Analyzing stability of equilibrium points in neural networks: a general approach

Wilson A. Truccolo[a], Govindan Rangarajan[b], Yonghong Chen[c,d], Mingzhou Ding[d,*]

[a]*Department of Neuroscience, Brown University, Providence, RI 02912, USA*
[b]*Department of Mathematics and Centre for Theoretical Studies, Indian Institute of Science, Bangalore 560 012, India*
[c]*Xi'an Jiaotong University, Xi'an 710049, China*
[d]*Center for Complex Systems and Brain Sciences, Florida Atlantic University, Boca Raton, FL 33431, USA*

Abstract

Networks of coupled neural systems represent an important class of models in computational neuroscience. In some applications it is required that equilibrium points in these networks remain stable under parameter variations. Here we present a general methodology to yield explicit constraints on the coupling strengths to ensure the stability of the equilibrium point. Two models of coupled excitatory–inhibitory oscillators are used to illustrate the approach.
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1. Introduction

We consider neural networks of the form

$$\dot{\mathbf{x}}^i = \mathbf{F}(\mathbf{x}^i) + \sum_{j=1}^{N} G_{ij}\mathbf{H}(\mathbf{x}^j), \tag{1}$$

where $\mathbf{x}^i$ is the M-dimensional state vector of the ith node. Each node can either be a single neuron ($M = 1$) as in Hopfield types of models (Hirsch, 1989; Wersing, Beyn, & Ritter, 2001), or a group of neurons ($M > 1$), representing, e.g. the cortical column of interacting excitatory and inhibitory neurons (Li & Dayan, 1999; Truccolo, Ding, & Bressler, 2000; Wilson & Cowan 1972). The dynamics of the individual node is given by $\dot{\mathbf{x}}^i = \mathbf{F}(\mathbf{x}^i)$ and $\mathbf{H} : R^M \rightarrow R^M$ is the coupling function. The coupling matrix is $\mathbf{G} = [G_{ij}]$ where G_{ij} gives the coupling strength from node j to node i.

Without loss of generality assume that the origin is a stable equilibrium point for the individual node and remains an equilibrium point for the network. The stability of the origin under coupling strength variations is the main

concern of the present work. This problem is mainly motivated by some computational considerations. For example, a class of models assert that the background state of the network, represented by the equilibrium point at the origin, should be quiescent in the absence of input (Baird, 1990; Buhmann, 1995; Carpenter, Cohen, & Grossberg, 1987; Destexhe, 1994; Li, 1994; Li, 1999; Li & Hopfield, 1989; Whittle, 1998; Yao & Freeman, 1990). External inputs, treated as a slowly increasing and then decreasing function of time, can lead the network through a Hopf bifurcation to an oscillatory state and then return it to its background or equilibrium state once the input has been removed. This natural reset mechanism, requiring the origin to be a stable equilibrium point, makes the network ready for the next computational cycle. To endow the oscillatory network the ability to differentiate patterns of inputs, statistical learning takes place wherein the coupling strengths between the network units change according to certain learning rules. Without careful consideration the learning related parameter changes can potentially alter the stability of the background state, thereby defeating the computational picture established earlier. It is thus desirable to have constraints on the individual coupling strengths that can be incorporated into the learning rules so that the stability of the equilibrium point is ensured for all time.

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* Corresponding author.

E-mail addresses: ding@walt.ccs.fau.edu (M. Ding); wilson_truccolo@brown.edu (W.A. Truccolo); ychen@walt.ccs.fau.edu (Y. Chen); rangaraj@math.iisc.ernet.in (G. Rangarajan).

Previous work on stability constraints have mainly concentrated on recurrent networks of the Hopfield type (Atiya, 1988; Chen & Amari, 2001; Fang & Kincaid, 1996; Feng & Brown, 1998; Guez, Protopopsecu, & Barhen, 1988; Hirsch, 1989; Hoppendsteadt & Izhikevich, 1997; Kelly, 1990; Liang & Wu, 1998; Matsuoka, 1991; Michel, Farrell, & Porod, 1989; Sugawara, Harao, & Noguchi, 1983; Wersing et al., 2001; Yang & Dillon, 1994) with $M = 1$. In this paper we consider a general approach that leads to stability bounds on the individual coupling strengths in recurrent networks with more complex local dynamics. Two explicit models of coupled neural populations will be used to illustrate our approach.

2. Theory

Our approach consists of three steps.

Step 1. For simplicity, let $\mathbf{F(0)} = \mathbf{0}$, $\mathbf{H(0)} = \mathbf{0}$, and the real parts of the eigenvalues of the Jacobian $\mathbf{DF(0)}$ be negative so that the origin is stable for the individual node.

Linearizing Eq. (1) around the origin gives (in matrix form)

$$\dot{\mathbf{S}} = \mathbf{DF}{\cdot}\mathbf{S} + \mathbf{DH}{\cdot}\mathbf{S}{\cdot}\mathbf{G}^{\mathrm{T}}, \tag{2}$$

where $\mathbf{S} = (\mathbf{x}^1, \mathbf{x}^2, ..., \mathbf{x}^N)$. According to the Jordan canonical form theory, the stability of Eq. (2) is determined by the eigenvalue λ of $\mathbf{G}$. Let the corresponding eigenvector from $\mathbf{G}^{\mathrm{T}}$ be $\mathbf{e}$ and let $\mathbf{u} = \mathbf{Se}$. The equation for $\mathbf{u}$ reads

$$\dot{\mathbf{u}} = [\mathbf{DF} + \lambda{\cdot}\mathbf{DH}]\mathbf{u}. \tag{3}$$

The origin of Eq. (1) is stable if this equation is stable for all the eigenvalues of $\mathbf{G}$. This is true even when the coupling matrix is defective (Hirsch & Smale, 1974).

Step 2. To proceed further we treat λ in Eq. (3) as a complex control parameter. Denote by Ω the region in the $\mathrm{Re}(\lambda) - \mathrm{Im}(\lambda)$ plane where all the eigenvalues of $(\mathbf{DF} + \lambda{\cdot}\mathbf{DH})$ have negative real parts. Clearly, the equilibrium point is stable if all eigenvalues of $\mathbf{G}$ lie within Ω. We henceforth refer to Ω as the stability zone. A schematic of Ω is shown in Fig. 1. We note that Ω is usually obtained numerically. For some situations analytical results are possible (see below).

Step 3. Thus far the stability criteria are stated in terms of the eigenvalue of $\mathbf{G}$. The goal in this work is to directly constrain the coupling strengths themselves. This is done by making use of the Gershgörin disc theorem (Horn & Johnson, 1990).

Given an $n \times n$ matrix $\mathbf{A} = [a_{ij}]$, the Gershgörin theorem states that all eigenvalues of $\mathbf{A}$ are located in the union of n discs (called the Gershgörin discs) where each disc is given by

$$\left\{ z \in C : |z - a_{ii}| \le \sum_{j \ne i} |a_{ji}| \right\}, \qquad i = 1, 2, ..., n.$$

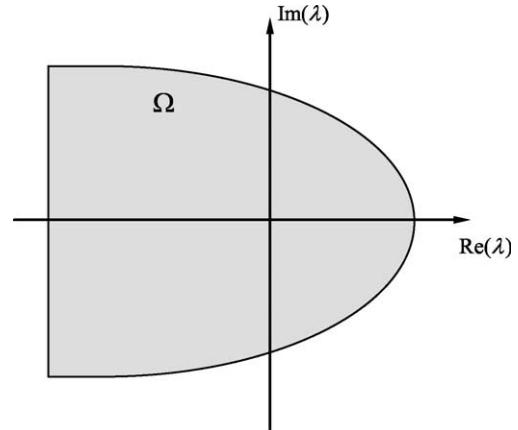
Fig. 1. Schematic of the stability zone.

Alternative forms of the n discs are (Horn & Johnson, 1990):

$$\left\{ z \in C : |z - a_{ii}| \le \sum_{j \ne i} |a_{ij}| \right\}, \qquad i = 1, 2, ..., n.$$

Combining the two, we have the form used in the remainder of this paper:

$$\left\{ z \in C : |z - a_{ii}| \le \frac{1}{2} \sum_{j \ne i} (|a_{ji}| + |a_{ij}|) \right\}, \tag{4}$$

$i = 1, 2, ..., n.$

This form is more intuitive since it involves incoming and outgoing coupling strengths for a given node.

The stability conditions for the equilibrium point can now be stated as follows:

(1) the center G_{ii} ($i = 1, 2, ..., N$) of every Gershgörin disc of $\mathbf{G}$ lies inside the stability zone Ω;
(2) the radius of every Gershgörin disc is shorter than the distance from the center of the disc to the boundary of Ω.

In other words, letting $\delta(x)$ denote the distance from point x on the real axis to the boundary of Ω, stability of the equilibrium point is ensured if

$$(G_{ii}, 0) \in \Omega, \qquad \frac{1}{2} \sum_{j \ne i} (|G_{ji}| + |G_{ij}|) < \delta(G_{ii}), \tag{5}$$

for $i = 1, 2, ..., N.$

3. Examples

3.1. The case of M = 1

When one dimensional systems are coupled together, the matrices $\mathbf{DF}$ and $\mathbf{DH}$ are reduced to real numbers.

Representing them by μ and ν, respectively, the stability zone is easily obtained as $\mathrm{Re}(\lambda) < -\mu/\nu$. The distance from the center of the ith Gershgörin disc to the boundary of Ω is given by $\delta(G_{ii}) = -\mu/\nu - G_{ii}$. Using Eq. (5) we obtain the stability conditions as

$$\frac{1}{2}\sum_{j\neq i}(|G_{ji}| + |G_{ij}|) + G_{ii} < -\mu/\nu. \tag{6}$$

This result was obtained before in Hirsch (1989) and Wersing et al. (2001).

3.2. A coupled oscillator model with $M = 2$

The general topology for the model is shown in Fig. 2. The basic unit in the model is a neural population consisting of either excitatory or inhibitory cells (Baird, 1990; Li, 2001; Li & Hopfield, 1989; Wilson & Cowan, 1972). The functional unit in the network is a cortical column consisting of mutually coupled excitatory and inhibitory populations. The columns are then coupled through mutually excitatory interactions to form the network.

A single column is described by two first order differential equations

$$\frac{\mathrm{d}x}{\mathrm{d}t} + ax = -k_{ei}Q(y, Q_m) + I,$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} + by = k_{ie}Q(x, Q_m). \tag{7}$$

Here x, y represent the local field potentials of the excitatory and inhibitory populations, respectively, and I is the input ($I = 0$ in the subsequent analysis). The constants a, $b > 0$ are the damping constants. The parameter $k_{ie} > 0$ gives the coupling gain from the excitatory (x) to the inhibitory (y) population whereas $k_{ei} > 0$ represents the strength of the reciprocal coupling. The nonlinear neuronal interaction is realized through the sigmoid function $Q(\cdot, Q_m)$ where Q_m is a parameter controlling the slope of the function. Here we only need to specify that $Q(0, Q_m) = 0$ and $Q'(0, Q_m) = 1$.
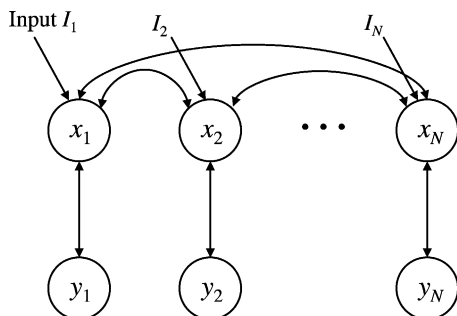

Fig. 2. Schematic of the network configuration.

The N columns are coupled together in the following fashion:

$$\frac{\mathrm{d}x_n}{\mathrm{d}t} + ax_n = -k_{ei}Q(y_n, Q_m) + \frac{1}{N}\sum_{p=1}^{N}c_{np}Q(x_p, Q_m) + I_n, \tag{8}$$

$$\frac{\mathrm{d}y_n}{\mathrm{d}t} + by_n = k_{ie}Q(x_n, Q_m),$$

where the columns are indexed by $n = 1, 2, ..., N$ and the coupling strength c_{np} is the gain from the excitatory population of column p to the excitatory population of column n.

Variables used in Eq. (3) can be explicitly evaluated for the present model as

$$\mathbf{DF} = \begin{pmatrix} -a & -k_{ei} \\ k_{ie} & -b \end{pmatrix}, \quad [\mathbf{G}]_{np} = \frac{c_{np}}{N}, \quad \mathbf{DH} = \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix}$$

where we have used the fact $Q'(0, Q_m) = 1$.

To discover the stability zone we study the eigenvalue α of the matrix $(\mathbf{DF} + \lambda \cdot \mathbf{DH})$ as a function of λ. The characteristic polynomial of this matrix is given by

$$f(\alpha) = \alpha^2 + \alpha(a + b - \lambda) + (k_{ei}k_{ie} + ab - b\lambda).$$

For an arbitrary coupling matrix $\mathbf{G}$, its eigenvalues λ could be complex:

$$\lambda = \lambda_R + i\lambda_I.$$

Then the characteristic polynomial becomes

$$f(\alpha) = \alpha^2 + \alpha(a + b - \lambda_R - i\lambda_I) + (k_{ei}k_{ie} + ab - b\lambda_R - ib\lambda_I).$$

The range of parameter values which gives $\mathrm{Re}(\alpha) < 0$ can be determined by applying the generalized Routh–Hurwitz criterion (Appendix A). Following this procedure, consider $-if(i\alpha)$:

$$\begin{aligned}-if(i\alpha) = {} & i\alpha^2 + \alpha(a + b - \lambda_R) - i\alpha\lambda_I \\ & - i(k_{ei}k_{ie} + ab - b\lambda_R) - b\lambda_I.\end{aligned}$$

This has to be put into the following standard form:

$$-if(i\alpha) = b_0\alpha^2 + b_1\alpha + b_2 + i[a_0\alpha^2 + a_1\alpha + a_2].$$

Comparing the two equations we get

$$a_0 = 1, \quad a_1 = -\lambda_I, \quad a_2 = -(k_{ei}k_{ie} + ab - b\lambda_R), \quad b_0 = 0,$$

$$b_1 = (a + b - \lambda_R), \quad b_2 = -b\lambda_I.$$

Applying the generalized Routh–Hurwitz criterion, we have $\mathrm{Re}(\alpha) < 0$ if the following two conditions are met:

$$\nabla_2 = \begin{vmatrix} 1 & -\lambda_I \\ 0 & (a + b - \lambda_R) \end{vmatrix} > 0$$

and

$$\nabla_4 = \begin{vmatrix} 1 & -\lambda_I & -(k_{ei}k_{ie}+ab-b\lambda_R) & 0 \\ 0(a+b-\lambda_R) & -b\lambda_I & 0 \\ 0 & 1 & -\lambda_I & -(k_{ei}k_{ie}+ab-b\lambda_R) \\ 0 & 0 & (a+b-\lambda_R) & -b\lambda_I \end{vmatrix} > 0.$$

Evaluating the above determinants and simplifying, we get

$$(a+b-\lambda_R) > 0,$$

$$(k_{ei}k_{ie}+ab-b\lambda_R)(a+b-\lambda_R)^2 - b\lambda_I^2(\lambda_R-a) > 0. \tag{9}$$

Solving the inequalities, the stability zone Ω (Fig. 3) is found to be the region to the left of the curve

$$\lambda_I^2 = \frac{(k_{ei}k_{ie}+ab-b\lambda_R)(a+b-\lambda_R)^2}{b(\lambda_R-a)}. \tag{10}$$

The pointed tip of the curve in Fig. 3 along the real axis is given by $(\min(a+b, a+k_{ie}k_{ei}/b), 0)$ and it corresponds to the symmetric coupling case.

The distance $\delta(G_{ii})$ from the center of the ith Gershgörin disc to the boundary is (Appendix B)

$$\delta(G_{ii}) = \sqrt{(a-G_{ii})^2 - b^2 - 2k_{ie}k_{ei} + 2\sqrt{k_{ie}k_{ei}[2b(a+b-G_{ii}) + k_{ie}k_{ei}]}}.$$

So the stability conditions (Eq.(5)) are given by

$$G_{ii} < \min(a+b, a+k_{ie}k_{ei}/b), \qquad \frac{1}{2}\sum_{j\neq i}(|G_{ji}| + |G_{ij}|) < \sqrt{(a-G_{ii})^2 - b^2 - 2k_{ie}k_{ei} + 2\sqrt{k_{ie}k_{ei}[2b(a+b-G_{ii}) + k_{ie}k_{ei}]}}.$$

Fig. 3. Stability zone for model Eq. (8).

We note that, since the boundary curve of the stability zone asymptotically approaches the straight line $\lambda_R = a$, we can use this line to define a new stability zone to obtain some simpler stability constraints. The distance to the new boundary is easily found to be

$$\delta_i = |a - G_{ii}|.$$

In this case, the stability condition simplifies to

$$\frac{1}{2}\sum_{j\neq i}(|G_{ji}| + |G_{ij}|) + G_{ii} < a, \qquad i = 1, 2, ..., N. \tag{11}$$

This simplified condition is a good approximation if $\min(a+b, a+k_{ie}k_{ei}/b)$ is sufficiently close to a. We further note that Eq. (11) is satisfied if

$$|G_{ij}| < a/N, \qquad i, j = 1, 2, ..., N.$$

That is, the equilibrium point is stable if
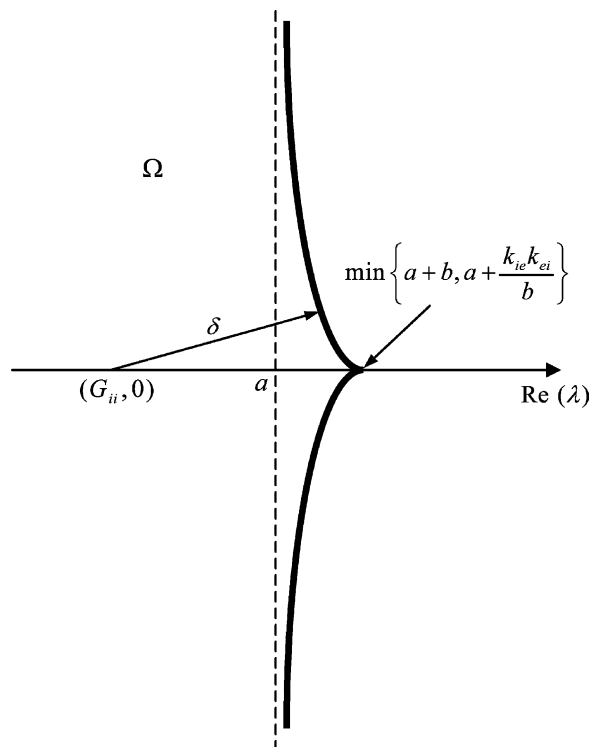
$$|c_{np}| < a \qquad \forall n, \ p = 1, 2, ..., N.$$

This simple stability bound on the individual coupling strengths can be very useful in practice.

3.3. A coupled oscillator model with M = 4

The previous model represents a neural population by a first order differential equation. This has the property that its impulse response has an instantaneous rise phase. Here we consider another model where the neural population is a second order differential equation possessing a finite rise and decay impulse response. Each individual column is described by a system of two second order differential equations (Freeman, 1975):

$$\frac{d^2x}{dt^2} + (a+b)\frac{dx}{dt} + abx = -k_{ei}Q(y, Q_m) + I,$$

$$\frac{d^2y}{dt^2} + (a+b)\frac{dy}{dt} + aby = k_{ie}Q(x, Q_m). \tag{12}$$

The parameters have the same interpretation as before. The N column equations are given by

$$\frac{\mathrm{d}^2 x_n}{\mathrm{d}t^2} + (a+b)\frac{\mathrm{d}x_n}{\mathrm{d}t} + abx_n$$

$$= -k_{ei}Q(y_n, Q_m) + \frac{1}{N}\sum_{p=1}^{N} c_{np}Q(x_p, Q_m) + I_n, \qquad (13)$$

$$\frac{\mathrm{d}^2 y_n}{\mathrm{d}t^2} + (a+b)\frac{\mathrm{d}y_n}{\mathrm{d}t} + aby_n = k_{ie}Q(x_n, Q_m),$$

where the same network topology in Fig. 2 applies.

We first consider the stability of the single column equations given in Eq. (12). When the input I is zero, the origin $x = 0$, $y = 0$ is an equilibrium point. In order to study its stability properties, we convert the above second order differential equations to the following system of first order differential equations:

$$\frac{\mathrm{d}z_1}{\mathrm{d}t} = z_2, \qquad \frac{\mathrm{d}z_2}{\mathrm{d}t} = -(a+b)z_2 - abz_1 - k_{ei}Q(z_3, Q_m),$$

$$\frac{\mathrm{d}z_3}{\mathrm{d}t} = z_4, \qquad \frac{\mathrm{d}z_4}{\mathrm{d}t} = -(a+b)z_4 - abz_3 + k_{ie}Q(z_1, Q_m),$$

where

$$z_1 = x, \qquad z_2 = \frac{\mathrm{d}x}{\mathrm{d}t}, \qquad z_3 = y, \qquad z_4 = \frac{\mathrm{d}y}{\mathrm{d}t}.$$

The Jacobian matrix $\mathbf{DF}$ is obtained as

$$\mathbf{DF} = \begin{pmatrix} 0 & 1 & 0 & 0 \\ -ab & -(a+b) & -k_{ei} & 0 \\ 0 & 0 & 0 & 1 \\ k_{ie} & 0 & -ab & -(a+b) \end{pmatrix}. \qquad (14)$$

Here we have used the fact that $Q'(0, Q_m) = 1$. For stability of the origin, the real parts of all eigenvalues of $\mathbf{DF}$ should be less than zero. The eigenvalues are determined from the characteristic equation:

$$\lambda^4 + 2(a+b)\lambda^3 + (a^2 + 4ab + b^2)\lambda^2$$
$$+ 2(a^2 b + ab^2)\lambda + k_{ie}k_{ei} + a^2 b^2 = 0.$$

Applying the Lienard–Chipart criterion (Appendix A), the real parts of all eigenvalues are negative if the following inequalities be satisfied:

$$a^2 b^2 + k_{ie}k_{ei} > 0, \qquad 2a^2 b + 2ab^2 > 0, \qquad 2a + 2b > 0,$$

$$-4k_{ie}k_{ei} + 4ab(a+b)^2 > 0.$$

Since a, b, k_{ei}, $k_{ie} > 0$, the first three inequalities are automatically satisfied. After simplification, the last inequality can be written as:

$$k_{ie}k_{ei} < ab(a+b)^2. \qquad (15)$$

To summarize, the origin is stable for the single column equations if the above condition is satisfied. Henceforth, we will assume that this is true.

Next, we consider the stability of a network of coupled columns given in Eq. (13). Here

$$[\mathbf{G}]_{np} = \frac{c_{np}}{N},$$

and

$$\mathbf{DH} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}$$

As before, we examine the eigenvalue α of the matrix $\mathbf{DF} + \lambda \cdot \mathbf{DH}$ as a function of λ. The characteristic polynomial of this matrix is given by

$$f(\alpha) = \alpha^4 + 2(a+b)\alpha^3 + [(a+b)^2 + 2ab - \lambda]\alpha^2$$
$$+ [2ab(a+b) - \lambda(a+b)]\alpha + [a^2 b^2 - ab\lambda + k_{ie}k_{ei}].$$

For complex λ, we are not able to obtain an analytical form for the stability zone Ω, since the characteristic equation results in a eighth order polynomial when applying the generalized Routh–Hurwitz criterion. However, numerical results are always possible. Fig. 4 shows the stability zone Ω when $a = 0.22$, $b = 0.72$, $k_{ie} = 0.1$, $k_{ei} = 0.4$. After numerically finding the distance $\delta(G_{ii})$ from the center of the ith Gershgörin disc to the boundary curve, Eq. (5) can again be used to give the stability criteria.

If the coupling is symmetric, which implies that λ is real, the stability boundary is just the rightmost tip of the curve along the real axis in Fig. 4. Then the distance δ is given by the absolute difference between the coordinates of the tip point and the center of the ith Gershgörin disc. This tip can be determined as follows.
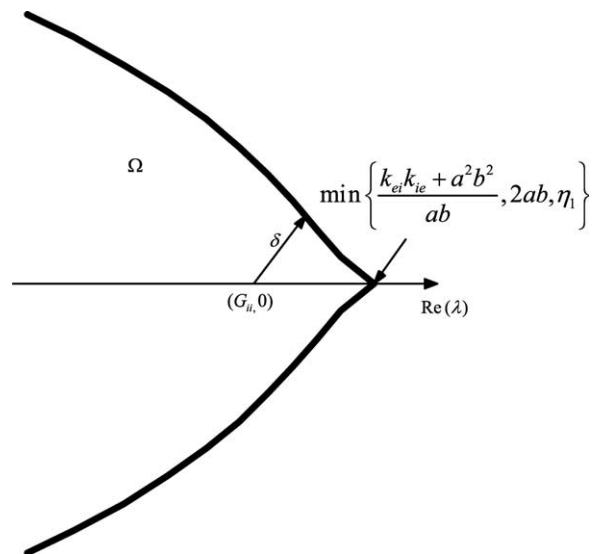

Fig. 4. Stability zone for model Eq. (13).

Again applying the Lienard–Chipart criterion (Appendix A), the real parts of all eigenvalues are negative if the following inequalities are satisfied:

$$a^2b^2 - ab\lambda + k_{ie}k_{ei} > 0,$$

$$2ab(a+b) - \lambda(a+b) > 0, \qquad 2(a+b) > 0, \qquad (16)$$

$$\lambda^2 - 2(a+b)^2\lambda + 4(a^3b + 2a^2b^2 + ab^3 - k_{ie}k_{ei}) > 0.$$

Since a, b are positive, the third inequality is automatically satisfied. After simplification, the first two inequalities become

$$\lambda < \frac{k_{ie}k_{ei} + a^2b^2}{ab}, \qquad \lambda < 2ab.$$

The last inequality is of the form

$$a_1\lambda^2 - a_2\lambda + a_3 > 0,$$

where

$$a_1 = 1, \quad a_2 = 2(a+b)^2, \quad a_3 = 4[ab(a+b)^2 - k_{ie}k_{ei}].$$

Note that a_1, a_2 are obviously positive. It turns out a_3 is also positive because of the local stability condition derived in Eq. (15). The quadratic function $a_1\lambda^2 - a_2\lambda + a_3$ with a_1, a_2, a_3 positive has a unique global minimum at $\lambda = a_2/2a_1$. Thus the minimum occurs at a positive value of λ. It is also seen that

$$a_2^2 - 4a_1a_3 = 4[(a+b)^4 - 4[ab(a+b)^2 - k_{ie}k_{ei}]].$$

This can be simplified as

$$a_2^2 - 4a_1a_3 = 4[(a^2 - b^2)2 + 4k_{ie}k_{ei}],$$

which is positive since $k_{ie}k_{ei}$ is positive. Thus both the zeros of the quadratic function (we will denote them η_1 and η_2 with $\eta_1 < \eta_2$) are real. Further, since $a_3 > 0$ and the global minimum occurs at a positive value, $\eta_2 > \eta_1 > 0$. Consequently, the last inequality is satisfied when $\lambda < \eta_1$ or $\lambda > \eta_2$ where

$$\eta_{1,2} = (a+b)^2 \pm \sqrt{(a^2 - b^2)^2 + 4k_{ie}k_{ei}}.$$

Note that η_1 is explicitly seen to be positive by applying Eq. (15). Further, $\eta_2 > (a+b)^2 > 2ab$. Thus the inequality $\lambda > \eta_2 > 2ab$ is not possible given the stability condition $\lambda < 2ab$ derived earlier. Therefore, the last inequality in Eq. (16) reduces to $\lambda < \eta_1$.

Summarizing, we get the following set of stability conditions:

$$\lambda < \frac{k_{ie}k_{ei} + a^2b^2}{ab}, \qquad \lambda < 2ab, \qquad \lambda < \eta_1.$$

Let

$$\kappa = \min\left\{\frac{k_{ie}k_{ei} + a^2b^2}{ab}, 2ab, \eta_1\right\},$$

then all these inequalities will be simultaneously satisfied if

$$\lambda < \kappa. \qquad (17)$$

Thus the rightmost tip of the boundary curve along the real axis is $(\kappa, 0)$. Therefore, the distance function $\delta(G_{ii})$ is given by

$$\delta(G_{ii}) = |\kappa - G_{ii}|, \qquad i = 1, 2, ..., N. \qquad (18)$$

Applying Eq. (5), we obtain the following stability condition for the present model with symmetric couplings:

$$\frac{1}{2}\sum_{j\neq i}(|G_{ji}| + |G_{ij}|) + G_{ii} \leq \kappa, \qquad i = 1, 2, ..., N. \qquad (19)$$

As we discussed before, this condition is satisfied if the individual coupling strengths obey the following stability constraints:

$$|c_{np}| < \kappa, \qquad \text{for } c_{np} = c_{pn}, \ n, p = 1, 2, ..., N. \qquad (20)$$

4. Conclusions

We have presented a general method for studying the stability of the equilibrium state in neural network models. When the single-neuron coupled networks, such as Hopfield type of models, are studied, the stability result from our general approach coincides with the known result found in the literature. As a harder application, two typical neural population models where the individual nodes are higher dimensional were considered. The stability of the first model, a coupled network of two-dimensional systems, was solved completely. For the second model, a coupled network of four-dimensional systems, stability criteria for symmetric coupling was given analytically. For the nonsymmetric case, our method was used to obtain numerical criteria. Through the above examples we have demonstrated that our general method is applicable to arbitrary neural networks where the individual nodes can themselves be high dimensional. When the dimension of the individual node is not too high, analytical results are possible.

From the stability criteria, we also derived simple bounds on the coupling strengths which ensure stability. These bounds put a limit on the magnitude of change that the coupling strengths can undergo in the process of statistical learning.

Acknowledgements

Appendix A

In this section, we state the Lienard–Chipart and generalized Routh–Hurwitz criteria. The statements are taken directly from Gantmacher (1964) and are given here for the sake of completeness.

A.1. Lienard–Chipart criterion

Consider a real polynomial

$$f(z) = a_0 z^n + a_1 z^{n-1} + \cdots + a_n,$$

with $a_0 > 0$. Necessary and sufficient conditions for all the zeros of the polynomial to have negative real parts can be given in any one of the following forms (Gantmacher, 1964):

(1) $a_n > 0, a_{n-2} > 0, \ldots; \Delta_1 > 0, \Delta_3 > 0, \ldots,$
(2) $a_n > 0, a_{n-2} > 0, \ldots; \Delta_2 > 0, \Delta_4 > 0, \ldots,$
(3) $a_n > 0, a_{n-1} > 0, a_{n-3} > 0, \ldots; \Delta_1 > 0, \Delta_3 > 0, \ldots,$
(4) $a_n > 0, a_{n-1} > 0, a_{n-3} > 0, \ldots; \Delta_2 > 0, \Delta_4 > 0, \ldots$

Here Δ_p is the Hurwitz determinant of order p given by the formula

$$\Delta_p = \begin{vmatrix} a_1 & a_3 & a_5 & \ldots & \\ a_0 & a_2 & a_4 & \ldots & \\ 0 & a_1 & a_3 & \ldots & \\ 0 & a_0 & a_2 & a_4 & \\ & & & \ddots & \\ & & & & a_p \end{vmatrix}, \qquad p = 1, 2, \ldots, n,$$

where $a_k = 0$ for $k > n$. In the literature, the equivalent Routh–Hurwitz criterion is usually used. But the Lienard–Chipart is better since the number of determinants that have to be evaluated is half the number that have to be evaluated for the Routh–Hurwitz criterion. This leads to a simpler set of inequalities that need to be evaluated. In the main text, we use the third form of the Lienard–Chipart criterion given above.

A.2. Generalized Routh–Hurwitz criterion

Consider a polynomial $f(z)$ with complex coefficients. Suppose that

$$f(iz) = b_0 z^n + b_1 z^{n-1} + \cdots + b_n + i(a_0 z^n + a_1 z^{n-1} + \cdots + a_n),$$

where $a_0, a_1, \ldots, a_n, b_0, b_1, \ldots, b_n$ are real numbers. If the degree of $f(z)$ is n, then $b_0 + ia_0 \neq 0$. Without loss of

generality, we may assume that $a_0 \neq 0$. Otherwise, we consider the polynomial $g(z) = -if(z)$ and repeat the analysis for this polynomial. Both $f(z)$ and $g(z)$ have the same set of zeros and so no information is lost. This is the case considered in the main text.

If $\nabla_{2n} \neq 0$, then all the zeros of $f(z)$ have negative real parts if

$$\nabla_2 > 0, \nabla_4 > 0, \ldots, \nabla_{2n} > 0,$$

where

$$\nabla_{2p} = \begin{vmatrix} a_0 & a_1 & \cdots & a_{2p-1} \\ b_0 & b_1 & \cdots & b_{2p-1} \\ 0 & a_0 & \cdots & a_{2p-2} \\ 0 & b_0 & \cdots & b_{2p-2} \\ \vdots & & \ddots & \vdots \end{vmatrix}, \qquad p = 1, 2, \ldots, n,$$

where $a_k = b_k = 0$ for $k > n$. Note that the condition $\nabla_{2n} \neq 0$ would be satisfied for a generic set of parameter values. This is especially true in our case where a_k, b_k are functions of system parameters.

Appendix B

The distance γ from the center $(G_{ii}, 0)$ of the ith Gershgörin disc to any point on the boundary of the stability zone is given by

$$\gamma^2 = (\lambda_R - G_{ii})^2 + \lambda_I^2$$

Substituting λ_I from Eq. (10) and differentiating with respect to λ_I, we have

$$\frac{d\gamma^2}{d\lambda_R} = 2(\lambda_R - G_{ii}) - \frac{(a + b - \lambda_R)^2}{(\lambda_R - a)}$$
$$+ \frac{[(\lambda_R - a)^2 - b^2](ab + k_{ie}k_{ei} - b\lambda_R)}{b(\lambda_R - a)^2}.$$

Setting $(d\gamma^2/d\lambda_R) = 0$, we get two solutions:

$$\lambda_R = a \pm b\sqrt{\frac{k_{ie}k_{ei}}{2b(a + b - G_{ii} + k_{ie}k_{ei})}}.$$

Since the boundary of Ω lies to the right of the point $(a, 0)$, we can discard the smaller solution. Substituting the remaining solution in the equation for γ^2 and taking the square root, we get the shortest distance as

$$\delta_i = \gamma_{\min} = \sqrt{(a - G_{ii})^2 - b^2 - 2k_{ie}k_{ei} + 2\sqrt{k_{ie}k_{ei}[2b(a + b - G_{ii}) + k_{ie}k_{ei}]}}, \qquad i = 1, 2, \ldots, N.$$

References

Atiya, A. F. (1988). Learning on a general network. In D. A. Anderson (Ed.), *Neural information processing systems*. New York: American Institute for Physics.

Baird, B. (1990). Bifurcation and category learning in network models of oscillatory cortex. *Physica D*, *42*, 365–384.

Buhmann, J. M. (1995). Oscillatory associative memories. In M. A. Arbib (Ed.), *The handbook of brain theory and neural networks*. Cambridge: MIT Press.

Carpenter, G. A., Cohen, M. A., & Grossberg, S. (1987). Computing with neural networks. *Science*, *235*, 1226–1227.

Chen, T., & Amari, S. (2001). Stability of asymmetric Hopfield networks. *IEEE Transactions on Neural Networks*, *12*(1), 159–163.

Destexhe, A. (1994). Oscillations, complex spatiotemporal behavior, and information transport in networks of excitatory and inhibitory neurons. *Physical Review E*, *50*(2), 1594–1606.

Fang, Y., & Kincaid, T. G. (1996). Stability analysis of dynamical neural networks. *IEEE Transactions on Neural Networks*, *7*, 996–1006.

Feng, J., & Brown, D. (1998). Fixed-point attractor analysis for a class of neurodynamics. *Neural Computation*, *10*, 189–213.

Freeman, W. J. (1975). *Mass actions in the nervous system*. New York: Academic Press.

Gantmacher, F. R. (1964). *Theory of matrices*. New York: Chelsea.

Guez, A., Protopopsecu, V., & Barhen, J. (1988). On the stability, storage capacity and design of nonlinear continuous neural networks. *IEEE Transactions on Systems, Man, Cybernetworks*, *18*, 80–87.

Hirsch, M. W. (1989). Convergent activation dynamics in continuous time networks. *Neural Networks*, *2*(5), 331–349.

Hirsch, M. W., & Smale, S. (1974). *Differential equations, dynamical systems, and linear algebra*. New York: Academic Press.

Hoppendsteadt, F. C., & Izhikevich, E. M. (Eds.), (1997). *Weakly connected neural networks*. New York: Springer.

Horn, R. A., & Johnson, C. R. (1990). *Matrix analysis*. Cambridge: Cambridge University Press.

Kelly, D. G. (1990). Stability in contractive nonlinear neural networks. *IEEE Transactions on Biomedical Engineering*, *37*, 231–242.

Li, Z. (1994). Modeling the sensory computations of the olfactory bulb. In E. Domany, J. L. van Hemmen, & K. Schulten (Eds.), *Models of neural networks II: Temporal aspects of coding and information processing in biological systems*. New York: Springer.

Li, Z. (1999). Visual segmentation by contextual influences via intra-cortical interactions in the primary visual cortex. *Network: Compu-tional Neural Systems*, *10*, 187–212.

Li, Z. (2001). Computational design and nonlinear dynamics of a recurrent network model of the primary visual cortex. *Neural Computation*, *13*(8), 1749–1780.

Li, Z., & Dayan, P. (1999). Computational differences between asymme-trical and symmetrical networks. *Network: Computional Neural Systems*, *10*(1), 59–77.

Li, Z., & Hopfield, J. J. (1989). Modeling the olfactory bulb and its neural oscillatory processings. *Biological Cybernetworks*, *61*, 379–392.

Liang, X. B., & Wu, L. D. (1998). New sufficient conditions for absolute stability of neural networks. *IEEE Transaction on Circuit Systems I*, *45*, 584–586.

Matsuoka, K. (1991). On absolute stability of neural networks. *Trans-actions of the Institute of Electrical Communication Engineering, Japan, J74-D-11*, 536–542.

Michel, A. N., Farrell, J. A., & Porod, W. (1989). Qualitative analysis of neural networks. *IEEE Transactions on Circuit Systems*, *36*, 229–243.

Sugawara, K., Harao, M., & Noguchi, S. (1983). On the stability of equilibrium states of analogue neural networks. *Transactions of the Institute of Electrical Communication Engineering, Japan, J66*, 258–265.

Truccolo, W. A., Ding, M., & Bressler, S. L. (2000). Stability constraints for oscillatory neural networks. *Neurocomputing*, *32/33*, 585–589.

Wersing, H., Beyn, W.-J., & Ritter, H. (2001). Dynamical stability conditions for recurrent neural networks with unsaturating piecewise linear transfer functions. *Neural Computation*, *13*, 1811–1825.

Whittle, P. (1998). *Neural nets and chaotic carriers*. New York: Wiley.

Wilson, H., & Cowan, J. D. (1972). Excitatory and inhibitory interactions in localized populations of model neurons. *Biophysics Journal*, *12*, 1–24.

Yang, H., & Dillon, T. S. (1994). Exponential stability and oscillation of Hopfield graded response neural network. *IEEE Transactions on Neural Networks*, *5*(5), 719–729.

Yao, Y., & Freeman, W. J. (1990). Model of the biological pattern recognition with spatially chaotic dynamics. *Neural Networks*, *3*, 153–170.