From view cells and place cells to cognitive map learning: the hippocampus as a spatio-temporal memory

P. Gaussier, A. Revel, J.P. Banquet (*), S. Leprêtre, V. Babeau, R. Borges
Neuro-cybernetic team, Image and Signal processing Lab. (ETIS),
6 av du Ponceau, 95014 Cergy Pontoise, France
(*) Neurosciences and modelisation institute,
INSERM 483, Jussieu, Paris
email: gaussier or revel @ensea.fr

Abstract

The first goal of this paper is to propose an abstract model of visual place recognition and homing behavior that emphasizes common characteristics of insect and mammal visual navigation. In the case of mammals, the model and robotic experiments show that "place cells" could be learned in the perirhinal and entorhinal cortex. The role of the hippocampus (Hs) could not be specifically dedicated to navigation or map building. Conversely, in the second part of the paper, we show the role of Hs could be to learn and predict transitions between states. This transition prediction could be important for novelty detection and, above all, crucial to merge in a coherent system planning and sensori-motor systems. A neural architecture embedding this model has been successfully tested on an autonomous robot, during navigation and planning in an open environment.

1 Introduction

This paper is dedicated to hippocampal function during visual navigation. In the first part, a theoretical and transversal model for place recognition and homing behavior emphasizes common characteristics of visual homing in insects and mammals that could result from different kinds of merging between "what" and "where" features extracted from the visual flow. An original implication of this model is that directional place recognition in mammals could be performed before the hippocampus, at the level of the entorhinal cortex, with information coming from the perirhinal cortex. In this context, the hippocampus (Hs), usually supposed to perform such a recognition, appears not to be specifically dedicated to spatial navigation.

According to robotic and biological constraints related to complex action selection problems, we will show that Hs is an ideal structure to learn the transitions between states defined by the merging of multimodal information, whatever its nature is (places in the case of navigation). In fact, Hs could participate in the selection of a transition-state among all possibilities, allowing to choose the correct action during planning. The presence in the hippocampus of neurons that react when the animal is at a particular place, does not deny this explanation. Indeed, "place cells" activity in CA [30] could result from transition detection or prediction rather than place recognition performed earlier in the Dentate Gyrus (DG) and/or in the Entorhinal Cortex (EC).

The second part of the paper addresses the problem of action selection and goal seeking in a complex environment. The issue of connecting sensory-motor and planning systems is explored through the construction by an animat (animal-automat – see [37]) of an abstract model of cognitive map (based on the place recognition model previously described). In particular, associating the recognition of a transition between two places (or two states) and not a "steady state" with an action is shown to be crucial. Transition detection, storage, and recognition are fundamental for an unambiguous connection between sensory-motor and planning systems. In conclusion, a global model of visual place recognition and action planning is discussed according to the neurobiological data related to the perirhinal cortex, the entorhinal cortex (EC), Hs and the prefrontal cortex.

2 A general model for visual place recognition

In this section, we try to reconcile models of visual navigation in insects and mammals. Of course, we do not claim that insects and mammals use the same kind of visual information to navigate or have the same structures to compute a place recognition. Instead, the abstract model of place recognition presented allows a graded transition from insect to mammal processes.

The gradual increase in complexity of the model is related to the number of vision primitives and pattern recognition capabilities.

In the studies of insect homing behavior, it has been shown that insects can use very simple landmarks (e.g. black cylinders) to navigate back to their nest. Experiments have shown that if the cylinders (the landmarks) are translated, the insect searches for the nest entrance at the geometrical position originally associated with the cylinders. Isotropic expansion of the experimental setup does not modify the place the insect searches for the nest [49, 11]. Conversely, when the nest entrance can only be located according to a single landmark, then, expanding twice the size of the landmark will induce the animal to search the nest entrance two times farther from the landmark than before. The same kind of experiments have been successfully performed with birds and mammals e.g. rats [30].

Models explaining navigation capabilities of insects or mammals do not rely on the same assumptions [11, 39]. For instance, models of human navigation deal with landmark recognition, measure of the landmark displacement, declarative knowledge linked to the use of an explicit map, and so on. On the contrary, insect models are based on the idea that perceived panoramas are directly matched as a whole with stored panoramas. Models of rodent navigation are also different because rodent vision is less efficient than primate vision and their cortex less developed. Whether insects and rodents identify landmarks or merely use global patterns is difficult to decide. Yet, the visual performances of rats seem close to that of humans:

> "one must be impressed by the similarity of the rat's discriminative behavior to the perceptual impressions of the human observer. If a series of patterns is ranked in order of the conspicuousness of the figures for the human eye, that order will have a high predictive value for the rate at which the rat can learn the figures. Stimuli to which the rat transfers in equivalence test are obviously similar for man" (K.S. Lashley [35] p 181).

More specifically, during tasks involving object recognition, rats use head movements to bring the stimuli onto the temporal retinal region of binocular overlap [34]. The main difference between rat and human vision seems to be mostly quantitative: -the rat's total view field is about 320 degrees [28] (180 degrees for humans); -rat visual acuity is 50 times worse than human acuity, and obviously its brain is far less developed. The diversity of results about insects' visual perception makes comparison more difficult even though common characteristics with mammals can be found: insects are able to focus their attention, to perceive virtual edges, to learn complex visuo-motor associations [56]... Yet, these results must be contrasted with Wehner claims about the simplicity of the insects visual system [55].

In the present model, we would like to show that all these points of view can be unified if we consider that visual place recognition is the result of a more or less complex merging of visual information including "object" recognition ("what" pathway in mammals) and "object" location ("where" pathway). Obviously the notion of "object" may be supposed to be more complex for mammals and primates than for insects but our model suggests it could be not fundamentally different.

2.1 Basic insect models

Our abstract model derives from classical models of insect navigation (see Cartwright and Collett algorithm for instance [11]). These models are mainly based on optical flow-like techniques in which summation of the displacements in the visual field of particular cues is used to compute movement direction which allows the insect to reach the learned location [11, 55] (see fig. 1).

The low level visual treatment is simply an "object/feature" detector using features such as gradient information to detect a transition between two areas. The useful information is the azimuth of the "object/feature" according to a given absolute direction provided by the sun light polarity for instance. The possibility that insects directly use the perceived panorama as a whole cannot be discarded, but the limitations of such a global comparison between stored and perceived panoramas prohibits its use for decision making when the distance to the learned location is large (very low tolerance to object displacements, variations of lights and shadows and object scale variations). That is the reason why the promoters of a direct use of global panoramic information say that insects seem to rely on path integration to reach the nest area and then start to rely on global panorama matching.

Cartwright and Collett algorithm has been successfully used to control autonomous robots and proved to be able to deal with very low visual information for homing behavior [39]. Its main feature is that the movement direction is directly computed as a sum of the direction variation of the vertical edges detected. Unfortunately important limitations appear and need to be overcome in order to get flexible navigation capabilities:

- the model does not deal with appearance or disappearing of new features. The algorithm considers that a given feature has to be matched with the nearest feature on the ring of neurons. If objects are introduced and/or occluded, the global distribution of the local features can be very different. A categorization of the local features could really

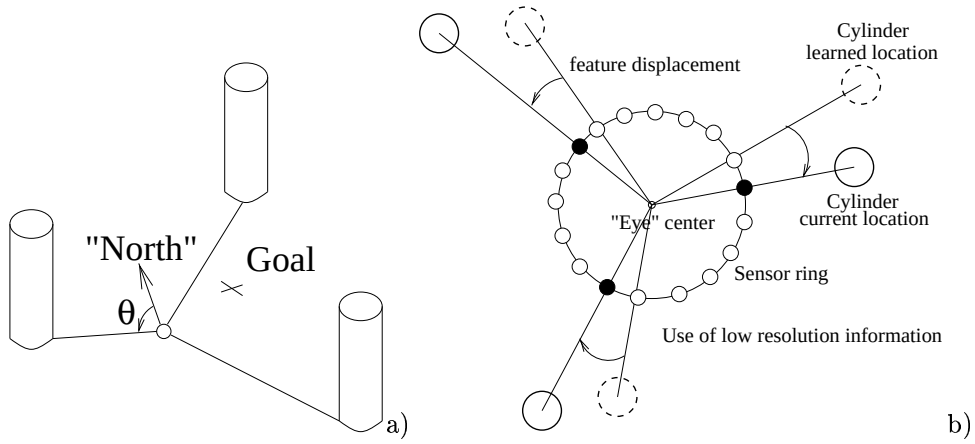

Figure 1: Paradigm of the Optical flow like techniques (Cartwright & Collett). a) represents a typical experimental setup with 3 identical block cylinders that the insect will use as landmarks. Absolute direction "North" can be obtained from sunlight polarity. b) shows the variation of input information in a simplified model of the insect compound eye. Black circles represent the neurons activated by the local landmarks "recognition". When the animal moves from one place to the other, the apparent motion of the landmarks on the compound eye can be computed and used to decide the rotation to adopt for returning to the learned place.

improve the performances by avoiding the matching of quite different local features.

- the same system cannot learn to return to several locations because there is no separation between place recognition and movement selection.

The need for autonomy means the animal must be able to learn to return to a given location but also to select actions according to drives. Unfortunately, in the Cartwright & Collett model, the actions result directly from the panorama transformations. The system has no action selection capabilities in order to decide to turn right or left according to a motivation. The addition of the capability of turning right, according to the recognition of a given pattern, implies to store twice almost exactly the same information. Because some kind of place recognition cannot be avoided, computational and memory considerations lead to introduce it as a separate stage of the navigation process.

2.2 An abstract model of visual place recognition

The abstract model starts from the following considerations. First, the topology of the visual information must be preserved (withhold an azimuthal coding). Second, the larger the number of landmarks recognized, the more accurate the displacement measure will be. Unfortunately, if recognition means the ability to recognize an object at a symbolic level (a phone, or a face), this process cannot be performed in parallel as it was performed in the extraction of visual primitives (edges, corners...). Indeed, the cost and the learning time would be too important (duplication of the material for the object recognition).

Nevertheless, if low level undifferentiated features are extracted in parallel and can be associated with each azimuth location (an absolute direction provided by a compass or by the polarity of the light or by the vestibular system...) then the place recognition Ack_k is computed as the complement to 1 of the sum of the distances between the expected location of a feature and the location of the nearest similar feature (eq. 1).

$$Act_k = 1 - \frac{1}{\pi N} \cdot \left(\sum_{i=0}^{N} \min_{j=0}^{N} \left| \theta_{ik}^{L} - \theta_j \right| \right) \qquad (1)$$

where θ_{ik}^{L} represents the orientation of one learned feature and θ_j the orientation of the corresponding feature in the current panorama (N is the number of landmarks). The activity Act_k is close to 1.0 when all features are in their learned orientation: the place is then recognized. The neuron activity decreases when the features are not at their correct location. Unfortunately even if the place does not look at all similar to the learned place, the measured activity will not tend to zero but will remain at a high positive value. For instance, if the learned place is at the center of an equilateral triangle shaped from 3 identical cylinders (3 features) then the worst recognition level will be obtained when the robot is to the infinity from the learned place. If no more features are visible, the activity will be 0. But if the robot is far away and continues to perceive some features, all these features will be seen in the same narrow part of the visual field. The activation level will be higher than $1 - \frac{3.\frac{2.\pi}{3}}{3.\pi} = 0.333$ because the azimuth error will not be farther than $\frac{2\pi}{3}$ from any learned azimuth. Fig. 2 shows a possible N.N. implementation of equation 1.

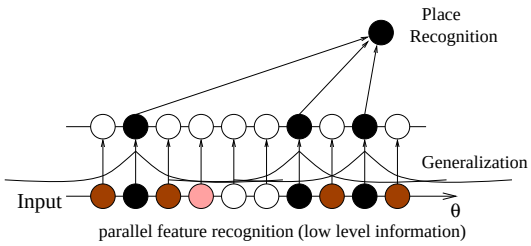

Figure 2: Level 1 model: Direct matching of low level undifferentiated visual information resulting from a parallel process. The visual information is expressed in an absolute referential independent from the robot orientation. On the input layer, the black circles represent the recognized landmarks (parallel extraction). The neighbors neurons are also activated according to their distance, in azimuth, to neurons associated with recognized landmarks. The second layer is just a copy of the first layer only represented for sake of homogeneity with the other models to be presented in the next figures. The third layer is devoted to place recognition. If the winner neuron learns the connection to its most activated inputs, it will have a relevant representation of the learned place (its output will decrease when the landmarks move from the learned azimuth to another apparent location on the input ring of sensors).

The network will be really equivalent to the formal equation if lateral diffusion of the features on the neuron ring is a maximum (max) operator (the diffusions from different sources must not be summed. The max of the contributions must be used). The effect of the lateral diffusion on the activity I_i of the neuron i of the ring is defined as follows:

$$I_i = \max_{j=0}^{N} \quad e^{\frac{\left((\theta_j^L - \frac{2\pi}{N} I_j) \bmod 2\pi\right)^2}{2\sigma}} \tag{2}$$

where θ_j^L represents the azimuth of the jth landmark in the environment. The neural computation associated with a place recognition is performed by a classical formal neuron:

$$Act_k = f\left(\sum_{i=0}^{N} W_{ik}.I_i^{abs}\right) \tag{3}$$

where W_{ik} are the neuron k weights and f is a non linear function that returns a null value for negative inputs. I_i^{abs} is the activity of the input neurons associated with the recognition of one feature under the orientation $\frac{2\pi i}{N}$. The input information is supposed to be independent of the system orientation. If the animal or the robot is rotated 90 degrees left, then all sensor information is rotated 90 degrees to the left so that the N.N. input are invariant to the system orientation.

$$I^{abs} = tr\,(I, \theta) \tag{4}$$

where $tr(x)$ represents an operator allowing to translate in a circular manner the components of the I vector according to the robot orientation θ. In a first approximation, the weights W_{ik} can be supposed to be 1 (if a feature has been learned under the considered azimuth) or 0, but to avoid comparison problems between neurons associated with different places, it is better to introduce a weight normalization $W_{ik} \leftarrow \frac{W_{ik}}{\sum_{i=0}^{N} W_{ik}}$.

This set of equations defines a model of how insects and simple animals with poor visual systems may recognize a place. We will name it the level 1 model. A more realistic and efficient model could suppose that some animals have the ability to differentiate few kinds of features. If an animal has the capability of recognizing two different kinds of features and detects that they are both present in the image, then, the discrimination capability will be much more important (at least twice better). As shown in fig. 3, the N.N. does not need to be changed drastically in order to deal with this new degree of freedom.

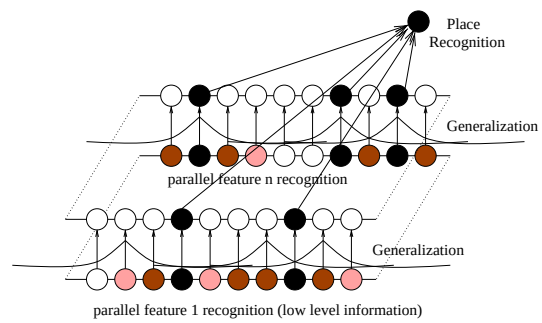

Figure 3: Level 2 model: Direct matching of low level information extracted in parallel (same comments as for fig. 2)

In terms of complexity, it will be called the level 2 of our model. Its formal description is the same as for the level 1. The only difference is that the input space has one more dimension associated with the different features which are extracted in parallel (see fig. 3).

In the case of an even more sophisticated visual system, another level of visual recognition integrating several local features can be added (level 3 complexity in our model). In this case, because of the computational and memory requirements previously discussed, the system can recognize very few objects at the same time. The exploration of the visual scene has to be sequential and a kind of buffer to store the previously recognized information has to be introduced. Fig. 4 presents such a network. We have to suppose the existence of a mechanism that controls the focus of attention (internal moving spot light or ocular saccades or head/body rotations.). The system must also possess the capability of matching the perceived local view with already stored views and to store on-line and autonomously new views. A Winner Take All (WTA) group or an ART network [10] can be used. Like in the

previous systems, the lower layer in fig. 4 provides information about the object location in the visual field (its azimuth for instance).

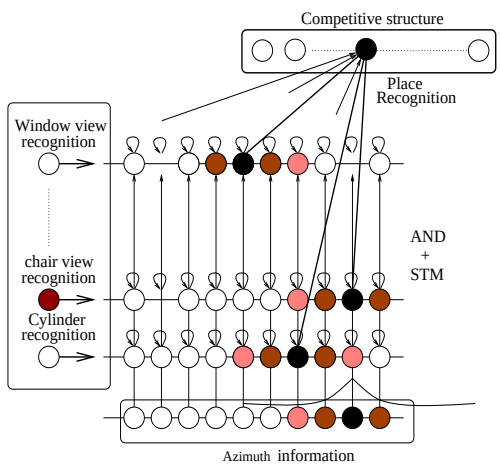

Figure 4: Level 3 model: Merging of "What" and "Where" information for place recognition in the case of an high-level visual system. The lateral diffusion allows to measure the difference between the learned azimuth and the current azimuth.

But now, the second group of neurons receives both object recognition information and their azimuth. A one by one product between those two kinds of information is performed on that layer so that a particular neuron is activated only when a given object is perceived under a given azimuth. The formal computation of this group of neurons can be represented by the activity in a matrix of neurons M computed as follows:

$$M = \sum_{i=1}^{N} Rec_i . Az_i^T \tag{5}$$

where Rec_i and Az_i are respectively the recognition and the Azimuth vector associated with the perceived local view. The effect of the sum is similar to a temporal integration without decay and with a reset to 0 after each panorama exploration. An inhibition of the previously explored focus points guarantees the system cannot focus twice on the same point during the panorama exploration. So M only contains values between 0 and 1. The recognition of a learned local view is associated with a strong activation of the corresponding component in the matrix. A memory at the level of the neuron is supposed to maintain the activity until a reset is triggered at the beginning of new panorama exploration. Different neurons will win for different azimuths or different recognized objects. The activity of the "place cells" P_k when the robot is at the location (x,y) can be expressed by the following equation:

$$P_k(x,y) = 1 - \frac{\sum_{i=1}^{N_k} V_{i,k} . f\left(\left|\Theta_{i,k} - \theta_i(x,y)\right|, v_i(x,y)\right)}{\pi N_k} \tag{6}$$

An intuitive understanding of this measure can be seen fig. 5 where the negative term of the equation is plotted with respect to the robot position.

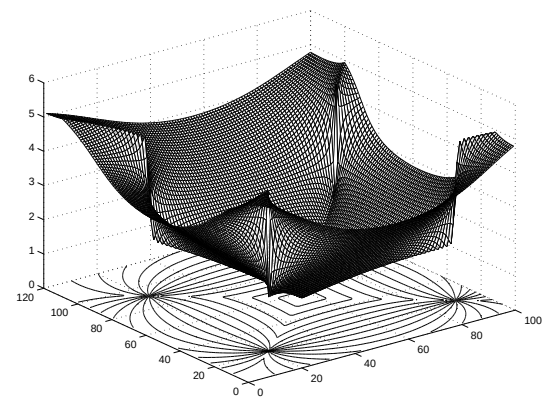

Figure 5: Simulation of the error of a "place cell" response computed according to the negative part of eq. 6. In that example, the learned location is associated with the point (50,50). 4 recognizable landmarks are located at positions (20,20),(20,90),(90,20) and (90,90). The shape can be seen as an attraction basin centered on the learned location.

In this equation, N_k is the number of visible landmarks when the robot is at the learned place k (field corresponding to P_k). $\Theta_{i,k}$ represents the learned value of the landmark i azimuth from the learned place k. θ_i is the value of the same landmark azimuth for the current robot location (x,y). All the angles are expressed in radians and measured from an absolute direction (the north for instance). $|\Theta_{i,k} - \theta_i(x,y)|$ is computed modulo π, $V_{i,k}$ is set to 1 when the landmark i is seen from the learned location k and 0 otherwise (the same rule applies to v_i for the current location). When learned landmarks are not recognized, we can have $V_{i,k} = 1$ and $v_i = 0$. f is a non linear function to account for landmark recognition:

$$f(\theta, v_i) = \begin{cases} \theta & if \quad v_i = 1 \\ \pi & if \quad v_i = 0 \end{cases}$$

The error associated with a landmark azimuth is maximal when the landmark cannot be found (landmark not visible for instance: $f(\theta, 0) = \pi$). Eq. 6 gives a growing activity P_k that tends to 1 when the azimuths θ_i associated with the current location are close to the stored $\Theta_{i,k}$.

In the case where the system uses this sequential mechanism of object identification and where all objects are similar, there is no need to add another mechanism to discriminate between objects. If all objects

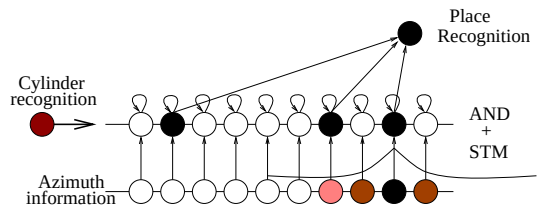

Figure 6: Sequential "recognition" of the cylinders allowing the recognition of a place (case of identical and distant landmarks).

have the same label then, a single line will be activated on the "what&where" representation. The resulting representation (see fig. 6) is exactly the same as the one we used in the level 1 of our model for an insect-like place recognition! The system can have problems in case of symmetrical situations but if the number of "cylinders" remains low and does not change, the place recognition will be correct.

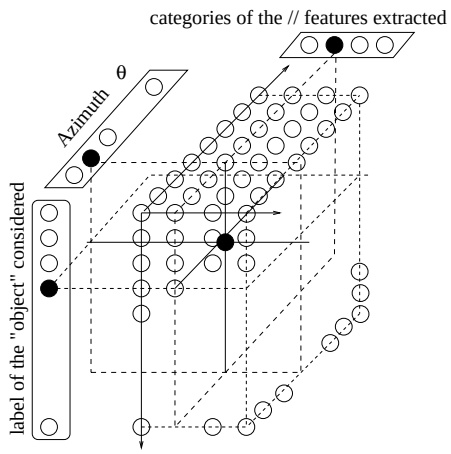

Figure 7: Representation of the visual information factorization in our model. The activation of a neuron in the matrix is the result of the co-occurrence of the 3 kinds of information. To exploit the label or "what" dimension, there is a need for a neuron dynamical memory to maintain active the neurons while the system explores other parts of the visual scene. The apparent size of the objects (not taken into account here) could be represented by a 4th axis similar to the azimuth axis.

To sum up, our place recognition model, is a proposition about how visual information can be factorized. The model can be seen as a 3 dimensional representation (see fig. 7) of the visual information connected to "place cell" neurons that learn particular configurations of this 3D matrix (the representation is invariant to the robot orientation). The dimensions are:

- the azimuth of the feature
- the feature category (the kind of feature extracted if there are several low level feature extractors)
- the label of the "object" associated with the location provided by the first dimension: the azimuth

Classical models of visual place recognition can be seen as simplification, or computation on a particular projection of our representation. If the matrix is degenerated to the single first dimension (the azimuth) then we come back to the Cartwright and Collett model. If we consider the 2 dimensional matrix: $[azimuth \times features]$ we obtain models that looks like what is considered in rodents. If we consider $[azimuth \times label]$ we come back to the level 1 model and to something that looks like primate object recognition capability. At last, if we consider a learning mechanism on the complete 3 dimensional representation then, we could have the possibility of understanding what are the important features according to a particular task (navigation, complex object identification).

2.3 Robotic implementation of place recognition

Our merging and place recognition models have been implemented on a mobile robot (see fig. 8) in order to test their efficiency.

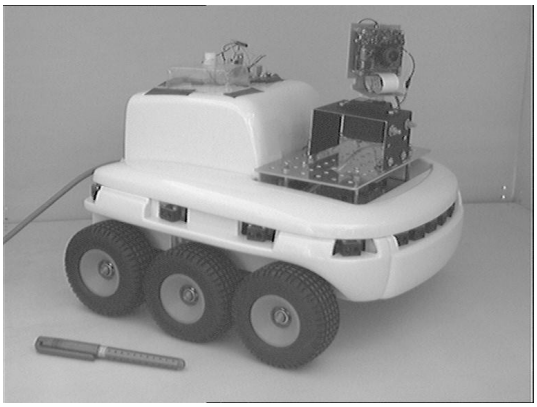

Figure 8: Photo of our six-wheeled Koala robot (size 32 cm x 32 cm) from KTeam SA. The magnetic compass is visible on the top. The CCD camera is mounted on a servo-motor to control the direction of gaze.

To take a panorama, the CCD camera can pan from +90 to -90 degrees. This system allows to build a panoramic image up to 300 degrees wide (fig. 9). Several kinds of visual processing have been developed [16]. They involve very rough perception or, on the contrary, complex visual processing such as log-polar transform of the visual input, gradient extraction, feature point detection, ... In this paper, we will only deal with the simplest one that directly works with the grey level image, which is good enough for the present demonstration.

The azimuths of the possible landmarks are chosen at the maxima of the vertical gradient at a very low reso-

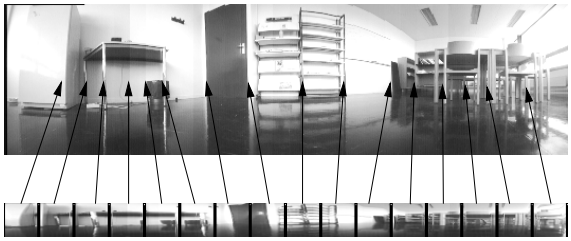

Figure 9: 16 examples of 32×32 local views learned as landmarks from a 300 degrees panoramic image.

lution (see fig. 9). They are corrected according to the value of a magnetic compass (gyroscopic information could also be used). Any a priori selection mechanism of "interesting" landmark can be used. The perceived local views are centered around those points. For each selected focus point, a 32×32 pixels local view is built by averaging the 148×288 pixels of the corresponding panoramic image part (see fig. 9). The $\mathbf{y}$ axis is just scaled whereas a logarithmic transform is used for the $\mathbf{x}$ axis (no need of a complete log-polar transform since there will not be object rotation problems in the camera plane). Then, each current local view is compared with each learned local view. This comparison is made by computing the norm of the difference between the grey levels of pixels of the two local views. The best corresponding local views are used as landmarks, i.e. their positions in the image are compared with the ones in the learned panorama.

All possible landmarks are used. As a result, the number of object-landmarks found in the image can change from one image to the next. The system can consider a human or an animal as a landmark! This is not a problem since the presence of a landmark, not present during learning will have no effect on the place recognition (see eq. 3 and 6). Obviously, the presence of new landmarks can hide learned landmarks. In that case, the recognition level of the associated places will decrease. But because the robot learns at least 15 landmarks[1], the lack of 5 of them will not introduce an excessively large variation in the neuron activities. It might be noticed that the correct recognition of 2 landmarks is enough for a correct place recognition. If the errors are not coherent, they can be interpreted as noise on the neuron response. In the opposite case, the system will fail because large coherent errors mean the perceived situation looks like a massive displacement of the landmarks (rotation or translation of the room)!

The interest of these experiments for our understanding of animal visual navigation lies in the opportunity to record the response of each neuron coding for

[1] The number of visible objects or landmarks depends directly on the visual scene complexity. The presence of 15 "landmarks" is a lower bound (in average). The system can find up to 40 landmarks (intrinsic limitation of the landmark detection system).

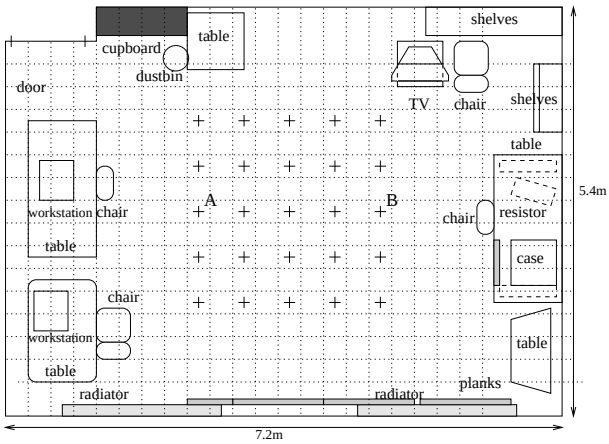

Figure 10: The room in which the experiments are performed. The little crosses represent the places where the robot has learned (see fig. 11 and 12).

place recognition (we may consider them as artificial "place cells" – see below) in a completely controlled situation. Fig. 11 shows the activity of 25 neurons associated with 25 different places. This activity is the response of the neurons according to their direct input (recognition level of the landmark and information about their azimuth). Learning was supervised with each neuron associated with a particular location in a 5×5 grid of the room used for the experiments (see plan fig. 10). The different curve lines show that a neuron may be activated even if the current view is far from the learned one, and that there are no local minima. Fig. 12 shows what happens after a strict competition. For a given location, only the winner neuron remains activated (it keeps its previous value while the others are reset to 0). This activity looks very much like the shape of place cell activity that has been recorded in the rat hippocampus for several decades [30] (we will come back to this kind of comparison in the next section). The results show the model allows to obtain a segregation of the place locations in a real environment from the sole visual information.

The most interesting result is that the gradient of the place recognition level can be used very far away from the learned location (more than 2 or 3 m in our case). In the following experiment, a supervised triggering of the place learning is used so that the robot learns only two places A and B which are 240 cm away from each other (see fig. 10). The robot learns 20 local views or landmarks from those two locations. Even if the same object can be perceived from A and B, the robot learns two different views for the object (the vigilance threshold is set very high). Next, the robot moves on a straight path between those two places and the activation level of the two place cells is recorded. Fig. 13 shows the average of the 2 neuron responses computed from five different measures at each location

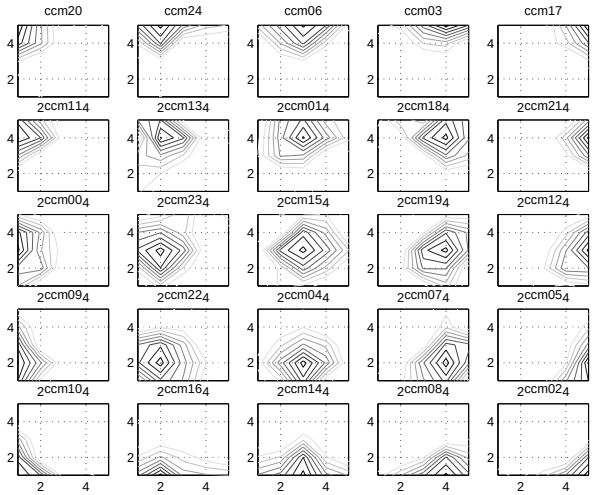

Figure 11: 25 neurons, 25 places, 5 measures averaged per place, diffusion 35 degrees. Neurons are considered to be isolated (activation only comes from the direct input). Learning was supervised: each neuron is associated with a particular location in a 5×5 paving of the room in which the experiments have been carried out. Each rectangle is a map of the room. The curves show the activity of the neurons corresponding to the crosses of fig. 10.

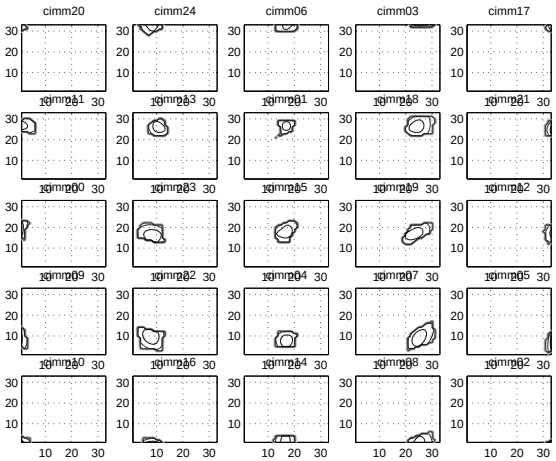

Figure 12: Same setup as in fig. 11. A competition between neurons is introduced. Only the winner neuron remains activated while the others are set to 0 (no activity enhancement used).

on the line. The standard deviation comes from the uncertainty on the "landmark" recognition in case of ambiguous local views. The two curves decrease almost monotonously on more than 2 meters, which means the information learned in A and B is relevant when the robot is far from those locations. A gradient following technique or any other efficient technique could be used to return to the learned places [18]. The neuron does not only represent the recognition of a place but also provides information about the distance to that place. Another interesting result of this experiment lies in the importance of a non linear measure of the azimuth variation for a given landmark between its learned and perceived location. Indeed, in fig. 13 a) landmarks are supposed not to be recognized if their azimuth variation is greater than 38 degrees while in fig. 13 b) the threshold is about 276 degrees. In the first case, the place recognition curve is sharp and precise around the learned place, but becomes difficult to use for distances longer than 1m. Conversely, in the second case, with an important tolerance on the azimuth variation, the measure remains correct over several meters but is obviously relatively "flat" close to the learned locations. Hence, during a homing behavior, it can be useful to use a large diffusion when the robot is far from the goal (low recognition level of that goal) and decrease the diffusion as the robot comes closer to the goal. We successfully use this kind of techniques on our robot.

These results must be contrasted with those obtained using only the information about the azimuth of the landmarks and not their identification (level 1 of the model). Fig. 13 c) shows clearly that this kind of information can be used when the robot is close to the learned place but is of no use farther (no generalization capability). This experiment shows also that algorithms directly inspired from Cartwright and Collett model can work correctly if there are not too many landmarks. When there are more than 10 possible landmarks, the problems of landmark selection and landmark matching become non trivial and other mechanisms need to be introduced in the algorithm (learning intermediate places but with the problem of no generalization or introducing a mechanism to recognize relevant landmarks [6]).

A last robotic experiment can be useful for understanding some differences between rodent and monkey perception of their visual environment. In this new experiment, the visual field of the system is limited to 180 degrees. Then the activity of the neurons associated with the recognition of the "what&where" representation are no longer place cells but react like view cells and have very similar properties than the "view cells" recorded by E. Rolls ([42, 43]) in the monkey hippocampus (see fig 14). The neuron response seems to be defined by the view of the environment and not by the place where the robot was.

This experiment shows something that was already true in the previous experiment but more difficult to see: our place cells are directional and their directionality depends on the field of view. For large fields of view (about 300 degrees) and for a given location, the activation of a place cell decreases a little when the robot orientation is at 180 degrees of the orientation used for learning (if the landmarks are uniformly distributed). For smaller visual fields, it happens more

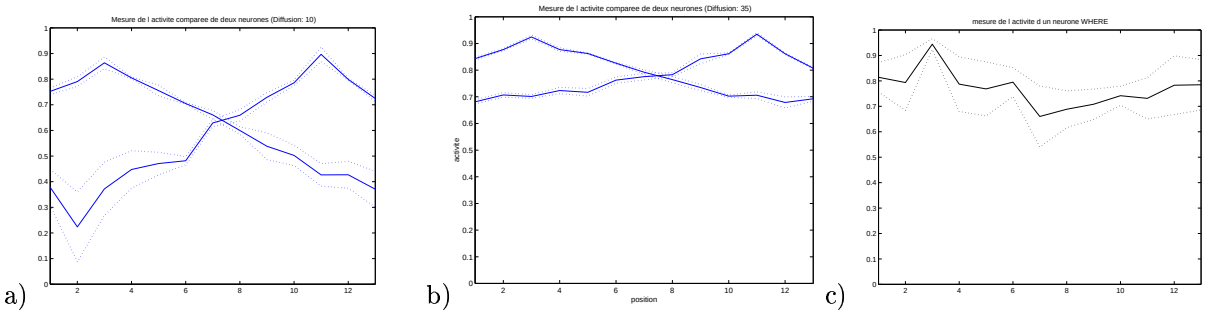

Figure 13: a) and b) Responses of two places cells while the robot is moving on a straight line (dashed lines represent the standard deviation computed over 5 trials). The diffusion is respectively about 38 degrees a) and 276 degrees b). The 2 peaks are associated to the 2 learned locations (x_A=3 and x_B=11 distant 240cm apart). c) Response of a place cell computed according to the sole azimuth information of the landmarks (the learned location is at x=3, the highest peak). The landmarks are all considered to be the same. The diffusion is about 38 degrees.

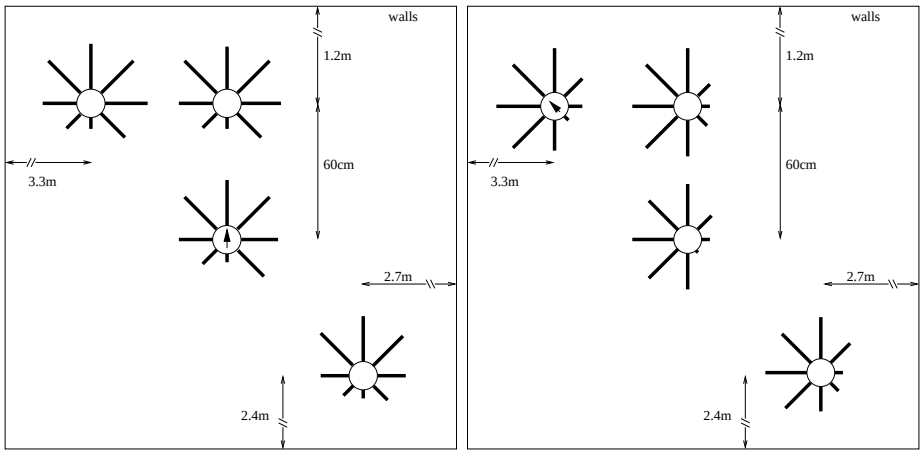

Figure 14: Record of 2 "view cells" according to the robot location and orientation in our experiment room (arrow represents the position and direction of the learned view). The black bars represent the neuron or "view cell" activation in direction of view. The robot uses the same algorithm as for place recognition. The robot field of view is simply reduced from 300 to 180 degrees.

easily that landmarks disappear from the field of view.

2.4 Discussion of the model

The meaning of the robotic results presented here question a lot if we compare them to animal visual navigation. First of all, our results, like others obtained in neurobiology these last years, confirm that visual information is very important for place recognition. In contradiction with McNaughton and others [36], it appears to us simpler to imagine a model of place cells mainly based on visual information but where the idiothetic information would be used to increase performance or to maintain a coherent activity when the light is off or when the environment is visually non discriminant (corridor situations or very poor visual environments like those used for most of the neuropsychological studies about navigation...). Another argument in favor of the preeminence of visual information is the fact that rodents reset their odometric information according to visual information if there is a strong contradiction between them [13]. This kind of merging has still not been performed in our robotic experiment but it will be of very high importance for complex navigation tasks.

Other information like apparent size could also be used to improve the system performances and provide information about landmarks' distance. But, as pointed out by Zipser [57] the sole distance information cannot be used to distinguish between mirror situations. Information about the relative locations of the objects from each other are very important. Moreover, distance information obtained from vision is less precise than azimuth information. One of the main argument of Burgess, Recce and O'Keefe model in favor of the use of distance information for place recognition was to account for the results that an expansion in a single direction of the experimental setup induces a splitting of the place fields [8]. Their explanation is that if a neuron takes distance information from two different walls and if the distance between the 2 walls

increases then, the neuron will have two maxima of activation from the two locations associated with the learned distances.

If place cell activation is computed according to our model (see eq. 6) then, it is not possible to account for O'Keefe and Burgess experiment: the place fields remain robustly associated with the same location! That means absolute azimuth information must not be used if the model has to account for this kind of drawback. The same "problem" also remains if a given landmark is taken as referential to measure the angles (see fig. 15). This kind of robustness of place fields in our model is interesting for robotic applications but disagrees with the biological data!

Interestingly, if the angles are measured from one landmark to the next (each landmark is used as a reference to measure the azimuth of the next landmark) then we observe the splitting of the place field in two when the environment is enlarged (see fig. 15 c) and d)). In that case, to explain the splitting of the place field in two, we will consider that the landmarks are the 4 corners of the workspace (a box) and not the walls by themselves as in Burgess, Recce and O'Keefe's model. Then, a place is defined as the location where the angles between landmarks remain constant. Because the angles are measured between the current location and two particular landmarks, the places where an angle remains constant is an arc of a circle. If the box dilatation is homogeneous, the dilatation of 3 circle radius will be identical for all of them and the 3 circles will continue to intercept each other at the same location. On the contrary, if the dilatation only happens in the x direction, the places where the angle associated with L3 and L4 will not change while the places where the angle between L1 and L2 remains the same will change because the distance between L1 and L2 changes. As a result, there is no longer a unique intersection of the 3 circles. 2 locations of intersections between the two pairs of circles solution appear and constitute the places where there is a minimum of error in the place recognition. Then, the associated place cell has 2 local maxima of activation and our model could be considered as an alternative explanation to account for place field splitting. As a preliminary conclusion, we can only say that our abstract model does not disagree with neurobiological evidence. Questions that remain are: is the rodent visual system complex enough to make our model plausible? How is it possible to embody our abstract model in the neurobiological structure?

First of all, it appears that the whole field luminance is not much used by normal rats [31, 25]. We can conclude they use something more complex than the level 1 of our model. Rats must be able to use some kind of landmark identification but "it is not clear, however, how these distant cues are processed. They might be fixated sequentially or processed in peripheral vision as either stationary of self produced movement cues." ([32] p 293). The landmark identification performed by rodents could involve only few parallel and low level feature extractors (like in the level 2 of our model). Indeed there are also some suggestions that the rat temporal cortex may be involved in peripheral and not central vision [32]. But, there exists in the rodent lateral posterior cortex an area called Te2 (Krieg's area 36, Zilles's area Te2) that has some resemblance to inferotemporal cortex of the monkey. It projects to perirhinal region [12] and receives projections from the entorhinal cortex [33].

These connections are mainly similar to those of the monkey. Lesions to the posterior parietal cortex (PPC) involve a "deficit in perceiving the spatial relations between objects, such that the animals do not orient themselves accurately with respect to spatial information. This deficit is reminiscent of similar deficits in humans and non human primates. The posterior parietal deficit is likely dissociable from the frontal or hippocampal deficits in that there is no additional memory deficit after PPC lesions [32]. From the anatomical data, it is not possible to say that complex object recognition cannot be used for navigation, but the ablation of Te2 region does not perturbate navigation task like in the Morris swimming pool. On the contrary, it suppresses the capability of associating the recognition of a complex object with an action, like jumping in the direction of the object or avoiding it. It is thus possible to conclude that there are in rodent and monkeys two distinct visual processing routes: one for the spatial guidance and one for the kind of visual analysis required for object recognition [38, 32]. Obviously, all these features can be much more complex in the primate or the human brain with the possibility of more cognitive function in PPC (spatial rotation, map visualization...). In conclusion, animals such as insects (ants, wasps, bees...), rodents and primates can use, at the same time, more or less complex (or integrated) visual information that our generic model accounts for. It seems very interesting there exists a path from simple to complex visual navigation linked with a more or less elaborated or complex merging of visual information.

Now, we can try to address the second question about how to fit our model in the biological structure. Our starting point is that nearly every neocortical area has reciprocal connections with the perirhinal cortex which is the major route to hippocampus and amygdaloid formation [43]. Hence, the perirhinal cortex or the parahippocampus could be the places where local configurations of different kind of information is recorded (like "what" and "where" information).

In the case where only low level and parallelly extracted visual information is used, this merging can be seen as a first step towards information integration

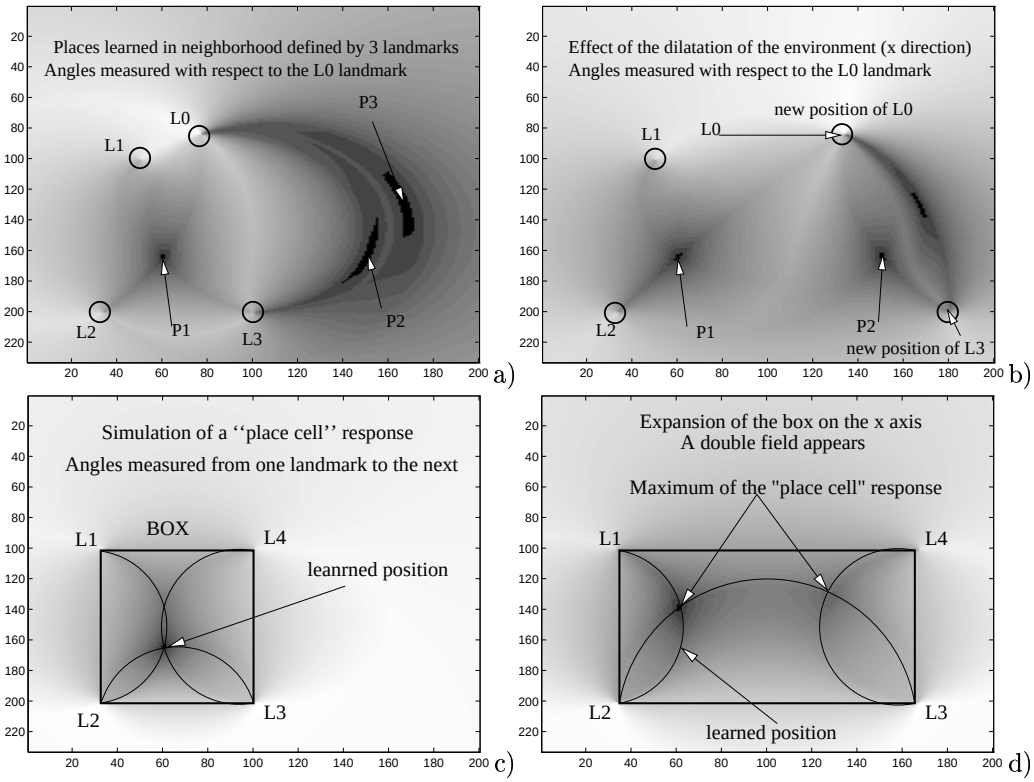

Figure 15: a) Simulation of 3 place fields on a flat surface (coordinates expressed in an arbitrary metric) before environment dilatation when the landmark L0 is taken as the reference to measure the angles. The grey level represents the level of neuron activation according to the simulated robot location (areas associated with higher activities are represented by darker areas). b) Place fields after environment dilatation. c) and d) Simulation of the effect of a box dilatation on 1 place field when angles are measures from one landmark to the next: c) before box dilatation, d) after dilatation splitting in two of the place field. The arc of circles represent the location where there is no error on a given angle or neuron input.

in order to recognize some kind of more complex local views. When more abstract visual information is available, the merging of the "what" and "where" information needs the presence of sigma-pi unit [44]. The same holds if we suppose that other contextual information is used. It will have a modulation effect on the more spatial information and a product operator would be of a great help. Hence, we can propose a very hypothetical model of the place recognition in which *the parahippocampus is used to store experienced configurations while the place recognition is performed in the entorhinal cortex.*

But it remains striking that the place cells found in the rat hippocampus are restricted to an area about 10 to 20 cm while we insist on the possible availability of a continuous place recognition information that can be used on several meters (at least 2m, 10 times the diameter of the observed place fields)! In a simple open environment the sole use of the discrete place recognition performed in the hippocampus means the animal is only able to recognize its very location and cannot have any idea about its distance to a particular location like a goal or the platform in the case of the Morris swimming pool. We know this information could be available at a very low cost! As a result, models of rat navigation based on hippocampal place cell always involve cognitive maps [53] that can be represented as a graph linking neighboring places. Unfortunately to come back to a goal location, a robot using these models will have to already know a path linking the current location with the goal location. A priori generalization is then not possible and if mammals were all using only this kind of strategy, they would have less navigation insight than insects! On the contrary, as shown in fig. 16, it is sufficient with the Perception-Action (PerAc) architecture (for more details see [24]) to learn only 3 place-cell / action associations in the immediate neighborhood of a goal to allow the robot to come back to the goal from any location in the open space around the goal (even if the robot never experienced this location before).

Is it possible that the "real" place cells or the precursors of the hippocampus "place cells" would exist before the hippocampus? According to our model those cells might react over very long distances and would not appear at first sight as really place-specific because hip-

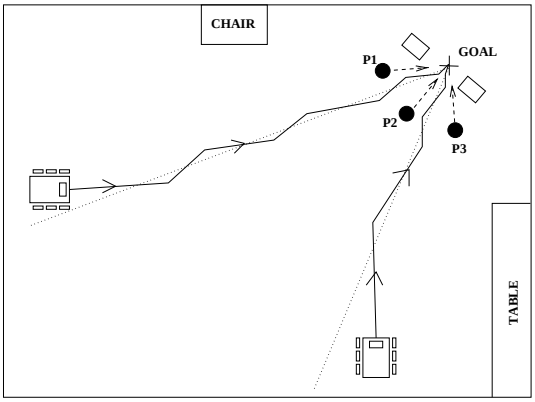

Figure 16: Schematic representation of a robotic experiment in which our robot learns 3 locations around a goal (the black circles) associated with the actions that allow it to reach the goal. When the robot is far from the goal, the competition between place cells allow the robot to reach the goal whatever its starting position is (see [18] for more details). The 2 long straight lines represent the frontiers of the place "recognition" areas associated with the 3 place cells.

pocampal place fields are more localized and sharper than the tuning curves of our model's cells. It would be only at the level of the entorhinal cortex that the competition would allow to measure activities that look like "directional place cells". Now, the problem is now to study how this place or view recognition mechanism can be used in the case of a motivated navigation in a complex environment.

3 A planning model based on transition detection

Using the "place cell" learning mechanism presented above, a given environment can be paved with place fields so that for each subpart of the environment a given place cell responds. Furthermore, each "place fields" can be associated with a basin of attraction, and is thus potentially reachable (provided it is recognized, and that there is an open space between the place the animat actually is and the one it wants to reach). Therefore, if some of those places are associated with specific motivations ("hunger" or "thirst" for instance – see figure 17), the modulation of the recognition by the motivation level allows the animat to reach the appropriate place. This simple action selection mechanism still works even if there are obstacles on the trajectory, provided a reflex obstacle avoidance system competing with the goal attraction mechanism [17].

The main difficulties arise when the animat cannot perceive directly where the goal is, for instance when there is a wall or a huge object. As the animat cannot see the goal, it cannot generalize the "good" movement to perform from what it has learned next to the goal. An intermediate step consisting in learning how to reach places from where it is possible to see the goal is necessary. Behaviorists have proposed that it could be performed by learning what they call "conditioning chains": they suggest that from place to place, the movements leading to the goal could be reinforced (it is interesting to notice that this mechanism is similar to Q-learning techniques [54]).

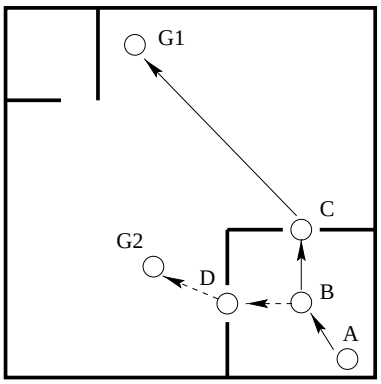

Figure 17: Example of a complex environment showing the need for a planning mechanism. Circles (and the associated capital) represent learned places and arrows show the movement leading from one place to another. 2 goals G1 and G2 associated to 2 different motivations are also present. Conditioning alone cannot explain the capacity of the animat to choose between 2 possible movements in B (the dotted arrows represent the alternative movements), a planning or anticipation mechanism must be added.

This explanation can still stand even if, at given places, there are several possible routes (but a single motivation). For instance, in figure 17, if the animat finds a new goal G_2 which is closer than G_1, the route can be reinforced more efficiently since it is closer (short delay between reinforcement signals). Yet, in case G_1 and G_2 are associated with 2 different motivations, the "conditioning chain" explanation does not work anymore. For instance, if G_2 is associated with "thirst", links BC and BD will be reinforced (maybe BD will be reinforced more since G_2 is closer) and there would be no way to distinguish the action leading to G_1 from the action leading to G_2. One can think of using a modulation mechanism as the one we propose above, but in this case, there should be as many place-cells or action coding as motivations!

3.1 Learning a cognitive map

In fact, the ultimate problem of the above model is that it does not explain latent learning. Indeed, in the 30's, Tolman performed a maze experiment with rats, which consisted in comparing the results of rats that

were always rewarded while another group of rats was only rewarded after 11 days [51]. According to the behaviorism paradigm, rats of the first group should have had much better results than rats of the second group. Yet, after the eleventh day, the rats of the second group had results equivalent to those of the first group. Thus, it seems that, although they were not rewarded before the eleventh day, rats have learned ("latent learning") an internal representation of the maze (called "cognitive map"). The definition of the "cognitive map" is controversial. In particular, some consider that this kind of map must be in Cartesian coordinates [15]. Yet, Schmajuck proposed a definition which is, in our opinion, more appropriate [45]:

> "...The cognitive map [...] is a topological map, i.e, it represents only the adjacency, but not distances or directions, between places... The cognitive map allows the combination of information about spatially adjacent places, and thereby the inference of the connections to remote places."

Let us come back to our "place cell" model: how is it possible to *learn* a "cognitive map" starting from our implementation of the recognition of places? In fact, it is rather easy if we consider that neurons of the place recognition map are fully interconnected. Then, when a place is recognized, it is coded on a neuron i. When a new place appears, it is coded on j, and a simple Hebbian rule allows the learning of the time relationship (and thus the topological relationship) between these two situations. If x_i is neuron i activity and $\overline{x}_i$ its corresponding short term memorization (τ time constant) with:

$$\tau \cdot \frac{d\overline{x}_i(t)}{dt} = -\overline{x}_i(t) + x_i(t) \tag{7}$$

the Hebbian learning rule is given by:

$$\frac{dW_{ij}}{dt} = -\lambda W_{ij} + (C + \frac{dR}{dt}) \cdot (1 - W_{ij}) \cdot \overline{x}_i \cdot x_j \tag{8}$$

where C is a positive constant (speed of the associative learning) and λ the decay factor. The weight modification also depends on the variation of the reinforcement signal R. If the reinforcement decreases while the robot is moving from one place to the other then, the associated link will be less reinforced than in the normal case. $(1 - W_{ij})$ is a saturation term to ensure $W_{ij} \leq 1$. By generalizing the mechanism, a graph of the spatial relationships between places is constructed.

Planning requires also to learn the link between the recognition of a given place and the satisfaction of a motivation (that will be used as a goal). For this purpose, it must be considered that the recognition of this place is associated with the activation of a given "motivational" neuron. The links between the motivational neuron and the recognition of the situation can be reinforced with a Hebbian rule. Then, a solution for the planning process can be the back-propagation of the motivation activity within the map (as for resistive grids [7]). For a proper functioning of the planning process, the activity of a neuron in the cognitive map (x_i) must be a function of its topological distance (number of intermediate places for instance) to the goal. We propose:

$$x_i = \max_j (W_{ij} \cdot x_j) \tag{9}$$

We assume that neuron activity is bounded by 1 and that the value of weights is bounded with a value W_{max} which is lower than 1 (see above). Before stabilization of the algorithm, there must be several iterations. The 2 phases of planning algorithm are:

- Initialization: i_0 is the motivational neuron, $x_{i_0}(0) \leftarrow 1$ and $x_i(0) \leftarrow 0$, $\forall i \neq i_0$
- Do $\forall i,\ x_i(t+1) \leftarrow \max(W_{ij} \cdot x_j(t))$ While the net is not stable (maximal distance between the current node and the goal in connections number)

The use of the cognitive map could be the following: after backpropaging the motivations from the goals to all the sub-goals or known places, the system tries to recognize its current location (the most activated "place-cell" is the nearest learned place from the current robot location). Then, it selects as a sub-goal the most activated node on the "cognitive map" directly linked with its current location. To reach that place, a gradient following technique can be used (moving in the direction that maximizes the activity of the place cell coding for the sub-goal the system wants to reach) When the system enters in the vicinity of the next sub-goal, the process is repeated (selection of the next sub-goal...) until it reaches the nearest goal relative to its starting location. This neural algorithm is formally equivalent to Bellman's shortest graph distance algorithm [5] and it has been shown to be very efficient in simulation to solve complex action selection problems including opportunistic choices and contradictory motivations [20, 40].

If the place-recognition neurons were directly connected to each other with recurrent connections so they can be also used as a cognitive map, the meaning of the neuron activity would become ambiguous: the neuron activity would represent a mixing between the distance to the associated learned places and the distance to the goal (the feed-forward and the backward computation would be mixed together).

A solution consists in separating the process in two functional levels so as to separate the two information

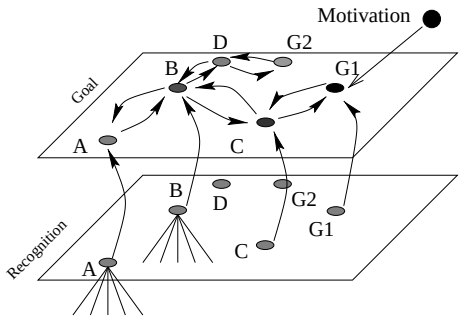

Figure 18: Building of a "cognitive map". During learning, the information goes from recognition to "goal" level to allow the learning of the map (topology learning between A, B, C and G_1...). During planning, the activation of a motivation is back-propagated on the map.

flows: one corresponding to the "goal" level, another corresponding to the recognition of the current place. During learning, the information must flow "bottom-up" from the recognition level ($P_k(x, y)$ activity) to the "goal" level so as to allow cognitive map learning (one-to-one connection between the neurons of the 2 levels). Conversely, during planning, the information coming from the "goal" level must go "top-down" in order to select the action to perform (see figure 18). Interestingly, this functional organization corresponds to the neurobiological model of cortical columns proposed by Burnod [9]. But the need for 2 functional levels does not mean necessarily an anatomical separation. For instance, neuromodulations can be used to inhibit the effect of a particular kind of inputs during critical periods. We will come back to this point in the discussion of the brain regions that could implement such a cognitive map, but the possibility that CA3 recurrent connections could play that role is not impossible and is the basis of most of the navigation models using hippocampus (see [53] for a review).

3.2 Need for transitions coding

Until this point, we have not considered action learning and selection aspects. Animal studies have shown, that rats were able, at "strategic locations" (T-junctions of a maze for instance), to try for a short distance the different possible ways, and come back to the junction, and finally choose the more appropriate action to reach the goal [50]. This mechanism, known as "Vicarious Trial and Error" (VTE), can be understood as a way to estimate the local gradient on the cognitive map ([45, 46]). But these systems rely on an external mechanism to analyze the cognitive map activity and to decide of the correct movement. In fact, in these systems, the action only results from a gradient descent and cannot be controlled willingly. To overcome this problem and the limitations of gradient descend techniques (which are not efficient in a robotic context [18]) it is important the system can learn to select a particular movement in a given situation. Our problem is then about the "embodiment" of the cognitive map in the sensory-motor system, i.e the problem of connecting it correctly to the "place-cells" and to the movement selection mechanism.

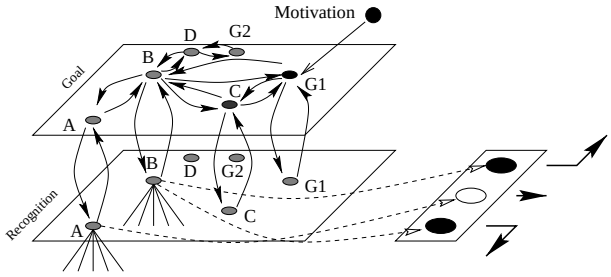

Figure 19: Planning is impossible by using only steady states recognition. Indeed, a situation can be linked with two different movements, and it is thus impossible to decide which action must be selected.

A first idea could be to decide that each place recognition cell has to be linked with the movement allowing to go to the next place. Yet, during planning, the system must use the information coming from the goal level to perform the action sequence allowing to reach this goal. If one place is linked to several actions, the correct action cannot be selected. For instance, if the animat starts from A on fig. 17, when it arrives in B there is no way to choose which action must be performed (B is linked with two movements! — see fig. 19).

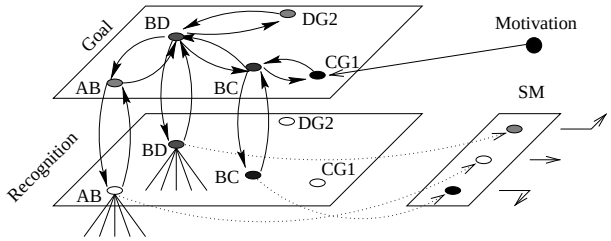

Figure 20: Use of the transitions for actions planning. At a given place, there are several possible transitions which are likely to be recognized by the recognition system. Thanks to the back-propagation of the motivation activity, the recognition can be biased in order to propose the appropriate movement to reach the goal (impossible with steady states, see fig. 19).

As there are action selection problems due to the association of two movements with a single place recognition, the solution is to build a representation which can disambiguate movement selection. Besides, this representation must take into account both the start and end points. A solution consists in building a representation of the *transition between two situations* (see figure 20).

Let AB be the internal representation of the transition between A and B. The associated action is the movement allowing to go from A to B (learned using a conditioning rule [22]). The idea of this representation has been inspired by a neurobiological model of timing and temporal sequences learning [1, 2, 21]. As the internal representation is elaborated from transition recognition and not only from scene recognition, an internal representation is necessarily linked with only a single movement. In situation B, for instance, the animat may turn left (arrives in C) or turn right (arrives in D). Transitions BC and BD will be created and respectively associated with "turn left" and "turn right" movements.

During exploration, the "recognition" level creates an internal representation for each transition between places and associates the movement allowing to go from one to the other. Besides, at the "goal" level, connections between representations are learned so as to create a graph of the topological relationships between the transitions. When the animat reaches the goal, it learns the association between the recognition of the last transition and the motivation satisfaction. During planning, the motivation back-propagation towards the current state allows the activation of the graph nodes, thereby indicating the movement that is necessary to perform in order to reach the goal.

3.3 Transition prediction system

The planning mode, requires (at variance with the exploration mode) to decide what movement to perform to reach the goal. Therefore, the system must allow a prediction of the place(s) which can be reached from the current location [1, 21]. We propose a neural implementation (see fig. 21) which consists in a map whose neurons are, on the one hand, linked with the derivative of the current place recognition[2] and, on the other hand, with the memory of the previous input. The neurons connectivity is shown fig. 21. The activity of neurons of this map is simply obtained adding the activity of each input, and then, thresholding the result. The initial weights and the threshold must be chosen so that the activity of a single input cannot activate the neuron, but both can. This system can also be used to learn to predict the possible transitions. This can easily be done assuming the link between the delayed input and the map can be reinforced enough (by Hebbian learning for instance), in order to be able to activate the neuron when only the delayed input is presented (simulation results can be found in [41]).

[2]The direct input vanishes if the animat remains at the same place. We suppose this derivation could be performed in EC.

3.4 Experimental results

We have tested this architecture in the open environment detailed in figure 22.

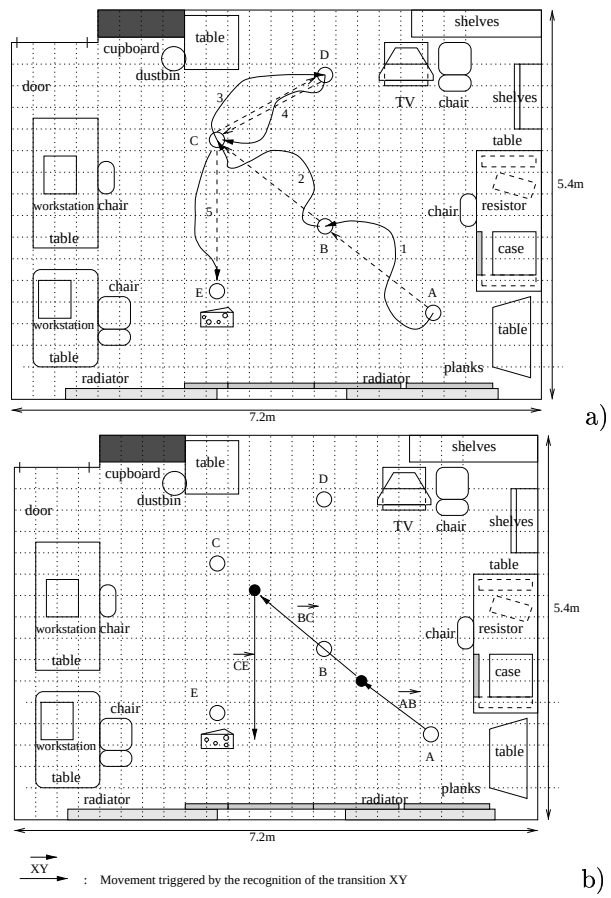

Figure 22: a) The robot path during the exploration and the latent learning of the cognitive map. b) Sequence of actions when the robot starts again from A and used the diffusion of the motivation on the cognitive map to plan its actions.

In a first phase, the robot explores the environment at random and at the same time learns the places A, B, C, D, and E when the activation of the already learned places becomes smaller than a given threshold (vigilance level). The cognitive map is elaborated over time, creating a new node for each new transition and linking nodes consecutively encountered. In the present experiment, the robot learns and links together the transitions AB, BC, CD, DC and CE (see fig. 23). The movement associated with a given transition is obtained after path integration of the robot movements from the previous activated place to the next one. The path integration is reseted when the robot discovers a new place or arrives to a known place.

It can be noticed that a single path has been learned in this very simple experiment. Nevertheless, it appears to be a very interesting case to show the capability of opportunistic behavior of the algorithm. Indeed,

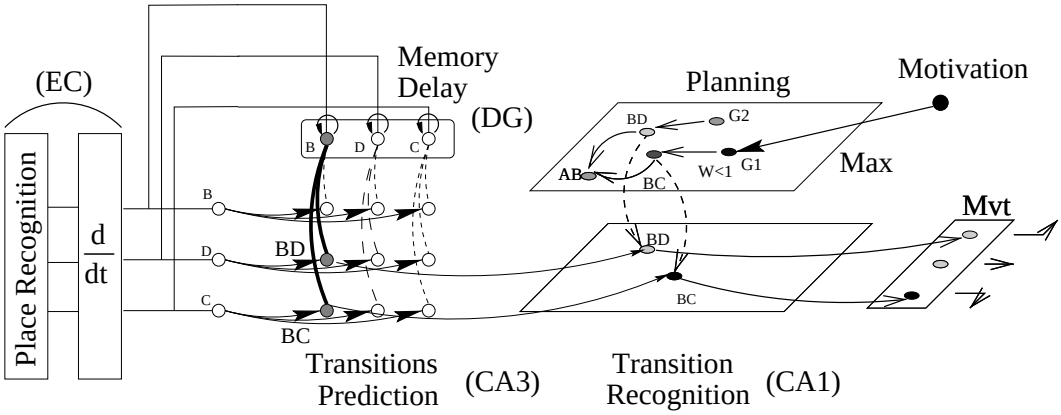

Figure 21: Overview of the planning architecture using transition detection: the recognized place and the past recognized place trigger the learning of one neuron in the transition prediction group (CA3). When only the memory of the previous place (DG) is available the same group (CA3) predicts all the possible transitions. Finally, these transitions are proposed to the transition recognition group (CA1) and the planning system can bias the recognition so as to perform the relevant movement.

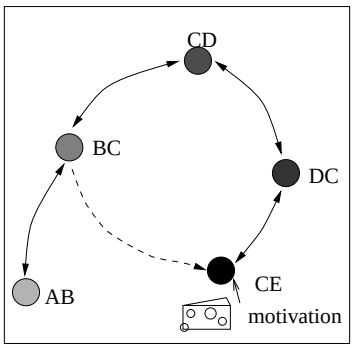

Figure 23: Cognitive map built after the exploration of the environment shown fig. 22. Note that there is no direct connection between the neuron coding the transition BC and the neuron coding the transition CE (because it was not experienced by the robot during the exploration). With the transition prediction system, the robot can nevertheless choose the transition CE after the transition BC because of its opportunistic behavior (recognition of C allows to predict CD and CE).

according to the graph, there is no reason for the robot to go directly from C to E. It should go first in D!

After this short exploration of the room, the robot is brought back to the starting point and the motivational neuron is activated. Because of the learning, the motivation is back-propagated on the cognitive map. At the same time, the robot recognizes from the sole visual panorama its current location (the most activated place cell). This recognition is used to "predict" all the possible transitions from the current location. When several transitions are possible the goal back-propagation on the cognitive map allows to bias the competition between the predicted transitions (through the top-down connections). The best transition according to the planning system is then selected. When the robot starts from A, only the transition AB is possible so the robot moves in the direction AB until it recognizes B. Then, the transition BC is proposed and the robot moves in that direction. Later, when the robot arrives in C, it predicts from C the transition CD but also the transition CE. Because the planning node CE is most activated than the node CD (nearer to the goal), the recognition of the transition CE wins and the robot triggers the movement in the direction CE (top-down bias of the planning system on the transition recognition system). Hence, it performs a "shortcut" in the graph. This new path (link between BC and CE) is besides learned on the cognitive map after the robot arrives in E.

Current robot experiments deals with navigation between several rooms. In simple cases, like moving from room A to the corridor and selecting the room B or C according to a particular motivation, the system works quite correctly. But a lot of work remains to be done, first, to select correctly the places to be learned (for instance to learn to pass correctly through a door) and next, to deal with visually ambiguous locations that appear in long corridors or in dark conditions (the place recognition has to take into account odometric information). Finding a low cost way to introduce odometric information in the planning system will also be very important to allow real short-cut like going directly from A to G in the experiment presented fig. 22.

4 Discussion and conclusion

In this paper, we have proposed a neurobiologically plausible architecture which could explain some animals' visual navigation abilities. Starting from the bi-

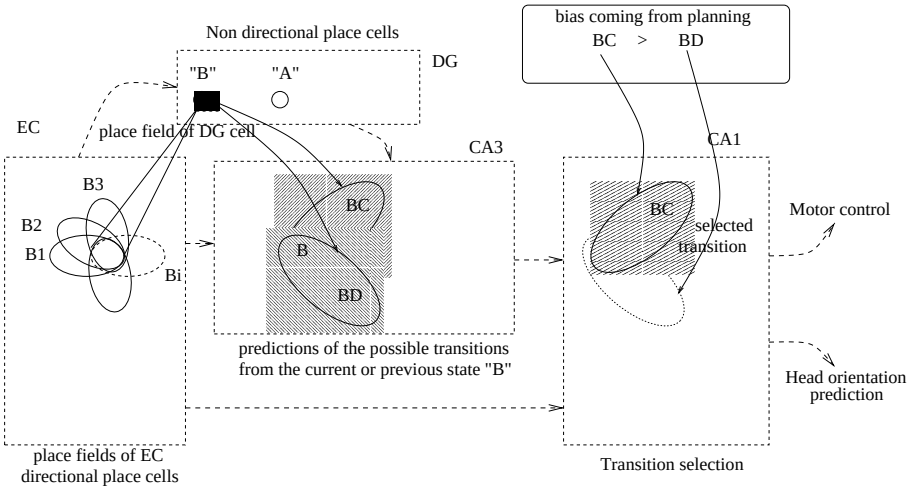

Figure 24: Relative size of the different place fields in the rodent hippocampus: according to neurobiological evidence, there could be directional place cells in the entorhinal cortex (EC). The Dentate Gyrus (DG), due to its time integration capability, could integrate those information to build place cells without orientation preference (classical place cells). CA3 could build transition cells as described in our model. According to the different neurons functionality, the place fields associated to DG granular cells should be smaller than the place fields of the CA3 pyramidal cells that are larger than the place fields of CA1 pyramidal cells.

ology of insect and mammal vision system, we have elaborated a generic abstract model. Our model accounts for navigational abilities of both species provided the input and its processing are either simple (rough recognition and no integration) for insects, or complex (association of object recognition and spatio-temporal integration) for mammals. This model is mainly inspired from the "place cells" found in rat hippocampus but it can also account for "view cells" found in the monkey hippocampus if simply the system field of view is reduced from 320 to 180 degrees. Yet, it is argued that "place cells" and "view cells" could exist before the hippocampus (in EC for instance). We propose that Hs is mainly devoted to learning and predicting transitions between steady states which are crucial when planning abilities are required (navigation in a maze like environment for instance).

We can try to compare this model with neurobiological data. In particular, in support of the temporo-spatial planning function of prefrontal cortex, it has been shown that rats with medial pre-frontal (MF) lesions have impaired performances for a variety of delay-type tests including delayed response [32]. They have also difficulties for the acquisition of any spatial maze task in which they have been tested [4, 27, 31]. Our proposal is that the cognitive map could be elaborated and/or implemented in the prefrontal cortex but that the internal representations of transitions could be coded in CA3. Indeed there is neurobiological evidence that the pre-frontal cortex has extensive connections to and from CA1 (which is consistent with our model – [14, 48]). However, it has also be shown that MF rats succeed in solving Morris swimming pool task. This does not contradict our model, since navigation in the Morris pool can be explained simply by a direct association between "place cells" and actions (see [23, 24, 19, 17, 18]). The rat capability of reaching the platform even after Dentate Gyrus (DG) and CA3 and CA1 ablation (even if its performances are impaired) could be explained by the existence of place cells in the entorhinal cortex. The impairment of the performances could result from the incapacity either to merge odometric information or to plan a short trajectory or both, because of an incapability of predicting the possible transitions from the current state.

We believe the hippocampus must not be thought of as devoted only to navigation. It rather seems to be a structure involved in a more generic function of integration of spatio-temporal information, transition detection, and novelty detection (an error in the prediction is detected and the input considered as a novelty). In particular, Hasselmo has proposed a model of novelty detection involving the hippocampus and a structure called the septum (responsible for cholynergic (ACh) modulation– [26]). Indeed, there is biological evidence that a mismatch of recognition in CA3 (resp. CA1) makes the corresponding region of the septum react and modulate the activity of CA3 (resp. CA1) in order to learn a new pattern. Due to links with the pre-frontal cortex, the activity of the septum can also be modulated according to a vigilance or motivational level. In our model, we have used this inspiration to account for the stabilization of the transition learning [3].

More precisely, DG granular cells (fig. 24) could integrate information linked with the directional place cells of EC to build place cells with no preferential orientation (classical place cells). At last, CA3 pyramidal cells could build transition cells as described in our model. This could explain why the place fields associated with neurons in DG are smaller than those associated with CA3 neurons. In fact, CA3 neurons should react not only when the animal is at a particular location, say B, but also when it moves from B to C or from B to D (see fig. 24). If transition selection really happens in CA1, it should be also possible to notice smaller place fields in CA1 than in CA3.

Besides, what is the role of the recurrent CA3 connections? Are they used as an auto-associative memory (for the completion of distributed patterns)? Or are they used as an "hetero-associative" memory that could predict a sequence of possible transitions? In the present model, both solutions are possible but it would be simpler to imagine the CA3 recurrent connections as an auto-associative memory. Otherwise, the problem would be to control the diffusion of activation first, during the learning phase, then during the exploitation phase. It is complex to manage but this is not impossible to imagine. Other models use sequence learning as either a memory system [29, 47] or a way to learn graphs or maps [52]. In these models, only the events that co-occur during the same theta phase are linked together and reactivated during the successive theta cycles. But do their results justify the complexity of their system (difficulty to get back the stored information or to add on-line new information)?

Another important question is how the pre-frontal cortex and the hippocampus really interact. To have a chance of solving these questions and developing more "intelligent" controllers for autonomous robots, it is necessary to come back to neurobiological data, searching evidence and inspiration that can help us to improve our model. Yet, it must be emphasized that the neurobiological aspect is also enriched by the computational aspect and vice versa. Our model has been progressively tested on computer simulations as well as in robotic experiments. But the main interest is possibly not the proposed model, which will be improved or corrected, but the fact that the strategy we use (neurobiological modeling associated with robotic experiments) allows to ask new questions that, we hope, will be of interest for neurobiology and ethology communities.

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