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Review

Statistical mechanics of the neocortex

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ABSTRACT

We analyze neocortical dynamics using field theoretic methods for non-equilibrium statistical processes. Assuming the dynamics is Markovian, we introduce a model that describes both neural fluctuations and responses to stimuli. We show that at low spiking rates, neocortical activity exhibits a dynamical phase transition which is in the universality class of directed percolation (DP). Because of the high density and large spatial extent of neural interactions, there is a "mean field" region in which the effects of fluctuations are negligible. However as the generation and decay of spiking activity becomes *balanced*, there is a crossover into the critical fluctuation driven DP region, consistent with measurements in neocortical slice preparations. From the perspective of theoretical neuroscience, the principal contribution of this work is the formulation of a theory of neural activity that goes beyond the mean-field approximation and incorporates the effects of fluctuations and correlations in the critical region. This theory shows that the scaling laws found in many measurements of neocortical activity, in anesthetized, normal and epileptic neocortex, are consistent with the existence of DP and related phase transitions at a critical point. It also shows how such properties lead to a model of the origins of both random and rhythmic brain activity.

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1. Introduction

One of the main challenges for 21st century science is to understand how the brain works. This is no easy task. The major structure of the human brain, the neocortex, comprises about 75% of all neurons in the central nervous system. There are approximately 3.10^{10} neurons in the neocortex, each supporting up to 10^4 synaptic contacts. Histological studies (Sholl, 1956) show it to be close packed with neurons and neuroglial cells, occupying a volume of about 3000 cc. Sholl's studies indicate that the connections of individual cells are not nearly so important as the global pattern of connectivity in populations. Taken together, this suggests we can characterize connections in terms of probabilities. A similar conclusion about the statistical nature of neocortical activity is derived from physiological studies of cellular and population responses. At the cellular level, discharge patterns are extremely variable, especially in unanesthetized animals. Population records also show considerable variability in both spontaneous and evoked activity. There is thus the appearance of randomness in most, if not all, neocortical networks, both in the details of connectivity, and in recorded activities. Such an appearance of randomness is most likely not the result of "noise", but of the very large number of degrees of freedom or *entropy* inherent in the neurodynamics of some 10^{10} neurons. In fact if we characterize the activity of each neocortical neuron as either *quiescent* – at rest in a subthreshold state, *active* – producing an action potential or spike, or *refractory* – returning to rest, then there are approximately 10^{37} different configurations of neocortical activity.

This suggests that the methods of modern statistical mechanics (Itzykson and Drouffe, 1989) need to be applied to understand such activity. In particular the methods of Euclidean quantum field theory have proven extremely useful in understanding the physics of phase transitions, i.e. physics near "critical points". It is our hypothesis that criticality is of some importance for the dynamics of the brain. It stands to reason that these same methods should bear fruit in this area. We begin in Section 2 with a discussion of criticality and continue in Section 3 with experimental support for our claim. We continue in Sections 4 through 10 with a discussion of the models we will analyze and our results, followed by a discussion of other theoretical and modeling approaches in Section 11. Finally, we discuss some ramifications of our work.

2. Criticality in neocortex

Given such a large configuration space, the problem of understanding how the neocortex works seems overwhelmingly difficult. To make progress we require some way to organize the complexity