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Decoding the Grid Cells for Metric Navigation Using the Residue Numeral System

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Knowing that the grid cells in the dorso-lateral band of the medial entorhinal cortex are a necessary component of rat's ability to perform path integration and homing, we explore the idea proposed by Fiete et al. (2008, *J. Neurosci.*, 28(27):6858) that they might encode the coordinates of the rat in a Residue Number System. We show that the decoding network based on a gradient descent they propose to use for that purpose does not operate satisfactorily, and thus propose a network using a direct approach derived from the Chinese Remainder Theorem.

1 Introduction

Rodents are able to directly come back to their departure point after having explored an unknown environment, even in the absence of visual or other allocentric cues, exhibiting the so-called *homing* navigation strategy [3]. They achieve this using path integration (or dead-reckoning), i.e. the integration of self-movement information derived from proprioceptive inputs, efferent copy of movement orders and vestibular information, so as to continuously estimate their position relative to their departure point.

The neural substrate of this integration mechanism is thought to be the recently discovered grid cells (GC) [7] in the dorso-lateral band of the medial entorhinal cortex (dMEC). These cells fire according to a repeating equilateral triangular pattern (fig. 1, left) in the locomotion plane, characterized by a given period (the distance between two maximal response sites) and a given orientation (of one of the triangle sides with regard to an allocentric reference). Nearby cells in the dMEC have the same period and orientation but a different phase and are thus thought to belong to the same grid, while increasing grid sizes have been observed when recording cells along a dorsal to ventral axis. This spatial pattern of activity takes into account self-movement information, as it has been shown that it is preserved in absence of

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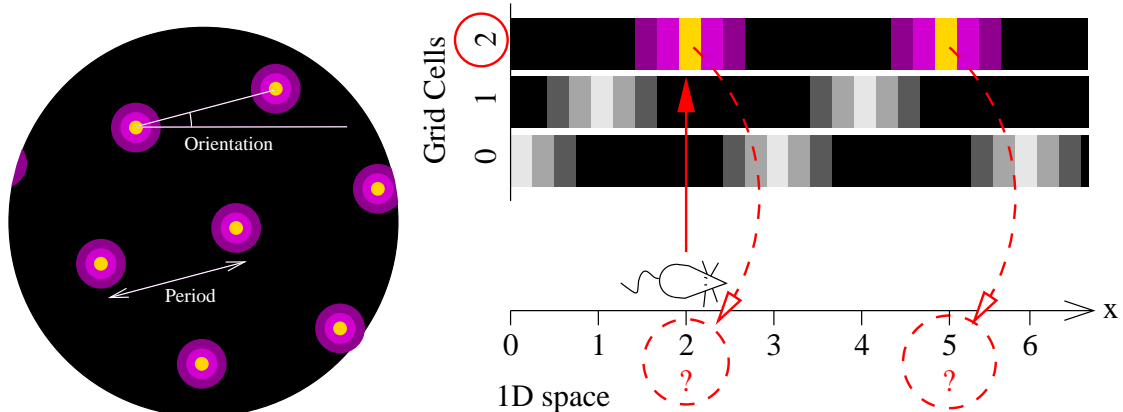


Figure 1: *Left*: Grid cell firing pattern schema. A grid cell recorded while the rat locomotes (here in a circular arena) fires with an equilateral triangular pattern characterized by a period and an orientation. *Right*: Grid cells as a modulo operator. Considering the 1D case, with a grid of period 3, the current rat position is encoded (plain arrow) by neuron 2, but neuron 2 represents all positions $2 \text{ modulo } 3$ (hashed arrows), adapted from [4].

any visual cue, despite a spreading of the bumps of activity, caused by accumulation of errors by the integration process.

The dMEC is an essential part of the path integration/homing system, as it has been shown that animals with an enthorinal lesion are unable to perform homing [10]. Interestingly, the hippocampus does not seem to be an essential component of path integration, as hippocampectomized rats can still perform homing [1]. Consequently, the intrinsically metric homing navigation strategy does not require functional place cells –that are a topological code of the rat position rather than a metric one– to operate. How to perform homing using the GC activity solely is a yet unanswered question, as most existing models of navigation including the GCs (like the very first one [6]) use them to generate place cells, which can then be exploited to navigate with topographical strategies, like place recognition triggered response or path planning (see [8, 9] for reviews on this matter). A computational model of homing should be able to extract directly from the grid cells the current position with regard to the departure point, so as to be able to generate the opposite locomotor command.

In the following, we propose a computational model able to extract directly from the activity of a set of grid cells the current coordinates of the animal, that can be used to control the homing behavior.

2 Model

2.1 The initial idea

In a recent paper, Fiete et al. [4] proposed a new way to interpret the GC activity: they could be considered as performing the 2D equivalent of modulo operator. When considering one axis of a given grid, the currently most active neuron in this grid provides the residue of the division of the current coordinate of the rat on this axis by the grid period (fig. 1,

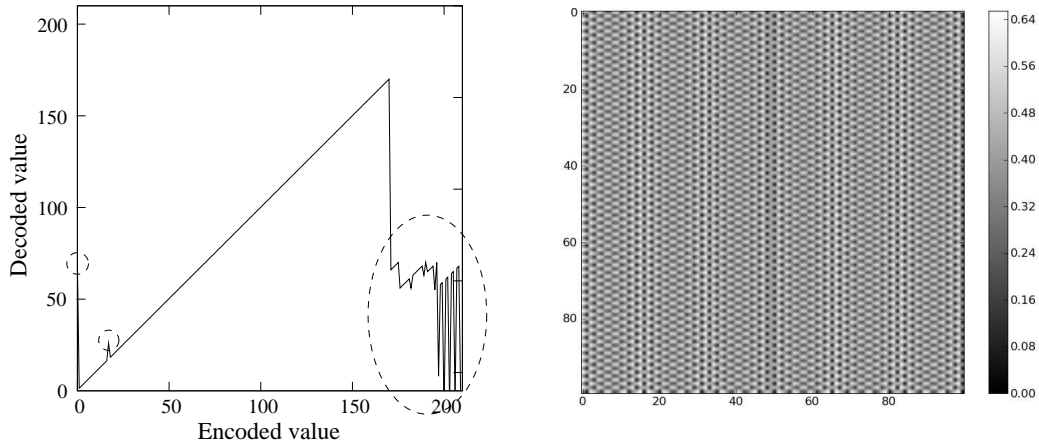


Figure 2: *Left*: The Sun & Yao [13] model fails to decode correctly all the encoded values, errors, away from the diagonal, are highlighted by hashed ellipses. *Right*: Decoding errors (in *cm*) generated by our model on a $100 \times 100m$ surface.

right). The information from one grid allows to locate the animal modulo this grid's period, but the information provided by a set of N grids of periods $(\lambda_1, \dots, \lambda_N)$ corresponds to a well known number encoding system, the Residue Number System (RNS). The RNS is based on the Chinese Remainder Theorem (CRT) which states that given a set of residues (r_1, \dots, r_N) and a set of pairwise coprimes $(\lambda_1, \dots, \lambda_N)$ (with $\Lambda = \prod_{i=1}^N \lambda_i$), there exist a unique integer x modulo Λ so that $\forall i \in [1, N], x \equiv r_i \pmod{\lambda_i}$. Thus, given the N aforementioned λ_i any number in $[0, \Lambda[$ can be encoded as the set of residues r_i . Note that this can be generalized to non coprime pairwise periods, in which case the Λ is the least common multiple (lcm) of the periods. If we consider a set of grids of identical orientation and different periods, and use them as modulo operators, one should be able to extract the coordinate x of the animal on one of their axes. Doing this operation on two axes of these grids provides a coordinate system sufficient to locate the animal in space, as long as it does not travel distances exceeding the periods' lcm.

Fiete et al. did not provide a computational implementation of their idea, but suggested to decode the activity of a set of grids using a neural network model proposed by Sun & Yao [13]. However, this model computes x by performing a gradient descent on an discontinuous energy function with multiple local minima:

$$E(r) = \sum_{i=1}^N \frac{1}{2} |x \bmod \lambda_i - r_i|^2 + \frac{1}{2AR} x^2 \quad (1)$$

Such a function being unadequate for a gradient descent, it work quite poorly as it easily get stuck in local minima. For example, with a set of periods 2, 3, 5, 7, fig. 2 (left) shows the decoding of all the positions in $[0, \Lambda = 210[$, where numerous values are not correctly decoded.

2.2 TRC-based model

We propose a decoding scheme based on an explicit use of the basic mathematics associated to the CRT. Consider the $\hat{\lambda}_i = \frac{\Lambda}{\lambda_i} = \prod_{j \neq i} \lambda_j$: they are pairwise coprimes, and according to

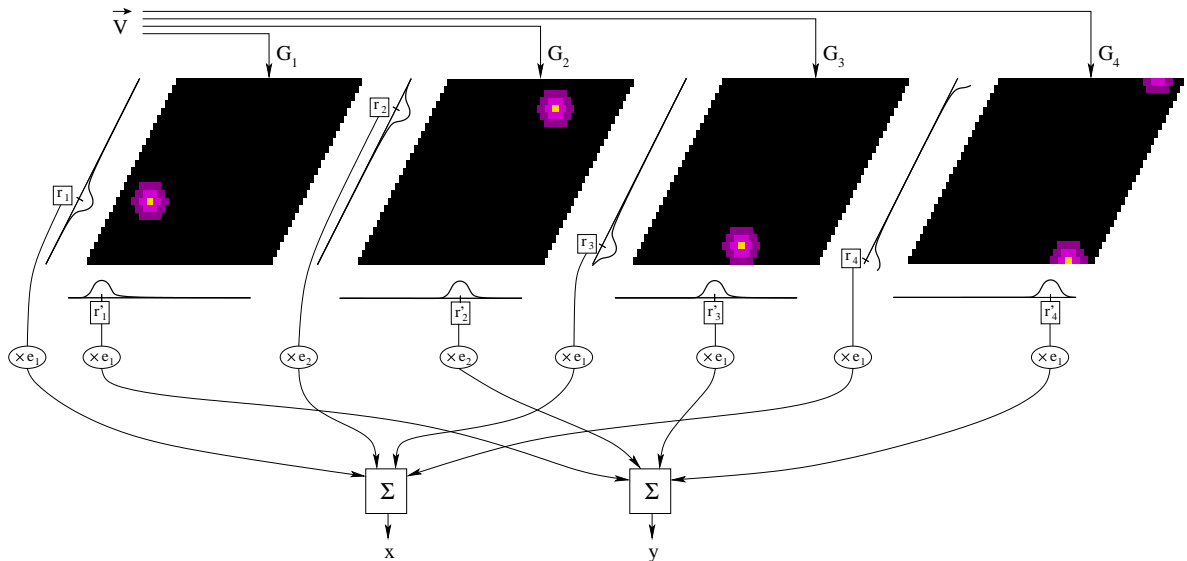


Figure 3: Grid cells decoding model. The speed V of the simulated animal displaces the activity in the four grids (25×25 neurons), the gains G_i define the grid periods (38, 50, 62 and 74cm). The circular barycenters r_i and r'_i of the grid activities projected on one of their axes are the residues used with the e_i weights to decode the coordinates (x, x') (note that this reference frame is not orthogonal).

Bezout's theorem, u_i and v_i exist such that $u_i \lambda_i + v_i \lambda_i = 1$. If we define $e_i = v_i \hat{\lambda}_i$, x can be computed as the following weighted sum:

$$x = \sum_{i=0}^N e_i r_i \quad (2)$$

A similar solution holds when using non-pairwise coprime periods.

We built a computational model to show the efficiency of the Fiete et al. RNS idea, using the direct RNS computation (eqn. 2). This model (fig. 3) operates in 2D and uses real residue values extracted from grid cells. It uses velocity inputs provided to 4 grids, based on the model proposed in [12]. These grids have realistic periods of 38cm, 50cm, 62cm and 74cm, theoretically allowing the unique decoding of values over more than 5km; they all have the same orientation, which also seems to be realistic [2]. The position of the maximum activity on two of the three axes of the grids is obtained by summing the activity of all cells projected on these axes and computing the circular barycenters of the resulting vectors. These values correspond to the residues r_i , which are then sent to two neurons, whose synaptic weights were set to e_i .

The simulations performed with this model show that a simulated rat is able to compute its position in 2D. The errors, caused by the discretization of the grids, have an average of 0.39cm ($std = 0.19$) (fig. 2, right), a value which seems acceptable with regards to the size of a rodent.

3 Discussion & Conclusion

Based on the idea –proposed by Fiete et al. [4]– that the grid cells could be considered as an encoder of the position of animal using a residue number system, we propose a computational model performing the decoding of this position, to be used as a command for the locomotor system in a homing navigation strategy. We also establish that the residue-to-decimal decoder proposed in [13] does not operate efficiently.

Our simulations were conducted without noise in the speed measurements. In reality, such noise affects the grid updating and is fought with resets of the grid activity in places identified by learnt allocentric cues [7]. Such stabilization mechanisms are present in most GC models, and are either based on direct visual inputs or on interactions with the multimodal place cells [11]. This does not affect the validity of proposed decoding scheme, which should of course be connected to a grid cell model including a stabilization mechanism.

Finally, a computational model –anterior to the discovery of the grid cells [5]– proposed to learn the coordinates corresponding to each place cell of a hippocamp model, so as to thereafter enable metric navigation. We showed here that the grid cells, providing inputs to the place cells, are sufficient to perform metric navigation, with the advantage that no prior associative learning phase is necessary, in accordance with observations of homing behavior performed by rodents in new and unexplored environments.

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