Temporal sequence learning and the hippocampus: A continuous attractor model of location based learning in sequential activation of place cells

Alex Hoggarth*, Ranga Rankaduwa*, Alan Fine (P), and Thomas Trappenberg

Neuroscience Institute, Dalhousie University, Halifax NS Canada
E-mail: tt@cs.dal.ca
*These authors contributed equally to this paper

Abstract— Previous multi-modular models of the hippocampus with point attractor networks have shown a robust ability to learn long sequences. Here we extend this framework to continuous attractor networks that have been implicated in place fields. We discuss their relation to recent physiological findings of sequence recall in rodents.

Keywords— Hippocampus, Neural Network, Continuous Attractor, Heteroassociation

1 Introduction

Although there is some consensus that the hippocampus is involved in spatial memory and learning, the precise processes and mechanisms are still under debate. In recent years many studies have linked memory consolidation and retrieval to the hippocampus. Hippocampal replay during sleep has been considered necessary for consolidation (strengthening of synaptic associations) of new memories in the cortex [1]. More recently, replay (synaptically driven reactivation of cells involved with the learned memory) has been observed during both the awake and resting states [2]. Robust and frequent replay in periods of awake rest as well as during reward-based tasks [3] suggests that consolidation is not limited to sleep. Studies have found that awake replay, mostly associated with memory retrieval, can be stimulated by sensory input as a cue for the associated memory recall [4].

Replay stimulated by a subject's spatial location can provide the stored information required to navigate or interpret their current and future spatial environments. Replay of a firing sequence in place neuron fields could be linked to storage of memories related to navigational tasks and implicated in retrieval of a navigation sequence prior to the traversal of a learned path [5]. In addition to replay of a learned pattern in the forward direction in the time leading up to a navigational task, there may be mechanisms for replay in the reverse direction after the traversal of a sequence of locations, involved in consolidation [6].

Lawrence et al. [7] proposed a network, similar to that of Jensen and Lisman [8], incorporating a hetero-associative connection between modules in contrast to an autoassociation. Each independent module remained implemented as a Hebbian trained point attractor neural network connected through recurrent autoassociations (Fig 1A). Their model learned long discrete sequences of random patterns rapidly and efficiently, in control and noisy conditions [7].

Here, we build on the model of Lawrence et al. to simulate the neural network activity of place cells in the hippocampus, testing whether a point attractor neural network can be transformed into a robust reliable continuous attractor neural network for computational modeling of sequence memory. We do this implementing a continuous Gaussian input pattern as in the Dynamic Neural Field model [9], thus transforming each module within the network from a point attractor to a continuous attractor. Thus, our proposed architecture is used to simulate the synaptic activity of the place cells as the cognitive map is formed (encompassing both learning and replay functions) when the subject follows a spatial path [10].

We show that this architecture can rapidly learn and replay sequences of place fields effectively. Furthermore we show that associations can be made between patterns further apart than the immediately preceding and succeeding patterns; such distal associations may be essential for goal based spatial memory and behaviour.

2 Results

Our simulation showed that the network can recall sequences of Gaussian patterns.

To test how well this network can learn sequences of different speeds we altered the relative distance between subsequent patterns. Thus for each successive iteration of the sequence, the maximally activated node is a further distance away. We refer to the distance of consecutive patterns as shift value. We tested the network using shift values of one to fifty nodes (after fifty nodes, the test would be repeating itself, as the Gaussian patterns composing the input are periodic). The rate of pattern replay, calculated as the distance between two maximally activated nodes during a set number of iterations, gradually increased as expected with increasing pattern shift, until a shift of approximately 25 nodes (Fig 1B). This showed substantial robustness, as the network was able to retain the sequence with up to one quarter of the pattern shifted per iteration. Replay rate increased linearly over these first 25 calculations and then dropped abruptly, indicating that the network was no longer holding the pattern and had broken down in terms of recall ability.

To test the robustness of the network, we studied the ability of the network to recall a pattern when the initial input sequence was altered to represent noisy variation in firing amplitude. The network retained a high degree of recall to approximately 22 shifted patterns. The rate of pattern replay does not increase linearly with noisy input compared to the control condition (static peak heights). These results show the model can reliably replay noisy patterns with a small change in linearity of recall, showing network stability important for biological plausibility. The heteroassociative network remains operational with large pattern shifts, displaying accurate sequence recall when moving through a pattern at greater speed.

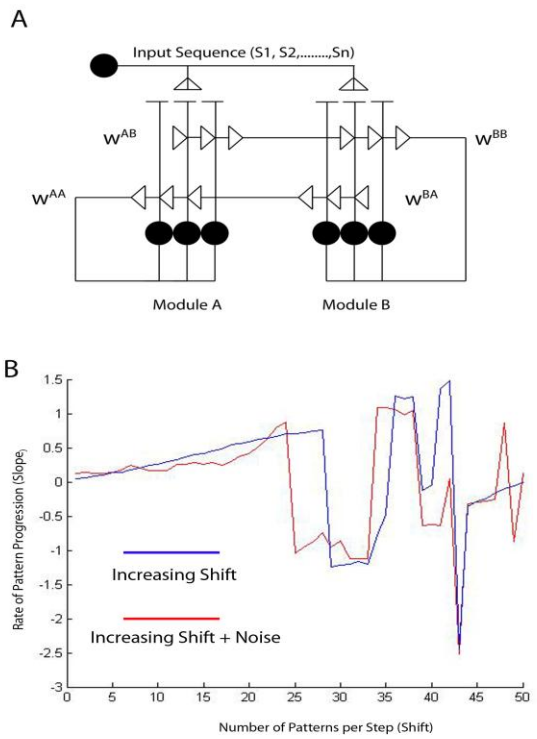

Figure 1: (A) Network Schematic – Hebbian trained continuous attractor networks (Module A and B) containing recurrent intramodule autoassociations (w^{AA}, w^{BB}), an intermodule autoassociation (w^{BA}) and an intermodule heteroassociative link (w^{AB}). (B) Results of the network recall ability test with increasing pattern shift comparing control and noisy conditions. Without noise the network retains the sequence up to 25 patterns per step whereas in the noisy conditions only 22 patterns per step were successfully retained.

3 Discussion

A continuous attractor model can achieve in viable sequence learning. The benefits of the bi-modular attractor network [6], namely automatic transitions between patterns in a sequence in the absence of a designated time constant, are evident in our continuous attractor model, which can effectively learn and replay sequences of highly structured continuous patterns.

Our results were obtained with modules each containing one hundred nodes. The optimal number of nodes is a subject of contention in neural modeling, and it is possible that variations in node number may affect network learning and recall. Modules containing hidden layers of nodes or multiple auto- or hetero-associations may also be effective at storing and replaying ordered sequences of patterns.

An interesting aspect of our results was the lack of occurrence of replay in the reverse direction. Reverse replay has been observed in place node neural fields in biological experimentation [7], and it has been postulated that a singular network can replay a sequence in the forward direction preceding motor activity, as well as in the reverse direction (assumed to be for consolidation purposes) following traversal of a path [6]. Reverse replay has been implicated in associating reward or consequence following movement along a path [5]. Parameter-dependent alternation between forward and reverse replay in a manner consistent with known models of hippocampal network behavior has yet to be successfully implemented [5]. It has been shown that reverse replay does occur biologically in a context dependent manner, with little reverse replay observed in the sleep state relative to the waking, active state [8]. These findings suggest that a pattern once stored can be dynamically recalled in either the forward or reverse direction. We, however, were unable to detect reverse replay in this study. Our findings show that a bimodular continuous attractor network using a heteroassociation is an effective mechanism for sequence memory. Further research incorporating parameter dependent reverse replay, along with biological correlates, would support the hypothesis that such networks exist in the hippocampus.

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