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Traveling Bumps and Their Collisions in a Two-Dimensional Neural Field

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A neural field is a continuous version of a neural network model accounting for dynamical pattern forming from populational firing activities in neural tissues. These patterns include standing bumps, moving bumps, traveling waves, target waves, breathers, and spiral waves, many of them observed in various brain areas. They can be categorized into two types: a wave-like activity spreading over the field and a particle-like localized activity. We show through numerical experiments that localized traveling excitation patterns (traveling bumps), which behave like particles, exist in a two-dimensional neural field with excitation and inhibition mechanisms. The traveling bumps do not require any geometric restriction (boundary) to prevent them from propagating away, a fact that might shed light on how neurons in the brain are functionally organized. Collisions of traveling bumps exhibit rich phenomena; they might reveal the manner of information processing in the cortex and be useful in various applications. The trajectories of traveling bumps can be controlled by external inputs.

1 Introduction

A neural field model is a continuous version of a neural network model describing the spatiotemporal patterns of populational neuronal firing activities. Classical studies include Wiener and Rosenblueth (1946) and Farley and Clark (1961). Its modern version was first proposed by Wilson and Cowan (1973), and mathematical studies were done by Amari (1977) and Kishimoto and Amari (1979). Since then, a large number of studies have been conducted on the dynamics of excitation in neural fields (see Ermentrout, 1998; Doubrovinski & Herrmann, 2009; Coombes, 2005, for reviews), in particular, on phenomenology, including sets of standing bumps (Amari, 1977; Laing, Troy, Gutkin, & Ermentrout, 2002), moving bumps (Zhang, 1996; Fung, Wong, & Wu, 2010), traveling waves, and wave fronts (Amari, 1977; Ermentrout & McLeod, 1993; Pinto & Ermentrout, 2001), spiral waves (Huang et al., 2004; Laing, 2005) and breathers (Folias & Bressloff, 2004, 2005), and on applications including traveling waves in brain slices (Richardson, Schiff, & Gluckman, 2005), working memory (Laing et al., 2002), head direction cells (Zhang, 1996), visual hallucinations (Ermentrout & Cowan, 1979), motion perception (Giese, 1998), robotic control (Erlhagen & Bicho, 2006), movement preparation (Erlhagen & Schöner, 2002), and population coding (Wu, Amari, & Nakahara, 2002).

There are two different types of activity in neural field models. One is wavelike, spreading over the entire field and including repetitive wave patterns, traveling waves, spiral and breathing waves, and self-reproducing radial waves. This type is observed in many situations, including epilepsy and hallucinations. The other is a localized excitation behaving like a particle. It is assumed in working memory theory that such particle-like activities are used as excitations (standing bumps) to keep a memory of outside stimuli as a persistent excitation of local positions. When the field sustains a stable moving particle represented in the form of a localized region of excitation, we may call this excitation a traveling bump.

As particle-like patterns, traveling bumps or localized traveling waves deserve investigation since they are observed as spatiotemporal patterns of populational neuronal firing activities in many brain areas (Delaney et al., 1994; Ermentrout & Kleinfield, 2001; Prechtl, Cohen, Mitra, Pesaran, & Kleinfeld, 1997; Wu, Guan, & Tsau, 1999; Wu, Huang, & Zhang, 2008). Amari (1977) proved the existence of a traveling wave in a 1D field consisting of layers of excitatory neurons and inhibitory neurons. Pinto and Ermentrout (2001) modified Amari's model, using only one spatial convolution term. The model fits the traveling waves measured in brain slices in their experiments. They obtained a traveling wave solution to their model by using perturbation methods. They also showed that the velocity of the traveling waves is a decreasing function of the firing threshold (a constant in their model). Later, this prediction was confirmed in experiments on neocortex slices (Richardson et al., 2005). Thus, the neural field model provides a possible answer to the question: How do traveling waves emerge in a neural network?

However, although Amari (1977) and Pinto and Ermentrout (2001) were mostly done in one dimension (1D), neurons are believed to be distributed in at least two dimensions (2D). Therefore, it is desirable to extend the range of study from 1D to 2D to find more interesting dynamical phenomena and richer applications. So far, target waves (Huang et al., 2004, Folias & Bressloff, 2004), spiral waves (Huang et al., 2004; Laing, 2005), and breathers (Folias & Bressloff, 2004, 2005) have been found in the 2D Pinto and Ermentrout (2001) model. In this study, we show the existence of multiple stable traveling bumps, their collisions, and their trajectory control in the 2D Pinto and Ermentrout (2001) model.

2 2D Neural Field

Let $\mathbf{x} = (x, y)$ be the coordinates of a 2D field and $u(\mathbf{x}, t)$ and $v(\mathbf{x}, t)$ be excitatory and inhibitory variables at position $\mathbf{x}$. The activation-inhibition mechanism is described as

$$\frac{\partial u(\mathbf{x}, t)}{\partial t} = L_{uu}\left[u(\mathbf{x}, t)\right] + L_{uv}\left[v(\mathbf{x}, t)\right] \tag{2.1}$$

$$\frac{\partial v(\mathbf{x}, t)}{\partial t} = L_{vu}\left[u(\mathbf{x}, t)\right] + L_{vv}\left[v(\mathbf{x}, t)\right], \tag{2.2}$$

where L_{uu}, L_{uv}, L_{vu}, and L_{vv} are operators representing interactions of the field variables. The reaction-diffusion equation uses the linear Laplacian diffusion mechanism for spatial interactions, together with pointwise nonlinear interactions, whereas the equation of a neural field uses nonlocal interactions due to the synaptic connections of neurons, represented by a spatial convolution of the type

$$L_{uu}\left[u(\mathbf{x}, t)\right] = \int w\left(\mathbf{x} - \mathbf{x}'\right) f\left[u\left(\mathbf{x}', t\right)\right] d\mathbf{x}', \tag{2.3}$$

where f is a nonlinear function.

The typical equations for a 2D neural field are as follows:

$$\begin{aligned} \frac{\partial u(\mathbf{x}, t)}{\partial t} = & \int w_1\left(\mathbf{x} - \mathbf{x}'\right) f_1\left[u\left(\mathbf{x}', t\right) - h_1\right] d\mathbf{x}' \\ & - \int w_2\left(\mathbf{x} - \mathbf{x}'\right) f_2\left[v\left(\mathbf{x}', t\right) - h_2\right] d\mathbf{x}' \\ & - u(\mathbf{x}, t) + I_u(\mathbf{x}, t), \end{aligned} \tag{2.4}$$

$$\begin{aligned} \frac{\partial v(\mathbf{x}, t)}{\partial t} = & \int w_3\left(\mathbf{x} - \mathbf{x}'\right) f_3\left[u\left(\mathbf{x}', t\right) - h_3\right] d\mathbf{x}' \\ & - \int w_4\left(\mathbf{x} - \mathbf{x}'\right) f_4\left[v\left(\mathbf{x}', t\right) - h_4\right] d\mathbf{x}' \\ & - v(\mathbf{x}, t) + I_v(\mathbf{x}, t). \end{aligned} \tag{2.5}$$

Here, $u(\mathbf{x}, t)$ and $v(\mathbf{x}, t)$ are the firing rates of excitatory and inhibitory neurons, respectively, at position $\mathbf{x}$ and time t. The convolutive functions $w_1(\mathbf{x} - \mathbf{x}'), \ldots, w_4(\mathbf{x} - \mathbf{x}')$ represent the synaptic efficacies from position $\mathbf{x}'$ to $\mathbf{x}$. The functions $f_1, \ldots, f_4$ denote the activation functions of neurons. They are activated by $u(\mathbf{x}, t)$ and in turn inhibited by $v(\mathbf{x}, t)$. $I_u(\mathbf{x}, t)$ and $I_v(\mathbf{x}, t)$ are inputs from the outside. We shall study the dynamical behaviors of a homogeneous neural field where $I_u(\mathbf{x}, t)$ and $I_v(\mathbf{x}, t)$ are constants I, in particular, $I = 0$. Nonconstant $I_u(\mathbf{x}, t)$ and $I_v(\mathbf{x}, t)$ will be used for setting the initial conditions and also for controlling the trajectory of bump solutions.

The activation functions are sigmoidal functions or Heaviside functions satisfying

$$0 \leq f_i(u) \leq 1, \quad \text{for } i = 1, 2, 3, 4, \tag{2.6}$$

and the synaptic efficacy functions $w_i(\mathbf{x}) \geq 0$ are radial symmetric, that is, $w_i(\mathbf{x})$ are functions of $\|\mathbf{x}\|$, for $i = 1, 2, 3, 4$. Hence, the 2D neural field is homogeneous and isotropic (rotationally invariant).

We shall show dynamical behaviors existing in a specific simple field (Pinto & Ermentrout, 2001). Note that it is plausible that such phenomena are common to other neural field models of nonlocal excitation and inhibition (adaptation) mechanisms.

The neural field model can be regarded as a special case of the field equation with excitation and inhibition mechanisms, similar to the standard reaction-diffusion equation. Hence, the neural field and reaction-diffusion models share lots of common dynamical characteristics in stationary and moving patterns (Vanag & Epstein, 2007). While the reaction-diffusion equation is restricted within local interactions due to diffusion, the neural field model has a spatially wide range of interactions (i.e., nonlocal interactions) that exhibits richer dynamical phenomena. Our study shows traveling bumps and their collisions, and we hope that it presents a new direction of research for 2D neural field models. (Also see Nishiura, Teramoto, & Ueda, 2003, 2005, 2007, and Ei, Mimura, & Nagayama, 2006, for the various collision and scattering phenomena of traveling spots in the reaction-diffusion equation with three components.)

3 Dynamical Phenomena of Traveling Bumps in a 2D Neural Field

We use the following simple equations comprising a two-dimensional extension of the model given by Pinto and Ermentrout (2001), Folias and Bressloff (2004, 2005), Huang et al. (2004), Laing (2005), and

Richardson et al. (2005):

$$\frac{\partial u(\mathbf{x},t)}{\partial t} = -u(\mathbf{x},t) + \int w\left(\mathbf{x}-\mathbf{x}'\right) f\left[u\left(\mathbf{x}',t\right) - h\right] d\mathbf{x}' \\ -v(\mathbf{x},t) + I_u(\mathbf{x},t), \tag{3.1}$$

$$\frac{\partial v(\mathbf{x},t)}{\partial t} = \alpha u(\mathbf{x},t) - \beta v(\mathbf{x},t) + I_v(\mathbf{x},t). \tag{3.2}$$

The parameters are:

$$\alpha = 0.6, \quad \beta = 0.8/3, \quad h = 3.0,$$
$$w(x,y) = 7.32e^{-\frac{x^2+y^2}{2}}, \quad f[u] = \frac{1}{1+e^{-2(u-4)}}. \tag{3.3}$$

For the numerical experiments for figure exhibition, we discretized the model (see equations 3.1 and 3.2) into a 200×200 grid with cyclic boundary conditions, using the fourth-order Runge-Kutta method in Matlab. The spatial resolution was 0.1, and the time step unit was 0.1.

3.1 Stable Traveling Bump. Our numerical experiments suggest that the field can be tristable, admitting the quiescent state, a stable traveling bump (see Figure 1), and a traveling band solution growing to infinite length. We set the initial excitation region with a length l, which is a natural stimulus such as excitatory stimuli around a position and inhibitory stimuli at a slightly different positions. The stimuli are not symmetric enough to generate a traveling bump. When l is too large, the bump converges to the traveling band solution obtained with the corresponding 1D model. When l is close to the characteristic scale l_0, it converges to a traveling bump with a fixed shape. When l is too small, the bump shrinks and disappears, converging to a quiescent state (see Figure 2). In the parameter region around $h \sim 3.0$, starting with a fixed initial excitation region with a length $l = l_0 \sim 9$ (90 grids in the numerical simulation with spatial resolution 0.1), traveling bumps occur. Furthermore, with the initial condition $l = l_0$ in this parameter region, the traveling bump is locally stable; that is, it resists small perturbations. By adding large perturbations, it converges to either the traveling band solution or the quiescent state, implying that the field is tristable.

A traveling bump has a crescent shape. The curvature of the excited region is positive in the front area and negative in the rear area. Such a crescent shape is typically observed in, for example, chemical reactions (Schenk, Or-Guil, Bode, & Purwins, 1997; Vanag & Epstein, 2007), patterns of seashells (Meinhardt & Klinger, 1987), and barchans in sand dune (Schwammle & Herrmann, 2003), caused by symmetry breaking by forward motion. The

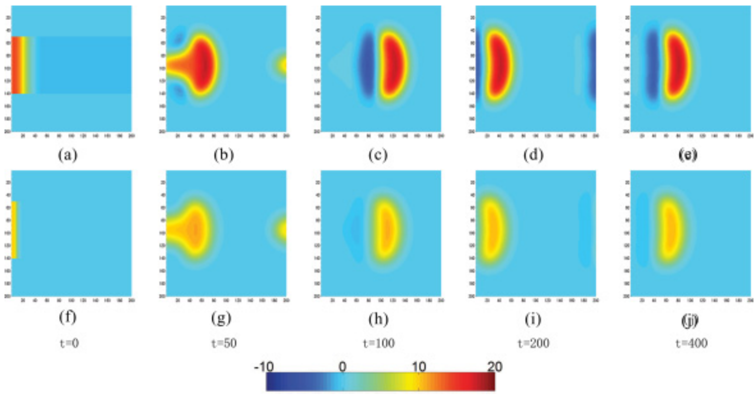

Figure 1: (a–e) Stable traveling bump of u. (f–j) Stable traveling bump of v. Color denotes the value of $u(x, y, t)$ and $v(x, y, t)$. The initial excitation region was $l = l_0$ (90 grid points in the numerical simulations). The boundary condition is cyclic, and the entire space is on a torus.

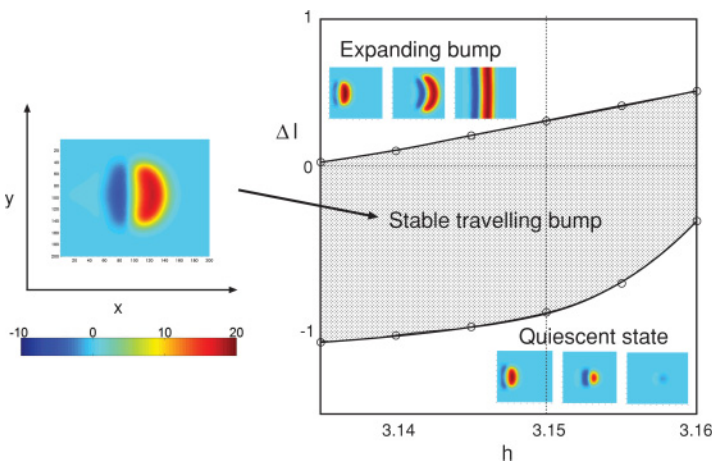

Figure 2: Stable traveling bump and phase diagram.(Left) x and y are the coordinates of the field of $u(x, y, t)$. A snapshot of a stable traveling bump at the time step $t = 100$ is depicted. Color denotes the value of $u(x, y, t)$. (Right) The horizontal axis is the threshold parameter h, and the vertical axis is perturbation to the bump shape given by the initial condition of length l. The traveling bumps occur in the parameter region around $h \sim 3.0$, starting with a fixed initial excitation region with length $l = l_0 \sim 9$. To check the stability of a traveling bump, we uniformly add a positive and negative perturbation to u with size Δl. When Δl is a large, positive number, the bump grows into the band solution, and when it is a large, negative number, it disappears into the quiescent state, implying that the field is tristable.

origin of the shape and the length scale in our case may be analyzed better by comparing the local structure in 1D neural field model with excitatory coupling (Drover & Ermentrout, 2003).

In the 2D two-component reaction-diffusion equation, the existence of spatially localized traveling objects has not been reported with more than local operators (Vanag & Epstein, 2007). It is known that global operators added to two-component systems may induce a single stable traveling bump but not induce multiple solutions (Schenk et al., 1997), while many three-component systems with local operators show multiple traveling bumps. Here, we show an example of multiple stable traveling bumps in a 2D neural field model. It is a two-component system with nonlocal operators. In our case, the spatial convolution term plays the role of the third component to stabilize the bump, and nonlocal interaction supports multiple solutions. Exact nonlinear analysis will be done elsewhere.

3.2 Collisions of Traveling Bumps. A number of traveling bumps may coexist in a field, and they strongly interact when they are close. The typical interaction is a collision. When two bumps collide, they fuse into a single bump. The resulting bump converges to one of the tristable states depending on the collision angle (see Figure 3). We found no standing objects other than the traveling bumps in the parameter settings (see equation 3.3) so that even with complex collisions, the resulting output is thought to be only one of the following: (a) quiescent state, (a) stable traveling bump, or (a) growing band solution.

Eight other types of collisions are collected in Figure 4, showing patterns before, in, and after collisions. For collisions of three or more bumps, the temporal sequence of the collision is vital to the subsequent behavior. For example, types d and g are collisions of two horizontal traveling bumps coming toward each other and a vertical traveling bump coming toward them. Depending on the timing of the vertical traveling bump's arrival, different behaviors occur after the collision. Types g and h are collisions of three horizontal traveling bumps. Two traveling bumps collide before the arrival of the third one. In type g, the field eventually converges to a quiescent state after the collision, whereas in type h, an expanding bump emerges after the collision.

3.3 Control of Traveling Bumps. In obtaining stable traveling bumps, the external inputs I_u and I_v are put equal to 0, which means their dynamical phenomena represent spontaneous neural activities. In this section, we use external inputs to control traveling bumps spatially and temporally. External inputs are also used for setting an initial state. Neural excitations are extinguished by giving a constant negative external input to the whole field.

Figure 5 shows an example of how the trajectory of a traveling bump is altered by inputs I_u and I_v.

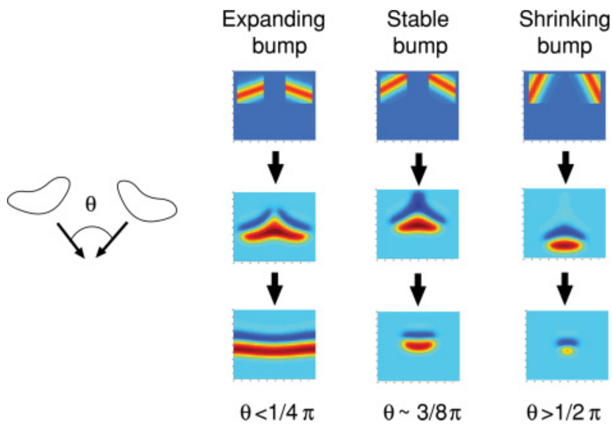

Figure 3: Collision of bumps. When two bumps collide (upper row), they fuse into a single bump (middle row). The parameters are fixed as in equation 3.3. The resulting bump converges to a growing band solution, with a collision angle less than $\frac{1}{4}\pi$, or to a quiescent state, with a collision angle more than $\frac{1}{2}\pi$, or it survives, with a collision angle around $\sim \frac{3}{8}\pi$ (bottom row).

Let us define the center of gravity of a traveling bump $u(\mathbf{x}, t)$ by

$$\mathbf{r}(t) = \frac{1}{M}\int \mathbf{x} f[u(\mathbf{x}, t) - h]\, d\mathbf{x}, \tag{3.4}$$

where

$$M = \int f[u(\mathbf{x}, t) - h]\, d\mathbf{x}. \tag{3.5}$$

When the bump moves stationarily, the velocity $d\mathbf{r}(t)/dt$ is a fixed constant. Assume that a control signal $I_u(\mathbf{x})$ added to the field at time 0, $u(\mathbf{x}, t)$ is altered by $\delta u(\mathbf{x}, t)$ after time δt,

$$\delta u(\mathbf{x}, 0) = I_u(\mathbf{x})\delta t. \tag{3.6}$$

This causes an extra change $\delta\mathbf{r}$ to the center of gravity of the traveling bump, which can be written in the form

$$\delta\mathbf{r} = \delta t \int k(\mathbf{x}) I_u(\mathbf{x})\, d\mathbf{x}. \tag{3.7}$$

The function $k(\mathbf{x})$ is the influence function of external stimuli, and it shows the influence of a unit stimulus added at $\mathbf{x}$ on the center of gravity.

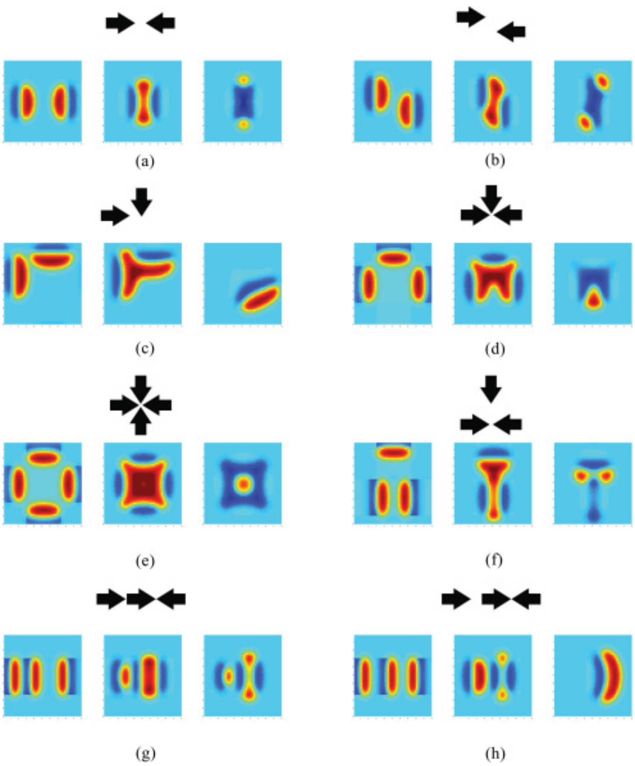

Figure 4: Collision types (a–h) Patterns before, in, and after collision. The parameters are fixed as in equation 3.3. Types d and g are collisions of two horizontal traveling bumps coming toward each other and a vertical traveling bump coming toward them. Types g and h are collisions of three horizontal traveling bumps. In type g, the field eventually converges to a quiescent state after the collision, whereas in type h, an expanding bump emerges after the collision.

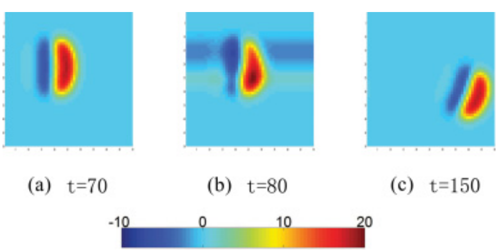

Figure 5: Control of a stable traveling bump. The parameters are fixed as in equation 3.3. External perturbations are added to u, v at the time step72.

The influence curve is calculated from the subsequent variation due to δu:

$$\delta \mathbf{r} = \delta \left[\frac{\mathbf{x} f(u-h)\, d\mathbf{x}}{M(u)} \right] \tag{3.8}$$

$$= \frac{1}{M} \int \mathbf{x} f'[u(\mathbf{x}) - h] \delta u \, d\mathbf{x} - \frac{1}{M^2} \int \mathbf{x} f[u(\mathbf{x}) - h] \, d\mathbf{x} \delta M \tag{3.9}$$

$$= \frac{\delta t}{M} \int (\mathbf{x} - \mathbf{r}) f' [u(\mathbf{x}) - h] \, I_u(\mathbf{x}) \, d\mathbf{x}. \tag{3.10}$$

Hence, the influence curve is

$$k(\mathbf{x}) = \frac{1}{M} (\mathbf{x} - \mathbf{r}) f' [u(\mathbf{x}) - h], \tag{3.11}$$

which shows that the influence is large at the positions $\mathbf{x}$ where f' is large.

Now let us consider $I_u(\mathbf{x}) = I = \text{const}$ as a special case. Imagine a bump moving in the x-direction. Then new application of I causes a change of the center of gravity by δs in the x-direction. This is calculated as

$$\delta s = \delta t \frac{I}{M} \int x f'[u(x) - h] \, dx \tag{3.12}$$

$$= -\delta t \frac{I}{M} \int f[u(x) - h] \, dx \tag{3.13}$$

$$= -\delta t I. \tag{3.14}$$

This shows that the velocity s of the bump changes as a result of this perturbation by the above equation.

4 Discussion

In addition to standing bumps, moving bumps, spiral waves, breathers, and target waves, this study has found a new pattern, called a traveling bump, in a 2D neural field. In our numerical experiments, it seems that standing bumps do not exist in the model and target waves do not coexist with traveling bumps within the same parameters set. Whether it is possible to use external inputs to switch from one solution to another, say, from traveling bumps to spiral waves, is not known. More mathematical analysis of traveling bumps and their controls will have to be conducted to determine an answer.

Apart from the model we used, there are three other similar neural field models with excitation-inhibition mechanisms:

- Excitatory neurons and inhibitory neurons (Amari, 1977):

$$\frac{\partial u(\mathbf{x},t)}{\partial t} = -u(\mathbf{x},t) + \int w_1(\mathbf{x}-\mathbf{x}') f[u(\mathbf{x}',t)-h_1]\,d\mathbf{x}' - \int w_2(\mathbf{x}-\mathbf{x}') f[v(\mathbf{x}',t)-h_2]\,d\mathbf{x}' \tag{4.1}$$

$$\frac{\partial v(\mathbf{x},t)}{\partial t} = -\alpha v(\mathbf{x},t) + \beta f[u(\mathbf{x}',t)-h_3] \tag{4.2}$$

- Excitatory neurons with adaptive synapses (Kilpatrick & Bressloff, 2010):

$$\frac{\partial u(\mathbf{x},t)}{\partial t} = -u(\mathbf{x},t) + \int w(\mathbf{x}-\mathbf{x}') v(\mathbf{x}',t) f[u(\mathbf{x}',t)-h_1]\,d\mathbf{x}' \tag{4.3}$$

$$\frac{\partial v(\mathbf{x},t)}{\partial t} = -\alpha v(\mathbf{x},t) - \beta v(\mathbf{x},t) f[u(\mathbf{x},t)-h_2] + \gamma \tag{4.4}$$

- Excitatory neurons with an adaptive threshold (Coombes & Owen, 2005)

$$\frac{\partial u(\mathbf{x},t)}{\partial t} = -u(\mathbf{x},t) + \int w(\mathbf{x}-\mathbf{x}') f[u(\mathbf{x}',t)-v(\mathbf{x}',t)]\,d\mathbf{x}' \tag{4.5}$$

$$\frac{\partial v(\mathbf{x},t)}{\partial t} = -\alpha v(\mathbf{x},t) + \beta f[u(\mathbf{x},t)-h] + \gamma \tag{4.6}$$

If we use $\beta u(\mathbf{x},t)$ instead of $\beta f[u(\mathbf{x},t)-\theta_0]$ in equation 4.5, model 3 is equivalent to the Pinto and Ermentrout (2001) model. Whether stable traveling bumps can exist in models 1, 2, and 3 is not known.

Using the parameter set in equation 3.3 for the Pinto and Ermentrout (2001) model, we found the stable traveling bumps. Our work demonstrates the existence of traveling bumps in a 2D neural network consisting of identical neurons. The stability of these localized traveling excitations does not require any geometric restriction or boundary to prevent them from propagating away, and this fact may shed light on how neurons in brain are organized.

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