



## An attractor model for hippocampal place cell hysteresis

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### Abstract

It is well-known that identical sensory input under different perceptual, behavioral or contextual conditions can produce distinct patterns of activity in the place cells of the rodent hippocampus. However, the mechanisms underlying this have not been completely clarified. A recent experiment has shown that place cell activity on a 3-arm maze exhibits hysteresis as the maze is rotated with respect to distal cues. The apparent angular extent of a place field is greater when a maze arm rotates out of it than when it rotates back into the field. In this report, we present a simple attractor-based model of the hippocampus that reproduces this hysteresis phenomenon. The model allows us to make predictions about changes in the hysteresis effect as the animal becomes more familiar with the maze in several orientations. It also has implications for the place field remapping phenomenon seen in many hippocampal experiments. © 2001 Elsevier Science B.V. All rights reserved.

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### 1. Introduction and background

Primary cells in the rodent hippocampus show place dependent firing, with the region of high activity called a place field. Extensive experimental studies have shown that hippocampal place representations depend in a complex fashion on external, vestibular, motivational, behavioral and contextual cues [5,16,9,3,17,7,1]. In some

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instances, identical sensory situations can generate distinct representations in the same environment [13], where either the perception of the animal or the context play a role. Other non-linear effects can also arise, e.g. dissociation of the external and vestibular sensory cues produce different results, depending on the magnitude of discrepancy between the two [6,13,15]. Several computational models have addressed these issues. These include reference frames [10], charts [14], and latent attractors [8,4]. However, the large range of experimental results is very difficult to explain with any single theory, probably because multiple mechanisms are at work. In this paper we present a computational model of the rodent hippocampus aimed at explaining the process underlying a very recent experimental result [12] showing a non-linear hysteresis phenomenon in place cell activity. This effect is in line with previous predictions of our model of the hippocampus for context-dependence [8,4], and constitutes further evidence of the presence and effect of attractors in the hippocampus.

## 2. Experimental results

The experimental apparatus [12] consists of a 3-arm maze (Y maze, Fig. 1(a)), surrounded by rich distal cues in the recording room. The rat's task is to run for food at the end of each arm in a non-repetitive manner. During recordings from CA3/CA1 cells, the maze is rotated slowly in eight increments of  $15^\circ$  clockwise until it is again in the initial position, but with different arms. After a short break for the rat, the maze is rotated back counterclockwise in the same eight increments. Initially, and after each rotation, the rat is allowed to sample each arm at least four times so that reasonable place field estimates are obtained. The primary result is that place fields recorded in the initial orientation show greater angular extent when the maze rotates out of them than when it rotates back in (Fig. 1(b) and (c)). Thus, the place fields show spatial hysteresis. An interesting aspect of this result is that, in the region of hysteresis, identical positions (i.e. visual information) produce different place activity depending on the direction of maze rotation. This offers further evidence that place cell activity is not determined solely by external sensory information, but, in this case, also by recent experience, suggesting the presence of attractor dynamics in the system.

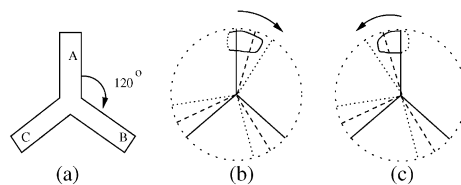


Fig. 1. (a) Maze configuration; (b,c) example of place field hysteresis: (b) clockwise rotation, (c) counterclockwise rotation.

### 3. Theoretical model

Our model explains the hysteresis effect through attractors supported by the recurrent connections of the CA3 region which can undergo potentiation as the animal experiences new maze orientations. Thus, when the rat learns the Y maze task in the initial orientation, cells that fire together or within short intervals acquire stronger interconnections than cells that fire far apart in time and space, setting up a series of continuous attractors over the maze [2,14,10,11]. However, the inertial effect of this is masked by the external sensory input which updates place cell activity as the animal moves around.

Consider the maze in the original position ( $0^\circ$  rotation), and designate the attractors on Arm  $A$  as  $A_0$ . The active group in  $A_0$  comprises place cells with centers on Arm  $A$  in the starting orientation. When the maze is first rotated  $15^\circ$  clockwise, there is competition for firing between cells of  $A_0$ —with strong recurrent connections but slightly reduced external sensory input—and cells with centers in the new position of the maze that receive high sensory input but have not yet developed strong recurrent connections because they have not experienced this situation before. The slight advantage for the latter group in terms of external stimulus is overcome by the recurrent advantage of the original cells, and firing in the  $15^\circ$  position remains confined mostly to  $A_0$ . When the maze is rotated further into the  $30^\circ$  position, the situation changes, and the attractor dynamics of the original place cells cannot make up for their now seriously reduced sensory drive. Thus, new place cells with centers near the  $30^\circ$  position of the arms become active and the place fields active in the original orientation disappear. Synaptic potentiation now occurs in the recurrent connections between the newly active cells, creating a new attractor,  $A_{30}$ , in the new position. When the maze is rotated back counterclockwise from the  $30^\circ$  position to the  $15^\circ$  position, it is  $A_{30}$  which persists because of attractor dynamics. Then, when the position returns to  $0^\circ$ , the cells of  $A_0$  reassert themselves, and the original starting configuration is recovered. Thus, while place activity in the  $0^\circ$  and  $30^\circ$  positions is consistent during clockwise and counterclockwise rotation, the cells active in the  $15^\circ$  position are  $A_0$  cells during clockwise rotation and  $A_{30}$  cells during counterclockwise rotation. This is precisely the hysteresis effect seen experimentally. In terms of  $A_0$  cells, it looks as though they fire at  $15^\circ$  as the maze moves out of their fields (clockwise), but not when the maze moves back in (counterclockwise) (see Fig. 1(b) and (c)).

The angles of rotation used in the discussion above are for illustration only, and do not carry any particular biological or behavioral significance. In both experiment and simulation, the observed hysteresis is gradual, with place cells decreasing their activity over  $30^\circ$  or even more rather than switching off abruptly.

### 4. Simulation and results

The model used to simulate the hysteresis effect consists of a single layer of  $N_c$  place cells (as in the CA3). Place field centers,  $c_i$ , are uniformly distributed on a circular area with a radius equal to the maze radius,  $R_m$ . Distal cues are represented by

$N_1$  landmarks,  $L_k$ , characterized by their position, distributed uniformly along the circular wall of the simulated room of radius  $R_1$ . The following parameter values are used in simulation:  $R_m = 20$ ,  $R_1 = 40$ ,  $N_1 = 12$ , and  $N_c = 484$ .

Each cell receives external input as well as recurrent stimulus from other place cells. The external sensory input comes from the distal cues, with each cell responding to a random number of landmarks (between  $l_{\min}$  and  $l_{\max}$ ) chosen from the most  $n_1$  cues closest to its field center. Thus, the external input to cell  $i$  is

$$h_i^{\text{ext}}(t) = \exp\left(-\sum_{k=l_{\min}(i)}^{l_{\max}(i)} w_k \frac{[d(p(t), L_k) - d(c_i, L_k)]^2}{2\sigma_{\text{ext}}^2}\right), \quad (1)$$

where  $w_k \in [0, 1]$  encodes the significance of landmark  $k$ ,  $d(p(t), L_k)$  is the distance between the animal's position at time  $t$  and the landmark,  $d(c_i, L_k)$  is the distance between the cell center and the landmark, and  $\sigma_{\text{ext}}^2$  parameterizes the width of the field.

The recurrent connections between cells are chosen randomly with probability of connection  $p_c$ . The weight from cell  $j$  to cell  $i$  is set as:  $w_{ij} = g \exp(-d(c_i, c_j)/(2\sigma_w^2))$ , where  $d(c_i, c_j)$  is the distance between the field centers of  $i$  and  $j$ , and  $g$  is a gain parameter distributed uniformly in an interval. For connections between cells with centers on the initial position of the maze, the interval for  $g$  is close to 1 (i.e. the attractors are stronger due to the rat's familiarity with this position), while for other connections,  $g$  is distributed closer to 0, since those cells have never fired together. The total input to a cell is formed by the sum of external and recurrent components.

The neuron output is binary, with a competitive updating rule that fires the  $K$  most active neurons, where  $K$  represents a small fraction (2%) of the size of the network. As the simulated rat moves on the maze, a Hebbian learning rule updates the weights, such that, as the maze rotates, attractors outside the maze are formed and strengthened:  $\Delta w_{ij} = \lambda \exp(-d(c_i, c_j)/(2\sigma_w^2))$ , with  $\lambda$  the learning rate. Because no forgetting is included in this simple rule, a maximum upper bound is imposed on the weight values. Also, the weights are increased faster ( $\lambda = 0.4$ ) for cells with centers outside the familiar position of the maze, as compared with the rest of the cells ( $\lambda = 0.03$ ). This simulates the effect of synaptic saturation, with a slower learning rate for already potentiated synapses.

Fig. 2 shows how the mean spatial firing rate of cells with centers on the initial position of the maze arms varies with the rotation angle. The hysteresis phenomenon can be seen in two cases, corresponding to Fig. 1(b) and (c). First, when the maze is rotated clockwise the place cells fire for larger angular extent than when the maze comes back (Fig. 2 (right side)). Second, as Arm  $C$  moves into the original position of Arm  $A$  ( $120^\circ$  rotation), cells fire later than when it is rotated out (Fig. 2 (left side)).

Fig. 3 shows the place field of a cell situated on Arm  $B$ , as the maze is rotated in both directions. The place fields on the first row correspond to the first four rotations of the maze during clockwise rotation ( $B_0, B_{15}, B_{30}, B_{45}$ ). The cell fires on the first three positions, though the place field shrinks, and the overall mean firing rate decreases. The bottom figures (Fig. 3(e–h)) show the place field as the maze is rotated counterclockwise through the same positions ( $B_{-75}, B_{-90}, B_{-105}, B_{-120}$ ). The cell starts firing only at  $B_{-105}$ , and becomes fully active only at  $B_{-120}$ .

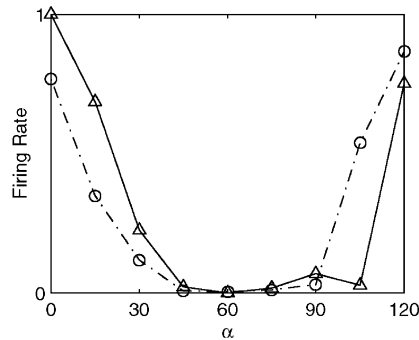


Fig. 2. Dependence of place cell spatial firing rate with rotation angle ( $\alpha$ ): ( $\Delta$ , solid line) clockwise rotation, and ( $\circ$ , dashed line) counterclockwise rotation. Each point represents the normalized mean firing rate over all possible locations of all cells that had place centers on the  $0^\circ$  position of the maze arms. The normalization factor is the mean spatial firing rate at  $0^\circ$  maze position, at the start of the clockwise rotation.

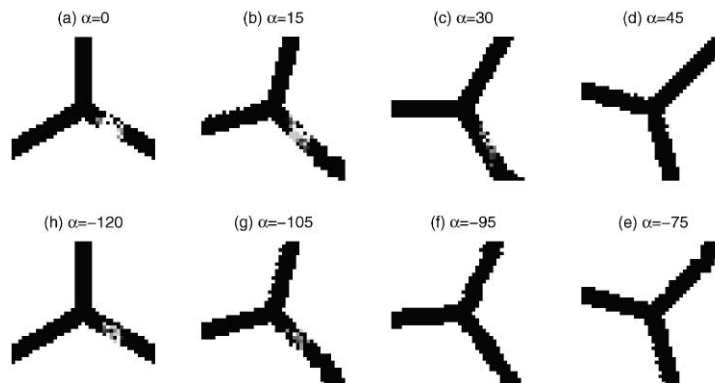


Fig. 3. Place field hysteresis: (a–d) clockwise rotation: (a)  $0^\circ$ , (b)  $15^\circ$ , (c)  $30^\circ$ , (d)  $45^\circ$ ; (e–h) counterclockwise rotation: (e)  $-75^\circ$ , (f)  $-90^\circ$ , (g)  $-105^\circ$ , (h)  $-120^\circ$ .

## 5. Conclusions and discussion

The scenario outlined above has implications for the dynamics of cognitive maps in changing environments. Many hippocampal theories ([10,11,14,8,4]) are based on the existence of attractors or maps for each distinctively perceived environment, formed by currently active place cells. The framework we describe allows us to generate testable hypotheses about the plasticity of these attractors. For example, if plasticity in the recurrent connections between place cells involves depotentiation (forgetting) as well as potentiation, the hysteresis effect would show a strong dependence on the timing and duration of the maze rotation episodes, but would persist almost unaltered as the animal is tested over long periods.

We have shown how a simple attractor model of the rodent hippocampus is able to emulate a nonlinear, hysteresis effect seen experimentally in place cells recordings. The model also enables us to better understand the mechanisms that may underlie hippocampal place representations.

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