Nonlinear Analysis: Real World Applications 14 (2013) 997–1025

Contents lists available at SciVerse ScienceDirect

Nonlinear Analysis: Real World Applications

journal homepage: www.elsevier.com/locate/nonrwa

Effect of localized input on bump solutions in a two-population neural-field model

Muhammad Yousaf[a,b], John Wyller[a,*], Tom Tetzlaff[c], Gaute T. Einevoll[a]

[a] Department of Mathematical Sciences and Technology, Norwegian University of Life Sciences, P.O. Box 5003, N-1432 Ås, Norway
[b] Department of Mathematics, COMSATS Institute of Information Technology, Lahore, Pakistan
[c] Inst. of Neuroscience and Medicine (INM-6), Computational and Systems Neuroscience, Research Center Jülich, Germany

ARTICLE INFO

Article history:
Received 8 March 2012
Accepted 24 August 2012

Keywords:
Two population neuronal-field models
Localized input
Bump solutions (see below)
Localized solution
Integro-differential equation
Stability analysis
Fourth-order Runge–Kutta method

ABSTRACT

We investigate a two-population Wilson–Cowan model extended with stationary and spatially dependent localized external inputs and study the existence and stability of localized stationary (bump) solutions. The generic situation for this model in the absence of external inputs corresponds to two bump pairs, one narrow and one broad pair. For spatially wide localized external inputs we find this generic picture to be unchanged. However, for strongly localized external inputs we find that three and even four bump pairs, all with symmetric activity profiles around the center of the localized external input, may coexist. We next investigate the stability of these bump pairs using two different techniques: a simplified phase–space reduction (Amari) technique and full stability analysis. Examples of models, i.e., choices of model parameters, exhibiting up to three stable bump pairs are found. The Amari technique is further found to be a poor predictor of stability in the case of strongly localized external inputs. The bump-pair states are also probed numerically using a fourth order Runge–Kutta method, and an excellent agreement is found between numerical simulations and the analytical predictions from full stability analysis.

1. Introduction

Experiments have implicated persistent neuronal firing as a possible substrate for short-term memory [1–3], and this has spurred significant interest among modelers in investigating persistent neural-network activity [4–7] and, in particular, spatially localized activity solutions, ‘bumps’, of neuron network models [7,8]. In recurrent networks such localized stationary states are naturally formed by a combination of (i) a strong and localized recurrent excitation boosting the bump and (ii) a spatially more extended ‘lateral’ inhibition preventing the bump from growing in size [9]. Neuronal field models have provided a powerful and versatile tool for the investigation of the properties of such bump states [8–13], and a large number of studies have used such models to study generic properties of bumps such as conditions for their existence and stability [14–27].

Most of these studies have focused on the generic properties of bumps for spatially homogeneous, i.e., translationally invariant, networks without external inputs. In some studies homogeneous inputs have been included [9,14,20]. However, as such inputs do not violate the translational invariance of the model, few new qualitative features are introduced, and the effects are akin to changing the effective firing threshold in the neural-field firing-rate functions. A more interesting situation

---

* Corresponding author. Tel.: +47 64965489; fax: +47 64965401.
E-mail address: John.Wyller@umb.no (J. Wyller).

1468-1218/$ – see front matter © 2012 Elsevier Ltd. All rights reserved.
doi:10.1016/j.nonrwa.2012.08.013

arises when the external input is spatially localized as this breaks the translational invariance. Further, the situation with such localized inputs is expected to be common in real neural networks, for example, in primary visual cortex where such inputs must underlie the prominent retinotopic organization [28]. Models with localized inputs have been explored in the context of orientation tuning in visual cortex [29,30]. In a more general setting, Folias and Bressloff [19] analyzed bumps in a one-population model with spatially localized external inputs and found that (i) sufficiently large inputs can stabilize bump states and (ii) that reduction of the input amplitude may induce a Hopf instability and the conversion of stable bumps into breather-like oscillatory waves.

In the present study we investigate the effects of spatially localized external inputs on bump states in a two-population Wilson–Cowan like model with one excitatory and one inhibitory population. We have previously investigated bump states in this model without external inputs [24,27], and an interesting feature is the key role played by the inhibitory time constant in determining the stability of bumps. The bumps are found to be stable only for inhibitory time constants below a critical value, about three times the excitatory time constant for the example in [24], while the bumps are converted to stable breathers through a Hopf bifurcation at the critical value. This crucial dependence on the ratio of inhibitory and excitatory time constants, which obviously cannot be addressed in a one-population model, has previously been seen in extensive network simulation of integrate-and-fire neurons [4,6].

The model investigated is a direct extension of the model studied in [24] with spatially dependent external inputs added to the equations describing the dynamics of both the excitatory and inhibitory populations:

$$
\begin{aligned}
\frac{\partial}{\partial t}u_e(x,t) &= -u_e(x,t) + \int_{-\infty}^{\infty}\omega_{ee}(x'-x)P_e(u_e(x',t)-\theta_e)dx' \\
&\quad - \int_{-\infty}^{\infty}\omega_{ie}(x'-x)P_i(u_i(x',t)-\theta_i)dx' + h_e(x) \\
\tau\frac{\partial}{\partial t}u_i(x,t) &= -u_i(x,t) + \int_{-\infty}^{\infty}\omega_{ei}(x'-x)P_e(u_e(x',t)-\theta_e)dx' \\
&\quad - \int_{-\infty}^{\infty}\omega_{ii}(x'-x)P_i(u_i(x',t)-\theta_i)dx' + h_i(x).
\end{aligned}
\tag{1}
$$

Here $u_e(x,t)$ and $u_i(x,t)$ are excitatory and inhibitory activity levels, $\omega_{mn}(x)$ the distance-dependent connectivity strengths, P_e and P_i the firing-rate functions for the excitatory and inhibitory populations, θ_e and θ_i the threshold values for firing of these excitatory and inhibitory populations, and τ the relative inhibition time, i.e., the ratio between the inhibitory and the excitatory time constants. (The excitatory time constant is, for convenience, set to unity.), Finally, $h_e(x)$ and $h_i(x)$ represent the new elements introduced to the model used in [24], i.e., stationary, localized external inputs.

The generic situation for the case without external inputs consists of two bump pairs, one narrow bump pair and one broad bump pair [24]. For spatially wide localized external inputs we find this generic picture to be unchanged. However, for strongly localized external inputs a more interesting situation emerges: here three and even four bump pairs may coexist. We next investigate the stability of these bump pairs. The two techniques used in [24], namely the simplified phase–space reduction technique (the so called *Amari* technique) and full stability analysis, are considered, and we find that the Amari technique fails to produce the correct stability results in the case of strongly localized external inputs.

The paper is organized as follows: In Section 2, we discuss the two population model (1) in some detail. We show that the solution of the initial value problem of this system is globally bounded and that spatially dependent external inputs represent a symmetry breaking effect i.e. the translational invariance property is violated. The existence and uniqueness of localized stationary solutions (bumps) for a given pair of threshold values subject to the spatially dependent external input are addressed in Section 4. Here and in the rest of the paper it is assumed that the firing rate functions are given by means of the Heaviside functions. In Section 5 we investigate the stability of these bumps analytically by using the Amari approach and full stability analysis. Section 6 is devoted to numerical simulations, where the time evolutions of localized structures are investigated by using a fourth order Runge–Kutta method. Section 7 contain a summary of the results and an outlook. Appendix A contains the detailed derivation of the growth rate equations in the full stability analysis in Section 5, Appendix B gives the description of the numerical code underlying the numerical simulations of Section 6, while Appendix C contains the technical details underlying the discussion on the discrepancy between the Amari analysis and full stability analysis.

2. Model

The model described by (1) can more compactly be written as

$$\frac{\partial u_e}{\partial t} = -u_e + \omega_{ee}\otimes P_e(u_e-\theta_e) - \omega_{ie}\otimes P_i(u_i-\theta_i) + h_e \tag{2a}$$

$$\tau\frac{\partial u_i}{\partial t} = -u_i + \omega_{ei}\otimes P_e(u_e-\theta_e) - \omega_{ii}\otimes P_i(u_i-\theta_i) + h_i \tag{2b}$$