

3.1 Place cells

In a first version of the model, we first assume that place fields are uniformly distributed in the environment. As the animat moves in a continuous manner within the environment, only a subset of its place cells is active, in accordance with experimental data. Such a process, which keeps the total activity within the hippocampus very low, is thought to involve inhibitory interneurons, both through feedforward and feedback pathways, that are not explicitly modeled here (Marr, 1969; Sharp, 1991).

In practice, 5 place cells, defined as those whose place field centers are closest to the current position of the animat (Fig. 4a), emit a spike.

Include Figure 4 around here

We have previously suggested that the role of dentate gyrus is to act as a short-term memory of the sequence of visited places and consequently to activate place cells in the CA3 region of the hippocampus through the strong mossy fiber synapses (Trullier and Meyer, 1997b). Here, we do not explicitly simulate the dentate granular cells but we assume that place cells fire at specific phases with respect to the theta rhythm as the result of the activation by the dentate gyrus, that is, in the same temporal order as the sequence of visited places. In other words, if a place cell starts firing after a silent period (i.e. the animat enters the corresponding place field), we assign it the latest phase in the theta cycle. If it fires again at the next simulated time step (i.e. the animat hasn't moved out of the place field yet), its phase is decreased. This simulates phase precession and the fact that place cells fire within each theta cycle in the order of the experienced place sequence (Fig. 4b).

Each simulated timestep, that is, each movement of the animat, corresponds to one theta cycle (as in the model of (Burgess et al.) [1994]).

In a parallel version of the model, we introduced a mechanism by which the animat could recruit place cells according to the local complexity of the environment. Such a possibility has already been considered by Poucet (1993) and similar functionalities have been implemented by Touretzky and Redish (1996). In this approach, they enabled us to save computation time by simulating only the needed place cells.

We first assume that the animat uses wall corners as landmarks and that, although there may be many such landmarks in the environment, the animat is able to recognize them individually. Place cells' activities now depend on the distances to a certain number of these landmarks. In our simulations, we used the following activation function:

$$act = \prod_{i=1}^{n} exp(-\frac{(d_i - d_i^*)^2}{\sigma^2})$$

n is the number of landmarks associated with the place cell, d_i is the transform of the distance between the current position of the animat and landmark i ($d_i = exp(-\text{actual distance})$ so that $0 \leq d_i \leq 1$), d_i^* is the same transform but for the distance between the location where the place cell has been recruited and landmark i and σ is a parameter that grossly determines the size of the resulting place fields. When a landmark is not visible, d_i is arbitrarily set to -0.1. The place cells with activities above a given threshold are then allowed to emit a spike, in the limit of the 5 most activated place cells. In practice, wall corners in the simulation are assigned unique IDs and at each simulated timestep, the animat gets the list of IDs corresponding to the visible landmarks, along with their respective distances to the animat's position.

When there are fewer than 5 place cells with activities above the threshold, a new place cell is recruited in order to better represent the current location (Fig. 5). This new place cell "learns" the distances between the animat and the visible landmarks.

Include Figure 5 around here

No difference in performance was found between the two models that only differ in the way place cells are simulated (Fig. 6). As a consequence, we will indifferently use the figures corresponding to the results of both models in the remaining of the paper.

Also, simulating the fact that place cell activities depend upon distances to visible landmarks was done for illustrating how place cells could be recruited as the animat explores the environment and studying how the resulting representation depended upon the local complexity of the environment. As a consequence, no effort was made to take into account problems such as sensory aliasing or the orientation-dependence of the views. These points will be dealt with in future work, involving a real mobile robot. However, we believe that the number of landmarks will be large enough to enable identification or measurement errors on a few landmarks.

Include Figure 6 around here

3.2 Topological representation

The CA3 region of the hippocampus has a dense recurrent connectivity with plastic synapses (Rolls, 1995). Like Schölkopf and Mallot (1995), we assume that these synapses can be gated by head-direction information and that the propagation of activity from a pre-synaptic cell to a post-synaptic cell, as well as synaptic modification of the connection, occur only if the animat is oriented in the direction corresponding to the gating head-direction information. Thus, as the animat explores its environment, synapses connecting place cells corresponding to place fields it traverses are modified. Synaptic weights are enhanced (Long-Term Potentiation or LTP) if both pre- and post-synaptic cells are active at successive phases (Fig. 3, bottom, Fig. 4c). They are depressed (Long-Term Depression or LTD) if either the pre- or the post-synaptic cell is active while the other is silent. Accordingly, they progressively stabilize at a value that reflects the overlap between place fields, if the place fields are oriented in the appropriate direction. For instance, the connection gated by the "northward" information between place cell a and place cell b in Figure 7 has been enhanced during exploration because the animat went from place field A, corresponding to a, to place field B, corresponding to b, as it was moving northward. Similarly, the connection gated by the "eastward" information between place cell a and place cell c has been enhanced. However, the connection gated by the "northward" information between a and c has almost not been enhanced (if it were, it would be because the animat traversed through the overlapping region between place fields A and C while facing North) and all connections between place cell a and place cell d have been depressed because place fields A and D are too far apart from each other.

Include Figure 7 around here

In the end, the population of CA3 place cells with their recurrent synapses can be viewed as a directed graph, where nodes are places and links represent the fact that nodes are adjacent – such links being labeled by head-direction information. In other words, it is a topological representation of the environment (Fig.8a).

Include Figure 8 around here

3.3 Goal representation

Such a topological representation can be used to predict the places that can be reached from the current place, when moving in a certain direction. Propagation of activity through a topological graph is a mechanism that has been used (e.g. [Matarić, 1991] and [Schmajuk and Thieme, 1992]) for path planning. However, in such approaches, either the signal propagates back from the goal, which implies that there's a mechanism triggering the place cell that represents the goal place (which seems not to be the case according to experimental data), or the signal propagates forward from the current place, but there must be a mechanism to detect that the goal place has been reached by the prediction (a mechanism for which there is also no experimental support).[2]

[2] For a discussion on the biological plausibility of these models and of others, as opposed to ours, the reader is referred to (Trullier and Meyer, 1997b) and to (Trullier et al., 1997).

Alternatively, Burgess et al. (1994) hypothesized the existence of so-called goal cells, downstream of the hippocampus, that would code for the animat's position with respect to the goal, based on the information coming from the place cells. For instance, the "East" goal cell would fire when the animat is to the East of the goal. In the model they proposed, Burgess et al. used phase coding to reinforce the connections from specific place cells to the goal cells. To learn a specific location it will need to return to later on (a goal location), their animat, upon finding such a location, looks about in all directions. In each of these directions, modification of the connections between place cells and the corresponding goal cell is forced to occur at the end of the theta cycle. As a consequence, only the place cells that fire at a late phase, that is, place cells that have place fields lying in front of the animat are involved in the process. The "place field" of a goal cell can then be defined as the sum of the place fields of the associated place cells – cells from which the connections have been reinforced – and indeed lies in the direction the animat is facing, with respect to the goal location. However, each of these place cells that fire at a late phase must have their place fields containing the goal location (when theta rhythm is present, a place cell only fires if the animat is within the corresponding place field). In other words, the "place fields" of goal cells cannot extend at a great distance from the goal because the size of place fields are limited. As a consequence, navigation abilities are extremely dependent upon the size of the place fields and the environment has to be small enough. This is because the model of Burgess et al. does not encode any spatial relationship between places and cannot predict all the places that lie ahead of the animat. Furthermore, no mechanism for dealing with obstacles is proposed.

Include Figure 9 around here

In this work, we propose to combine the mechanism of signal propagation with the existence of goal cells. As in the model of Burgess et al., the animat, upon finding a goal location, looks about in all directions. In each of these directions, the activity of the place cell representing the goal location – where the animat currently is – is propagated within the CA3 network, through the connections that are gated by the current head-direction information and for which the synaptic weights are above a certain threshold. The later condition ensures that synaptic weights that have been modified through erroneous or noisy learning are not taken into account. (Fig. 8b, Fig. 9). *All* the place cells that represent locations *in the direction the animat is facing* are thus activated. They represent, as an ensemble, the corresponding region with respect to the goal (West in Figure 8b), regardless of distance from the goal. The connections from these activated place cells to the respective goal cell are enhanced through a Hebbian learning rule, at each iteration of the propagation phase. As a consequence, the synaptic weight between a given place cell and a given goal cell is an inverse function of the distance from the goal to the preferred location of the place cell. A certain form of metric information is thus present in the model. For instance, in Figure 9, the propagation phase takes 38 steps (at the 39th step, no more non-activated place cell is triggered). Thus, the connections from the place cells representing the goal location and the "East" goal cells are enhanced 38 times, while the connections from the place cells representing the North-East corner of the environment are enhanced only once or twice.

We will say that the activated place cells, from which the connections to the goal cell have been modified, are *associated* with the goal cell.

Subsequently, any of the associated place cells becomes able to trigger the firing of the goal cell. In other words, the firing of the place cell corresponding to the location of the rat will activate the appropriate goal cells that will represent where the animat is with respect to the learned goal. For instance, Figure 8c shows a place cell that has been associated with, and thus activates, the "South" and the "South-West" goal cells. This means that the animat is at the South-South-West of the goal.

Rats, upon finding a reward, often look all around, as if to learn the configuration of cues visible from there. They might also propagate the information corresponding to where they are in the cognitive graph, in different directions. When the rat is not moving, hippocampal activity usually goes into another mode, called LIA (Large-amplitude Irregular Activity) where many more cells fire at the same time. This mode is usually associated with a "recall mode" (Buzsáki, 1989). Our animat is supposed to learn the connections between place cells and goal cells during such periods.

4 Navigating with a Cognitive Directed Graph

The animat moves in a continuous manner in a continuous environment containing obstacles. Its movement is specified by its constant velocity and the maximum angle by which it can rotate at each simulated time step. An obstacle avoidance mechanism based on the use of optical flow (Duchon, 1996) is also called upon when the animat is too close to a wall. Figure 10 shows an example of the exploratory trajectory of the animat.

Include Figure 10 around here

In practical simulations, the animat is assumed to be equipped with a 120° field of view. It measures the distance to obstacles, within a certain range, in 49 directions (every 2.5° between -60° and +60°). The limit on the range of the measurement ensures that only close obstacles are taken into account. Following Duchon (1996), we use an approximation of the optical flow at these 49 points by ignoring the rotational component and taking the translational component. The optical flow is thus expressed as follows:

$$\dot{\beta} = \frac{|h| sin\beta}{d}$$

where $\dot{\beta}$ is the angular speed, h the speed of the animat (movement is considered to be colinear to the optical axis), β is the angle with respect to the optical axis where the optical flow is sampled, and d is the distance to the obstacle in the direction of β. The optical flow is zero if no obstacle is detected.

The local navigation strategy proposed by Duchon (1996) consists in trying to equate the average magnitude of optical flow measured on each side of the optical axis (the movement direction). If there are nearby obstacles on one side, they will generate more optical flow, and they will force the animat to turn away.

When there are nearby obstacles on both sides, it means the animat cannot turn to avoid them. The animat should then turn around 180°. Duchon (1996) proposed to implement a "tau-reflex", a mechanism triggered when the time-to-collision, usually named τ (Lee, 1976), is too low. The time-to-collision can be approximated by $\tau \approx \beta/\dot{\beta}$.

When the local obstacle avoidance mechanism is not called upon, the animat turns by a random angle drawn from a uniform distribution between -30 and +30°.

Include Figure 11 around here

Once the topological representation is acquired (the animat has explored for a fixed length of time), the animat looks for reward. When it finds one, it recruits a set of goal cells to learn the goal location. Figure 11 illustrates the result of the propagation of the signal from the goal location in the 8 directions. The theoretical activity field of a goal cell has a conical shape (Fig. 8b). In practice, the way the signal propagates strongly depends on the distribution of the place fields and the degree of accuracy of the topological representation (the synaptic weights fluctuate as exploration goes on and some weights can be erroneous due to the lack of exploration or due to the wrong activation of some place cells).

As illustrated by Figure 8c, a set of goal cells code the direction to the goal. This type of coding is called "population coding" (Georgopoulos et al., 1986). The activity of each goal cell is proportional to the sum of the synaptic weights of the connections coming from all the associated place cells that are active. The direction indicated by the set of the goal cells is a weighted average of the preferred directions:

$$\alpha = arg_{\alpha}(\sum_{i=1}^{8} GC_i * \vec{d_i})$$

where α is the direction coded by the set of goal cells, GC_i is the activity of goal cell i and $\vec{d_i}$ is the direction opposite to the label of the corresponding goal cell i (e.g. South for the North goal cell).

Include Figure 12 around here

However, as can be deduced from the working principle of Figure 8, the information from a goal location propagates in a restricted range of directions (within 45° around the direction the animat is facing), and can only partially skirt around obstacles (Fig. 9). In the example of Figure 12, where the vector field illustrates for every position in the environment the direction coded by the set of goal cells, we can see that the animat would be lost if put at location A. None of the eight goal cells would fire when the animat is in A and the system would be clueless as to the direction pointing towards the goal.

Include Figure 13 around here

We thus introduce the notion of subgoal. When the animat is trying to reach the goal, it can be in two modes. If some goal cells are firing and provide the direction towards the goal, it follows this direction; if no goal cell fires, the animat starts moving randomly to look for information. At the location where it finds information, it recruits a new set of goal cells (subgoal cells) and learns the connections from the CA3 place cells to these subgoal cells in the same way it learned the connections from the place cells to the first set of goal cells. It then proceeds and follows the direction coded by the first set of goal cells. If it succeeds in reaching the goal, it validates the set of subgoal cells. If it moves again into a region without information, it removes the newly recruited set and starts looking for information again. Figure 13 illustrates this process: when the animat is at position A, the first set of goal cells doesn't provide any information. The animat thus moves randomly in search of information (trajectory 1). When it finds information, it recruits a new set of (sub)goal cells. It then proceeds and follows the direction indicated by the first set of goal cells (trajectory 2). This brings the animat back to a region where the first set of goal cells is silent. This means that the subgoal is inefficient. The animat thus discards it and looks for information again (trajectory 3). It finds some, recruits a set of (sub)goal cells and succeeds in reaching the goal (trajectory 4). This latter subgoal is validated.

If the environment contains more obstacles, the animat will have to recruit other sets of subgoal cells. As a consequence, at any given position in the environment, more than one set of (sub)goal cells can be active, for the same goal (this is for instance the case at the upper-left corner of the environment in Figure 13 where the set of goal cells and the set of subgoal cells are both active). The animat has to choose which direction to follow. Thus, we introduce yet another mechanism. When the animat is lost and looking for information, it recruits a new set of subgoal cells as soon as one of the existing sets is active. We will say that the new set is *associated* with this active set. For instance, the first subgoal will be associated with the goal, the second subgoal with the first, etc. Some kind of distance information is implicitly coded in this association. The set of goal cells leads to the goal and is at distance 0 from the goal. The first set of subgoal cells leads to a position where the set of goal cells will be active, so the first subgoal is at (topological) distance 1 from the goal. The second subgoal is thus at (topological) distance 2 from the goal, and so on.

At the position where a new set of (sub)goal cells is recruited, the associated set of (sub)goal cells provides some kind of distance information. The activities of the (sub)goal cells depend on the synaptic weights of the connections from the associated place cells, which are proportional to the inverse of the number of iterations it required the signal from the (sub)goal to reach the corresponding place cells. In other words, the activities of the (sub)goal cells indicate how far the animat is from the (sub)goal. Thus, we use a "symbolic" mechanism by which a newly recruited set of (sub)goal cells stores the distance information to the goal as the combination of two terms: the distance information provided by the associated set of (sub)goal cells (zero for the first set of goal cells) and the distance from the associated (sub)goal to the current location where the new set is recruted, computed from the activities of the (sub)goal cells of the associated (sub)goal.

For instance, in the example of Figure 13, the distance from the goal (G) to the subgoal (S) is 12 iterations, as can be deduced from Figure 9 (S is situated somewhere between the area covered by the propagation at iteration 10 [Fig. 9c] and the area covered by the propagation at iteration 20 [Fig. 9d]). The correspondence with the activities of the goal cells at position S must take into account the maximum number of iterations (38 in this case), because the synaptic weights from the place cells at position S to the East goal cell have grown by an amount of 26 (38−12) step-increases.

Include Figure 14 around here

Figure 14 shows how our model performs in the example environment we've been using so far. Note that the trajectories are not straight to the goal. This is due to the scale of the place cell representation, to the fact that exploration is never quite exhaustive, and to the fact that all connections are not stabilized at their theoretical values.

Figure 15 shows other examples of environments that require several subgoals.

Include Figure 15 around here

5 Discussion

There is no comprehensive theory of the hippocampus yet and there are still many controversies on apparently contradictory experimental results (probably stemming from differences in the paradigms and the protocols used). It seems however that there is some agreement as to the idea that the hippocampus is involved in different kinds of memory processes, one of which being spatial memory (O'Keefe and Nadel, 1978; Nadel, 1991).

We have followed Muller et al. (1996) in speaking of the hippocampus as a "cognitive graph" instead of as a "cognitive map" – which is more often used. This allows us not to assume an underlying metric representation which would resemble a "map-in-the-head" (Kuipers, 1982), thus contradicting the viewpoint of Touretzky and Redish (1996), which states that place cells are attached to a Cartesian coordinate system. However, we took from these authors the idea of recruiting place cells as the animat explores its environment. We also contradict the theory proposed by Samsonovich and McNaughton (1997) according to which connections between place cells are defined *a priori* (charts) so that the population activity of place cells can propagate from place cell to place cell in relation with the animal's movements (path integration). In this latter view, the sensory information associated with each place is learned only on top of this strict predefined spatial representation.

We believe that the hippocampus simultaneously learns two things:

- The relationships between the different stimuli that form a configuration (a situation or an episode) and a specific time or a specific place.
- The temporal as well as spatial relationships between different configurations.

The model presented here focused on the second aspect, and the first aspect was quickly dealt with through the mechanism by which place cells are recruited during exploration.

5.1 Other computational models of the hippocampus

Simultaneously building a place representation and a spatial representation (relationships between places) raises a coherency problem that no other computational model, to our knowledge, has tackled yet. Basically, the problem stems from the fact that connections between place cells, which have been established at a given exploratory stage, may need to be modified at a later stage, if new places and new topological links are discovered in the environment (Fig. 16). In this work, this problem has been solved by the fact that each position is represented by several place cells (as in the real hippocampus), by the fact that each connection has a small influence on the overall process and by the use of learning processes that gradually weaken or strenghten place cell connectivity.

Include Figure 16 around here

The model of Matarić (1991) and that of Kuipers and Byun (1991) rely on stereotyped low-level behaviors (wall-following, guidance strategies) in order to define what a place is (left-wall, right-wall, corridor). Thus, although their animats are building a place representation during exploration, along with a topological or metric spatial representation, there's no chance that such representation will change during the exploratory process. In these models, any learned connection between two place cells corresponds to topological links between places in the environment that will never get questioned later on.

Likewise, in the model of Touretzky and Redish (1996), place cells are recruited during exploration but there is no need for a spatial representation to be learned since an underlying Cartesian coordinate system defines all spatial relationships between places.

Wallenstein and Hasselmo (1997) proposed an attractive model of the hippocampus as a memory for sequences. Although not a complete model of animal navigation, the model suggests how place cells might be "recruited" in a biologically plausible way and how sequences might be simultaneously learned. In their model, pyramidal cells in the CA3 region of the hippocampus spontaneously discharge at a very low frequency (15% of all pyramidal cells are active at any one time). As a consequence, when a sequence of items is presented through a direct stimulation of specific pyramidal cells, other cells, discharging spontaneously, get associated with the former cells through a classical Hebbian learning mechanism (LTP of the synaptic connections). These latter neurons then discharge persistently during specific portions of the sequence. If the sequence corresponds to a linear trajectory of the rat, specific portions correspond to place fields. This might explain how place fields develop during exploration. However, Wallenstein and Hasselmo reported that phase precession could only be found in the simulated place cells that were directly stimulated, but not in the ones that developed, although the latter were necessary for the recall process.

There are, to our knowledge, only two other models based on hippocampal place cells that can cope with continuous environments with obstacles. Gerstner and Abbott (1996) proposed a model where the activity of place cells is modulated by the animat's position *and* by the goal location. This implies that each place cell gets information about where the goal is. This is not what is thought to happen in the rat hippocampus. Speakman and O'Keefe (1990) have indeed shown that place cell activity is independent of goal locations. By contrast, our model, like the one by Burgess et al. (1994), exhibits *latent learning*. It doesn't need the presence of any reinforcement to build a spatial representation of the environment, which is, by essence, independent of goal locations. Then, the animat can recruit as many sets of (sub)goal cells as needed to be able to return to as many goals as needed, without ever changing the underlying spatial representation.

The other model that is based on hippocampal place cells and can cope with continuous environments with obstacles is the one by Muller et al. (1996). It learns what Muller et al. also called a "cognitive graph", from distinct but overlapping places. In this model, the animat moves around in the environment and reinforces the synaptic connections between simultaneously active place cells. These synaptic weights reflect the degree of overlap between place fields (the inverse of the distance between place field centers). However, learning is symmetric (correlational learning) because it relies on simultaneously active place cells and there is no difference in the resulting representation between a movement from place A to place B from a movement from place B to place A. The model thus cannot be used to predict the animat's future positions from the current position. As a consequence, in order for the animat to return to a goal while avoiding obstacles, Muller et al. had to introduce a biologically unrealistic graph search algorithm stemming from Artificial Intelligence research on path planning. We proposed in our model a biologically-plausible mechanism to "read out" the cognitive graph, a mechanism that is modified and extended from the original idea of Burgess et al. (1994).

Beside these two models, several others among the existing computational models of animal navigation (Trullier et al., 1997) consider the hippocampus as an hetero-associative network in the spatial domain, that is, a network that learns how places are connected to one another and thus corresponds to a topological representation of the environment. We already briefly mentioned the models by Matarić (1991) and by Schmajuk and Thieme (1992).

5.2 Biological plausibility and experimental predictions

This model, together with its extended version (Trullier and Meyer, 1997b), relates more closely to the rat hippocampal architecture and to physiological mechanisms than previous models. As we previously suggested (Trullier and Meyer, 1997b), we can make several experimental predictions.

We first propose that phase precession in the CA3 region is forced by dentate gyrus and enables sequence learning. This hypothesis implies that phase precession also occurs in dentate gyrus, which it does (Skaggs et al., 1996). But it also implies that, if we simultaneously record several dentate granular cells and several CA3 pyramidal cells, we should be able to see that place cells whose place fields overlap those of the dentate granular cells fire just after the granular cells, a correlation supporting the idea that the recorded granular cells force the discharge of the recorded place cells.

We also propose that the learning of the goal location occurs during another state of hippocampal activity, namely LIA (Large-amplitude Irregular Activity), observed in particular during awake immobility of the rat, and which is usually associated with "recall" by the hippocampus of previously learned episodes (Buzsáki, 1989). During such a state, a large number of pyramidal cells in the CA3 region are activated (but far from all). We thus propose that this state is the result of a signal propagation within the CA3 region that activates all the place cells whose place fields lie ahead of the animat. If we simultaneously record a lot of CA3 (not CA1) place cells during LIA, we should be able to see a tendency of the activation to be limited to specific place cells.

In the spatial domain, Redish (1997) also suggested a role for LIA. According to his theory, the hippocampus is not necessary for the on-going process of navigation but is involved in the definition and the retrieval of the spatial context. In other words, the hippocampus is used to recognize a specific familiar environment, but not to navigate. More specifically, Redish suggested that during LIA, the hippocampus is in a self-localization process. Many place cells would discharge at first, corresponding to many different hypotheses as to where the animal actually is. Then, a pseudo-winner-take-all mechanism between place cells would lower the global activity, keeping only a "coherent" population of place cells active in a kind of relaxation process. Such a theory doesn't provide a way of exploiting such a spatial representation in order for the rat to navigate. What we proposed is that LIA allows the spatial information to be transferred from the hippocampus to downstream of the hippocampus, by defining where the goal is with respect to each known place.

Apart from place cells that code for locations in an absolute reference frame, our model doesn't include representations for objects or specific places. In particular, obstacles are *not* represented internally but obstacle avoidance emerges from the fact that some pairs of place cells are not connected because of the obstacles. The positions of subgoals are also not represented explicitly. The animat seems to move from subgoal to subgoal, closer and closer to the goal, but doesn't actually "recognize" that a subgoal has been reached. This is the result of the competition between sets of goal cells. In fact, our model doesn't actually perform "path planning": it doesn't have to choose among a certain number of different paths. Consequently, our model rather belongs to the category of navigation models that we called "place recognition-triggered response" (Trullier et al., 1997).

Our current model is not meant to cope with dynamically-changing environments. Once a set of goal cells is learned, the animat exploits the information this set provides, without comparing with new sensory information. Real animals, on the contrary, constantly update their internal representations. In particular, if obstacles move, disappear or appear, they restart a new phase of exploration. We are currently looking into this kind of process to improve our model.

6 Conclusion

We have proposed a new model of the rat hippocampus based on several ideas from different models previously published by others in the literature. We have been able to show that such a model can successfully navigate in continuous environments containing obstacles. We also have shown that our model is based on biologically-plausible architecture and mechanisms. Furthermore, we made several experimental predictions based on our new way of interpreting the roles of the different structures in the rat hippocampal formation.

We are still working however on ways to include other mechanisms, so that our model can cope with dynamically-changing environments.

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Captions

Figure 1 Phase shift in place cell firing during the rat's movement, as discovered by O'Keefe and Recce (1993). The horizontal axis represents both space (top, rat's movement) and time (bottom, theta cycles and spikes). When the rat is at A (it runs from left to right in this overhead view), the place cell corresponding to place field PF1 fires **late** in the theta cycle (spikes shown as vertical bars). In B, this cell fires at the **middle** phase and, when in C, at the **early** phase of the theta cycle. C also corresponds to the point of entry into place field PF2 with respect to the heading direction. The corresponding place cell fires **late** in the theta cycle. (Schematized on the basis of data from O'Keefe and Recce (1993) and from Skaggs et al. (1996))

Figure 2 Phase precession explained by sequence learning. Each bin in this grid-like world corresponds to a unique place. The rat has learned the sequence of places from A to J. It subsequently moves from A to J (top): when it is in A, it recalls the sequence from A to G (bottom); when it is in B, it recalls the sequence from B to H; and so on. Each movement and each prediction phase take a full theta cycle. Thus, the representation of the current place starts a new theta cycle and the prediction of place E comes earlier and earlier in the cycle (dotted arrow), i.e. the phase of firing of the place cell corresponding to E diminishes.

Figure 3 Architecture of the proposed model. (Top) We assume that the entorhinal cortex sends information about the spatial configuration of landmarks to the dentate gyrus and to the CA3 region through the perforant path. The dentate granular cells store this information as a short-term memory, in the correct temporal order corresponding to the temporal sequence of visited places (not explicitly simulated in this paper). This information is forced onto the CA3 pyramidal cells (large triangles) through the strong mossy fibers. These CA3 place cells then send projections (presumably through CA1 and subiculum) to putative goal cells. Small triangles are plastic synapses and small arrows on some synapses indicate that these synapses are gated by head-direction information. (Bottom) When the rat moves from place A to place B, as it is heading North (left), place cell A and place cell B fire in order (right, filled triangles). At the same time, the connection from place cell A to place cell B, gated by North head-direction information (small filled triangle with labeled arrow) is reinforced. (North is arbitrary and refers to a reference direction within the head-direction representation system.)

Figure 4 Activation of a subset of place cells for a given position of the animat and synaptic learning. Each circle represents the preferred position of a place cell (position of peak activation). (a) At each timestep, t, t+1 and t+2, 5 place cells (grey circles) emit a spike. These 5 cells are those for which the preferred positions are closest to the current position of the animat (arrow). The big circle is for illustration; its radius has been adjusted, so that it includes 5 place field centers. (b) These activated place cells (circles with continuous lines) are associated with specific phases of firing (numbers within the circles). The phase arbitrarily precesses from 3 to 1. (c) Synaptic weights of connections between cells that emit a spike at successive phases are enhanced. Those of connections between pairs of cells in which only one has been active are depressed.

Figure 5 Recruiting a new place cell and associating it with visible landmarks. When there aren't "enough" place cells to represent the current location (fewer than 5 place cells have their activities above a certain threshold), a new place cell is recruited. This new place cell "learns" the distances (dotted lines) between the current position of the animat (black dot) and each of the visible landmarks (wall corners).

Figure 6 Comparison between the way places are represented in our two models. (Left) Place fields are uniformly distributed in the environment, regardless of possible obstacles. (Right) Place cells are recruited as the animat explores the environment. At the end of the exploration, place fields are distributed almost uniformly. Their positions depend on the complexity of the environment (obstacles), that is, on where the landmarks are visible.

Figure 7 The modified connection between two place cells in neural space corresponds to the facts that the corresponding place fields are neighbors and that the place field of the post-synaptic cell is in the direction corresponding to the head-direction that modulates the connection, with respect to the place field of the pre-synaptic cell.

Figure 8 Summary of the principles of our model. The simulations are decomposed into three phases, corresponding to exploration (a), association with a goal location (b), and exploitation (c). (a) As the animat moves randomly, connections between place cells are modified to reflect the topological organization of the corresponding place fields. Direction information is also included. (b) At a goal, the information corresponding to the current place is propagated through the head-direction gated synapses. All the place cells lying in a specific direction with respect to the current goal location are triggered and are then associated with one goal cell. (c) Each place cell triggers the firing of the appropriate goal cells. These goal cells code, as a population, the direction to follow to return to the goal. (We used a grid-like world for illustration purposes. Also note that place cells are not topographically organized in the rat hippocampus. They are placed topographically here to ease the visibility of the learned connections.)

Figure 9 Signal propagation from the goal location towards the East. (a) Initially, 5 place cells corresponding to the current position of the animat (arrow) are active. The first figure illustrates the extent of the combined place fields of these 5 cells, around the goal location. (b-f) The signal from these place cells propagate through the recurrent connections that are gated by the current head-direction information (East in this case) and for which the synaptic weights are above a certain threshold.

At each iteration of this propagation phase, the currently active cells trigger neighboring connected cells. The successive figures illustrate the extent of the combined place fields after 5, 10, 20, 30 and 38 iterations. At the 39th iteration, no other non-active place cell was triggered. As a consequence, the propagation phase stops.

Figure 10 An example of the exploratory behavior.

Figure 11 Activity fields of 8 goal cells. Each goal cell is connected to all the place cells and the synaptic weights are initially set to zero. When the animat learns the goal location, the signal from the place cells corresponding to the goal location is propagated in 8 directions and the synaptic weights are modified so that place cells whose place fields lie in a given direction with respect to the goal location are associated with the corresponding goal cell. As a consequence, the activity field of a goal cell is equivalent to the combined place fields of the associated place cells. Each of the eight figures illustrate the extent of the activity fields of the 8 goal cells.

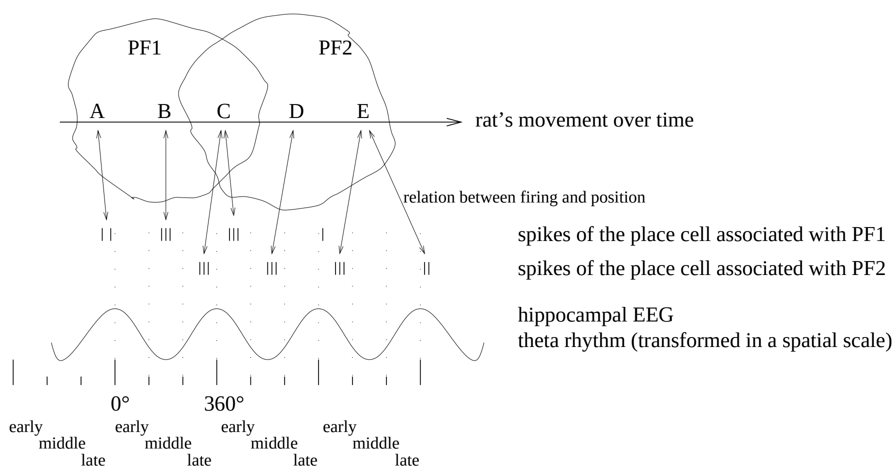
Figure 12 Vector field generated by the goal cells learned at the goal location. This vector field is generated by virtually putting the animat in each position within the environment and computing the direction it would follow by measuring the output of the goal cells. The limit between the region where there is information (arrows) and the region where there is none is not a straight line because place fields are scattered randomly, because place fields have a certain extent, and because synaptic weights have been learned with some noise. For instance, a place cell whose place field is at B received the information from the goal location when the animat was facing North-East but its place field extends behind the corner. As a consequence the place cell corresponding to place C was also activated and so on.

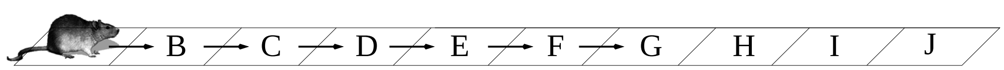
Figure 13 (a) 4 successive trajectories in the process of creating a subgoal. At the end of path 1, the animat recruits a set of subgoal cells but this turns out to be inefficient, since path 2 leads back the animat into the "silent" zone. The animat recruits another set of subgoal cells at the end of path 3, which proves successful, since path 4 leads to the goal (G). (b) Vector field illustrating the directions indicated by the set of (sub)goal cells that were recruited at position S and which proved efficient.

Figure 14 Resulting trajectory during exploitation.

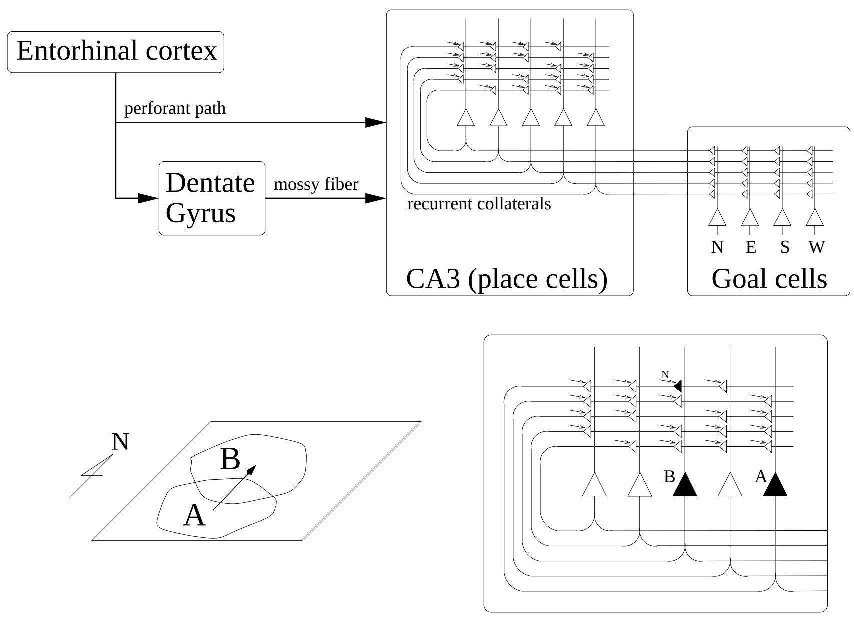
Figure 15 Trajectories during exploitation within two other environments (a,c) and the respective positions of the recruited subgoals (b,d). The dotted lines indicate where the corresponding set of (sub)goal cells (label near the line) stops being active. Note that in the second environment containing an inversed U-shaped obstacle, the animat has recruited 4 ensembles of goal cells (G, 1, 2 and 3). The region where the ensemble of subgoal cells 1 is active extends to both sides of the region covered by the ensemble of goal cells G. As a consequence, both subgoals 2 and 3 were associated with subgoal 1. When the animat is in the North-East corner of the environment (A), it moves towards subgoal 3 and then to subgoal 1, instead of using a theoretically shorter path to the other side of the obstacle. Indeed, its internal spatial representation indicates that $d_1 + d_3$ is shorter than $d_1 + d_2$. This distance information is approximate and is given by the numbers of iterations the propagation phases took from each subgoal and in each direction (see text for detail).

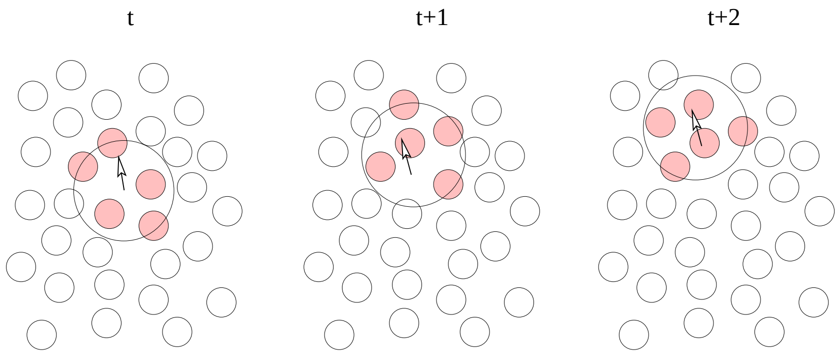
Figure 16 Interference and coherence problem between the elaboration of a place representation and the learning of the corresponding topological representation. The place representation can evolve during exploration (top left and top right). Place fields can move with respect to one another, new ones can appear or others disappear, for instance through a competition mechanism among the place cells. As a consequence, the connections that were learned during the early stage of exploration (bottom left) can become erroneous (bottom right, dashed arrows), while new connections have to be learned (bottom right, solid arrow). This implies that the animat has to explore the environment extensively.


PF1
PF2
A
B
C
D
E
rat's movement over time
relation between firing and position
spikes of the place cell associated with PF1
spikes of the place cell associated with PF2
hippocampal EEG
theta rhythm (transformed in a spatial scale)
0°
360°
early
middle
late
early
middle
late
early
middle
late
early
middle
late

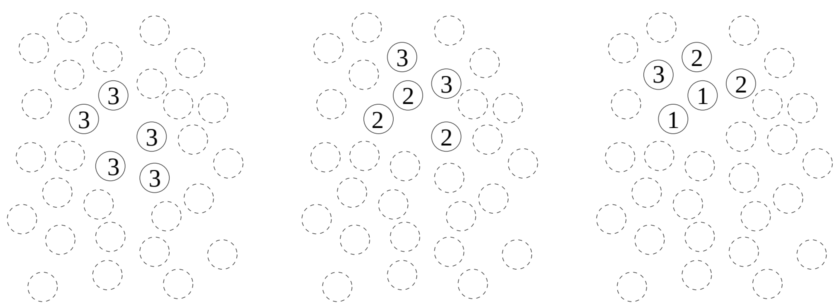


A → B → C → D → E → F → G
B → C → D → E → F → G → H
C → D → E → F → G → H → I
...

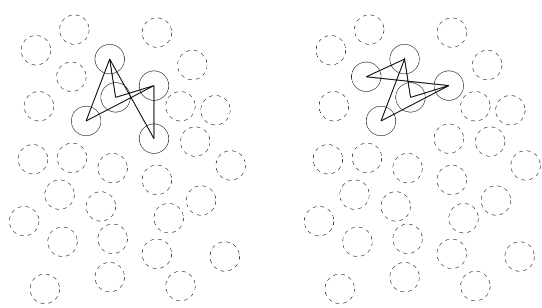

Entorhinal cortex
perforant path
Dentate
Gyrus
mossy fiber
recurrent collaterals
CA3 (place cells)
N
E
S
W
Goal cells
N
B
A
N
B
A



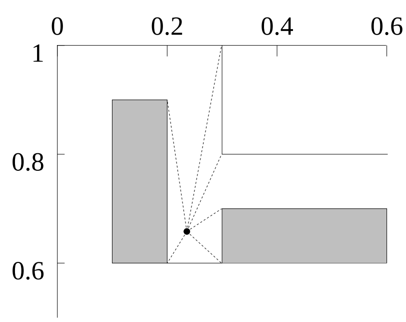
(a) Activated place cells



(b) Phase of the activated place cells



(c) Learned connections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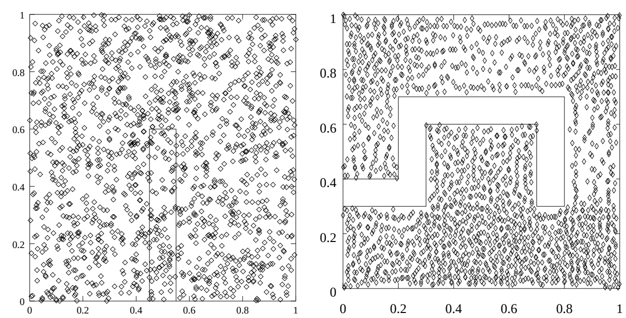
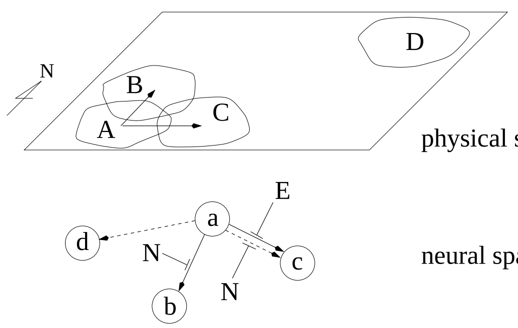
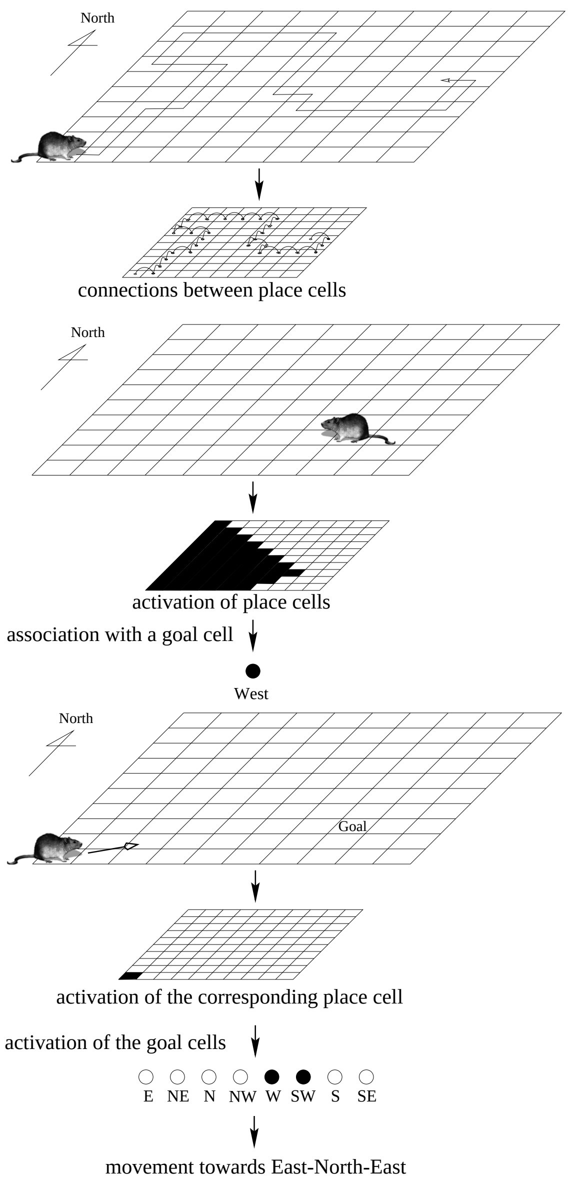
1
0.8
0.6





physical space

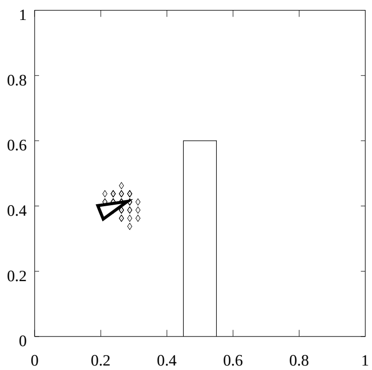
neural space


North
connections between place cells
North
activation of place cells
association with a goal cell
West
North
Goal
activation of the corresponding place cell
activation of the goal cells
E NE N NW W SW S SE
movement towards East-North-East

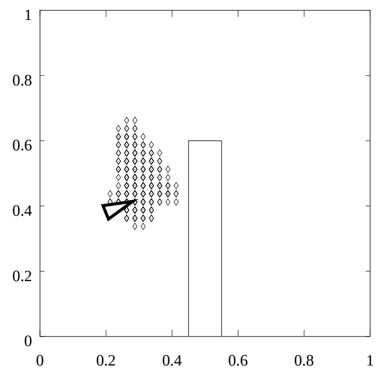
(a)

(b)

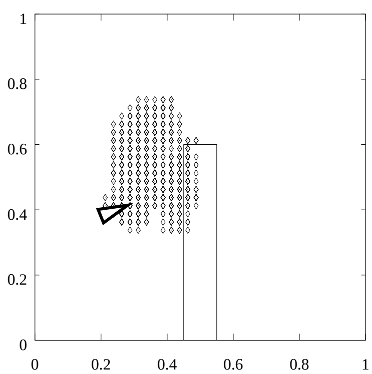
(c)



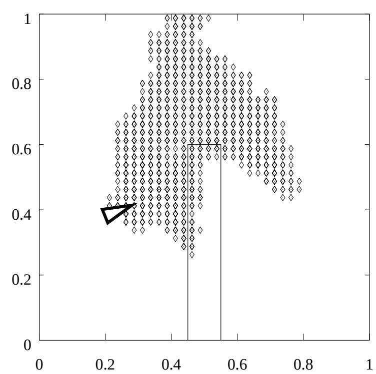
(a) initial state



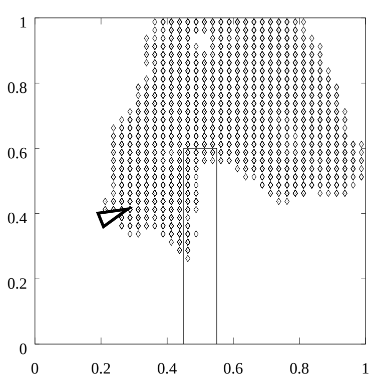
(b) after 5 iterations



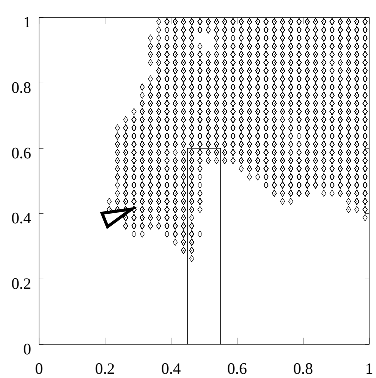
(c) after 10 iterations



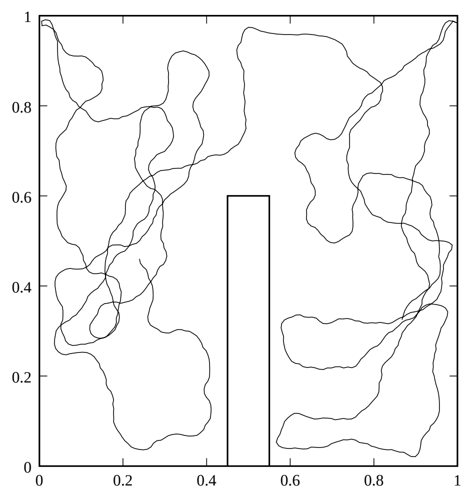
(d) after 20 iterations



(e) after 30 iterations



(f) after 38 iterations



1
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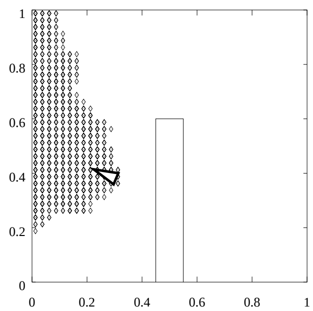
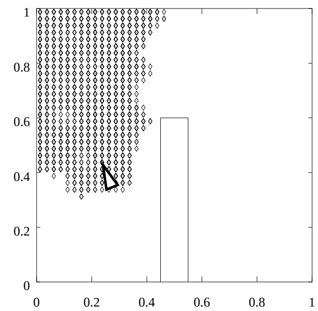
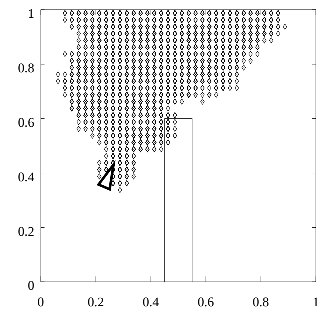
0
0.2
0.4
0.6
0.8
1



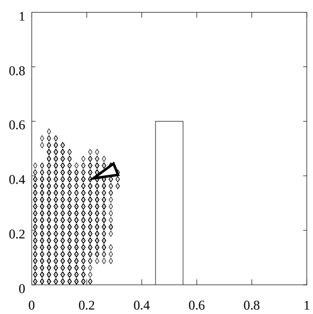
(g) North-West



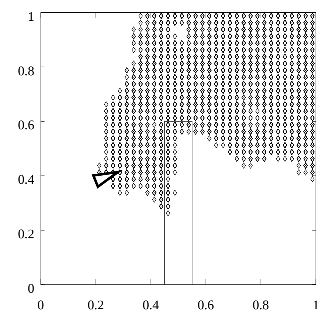
(h) North



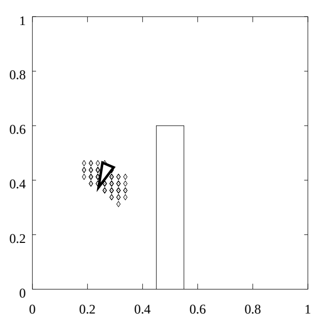
(i) North-East



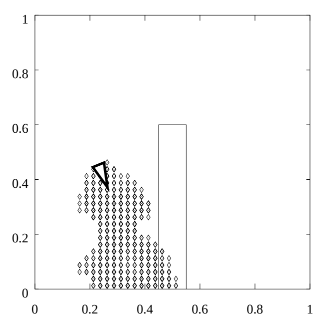
(j) West



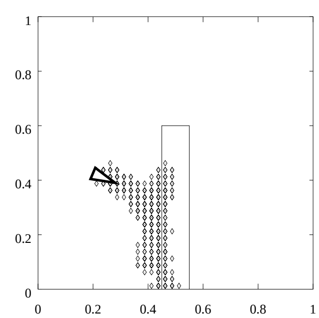
(k) East



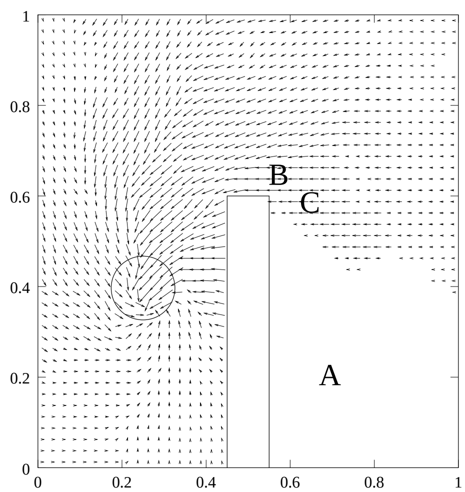
(l) South-West



(m) South



(n) South-East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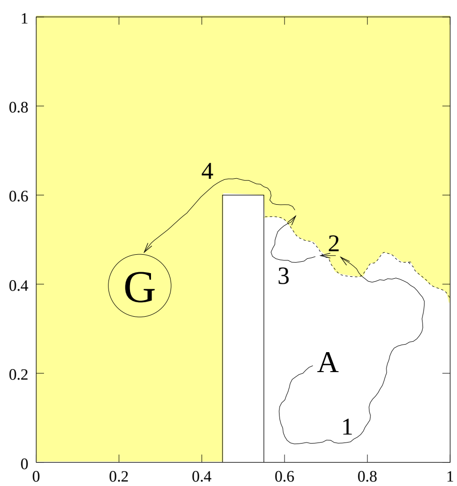
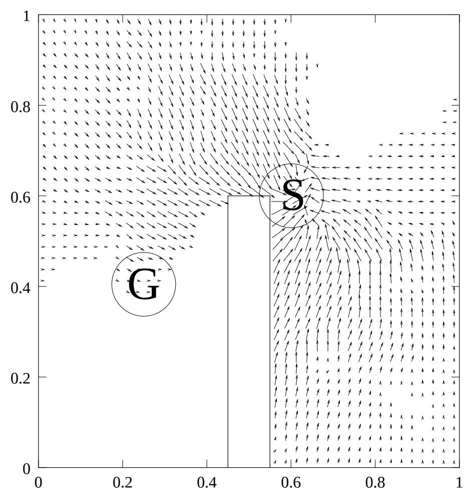
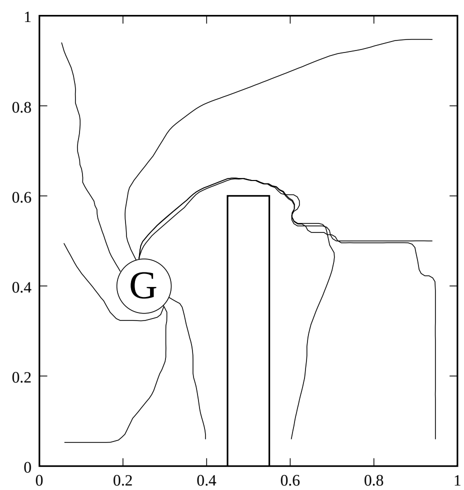
1



(o)



(p)


G
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0.2
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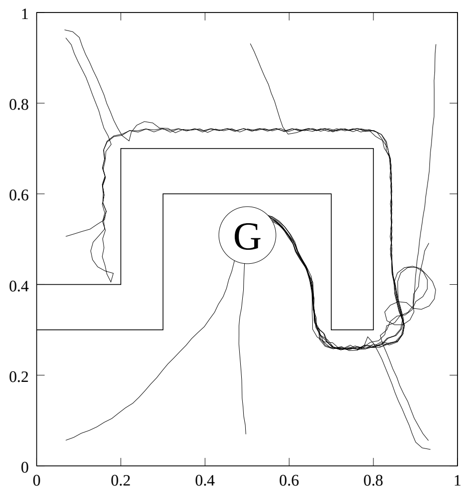
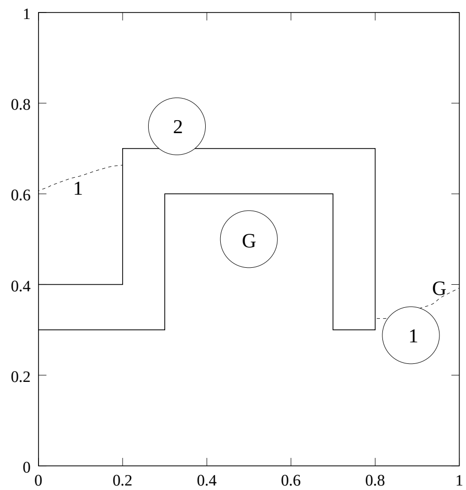
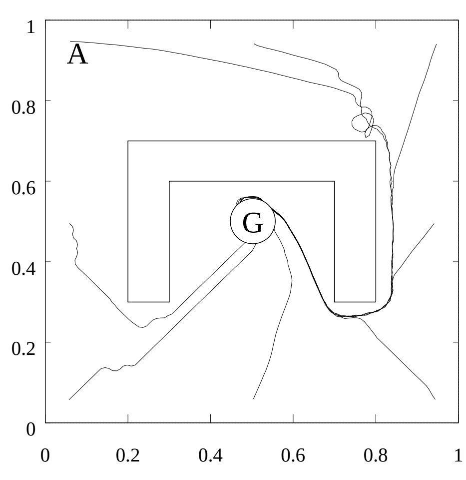
0.6
0.8
1



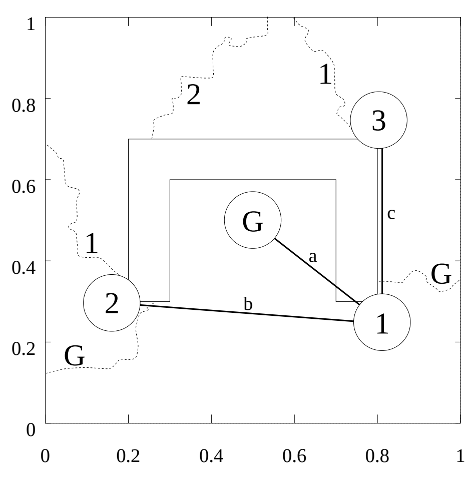
(q)



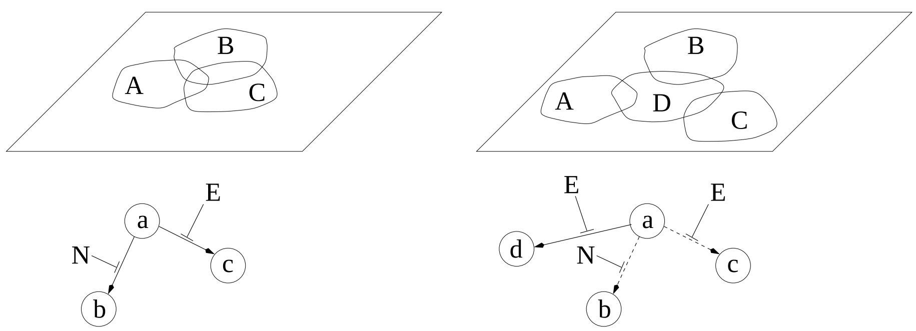
(r)



(s)



(t)


A
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