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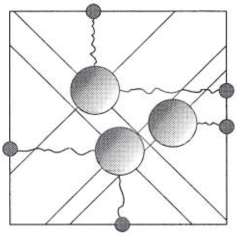

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A Point Process Approach to Cortical Networks

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Abstract

The "cognitive" properties of some artificial neuronal networks have introduced attractive models for cortical function. We discuss an extended framework for the description of biological nerve nets such that a direct comparison with the signals from electrophysiological recordings on the level of individual nerve cells becomes feasible. The mathematical analysis of these models leads to explicit conditions on their biophysical parameters giving rise to unexpected conclusions. We demonstrate that the "dynamic repertory" of a system of interacting spiking neurons is dramatically enhanced, if signals are admitted to have a time structure. Some possibilities of a spatio-temporal code in presence of plastic synapses and an appropriate learning rule are discussed.

1 Spatio-temporal patterns of action potentials

There is wide consensus that neurons in the neocortex exchange information by means of action potentials. In contrast to the highly reproducible waveform of spikes from an individual neuron, however, the timing of their occurrence is far from deterministic. As is known from single cell recordings both in slice preparations and in intact brains of behaving animals, there is a considerable variabilty in neuronal responses to repeated presentations of identical stimuli. Any theory of cortical function must therefore account for the specific properties of a stochastic code relying on identical point-like events distributed in space and time.

We explore the spatio-temporal dynamics of cortical activity by using an abstract network model, which is compatible with the notion of interacting stochastic point processes. Any such system may be viewed as a Markov process, whose "state" at a given time instance is the spatio-temporal pattern of all previously generated spikes. The "transition probabilities" specify how a pattern gradually evolves in time. The infinitesimal parameters of the process, usually called point process "intensities", are given by the spike probability normalized for an infinitesimal time interval, conditional on the pattern of previously generated action potentials. If these parameters exist, the resulting master equation is readily solved. This general framework sets the stage for a quantitative assessment of otherwise untractable network phenomena.

By taking account of redundancies in the state space, one arrives at a point process model for neuronal function which is of "integrate-and-fire" type. Each cell has its own state space with a "linear" structure and a "nonlinearity" transforming states into rates. The rates, in contrast to the situation in many ad hoc models in use, do not specify averages over a longer period of time, but are considered as instantaneous measures of neuronal excitation. In simple cases, the physical nature of the states can be identified with the help of experiments.

2 Physical states and system identification

By all available evidence, the class of point processes having infinitesimal parameters is sufficiently rich to comprise appropriate models for cortical function on different levels of abstraction. Each specific model amounts to an interpretation of the infinitesimal parameters in terms of biophysical properties of nerve cells. We use the solutions of the general master equation to obtain numerical fits of the parameters of such models to experimental observations. Further analysis of the fitted model's behavior can be expected to yield information on the role of subthreshold processes for the emergence of collective behavior.

Adopting this aproach, we can account for the details of spike generation upon direct current injection in regular spiking neurons, which constitute the major cell type in neocortex [3]. Using systematic variation of injected current in a slice preparation as an experimental paradigm, we identified membrane current, rather than membrane potential, as the significant physical state variable. The model parameters correspond to post-spike hyperpolarization currents, the constant current injected through the electrode, and a characteristic function translating the total membrane current into the point process intensity [5]. There is strong experimental evidence that this current-based description extends to synaptic interaction in terms of excitatory postsynaptic currents [4].

3 Analysis of the network model

In a model network of regular spiking neurons, a stable low level of activity is maintained whenever the post-spike hyperpolarization exceeds the total amount of excitation and inhibition received by each neuron. This hypothesis and its consequence are both in accordance with our knowledge of physiology in the cortex, where synaptic couplings are sparse and weak. Surprisingly though, inhibitory neurons are not required for stability, all rate control might be taken care of by "auto-inhibition". Yet another interesting aspect of this parameter constellation is that the coefficient of variation for the inter-spike interval distribution of single neuron spike trains increases with the total amount of recurrent excitation in the network. Again, no inhibitory neurons are necessary to achieve coefficients as obtained from *in vivo* data. This result is in contrast to some recent observations in the literature [6, 7].

It may be useful to characterize a single cortical pyramidal cell as a stochastic oscillator. The reason for this is not only its regular firing behavior upon DC stimulation, but also its response to transient inputs. In fact, the susceptibility of the model neuron to synaptic inputs shows a distinct phase preference, leading to pronounced resonance phenomena. In addition, the characteristic function translating current into neuronal excitation turns out to be convex, causing the neuron to prefer synchroneous inputs over asynchroneous ones. From this one correctly predicts that transient synchronization of groups of neurons should be part of the dynamic repertory for recurrent networks of regular spiking neurons.

Computer simulations of sparsely connected networks with random topology show that one can indeed distinguish two time scales of synchronization phenomena. At the macroscopic time scale (tens to hundreds of milliseconds), subgroups of neurons may exhibit transient states of "loose" spike synchronization, without appreciable effects on the average rates. Such "assemblies" desynchronize and reorganize periodically upon persistent stimulation. Within the periods of enhanced group activity, one can observe complex spatio-temporal patterns on a millisecond time scale reoccurring with great precision. Similar findings, both at the macroscopic time scale [8] and at the level of millisecond spike patterns [1, 2], have been reported from multi-neuron recordings in the prefrontal cortex of the behaving monkey.

4 Plasticity of time structure

Adaptive properties of a nervous system are most valuable for contolling the agent's behavior in a highly variable environment. We began to investigate the possibilities of plasticity in time structure of neuronal signals by introducing physiologically inspired Hebb-like synapses into our stochastic networks. In the context of point process models with physiological parameters, this leads to a learning rule of covariance type. From numerical simulations we conclude that the weakening of synapses connecting out-of-phase neurons can serve to maintain a stable total amount of excitation within such networks. No artificial normalization of synaptic strengths is necessary. By employing a measure for the "distance" between spatio-temporal patterns which naturally emerges from point process theory we can demonstrate that the mere presence of plastic synapses can have useful consequences. Among other things, one observes the imprinting of temporally extended stimulus patterns, as well as the automatic generation of discriminating representations for distinct stimuli which are presented sequentially.

5 Conclusions

We show that neuronal network models using generalized "integrate-and-fire" dynamics are a mathematical consequence of the assumption that neurons communicate by the use of action potentials. The corresponding dynamical equations are completly solved thus enabling a fit of the model parameters to electrophysiological recordings. A simple parametric characterization of single neuron function is achieved by fitting the model to the regular spiking behavior of cortical pyramidal cells. A number of fundamental properties of recurrent cortex-like networks assembled from such neurons can be predicted, most notably their ability to maintain stable low rates of activity without the help of inhibitory neurons.

Computer simulations indicate that high precision spatio-temporal patterns, embedded in periods of enhanced cooperative group activity, may play a role for coding and computation in such networks. Plasticity of the temporal structure of such patterns is achieved by introducing Hebb-like synapses into the network. The resulting properties brings the point process model close to what general abstract neuronal networks are known to be capable of. By further exploiting our model system's known mathematical structure we expect to derive quantitative predictions to be applied to more complex experimental paradigms involving neural structures with nonrandom topology and plastic properties.

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