Sequence association in two-layered feedforward neural network

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Abstract – Here we study the properties of robustness of two-layer feedforward network that stores association between two sequences in the two layers. Our work shows that robustness comes from the overlapping feedforward projections from the first to the second layer in the network. Recurrent connections in the second layer further improve robustness, while noise is decreasing it. Incorporating biological aspects of neural network in more detail in network dynamic may improve neural networks in engineering applications.

Keywords – Robustness, Noise, Overlapping Projections, Sequence Association.

I. INTRODUCTION

Sequence association is of crucial importance for information processing and memory, if information is encoded in sequences. Many, if not most, cognitive processes, such as consolidation, for instance, required processing in multiple layers. Therefore, sequences have to propagate from one region to another. Since the brain is exposed to internal and surrounding noise, strong resistance to sequence distortions are required, as the information encoded in the sequences not to be lost in transmission. Our results show that robustness of sequence association is possible and therefore memory processing in multi-layer networks is possible in principle, which is required by any theory that represents episodic memories by sequences of neural activity rather than near instantaneous activity patterns.

As mechanism for the consolidation of episodic memories in hippocampus, replay of sequential activity patterns was proposed [1]. It is thought that replay sequences originate in one area and trigger neuronal sequences downstream, e.g., in other area, like neocortex [2]. The precise sequential ordering of neuronal sequences might be corrupted under physiological conditions as internal noise or external interference . It remains an open question how robustly the activation of a corrupted sequence in one brain area can induce the associated sequence in the second area. Here we study this question in a two-layer feedforward network that stores the association between two sequences in the two layers. First one sequence is stored in the input layer, afterwards the second sequence and the association between the two is stored in the second layer and interlayer weights. After the storage, whenever the first sequence is activated, the second is automatically activated also.

II. MODEL

We degrade the input sequence incrementally and observe the sequence induced in the output layer. We measure the similarity of sequences with the Spearman rank-order correlation. The correlation takes values from -1 to 1, when sequences are reversed and same respectively. Small correlation or around 0 value, means that the sequences are random permutations of each other. Surprisingly, we find that even when the input sequence is highly corrupted, the retrieved output sequence is similar to the associated sequence. This result is specific to the stored association and not found for random sequences. Our work shows that neuronal sequences in one area can robustly trigger sequences in a second area if the association between the sequences is stored in the network. Incorporating biological details of neural network improves robustness of association of neural network [3].

We use neural network model with two layers consisting of excitatory and inhibitory units [4]. These units represent populations of neurons and have heterogeneous parameters, unless otherwise stated in the Results. To study the robustness systematically, we examined the relationship between the output correlation and the input correlation (Fig. 1).



Fig.1 Graphical presentation for network robustness

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Fig. 2. *Examples of input and output sequences.* **a)** Input sequence applied repetitively to the first layer, and **b**) output sequence in the second layer that was associated with that input sequence. **c**) Distorted test input sequence, and **d**) retrieved output sequence.

By input and output correlation we mean the correlation between the test sequences and their respective reference sequences. If for large changes of input correlation we obtain low changes in the output correlation then the network is robust (black line), for the opposite case we get non-robust network (gray line). We therefore generated 650 input sequences with input correlations roughly uniformly distributed in [-1,1], applied them on the first layer and recorded the invoked sequence in the second layer. In most our simulations, we stored associations between a sequence in the first layer, say units 1 to 80 (Fig. 2a), and a sequence in the second layer, say units 1 to 20 (Fig.2b), in the connection weights of the network as described in [4]. We examined the robustness of sequence association by applying perturbed sequences in the first layer (input sequences) (Fig.2c) and observing the evoked sequences in the second layer (output sequences) (Fig.2,d).

To quantify the differences between two sequences, we calculated the Spearman rank order correlation ρ between the activation times of the units in the two sequences. Since the units' activities are continuous variables, we had to define when the units are considered to have become active. Here we used the time of the first local maximum in a unit's activity. We then fit a sigmoid function to the relationship between output and input correlations

$$F1(x) = \frac{2}{1 + be^{-cx}} - 1 \tag{1}$$

and quantified the robustness by the parameter c. The closer the curve is to the maximal robustness, i.e., a sign function, the larger the robustness parameter c. Equation (1) is convenient for fitting the data for robust sequence association, but is not appropriate for non-robust relationships. In these cases, we use another fitting function instead

$$F2(x) = b' \tan(c'x) \tag{2}$$

We performed model selection based on the Akaike Information Criterion (AIC) to decide in each case whether (1), (2), or a combination of both

$$F(x) = F1(x) + F2(x)$$
 (3)

best accounted for the input-output relationship. The noise is given by

$$\dot{\eta}_j = \frac{-\eta_j}{\tau_\eta} + \xi_j \qquad (4)$$



Fig. 3: Overlapping feedforward projections largely account for robustness of sequence association. a) The connection strengths matrix after learning sequence association shows overlapping projection pattern. b) Constructed connection strengths with overlapping projection pattern. c) Constructed connection strengths with same number of projections as in a), but random, non-overlaping projections. d) Input-output relationship of three networks with different connectivities: learned connections weights (black), four connections per unit with overlap of three (red), and four random connections per unit (blue). Shown for each network are points representing input and output sequence pairs and lines representing the best-fit sigmoid function. e) Robustness parameter c for connections with overlap, and parameter c' for random distribution of connections.

where ξ_j is white noise process with zero mean and unit standard deviation (std) [4]. The parameter τ_{η} allow us to adjust the noise level. We were increasing the std of the noise to observe its influence on robustness.

III. RESULTS

Having found that sequence association is robust, we further examined the origin of this robustness. The matrix of learned connections indicates that only few first layer units send projections to the second layer, and those that do have systematically overlapping projections (Fig. 3a). For instance, if the first unit in the input sequence projects to units 1-4 in the output sequence, unit 2 in the input projects to units 2-5 in the output. To test whether this connectivity pattern was responsible for robustness, we studied robustness in networks where we constructed a connection matrix with overlapping connectivity pattern (Fig. 3b), instead of learning the sequence association. Indeed, sequence association in the constructed network showed robustness (Fig. 3c, red points), close to the network with learned connections (Fig. 3c, black points). As a control, we performed the same analysis with a network, in which each unit in the first layer projects randomly to the same number (4) of units in the second layer (Fig. 3d). This control network exhibited a non-robust input-output relationship (Fig. 3c, blue points). So, the conclusion is that the overlap of connections preserves the correct sequence at the output.

To examine the influence of the number of connections. we repeated the above simulations for different number of outgoing connections from the input units (Fig. 3e). In every case, the model selection indicated that one of the simpler models, i.e., Eq. (1) or (2) was sufficient to fit the data. Equation (1) was the most appropriate model to describe the data for the robust cases, i.e., connections with overlap, and (2) best fit the data in the nonrobust cases, i.e., random connections. Based on the results of the model selection, either parameter c or c' are reported in Fig. 3e. Networks with overlapping connections have robust sequence association for a range of connection numbers, but a clear peak in robust is reached for small numbers of connections. Networks with random connections do not show robustness. We therefore conclude that overlapping connectivity is crucial for the robustness of sequence association.

Next, we studied how the robustness is affected by the noise in the network dynamics and the heterogeneity in the dynamics parameters. When we increased the standard deviation of the noise process, we saw a lower robustness in the sequence association as evidenced by a shallower slope in the input-output relationship as compared to (Fig.4a,b). Larger standard deviations in the noise process consistently led to lower robustness in the sequence association. This relationship was captured by the robustness parameter c (Fig. 4c). In these analyses, the parameters were averaged across 60 repetitions of sequence storage and subsequent analysis of the input-output relationship. Repetition was



Fig. 4: The impact of the noise process on the robustness of sequence association. a,b) These two examples show that more noise in the network leads to less robust sequence association, as evident in the steeper slope of the input-output relationship for (a) as compared to (b) and in the robustness parameter, vs. std, c) The robustness parameter c declines as a function of the standard deviation of the noise process for homogeneous (dashed line) and heterogeneous (solid line) network parameters. d) The fit parameter b is not related to the robustness of sequence association.

required to sample across different realization of the noise process and, in the heterogeneous case, of the parameters in the units' dynamics (solid line). As expected, the other parameter b in the curve fitting did not depend on the noise process (Fig. 4d). These results show that, first, the robustness decreases with increased noise; and second, heterogeneity in the dynamics parameters within the tested range does not significantly affect robustness.

We return to the network with learned sequence associations to study the effect of network properties that we excluded in the first analysis above, namely ongoing plasticity between layers during testing and E2-E2 connections. We found robustness in a test case with, even when both plasticity and recurrent connections are enabled (Fig. 5a). As above, robustness was observed only for the stored sequence, not when tested with random reference sequences (Fig. 5b). To facilitate a direct comparison of the networks with different features, we plotted the robustness as a function of the noise standard deviation for six different network types (Fig. 5c). Including E2-E2 connections yielded higher robustness than the purely feedforward network (Fig. 5c, green lines). However, adding ongoing plasticity on top of E2-E2 connections did not further increase robustness (Fig. 5c, blue lines). We did not observe systematic differences between networks with homogeneous and those with heterogeneous parameters (Fig. 5c, dashed and solid lines, respectively). That recurrent E2-E2 connections increase robustness of sequence association makes intuitive sense since the recurrent connections store the output sequence in addition to the feedforward E1-E2 connections. It is not immediately obvious why ongoing plasticity has little effect on robustness.

We therefore directly studied the plasticity that occurred in the network. We computed the average absolute change in E1-E2 connection strength during both learning and testing phases (Fig. 5d). The connections show large changes early during training, which then asymptotes at a low level. During testing only small changes are seen, which are probably due to random fluctuations in unit activity resulting in random prepost pairings. This result indicates that during the testing phase (Fig.5d), the neural activity does not drive large changes in connection strengths probably because there are no consistent pairings of pre- and postsynaptic activity that deviate from the stored activity pattern. As a consequence, ongoing plasticity does not improve robustness, nor does plasticity harm robustness, which is somewhat surprising since testing was done using corrupted input sequences.



Fig. 5: Sequence association in network with recurrent E2-E2 connections and ongoing plasticity. a) Example for robust sequence association, . b) Robustness is observed only for the stored sequences, or similar ones. c) Robustness vs. standard deviation of noise process for six different cases. The three colors represent different combinations of the two network features: recurrent E2-E2 connections and ongoing plasticity as indicated in inset; the line type indicates homogeneous (dashed line) or heterogeneous (solid line) network parameters. The red lines represent the same data as in Fig. 4c and are replotted for easier comparison. d,e) Average absolute change in connection strengths during the learning (d) and the testing (e) phase.

IV. CONCLUSION

We found that a purely feedforward network associates the input and output sequences robustly. There are, however, open questions and limitations to our study. When looking at all possible permutation of a reference sequence with many elements, the number of sequences with a correlation around zero is much larger than the number of correlations close to 1 or -1. Future work will be need to investigate the influence of the statistics of the input sequences on the robustness.

The potential influence of the procedure for assigning a unique time of activation to each unit's activity. here we used the first local maximum of the activation. Other potential measures could have been used, such as the first time of crossing a certain threshold, the median time of the activity distribution, or the time of the absolute maximum. Since there is no universally agreed upon measure for rate-based units, it is speculative at this point. This ambiguity could be resolved by using spiking neuron models, where the sharp spikes allow a clear definition of times of activity. In our study we used only one fixed set of network parameters network, including a relatively modest network size, since the network dynamics and analyses require extensive numerical calculations. Future work is needed to study robustness of sequence association for different network parameters, especially different network sizes and different level of inhibition.

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