



## A latent attractors model of context selection in the dentate gyrus–hilus system

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### Abstract

Primary neurons in all parts of the rodent hippocampus show location-specific patterns of activity called place fields, thus forming a distributed representation of place. Paradoxically, environments with very similar sensory cues can produce distinct place representations. The origin of this context dependence is not known. In this paper, we speculate that the dentate gyrus–hilus (DGH) system, with its disynaptic recurrent connectivity plays a central role in creating context-dependent place representations. We show that a simple system architecture can support distinct and consistent place representations for similar environments. © 1999 Elsevier Science B.V. All rights reserved.

*Keywords:* Hippocampus; Place cells; Spatial representation; Localization; Context

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### 1. Introduction

The rodent hippocampus is believed to play a crucial role in spatial cognition, and hippocampal place cells [12] have been the object of great interest. The sensory, behavioral, and motivational correlates of place fields throughout the hippocampus have been elucidated experimentally [5,10,18,13,14,11], and have led to elegant computational models [19,15]. In this paper, we present a connectionist model for a very intriguing and poorly understood aspect of place fields: dependence on spatial context.

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## 2. Motivation

This research is motivated by three observations: (1) Only a subset (20–50%) of cells in CA3 and CA1 show place fields in a given environment [18]; (2) While sensory cues have decisive control over place fields [12,5,10], the fields are not *determined* by these cues, and environments with identical sensory cues can produce distinct place fields if the animal perceives them as different environments [13]; (3) Once a place representation has been activated, it is very robust against changes in visual cues, and if it does change, the switch is to a significantly different representation [1,3].

These observations suggest that place fields form via the combination of two effects: (1) *Informational*: Specific sensitivity of individual cells to conjunctions and disjunctions of features from sensory, vestibular, directional, motivational, and motor information; and (2) *Contextual*: Global selection of a cell group for activity.

## 3. Theoretical model

Context dependence in place fields suggests the existence of a multi-stable attractor-based context system in the hippocampus. This system must attend to the same information as the CA3 place cells and exert a strong – but not exclusive – influence over them. It must also be able to learn salient sensory cues, recognize them, and switch in response to them. The need to retain context dependence over long durations and the requirement of responding smoothly to varying sensory stimuli are in conflict, and we suggest that the conflict is resolved through a hierarchical strategy.

We hypothesize that the dentate gyrus–hilus (DGH) system functions as a multi-attractor neural network for the recognition and stable encoding of context. The CA3 has previously been suggested as the site for such processing [7,9,15], but we prefer the DGH system because it is situated prior to CA3 in the hippocampal information stream, and there is evidence for context dependence in DG granule cell place fields [8]. Also, the architecture of the DGH system supports excitatory recurrence and very subtle inhibitory control of different neural populations [16,4,2,6] – both features necessary for context representation.

We model the DGH system as a recurrent system of granule–mossy–granule cell connections with various inhibitory subsystems. Both the DG and H are organized into distributed non-disjoint excitatory cell groups [17]. Cells in the same group tend to activate each other and depress those in other groups, and only a limited number of cells can be active at a time. Thus, once a group is sufficiently active, activity will tend to stay within that group until strongly perturbed. When afferent activity from the EC is present, the effect of the recurrent system is to focus firing within a metastable subset of granule cells. We call this the “latent attractor effect”, since the effect of the EC activity is channelled by an attractor which cannot sustain itself autonomously, but whose effect is unmasked by the afferent input.

At the beginning of an episode, a particular pattern of sensory input from the EC (a “recognition stimulus”) excites granule cells within a specific group, focusing future activity within this group. For the duration of the episode, then, granule cells are

driven primarily by the afferent input, but cells that are not part of the selected group are effectively suppressed. Place is, thus, coded with a two-level hierarchical representation. At the first, coarser level, each context is represented by the selection of an active cell group. Within this, individual cells are fired by sensory and ideothetic afferent information.

#### 4. Computational model

The environment is an  $M \times M$  grid on which the simulated animal moves randomly. The network has three layers: EC, DG, and H (hilus). The EC layer is modeled at a purely phenomenological level, based on the known characteristics of EC place fields [13]. Each cell is given a broad, noisy Gaussian place field with a randomly chosen center and random shape and orientation. As the animal moves on the grid, each EC cell's activity just reflects its place field.

The DG layer receives excitatory input from EC and focused excitatory as well as global inhibitory input from H. DG cells, which are modeled as discrete-time binary threshold units, are fired by a  $k$ -of- $N$  rule simulating competitive firing. Since the input from H represents a feedback, it has a delay of 1 time step. H layer neurons are also modeled as simple threshold units.

$N$  cell groups are chosen from both the DG and H excitatory cells, with no restrictions on overlaps. All groups in the same layer are of identical size. Granule-to-mossy and mossy-to-granule cell connectivity is uniform random with a fixed probability of connection. Cell groups are implemented by setting all existing cross-group connections to low values and all within-group connections to high values. To determine the utility of the proposed group structure, we also simulated an equivalent network without groups.

To investigate the networks, we simulated each system in two environments,  $A$  and  $B$ , with identical EC place fields. They were distinguished only by providing different inputs to DG at the beginning of the episode – signifying context. The networks were evaluated based on two criteria: (1) *Context separation*, which measured the difference between the DG place representations for the two environments; and (2) *Localization*, which measured how well the place representation in  $A$  could be used to track the simulated animal's true position via Bayesian maximum-likelihood estimation [20], thus indicating the quality of the place representation. Clearly, an acceptable system should show good performance on both criteria.

#### 5. Results

Fig. 1 shows the performance of a network with 300 EC neurons, 1000 DG neurons, and 500 hilus neurons in  $20 \times 20$  environments. We fix the strength of the H input to DG and systematically vary the strength of the EC input, thus changing the relative weight,  $R$ , given to sensory (EC) and context (H) information. Context separation was measured by the mean Hamming distance between place representations for

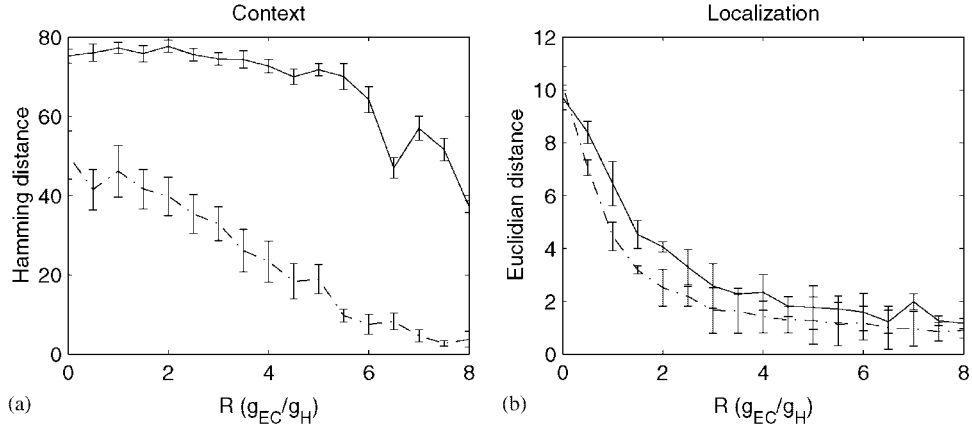


Fig. 1. The context separation and localization error of the network with groups (solid line) and the equivalent network without groups (dashed line). Parameters  $g_H$  and  $g_{EC}$  denote the gains of the inputs to DG from H and EC, respectively.

corresponding locations in  $A$  and  $B$  along a random path. The representations were based on reconstructed place fields for the same 300 DG cells in both environments. Localization was measured by  $e$ , the mean tracking error when reconstructed DG place fields were used to estimate the animal's position during a random traversal of environment  $A$ . The place field for cell  $i$  in a given environment was estimated as:

$$f_i(u, v) = P(z_i(t) = 1 | x(t) = u, y(t) = v) \approx \frac{\sum_t z_i(t) \delta_{uv}(t)}{\sum_t \delta_{uv}(t)},$$

where  $(x(t), y(t))$  is the animal's position at time  $t$ ,  $z_i(t)$  is the output of cell  $i$ , and  $\delta_{uv}(t) = 1$  if  $x(t) = u$ ,  $y(t) = v$  and 0 otherwise.

Fig. 1 shows that the non-group network trades off good context separation at low  $R$  for good localization at high  $R$ . However, the group network is able to simultaneously achieve both criteria over a wide range of  $R$ . The group architecture makes this possible by ensuring that the context information in the recurrent DG–H–DG loop acts only as a selective mechanism, leaving individual cells (in the selected group) to respond to afferent (EC) input without interference.

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