Sharpening the spatial tuning curves of place cells in a feed-forward network: the possible role of theta oscillation-based dynamics in the hippocampus

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Activity of the principal cells of the hippocampus during exploratory behavior is known to encode for the spatial location of the rat both by their firing rates[1,2] and by the precise timing of their discharges relative to the ongoing theta rhythm field potential-oscillation, provided by the phase precession effect[3,4]. Such 'place cells' with doubly (rate and phase) coded firing patterns were found in all three subregions of the hippocampus: in the dentate gyrus (DG), in CA3 and in CA1[4,5]. These subregions possess different anatomical layouts, and are mainly connected by excitatory feed-forward connections in the DG→CA3→CA1 loop[6]. Moreover, the cortical input of the hippocampus is only weakly correlated with the location of the animal[7], and place cell activity was shown to persist in downstream areas (CA3 and CA1) even in the absence of upstream place specific activity (DG[8] and CA3[9], respectively). Thus, place cells in each hippocampal area appear to bear significant autonomy in generating spatially coded firing and to only a smaller extent rely on topographical input or on a specific arrangement of intra-regional connections. Although a huge body of experimental and model works has accumulated in this field over the past years[10,11], no theory has yet been able to explain this autonomous doubly coded place specific activity throughout different areas of the hippocampal loop.

In this work, a simple feed-forward network was simulated, where the layers of the network corresponded to different hippocampal subfields, and were connected with realistic convergence and divergence ratios. This network architecture was shown to have two distinct modes of operation. In the 'classical mode', only the rate code of place cell firing could be considered: postsynaptic neurons simply summed the activity of their presynaptic partners, and thus place-specific activity in each layer depended on correctly formed spatial tuning curves in its afferent layer, with tuning curves in downstream areas being usually more blurred than in upstream areas due to the convergence of feed-forward connections. In 'theta mode', two consequences of the hippocampal theta oscillation were

taken into account. First, firing probability of interneurons was modulated by the phase of theta oscillation[4,12], and thus synaptic transmission between layers could only be effective in a short time window within each theta cycle. Ensemble activity of phase precessing place cells in this time window was shown to be strongly correlated with the velocity of the animal. Second, somatic membrane potential of place cells oscillated in the substhreshold regime with theta frequency[13], while the denritic membrane sustained intrinsic membrane potential oscillations, frequency modulated in the theta range by the level of depolarization[14]. Thus, as shown in our previous work[15], neurons of each layer were capable to generate place specific firing patterns, simultaneously rate and phase coded, by relying primarly on the velocity-correlatedness and only weakly on the location-correlatedness of the activity in their afferent areas. This predicts that hippocampal subregions show considerable autonomy in maintaining properly tuned firing rate curves in their place cells, and perform effective sharpening of these tuning curves compared to the classical operational mode.

A comparison of our results to the most widely accepted, attractor neural network (ANN) description of hippocampal place cells[10,16,17] is given. In those models, the sharpening of tuning curves is accomplished by intranetwork dynamics based on dense and topographical lateral connections between place cells. Hence they may be directly applicable to CA3 only where recurrent collaterals can be found[6], yet the functionality of these collaterals under physiological conditions is not clear[18]. In our model recurrent collaterals are not necessary for sharp tuning curves but may play other roles in the dynamics of the network. We also find that, as opposed to our model, simultaneous reproduction of the rate and phase code of place cells can be problematical in ANNs. Further quantitative predictions of the two models are also compared and matched to experimental data in detail. Finally, our proposed 'one architecture–two dynamical modes' scenario is also discussed from an evolutionary perspective.

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