Localized activity patterns in two-population neuronal networks

Patrick Blomquist*, John Wyller, Gaute T. Einevoll

Department of Mathematical Sciences and Technology, Norwegian University of Life Sciences, P.O. Box 5003, N-1432 Ås, Norway

Received 9 November 2004; received in revised form 26 April 2005; accepted 3 May 2005

Communicated by A. Doelman

Abstract

We investigate a two-population neuronal network model of the Wilson–Cowan type with respect to existence of localized stationary solutions ("bumps") and focus on the situation where two separate bump solutions (one narrow pair and one broad pair) exist. The stability of the bumps is investigated by means of two different approaches: The first generalizes the Amari approach, while the second is based on a direct linearization procedure. A classification scheme for the stability problem is formulated, and it is shown that the two approaches yield the same predictions, except for one notable exception. The narrow pair is generically unstable, while the broad pair is stable for small and moderate values of the relative inhibition time. At a critical relative inhibition time the broad pair is typically converted to stable breathers through a Hopf bifurcation. In our numerical example the broad pulse pair remains stable even when the inhibition time constant is three times longer than the excitation time constant. Thus, our model results do not support the claim that slow excitation mediated by, e.g., NMDA-receptors is needed to allow stable bumps.

© 2005 Elsevier B.V. All rights reserved.

PACS: 87.19.Lu, 89.75.Kd, 02.30.Rz

Keywords: Pattern formation, Integro-differential equations, Short term memory, Neuroscience

1. Introduction

Experimental observations have established persistent neuronal activity in prefrontal cortex as a neural process underlying short-term, working memory (for a review, see Ref. [1]). In particular, localized persistent activity, or "bumps", in cortical networks may serve as memory storage. Numerous modelling studies have examined...
the existence and stability of such bumps, and both firing-rate and spiking-neuron models have been considered [2–27]. An excellent and current review of bumps in neural firing-rate models (as well as waves and other patterns) is provided by Ref. [27].

In an early study Amari [3] proved analytically the existence and stability of such bumps in a simplified rate model of the lateral inhibition (LI) type in one spatial dimension,

\[ u_0(x, t) = -u_0(x, t) + \int_{-\infty}^{\infty} \omega(s - x')P(u(x', t)) \, dx' + h(x, t) \tag{1} \]

Here \( u(x, t) \) denotes the “synaptic input” to a neural element at position \( x \) and time \( t \), and \( u_i(x, t) \) is the corresponding time derivative. The non-negative function \( P(u) \) gives the firing rate of a neuron with input \( u \). The function \( s(x, t) \) represents a variable external input while the parameter \( h \) represents a constant external input applied uniformly to all neurons. The synaptic connectivity function \( \omega(x) \) determines the coupling between the neurons, and in LI networks this typically has a characteristic “Mexican-hat shape”: nearby neurons excite each other (recurring excitation) while more distant neurons inhibit each other (lateral inhibition). For the case where the firing-rate function \( P(u) \) is chosen to be the Heaviside step function, Amari [3] proved the existence of stable bumps in such a LI network; stable bumps are sustained by local recurrent excitation and localized by lateral inhibition.

More recent studies have investigated existence and stability of a variety of bump types in generalized Amari-type models where different synaptic coupling functions \( \omega(x) \) and firing-rate functions \( P(u) \) have been considered [10, 15, 16, 18, 21, 23, 24]. Effects of axo-dendritic synaptic processing have also been studied [16].

In LI-models of the Amari type the spatially extended inhibition models in a simplified way the excitation of and consequent return inhibition from inhibitory interneurons surrounding the excitatory model population. This one-population model for excitatory neurons can be seen to correspond to a two-population model incorporating an additional inhibitory population, in the limit where the inhibitory time constant goes to zero [13]. A crucial question is thus whether bumps found to be stable in “instantaneous-inhibition” Amari models are stable also when models incorporating more realistic inhibitory delays are considered [13].

Recent modelling studies with spiking-neuron networks have focused on requirements for bump stability in the context of working memory. Compte et al. [9] considered a two-population network of leaky integrate-and-fire neurons and found that the recurrent synaptic excitation should primarily be mediated by the slower NMDA-receptors to achieve stability; with the faster AMPA-receptors dominating, the excitation would be too fast compared to the GABA\(_B\)-mediated inhibition and bump stability would be lost (see also discussions in [1, 28]). However, Gutkin et al. [11] found that bump stability could be achieved also with AMPA-receptors when networks based on biologically more realistic neuron models were used.

To study the effects of excitation and inhibition times on bump stability in a rate model, one must go beyond the one-population Amari-type model. Pinto and Ermentrout [13] studied the existence and stability of bumps in the following two-population model:

\[ \dot{u}_e(x, t) = -u_e + \int_{-\infty}^{\infty} \omega_e(s - x')P(u_e(x', t) - \theta) \, dx' - \int_{-\infty}^{\infty} \omega_i(s - x')u_i(x', t) \, dx', \tag{2a} \]

\[ \tau \dot{u}_i(x, t) = -u_i + \int_{-\infty}^{\infty} \omega_i(s - x')P(u_i(x', t) - \theta) \, dx'. \tag{2b} \]

Here \( u_e(x, t) \) and \( u_i(x, t) \) represents the synaptic input to an excitatory and an inhibitory neural element respectively, and \( \theta \) the inhibitory time constant (measured relative to the excitatory time constant). Compared to the analogous two-population model studied by Wilson and Cowan [2] this model (i) neglects a term describing recurrent inhibition (\( s \rightarrow i \)) and (ii) assumes a linear firing-rate function for the inhibitory population. These assumptions allow for a reduction of the two-equation system to a single equation in the mathematical analysis of the existence and stability of bumps. For their model Pinto and Ermentrout found that the inclusion of the more realistic inhibitory dynamics resulted in a loss of stability. They thus concluded that their work did not support the hypothesis that
sustained activity in prefrontal cortex is a result of the dynamics in an LI network (even though it could not be ruled out completely since an attempt to quantify the necessary speed of inhibition to maintain stability was not made).

In the present work we consider the following two-population model,
\[
\begin{align}
\partial_t u_i &= -u_i + \int_{-\infty}^{\infty} a_i(x - x') P_e(u_i(x', t) - \theta_e) dx' - \int_{-\infty}^{\infty} a_i(x - x') P_i(u_i(x', t) - \theta_i) dx', \\
\partial_t v_i &= -v_i + \int_{-\infty}^{\infty} b_i(x - x') P_e(v_i(x', t) - \theta_e) dx' - \int_{-\infty}^{\infty} b_i(x - x') P_i(v_i(x', t) - \theta_i) dx',
\end{align}
\]
where the dynamics of the excitatory and inhibitory populations are modelled in a symmetric way. We limit ourselves to the case where \(P_e\) and \(P_i\) are Heaviside step functions, but allow for different threshold values \(\theta_e\) and \(\theta_i\). This model is analogous to the Wilson–Cowan model [2] where the dynamical variables represent firing rates and not (as here) synaptic inputs. In Wilson and Cowan [2] numerical examples of stable bumps were given, but a systematic study of conditions for the existence and stability of such bumps was not pursued.

We address the same type of questions as in Pinto and Ermentrout [13], i.e., conditions for existence and uniqueness of pairs of spatially symmetric bumps of excitatory and inhibitory neuronal firing for a given set of threshold values. In particular we focus on the stability of such bumps, and how it depends on the dynamics of the inhibitory compared to the excitatory population.

In Section 2, we formulate the model and show that a general feature is that the solutions are bounded. Section 3 is devoted to the study of the existence and uniqueness of stationary symmetric localized pulses, and we prove that such pulses will always exist, i.e., for any choice of synaptic coupling functions \(a_{e,i}(x)\) there will always exist a set of threshold values \((\theta_e, \theta_i)\) which assures a stationary pulse. From the proof, it also follows that by choosing appropriate threshold values one can construct an excitatory pulse accompanied by an arbitrarily narrow inhibitory pulse.

We further investigate the stability of these stationary bumps, using two different approaches: The first approach is based on the formal arguments for stability elaborated by Amari [3] and later used by Pinto and Ermentrout [13]. One identifies each stationary pulse with its width. An autonomous dynamical system, which is consistent with the model equations, for the variation of the width parameters is then derived. The equilibrium point of this system corresponds to the widths of the stationary pulses, and it is conjectured that the stability properties of the pulses can be inferred from the stability properties of the pulse-width equilibrium. The result from this analysis is presented in Section 4. There we find that bumps which are stable for fast inhibition (i.e., not too large \(\tau\)) can lose its stability at a critical value for \(\tau\), \(\tau_c\), through a Hopf bifurcation.

The second approach given in Section 5 is based on a standard linearization procedure with the full set of model equations and the known stationary bumps as a starting point, in a way identical to the technique presented in [13]. Notice that this approach for investigating stability can be generalized to cover the travelling wave stability, using the Evans functions approach elaborated in [19].

The results from the two stability-analysis approaches are compared in Section 6, and it is shown that Amari’s approach and the full stability analysis in most, but not all, cases yield the same result. Moreover, we identify a parameter regime where results from the two stability analyses agree and bump stability is lost through a supercritical Hopf bifurcation with the generation of stable breathers.

For the question of whether bumps can be stable in realistic cortical networks and thus function as a substrate for working memory, the numerical value of \(\tau_c\) is essential. In Section 7 we consider a numerical example where \(\tau_c\) typically is around 3. This means that bumps can be stable even if the inhibitory time constant is three times as large as the excitatory time constant; a requirement that likely can be fulfilled with GABA\(_a\)-mediated inhibition even if the recurrent excitation is mediated by AMPA-receptors [1]. This result appears to differ from the corresponding result for the model studied in [13] where bump stability (in their numerical examples) was lost already for values of \(\tau\) much less than 1. Thus the conclusion regarding the possibility for LI networks to be a substrate for working memory appears to be different for these two models.
The final Section 8 contains a summary and conclusion. In Appendix A we describe the numerical scheme underlying the computations in Section 7, and present some tedious mathematical derivations in Appendix B and C.

2. Model

We generalize the model studied by Pinto and Ermentrout [13] by including a recurrent inhibitory term in the inhibitory equation as well as assuming the coupling from inhibitory to excitatory neurons to be nonlinear. We also allow the threshold, \( \theta_e \), for the excitatory population and the threshold, \( \theta_i \), for the inhibitory population to be different. Our model thus reads

\[
\begin{align*}
\partial_t u_e &= -u_e + \omega_{ee} \ast P_e (u_e - \theta_e) - \omega_{ie} \ast P_i (u_i - \theta_i) \\
\tau \partial_t u_i &= -u_i + \omega_{ei} \ast P_e (u_e - \theta_e) - \omega_{ii} \ast P_i (u_i - \theta_i).
\end{align*}
\]

Here the functions \( u_e = u_e(x, t) \) and \( u_i = u_i(x, t) \) model the synaptic input to excitatory and inhibitory neurons, respectively. \( P_e \) and \( P_i \) model the corresponding firing-rate functions. These functions constitute a one-parameter family of increasing functions mapping the set of real numbers onto the unit interval, where the parameter involved measures the characteristic variation length of the functions. When the typical width approaches zero, the functions \( P_m \) are assumed to approach the Heaviside step function \( H \). In the present paper we will approximate the firing rate functions with the Heaviside step function. The parameters \( \theta_e \) and \( \theta_i \) play the role as the threshold values for firing of the excitatory and inhibitory populations, respectively, which by assumption may be different. \( \omega_{mn} \ast f \) denotes the convolution integral defined as

\[
(\omega_{mn} \ast f)(x) = \int_{-\infty}^{\infty} \omega_{mn}(x-y)f(y)\,dy, \quad m, n = e, i
\]

and the functions \( \omega_{mn} \) are the connectivity functions, which are assumed to be real valued, positive, bounded, symmetric, and to satisfy the normalization condition \( \int_{-\infty}^{\infty} \omega_{mn}(x)\,dx = 1 \). In addition, they can generically be expressed as

\[
\omega_{mn}(x) = \frac{1}{\sigma_{mn}} \Phi_{mn}(\xi_{mn}), \quad \xi_{mn} = \frac{x}{\sigma_{mn}}
\]

where the parameter \( \sigma_{mn} \) describes the spatial extension, i.e., synaptic footprint, and \( \Phi(\xi_{mn}) \) is a non-dimensional scaling function. Finally, the parameter \( \tau \) is the ratio between the inhibitory and excitatory time constants, which we from now on refer to as the relative inhibition time.

As examples on localized connectivity functions of the type (6) we have the Gaussian

\[
\Phi_{mn}(\xi_{mn}) = \frac{1}{\sqrt{2\pi}} \exp\left(-\xi_{mn}^2\right)
\]

and the exponential decay

\[
\Phi_{mn}(\xi_{mn}) = \frac{1}{2} \exp(-|\xi_{mn}|).
\]

Pinto and Ermentrout [13] address the problem of existence and uniqueness of stationary, symmetric, localized stationary pulses (“bumps”) as well as stability of these solutions using both a generalized version of the Amari approach and a direct linearization procedure. In the present paper we will investigate the same type of questions.
We first point out a boundedness property for the solutions of the initial value problem of the system. Now, since by the conditions imposed on $\omega_{mn}$

$$0 \leq \int_{-\infty}^{\infty} \omega_{mn}(y-x)H(f(y,t) - \theta_m)\,dy \leq \int_{-\infty}^{\infty} \omega_{mn}(y-x)\,dy \leq 1$$

for any function $f$, we find the explicit bounds

$$\left( V_e(x) + 1 \right) e^{-t} - 1 \leq u_e(x,t) \leq \left( V_e(x) - 1 \right) e^{t} + 1$$

and

$$\left( V_i(x) + 1 \right) e^{-t/\tau} - 1 \leq u_i(x,t) \leq \left( V_i(x) - 1 \right) e^{-t/\tau} + 1$$

for the solution-components $u_e$ and $u_i$, where $(V_e(x), V_i(x))$ is the initial condition of (4). Notice that the results (10) also hold true in the general case of firing rate functions possessing values between 0 and 1. From this result we can draw the following conclusion: Since the initial data by assumption obeys

$$|V_e(x)| \leq 1, \quad |V_i(x)| \leq 1$$

for all $x \in \mathbb{R}$, then

$$|u_e(x,t)| \leq 1, \quad |u_i(x,t)| \leq 1$$

for all $x \in \mathbb{R}$, uniformly in $t \geq 0$. This property has the following immediate consequences: If $\theta_m > 1$, $m = e, i$, the non-locality does not contribute to the time evolution of $u_m$. The global evolution of $u_m$ is described as exponential decay. For $-1 \leq \theta_m \leq 1$, only the range for which $u_m(x,t) \geq \theta_m$ contributes to the nonlocal terms. Finally, for $\theta_m < -1$, all neuronal elements are above threshold and contribute to the nonlocal terms.

The boundedness result (12) indeed shows that the nonlinear stage of the instabilities we detect by a linearization procedure, has to be saturated.

3. Existence and uniqueness of stationary localized solutions

In this section we investigate for the model conditions for existence and uniqueness of pairs of excitatory and inhibitory symmetric, localized pulses termed “bumps”, by generalizing arguments presented in Pinto and Ermentrout [13]. In the following it is assumed that $0 < \theta_m \leq 1$ ($m = e, i$). We conveniently separate the existence issue from the uniqueness problem.

1. The existence issue is a global problem, and it can be posed as follows: Determine the set of threshold values for firing which produce “bumps”—solutions of (4).

2. The uniqueness problem can be formulated as follows: Suppose we have proven the existence of “bumps”. Then the task consists of giving conditions for having a one-to-one correspondence between the threshold values and the “bumps”. This latter issue turns out to be a local problem.

3.1. Existence theory

We first investigate the possibility of having localized stationary, symmetric solutions of the system (4) and proceed as follows:

1. The firing rate functions $P_e$ and $P_i$ are approximated with the Heaviside step function, i.e., $P_m = H$ ($m = e, i$).

2. The solutions of (4) are assumed to be time-independent, i.e., $u_m(x,t) = U_m(x)$, $u_i(x,t) = U_i(x)$ where $U_m(x)$ and $U_i(x)$ are smooth, bounded functions satisfying the following symmetry and limit conditions:
\[ U_m(x) = U_m(-x), \text{ for } m = e, i \]
\[ U_m(\pm\infty) = 0, \text{ for } m = e, i \]

There are unique points denoted by \( a, b \geq 0 \) such that
\[ U_e(x) > \theta_e \text{ (} |x| < a \text{ or } |x| > a \text{) (13a)} \]
\[ U_i(x) > \theta_i \text{ (} |x| < b \text{ or } |x| > b \text{)} \]

Notice that the conditions imposed above imply that we only consider single bump solutions.

The parameters \( a, b \) measure the widths of the pulses and hereafter we refer to these parameters as the pulse widths of \( U_e(x) \) and \( U_i(x) \). By making use of the stationarity ansatz described above, we now find that \( U_e(x) \) and \( U_i(x) \) can formally be expressed as
\[ U_e(x) = \int_{-a}^{a} \omega_{ee}(x-x') \, dx' - \int_{-b}^{b} \omega_{ie}(x-x') \, dx' \]  
\[ U_i(x) = \int_{a}^{a} \omega_{ei}(x-x') \, dx' - \int_{b}^{b} \omega_{ii}(x-x') \, dx'. \]

Now, by combining the remaining assumptions on pulses \( U_e(x) \) and \( U_i(x) \) we find that the conditions which must be fulfilled in order to have stationary symmetric solutions read
\[ f_e(a, b) = \theta_e \] \[ f_i(a, b) = \theta_i \]

where \( f_e \) and \( f_i \) are given as
\[ f_e(a, b) = W_{ee}(2a) - W_{ee}(a + b) + W_{ee}(a - b) \] \[ f_i(a, b) = W_{ei}(a + b) - W_{ii}(b - a) - W_{ii}(2b). \]

Here \( W_{jk}(\xi) \) is defined as the integral
\[ W_{jk}(\xi) = \int_{-\xi}^{\xi} \omega_{jk}(y) \, dy. \]

In contrast to \( \omega_{jk} \), which is an even function, \( W_{jk} \) is an odd function.

In Fig. 1, we display numerical examples of pulses when the connectivity functions are given as Gaussians (6) and (7).

The key problem now consists of investigating for which threshold values \( \theta_m \) where \( 0 < \theta_m \leq 1 \) \((m = e, i)\) the system (15) possesses solutions. We conveniently translate this problem into a mapping problem as follows:

Introduce the subset \( \Sigma \) of \( \mathbb{R}^2 \) as
\[ \Sigma = \{(a, b) | a \geq 0, b \geq 0\} \]

and the unit square
\[ I = [0, 1] \times [0, 1] \]
in the \((\theta_e, \theta_i)\)-plane.

From now on we refer to \( \Sigma \) as the pulse width set and \( I \) as the threshold value set. We also assume that the connectivity functions \( \omega_{mn} \) are continuous for all \( x \in \mathbb{R} \) except for a possible set of measure zero, which means that the vector field \( \mathbf{F} : \Sigma \to \mathbb{R}^2 \) defines a continuous mapping. Then we show that for all choices of connectivity
functions and synaptic footprints, there is a set of localized, stationary symmetric solutions of the model equations (4):

**Theorem 1.** Let $F : \Sigma \to \mathbb{R}^2$ be the continuous mapping from the pulse width set $\Sigma$ to the threshold value set, defined as

$$\theta = F(a)$$

(20)

where

$$a = \begin{bmatrix} a \\ b \end{bmatrix}, \quad \theta = \begin{bmatrix} \theta_e \\ \theta_i \end{bmatrix} \quad \text{and} \quad F = \begin{bmatrix} f_e \\ f_i \end{bmatrix}$$

(21)

with the component functions $f_e$ and $f_i$ given as (16a) and (16b). Then $F(\Sigma)$ is bounded and $\mathbb{F}(\Sigma) \cap 1 \neq \emptyset$.

(22)
We first prove that $F[wSigmag]$ is bounded. The triangle inequality yields
\[
|f_e (a,b)| \leq |W_{ee} (2a)| + |W_{ei} (a+b)| + |W_{ie} (a-b)|, \quad (23a)
\]
\[
|f_i (a,b)| \leq |W_{ei} (a+b)| + |W_{ii} (2b)|. \quad (23b)
\]

Now, since the connectivity functions by assumption are symmetric and satisfy the normalization condition, we have
\[
|W_{jk}(\xi)| \leq \frac{1}{2}. \quad (24)
\]

Hence
\[
|f_e (a,b)| \leq \frac{3}{2}, \quad |f_i (a,b)| \leq \frac{3}{2}. \quad (27)
\]

Next, we prove that the intersection between the image set $F[wSigmag]$ and the threshold value set $I$ is non-empty. We find that the image of the positive $a$-axis under the mapping $F$ is given as
\[
\gamma(a) = F(a,0) = \begin{bmatrix} f_e(a,0) \\ f_i(a,0) \end{bmatrix} = \begin{bmatrix} W_{ee}(2a) \\ 2W_{ii}(a) \end{bmatrix}. \quad (25)
\]

The boundary curve $\gamma(a)$ has the following properties:
\[
\gamma(0) = 0, \quad \gamma(a \to \infty) = \begin{bmatrix} 1 \\ 2 \end{bmatrix}. \quad (26)
\]

Moreover, this curve is the graph of a strictly increasing function $G$ given as
\[
\theta_i = G(\theta_e) \quad \text{where} \quad \theta_e = W_{ee}(2a), \quad \theta_i = 2W_{ii}(a).
\]

Hence, the image of the positive $a$-axis is contained in the threshold value set $I$. Now, since $\Sigma$ is simply connected and $F$ is a continuous mapping, we can conclude that
\[
F[w\Sigma] \cap I \neq \emptyset. \quad (27)
\]

This result means that it always exists a subset of $I$ (which we will term the set of admissible threshold values) for which the system (15) has solutions. For this set of $(\theta_e, \theta_i)$-values we have localized symmetric pulses. Notice that the proof of the theorem shows that an finite width excitatory pulse may coexist with arbitrarily narrow inhibitory pulse ($b \to 0$).

We will now prove that inhibitory stationary pulses cannot coexist with an arbitrarily narrow excitatory pulses ($a \to 0$) for $0 < \theta_e \leq 1 \, (m = e, i)$. This result is represented in terms of the present mathematical terminology as follows: The intersection of the image of the positive $b$-axis, with $a = 0$, under the mapping $F$ and the threshold value plane $I$ is empty. We prove this result as follows: First, simple computation reveals that
\[
\Sigma = F(0,b) = \begin{bmatrix} f_e(0,b) \\ f_i(0,b) \end{bmatrix} = \begin{bmatrix} -2W_{ee}(b) \\ W_{ii}(2b) \end{bmatrix}. \quad (28)
\]
where the components are negative for all $b > 0$. The image curve $\Gamma$ has the properties

$$\Gamma(0) = 0, \quad \Gamma(b \to \infty) = \begin{bmatrix} -1 & 1 \\ 1 & -2 \end{bmatrix}. \quad (29)$$

Moreover, this image curve is the graph of a strictly increasing function. Hence, the image curve $\Gamma(b)$ is totally located in the third quadrant, from which it follows that the intersection between $I$ and the image curve is empty. Thus, finite width inhibitory pulses cannot coexist with very narrow excitatory pulses ($a \to 0$).

3.2. Uniqueness theory and pulse pair generation

3.2.1. Uniqueness theory

Let us assume that the threshold values $(\theta_e, \theta_i)$ belong to the admissible subset of threshold values. This means that (20) possesses a solution which will be denoted by $(a_{eq}, b_{eq})$. We will address the question about uniqueness of the pulse pair solutions. We proceed as follows: Assume that the connectivity functions $o_{mn}$ are continuous. Then the vector field $F$ where the component functions are given by (16), is continuous differentiable. Then, by the inverse function theorem this vector field is locally one-to-one and onto, provided the Jacobian of $F$ evaluated at $a_{eq} = (a_{eq}, b_{eq})$ is non-singular, i.e.,

$$\det \left[ \frac{\partial F}{\partial a} \right] (a_{eq}) \neq 0. \quad (30)$$

This is clearly a local problem in the sense that the theorem states that there is an open neighborhood of $a_{eq}$ which is mapped one-to-one and onto an open neighborhood of the threshold values $(\theta_e, \theta_i)$. Geometrically, the solution of the system (20) satisfying the condition (30) emerges as a transversal intersection between the level curves $f_e(a,b) = \theta_e$ and $f_i(a,b) = \theta_i$. From now on we refer to the condition (30) as the transversality condition.

3.2.2. Pulse pair generation

The breakdown of the transversality condition (30) is connected to the process of the pulse pair generation in a way which is analogous to the problem of generation of two standing pulses for a given admissible threshold value through a bifurcation process detailed in [13].

We first search for admissible threshold values $(\theta_e, \theta_i)$ which correspond to a situation where the level curves $f_e = \theta_e$ and $f_i = \theta_i$ are tangent to each other. We proceed as follows: One determines positive solutions of the system of equations

$$\det \left[ \frac{\partial F}{\partial a} \right] (a, b) = 0 \quad (31a)$$

$$f_e(a, b) = \theta_e \quad (31b)$$

for a given set of connectivity functions $o_{mn}$ and synaptic footprints $\sigma_{mn}$ when $\theta_e$ varies through the unit interval. The next step consists of computing the corresponding $\theta_i$-value by means of the formula $f_i(a, b) = \theta_i$ under the constraint $0 < \theta_i \leq 1$. This process generates a separatrix curve in the set of admissible threshold values.

Now, with a proper adjustment of the threshold values around this separatrix curve, we go from a situation with no intersection of the level curves $f_e = \theta_e$ and $f_i = \theta_i$ to a tangent situation as described by (31) and finally end up with two transversal intersection points, from which it follows that we get two pulse pairs locally for a certain range of threshold values. In Fig. 2 we see a numerical example of a threshold subset that corresponds to solutions of (20), where the subset is bounded by (23) and (31a).
Fig. 2. Illustration of existence and non-existence of pulse pair solution(s) for different threshold values. The subset, denoted (i), of the threshold value set producing two pulse pair solutions (narrow and broad pulse pair) is contained in the grey region. Curve segment (ii) corresponds to the situation where \( b \to 0 \) for the narrow pulse pair, cf. (25). Curve segment (iii) corresponds to only one pulse pair solution, see (31a) for the criterion. The connectivity functions are Gaussian (6) and (7) with synaptic footprints \( \sigma_{ee} = 0.35, \sigma_{ei} = 0.48, \sigma_{ie} = 0.60 \), and \( \sigma_{ii} = 0.69 \).

Note that in the region below the dashed line in Fig. 2, there are no bumps solution, while in the region above the solid line there may exist a single bumps pair solution. However, here we focus on the regime where two pairs of bumps exist (grey region in Fig. 2).

4. Amari approach to pulse stability

A pulse pair \( (U_e(x), U_i(x)) \) is identified with the intersection point \( (a,b) \) between the level curves \( f_e(a,b) = \theta_e \) and \( f_i(a,b) = \theta_i \). This is the starting point for the stability analysis approach originally developed by Amari [3] and later used by Pinto and Ermentrout [13]. It is conjectured that the stability properties of pulse pairs can be inferred from the stability properties of the intersection point \( (a,b) \). To do this, it is necessary to prescribe the dynamical evolution of the pulse-width coordinates \( (a,b) \) in a way consistent with the system (4).

4.1. Stability analysis

Let us assume that \( (\theta_e, \theta_i) \) belongs to the set of admissible threshold values, which means that the system \( f_e(a,b) = \theta_e \) and \( f_i(a,b) = \theta_i \) possesses at least one solution. This solution is denoted by \( (a_{eq}, b_{eq}) \). Following Amari [3] and Pinto and Ermentrout [13] we assume that the perturbed pulses are described by time-dependent pulse-width coordinates \( (a(t), b(t)) \), satisfying the same threshold value conditions as the stationary pulse pairs:

\[
\begin{align*}
u_e(a(t), t) &= \theta_e, \quad u_i(b(t), t) = \theta_i.
\end{align*}
\]

Then, by differentiating (32) with respect to \( t \) and using (4) with firing-rate functions approximated with Heaviside step function, we find

\[
\begin{align*}
|\partial_t u_e(a(t), t)| &= -\theta_e + \int_{-\infty}^{\infty} \omega_e(a - x') H(u_e(x', t) - \theta_e) \, dx' - \int_{-\infty}^{\infty} \omega_i(a - x') H(u_i(x', t) - \theta_i) \, dx' \\
&= f_e(a, b) - \theta_e,
\end{align*}
\]
Notice that the equilibrium point of the system (33) and (34) determines the widths of the “bumps”. The next step consists of studying the stability properties of this point. In order to do that, we proceed in the standard way by computing the Jacobian of the vector field defining the pulse width autonomous dynamical system (33) and (34) evaluated at the equilibrium point \((a_{\text{eq}}, b_{\text{eq}})\). In the process of doing this, the slopes \(\partial x u_e(a,t)\) and \(\partial x u_i(b,t)\) are expressed in terms of the values of these slopes evaluated at the equilibrium points:

\[
\partial x u_e(a,t) \approx -|U'_e(a_{\text{eq}})|, \quad \partial x u_i(b,t) \approx -|U'_i(b_{\text{eq}})|.
\]

(35)

Here we have taken into account that the slope of the pulses evaluated at the pulse widths is negative. The dynamical system for the pulse widths now reads

\[
\begin{align*}
\tau |U'_e(a_{\text{eq}})| \frac{da}{dt} &= f_e(a,b) - \theta_e, \\
\tau |U'_i(b_{\text{eq}})| \frac{db}{dt} &= f_i(a,b) - \theta_i.
\end{align*}
\]

(36a) (36b)

We readily find that the Jacobian evaluated at the equilibrium points can conveniently be written on the compact form

\[
J_A = \frac{\partial F}{\partial (a,b)}|_{(a_{\text{eq}},b_{\text{eq}})} = \begin{bmatrix} \beta_A & -\eta_A \\ \mu_A & \alpha_A - \beta_A \end{bmatrix},
\]

(37)

where \(\alpha_A, \beta_A, \eta_A\) and \(\mu_A\) are defined as

\[
\begin{align*}
\alpha_A &= 2 \omega_{ee} (2a_{\text{eq}}) + \omega_{ee} (a_{\text{eq}} - b_{\text{eq}}) \frac{U'_e(a_{\text{eq}})}{|U'_e(a_{\text{eq}})|} + \omega_{ee} (a_{\text{eq}} + b_{\text{eq}}) \frac{U'_e(a_{\text{eq}})}{|U'_e(a_{\text{eq}})|}, \\
\beta_A &= 2 \omega_{ee} (2a_{\text{eq}}) + \omega_{ee} (a_{\text{eq}} + b_{\text{eq}}) \frac{U'_e(a_{\text{eq}})}{|U'_e(a_{\text{eq}})|} + \omega_{ee} (a_{\text{eq}} - b_{\text{eq}}) \frac{U'_e(a_{\text{eq}})}{|U'_e(a_{\text{eq}})|}, \\
\eta_A &= \omega_{ee} (a_{\text{eq}} + b_{\text{eq}}) \frac{U'_e(a_{\text{eq}})}{|U'_e(a_{\text{eq}})|} + \omega_{ee} (a_{\text{eq}} - b_{\text{eq}}) \frac{U'_e(a_{\text{eq}})}{|U'_e(a_{\text{eq}})|}, \\
\mu_A &= \omega_{ee} (a_{\text{eq}} + b_{\text{eq}}) \frac{U'_i(b_{\text{eq}})}{|U'_i(b_{\text{eq}})|} + \omega_{ee} (b_{\text{eq}} - a_{\text{eq}}) \frac{U'_i(b_{\text{eq}})}{|U'_i(b_{\text{eq}})|}. 
\end{align*}
\]

(38a) (38b) (38c) (38d)

and, hence, the characteristic equation assumes the generic form

\[
\tau \lambda^2 + (\alpha_A - \beta_A) \lambda + \gamma_A = 0,
\]

(39)

where

\[
\gamma_A = -\alpha_A \beta_A + \mu_A \eta_A = \tau \det(J_A).
\]

(40)

In order to indicate that the present stability analysis relies on the Amari approach, we have introduced the subscript ‘A’ in the parameters in (37)-(40).
Table 1

<table>
<thead>
<tr>
<th>$\gamma_A$</th>
<th>Stability properties</th>
</tr>
</thead>
<tbody>
<tr>
<td>$&lt; 0$</td>
<td>Saddle point</td>
</tr>
<tr>
<td>$&gt; 0$</td>
<td>Stability for $\tau &lt; \tau_{cr}$</td>
</tr>
<tr>
<td></td>
<td>Instability for $\tau &gt; \tau_{cr}$</td>
</tr>
</tbody>
</table>

Here $\tau_{cr} = \alpha_A / \beta_A$.

In the following we assume that the connectivity functions $\omega_{ei}$ and $\omega_{ie}$ are decreasing for positive arguments. Hence, since these functions are even, we always have $\omega_{ei}(a_{eq} - b_{eq}) \geq \omega_{ei}(a_{eq} + b_{eq})$ and $\omega_{ie}(a_{eq} - b_{eq}) \geq \omega_{ie}(a_{eq} + b_{eq})$, from which it follows that $\mu_A, \alpha_A, \eta_A, \beta_A > 0$. Notice however that $\gamma_A$ may have both signs.

According to standard 2D stability theory, the stability properties depend on the invariants of the Jacobian $J_A$, i.e., $\gamma_A = \tau \det(J_A)$ and $tr(J_A) = \beta_A - \tau \alpha_A$. Given the sign properties of the parameters involved, we get the classification scheme for stability as summarized in Table 1.

4.2. Hopf bifurcation theory

According to the results of the previous subsection (Table 1) the critical relative inhibition time $\tau_{cr}$ determining the transition from stability to instability, is given by

$$\tau_{cr} = \frac{\alpha_A}{\beta_A}, \tag{41}$$

provided $\gamma_A > 0$. This critical relative inhibition time represents a generic Hopf bifurcation point in the classical bifurcation-theory sense, since in this case $\frac{d}{d\tau} tr(J_A)|_{\tau=\tau_{cr}} = \tau_{cr}^{2}\mu > 0$. In the present context this bifurcation is interpreted as conversion of stable “bumps” to pulses with an internal oscillating width, i.e., “breathers”, as the relative inhibition time $\tau$ passes $\tau_{cr}$, corresponding to the excitation of a limit cycle.

In Pinto and Ermentrout [13] it is pointed out that numerical simulations of their set of model equations show that unstable pulsating “bumps” are formed as the relative inhibition time exceeds a critical threshold value in the Hopf bifurcational sense. This indicates that the actual bifurcation is a subcritical Hopf bifurcation. Here we will investigate the stability properties of the limit cycle formed at the bifurcation point by means of standard normal form theory applied to the Amari system (36). We proceed as follows [29]: The vector field defining (36) is Taylor-expanded about the equilibrium point $(a_{eq}, b_{eq})$. This yields

$$\frac{du}{dt} = J_A \cdot (u - u_{eq}) + G(u) \tag{42}$$

where we have adopted the notation

$$u = \begin{bmatrix} a \\ b \end{bmatrix}, \quad u_{eq} = \begin{bmatrix} a_{eq} \\ b_{eq} \end{bmatrix} \tag{43}$$

Finally, $J_A$ is the Jacobian given by (37) and the vector field $G$ contains the nonlinear contributions. The next step consists of transforming the pulse width dynamics to a center manifold coordinate system $(v, w)$. This is done by means of the substitution

$$v = \tilde{u} + P \cdot \tilde{u} \tag{44}$$

where

$$P = \begin{bmatrix} \eta_A & 0 \\ \beta_A & \Omega \end{bmatrix} \tag{45}$$
and
\[ v = \begin{bmatrix} v \\ w \end{bmatrix} \] (46)

which results in
\[ \frac{d}{dt} \begin{bmatrix} v \\ w \end{bmatrix} = \begin{bmatrix} 0 & -\Omega \\ \Omega & 0 \end{bmatrix} \begin{bmatrix} v \\ w \end{bmatrix} + \begin{bmatrix} g(v, w) \\ h(v, w) \end{bmatrix} \] (47)

with \( \Omega > 0 \) given by
\[ \Omega^2 = \text{det}(J_A)|_{\tau = \tau_{cr}}. \] (48)

The scalar functions \( g \) and \( h \) are the components of the vector field \( \vec{G} \) expressed in terms of the center manifold coordinates \( (v, w) \) via the substitution (44). These functions obey the conditions
\[ \begin{align*}
g(0, 0) &= g_v(0, 0) = 0, \\
h(0, 0) &= h_v(0, 0) = 0.
\end{align*} \] (49) (50)

The center manifold reduction finally yields the normal form for the Hopf bifurcation, which conveniently can be expressed in terms of polar coordinates \( v = r \cos \phi, w = r \sin \phi \) as [29]
\[ \begin{align*}
\frac{dr}{dt} &= \delta (\tau - \tau_{cr}) r + \vartheta r^3, \\
\frac{d\phi}{dt} &= \Omega_{\tau} + \Omega_{\tau'} + \gamma r^2.
\end{align*} \] (51)

from which it is evident that only \( \delta \) and \( \vartheta \) influence the stability of the limit cycle: This cycle is stable (unstable) provided \( \vartheta < 0 (\vartheta > 0) \). Normal form theory for 2D systems also enables us to compute the coefficients \( \vartheta \) and \( \delta \) by means of the formulas
\[ \delta = \frac{1}{2} \frac{d}{dt} tr(J)|_{\tau = \tau_{cr}} = \frac{1}{2} \tau_{cr}^2 > 0 \] (52)

and [29]
\[ \vartheta = \frac{1}{16} [g_{uu} + g_{uw} + g_{uw} + h_{uw}] + \frac{1}{16} \frac{d}{dt} [g_{uu}(h_{uw} g_{uw}) - h_{uu}(g_{uw} g_{uw}) - g_{uw} h_{uw} + g_{uw} h_{uw}] \] (53)

where all the partial derivatives involved are evaluated at the equilibrium point \((0, 0)\). Notice that in order to estimate the frequency of the limit cycle oscillations as \( \tau \to \tau_{cr} \), it is necessary to compute the nonlinear frequency shift parameter \( \Gamma \) in a similar way as \( \vartheta \). This is not done here, however.

Fig. 3 shows the set of admissible threshold values (Fig. 3a) and the corresponding pulse widths (Fig. 3b) for the same connectivity functions as for the example pulses in Fig. 1. The corners A, B and C in Fig. 3a correspond to the corners A’, B’ and C’ in Fig. 3b, respectively, through the mapping process
\[ (\theta_e, \theta_i) \to (a, b), \quad f_1(a, b) = \theta_e, \quad f_2(a, b) = \theta_i. \]

The following features are apparent:

1. The curve segment AB (A’B’) of the boundary in Fig. 3a (Fig. 3b) corresponds a broad pulse pair coexisting with a narrow pulse pair where \( b \to 0 \).
Fig. 3. The set of admissible threshold values and corresponding pulse widths, see system (20), with Gaussian connectivity functions with synaptic footprints given by $\sigma_{ee} = 0.35$, $\sigma_{ei} = 0.48$, $\sigma_{ie} = 0.60$ and $\sigma_{ii} = 0.69$. Stability analysis of these bumps solutions are based on the Amari approach. The points A, B and C in (a) correspond to $A'$, $B'$ and $C'$ in (b), respectively. In (b) red points corresponds to narrow unstable pulse pairs, blue points to broad pulse pairs which are converted to stable breathers ($\vartheta < 0$) at $\tau = \tau_{cr}$, and black points to broad pulse pairs which are converted to unstable breathers ($\vartheta > 0$) at $\tau = \tau_{cr}$ (normal form theory).

2. The curve segment BC (B'C') of the boundary in Fig. 3a (Fig. 3b) corresponds to the situation when the level curves $f_e = \theta_e$ and $f_i = \theta_i$ are tangent to each other (non-transversal intersection), and hence we only obtain one pulse pair in this situation. Along this segment $\gamma_A = 0$.

Fig. 3b shows the subsets of the pulse width set for which $\gamma_A > 0$ and $\gamma_A < 0$, respectively. This plot shows all pulse pairs generated by considering threshold values $\theta_m$ in the interval [0,0.25]. The red pointed region in the pulse width set corresponds to narrow pulses which are subject to a saddle point instability. The region with blue (black) points corresponds to equilibrium widths $(a_{eq}, b_{eq})$ for which $\vartheta < 0$ ($\vartheta > 0$), and consequently, according to normal form theory, the broad pulses are converted to stable (unstable) breathers at $\tau = \tau_{cr}$.

Thus, to conclude, the Amari analysis predicts that narrow pulse pairs are expected to be subject to an instability of the saddle point type, while the broader pulse pairs are stable for low $\tau$ and converted to breathers as $\tau$ passes the critical value $\tau_{cr}$. In addition, this analysis indicates that there are possibilities of having both stable and unstable breathers excited at the Hopf bifurcation point $\tau = \tau_{cr}$.
5. Full stability analysis

In this section we study the stability of the pulse pairs with the full set of model equations (4) as a starting point, using a standard linearization procedure in a way identical to the one presented in Pinto and Ermentrout [13]. It is shown that one ends up with two eigenvalue equations of the same type as (39). These equations constitute the basis of the stability analysis. We compare the results of this approach with the simplified Amari analysis presented in the previous section.

5.1. Linearized non-local equations

Let $U^e$ and $U^i$ be a steady state pulse pair solution of (4), i.e.,

\begin{align}
U^e &= a_{\delta} \ast H(U^e - \theta_e) - a_{\omega} \ast H(U^i - \theta_i), \\
U^i &= a_{\delta} \ast H(U^i - \theta_i) - a_{\omega} \ast H(U^i - \theta_i).
\end{align}

(54a)

(54b)

We introduce the perturbed state

\begin{align}
\psi(x, t) = U^e(x) + \chi(x, t), \\
u(x, t) = U^i(x) + \psi(x, t).
\end{align}

(55)

Taylor expansion about the equilibrium state ($U^e$, $U^i$) yields

\begin{align}
H(U^e - \theta_e + \chi) &= H(U^e - \theta_e) + \delta(U^e - \theta_e) \chi + \ldots, \\
H(U^i - \theta_i + \psi) &= H(U^i - \theta_i) + \delta(U^i - \theta_i) \psi + \ldots.
\end{align}

(56a)

(56b)

Since, by assumption $|\chi| \ll |U^e - \theta_e|$ and $|\psi| \ll |U^i - \theta_i|$, we retain only the two lowest order terms in the expansion. Here $\delta$ denotes the Dirac function. When inserting these approximations into (4) and taking the equilibrium condition (54) into account, one deduces the linearized non-local evolution equations for the disturbances ($\chi, \psi$)

\begin{align}
\partial_t \chi &= -\chi + a_{\omega} \ast (\delta(U^e - \theta_e) \chi - a_{\omega} \ast (\delta(U^i - \theta_i) \psi) \\
\partial_t \psi &= -\psi + a_{\omega} \ast (\delta(U^i - \theta_i) \chi - a_{\omega} \ast (\delta(U^i - \theta_i) \psi).
\end{align}

(57a)

(57b)

5.1.1. Eigenvalues

We then look for solutions of the form

\begin{align}
\chi(x, t) &= e^{\lambda t} \chi_1(x), \\
\psi(x, t) &= e^{\lambda t} \psi_1(x)
\end{align}

(58a)

(58b)

of the system (57) and get

\begin{align}
(1 + \lambda) \chi_1(x) = a_{\omega} \ast (\delta(U^e - \theta_e) \chi_1) - a_{\omega} \ast (\delta(U^i - \theta_i) \psi_1) \\
(1 + \lambda) \psi_1(x) = a_{\omega} \ast (\delta(U^i - \theta_i) \chi_1) - a_{\omega} \ast (\delta(U^i - \theta_i) \psi_1).
\end{align}

(59a)

(59b)

Here $\lambda$ plays the role of growth rate ($Re\lambda > 0$) or decay rate ($Re\lambda < 0$) of the disturbances ($\chi(x, t), \psi(x, t)$) imposed on the stationary pulse pair state ($U^e(x), U^i(x)$).

Again we exploit the identification of the equilibrium pulse pairs ($U^e(x), U^i(x)$) with pulse width coordinates ($a_{\delta}, b_{\delta}$), through the equations $U_{eq}(x) = \theta_{\omega}, 0 < \theta_{\omega} \leq 1, m = e, i$. We assume that the latter set of equations possesses one and only one solution ($a_{\delta m}, b_{\delta m}$) for which $a_{\delta m} > 0$. By making use of this assumption we can
evaluate the convolution integrals \( \omega_{mn} \). The details in this evaluation is shown in Appendix B, and we end up with

\[
(1 + \lambda)\chi(x) = \frac{1}{|U(\theta_{\alpha})|} \left[ \omega_{\alpha}(x - a_{\alpha})\chi(-a_{\alpha}) + \omega_{\alpha}(x - a_{\alpha})\chi(a_{\alpha}) \right]
- \frac{1}{|U(b_{\alpha})|} \left[ \omega_{\alpha}(x + b_{\alpha})\psi(-b_{\alpha}) + \omega_{\alpha}(x - b_{\alpha})\psi(b_{\alpha}) \right]
\]

\[
(1 + \lambda)\psi(x) = \frac{1}{|U(\theta_{\alpha})|} \left[ \omega_{\alpha}(x + a_{\alpha})\chi(-a_{\alpha}) + \omega_{\alpha}(x - a_{\alpha})\chi(a_{\alpha}) \right]
- \frac{1}{|U(b_{\alpha})|} \left[ \omega_{\alpha}(x + b_{\alpha})\psi(-b_{\alpha}) + \omega_{\alpha}(x - b_{\alpha})\psi(b_{\alpha}) \right].
\]

The relations (60) imply the equivalence

\[
\chi(a_{\alpha}) = \chi(-a_{\alpha}) = \psi(b_{\alpha}) = \psi(-b_{\alpha}) \equiv 0 \Rightarrow \chi(x) = \psi(x) \equiv 0.
\]

Then, since we consider non-trivial spatial disturbances \((\chi(x), \psi(x))\) the condition

\[
\sum = \begin{bmatrix} \chi(a_{\alpha}) \\ \chi(-a_{\alpha}) \\ \psi(b_{\alpha}) \\ \psi(-b_{\alpha}) \end{bmatrix} \neq 0
\]

has to be satisfied. The problem now consists of determining the eigenvalue \( \lambda \) for which (62) is fulfilled. We proceed as follows: By letting \( x = \pm a_{\alpha} \) and \( x = \pm b_{\alpha} \) in (60a) and (60b), respectively, we find

\[
(1 + \lambda)\chi(a_{\alpha}) = \frac{1}{|U(\theta_{\alpha})|} \left[ \omega_{\alpha}(0)\chi(a_{\alpha}) + \omega_{\alpha}(2a_{\alpha})\chi(-a_{\alpha}) \right]
- \frac{1}{|U(b_{\alpha})|} \left[ \omega_{\alpha}(a_{\alpha} + b_{\alpha})\psi(-b_{\alpha}) + \omega_{\alpha}(a_{\alpha} - b_{\alpha})\psi(-b_{\alpha}) \right]
\]

\[
(1 + \lambda)\chi(-a_{\alpha}) = \frac{1}{|U(\theta_{\alpha})|} \left[ \omega_{\alpha}(2a_{\alpha})\chi(a_{\alpha}) + \omega_{\alpha}(0)\chi(a_{\alpha}) \right]
- \frac{1}{|U(b_{\alpha})|} \left[ \omega_{\alpha}(a_{\alpha} + b_{\alpha})\psi(-b_{\alpha}) + \omega_{\alpha}(a_{\alpha} - b_{\alpha})\psi(-b_{\alpha}) \right]
\]

\[
(1 + \lambda)\psi(b_{\alpha}) = \frac{1}{|U(\theta_{\alpha})|} \left[ \omega_{\alpha}(a_{\alpha} - b_{\alpha})\chi(a_{\alpha}) + \omega_{\alpha}(a_{\alpha} + b_{\alpha})\chi(-a_{\alpha}) \right]
- \frac{1}{|U(b_{\alpha})|} \left[ \omega_{\alpha}(0)\psi(b_{\alpha}) + \omega_{\alpha}(2b_{\alpha})\psi(-b_{\alpha}) \right]
\]

\[
(1 + \lambda)\psi(-b_{\alpha}) = \frac{1}{|U(\theta_{\alpha})|} \left[ \omega_{\alpha}(a_{\alpha} + b_{\alpha})\chi(a_{\alpha}) + \omega_{\alpha}(a_{\alpha} - b_{\alpha})\chi(-a_{\alpha}) \right]
- \frac{1}{|U(b_{\alpha})|} \left[ \omega_{\alpha}(2b_{\alpha})\psi(-b_{\alpha}) + \omega_{\alpha}(0)\psi(-b_{\alpha}) \right].
\]
The system (63) is easily recognized as a linear homogeneous system of equations, \[ A \cdot X = 0 \] (64)

where the matrix \( A \) is given by

\[
A = \begin{bmatrix}
A_1 - (1 + \lambda) & B_1 & -C_1 & -D_1 \\
B_1 & A_1 - (1 + \lambda) & D_1 & -C_1 \\
E_1 & F_1 & -G_1 - (1 + \lambda \tau) & -H_1 \\
F_1 & E_1 & -H_1 & -G_1 - (1 + \lambda \tau)
\end{bmatrix},
\]

(65)

from which it follows that \( \lambda \) is an eigenvalue of a 4 \times 4 matrix. For convenience, we have introduced the parameters \( A_1, B_1, C_1, D_1, E_1, F_1, G_1 \) and \( H_1 \) defined as

\[
A_1 = \frac{\alpha_X(0)}{[U]^2[a_{2q}]}, \quad B_1 = \frac{\alpha_X(2a_{2q})}{[U]^2[a_{2q}]},
\]

(66a)

\[
C_1 = \frac{\alpha_0(a_{2q} - b_{2q})}{[U]^2[a_{2q}]}, \quad D_1 = \frac{\alpha_0(a_{2q} + b_{2q})}{[U]^2[a_{2q}]},
\]

(66b)

\[
E_1 = \frac{\alpha_0(a_{2q} - b_{2q})}{[U]^2[a_{2q}]}, \quad F_1 = \frac{\alpha_0(a_{2q} + b_{2q})}{[U]^2[a_{2q}]},
\]

(66c)

\[
G_1 = \frac{\alpha_Y(0)}{[V]^2(b_{2q})}, \quad H_1 = \frac{\alpha_Y(2b_{2q})}{[V]^2(b_{2q})}.
\]

(66d)

Now, let

\[
P = \begin{bmatrix}
1 & 1 & 0 & 0 \\
1 & 1 & 1 & 1 \\
0 & 0 & 1 & 1 \\
1 & 1 & 0 & 0 \\
0 & 0 & 1 & -1
\end{bmatrix},
\]

(67)

and introduce the substitution

\[
Y = P \cdot X
\]

(68)

where

\[
Y = \begin{bmatrix}
X_0(a_{2q}) \\
\psi_0(a_{2q}) \\
X_0(b_{2q}) \\
\psi_0(b_{2q})
\end{bmatrix}.
\]

(69)
The subscripts e and o refer to the even and odd parts, respectively, of the functions $\chi_1$ and $\psi_1$. The similarity transformation (68) conveniently transforms $A$ to the block-diagonal matrix $PAP^{-1}$ given by

$$
PAP^{-1} = \begin{bmatrix}
A_1 + B_1 - \lambda - 1 & -C_1 - D_1 & 0 & 0 \\
F_1 + E_1 & -G_1 - H_1 - \lambda \tau - 1 & 0 & 0 \\
0 & 0 & A_1 - B_1 - \lambda - 1 & -C_1 + D_1 \\
0 & 0 & -F_1 + E_1 & -G_1 + H_1 - \lambda \tau - 1
\end{bmatrix}. \quad (70)
$$

Then, we find that

$$
\det(PAP^{-1}) = [\tau \lambda^2 + (\alpha L + \beta L \tau) \lambda + \gamma_L] [\tau \lambda^2 + (\alpha'_L - \beta'_L \tau) \lambda + \gamma'_L] \quad (71)
$$

and hence the eigenvalues $\lambda$ are solutions to the quadratic equations

$$
\tau \lambda^2 + (\alpha_L - \beta_L \tau) \lambda + \gamma_L = 0 \quad (72a)
$$

$$
\tau \lambda^2 + (\alpha'_L - \beta'_L \tau) \lambda + \gamma'_L = 0. \quad (72b)
$$

Here

$$
\alpha_L = 1 + G_1 + H_1, \quad (73a)
\beta_L = -1 + A_1 + B_1, \quad (73b)
\gamma_L = 1 - (A_1 + B_1)(1 + G_1 + H_1) + G_1 + H_1 + (C_1 + D_1)(E_1 + F_1), \quad (73c)
$$

and

$$
\alpha'_L = 1 + G_1 - H_1, \quad (74a)
\beta'_L = -1 + A_1 - B_1, \quad (74b)
\gamma'_L = 1 - (A_1 - B_1)(1 + G_1 - H_1) + G_1 - H_1 + (C_1 - D_1)(E_1 - F_1). \quad (74c)
$$

Here the subscript 'L' is used in order to indicate that the stability analysis is based on the linearization procedure of the full model as opposed to the simplified Amari approach. In the following we will make use of the following properties:

1. From the definitions of $\beta_L$ and $\beta'_L$, it follows that $\beta_L \geq \beta'_L$.
2. From the definition of $\alpha_L$ and $\alpha'_L$, it follows that $\alpha_L > 0$ and that $\alpha'_L \leq \alpha_L$. Moreover, since $\omega_{ii}$ by assumption is a decreasing function for positive $x$, $\alpha'_L > 0$. Thus we can conclude that $\alpha'_L \geq \alpha_L \geq 0$.
3. One can prove that $\gamma'_L \equiv 0$. The proof of this is presented in Appendix C. This result reflects the translation invariance of the pulse solutions, in the same way as observed in Pinto and Ermentrout [13].

6. Amari approach versus full stability analysis

In this section, we discuss the relationship between the Amari approach (Section 4) and the full stability analysis (Section 5). We first notice the structural equivalence between the eigenvalue problems (39) and (72a), i.e., they can both be written on the form

$$
\tau \lambda^2 + (\alpha_i - \beta_i \tau) \lambda + \gamma_i = 0, \quad (i = A, L) \quad (75)
$$
where the subscripts $i = A$ and $i = L$ correspond to the Amari eigenvalue equation (39) and the quadratic equation (72a), respectively. In Appendix C it is proved that

$$
\alpha_A = \alpha_L, \quad \beta_A = \beta_L, \quad \gamma_A = \gamma_L.
$$

(76)

by means of some straightforward, but tedious algebraic computations. From now on we use the notation

$$
u \equiv \nu_A = \nu_L, \quad \beta \equiv \beta_A = \beta_L, \quad \gamma \equiv \gamma_A = \gamma_L.
$$

(77)

Hence, the only difference between the two stability approaches consists of the presence of the additional eigenvalue equation

$$
\tau \lambda^2 + (\alpha' - \beta') \lambda = 0
$$

(78)

in the full stability analysis, where we here and in the sequel for convenience employ the notation $\alpha' \equiv \alpha'_L$ and $\beta' \equiv \beta'_L$. The presence of equation (78) may affect the conclusions with respect to the stability/instability of the pulse pairs.

Here we will show that we can use the Amari analysis to predict stability versus instability of the pulse pairs, with one notable exception.

1. When $\gamma$ is negative we have a saddle point instability, irrespective of the properties of the roots of (78). Both the pulse widths and the synaptic footprints regulate the magnitude of $\gamma$.

2. In the complementary regime, i.e., when $\gamma$ is positive, one has to separate the discussion into the following subcases:

- $\beta > 0 \geq \beta'$.

Even though $\beta$ according to the Amari analysis always is positive, $\beta'$ may be non-positive. In this case the equation (78) gives a negative value for the non-zero eigenvalue. But, since $\beta > 0$, there is a Hopf bifurcation point at a critical $\tau$-value for (75), given by $\tau = \tau_{cr} = \frac{1}{2}$. In this case the stability situation is governed by (75).

- $\beta \geq \beta' > 0$.

If $\beta' > 0$, the following picture emerges: There are two different critical $\tau$-values, $\tau_{cr}$ and $\tau'_{cr}$, given as

$$
\tau_{cr} = \frac{\alpha}{\beta} \quad \text{and} \quad \tau'_{cr} = \frac{\alpha'}{\beta'}.
$$

(79)

Motivated by the results of the Amari approach, we will term $\tau_{cr}$ the Hopf bifurcation point.

For $\beta', \gamma > 0$, we can now infer that the Amari approach is applicable if

$$
\tau_{cr} \leq \tau'_{cr}.
$$

(80)

One shows this as follows: Let us vary $\tau$. When $\tau$ exceeds the Hopf bifurcation point $\tau_{cr}$, the real part of the eigenvalues of (75) changes from negative to positive, while the nontrivial eigenvalue of (78) remains negative. Hence the question about stability versus instability of the “bumps” can solely be based on (75).

In the complementary regime, i.e., when

$$
\tau_{cr} > \tau'_{cr},
$$

(81)

the Amari approach predicts stability for the range $\tau_{cr} < \tau < \tau_{cr}$, whereas the full linear stability analysis yields instability in the same range of relative inhibition times. Hence the Amari approach gives correct stability predictions except when $\gamma > 0, \beta \geq \beta' > 0$ and $\tau_{cr} < \tau < \tau_{cr}$.

In Fig. 4 the applicability of Amari approach is demonstrated for the admissible set of threshold values when the connectivity functions are as in Figs. 1–3. The following features are apparent: One can identify compact subsets in
both the threshold value set and the pulse width set for which $\tau_0 > \tau_{cr}$. This regime contains a subset corresponding to broad pulses converted to unstable breathers for $\tau = \tau_0$, according to Amari analysis. However, according to the full stability analysis, the Amari analysis is not applicable here. Thus we do not expect to observe the unstable breathers predicted by Amari analysis, since the broad pulse pairs in this regime become unstable when $\tau$ passes $\tau_{cr}$.

7. Numerical stability results

In principle, the stability/instability of pulse pairs $(U_e(x), U_i(x))$ can now be determined by means of the results obtained in the previous sections. More specifically, one proceeds as follows:

1. Derive the formulas for the component functions $f_e$ and $f_i$ for a given set of connectivity functions $\omega_{mn}$ and synaptic footprints $\sigma_{mn}$ by means of the formulas (16) and (17).
2. Determine the pulse width coordinates \((a_{eq}, b_{eq})\) of the pulse pairs \((U_e(x), U_i(x))\) by solving the system (15) for a given set of admissible threshold values \((\theta_e, \theta_i)\).

3. Compute the parameters \(\alpha, \beta, \gamma, \alpha', \beta'\) by means of the expressions (66a), (66b), (66c), (66d), (73a), (73b), (73c), (74a) and (74b).

4. Use the classification scheme described in Section 6 to infer conclusions about stability/instability of the “bumps” solutions.

In general, due to the complicated mathematical structure involved it is difficult to extract generic conclusions with respect to the stability/instability of the “bumps”. In most cases one has to rely on numerical computations.

We follow the four step procedure described above for the example shown in Fig. 1:

1. The synaptic footprints are chosen to be \(\sigma_{ee} = 0.35, \sigma_{ei} = 0.48, \sigma_{ie} = 0.60, \sigma_{ii} = 0.69\) (82) and all the connectivity functions are assumed to be Gaussians (6) and (7).

2. The threshold values for firing are chosen as \(\theta_e = 0.12, \theta_i = 0.08\) (83).

This choice of threshold values yields two solutions of the system (15), which indeed correspond to the situation with two separate pulse pairs, as explained in Section 3. The pulse width coordinates are \((a_{1eq}, b_{1eq}) = (0.066, 0.045)\) and \((a_{2eq}, b_{2eq}) = (0.179, 0.183)\). For convenience and in analogy with [13], we term the pulse pair corresponding to \((a_{1eq}, b_{1eq})\) as the narrow pulse pair, and \((a_{2eq}, b_{2eq})\) as the broad pulse pair.

3. The parameters \(\alpha, \beta, \gamma, \alpha'\) and \(\beta'\) have been computed separately for each pulse pair. We find the parameter set \(\alpha = 36.81, \beta = 15.36, \gamma = -58.03, \alpha' = 1.31, \beta' = 0.17\) (84) for the narrow pulse pair, while we get \(\alpha = 5.63, \beta = 1.86, \gamma = 1.97, \alpha' = 1.65, \beta' = 0.38\) (85) for the broad pulse pair. Hence, we can conclude that the narrow pulse pair is unstable in the saddle-point sense since \(\gamma < 0\). The broad pulse pair is stable for small and moderate relative inhibition times. When the relative inhibition time exceeds a critical \(\tau\) value, the broad pulses become unstable. First, it should be noticed that both \(\beta\) and \(\beta'\) are positive, so that we are in the regime where there are two critical relative inhibition times, \(\tau_{cr} = \frac{\alpha}{\beta}\) and \(\tau_{cr}' = \frac{\alpha'}{\beta'}\). Secondly, since \(\tau_{cr} = 3.03, \tau_{cr}' = 4.36\), (86) we have \(\tau_{cr} < \tau_{cr}'\), and hence the change from stability to instability occurs as the relative inhibition time exceeds \(\tau_{cr}\) Notice that since \(\tau_{cr} < \tau_{cr}'\), Amari’s stability analysis can be used to reach the conclusion regarding the stability properties of the broad pulse pair.

We have carried out numerical simulations of the full system of equations (4) with the stationary pulse pair \((U_e(x), U_i(x))\) as initial condition, using the set of input parameters listed above. These simulations are based on a split step approach where the time evolution is resolved by means of fourth order Runge-Kutta in time. At each time step, \(t_j\), we numerically detect the pulse widths of each pulse by means of the constraint equation \(u_m(a(t_j), t_j) = \theta_m\) for \(m = e, i\) (87).
Fig. 5. Pulse evolution with connectivity functions and threshold values as in Fig. 1. (a) Broad excitatory (left) and inhibitory (right) stable pulse at $\tau = 3$. (b) Broad excitatory (left) and inhibitory (right) stable pulse converted to breather at $\tau \approx \tau_{cr}$. (c) Broad excitatory (left) and inhibitory (right) stable pulse collapses at $\tau = 3.5$.

Notice that the numerical algorithm elaborated in Appendix A is applicable even in the case where one or both of the pulses vanishes, i.e., $a(t_j) = 0$ or/and $b(t_j) = 0$, which means that the corresponding nonlocalities have no effect on the evolution of the pulses. Figs. 5c and 6c show a rapid decay of the amplitudes with time for maximal amplitudes in the vicinity of threshold values.

The results can be summarized as follows for a broad stationary pulse pair as initial condition.

For $\tau < \tau_{cr}$, both the excitatory and inhibitory pulse remain unchanged (Fig. 5a). When $\tau \approx \tau_{cr}$, the pulses are converted to breathers (Fig. 5b). Finally, for $\tau > \tau_{cr}$, the excitatory and inhibitory pulses collapse (Fig. 5c) after the initial linear instability stage. Thus, we can conclude that the numerical simulations confirm the predictions deduced from the linear stability analysis.

Next, we consider the time evolution of the narrow pulse pair. For $\tau < \tau_{cr}$, we observe that the narrow pulses are converted to broad pulses (Fig. 6a). This process is identified with a heteroclinic orbit in the pulse width set (Fig. 6d). When $\tau \lesssim \tau_{cr}$, the pulse pair approaches the stable broad pulse pair in an oscillatory manner, signalling that we are in the vicinity of the Hopf point (Fig. 6b and c). For $\tau > \tau_{cr}$, the excitatory and the inhibitory pulses collapse (Fig. 6c and d).
Fig. 6. Evolution of unstable narrow pulse pairs with connectivity functions and threshold values as in Fig. 1. (a) Narrow excitatory (left) and inhibitory (right) pulse convert to broad inhibitory pulse at $\tau = 2.5$. (b) Narrow excitatory (left) and inhibitory (right) pulse convert to stable excitatory and inhibitory breathers at $\tau = 3.0$. (c) Narrow excitatory (left) and inhibitory (right) pulse collapse at $\tau = 3.5$. (d) Heteroclinic orbit in the pulse width plane for $\tau = 2.5$ and $\tau = 3.5$. For $\tau = 3.5$, we observe pulse pair collapse in the pulse width set. (e) Same as (d) for $\tau = 3.0$. The pulse width of the narrow pulse pair approaches the pulse width of the broad pulse pair in an oscillatory manner, signalling that we are in the vicinity of the Hopf point at $\tau = 3.0$. 

}\end{figure}
Fig. 7. Colormap of $\min(\tau_{cr}, \tau'_{cr})$ for broad pulse pair (cf. Fig. 1) as a function of excitatory and inhibitory threshold values.

Based on these numerical results, we conjecture that the attraction of the narrow pulse pair solutions to the broad pulse pairs is a generic property of the system (4) under consideration for $\tau < \min(\tau_{cr}, \tau'_{cr})$. Moreover, we expect that the narrow pulses are converted to stable breathers at $\tau \approx \tau_{cr}$ (if $\tau_{cr} < \tau'_{cr}$), and that they collapse for $\tau > \tau_{cr}$ after the initial linear instability regime.

Every threshold value coordinate in the subset in Fig. 2 corresponds to a narrow and a broad pulse pair. The stability of the broad pulses depends on the parameter $\tau$. In Fig. 7 we see how the value of $\min(\tau_{cr}, \tau'_{cr})$ changes through the threshold value subset by plotting a colormap of $\min(\tau_{cr}, \tau'_{cr})$ on top of the admissible threshold value set. The figure shows that the critical $\tau$ value remains relatively constant in the range 2.5–3.5, except for threshold values close to the corner B.

8. Discussion

In the present paper we have studied a Wilson–Cowan like extended version of the nonlocal, nonlinear two-population rate model (2) considered by Pinto and Ermentrout [13] in their investigation of existence and stability of “bumps”. In contrast to (2), our model (4) contains nonlinear coupling between interneurons, and a nonlinear coupling from inhibitory to excitatory neurons. We also allow the threshold for firing of excitatory and inhibitory neurons to be different. Our findings can be summarized as follows:

The solutions of the initial value problem of the model (4) satisfy a boundedness condition (10), which in turn implies that any instability detected by means of linear analysis has to be saturated.

For any set of connectivity functions there is a set of threshold values for firing for which stationary, symmetric excitatory and inhibitory potentials (termed “bumps”) exist. The set of such threshold values is called the set of admissible threshold values. We have focused on the case of two pulse pair configurations termed the narrow pulse pair and the broad pulse pair exist. The possibility of having coexistence of arbitrarily narrow excitatory pulses together with finite size inhibitory pulses are excluded. However, the model allows the opposite situation to take place, i.e., that finite size excitatory pulses may coexist with extremely narrow inhibitory pulses.

Generation of pairs of “bumps” appears as a bifurcation process in the set of admissible threshold values, where a curve in this set plays the role as bifurcation curve. This process is analogous to the one shown in [13].
The stability of the pair of “bumps” is studied by means of Amari’s simplified approach, i.e., by investigating the stability of the pulse widths of the pulses. This stability analysis is based on a quadratic eigenvalue equation where the relative inhibition time plays the role as control parameter. The narrow pulse pairs are generically unstable of the saddle point type, while the broad pulse pairs are shown to be stable for small and moderate values of the relative inhibition time. Regimes producing change from stability to instability through a Hopf bifurcation are identified. Moreover, the stability of the limit cycle formed at the bifurcation point is addressed using the theory of normal forms for 2D systems. Numerical investigation of the outcome of our Amari-type analysis confirm that both stable and unstable breathers can be excited at the Hopf bifurcation point (cf. Fig. 3b).

The stability analysis based on Amari’s approach is paralleled by a rigorous stability analysis of the “bumps” using the full set of equations (4) and the “bumps” as a starting point. It is readily shown that the eigenvalue problem factorizes into a product of two quadratic polynomials of which one is identified with the Amari eigenvalue problem. A scheme for determining the stability is then devised, and it is shown that the Amari approach and the full analysis yield the same predictions, with one notable exception.

The stability of “bumps” is investigated numerically by means of a split step scheme where the time evolution is resolved by means of a fourth order Runge–Kutta method. This investigation reveals that narrow “bumps” seem to be unstable for all relative inhibition times, while broad “bumps” are stable for small and moderate relative inhibition times. However, when the relative inhibition time exceeds a certain threshold, the “bumps” become unstable. One notices that this feature also appears in [13]. In some of our numerical investigations this threshold is lower than the threshold for stability predicted by the Amari approach.

We also observe stable breathers numerically as $\tau$ passes the Hopf bifurcation point $\tau_{cr}$ predicted by the Amari approach. However, the unstable breathers are not expected to be seen at this point, since full stability analysis predicts that the broad pairs corresponding to these breathers have become unstable for relative inhibition times below the Hopf bifurcation point.

The observation of stable breathers in our model contrasts the numerical observations of the model (2) reported in [13] where only unstable periodic solutions were seen, suggesting a subcritical Hopf bifurcation. A similar conclusion was reached in [27]. Stable breathers could be generated in a similar model, however, by inclusion of localized inputs breaking the spatial homogeneity [20]. Interestingly, Coombes and Owen [26] recently observed stable breathing solutions in a homogeneous model with a Mexican-hat like connectivity when a dynamic firing threshold was incorporated. This could hint that our observation of stable breathers is related to the incorporation of two independent firing thresholds in the present model (4). However, we have observed stable breathers in our model even when $\theta_e = \theta_i$, for example, $\theta_e = \theta_i = 0.2$, with the same synaptic footprints as in Fig. 1. Notice that this situation is outside the generic two pulse pair regime displayed in Fig. 2. One can show that this choice of threshold values $(\delta_\theta, \theta)$ gives rise to a single pulse pair solution. However, the same stability analysis as elaborated in this paper is applicable in this case.

In our numerical example in Section 7 we found $\tau_{cr}$ to be 3.03. Thus stable bumps were found to exist even with an inhibitory time constant a factor three larger than the excitatory time constant. This contrasts the analogous result from the analysis of the model considered by Pinto and Ermentrout [13] where $\tau_{cr}$ was found to be significantly smaller than one. Thus, our model results do not support the claim that slow excitation mediated by say NMDA receptors is needed to allow stable bumps [9].

Hansel and Mato [30] studied stability of persistent states in large networks of spiking excitatory and inhibitory neurons of the quadratic integrate-and-fire type. In their two-population model without any spatial structure they found that so called asynchronous persistent states could be obtained more easily when inhibitory–inhibitory interactions were included. We have not done a systematic study of the parameter-dependence of bump stability in our rate model. However, since rate models are expected to be able to describe asynchronous states, Hansel and Mato’s observation suggests that the larger range of $\tau$ allowing stable bumps in our model may stem from the inclusion of the inhibitory–inhibitory interaction, i.e., $w_{ij}(x) \neq 0$. This interaction was absent in the model studied by Pinto and Ermentrout [11].
Acknowledgements

The authors will like to thank Wieslaw Krolikowski, Yuri Kivshar, Andrey Miroshnichenko and Hans Ekkehard Plessser for many fruitful and stimulating discussions during the preparation phase of the present paper. Most of the figures in the present paper is generated by means of the supercomputer Caspar at the Norwegian University of Life Sciences. P. Blomquist was supported by the Research Council of Norway under the grant No. 160011/V30. J. Wyller acknowledges support from Centre for Integrative Genetics and the Research Council of Norway under the grant No. 153405/432. The present work was completed in 2003/04 when J. Wyller was a Visiting Fellow at Nonlinear Physics Centre and Laser Physics Centre, Australian National University. We will like to thank the reviewers for constructive remarks.

Appendix A. Runge–Kutta split step method

Here we design a numerical code for the initial value problem of system (4) with all the firing rate functions approximated with the Heaviside step function. The code is based on a so-called split-step approach. The starting point is to study the time evolution on a time interval referred to as the time stepping length. The non-localities which contain the nonlinear effects are treated as constants on this particular interval. The time-evolution which is described by a set of ordinary differential equations, can be resolved by means of a finite difference scheme for such equations. Here we will employ the fourth order Runge–Kutta method in order to solve this problem.

We discretise the time interval, i.e., introduce the sequence \( \{t_j\}_{j=0}^N \) where \( t_0 \equiv 0 \) and the time stepping length \( \Delta t_j \equiv t_{j+1} - t_j \). Let \( \mathbf{X} \) and \( \mathbf{F}(\mathbf{X}) \) be the 2D vector fields defined as

\[
\mathbf{X}(x,t_j) = \begin{pmatrix} u_e(x,t_j) \\ u_i(x,t_j) \end{pmatrix}, \quad \mathbf{F}(\mathbf{X}) = \begin{pmatrix} f_j \\ g_j \end{pmatrix}
\]

where the components \( f_j \) and \( g_j \) are given as

\[
f_j = -u_e(x,t_j) + \Phi_j \quad \text{(A.1a)}
\]

\[
g_j = -\frac{1}{\tau} u_i(x,t_j) + \frac{1}{\tau} \Psi_j \quad \text{(A.1b)}
\]

with

\[
\Phi_j = \Omega_{ee}(a(t_j) + x) + \Omega_{ei}(a(t_j) - x) - \Omega_{ie}(b(t_j) + x) - \Omega_{ii}(b(t_j) - x) \quad \text{(A.2a)}
\]

\[
\Psi_j = \Omega_{ee}(a(t_j) + x) + \Omega_{ei}(a(t_j) - x) - \Omega_{ie}(b(t_j) + x) - \Omega_{ii}(b(t_j) - x) \quad \text{(A.2b)}
\]

and

\[
\Omega_{\text{exc}}(x) \equiv \int_0^\beta u_{\text{exc}}(y) dy = \int_0^{\tilde{\xi}_{\text{exc}}} \Phi_{\text{exc}}(\tilde{\xi}) d\tilde{\xi} \quad \text{(A.3)}
\]

where we have taken into account the generic form of the connectivity functions \( u_{\text{exc}}(x) = \sigma_{\text{exc}}^{-1} \Phi_{\text{exc}}(\xi_{\text{exc}}) \).

The width coordinates \( a(t_j) \) and \( b(t_j) \) appearing in the expressions \( \Phi_j \) and \( \Psi_j \) satisfy the constraints

\[
u_e(a(t_j), t_j) = \theta_e, \quad u_i(b(t_j), t_j) = \theta_i \quad \text{(A.4)}
\]

The fourth order Runge–Kutta code can now be formulated as follows:
1. Compute the iteratively defined vector fields $k_n$, $n = 1, 2, 3, 4$ defined by the sequence

\[ k_1 = \Delta t_j \cdot F(X) \] (A.5a)

\[ k_2 = \Delta t_j \cdot F(X + \frac{1}{2} k_1) \] (A.5b)

\[ k_3 = \Delta t_j \cdot F(X + \frac{1}{2} k_2) \] (A.5c)

\[ k_4 = \Delta t_j \cdot F(X + k_3) \] (A.5d)

2. Then the iterate $X_{j+1}$ approximating the solution of the system (4) is given by means of the formula

\[ X_{j+1} = X_j + \frac{1}{6} k_1 + \frac{1}{2} k_2 + \frac{1}{2} k_3 + \frac{1}{6} k_4 \] (A.6)

Notice that one has to track both the iterates $u(x, t_j)$ and the widths $(a(t_j), b(t_j))$ in the time stepping process. The iteration procedure can be described as follows:

- Compute the initial widths $(a(0), b(0))$ by means of the initial condition $(U_e(x), U_i(x))$ and (A.4), i.e., solve the system $U_e(a(0)) = \theta_e, U_i(b(0)) = \theta_i$.
- Determine the iterate $(u_e(x, t_1), u_i(x, t_1))$ by means of the iteration scheme (A.5) and (A.6) with the components of the vector field $F(X)$ given by (A.1) with $t_0 = 0$ and $t_1 = \Delta t_0$, i.e., plug in the initial condition $(U_e(x), U_i(x))$ and the initial widths $(a(0), b(0))$ found in the previous step into (A.1).
- Compute the width coordinates $(a(t_1), b(t_1))$ by solving the system $u_e(a(t_1), t_1) = \theta_e, u_i(b(t_1), t_1) = \theta_i$.
- Find the iterates $(u_e(x, t_2), u_i(x, t_2))$ using (A.5), (A.6) and (A.1) with $t_2 = t_1 + \Delta t_1$.
- Compute the width coordinates $(a(t_2), b(t_2))$ by solving the system $u_e(a(t_2), t_2) = \theta_e, u_i(b(t_2), t_2) = \theta_i$.

etc.,

\[ \vdots \]

- Find the iterates $(u_e(x, t_j), u_i(x, t_j))$ using (A.5), (A.6) and (A.1) with $t_j = t_{j-1} + \Delta t_{j-1}$.
- Compute the width coordinates $(a(t_j), b(t_j))$ by solving the system $u_e(a(t_j), t_j) = \theta_e, u_i(b(t_j), t_j) = \theta_i$.

\[ \vdots \]

- Find the iterates $(u_e(x, t_{j+1}), u_i(x, t_{j+1}))$ using (A.5), (A.6) and (A.1) with $t_{j+1} = t_j + \Delta t_j$.

etc.,

\[ \vdots \]
Notice that the split step iteration scheme for the model (4) presupposes a one-to-one correspondence between the pulse width iterates \((a(t_j), b(t_j))\) and the threshold values \((\theta_x, \theta_y)\) as long as \(a(t_j) > 0, b(t_j) > 0\). By continuity, this property is always fulfilled for the initial time steps if the system \(U_i(a(0)) = \theta_x, U_i(b(0)) = \theta_y\) possesses a unique solution.

Notice also that the tracking of the width coordinates enables us to show numerically the existence of stable symmetric stationary solutions which act as attractors as well as breathers excited at the Hopf bifurcation point. The numerical code is also applicable in the case of pulse amplitudes becoming smaller than the threshold values. From (A.2) and the fact that the functions \(\Omega_m, \Omega_n\) are odd it follows that \(a(t_j) = 0\) and \(b(t_j) = 0\) is equivalent to no effect of the corresponding nonlocal interactions. In fact, in the numerical examples in Figs. 5c and 6c the excitatory couplings \(\Omega_m, \Omega_n\) vanish at certain time \(t_e\) (where \(\Omega_m, \Omega_n\) are still non-zero), resulting in a decay faster than purely exponential for \(t > t_e\).

Finally, consider a localized and spatially symmetric initial condition for the model, i.e., \(u_m(x, 0) = U_m(x)\); \(m = c, i\), where \(U_m(x) = U_m(-x)\). Then it is easy to prove by means of the induction principle applied to the numerical code formulated above, that all the iterates \(u_m(x, t_j)\) are symmetric with respect to \(x\).

Appendix B. Evaluation of the convolution integrals appearing in the full stability analysis

The convolution integrals appearing in (57) assume the form \(\omega * (\delta(x - \theta))\), i.e.,

\[
\omega * (\delta(x - \theta)) = \int_{-\infty}^{\infty} \omega(\xi) \delta(x - \theta - \xi) d\xi.
\]

This integral is conveniently decomposed into two parts:

\[
\omega * (\delta(x - \theta)) = \int_{0}^{\infty} \omega(\xi) \delta(x - \theta - \xi) d\xi + \int_{-\infty}^{0} \omega(\xi) \delta(x - \theta - \xi) d\xi
\]

We assume that the function \(u(\xi)\) satisfies the conditions

1. \(u(\xi) = u(-\xi)\)
2. \(u'(\xi) < 0\) for \(0 < \xi < \xi_1\)
3. \(u'(\xi) > 0\) for \(\xi > \xi_1\)
4. \(\xi = u^{-1}(y), \quad dy = u'(\xi)d\xi\)
5. \(u(0) = \gamma_0, \quad u(\xi_1) = \gamma_1(>0)\), \(u(\infty) = 0\)
6. \(u(\theta) = \theta \Rightarrow a = u^{-1}(\theta)\)
7. \(u(x) = u(-x)\)

The second term of (B.2) can then conveniently be rewritten as a sum of two integrals:

\[
\int_{0}^{\infty} \omega(x - \xi) \delta(x - \theta - \xi) d\xi = \int_{0}^{\gamma_0} \omega(u^{-1}(y) - \xi) \delta(y - \theta - \xi) dy + \int_{\gamma_1}^{\infty} \omega(u^{-1}(y) - \xi) \delta(y - \theta - \xi) dy
\]

\[
= \int_{\gamma_0}^{\gamma_1} \omega\{u(u^{-1}(y) - \xi)\} \delta(y - \theta - \xi) dy + \int_{\gamma_1}^{\infty} \omega\{u(u^{-1}(y) - \xi)\} \delta(y - \theta - \xi) dy
\]

\[
= -\int_{0}^{\gamma_1} \omega\{u(u^{-1}(y) - \xi)\} [\theta - u^{-1}(y)]^{-1} dy + \int_{0}^{\gamma_1} \omega\{u(u^{-1}(y) - \xi)\} [\theta - u^{-1}(y)]^{-1} dy
\]

\[
= \int_{0}^{\gamma_1} \omega\{u(u^{-1}(y) - \xi)\} [\theta - u^{-1}(y)]^{-1} dy (B.3)
\]
The first of these integrals can easily be computed as follows: Introduce the extension
\[ f(y) = \begin{cases} \omega(u^{-1}(y) - x)z(u'(u^{-1}(y)))^{-1}, & \text{if } y_1 \leq y \leq y_0; \\ 0, & \text{otherwise.} \end{cases} \] (B.4)

Due to the properties of the \( \delta \)-function, one only gets a contribution from \( y = \theta \), i.e.,
\[ \int_{y_0}^{y_1} \omega(u^{-1}(y) - x)z(u'(u^{-1}(y)))^{-1} \delta(y - \theta) \, dy = \int_{-\infty}^{\infty} f(y) \delta(y - \theta) \, dy = f(\theta) \]
\[ = \omega(a - x)z(a)(u'(a))^{-1} 
   = -\omega(x - a)z(a)(u'(a))^{-1} \] (B.5)

The second integral is shown to be equal to zero by introducing the extension
\[ g(y) = \begin{cases} \omega(u^{-1}(y) - x)z(u'(u^{-1}(y)))^{-1}, & \text{if } y_1 \leq y \leq 0; \\ 0, & \text{otherwise.} \end{cases} \] (B.6)

and observing that \( \theta \) belongs to the interval \( y > 0 \), i.e., an interval where \( g(y) = 0 \). We then deduce the formula
\[ \int_{\infty}^{0} \omega(x - x)z(\xi)(u(\xi) - \theta) \, d\xi = \omega(a + x)z(a)(u'(a))^{-1} \] (B.7)
by means of the same technique as for the first term in (B.2).

**Appendix C. Proof of some identities**

Here we will prove that the coefficients appearing in the eigenvalue equations (39) and (72a) satisfy the conditions

1. \( a_A = a_L \)
2. \( b_A = b_L \)
3. \( \gamma_A = \gamma_L \)

Moreover, we will prove that \( \gamma_L' \) given as (74c) is identical to zero, i.e.,

4. \( \gamma_L' = 0 \).

In the following we will make use of formulas for the derivatives of \( U'_e(x) \) and \( U'_i(x) \). By using the formal expressions (14), i.e.,
\[ U_e(x) = \int_{-a}^{a} \omega_e(s - x) \, ds' - \int_{-b}^{b} \omega_e(s - x) \, ds' = \int_{-\infty}^{+a} \omega_e(y) \, dy - \int_{-b}^{+b} \omega_e(y) \, dy \] (C.1a)
\[ U_i(x) = \int_{-a}^{a} \omega_i(s - x) \, ds' - \int_{-b}^{b} \omega_i(s - x) \, ds' = \int_{-\infty}^{+a} \omega_i(y) \, dy - \int_{-b}^{+b} \omega_i(y) \, dy \] (C.1b)
we find
\[ U'_e(x) = \omega_e(s + a) - \omega_e(s - a) - \omega_e(s + b) + \omega_e(s - b) \] (C.2a)
\[ U'(s) = \omega \xi_x(s + a) - \omega \xi_x(s - a) - \omega \xi_x(s + b) + \omega \xi_x(s - b). \]  \hspace{1cm} (C.2b)

\section*{C.1.} \( \alpha_A = \alpha_L \)

The two parameters \( \alpha_A \) and \( \alpha_L \) are given as
\[
\alpha_A = \frac{2\omega \xi_x(2b) - \omega \xi_x(a + b) + \omega \xi_x(b - a)}{|U'(b)|}; \hspace{1cm} (C.3)
\]
\[
\alpha_L = 1 + \frac{\omega \xi_x(0) + \omega \xi_x(2b)}{|U'(b)|}; \hspace{1cm} (C.4)
\]
where
\[
|U'(b)| = |\omega \xi_x(a + b) - \omega \xi_x(b - a) - \omega \xi_x(2b) + \omega \xi_x(0)|. \hspace{1cm} (C.5)
\]

Since by assumption we know that the slope of \( U'(x) \) is negative for any pulse width coordinate \( b \), \( (C.5) \) can be rewritten as
\[
|U'(b)| = -|\omega \xi_x(a + b) - \omega \xi_x(b - a) - \omega \xi_x(2b) + \omega \xi_x(0)|. \hspace{1cm} (C.6)
\]
We hence get
\[
\alpha_A = -\omega \xi_x(a + b) + \omega \xi_x(b - a) + \omega \xi_x(2b) - \omega \xi_x(0) \hspace{1cm} (C.7)
\]

from which it follows that
\[
\alpha_A = \alpha_L. \hspace{1cm} (C.8)
\]

\section*{C.2.} \( \beta_A = \beta_L \)

The two parameters \( \beta_A \) and \( \beta_L \) are given as
\[
\beta_A = \frac{\omega \xi_x(a + b) - \omega \xi_x(2a) - \omega \xi_x(a - b)}{|U'(a)|}; \hspace{1cm} (C.9)
\]
\[
\beta_L = 1 - \frac{\omega \xi_x(0) + \omega \xi_x(2a)}{|U'(a)|}; \hspace{1cm} (C.10)
\]
where
\[
|U'(a)| = |\omega \xi_x(2a) - \omega \xi_x(a + b) + \omega \xi_x(a - b)|. \hspace{1cm} (C.11)
\]

Since the slope of \( U'_x(s) \) is negative for any pulse width coordinate \( a \), \( (C.11) \) can be rewritten as
\[
|U'(a)| = -|\omega \xi_x(2a) + \omega \xi_x(0) + \omega \xi_x(a + b) - \omega \xi_x(a - b)|. \hspace{1cm} (C.12)
\]
Thus we get
\[
\beta_A = \frac{\omega \xi_x(a + b) - \omega \xi_x(2a) + \omega \xi_x(0) - \omega \xi_x(a - b)}{-\omega \xi_x(2a) + \omega \xi_x(0) + \omega \xi_x(a + b) - \omega \xi_x(a - b)} \hspace{1cm} (C.13)
\]

from which it follows that
\[
\beta_A = \beta_L. \hspace{1cm} (C.14)
\]
C.3. $\gamma_A = \gamma_L$

The two parameters $\gamma_A$ and $\gamma_L$ depend on the connectivity functions in a complicated way. For convenience, we introduce the parameters $A_1$, $B_2$, $C_2$, $D_2$, $E_2$ and $F_2$ defined by

$$A_1 = \frac{\omega_1(2a)}{[U'_1(a)]}, \quad B_1 = \frac{\omega_1(a + b)}{[U'_1(a)]}, \quad C_1 = \frac{\omega_1(a - b)}{[U'_1(a)]}$$
$$D_2 = \frac{\omega_1(a + b)}{[U'_1(b)]}, \quad E_2 = \frac{\omega_1(b - a)}{[U'_1(b)]}, \quad F_2 = \frac{\omega_1(2b)}{[U'_1(b)]}$$

(C.15)

(C.16)

$\gamma_A$ and $\gamma_L$ can then be expressed as

$$\gamma_A = 2A_1D_2 - 2A_1E_2 - 4A_2F_2 + 2B_2E_2 + 2B_2F_2 + 2C_2D_2 - 2C_2F_2$$

(C.17)

$$\gamma_L = a_1f_L + \left( \frac{\omega_1(a - b)}{[U'_1(b)]} + \frac{\omega_1(a + b)}{[U'_1(b)]} \right) \left( \frac{\omega_1(a - b)}{[U'_1(a)]} + \frac{\omega_1(a + b)}{[U'_1(a)]} \right)$$

(C.18)

Moreover, the latter expression for $\gamma_L$ can easily be expressed in terms of $A_1$, $B_2$, $C_2$, $D_2$, $E_2$ and $F_2$ as

$$\gamma_L = (2F_2 - D_2 + E_2)(B_2 - 2A_1 - C_2) + C_2D_2 + B_2E_2 + B_1D_2 = 2A_2D_2 - 2A_2E_2 - 4A_3F_2 + 2B_2E_2 + 2B_2F_2 + 2C_2D_2 - 2C_2F_2 .$$

(C.19)

Hence

$$\gamma_A = \gamma_L .$$

(C.20)

C.4. $\gamma'_L = 0$

$\gamma'_L$ is given as

$$\gamma'_L = 1 - \left( \frac{\omega_1(0)}{[U'_1(0)]} - \frac{\omega_1(2a)}{[U'_1(0)]} \right) \left( 1 + \frac{\omega_1(0)}{[U'_1(b)]} - \frac{\omega_1(2b)}{[U'_1(b)]} \right)$$

$$+ \frac{\omega_1(a - b)}{[U'_1(b)]} + \frac{\omega_1(a + b)}{[U'_1(b)]} \left( \frac{\omega_1(a - b)}{[U'_1(a)]} + \frac{\omega_1(a + b)}{[U'_1(a)]} \right)$$

(C.21)

which can be rewritten on the convenient form

$$\gamma'_L = 1 + \frac{A_1 - B_1}{A_1 + B_1 + C_1} + D_1 + E_1$$

(C.22)

when introducing

$$A_1 = \omega_1(0)\omega_1(2b) - \omega_1(0)\omega_1(0) - \omega_1(2a)\omega_1(2b) + \omega_1(2a)\omega_1(0)$$

(C.23)

$$B_1 = \omega_1(a - b)\omega_1(a + b) - \omega_1(a - b)\omega_1(a - b) + \omega_1(a + b)\omega_1(a - b) - \omega_1(a + b)\omega_1(a + b)$$

(C.24)

$$C_1 = \omega_1(2a)\omega_1(a + b) - \omega_1(2a)\omega_1(a - b) - \omega_1(0)\omega_1(a + b) + \omega_1(0)\omega_1(a - b)$$

$$+ \omega_1(a + b)\omega_1(2b) - \omega_1(a + b)\omega_1(0) - \omega_1(a - b)\omega_1(2b) + \omega_1(a - b)\omega_1(0)$$

(C.25)

$$D_1 = \frac{\omega_1(2a) - \omega_1(0)}{[\omega_1(2a) - \omega_1(0) - \omega_1(a + b) + \omega_1(a - b)]}$$

(C.26)
\[ E_3 = \frac{\omega_{ii}(0) - \omega_{ii}(2\beta)}{\omega_{ii}(0) - \omega_{ii}(2\beta) + \omega_{ii}(a + B\omega_{ii}(a - B))}. \quad (C.27) \]

One can now prove that \(|A_3 + B_3 + C_3| = |U'_e(a)U'_i(b)|\). Then, by some tedious algebraic manipulations we can show that

\[ A_3 - B_3 \left[ A_3 + B_3 + C_3 \right] + D_3 + E_3 = -1 \quad (C.28) \]

which finally yields \(\gamma'_L = 0\) for every \(a\) and \(b\), and independent of the synaptic footprints, \(\sigma_{mn}\).

References


