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Edge of chaos and prediction of computational performance for neural circuit models

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Abstract

We analyze in this article the significance of the edge of chaos for real-time computations in neural microcircuit models consisting of spiking neurons and dynamic synapses. We find that the edge of chaos predicts quite well those values of circuit parameters that yield maximal computational performance. But obviously it makes no prediction of their computational performance for other parameter values. Therefore, we propose a new method for predicting the computational performance of neural microcircuit models. The new measure estimates directly the kernel property and the generalization capability of a neural microcircuit. We validate the proposed measure by comparing its prediction with direct evaluations of the computational performance of various neural microcircuit models. The proposed method also allows us to quantify differences in the computational performance and generalization capability of neural circuits in different dynamic regimes (UP- and DOWN-states) that have been demonstrated through intracellular recordings in vivo.
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1. Introduction

What makes a neural microcircuit computationally powerful? Or more precisely, which measurable quantities could explain why one microcircuit C is better suited for a particular family of computational tasks than another microcircuit C'? Rather than constructing particular microcircuit models that carry out particular computations, we pursue in this article a different strategy, which is based on the assumption that the computational function of cortical microcircuits is not fully genetically encoded, but rather emerges through various forms of plasticity ("learning") in response to the actual distribution of signals that the neural microcircuit receives from its environment. From this perspective the question about the computational function of cortical microcircuits C turns into the questions:

(a) What functions (i.e. maps from circuit inputs to circuit outputs) can particular neurons ("readout neurons", see below) in conjunction with the circuit C *learn* to compute.

(b) How well can readout neurons in conjunction with the circuit C generalize a specific learned computational function to new inputs?

We propose in this article a conceptual framework and quantitative measures for the investigation of these two questions. In order to make this approach feasible, in spite of numerous unknowns regarding synaptic plasticity and the distribution of electrical and biochemical signals impinging on a cortical microcircuit, we make in the present first step of this approach the following simplifying assumptions:

1. Particular neurons ("readout neurons") learn via synaptic plasticity to extract specific information encoded in the spiking activity of neurons in the circuit.
2. We assume that the cortical microcircuit itself is highly recurrent, but that the impact of feedback that a readout neuron might send back into this circuit can be neglected.[1]

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[1] This assumption is best justified if such readout neuron is located for example in another brain area that receives massive input from many neurons in this microcircuit and only has diffuse backwards projection. But it is certainly problematic and should be addressed in future elaborations of the present approach.

3. We assume that synaptic plasticity of readout neurons enables them to learn arbitrary linear transformations. More precisely, we assume that the input to such readout neuron can be approximated by a term $\sum_{i=1}^{n-1} w_i x_i(t)$, where $n-1$ is the number of presynaptic neurons, $x_i(t)$ results from the output spike train of the ith presynaptic neuron by filtering it according to the low-pass filtering property of the membrane of the readout neuron,[2] and w_i is the efficacy of the synaptic connection. Thus $w_i x_i(t)$ models the time course of the contribution of previous spikes from the ith presynaptic neuron to the membrane potential at the soma of this readout neuron. We will refer to the vector $\mathbf{x}(t)$ as the *circuit state at time t*. Note that the readout neurons do not have access to the analog state of the circuit neurons, but only to the filtered version of their output spike trains.

Under these unpleasant but apparently unavoidable simplifying assumptions we propose in Sections 4 and 5 new quantitative criteria based on rigorous mathematical principles for evaluating a neural microcircuit C with regard to questions (a) and (b). We will compare in Sections 6 and 8 the predictions of these quantitative measures with the actual computational performance achieved by 102 different types of neural microcircuit models, for a fairly large number of different computational tasks. All microcircuit models that we consider are based on biological data for generic cortical microcircuits (as described in Section 2), but have different settings of their parameters. It should be noted that the models for neural circuits that are discussed in this article are subject to noise (in the form of randomly chosen initial values of membrane voltages, and in the form of biologically realistic models for background noise, see the precise definition in Section 2, and exploration of several noise levels in Section 8). Hence the classical theory for computations in noise-free analog circuits (see, e.g., Siegelmann and Sontag (1994)) cannot be applied to these models. Rather, the more negative results for computations in analog circuits with noise (see, e.g., Maass and Orponen (1998), Maass and Sontag (1999)) apply to the circuit models that are investigated in this article.

For the sake of simplicity, we consider in this article only classification tasks, although other types of computations (e.g. online computations where the target output changes continuously) are at least of equal importance for neural systems. But actually, a theoretical analysis of the capability of neural circuits to approximate a given online computation (that maps continuous input streams onto continuous output streams), see Maass, Natschläger, and Markram (2002) and in more detail Maass and Markram (2004), has shown that the so-called separation property of circuit components is a necessary (and in combination with a condition on the readout also sufficient) condition for being able to approximate a given online computation that maps continuous input streams onto continuous output streams with fading memory. Hence one

can view the computational tasks that are considered in this article also as tests of the separation property of small generic circuits of neurons, and hence of their capability to serve as a rich reservoir of "basis filters" in the context of that theory, and hence as subcircuits for online computing with continuous output streams.

Several results of this article had previously been sketched in Maass, Legenstein, and Bertschinger (2005).

2. Models for generic cortical microcircuits

Our empirical studies were performed on a large variety of models for generic cortical microcircuits. All circuit models consisted of leaky-integrate-and-fire neurons[3] and biologically quite realistic models for dynamic synapses.[4] Neurons (20% of which were randomly chosen to be inhibitory) were located on the grid points of a 3D grid of dimensions $6 \times 6 \times 15$ with edges of unit length. The probability of a synaptic connection from neuron a to neuron b was proportional to $\exp(-D^2(a, b)/\lambda^2)$, where $D(a, b)$ is the Euclidean distance between a and b, and λ is a spatial connectivity constant. Synaptic efficacies w were chosen randomly from distributions that reflect biological data (as in Maass et al. (2002)), with a common scaling factor W_{scale}.

Linear readouts from circuits with $n - 1$ neurons were assumed to compute a weighted sum $\sum_{i=1}^{n-1} w_i x_i(t) + w_0$ (see Section 1). In order to simplify notation we assume that the vector $\mathbf{x}(t)$ contains an additional constant component $x_0(t) = 1$, so that one can write $\mathbf{w} \cdot \mathbf{x}(t)$ instead of $\sum_{i=1}^{n-1} w_i x_i(t) + w_0$. In the case of classification tasks we assume that the readout outputs 1 if $\mathbf{w} \cdot \mathbf{x}(t) \geq 0$, and 0 otherwise.

In order to investigate the influence of synaptic connectivity on computational performance, neural microcircuits were drawn from the distribution of circuits discussed above for 10 different values of λ (which scales the number and average distance of synaptically connected neurons) and 9 different values of W_{scale} (which scales the efficacy of all synaptic connections). 20 microcircuit models C were drawn for each of these 90 different assignments of values to λ and W_{scale}. For each circuit a linear readout was trained to perform one (randomly chosen) out of 2^{80} possible classification tasks on noisy variations u of 80 fixed spike patterns as circuit inputs u. See Fig. 1 for two examples of such spike patterns. The target performance of a linear readout with any such circuit was to output at time $t = 200$ ms the class (0 or 1) of the spike pattern from which the preceding circuit input had been generated (for some arbitrary partition of the 80 fixed spike patterns into two classes). Each spike pattern u consisted of 4 Poisson spike

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[2] One can be even more realistic and filter it also by a model for the short term dynamics of the synapse into the readout neuron, but this turns out to make no difference for the analysis proposed in this article.

[3] Membrane voltage V_m modeled by $\tau_m \frac{dV_m}{dt} = -(V_m - V_{\text{resting}}) + R_m \cdot (I_{\text{syn}}(t) + I_{\text{background}} + I_{\text{noise}})$, where $\tau_m = 30$ ms is the membrane time constant, I_{syn} models synaptic inputs from other neurons in the circuits, $I_{\text{background}}$ models a constant unspecific background input and I_{noise} models noise in the input. The membrane resistance R_m was chosen as 1 MΩ in all sections except for Section 8.

[4] Short term synaptic dynamics was modeled according to Markram, Wang, and Tsodyks (1998), with distributions of synaptic parameters U (initial release probability), D (time constant for depression), F (time constant for facilitation) chosen to reflect empirical data (see Maass et al. (2002), for details).