Physica D 239 (2010) 1048–1060

Contents lists available at ScienceDirect

Physica D

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

Stability of bumps in piecewise smooth neural fields with nonlinear adaptation

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ARTICLE INFO

Article history:
Received 7 December 2009
Received in revised form
23 February 2010
Accepted 25 February 2010
Available online 6 March 2010
Communicated by S. Coombes

Keywords:
Neural network
Synaptic depression
Spike frequency adaptation
Piecewise smooth dynamics

ABSTRACT

We study the linear stability of stationary bumps in piecewise smooth neural fields with local negative feedback in the form of synaptic depression or spike frequency adaptation. The continuum dynamics is described in terms of a nonlocal integrodifferential equation, in which the integral kernel represents the spatial distribution of synaptic weights between populations of neurons whose mean firing rate is taken to be a Heaviside function of local activity. Discontinuities in the adaptation variable associated with a bump solution means that bump stability cannot be analyzed by constructing the Evans function for a network with a sigmoidal gain function and then taking the high-gain limit. In the case of synaptic depression, we show that linear stability can be formulated in terms of solutions to a system of pseudo-linear equations. We thus establish that sufficiently strong synaptic depression can destabilize a bump that is stable in the absence of depression. These instabilities are dominated by shift perturbations that evolve into traveling pulses. In the case of spike frequency adaptation, we show that for a wide class of perturbations the activity and adaptation variables decouple in the linear regime, thus allowing us to explicitly determine stability in terms of the spectrum of a smooth linear operator. We find that bumps are always unstable with respect to this class of perturbations, and destabilization of a bump can result in either a traveling pulse or a spatially localized breather.

1. Introduction

Persistent, localized regions of neural activity have been proposed as substrates of several memory and sensory processes in the brain. Experiments in primate prefrontal cortex show that sensory cues can often lead to a spatially localized group of neurons persistently firing during a recall task. This "bump" of activity disappears once the task is complete [1–3]. Additionally, it has been suggested that the brain may keep the eyes still by representing eye position as an activity bump in the medial vestibular nucleus [4]. Also, visually evoked bumps of activity have been seen in striate cortex due to the orientation selectivity of recurrent connections [5]. There has been a great deal of work developing models that explain how such bumps of activity might arise and be sustained in a neuronal network [6–9]. One of the simplest models known to support stationary bumps is given by a scalar integrodifferential equation that represents averaged population activity in a spatially extended network of neurons [6]:

$$\tau\frac{\partial u(x,t)}{\partial t} = -u(x,t) + \int_{-\infty}^{\infty} w(x-x')f(u(x',t)-\theta)\mathrm{d}x' + I(x,t). \tag{1.1}$$

The variable $u(x,t)$ represents the local synaptic drive to a population of neurons at position x and time t, τ is the membrane time constant, $I(x,t)$ represents an external input, and $w(x)$ is a synaptic weight distribution. Usually w is a continuous function satisfying $w(-x) = w(x)$ and $\int_{-\infty}^{\infty} w(x)\mathrm{d}x < \infty$. The nonlinearity f denotes an output firing rate function. Typically, f is a bounded, positive monotone increasing function such as the sigmoid

$$f(u-\theta) = \frac{1}{1+\exp(-\eta(u-\theta))} \tag{1.2}$$

with gain η and threshold θ. Often, existence and stability of spatially localized solutions of Eq. (1.1) are conducted in the high-gain limit $\eta \to \infty$ such that f becomes the Heaviside function [6,9]

$$f(u-\theta) = \Theta(u-\theta) = \begin{cases} 0 & \text{if } u < \theta \\ 1 & \text{if } u > \theta. \end{cases} \tag{1.3}$$

It is then possible to establish existence of pulse solutions by explicit construction and to determine local stability in terms of an associated Evans function. The latter is obtained by linearizing the neural field equations about the pulse solution [10]. In the case of stationary pulses or bumps, local stability reduces to the problem of calculating the effects of perturbations at the bump boundary where $u(x) = \theta$.

Eq. (1.1) was first analyzed in detail by Amari [6], who showed that in the case of a Heaviside nonlinearity and a homogeneous input I the network can support a stable stationary bump solution

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doi:10.1016/j.physd.2010.02.016

when the weight distribution $w(x)$ is given by a so-called Mexican hat function with the following properties: $w(x) > 0$ for $x \in [0, x_0)$ with $w(x_0) = 0$; $w(x) < 0$ for $x \in (x_0, \infty)$; $w(x)$ is decreasing on $[0, x_0]$; $w(x)$ has a unique minimum on $\mathbb{R}^+$ at $x = x_1$ with $x_1 > x_0$ and $w(x)$ strictly increasing on (x_1, ∞). On the other hand, in the case of a purely excitatory network with $w(x)$ a positive, monotonically decreasing function, any bump solution is unstable and tends to break up into a pair of counterpropagating fronts. Following Amari's original analysis, the study of bumps in neural fields has been extended to multiple bump solutions in networks with oscillatory weight functions [11,12], two-dimensional bumps [13,12,14–16], and weakly interacting bumps [17]. There has also been some progress in studying the existence of bumps in scalar neural fields when the firing rate function is continuous in both infinite [18,19] and compact spatial domains [20].

One limitation of the scalar neural field model given by Eq. (1.1) is that it cannot support traveling pulses nor spatially structured oscillations when inhibition is blocked, which is inconsistent with a variety of *in vitro* experimental studies of disinhibited slice preparations [21]. These more complex forms of spatiotemporal dynamics can occur, however, when some of form of local negative feedback is included [22–27]. Pinto and Ermentrout proposed a neural field model with linear negative feedback that is analogous to the recovery variable in the Fitzhugh–Nagumo equation [22,19]. The existence and stability of stationary bumps can then be studied using a straightforward extension of the Amari analysis, since the bump solution is smooth in a neighborhood of the threshold crossing points. However, the analysis of bump stability is more complicated in the case of nonlinear forms of negative feedback such as synaptic depression [26] and spike frequency adaptation [23,25]. In these models, the amplitude of the feedback depends on the firing rate so if the latter is taken to be a Heaviside function, then the resulting dynamical system becomes piecewise smooth. In particular, it is no longer possible to determine stability by directly linearizing the neural field equations about a bump solution. Previous studies have thus constructed an Evans function for bump stability by linearizing the neural field equations with a smooth sigmoid (1.2) and then taking the high-gain limit [23,25,26]. However, the size of perturbations for which the linear theory remains valid vanishes in the high-gain limit, so that the Evans function approach does not fully capture the piecewise nature of the dynamics. Indeed, it is well known from the theory of piecewise smooth ordinary differential equations that fixed point solutions can abruptly appear or disappear, and the stability of a fixed point often depends on the properties of a piecewise linear operator [28].

In this paper, we follow a different approach to analyzing bump stability, in which the piecewise smooth nature of the dynamics in the high-gain limit is explicitly taken into account. It turns out that the way in which the piecewise smooth dynamics affects bump stability is strongly model dependent. In order to illustrate this, we study the linear stability of bumps in two different neural networks with piecewise smooth local negative feedback. In Section 2, bumps in a network with synaptic depression are examined. We first demonstrate that an Evans function approach is singular in the high-gain limit and underestimates the ability of synaptic depression to destabilize a bump. We then show how the linear stability of a bump can be analyzed in terms of solutions to a system of pseudo-linear equations, and use this to derive sufficient conditions for the instability of a bump. In the particular case of a network with a Mexican hat weight distribution, we show that sufficiently strong synaptic depression destabilizes a bump that is stable in the absence of depression. In Section 3, we study bumps in a network with spike frequency adaptation, which appears as a dynamic threshold in the firing rate function f. As with the network with depression, an Evans function approach breaks down in the high-gain limit, and we must resort to specifically addressing piecewise smoothness in stability calculations. In this case, we show that for a wide class of infinitesimal perturbations the activity and adaptation variables decouple in the linear regime, such that stability with respect to these perturbations can be determined using a straightforward modification of the standard Amari spectral equation [6]. We find that, in contrast to the stability analysis based on the high-gain limit of an Evans function [23,25], all bumps in the network are unstable, regardless of the strength of adaptation.

2. Neural network with synaptic depression

In this section, we analyze the existence and local stability of stationary bumps in a one-dimensional neural field model with synaptic depression. Synaptic depression is the process by which presynaptic resources such as chemical neurotransmitter or synaptic vesicles are depleted [29]. It can be incorporated into the scalar neural field model [6] by introducing a dynamic prefactor q in the nonlocal term according to [26,27]

$$\tau \frac{\partial u(x,t)}{\partial t} = -u(x,t) + \int_{-\infty}^{\infty} q(x',t) w(x-x') f(u(x',t)-\theta) \mathrm{d}x', \tag{2.1a}$$

$$\frac{\partial q(x,t)}{\partial t} = \frac{1-q(x,t)}{\alpha} - \beta q(x,t) f(u(x,t)-\theta). \tag{2.1b}$$

The factor $q(x,t)$ can be interpreted as a measure of the fraction of available presynaptic resources, which are depleted at a rate βf [30,31], and are recovered on a timescale specified by the constant α (experimentally shown to be 200–800 ms [32,33,30]). If we assume that the strength of a synapse is reduced by a factor $\eta = 0.05 - 0.9$ of its maximal value in response to a sustained input of rate $f = 1$ [32], then a simple steady-state calculation shows that $\beta \approx (1-\eta)/(\eta\alpha) \approx 0.0001 - 0.1\ (\text{ms})^{-1}$ for the given range of values of α. If we take $f = \Theta$ then the dynamics becomes piecewise smooth due to the presence of the Heaviside function Θ in the dynamical equation for the depression variable $q(x,t)$. In the following we set the time constant $\tau = 1$ which sets the unit of time to be of the order 10 ms.

2.1. Existence of bumps

On setting $f = \Theta$, a stationary solution $(U(x), Q(x))$ of Eq. (2.1) satisfies the pair of equations

$$U(x) = \int_{-\infty}^{\infty} Q(x') w(x-x') \Theta(U(x')-\theta) \mathrm{d}x', \tag{2.2}$$

$$Q(x) = 1 - \frac{\alpha\beta}{1+\alpha\beta} \Theta(U(x)-\theta). \tag{2.3}$$

Let $R[U] = \{x | U(x) > \theta\}$ be the region over which the field is excited or superthreshold. Exploiting the fact that any solution can be arbitrarily translated along the x-axis, we define a stationary bump solution of half-width a to be one for which $R[U] = (-a, a)$. Substituting Eq. (2.3) into (2.2) then yields

$$\begin{aligned} U(x) &= \frac{1}{1+\alpha\beta}[W(x+a) - W(x-a)], \\ W(x) &= \int_0^x w(y)\mathrm{d}y. \end{aligned} \tag{2.4}$$

As a simple example, we take a Mexican hat weight distribution given by the function

$$w(x) = (1-|x|)\mathrm{e}^{-|x|}, \tag{2.5}$$

which models short-range excitation and long-range inhibition as a function of distance in the connections between neural populations. Substituting the weight function (2.5) into the steady