Path Integrator Contributions to Hippocampal Map Formation

David S. Touretzky

Computer Science Department, Carnegie Mellon University, Pittsburgh, PA, USA

Abstract

Skaggs and McNaughton's (1998) experiment in which rats shuttled between two visually identical boxes provided a clear demonstration of stable partial remapping in hippocampal place cells. Any satisfactory theory of hippocampal map formation must account for both the degree of remapping and the stability of the partially remapped state. We suggest that a weak path integrator (PI) input causes the remapping observed in this experiment. A computer simulation shows that while Hebbian learning on CA3 recurrent connections can draw maps together, concurrent Hebbian potentiation of the PI projection onto CA3 helps to stabilize the partially remapped state.

Key words: hippocampus, cognitive map, place cells, path integrator

1 Introduction

Skaggs and McNaughton [1] reported that rats shuttling between two visually identical boxes connected by a corridor showed similar place codes in each

Email address: dst@cs.cmu.edu (David S. Touretzky).

box; see Figure 1. The degree of "partial remapping" between boxes varied somewhat from day to day, but with no discernible trend. This poses a problem for place cell theories in which the hippocampal map is a crossproduct of extrinsic (local view) and intrinsic (path integrator, or PI) variables, and failure to properly reset the PI upon reentry into an environment is what leads to remapping [2,3]. If the PI is not being reset upon each box entry, why isn't the remapping complete? On the other hand, if the PI is reset to an identical value upon each box entry, why is there any remapping at all? One possibility is that the rat remembers whether it entered the current box via a left turn (north box) or a right turn (south box), but it would have to retain that information throughout its visit. Here we consider a different explanation.

We suggest that the PI is not reset upon box entry, but exerts a relatively weak influence on map selection when visual cues are identical in two environments. The primary contribution of the PI to map formation is to help constrain the nascent place code to a proper 2D manifold. But the discrepancy in PI coordinates in the two boxes does induce some differences, hence partial remapping. Hebbian learning would then cause cells with fields in both boxes to become bound to two sets of path integrator coordinates. The PI thus both causes partial remapping and preserves it. We explore this hypothesis with a computer simulation.

2 Structure of the Model

We use a simple model in which place cells are driven by a combination of local view (feature detector) inputs, path integrator inputs, and recurrent connections. Pseuo-random wiring is used, so the model does not assume any
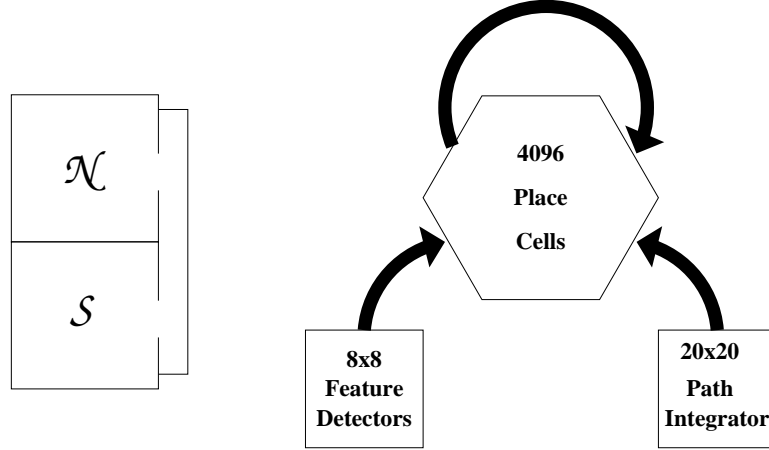
2

Fig. 1. Left: the two-box apparatus of Skaggs and McNaughton (1998): two visually identical boxes connected by a corridor. Right: structure of our place cell model. built-in structure beyond sparse connectivity. In other words, there are no pre-wired maps.

A box is represented as a 5×5 grid, giving 25 unique locations, and contains eight unique landmarks: four box corners and four wall midpoints. Since the two boxes are visually identical, the same landmarks are used in both. Each landmark has a set of eight Gaussian feature detectors tuned to specific distances from that landmark. Thus, there are a total of $8 \times 8 = 64$ feature detectors.

The path integrator is represented as a 20×20 array of units. The simulated rat's current position is indicated by the peak of a Guassian activity bump. The two adjacent 5×5 boxes are laid down on this grid, so that each of the 50 box locations has unique path integrator coordinates.

The model uses 4096 place cells, each of which randomly samples 16 feature detectors (2 of 8 for each of 8 landmarks), 40 path integrator units (out of 400 total), and 400 place cells (10% recurrent connectivity.) Instead of an explicit recurrent inhibition term, we calculate a dynamic threshold to maintan a
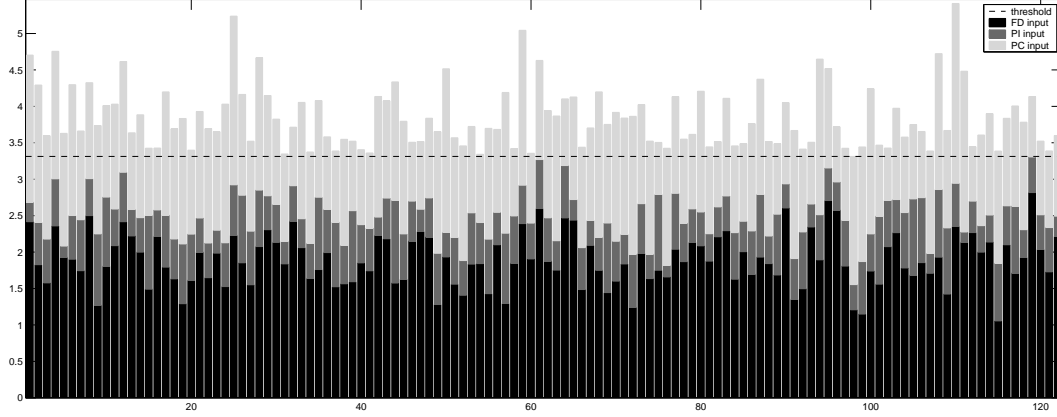
Fig. 2. Contributions of feature detector inputs (dark bars), path integrator inputs (medium bars), and recurrent projections (light bars) to the 122 place cells that were active when the simulated rat was in the center of the north box. Dashed line shows threshold set to achieve 3% activity rate; active cells required contributions from all three input sources in order to exceed the threshold.

3% activity rate over the place cell population, giving 122 active place cells. Figure 2 shows the contribution of each input type (feature detectors, PI, and and recurrent connections) after learning, for each of the 122 place cells active when the simulated rat is in the center of the north box.

In order to simulate the effects of map learning as the rat forages randomly in the box, we use the following procedure. Each location in the box is visited once, in random order. The location determines both the visual feature detector activity pattern and the path integrator activity pattern. These inputs drive the place cells, which are allowed to settle to a stable state. Then, we (1) increase the strengths of synapses from active PI units onto active place cells by an amount proportional to 2% of the PI unit's activation level (which ranges between 0 and 1), (2) decrease the strengths of active place cells' recurrent projections by 1%, but (3) increase the strengths of projections onto other *active* place cells by 40%. Then we pick another box location and continue the

4

learning process. After all locations in the current box have been visited, we switch boxes and repeat the procedure, then return to the first box, and then return to the second. Each box is thus visited twice, simulating the first day of exposure provided by Skaggs and McNaughton in their experiment.

3   Results

Treating the 5×5 array of box locations as a 25 element vector, each plot in Figure 3 shows activity pattern cross-correlations for 50 locations, 25 per box. These are organized in an L shape consisting of box 1-1, box 1-2, and box 2-2 correlations. The bottom left plot shows that prior to learning, there is a weak correlation in activity patterns for adjacent locations, and due to the PI input, an even weaker correlation between the two boxes. After learning (bottom right), the correlation between adjacent locations in a box is higher (i.e., the place code is more robust), and the correlation between boxes is also increased (less remapping).

Figure 4 shows that before learning, roughly half the active place cells had fields in both boxes. After learning, nearly 75% have fields in both boxes, indicating that the two maps have been brought closer together. But remapping has not been eliminated.

Examining the PI afferents of active place cells shows that many cells are bound to two sets of PI coordinates. So while the learning procedure was making the maps more similar by potentiating recurrent CA3 connections, it was also helping to stabilize both maps by strengthening connections from PI units active in either of the two boxes. By also potentiating PI projections onto
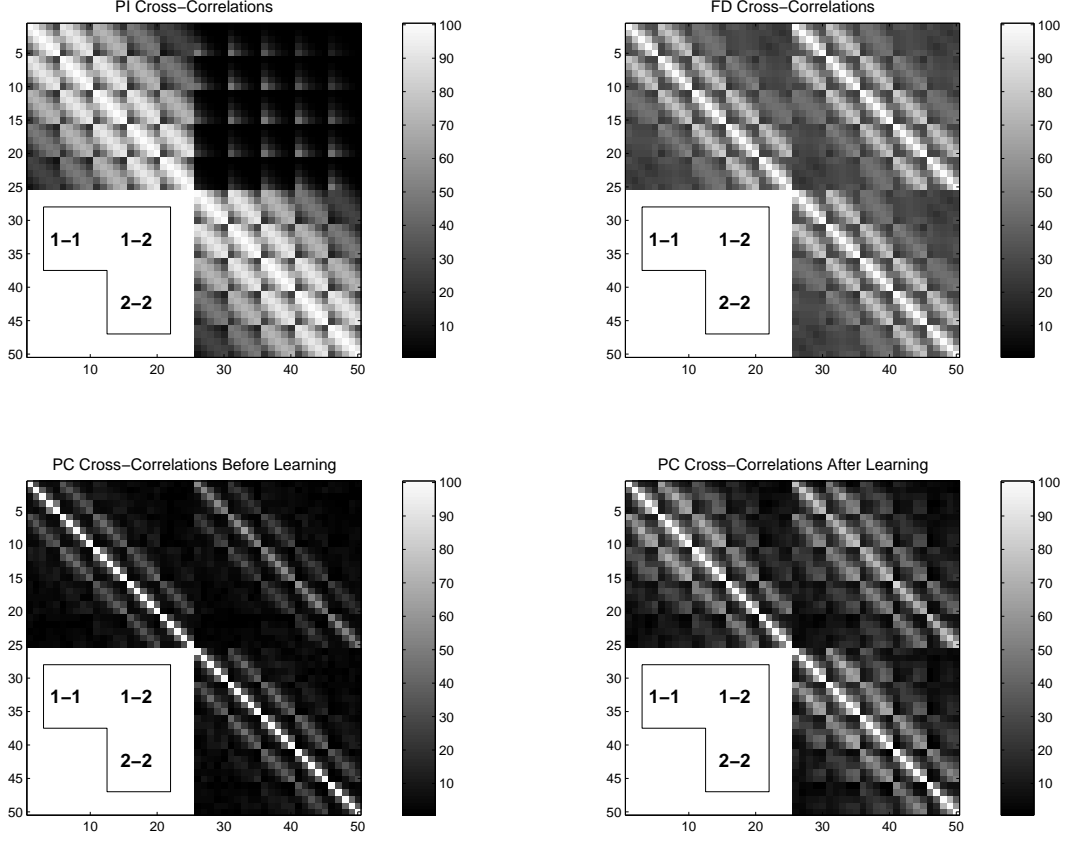
Fig. 3. Top left: cross-correlations of PI activity patterns for 50 locations, 25 per box. Top right: cross-correlation of feature detector activity patterns; since the boxes are visually identical, the across-box correlations are the same as the within-box correlations. Bottom: place cell activity pattern cross-correlations, (left) prior to learning, and (right) after learning.

place cells that were active in only one box, learning also helps to preserve the partially remapped state.

4 Discussion

We assume that the learning described in this model takes place during the initial formation of place fields as the rat explores the boxes for the first time. Whether learning acts to increase or decrease remapping depends on the
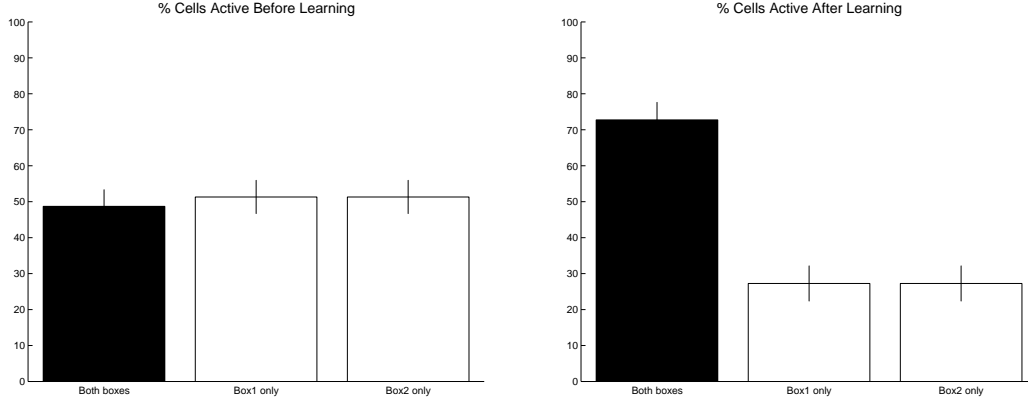
Fig. 4. Percentage of cells active in box 1, box 2, or both boxes, before learning (left) and after learning (right). Error bars indicate variance over 25 box locations.

relative rates of potentiation of place cells' recurrent connections vs. their path integrator connections. The model predicts that LTP-deficient rats should show greater amounts of remapping in the two-box experiment than normal rats, because of the lack of potentiation of recurrent synapses that would help to pull the maps together.

Skaggs and McNaughton found that the extent of remapping in their experiment showed no increasing or decreasing trend [1]. Other experiments have shown remapping that increases with increased exposure to the two environments, either abruptly after a delay [4], or gradually [5]. An increase in remapping with experience would appear to involve mechanisms other than Hebbian learning [6].

In Knierim's double cue rotation experiment [7], place code dissociation, individual place field splitting, and partial remapping are attributed to weak attractor dynamics. But they also imply a weak but nonzero PI influence. When some cells appear to follow local landmarks while others follow distal, the weak PI may remain bound to the distal reference frame and compete with local landmarks for control of place fields.

Acknowledgments

References

[1] W. E. Skaggs, B. L. McNaughton, Spatial firing properties of hippcampal CA1 populations in an environment containing two visually identical regions, Journal of Neuroscience 18 (20) (1998) 8455–8466.

[2] A. D. Redish, D. S. Touretzky, Cognitive maps beyond the hippocampus, Hippocampus 7 (1) (1997) 15–35.

[3] A. D. Redish, D. S. Touretzky, Separating hippocampal maps, in: N. Burgess, K. Jeffery, J. O'Keefe (Eds.), The Hippocampal and Parietal Foundations of Spatial Cognition, Oxford University Press, New York, 1999, pp. 203–219.

[4] E. Bostock, R. U. Muller, J. L. Kubie, Experience-dependent modifications of hippocampal place cell firing, Hippocampus 1 (2) (1991) 193–206.

[5] H. Tanila, M. L. Shapiro, H. Eichenbaum, Discordance of spatial representation in ensmbles of hippocampal place cells, Hippocampus 7 (6) (1997) 613–623.

[6] M. C. Fuhs, D. S. Touretzky, Synaptic learning models of map separation in hippocampus, Neurocomputing 32 (2000) 379–384.

[7] J. J. Knierim, Dynamic interactions between local surface cues, distal landmarks, and intrinsic circuitry in hippocampal place cells, Journal of Neuroscience 22 (14) (2002) 6254–6264.