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Dynamics of information and emergent computation in generic neural microcircuit models

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Abstract

Numerous methods have already been developed to estimate the information contained in single spike trains. In this article we explore efficient methods for estimating the information contained in the simultaneous firing activity of hundreds of neurons. Obviously such methods are needed to analyze data from multi-unit recordings. We test these methods on generic neural microcircuit models consisting of 800 neurons, and analyze the temporal dynamics of information about preceding spike inputs in such circuits. It turns out that information spreads with high speed in such generic neural microcircuit models, thereby supporting—without the postulation of any additional neural or synaptic mechanisms—the possibility of ultra-rapid computations on the first input spikes.

Keywords: Neural microcircuit; Spiking neurons; Information theoretic methods; Neural coding; Computational power; Dynamic synapses; Linear regression; Bayesian classifier

1. Introduction

Common analytical tools of computational complexity theory cannot be applied to recurrent circuits with complex dynamic components, such as biologically realistic neuron models and dynamic synapses. In this article we explore the capability of information theoretic concepts to throw light on emergent computations in recurrent circuit of spiking neurons (we refer to p. 429 of Panzeri, Rolls, Battaglia, & Lavis, 2001 for a discussion of advantages in using information theoretic methods in this context). This approach is attractive since it may potentially provide a solid mathematical basis for understanding such computations. But it is methodologically difficult because of systematic errors caused by under-sampling problems that are ubiquitous even in extensive computer simulations of relatively small circuits. Previous work on these methodological problems had focused on estimating the information in spike trains, i.e. temporally extended protocols of the activity of one or a few neurons. In contrast to that this paper addresses methods for estimating the information that is instantly available to a neuron that has synaptic connections to a large number of neurons. The proposed formalism to study simulated neural circuits has the advantage that it allows direct comparisons with experimental results on neural coding. In view of the very large existing literature on neural coding and relevant applications of information theory we cannot discuss here the preceding literature in detail. We refer to Borst and Theunissen (1999), deCharms and Zador (2000), Hertz (1999), Hertz and Panzeri (2003), Pola, Schultz, Petersen, and Panzeri (2003), and Rieke, Warland, van Steveninck, and Bialek (1997) for recent reviews. The dynamics of information in neural circuit models has previously been studied in Panzeri et al. (2001). In that study the speed of pattern completion was studied in a circuit model consisting of very realistic neuron models but static synapses. The network inputs consisted there of spatial patterns encoded by step currents, which represented fragments of more complete patterns from a fixed set of spatial patterns. Nevertheless, the results reported in that article about the speed of information processing are quite consistent with those reported in this article for the case where the network input consists of spike trains, and the fusion of information from several segments of these spike

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inputs is examined (rather than the fusion of information between static input patterns and information stored in synaptic weights as in Panzeri et al., 2001).

We will define the specific circuit model used for our study in Section 2 (although the methods that we apply appear to be useful for to a much wider class of analog and digital recurrent circuits). The combination of information theoretic methods with methods from machine learning that we employ is discussed in Section 3. The results of applications of these methods to the analysis of the distribution and dynamics of information in a generic recurrent circuit of spiking neurons are presented in Section 4. Applications of these methods to the analysis of emergent computations are discussed in Section 5.

2. Our study case: a generic neural microcircuit model

As our study case for analyzing information in high-dimensional circuit states we used a randomly connected circuit with sparse, primarily local connectivity consisting of 800 leaky integrate-and-fire (I&F) neurons, 20% of which were randomly chosen to be inhibitory. Constants of neurons and synaptic parameters were chosen to reflect the diversity of parameters reported in experimental studies (see Destexhe & Marder, 2004 for a discussion).[1] The 800 neurons of the circuit were arranged on two 20×20 layers L1 and L2.[2] Circuit inputs consisting of five spike trains were injected into a randomly chosen subset of neurons in layer L1 (the connection probability was set to 0.25 for each of the five input channels and each neuron in layer L1). We modeled the (short term) dynamics of synapses according to the model proposed in Markram, Wang, and Tsodyks (1998), with the synaptic parameters U (use), D (time constant for depression), F (time constant for facilitation) randomly chosen from Gaussian distributions that model empirical data for such connections. Parameters of neurons and synapses were chosen as in Maass et al. (2002) to fit data from microcircuits in rat somatosensory cortex (based on Gupta, 2000; Markram et al., 1998).

Since neural microcircuits in the nervous system often receive salient input in the form of spatio-temporal firing patterns (e.g. from arrays of sensory neurons, or from other brain areas), we have concentrated on circuit inputs of this type. Such firing pattern could for example represent visual information received during a saccade, or the neural representation of a phoneme or syllable in auditory cortex. Information dynamics and emergent computation in recurrent circuits of spiking neurons were investigated for input streams over 800 ms consisting of sequences of *noisy* versions of four of such firing patterns. We restricted our analysis to the case where in each of the four 200 ms segments one of two template patterns is possible, see Fig. 1. In the following, we write $s_i=1$ ($s_i=0$) if a noisy version of template 1 (0) is used in the ith time segment of the circuit input.

Fig. 2 shows the response of a circuit of spiking neurons (drawn from the distribution specified above) to the input stream exhibited in Fig. 1B. Each frame in Fig. 2 shows the current firing activity of one layer of the circuit at a particular point t in time. Since in such rather small circuit (compared for example with the estimated 10^5 neurons below a square millimeter of cortical surface) very few neurons fire at any given millisecond, we have replaced each spike by a pulse whose amplitude decays exponentially with a time constant of 30 ms. More precisely, the spike train from each presynaptic neuron was convolved with the kernel $e^{-\tau/30\ \mathrm{ms}}$. This models the impact of a spike on the receptors and the membrane potential of a generic postsynaptic neuron. The resulting vector $\boldsymbol{r}(t)=\langle r_1(t),\ldots,r_{800}(t)\rangle$ consisting of 800 analog values from the 800 neurons in the circuit is exactly the 'liquid state' of the circuit at time t in the context of the abstract computational model introduced in Maass et al. (2002). In the subsequent sections, we will analyze the temporal dynamics of the information contained in these momentary circuit states $\boldsymbol{r}(t)$.[3]

3. Methods for analyzing the information contained in circuit states

The mutual information $MI(X, R)$ between two random variables X and R can be defined by $MI(X, R)=H(X)-H(X|R)$, where $H(X)=-\sum_{x\in\mathrm{Range}(X)}p(x)\log p(x)$ is the entropy of X, and $H(X|R)$ is the expected value (with regard to R) of the conditional entropy of X given R, see e.g. Cover and Thomas (1991). It is well known that empirical estimates of the entropy tend to underestimate the true entropy of a random variable (see e.g. Panzeri & Treves,

[1] *Neuron parameters*: membrane time constant 30 ms, absolute refractory period 3 ms (excitatory neurons), 2 ms (inhibitory neurons), threshold 15 mV (for a resting membrane potential assumed to be 0), reset voltage 13.5 mV, constant nonspecific background current $I_b=13.5$ nA, input resistance 1 MΩ.

[2] *Connectivity structure*: We assumed that the neurons were located on the integer points of a three-dimensional grid in space, where $D(a, b)$ is the Euclidean distance between neurons a and b. The probability of a synaptic connection from neuron a to neuron b (as well as that of a synaptic connection from neuron b to neuron a) was defined as $C\exp(-D^2(a,b)/\lambda^2)$, where λ is a parameter which controls both the average number of connections and the average distance between neurons that are synaptically connected (we set $\lambda=2$, see Maass et al., 2002 for details). Depending on whether a and b were excitatory (E) or inhibitory (I), the value of C was 0.3 (EE), 0.2 (EI), 0.4 (IE), 0.1 (II).

[3] One should note that these circuit states do not reflect the complete current state of the underlying dynamical system, only those parts of the state of the dynamical system that are in principle 'visible' for neurons outside the circuit. The current values of the membrane potential of neurons in the circuit and the current values of internal variables of dynamic synapses of the circuit are not visible in this sense.