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Spontaneous and evoked activity in extended neural populations with gamma-distributed spatial interactions and transmission delay

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Abstract

The spatiotemporal dynamics of neural activity are studied using an integro-differential model of spatially extended neuronal ensembles. The model includes both synaptic and axonal propagation delay while spatial synaptic connectivities are represented by gamma distributions. This family of connectivity kernels has been observed experimentally and covers the cases of divergent, finite, and negligible self-connections. We give conditions for stationary and non-stationary instabilities for gamma-distributed kernels, which can be formulated in terms of the mean spatial interaction ranges and the mean spatial interaction times. We present novel mechanisms for Turing patterns and traveling waves, which result from the special shape of the gamma-distributed interactions. We give a numerical study of the propagation of evoked spatiotemporal response activity caused by short local stimuli, and reveal maximum response activity after the mean interaction time. This maximum occurs at a distance from stimulus offset location, which is equal to the mean interaction range.

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1. Introduction

The dynamics of neuronal activity is responsible for such major brain functions as perception, memory processes or motor coordination. The present study aims to gain some insight into the rich neuronal behavior by studying spatiotemporal neuronal dynamics caused by fluctuations and environmental external stimuli.

Fluctuations in space and time are always present due to the large number of interconnected neurons and are supposed to be responsible for large-scale coherent phenomena near unstable neural activity states. We mention the phenomena of hallucinations, which frequently result from specific circumstances such as fatigue or sleep deprivation [1] and which, in some cases, exhibits a shift of the neural state to an instability by increased neuronal excitation [2,3].

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For instance, Ermentrout and Cowan [4] introduced a mesoscopical neuronal field theory and explained visual hallucination patterns by loss of stability at bifurcation points.

In contrast, external stimuli may represent sensoric input as auditory speech or visual perceptions. For instance, during cognitive experiments encephalographic measurements reveal coherent evoked brain activity and indicate synchronous neuronal activity on a mesoscopic spatial level [5–9]. In this context, Freeman [10] has shown in an early study, that encephalographic activity relates to mesoscopic dendritic currents. Dipol and current source density models support these findings [11]. Hence, this study aims to study neuronal mechanisms on a spatially mesoscopic level.

Many studies investigating mesoscopic neuronal activity [12–20] treat synaptically coupled neuronal ensembles. This work follows the basic field approach of Jirsa and Haken [5], who combined the ensemble models of Wilson and Cowan [21] and Nunez [22]. This model considers a single type of neurons, which are interconnected by axons terminating at either excitatory or inhibitory synapses. Though the intrinsic delay due to axonal propagation had been introduced, it does not affect temporal and spatial dynamics. A recent work treating intracortical activity [23,24] extends the model by introducing synaptic response delay and thus adds a further time scale. It turns out, that the relation between synaptic and propagation delay affects the stability of the system.

In addition to the temporal scales, the synaptic connectivity kernels define the spatial scales of the neuronal field. In most studies, these connectivity kernels exhibit their maximum at zero distances, i.e. strong self-connectivity. Since experiments observed low probabilities [22] of local synaptic connections and the concerning effects of reduced self-connectivity has not been studied yet in a general form, we shall discuss the family of gamma-distributed connectivity kernels. This special type of spatial interaction may exhibit infinite, finite, and negligible probability densities of self-connections for diverse parameters. These cases shall be studied in the context of spontaneous and externally evoked activity.

The paper is organized as follows. The subsequent section presents the derivation of the field equation. In Section 3, stability conditions with respect to spontaneous fluctuations are derived analytically, followed in Section 4 by a numerical study of evoked responses caused by external stimuli. Section 5 summarizes the results and closes the work.

2. The model

The present study treats a three-section model of synaptically coupled neuronal ensembles. Here, one section represents the ensemble set of synapses, which convert the incoming presynaptic activity to postsynaptic potentials (PSP). The adjacent model section contains the ensemble set of trigger zones at somata converting PSPs to axonal pulse activity while the final one represents the set of axonal fibres linking trigger zones to distant synapses. In the following, these model sections are discussed in some detail.

2.1. Model derivation

Chemical synapses convert incoming action potentials to postsynaptic currents by emission of neurotransmitters [25]. Most excitatory synapses (e) emit neurotransmitters called glutamate, which enhance the activity of the postsynaptic cells while the neurotransmitter γ-aminobutyric (GABA) emitted by inhibitory synapses (i) diminishes the postsynaptic cell activity. In addition, synapses may bind to dendrites or the soma of the postsynaptic neuron. Hence, the efficacy of synapses is very diverse. Furthermore, there is evidence, that the dendritic morphology, such as compactness of arborization and branching patterns, affects the stability of connected neurons [14], e.g. due to propagation delays along spatially extended dendrites. In a simplified model, dendrites are electric conductors which exhibit passive spread of current through the dendritic tissue. According to this approach, Freeman [26] was one of the first to show, that the response of chemical synapses to incoming action potentials is approximately equivalent to the convolution of the action potential with an impulse response function $h_{e,i}(t)$. The presented approach accounts for this finding and neglects shunting effects.

In experimental practice single cell activation is obtained frequently as the number of action potentials exceeding a certain threshold potential during a time interval. Hence it is reasonable to assume action potentials at discrete times and the mean pulse rate at time t gives the number of action potentials in the interval. This description yields a coarse-graining in time. In addition, the model introduces spatial patches at location x each containing a fixed number of synapses (typically $\sim 10^4$). That means the activity discussed is coarse grained in space. Consequently, postsynaptic potentials averaged over time and space obey

$$\bar{V}^{e,i}(x,t) = \bar{g}_{e,i} \int_{-\infty}^{t} h_{e,i}(t-\tau)\bar{P}_{e,i}(x,\tau)\,d\tau, \tag{1}$$