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Driven by inhibition☆

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Abstract

We study the stability and information encoding capacity of synchronized states in a neuronal network model that represents part of the thalamic circuitry. Our model neurons have a Hodgkin–Huxley-type low threshold calcium channel, display post-inhibitory rebound, and are connected via GABAergic inhibitory synapses. Noise drives both the subthreshold non-spiking as well as the above threshold regularly spiking state into a self-organized, stochastically synchronized state. Neuronal firing is organized in stochastic clusters, with individual neurons hopping from cluster to cluster. The information content of the resulting spike trains consists of two separate contributions: the spike-time jitter around cluster firing times, and the hopping from cluster to cluster.

Keywords: Neural assemblies; Information theory; Inhibition; Noise

1. Introduction

The brain receives an enormous amount of information transduced by peripheral sense organs. This massive information influx is coded and decoded in ways that are not yet fully understood in cognitive neuroscience. Recent studies have focussed on specific neural substrates for binding mechanisms. Binding is the process by which the brain combines different aspects of sensory modalities of one object into one unified percept. The neural mechanisms that underlie synchronization in different parts of the

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brain are only partly understood. There is the suggestion that synchronization may be relevant to binding [9]. In most experiments to date one measures the activity of one neuron, or a small population of neurons. Periodic oscillations (field potential, or subthreshold intracellular) measured in these experiments are consistent with strong as well as weak synchronization. In strong synchronization all the neurons fire with a short time interval from each other. In weak synchronization the *average* neuronal activity is periodic, but without having each individual neuron firing at each period. Often theoretical analyses have, however, focussed on strong synchronization. Here, we conjecture that weak synchronization is robust against neuronal heterogeneities and synaptic noise, and consequently it is much more likely to occur in neuronal systems. Furthermore, we show that it can encode more information compared to strongly synchronized states. Here, we present numerical results of weak synchronization in a simple model of a network of thalamic neurons that supports our conjecture. We use a thalamic network, as an example, due to the wealth of modeling information that is already available. The mechanism we discuss here, however, has more general applicability.

The hallmark of weak synchronization is multimodal interspike interval (ISI) histograms (ISIH). The ISI occurs only near multiples of a particular time-scale, e.g. the period of the population activity T. Multimodality of the ISIH has been observed in the LGN [1], and it was attributed to the action of inhibitory neurons. Multimodal ISIH have also been found in model simulations of coupled inhibitory networks in the presence of noise [2] and in systems exhibiting stochastic resonance (SR) due to an external periodic drive [12]. In our work the periodic neuronal activity in the noise-driven system is internal and self-induced by the network. This mechanism is absent in unconnected single neurons, or in a single element with autosynaptic feedback. Recently, noise-induced periodic oscillations were also found in excitatory networks [4]. It has been suggested that the brain may encode information through an ensemble or cluster of neurons that fire within a short time of each other [10,5]. A particular neuron may be part of a cluster for a few cycles, before it joins another neuronal ensemble. This type of dynamics is very similar to the neuronal clusters that form in our model simulations described below. An important problem is how to quantify the information content of these binding-like cluster states. The Shannon entropy has been used as a measure of information content in investigations of sensory neurons in, for instance, crickets [3], and flies [6].

It is, nonetheless, not known how the brain processes information, and thus it is not clear whether the Shannon entropy is the correct quantity for this purpose. With this caveat in mind we still proceed to characterize the information content of our neural networks by calculating its well-defined Shannon entropy.

2. Methods

Our single neuron model equation contains a low threshold calcium current I_{Ca}, a general leak current I_{L}, a synaptic current I_{syn}, and a noise current $C_m\xi$,

$$C_m\frac{\mathrm{d}V}{\mathrm{d}t} = -I_{\mathrm{Ca}} - I_{\mathrm{L}} - I_{\mathrm{syn}} - C_m\xi \tag{1}$$

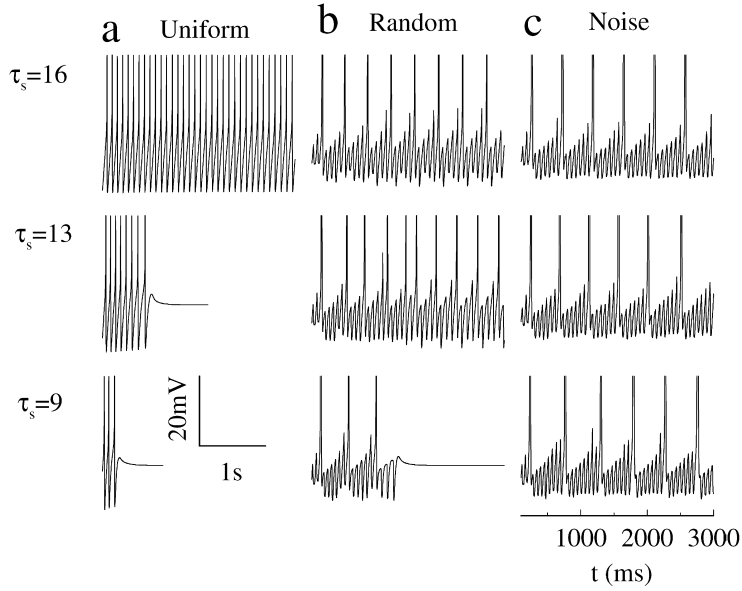

Fig. 1. Voltage traces for neuron one of an $N = 1000$ all-to-all connected neuron network with (a) uniform initial conditions, (b) random initial conditions, (c) uniform initial conditions with noise ($D = 0.02$, without the transient of 100 ms), for three different values of $\tau_s = 16, 13, 9$ (from top to bottom). A voltage and time scale bar is shown in the lower left graph.

together with the first-order (Hodgkin–Huxley type) kinetic equations for the activation m and inactivation h variables for I_{Ca} and the synaptic variable s. This yields a neuronal dynamics in terms of four variables, V, m, h, and s. We have used the kinetics for I_{Ca} and I_{syn} as specified in [7].

The neurons in our network are connected all-to-all by inhibitory GABAergic synapses. We have studied different sized systems, varying from $N = 1$ (a single neuron with autosynaptic feedback) to $N = 1000$. We also have included a Gaussian current noise, characterized by $\langle \xi \rangle = 0$ and

$$\langle \xi(t)\xi(0) \rangle = 2D\delta(t) \tag{2}$$

with D the strength of the noise. Unless stated differently the physiological total synaptic conductance used is $g_s = 2\,\mathrm{mS/cm^2}$, and the decay time of the synaptic channel $\tau_s = 16$ ms. The noise strength D is expressed in units of $\mathrm{mV^2/ms}$, time in ms, currents in $\mu\mathrm{A/cm^2}$, and voltage in mV.

The resulting differential equations are numerically integrated using a noise-adapted second-order Runge–Kutta algorithm [11].

3. Results

In Fig. 1 we show sample voltage traces of the first neuron in our network in different states. Of particular interest is the bottom row in the panel ($\tau_s = 9$). The

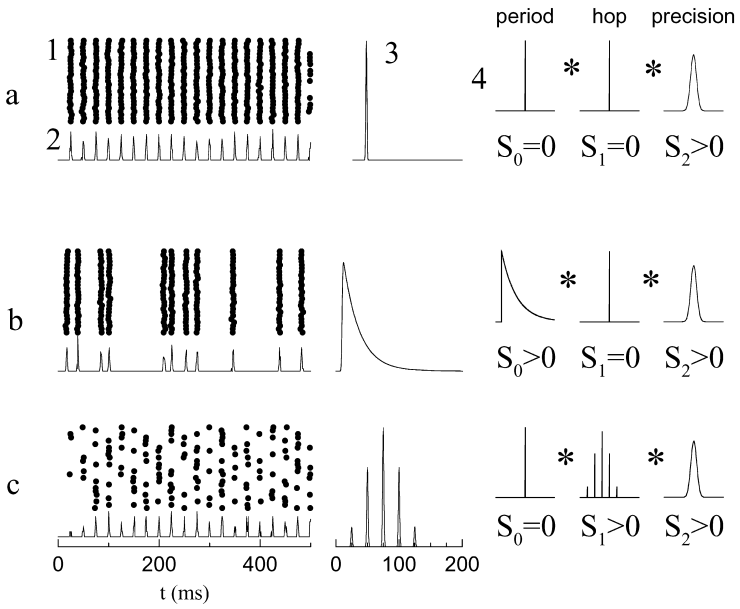

Fig. 2. Comparison of information content in synchronized oscillations. We consider (a) strongly synchronized and periodic, (b) strongly synchronized and aperiodic, and (c) weakly synchronized and periodic. For each case we plot (1) rastergram, (2) instantaneous firing rate, (3) the ISIH, and (4) the ISIH split into three components S_0, S_1, S_2. See text for details.

zero-noise oscillations are below threshold, but noise can induce, and is necessary to maintain, a stochastically synchronized state.

We have further studied the dependence of these oscillations on network parameters. We find that there is a difference between small (around 10 neurons) and large networks (a few hundred neurons), under the conditions of having a fixed total synaptic drive per neuron. For small networks one needs more noise to drive the subthreshold network into stable oscillations. These oscillations are very robust against increases in the noise level, however the fluctuations in the time between two cluster firings (cycle length) do increase with the amount of noise. For large networks strong noise causes an instability, the stable cluster size for a given amount of noise becomes too small to inhibit out of sync neuronal discharges. For intermediate noise strengths the neuronal dynamics self-organizes itself into a stochastically synchronized state. We also find that the farther the network is below threshold, more noise is necessary to induce a spiking state. The mechanism to create the oscillations is due to the competition between the excitatory de-inactivating, and the inhibitory effect of the synaptic drive. Each cycle will de-inactivate neurons, until they are excitable again. The neuron then has to await the decay of inhibition created by more excitable neurons. For some parameter values the latter stage is absent, and the dynamics is fully deinactivation dominated. The important time-scales in the dynamics are the

deinactivation time-scale τ_1 and the synaptic decay time τ_s. The cycle or population period scales directly with τ_s.

In Fig. 2 we compare the information content of weak versus strong synchronization in a cartoon. The information content of the ISIH can be divided up in three parts: S_0, the dispersion in cluster firing times; S_1, the hopping of neurons from cluster to cluster; S_2, the precision of firing times within a cluster. The information content is reduced when there are correlations between the ISIs [11]. For strong synchronization the information content is in the precision (or lack thereof) S_2. In that case more precision, that is better synchronization, corresponds to less information. However for weak synchronization the information is in S_1. Synchronization and information content can therefore be varied independently. Note that one could also code information in strongly synchronized oscillations by making them aperiodic (see Fig. 2c).

4. Discussion

In recent years considerable attention, as well as controversy, has been directed at studying the variability of neuronal discharge in the cortex [8]. It is beyond a doubt that neurons in vivo are noisy. The question is whether exact spike-times matter — that is, if the jitter in spike times represents information, for instance quantified by the Shannon entropy — or if only the average firing rate matters. If spike times *do* matter, then the synchronized discharge has a special significance. An important question is whether the nervous system is sensitive to synchronization or not. Our work is relevant in shedding light to this fundamental question in two ways. We have shown that noisy neurons can synchronize without the need of a strong external drive, and that the synchronized neuronal discharge has a potentially high information content. The brain thus has circuitry capable of synchronizing with heterogeneous components, and in the presence of noise. Whether the brain utilizes this mechanism to synchronize, and more importantly whether it uses the information in the precise temporal sequence is still an open question awaiting further study.

A detailed description of the results mentioned here, will be published elsewhere [11].

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