Beyond Bumps: Spiking Networks that Store Smooth n-Dimensional Functions

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Abstract

There are currently a number of models that use spiking neurons in recurrent networks to encode a stable Gaussian 'bump' of activation. These models successfully capture some behaviors of various neural systems (e.g., storing a single spatial location in parietal cortex). We extend this previous work by showing how to construct and analyze realistic spiking networks that encode smooth n-dimensional functions drawn from a finite functional space. These new networks can capture additional experimentally observed behavior (e.g., storing multiple spatial locations at the same time).

1 Introduction

Stable Gaussian shaped neuronal activities across a population of recurrently connected neurons without external perturbation, or stable 'bumps', have been successfully modeled by a number of researchers [8, 7, 6]. Bumps have been thought to be present in various neural systems including the head direction system [5], frontal working memory systems [8], parietal reach memory systems [4], and feature selective visual systems [3]. Many of these systems can store functions more complicated than a simple Gaussian bump. For example, there is evidence that parietal areas can hold multiple saccade targets in memory at the same time, suggesting that a multi-modal function is stored [2].

In this paper, we extend previous work on single bump networks by showing how to construct and analyze realistic spiking networks that can encode smooth n-dimensional functions drawn from a finite functional space. We begin our analysis with a one-dimensional network of simple rate-modeled neurons. We then show how it is possible to generate useful analytical results about this simple network. We discuss important extensions to the model, including how to implement the model in a spiking network (e.g., using integrate-and-fire neurons), and how to construct higher dimensional models. Notably, the approach we employ is a general one which can be applied to constructing and analyzing many different kinds of neural circuits [9, 10].

2 A simple rate model

We begin by representing the space of functions to be stored, $f(x)$, as a standard basis expansion:

$$f(x) = \sum_{n=1}^{D} A_n \chi_n(x). \tag{1}$$

$$A_n = \langle \chi_n f \rangle, \tag{2}$$

where $\langle \chi_n f \rangle = \int \chi_n(x) f(x) dx$.

We choose a finite number, D, of orthonormal basis functions, $\chi_n(x)$, to define the functional space. In our simulations, the functional space is constrained to have low spatial frequencies, resulting in smooth functions.

Next, we assume that the neurons form a highly overcomplete representation of this same functional space. The encoding functions for this representation are taken to be the neuron response functions:

$$a_i(x) = F_i\left[\left\langle \hat{\phi}_i f \right\rangle\right]. \tag{3}$$

$$f(x) = \sum_i^N a_i \phi_i(x) \tag{4}$$

Thus, the a_i are the neuron firing rates and must be positive. In order enforce this constraint, the firing rates are determined by passing the encoding process through a nonlinearity, F_i (e.g., rectification).

We find the decoding functions in the neuron space, $\phi_i(x)$, by minimizing the error between the two representations (i.e., the neuron space and orthonormal representations):

$$E = \left\langle \int \left[\sum_n A_n \chi_n(x) - \sum_i a_i \phi_i(x)\right]^2 dx \right\rangle_{A_n}. \tag{5}$$

We express the neuron decoding functions as a linear sum of orthonormal basis functions, $\phi_i(x) = \sum_j k_{ij} \chi_j(x)$, in order to ensure that they encode the same functional space. Minimizing the error in (5) gives:

$$\phi_i(x) = \Gamma_{in}^{-1} \chi_n(x), \tag{6}$$

where $\Gamma_{in} = \left\langle \hat{\phi}_i \chi_n \right\rangle$.

To store the function $f(x)$, we must ensure that the dynamics are stable. That is, we want to find weights that force the network to decode the same function it encodes from time step to time step. To facilitate analysis, we ignore the nonlinearity of the neuron response function in (3). This is justified because the functional space we are representing is positive definite. So, the weights needed to give stable dynamics can be found as follows:

$$a_i^{n+1} = \left\langle \hat{\phi}_i f^n \right\rangle \tag{7}$$

$$= \sum_j a_j^n \left\langle \hat{\phi}_i \phi_j \right\rangle$$

$$= \sum_j w_{ij} a_j^n. \tag{8}$$

The weights, in this case, are the projection of the encoding functions onto the decoding functions.

Notably, we can further analyze the dynamics of this network by finding the derivatives in the orthonormal space:

$$A_n^{k+1} = \left\langle \chi_n f^k \right\rangle \tag{9}$$

$$= \sum_i \gamma_{in} F_i[\sum_m \Gamma_{im} A_m^k], \tag{10}$$

where $\gamma_{in} = \langle \chi_n \phi_i \rangle$.

$$\begin{aligned} \frac{dA_n^{k+1}}{dA_m^k} &= \sum_i \gamma_{in} \frac{dF_i[\xi]}{d\xi} \frac{d\xi}{dA_m^k} \\ &= \sum_i \gamma_{in} \frac{dF_i[\xi]}{d\xi} \Gamma_{im} \approx \delta_{nm}. \end{aligned} \tag{11}$$

Our simulations have verified this result, which shows that the amplitudes, A_n, are dynamically remapped to themselves in spite of the nonlinear neuronal encoding procedure. In particular, assuming physiologically reasonable response functions, and using the weights as calculated in (8), this procedure results in a localized connectivity matrix that supports stable dynamics for functions of appropriate smoothness.

Notably, we have extended this analysis to account for the effects of noise by including a noise term in equation (11). This gives an expression for the diffusion characteristics in the amplitude space. We have shown that diffusion decreases as the square root of the number of neurons. Furthermore, in the limit of high spiking rates and a large number of neurons, we can model the dominant effect of the spike fluctuations using an equivalent noise level [1]. Again, these fluctuations lead to diffusion of the amplitudes. However, as noted in [8], the behavior is very different if the neurons become synchronized.

To verify and extend these further analyses we are in the process of simulating networks of noisy spiking neurons. Notably, the decoding and encoding functions are the same for the spiking model as those used in the rate model, and so, then, are the connection weights. The details of our implementation of this model in a spiking network follow [8].

Lastly, the extension of our analysis to higher dimensions is straight forward. In particular, equations (1) - (3) can be re-written using vector notation, and the remaining analysis will follow in a similar manner. We intend to verify this through additional simulations.

3 Conclusion

We have shown how to generate networks of spiking neurons that can store arbitrary smooth functions as defined by (1). We have given some examples of the kinds of analysis that can be carried out in the orthonormal space and yet help characterize the behavior of the high-dimensional neural network model.

Interestingly, these networks have produced an experimental prediction. Currently, memory experiments only record from neurons with stimuli at the center of their receptive fields. This results in a decrease in firing rate during the memory delay relative to the initial encoding of the stimulus. The networks we have generated reproduce this result, but they also include neurons whose firing rates increase when the stimuli is at the edge of the receptive field. We suspect, then, that a neuron tested with stimuli near the edges of its receptive field will also increase its firing rate during the memory delay period.

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