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Multi-bump solutions in a neural field model with external inputs

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HIGHLIGHTS

- Stable N-bump solutions in a field with N localized inputs are analyzed.
- Conditions for the shape of the input distribution ensure the existence.
- The effect of spatial interactions in a continuous attractor network is discussed.
- For a given finite field interval, the maximum number of bumps can be determined.
- The results are discussed in terms of a precise spatial memory mechanism.

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ABSTRACT

We study the conditions for the formation of multiple regions of high activity or "bumps" in a one-dimensional, homogeneous neural field with localized inputs. Stable multi-bump solutions of the integro-differential equation have been proposed as a model of a neural population representation of remembered external stimuli. We apply a class of oscillatory coupling functions and first derive criteria to the input width and distance, which relate to the synaptic couplings that guarantee the existence and stability of one and two regions of high activity. These input-induced patterns are attracted by the corresponding stable one-bump and two-bump solutions when the input is removed. We then extend our analytical and numerical investigation to N-bump solutions showing that the constraints on the input shape derived for the two-bump case can be exploited to generate a memory of $N > 2$ localized inputs. We discuss the pattern formation process when either the conditions on the input shape are violated or when the spatial ranges of the excitatory and inhibitory connections are changed. An important aspect for applications is that the theoretical findings allow us to determine for a given coupling function the maximum number of localized inputs that can be stored in a given finite interval.

1. Introduction

In recent years, the analysis of pattern formation in neural field models of cortical tissue has been a very active area of research in the emerging field of mathematical neuroscience (for reviews see [1,2]). These models take the form of nonlinear integro-differential equations on a spatially extended domain. Their dynamics is known to support a large variety of coherent structures observed in neural population activity including stationary "bumps" of localized excitation, as well as spatial or spatiotemporal oscillation patterns, and traveling waves. The mathematical analysis of field models has provided new insight into the conditions of excitatory and inhibitory interactions within neural populations, which ensure the existence and stability of these patterns. In a complementary line of research, bump attractors of neural population dynamics have been applied as models of cognitive processes such as visual attention, motor planning, decision making and working memory in biological and artificial agents ([3–10]; for reviews see [11,12]). In these applications, the neural fields are defined over continuous metric dimensions such as movement direction, retinal position, color or tone pitch. Due to the assumed translation invariance of neural interactions, the field supports a spatial continuum of persistent localized activity patterns known as a "continuous attractor" [13]. Transient input from external sensors representing information about a specific value along the coded dimension defines the field location where a self-stabilized bump evolves. While the peak position may serve a memory function in the case of a single cue, the situation is more complex when two or more localized stimuli are applied simultaneously.

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Since bumps are neutrally stable to perturbations in their position [14,13], the spatial interactions between several bumps in the field mediated by the recurrent architecture of the local network may lead to changes in their position. These interactions may thus result in a stationary pattern for which the number and positions of peaks do not match the number and locations of the external stimuli. As was previously qualitatively discussed by Amari [14] for the case of a connection function of "Mexican-hat" type (i.e., local excitation and surround inhibition), depending on the precise shape of the spatial couplings two input-induced local excitations separated by a certain distance may repel or attract each other. In the case of attraction, the two regions of excitation may eventually combine into a single bump at an intermediate position between the stimulated sites. While this behavior can be exploited to model for instance experimental findings in certain oculomotor decision tasks [8], it is obviously inadequate for the representation of a short-term maintenance of the two inputs (but see [15] for behavioral evidence of an attraction effect of neighboring items in working memory). In applications requiring the storage of a series of distinct cues with high precision [10,16], the impact of the mutual interactions between input-induced local excitations on the evolving memory representation should be minimal. Furthermore, since a single localized input may activate more than one bump, depending on its width, it is not only the relative position of the individual inputs that matters, but also their very size.

The main goal of the present study is to extend previous formal arguments for the existence and stability of multi-bump solutions in spatially homogeneous fields without external stimuli [17,18] to the case of a field dynamics in the presence of one or more localized inputs. More specifically, we establish conditions for the width and relative distance of the external stimuli, in terms of the coupling function, in order to ensure a precise multi-item memory representation in a continuous attractor network. The rigorous analysis allows us to better understand the pattern formation process when the conditions on the shape of the input distribution are violated. In particular, we study, both analytically and in numerical simulations, how changes in the spatial ranges of the excitatory and inhibitory couplings (e.g., during development and learning [15,7]) affect the field response to a given input distribution.

We investigate a particular formulation of a dynamic field first introduced and analyzed by Amari [14] and subsequently used in many applications [12,11]:

$$\frac{\partial u(x,t)}{\partial t} = -u(x,t) + \int_{-\infty}^{\infty} w(x-y) f\left(u(y,t)\right) dy - h + S(x,t). \tag{1}$$

Here, $u(x,t)$ represents the average level of activity (e.g., voltage) of a neuron at spatial position x and time t along a one-dimensional infinite domain. The nonlinear function $f(u)$ defines the firing rate of a neuron with activity u. The function $w(x)$ describes the coupling strength with neighboring neurons y, which is assumed to depend on the distance only, that is, $w(x|y) = w(x-y)$. The term $S(x,t)$ represents a transient external input with a spatial structure, whereas $-h < 0$ denotes a constant inhibitory input applied uniformly to the entire field. This global inhibition defines a homogeneous "resting" state for a neural field with $S(x) = 0\, \forall x$.

For the special choice of a Heaviside firing function and synaptic couplings of Mexican-hat type, Amari fully analyzed the existence and stability properties of a single-bump stationary solution of Eq. (1) with a unimodal and symmetric input distribution [14,19]. Since a stable bump co-exists with the stable resting state, a sufficiently strong transient input may switch between the two states, thus implementing a memory function. However, analytical and numerical studies have shown that a coupling function of Mexican-hat shape, which changes sign exactly once in the interval $(0,\infty)$, does not generally support a stable pattern of two or more regions of high excitation ([18], but see the discussion in [20,21] for large distances between bumps). In the present study we therefore apply a class of oscillatory coupling functions, previously introduced by Laing and colleagues [17], with an infinite number of positive zeros in $(0,\infty)$. The authors showed numerical evidence for the existence of multiple stable bumps in a homogeneous field without external input.

The paper is organized as follows: in Section 2 we review relevant results of previous studies on the existence and stability of one-bump and two-bump solutions and provide a detailed mathematical description of the model assumptions. In Section 3, we generalize Amari's analysis of a single bump in the presence of a localized input; for the class of oscillatory coupling functions, we determine conditions for the shape of the input $S(x)$ as well as for the global inhibition h, which guarantees the evolution of a stable region of local excitation. In Section 4, we extend the analysis for a specific value of h to the case of two-bump solutions of Eq. (1) with a bimodal, symmetric input. Based on the insight obtained from the analysis of the two-bump activation patterns, Section 5 presents analytical and numerical work on the existence and stability of input-induced N-bump solutions for $N \geq 2$. A brief summary of our results, as well as an outlook on future research, is presented in Section 6. In order to allow readers from applied areas to focus on the main findings, we present the mathematical proof of all theorems stated in the main text in Appendix A. The scheme for the numerical integration of Eq. (1) used in the simulations of the field model with external input is presented in Appendix B.

2. Model details and problem statement

We study the existence and the stability of steady state solutions of (1), i.e. solutions defined by

$$u(x) = \int_{-\infty}^{\infty} w(x-y) f\left(u(y,t)\right) dy - h + S(x). \tag{2}$$

In order to simplify the mathematical treatment of single-bump solutions, Amari chose the Heaviside activation function

$$f(u) = H_0(u) = \begin{cases} 0, & u \leq 0 \\ 1, & u > 0, \end{cases} \tag{3}$$

instead of a continuous function of sigmoidal shape. The main advantage is that the dynamics of a local excitation pattern can be understood by analyzing the much simpler motion equations of its boundaries. For the lateral connections between neurons, Amari used a coupling function $w(x)$ in which excitation dominates over smaller distances and inhibition over larger ones. Such a connectivity of "lateral inhibition" type satisfies the following properties:

(H_1) $w(x)$ is symmetric, i.e., $w(-x) = w(x)$ for all $x \in \mathbb{R}$.
(H_2) w is both continuous and integrable on $\mathbb{R}$.
(H_3) $w(x) > 0$ on an interval $(0,\bar{x})$, $w(x) < 0$ on $(\bar{x},\infty)$ and $w(\bar{x}) = 0$.
(H_4) $w(x)$ is decreasing on $(0,\bar{x}]$.

A concrete example of a coupling function satisfying (H_1)–(H_4) is a "Mexican-hat" function given by

$$w(x) = Me^{-m|x|} - Ne^{-n|x|}, \tag{4}$$

where $M > N > 0$ and $m > n > 0$ (Fig. 1, left).

Motivated by neuron labeling studies showing that the spatial coupling between groups of neurons in the prefrontal cortex forms approximate periodic stripes [22], Laing and colleagues [17,18]