Activity Affects Trace Conditioning Performance in a Minimal Hippocampal Model

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Abstract

Using a minimal hippocampal model, previous studies simulating trace conditioning have reproduced the empirically observed learnable trace interval and reproduced the number of training trials required for learning. However, these earlier studies did not address the effects of parameterization on performance. Here, we demonstrate a robust effect of average activity on trace conditioning performance.

Keywords: Neural Network; McCulloch-Pitts; Recall; Prediction; CA3

1. Introduction

Trace conditioning [4] requires the subject to use a tone stimulus (the CS) to correctly time an eyeblink in order to avoid a noxious airpuff (the UCS) that occurs following a temporal delay. This task is extremely valuable for theoretical study because it enables direct cross-species comparisons; the experimental setup is very similar when it is performed in animals to when it is performed in humans. Moreover, trace conditioning is a hippocampal dependent learning paradigm [7] that is undeniably non-spatial.

Previous studies have shown that a minimal model of hippocampal CA3 can learn trace conditioning [2], and that this model can reproduce the learnable trace intervals

and can also reproduce the time course of learning [5]. Although these studies required simulation parameters to be tuned in order to produce good performance, none of them have addressed the specific effects of parameterization on performance.

In our hippocampal model, the activity parameter, which specifies the number of neurons firing per simulation timestep, has been shown to positively correlate with place cell-like firing patterns called context neurons [3], and it also has been shown to be critical for configural task learning [8]. Here, we systematically vary activity in order to study the effect of this parameter on trace conditioning performance. We find that the activity setting is an important determinant of performance; a sufficiently high activity setting is required for a simulation to recall and to predict the UCS in a timely manner.

2. The model

The model used here is a minimal neural network model of hippocampal CA3 [1]. Neurons are binary McCulloch-Pitts threshold units, i.e. information transfer between neurons is {spike, no spike}. Connections between neurons are random and sparse. Specifically, there is a 10% probability of a connection existing from any one neuron to another. The connectivity matrix is set during the initialization of each simulation and is static thereafter.

The recurrent excitation of neuron j is:

$$Y_j(t) = \sum_{i=1}^{N} C_{ij} W_{ij}(t-1) Z_i(t-1) \quad (1)$$

where $Y_j(t)$ is the recurrent excitation to neuron j on timestep t, C_{ij} is a binary

constant specifying the presence of a connection from neuron i to neuron j, N is the number of neurons in the simulation (here, 1000 neurons), $W_{ij}(t-1)$ is the value of the weight of the connection from neuron i to neuron j on timestep (t-1), and $Z_i(t-1)$ is the binary firing state variable of neuron i on timestep (t-1). An external input, X_i, which represents the entorhinal and dentate afferents to neuron i of CA3, is very powerful. Activity on such an input line, $X_i(t) = 1$, forces the ith CA3 neuron to fire on timestep t; i.e. $Z_i(t) = 1$.

Activity control is implemented with a k-winners competitive rule, such that a fraction, a, of the neurons are active on each simulation timestep ($0 < a < 1$).

Modification of the excitatory recurrent synapses occurs after each simulation timestep according to a postsynaptic-dependent Hebbian rule that was derived from observations of LTP and LTD in the dentate gyrus:

$$W_{ij}(t) = W_{ij}(t-1) + \mu Z_j(t)\left(Z_i(t-1) - W_{ij}(t-1)\right) \quad (2)$$

where μ is set to 0.05 for all simulations in this study.

Each simulation has two phases: training and testing. There are two forms of external activation. First, the CS input pattern, consisting of a set of (300*a) neurons, fires for three timesteps. The CS is followed by the trace interval, consisting of 22 timesteps, during which there is no external input. Finally, the UCS pattern, which consists of another set of (300*a) neurons, fires for three consecutive timesteps. During each simulation, the network receives 200 trials on this sequence.

After training, the synaptic modification is turned off, and a test trial is run. The test input is the three-timestep pattern representing the CS. After the CS, the

simulation is allowed to run freely without any external input for 25 timesteps.

Prediction vs. Recall. We distinguish two measures of trace conditioning performance: recall and prediction. Recall is the ability of the simulation, during a test trial, to fire neurons in the UCS pattern during the same timesteps on which the UCS pattern would have been activated in training trials (timesteps 26-28). Prediction is the ability of the simulation to fire neurons in the UCS pattern during the timesteps preceding the timesteps on which the UCS pattern would have been activated in training trials. For this study, we limit our consideration of prediction to 3 timesteps, thus prediction refers to activity of the UCS neurons during timesteps 23-25. All simulations that produced prediction also produced recall, and recall is always stronger than prediction.

Definition of Context Length. In this study, we refer to a measure of the repetitiveness of neural firing called *context length* [3]. Context length is defined as the number of consecutive timesteps that an individual neuron fires in a single trial. For example, if a neuron fires on timesteps three through five, then that neuron's context length is three. If a neuron fires on only one timestep, then that neuron's context length is one. Previous studies [3, 6] have demonstrated a correlation between the mean context length of all of the neurons in the network and learning performance.

3. Results

A systematic sweep of activity demonstrates that the activity parameterization in simulations is critical for trace conditioning performance. Fig. 1 shows three test trial rastergrams, corresponding to simulations set to 5%, 10%, and 12.5% activity. When the activity setting is 5% (the leftmost rastergram), both recall and prediction fail; there is little activity in the UCS neurons during timesteps 26-28 and no activity in the UCS neurons during timesteps 23-25. When the activity setting is 10% (the center rastergram), there is robust recall but weak prediction – most of the UCS neurons fire during timesteps 26-28, but only a handful of neurons fire during timesteps 23-25. The 12.5% activity setting produces robust recall and good prediction, with nearly all UCS neurons firing during timesteps 26-28 and many UCS neurons firing during timesteps 23-25.

Fig. 2 plots recall and prediction as a function of activity. Activity has a robust effect on recall and prediction; both of these performance measures improve as activity is increased. Recall is relatively weak at low activity settings - activity of UCS neurons during timesteps 26-28 is approximately 15% and 30% average activity in the UCS neurons for the 5% and 7.5% activity settings, respectively. Increasing activity to 10% and then to 12.5% increases recall to approximately 66% and 80% average activity of the UCS neurons, respectively. Prediction is always weaker than recall, and is nonexistent at activity levels lower than 10%. At the 10% activity setting, prediction is 10% of the UCS neurons, which is not considered good performance because activity in the UCS neurons is not significantly higher than activity in the other neurons in the network. However, at the 12.5% activity setting,

predictive firing by the UCS neurons increases to 19%, which is assumed to be large enough for good performance.

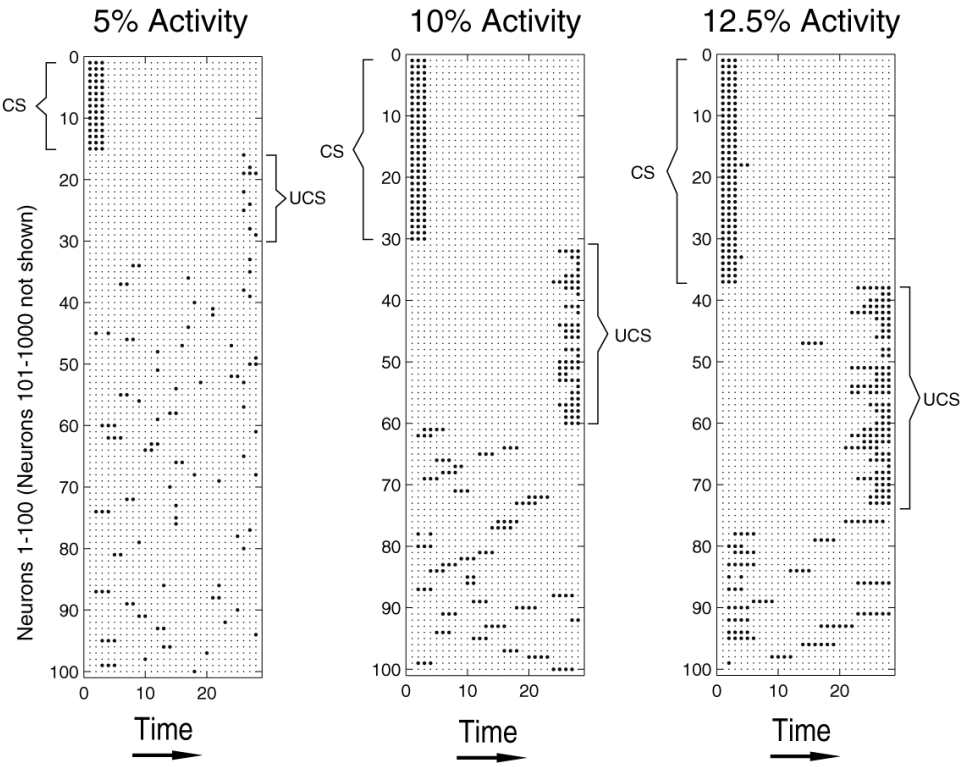

Fig. 1. Activity affects performance in post-training test trials. Only high activity simulations predict the UCS in a timely manner. These rastergrams compare neural firing during test trials for three different activity parameterizations. Left: At a relatively low activity parameterization (5%), the simulation shows little or no recall. Although there is some firing in the UCS pattern during timesteps 26-28, the magnitude of this firing is not significantly higher than in the other neurons in the network. Context length here is low - most of the displayed non-patterned neurons (here, neurons 31-100) do not fire repetitively in this trial. Center: With a higher activity parameterization (10%), the simulation shows good recall of the UCS pattern – a majority of UCS neurons fire at least twice during the timesteps when the UCS was presented during training (timesteps 26, 27, and 28). This higher activity setting leads to the emergence of place cell-like firing; context length has increased, with most of the displayed non-patterned neurons (here, neurons 61-100) firing for 2-4 contiguous

timesteps. However, the UCS is not well-predicted in this trial, as firing in all but one of the UCS neurons does not occur earlier than timestep 25. Right: Further increasing the activity parameterization to 12.5%, the UCS is well-recalled, and is predicted several timesteps in advance. Many of the UCS neurons fire during timesteps 21-25, predicting the UCS up to 5 timesteps in advance. Context length here is higher than in the 10% parameterization, with nearly all of the displayed non-patterned neurons (here, neurons 75-100) firing for 4-7 contiguous timesteps. On each rastergram, the sets of neurons that comprise the CS and UCS patterns are indicated by brackets on the left and right sides of the rastergram, respectively. Only the first 100 neurons out of 1000 total neurons are shown. Interconnectivity between these neurons is sparse and random - the spatial juxtaposition of neurons is not related to the connections between them. Simulation parameters: N = 1000, μ = 0.05, probability of connection = 10%, trace interval = 22 timesteps, and externally driven activity comprises 30% of total activity. Each simulation was trained for 200 trials before the displayed test trials were run.

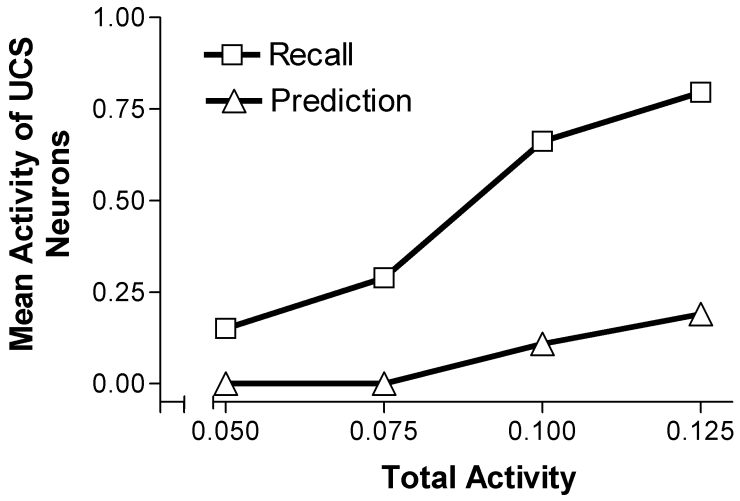

Fig. 2. Prediction and recall performance increase as a function of the activity parameterization. At the lower activity parameterizations, recall is weak and prediction is nonexistent: for the 5% and 7.5% activity parameterizations, test trial activity in the UCS patterns is relatively low during the 3 timesteps when the UCS was presented during training (timesteps 26-28), and there is absolutely no firing of UCS neurons during the 3 timesteps immediately preceding the 3 timesteps when the UCS was presented during training (23-25). Increasing activity to 10% and 12.5% successively increases both recall and prediction performance, with

prediction becoming robust at the 12.5% activity setting (see Fig. 1). Each point represents the average of 10 simulations. Simulation parameters here are identical to those listed in Fig. 1.

4. Discussion

Trace conditioning performance is sensitive to the activity parameterization of simulations. Sufficiently high activity settings are required for good prediction and recall performance. Furthermore, a higher activity setting is required for prediction than for recall alone.

Although recall and prediction are considered separate measures of performance in this study, prediction is more important for learning trace conditioning. In order to produce an eyeblink that blocks the UCS, the hippocampal sequence code must predict the UCS in advance of its onset; recall of the UCS that is simultaneous with UCS onset will not produce an eyeblink that blocks the UCS. Interestingly, context length is higher for the activity settings that produce good prediction, which is strongly suggestive of a key role for place cell-like firing in developing a sequential neural code that allows the hippocampus to bridge the trace interval.

In contrast to other studies [9], a drawback of this study is that time cannot be mapped into real time because none of the features of the model used here are explicitly matched to biological timescales. However, the model's minimal nature is also a positive feature, especially if one wants to move toward analytical insight into the evolution of context neurons and suitable encodings. Future studies can rectify timescale concerns by adding slightly more biological complexity to the model, explicitly matching timescales in the model to biologically observed values.

Acknowledgements

This work was supported by NIH MH48161, MH63855 and RR15205 to WBL; and NSF NGSEIA-9974968, NPACI ASC-96-10920, and NGS ACI-0203960 to Marty Humphrey.

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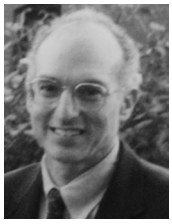

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