14
Investigation of Input–Output Gain in Dynamical Systems for Neural Information Processing

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14.1
Overview

The processing of sensory signals in the human cortex is currently the subject of numerous studies, both at an experimental and a theoretical level. These studies investigate the principles of interactions between pairs of cortical areas. Different theoretical models have been derived from the experimental results and then proposed, in order to describe the processing of stimuli in V1, the primary visual cortex.

Several models assume layers of discrete sets of neurons arranged in a regular grid structure to be coupled via feedforward and feedback connections. These local connection structures can be considered as local filters of parametrized spread, which implement local center-surround interactions as well as modulatory outer-surround ones. In such representations of two-layer architectures, at each location, pairs of neurons define a local recurrent system of two neurons that is driven by an external input to one of those neurons. In this contribution we provide an elementary mathematical investigation of the stability of a core model of feedforward processing that is modulated by feedback signals. The model essentially consists of a system of coupled nonlinear first-order differential equations. In this paper we will address the issues of the existence, asymptotics, and dependence on parameters of the corresponding solutions.

14.2
Introduction

The cerebral cortex is organized into different areas, each of them consisting of several layers of neurons that are connected via feedforward, feedback, and lateral connections. The human cortical architecure is organized in a hierarchical struc-

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ture of mutually interacting stages and the majority of cortical areas are connected bidirectionally, see [6], whereas *lateral connections* enable the interaction of neurons in the same layer.

Several empirical studies have investigated the principles of cortical interactions between pairs of bidirectionally coupled cortical areas, particularly at early stages in the processing hierarchy. For example, it has been shown that the analysis of input stimuli in the primate visual cortex is mainly driven by propagation and filtering along feedforward neural pathways. The output of such filtering processes are modulated by activations in a neighborhood in the spatial or feature domain (via lateral connections) as well by activations at stages higher up in the hierarchy (via fast-conducting feedback connections, see [8]).

Several authors have investigated the influence of higher cortical stages on responses in the primary visual sensory area of the cortex (commonly denoted by V1), and in particular, the shaping of feature selectivity of neurons at the earlier stage. Ample experimental evidence exists, [4, 9, 14, 15], which supports the view that the interaction between neural signals along different directions of signal flow can be characterized by basic properties such as driving feedforward processing and modulation of activation patterns by higher-order activities via top-down feedback processing. Several computational neural models that draw upon these empirical findings have been proposed. The feedforward and feedback processing along mutually excitatory connections raises the question of stability in such neural networks.

Most of the proposed developments have been derived on the basis of numerical and experimental investigations. In the present paper we consider the model proposed by Neumann and coworkers [1, 13, 17]. It features a modulatory feedback mechanism for feature enhancement along various dimensions of input signal features, such as oriented contrast, texture boundaries, and motion direction. These gain-enhancement mechanisms are combined with subsequent competitive mechanisms for feature enhancement. The architecture of this model is well-behaved, i.e. it complies with basic assumptions of the theory and, in particular, the neural activities appear stable for large ranges of parameter settings.

At a mathematical level, this model essentially consists of a coupled system of nonlinear first-order Ordinary Differential Equations (ODEs). No formal mathematical analysis of this neural model has yet been performed. The aim here is to discuss the existence and uniqueness of solutions to the systems, as well as to present an elementary stability analysis dependent on the settings.

The mechanisms of the considered model can be summarized as defining a cascade consisting of three computational stages, see Figure 14.1.

1. An initial (linear) feedforward filtering stage along any feature dimension.

2. A modulatory feedback activation from higher cortical stages (via top-down connections) or lateral intra-cortical activation (via long-range connections).

3. A final competitive center-surround interaction at the output stage.

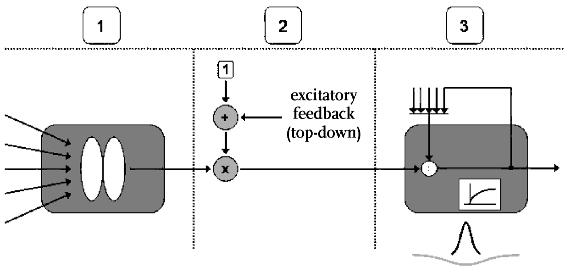

Fig. 14.1 Scheme of the model circuit composed of three sequential stages. For a mathematical description of the computational stages, see text.

The different steps can be adequately modeled by a coupled system of ordinary differential equations. The core equations can be summarized as follows:

$$\frac{\mathrm{d}c(t)}{\mathrm{d}t} = -c(t) + B\,\{s * \Gamma\}\,(t) \tag{14.1}$$

$$\frac{\mathrm{d}x(t)}{\mathrm{d}t} = -A\;x(t) + Bc(t)\left(1 + Cz^{\mathrm{FB}}(t)\right) \tag{14.2}$$

$$\frac{\mathrm{d}y(t)}{\mathrm{d}t} = -A\;y(t) + Bf(x(t)) - (D + Ey(t))\,\{f(x) * \Lambda\}\,(t)\;. \tag{14.3}$$

The evolution of the input filtering is described by (14.1): s denotes the feedforward driving input, c is the filtered input or simply the input and Γ is a filter which is properly selected for the current processing scheme and goals (here $*$ denotes the convolution operation). The first negative term on the r.h.s of all three equations represents a decay term.

The second stage, modeled in (14.2), computes the activity x of a model neuron in terms of its potential. Such activity is assumed to be driven by the input c plus a feedback input. The feedback signal z^{FB} is a function of the output stage y, namely $z^{\mathrm{FB}} = g(y)$. The core nonlinearity for selective modulatory enhancement of inputs c is generated by the gating mechanism $(1 + Cz^{\mathrm{FB}}(t))$, i.e. the feedback z^{FB} will be controlled by the input c in a multiplicative form. If no input is present, available feedback should not generate new activation, whereas if available input is not supported by any feedback, the feedforward activity should not be suppressed. In case both input as well as feedback activation are available, this always leads to an enhancement of activation at time t by an amount $c(t) \cdot C \cdot z^{\mathrm{FB}}(t)$ which is proportional to the product between feedforward and feedback activity.

The third stage describes, in (14.3), the evolution of the activity y of a second interacting neuron. A feedforward excitatory term $f(x)$ and an inhibitory term $(D + Ey(t))\,\{f(x) * \Lambda\}\,(t)$ are present. The inhibitory term accounts for the lateral connections from the first layer of neurons (the lower neuron in Figure 14.2) through the convolution of $f(x)$ with the inhibitory kernel Λ. The term $Ey(t)$ normalizes the x-activities in the pool of cells covered by the inhibitory kernel.

The parameters A, B, C, D and E are constants. The simplest choice for the function f in (14.3) is the identity function: $f(x) = x$. Another possible choice that results in a faster increase of the activity is $f(x) = x^2$. The function g in (14.2) accounts for net computational effects of higher stages taking y activities as input and transforming them nonlinearly, before feeding the result into the feedback signal pathway. A common choice for g is a sigmoid function.

For stationary input luminance distributions, $\mathrm{d}c(t)/\mathrm{d}t = 0$, and the resulting equilibrium term for c can be treated as a constant c_0 for the remaining two equations to describe activities x and y, respectively. Throughout we will impose this (quite restrictive) assumption, which dramatically simplifies the analysis of the system's time evolution.

In the case of stationary input, c is commonly referred to as *tonic input*: the input is switched on and is kept constant during the evolution process of the dynamical system. Under this assumption, (14.2) simplifies to read

$$\frac{\mathrm{d}x(t)}{\mathrm{d}t} = -A\,x(t) + Bc_0\left(1 + Cz^{\mathrm{FB}}(t)\right) . \tag{14.4}$$

Under certain circumstances (as, e.g. in the case of spatially constant input), the inhibitory convolution term $\{f(x) * \Lambda\}(t)$ of (14.3) can be simply replaced by a point evaluation, i.e. by $f(x)(t)$, thus neglecting lateral connections.[2] In the absence of lateral connections, we are thus led to consider

$$\frac{\mathrm{d}y(t)}{\mathrm{d}t} = -A\,y(t) + (B - D)f(x(t)) - Ey(t)f(x(t)) \tag{14.5}$$

instead of (14.3). Such a modified setting is clearly easier to investigate than a system with spatio-temporally varying external input. In order to fix the ideas, we will begin by studying this simplified model in Section 14.3. This will allow us to discuss elementary properties of the system using simple linear algebraical tools for the qualitative analysis of ODEs.

We can consider our model as a two-dimensional dynamical system with unknowns $x = x(t)$ and $y = y(t)$. A symbolic representation of this two-dimensional system given by (14.4)–(14.5) is shown in Figure 14.2. This basic unit, namely the recurrent connected pair of neurons x, y will be called *dipole* in the following. The dynamics of this two-dimensional system, which represents our basic unit, will be studied in Section 14.3.

It is, in fact, more realistic to consider (14.3), thus modeling (via the inhibitory kernel Λ) the lateral connections among neurons in the same hierarchical layer. A possible choice for this kernel is a Gaussian function. This can be interpreted as if the dipoles were mutually interconnected in a *ring* structure, as sketched in Figure 14.3. The mathematical properties of this ring architecture will be briefly discussed in Section 14.5.

2) Please note that $f(x(t)) \equiv f(x)(t)$ holds, since we have assumed a spatially constant input distribution within the extent of a spatial kernel Λ.

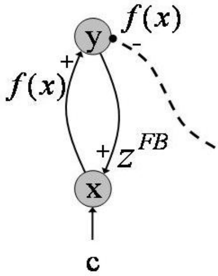

Fig. 14.2 The basic unit of our model: the dipole. Two neurons are coupled via feedforward and feedback connections. The solid line indicates excitatory connections, the dashed line indicates inhibitory connections. See text for details.

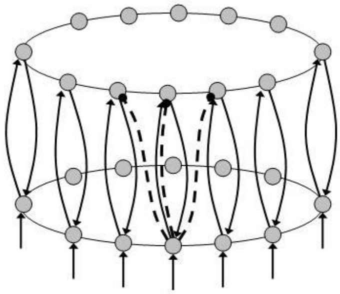

Fig. 14.3 The basic units are coupled recurrently to form a ring structure. See Figure 14.2 and text where the basic unit is isolated and explained.

14.3
The Basic Unit: Analytical Study of the Dipole

The model we consider consists of interconnected rings. Each ring arises as the coupling of smaller basic units, namely of recurrently connected pairs of neurons, which we call a *dipole*. The aim of this section is to investigate the behavior of a single dipole. In particular, we neglect the lateral connections and discuss the problem given by (14.4)–(14.5). Observe that in our model neurons are schematized as point-like, lumped structures: there is no delay in their interactions and, what is more important, their spatial structure is neglected. Although not quite realistic, this assumption greatly simplifies the mathematical description of the system; see [2] for a discussion of the relations between lumped and nonlumped models. For the case of stationary input, the initial value problem associated with the two-dimensional system introduced in (14.4)–(14.5) can be written in the more general form as

$$\begin{cases} \dot{x}(t) &=& -\alpha x(t) + \beta\big(1 + \gamma g(y(t))\big) \\ \dot{y}(t) &=& -\eta y(t) + \big(\delta - \varepsilon h(y(t))\big) f(x(t)) \\ x(0) &=& x_0 \in \mathbb{R} \\ y(0) &=& y_0 \in \mathbb{R}\,, \end{cases} \tag{14.6}$$

where $\dot{x}(t)$ and $\dot{y}(t)$ denote the time derivative of x, y. Here β depends on the input c_0, which we have assumed to be stationary. Moreover, the *activation parameters*

$\alpha, \gamma, \delta, \varepsilon, \eta$ are constants and f, g, h are real functions. In particular, g and f describe a feedback and feedforward activation, respectively. Thus, the initial value problem associated with (14.4)–(14.5) is actually only a special case of (14.6), after appropriate choice of parameters. We have preferred to perform qualitative analysis of this more general problem, instead on focusing of the special case introduced in Section 14.2.

In particular, the term $Bc(t)$ in (14.2) corresponds to β in the above problem. This is justified by the standing assumption that the input luminance distribution is stationary, and hence that $c(t) = c_0$, a constant. Therefore, $\beta = Bc_0$, and we can consider it as a *parameter* (which we are free to choose) depending on the (constant) input that we are feeding the system. We emphasize that our results do not hold in the general case when $\beta = \beta(t)$, i.e. if $c = c(t)$.

The above system of coupled first-order ODEs can be equivalently represented as a single Cauchy problem

$$\begin{cases} \dot{u}(t) &= F(u(t)) \\ u(0) &= u_0 \in \mathbb{R}^2 , \end{cases} \tag{CP}$$

to which we can apply standard mathematical results. Here $u := (x, y)$ and $u_0 := (x_0, y_0)$, while F is the nonlinear function on $\mathbb{R}^2$ defined by

$$F(x, y) := \begin{pmatrix} -\alpha x + \beta(1 + \gamma g(y)) \\ -\eta y + (\delta - \varepsilon h(y))f(x) \end{pmatrix} .$$

14.3.1
Well-Posedness Results

To begin with, we observe that the problem formulated above admits a solution, i.e. a pair $(x(t), y(t))$ satisfying (14.6).

Lemma 14.1 (The following assertions hold.)

(1) Let $f, g, h : \mathbb{R} \to \mathbb{R}$ be continuous. Then for all $x_0, y_0 \in \mathbb{R}$ there exists at least one solution of (14.6)*, locally in time.*

(2) Let moreover $f, g, h : \mathbb{R} \to \mathbb{R}$ be locally Lipschitz continuous. If $f(0) = h(0) = 0$, then there exists a unique solution of (14.6)*, locally in time.*

(3) Let finally $f, g, h : \mathbb{R} \to \mathbb{R}$ be globally Lipschitz continuous. If f or h is bounded, then the unique solution of (14.6) *is defined for all $t \in \mathbb{R}$.*

Proof

(1) The function F is clearly continuous. Thus, the assertion follows from Peano's existence theorem.

(2) Let $R > 0$ and $x, \tilde{x}, y, \tilde{y} \in B(0, R) := \{z \in \mathbb{R} : \|z\| \leq R\}$. Then one has

$$\begin{aligned}
\left\|F(x,y) - F(\tilde{x},\tilde{y})\right\| &\leq |\alpha|\|x - \tilde{x}\| + |\eta|\|y - \tilde{y}\| \\
&\quad + |\gamma|\|g(y) - g(\tilde{y})\| + |\delta|\|f(x) - f(\tilde{x})\| \\
&\quad + |\varepsilon|\|h(y)f(x) - h(\tilde{y})f(\tilde{x})\| \\
&\leq (|\alpha| + |\delta|L_f)\|x - \tilde{x}\| + (|\eta| + L_g)\|y - \tilde{y}\| \\
&\quad + |\varepsilon|\|h(y) - h(0)\|L_f\|x - \tilde{x}\| \\
&\quad + |\varepsilon|L_h\|y - \tilde{y}\|\|f(\tilde{x}) - f(0)\| \\
&\leq (|\alpha| + |\delta|L_f)\|x - \tilde{x}\| + (|\eta| + L_g)\|y - \tilde{y}\| \\
&\quad + |\varepsilon|L_f L_h R\|x - \tilde{x}\| + |\varepsilon|RL_f L_h\|y - \tilde{y}\| \;,
\end{aligned}$$

where L_f, L_g, L_h denote the Lipschitz constants of f, g, h, respectively. This shows that F is locally Lipschitz continuous, and the uniqueness of a local solution is as a consequence of the Picard–Lindelöf theorem.

(3) It suffices to observe that F is globally Lipschitz continuous under the above assumptions. □

Having proved the well-posedness of the system, we now investigate its stability properties. Along the nullclines of the system we have

$$\alpha x(t) = \beta + \beta\gamma g(y(t)) \qquad \text{and} \qquad \eta y(t) = \delta f(x(t)) - \varepsilon h(y(t)) f(x(t)) \;,$$

respectively.

As already mentioned in Section 14.2, the activation functions f and h are commonly assumed to satisfy $f(0) = h(0) = 0$. Accordingly, we deduce that $(\bar{x}, \bar{y}) \equiv 0$ is an equilibrium point provided that $\beta(1 + \gamma g(0)) = 0$ (the converse is true if $\alpha \neq 0$). As already mentioned, in many models g is a sigmoid function and, in particular, $g(0) = 0$. Therefore, we have just observed that in absence of input (i.e. if $\beta = 0$) the only stationary state is the inactive state (i.e. $x(t) = y(t) \equiv 0$). The aim of the following section is to prove the existence of stationary solutions to (14.6) also in the case of nontrivial input.

14.3.2 Linearization

We show that equilibrium points also appear in the case of $\beta \neq 0$, corresponding to constant but nonvanishing inputs. For the sake of simplicity, in the remainder of this note we impose the realistic assumption that

$$f(0) = g(0) = h(0) = 0 \;. \tag{14.7}$$

We consider (14.6) as a dynamical system dependent on the parameters $\alpha, \beta, \gamma, \varepsilon, \delta, \eta$. CE We are going to show that the choice of the parameters $\gamma, \delta, \varepsilon$ is irrelevant for the existence of a stationary state, whereas specific conditions have to be imposed on parameters α and η. We then find a curve of stationary states in a neighborhood of the origin. This allows us to discuss some basic bifurcation properties of our system.

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Theorem 14.1 *Let $\gamma, \delta, \varepsilon$ be fixed real numbers and f, g, h be given continuously differentiable activation function satisfying* (14.7)*. Then the following assertions hold.*

1. *For all parameters α_0, η_0 such that $\alpha_0\eta_0 \neq 0$ there exists a neighborhood U of $(\alpha_0, 0, \eta_0)$ and a continuous differentiable function $\kappa = (\kappa_1, \kappa_2)$ such that $(x, y) = (\kappa_1(\alpha, \beta, \eta), \kappa_2(\alpha, \beta, \eta))$ is a stationary state for all $(\alpha, \beta, \eta) \in U$.*
2. *The system has a bifurcation in $(\overline{x}, \overline{y}) = (0, 0)$ for $\beta = 0$ and all parameters α_0, η_0 such that $\alpha_0\eta_0 = 0$.*

Proof

(1) Fix $\gamma, \delta, \varepsilon \in \mathbb{R}$. Define a function $\Phi : \mathbb{R}^2 \times \mathbb{R}^3 \to \mathbb{R}^2$ by

$$\Phi\begin{pmatrix} (x, y) \\ (\alpha, \beta, \eta) \end{pmatrix} := \begin{pmatrix} -\alpha x + \beta + \beta\gamma g(y) \\ -\eta y + \delta f(x) - \varepsilon h(y) f(x) \end{pmatrix} .$$

In other words, for fixed parameters $\gamma, \delta, \varepsilon$ and for given α, β, η one has

$$\Phi\begin{pmatrix} (\cdot, \cdot) \\ (\alpha, \beta, \eta) \end{pmatrix} = F\big((\cdot, \cdot)\big) .$$

Then Φ is a continuously differentiable function, and its partial differential with respect to the first two variables is given by

$$D_{xy}\Phi\begin{pmatrix} (x, y) \\ (\alpha, \beta, \eta) \end{pmatrix} = \begin{pmatrix} -\alpha & \beta\gamma g'(y) \\ (\delta - \varepsilon h(y)) f'(x) & -\varepsilon h'(y) f(x) - \eta \end{pmatrix} \tag{14.8}$$

For $\beta = 0$ and arbitrary coefficients α_0, η_0 the vector $(x, y) = (0, 0)$ is an equilibrium point of the system (14.6) since

$$\Phi\begin{pmatrix} (0, 0) \\ (\alpha_0, 0, \eta_0) \end{pmatrix} = 0 .$$

In order to apply the implicit function theorem, compute the determinant of $D_{xy}\Phi$ in the point $((0, 0), (\alpha_0, 0, \eta_0))$. This is given by

$$det D_{xy}\Phi\begin{pmatrix} (0, 0) \\ (\alpha_0, 0, \eta_0) \end{pmatrix} = \det\begin{pmatrix} -\alpha_0 & 0 \\ \delta f'(0) & -\eta_0 \end{pmatrix} = \alpha_0\eta_0 , \tag{14.9}$$

because of the assumptions (14.7). By the implicit function theorem, there exist neighborhoods U of $(\alpha_0, 0, \eta_0) \in \mathbb{R}^3$ and V of $(0, 0) \in \mathbb{R}^2$ and a continuously differentiable function $\kappa : U \to V$ such that

- $\Phi(\kappa(\alpha_0, 0, \eta_0), \alpha_0, 0, \eta_0) = 0$ and
- for all $(x, y, \alpha, \beta, \eta) \in V \times U$ the point (x, y) is a stationary state with respect to parameters α, β, η if and only if $(x, y) = \kappa(\alpha, \beta, \eta)$.

(2) We have observed that the trivial state $(0, 0)$ is a stationary state if and only if $\beta = 0$. If $\alpha_0\eta_0 = 0$, then $\det D_{xy}\Phi((0, 0), (\alpha_0, 0, \eta_0)) = 0$ and the implicit function theorem fails to apply. Thus, the system has a bifurcation. □

By the above theorem it is possible to investigate the stability of our system by linearizing around the stationary state $(\overline{x}, \overline{y}) = (0, 0)$. To this end, we assume throughout that $\alpha\eta \neq 0$. By continuity, the asymptotic behaviour of the infinitely many stationary points whose existence has been proved in Theorem 14.1.(1) is the same of that of the stationary point $(0, 0)$. We can therefore restrict ourselves to investigating stability issues of (CP) for the case $(\overline{x}, \overline{y}) = (0, 0)$ and $\beta = 0$, only: we thus obtain the linearized Cauchy problem

$$\begin{cases} \dot{v}(t) &= DF(0,0)v(t) \\ v(0) &= u_0 \in \mathbb{R}^2 \, . \end{cases} \tag{lCP}$$

The Fréchet derivative $DF(0, 0)$ of F at $(0, 0)$ has been computed in (14.9): denoting by $T(t)$ the exponential of the 2×2 matrix $DF(0, 0)$, i.e.,

$$T(t) = \begin{pmatrix} e^{-t\alpha} & 0 \\ \delta f'(0)e^{-t\eta} & e^{-t\eta} \end{pmatrix} ,$$

the solution to (lCP) can be written as

$$v(t) = T(t)(x_0, y_0) \, .$$

This formula and the basic results from linear algebra yield interesting information about the asymptotic behaviour of the solution to (lCP) and hence, by the theorem of Hartman–Großman, also about the solution to (CP). Since the parameters have been assumed to be real, the relevant asymptotic behaviors are only determined by the sign of α and η.

This leads to the following, which holds for all parameters (α, β, η) inside the neighborhood U introduced in Theorem 14.1.

Theorem 14.2 *The following assertions hold for the linearized system (lCP) and all initial values $u_0 \in \mathbb{R}^2$, and hence also for the original system (CP) and all initial values in a neighborhood of the origin.*

1. *If $\alpha \geq 0$ and $\eta \geq 0$, then the solution is stable in the sense of Lyapunov, i.e.*

$$\|v(t)\| \leq \|u_0\| \quad \text{for all} \quad t \geq 0 \, .$$

2. *If $\alpha > 0$ and $\eta > 0$, then the solution is uniformly exponentially stable, i.e.*

$$\|v(t)\| \leq e^{-\max\{\alpha,\eta\}t}\|u_0\| \quad \text{for all} \quad t \geq 0 \, .$$

3. *If $\alpha\eta < 0$, then the solution with initial data $u_0 = \xi_{\text{unst}}$ (resp. $u_0 = \xi_{\text{stab}}$) is unstable (resp., exponentially stable), where ξ_{stab} and ξ_{unst} are the eigenvectors of $DF(0, 0)$ associated with $\max\{\alpha, \eta\}$ and $\min\{\alpha, \eta\}$, respectively.*
4. *If $\alpha < 0$ and $\eta < 0$, then the solution is unstable.*

In view of Theorem 14.2.(3), observe that the eigenspaces associated with α and η are spanned by $(1, \delta f'(0)/(\eta - \alpha))$ and $(0, 1)$, respectively, if $\alpha \neq \eta$.

In the above result we have denoted by $\|\cdot\|$ the Euclidean norm on $\mathbb{R}^2$, i.e. $\|(x, y)\| = \sqrt{x^2 + y^2}$ for all $x, y \in \mathbb{R}$. While it is true that all norms on $\mathbb{R}^2$ are equivalent, and hence the stability properties we have obtained are norm-independent, it may still be interesting to characterize dissipativity of the system with respect to more relevant norms: in particular, with respect to the $\|\cdot\|_1$ and $\|\cdot\|_\infty$ norms defined by

$$\|(x, y)\|_1 = |x| + |y| \qquad \text{and} \qquad \|(x, y)\|_\infty = \max\{|x|, |y|\} .$$

These norms have a more intuitive interpretation than $\|\cdot\|$: at a given time t, $\|(x(t), y(t))\|_1$ and $\|(x(t), y(t))\|_\infty$ give the total potential of the inhibitory–excitatory system and the higher of both inhibitory and excitatory potentials, respectively. By [12, Lemma 6.1] we obtain the following: If $|\delta f'(0)| \leq \min\{\alpha, \eta\}$, then the solution of ($lCP$) satisfies

$$\|v(t)\|_1 \leq \|u_0\|_1 \quad \text{as well as} \quad \|v(t)\|_\infty \leq \|u_0\|_\infty \quad \text{for all} \quad t \geq 0 .$$

14.4
The Basic Unit: Numerical Analysis of the Dipole

In this section we present some numerical simulations for the two-dimensional system introduced in (14.6). The analyis is made for a particular choice of functions f, g and h and for particular values of parameters. In particular, the constant input has been chosen in such a way that $\beta = 1$. Further, the parameters have been set to $\alpha = \eta = 1$, $\gamma = 10$, and $\varepsilon = 1$. The analysis has been made for different values of the gating parameter δ. The behavior for the cases $\delta = \pm 5$ has been plotted in the figures. The initial conditions are $x(0) = y(0) = 0$. The functions have been chosen as: $f(x) = x$, $g(y) = 1/(1 + \exp(-y)) - 0.5$ and $h(y) = y$. Given these functions, the nullclines of the system can be expressed analytically. The x-nullcline is given by

$$y = -\ln\left(\frac{10}{x+4} - 1\right)$$

while the y-nullcline has coordinates

$$y = \frac{\delta x}{1 - x}$$

In Figure 14.4a the activities x and y as a function of t are shown for $\delta = 5$. The neural activities increase and converge to a stable value for $t > 2$ ms. In Figure 14.4b the trajectory of the system from the initial condition to the final state is shown together with the nullclines of the system. In this case, the corresponding eigenvalues $\lambda_{1,2}$ of the matrix $D_{xy}\Phi$ given by (14.8) are both negative ($\lambda_1 = -0.98$ and $\lambda_2 = -6.9$), indicating that the solution is stable; in fact, it is a stable *node*. The same simulations

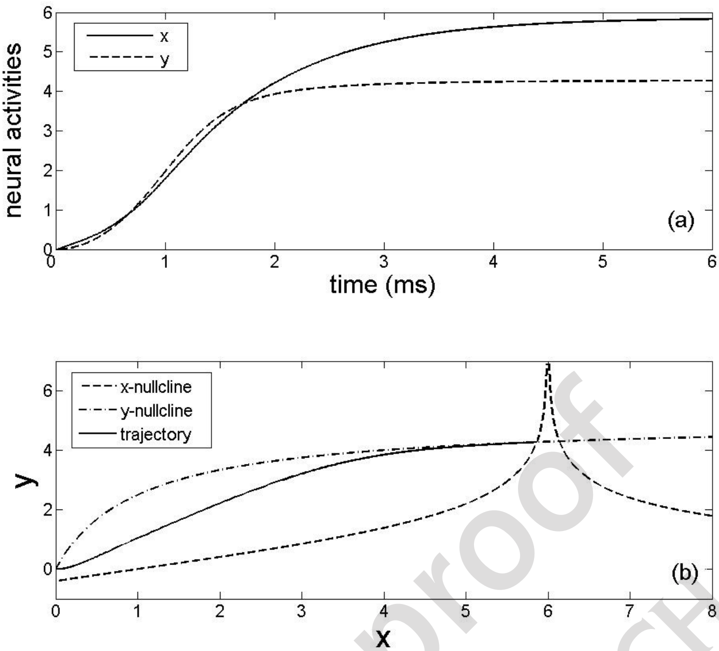

Fig. 14.4 (a): Neural activities as a function of time. The parameters have been set as follows: $\alpha = \eta = 1, \gamma = 10, \varepsilon = 1$ and $\delta = 5$. (b) Nullclines and trajectory of the system.

have been carried out for $\delta = -5$ (see Figure 14.5). In this case the corresponding eigenvalues are complex conjugate numbers ($\lambda_1 = -1.4 + 1.5i$ and $\lambda_2 = -1.4 - 1.5i$) with negative real part. The activities present an oscillatory behavior for $t < 3$ ms and converge to a stable value for $t > 3$ ms. Therefore, the system evolves to a stable state and the trajectory corresponds to a stable *focus* as can be seen in Figure 14.5b.

14.5
Model of a Recurrent Network

In this section we briefly discuss the case of a recurrent neural network. We thus allow for lateral connections among neurons of the same hierarchical level, see Figure 14.3. We avoid technicalities and refer the interested reader to a later paper for mathematical details.

In order to describe the behavior of a ring, we denote a given dipole in the ring by its angle $\theta \in [0, 2\pi)$ with respect to some fixed reference direction: we will therefore denote by $x_\theta(t)$ and $y_\theta(t)$ the potentials of the dipole with angular coordinate θ at time t.

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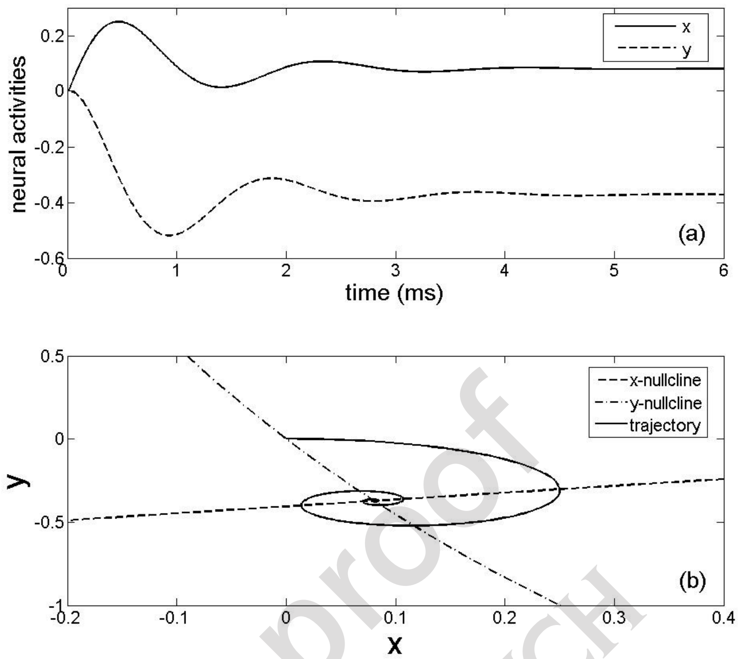

Fig. 14.5 (a) Neural activities as a function of time. The parameters have been set as follows: $\alpha = \eta = 1, \gamma = 10, \varepsilon = 1$ and $\delta = -5$. (b) Nullclines and trajectory of the system.

As explained in Section 14.2, the correct mathematical setting is that of a system of integro-differential equations corresponding to (14.4 and 14.3). Formulating it in greater generality, such that the initial-value problem associated with this system reads as a Cauchy problem, we have TS[a]

$$\begin{cases} \dot{x}(t) &= -\alpha x(t) + \beta\big(1 + \gamma g(y(t))\big) \\ \dot{y}(t) &= -\eta y(t) + \delta f(x(t)) \\ & \quad +(\varepsilon + \theta h(y(t)) \int_0^{2\pi} f(x(s))\Lambda(t-s)\,\mathrm{d}s \\ x(0) &= x_0 \\ y(0) &= y_0\,, \end{cases} \tag{14.10}$$

where Λ is a suitable integral kernel. In this setting, we are considering the distribution of the neuronal activity on a whole ring. Thus, we have to consider a state space more involved than $\mathbb{R}^2$ (which we have used in Section 14.3), taking account of the angular distribution of the activity. In fact, there are several possibilities: we choose to take as the phase space the product space $L^2_{\text{per}} \times L^2_{\text{per}}$. Here L^2_{per} is the linear space of square integrable 2π-periodic real functions. Observe that the initial data are not numbers but functions representing the initial distribution of the neuronal activity, i.e. $x_0, y_0 \in L^2_{\text{per}}$.

As in Section 14.3 we rewrite (14.10) as the differential equation

$$\begin{cases} \dot{u}(t) &= F(u(t)) \\ u(0) &= u_0 \in \mathbb{R}^2 , \end{cases} \tag{DP2}$$

in the infinite-dimensional space $L^2_{\text{per}} \times L^2_{\text{per}}$, to which we can apply standard results on existence, uniqueness, and stability. As in Section 14.3, $u := (x, y)$ and $u_0 := (x_0, y_0) \in L^2_{\text{per}} \times L^2_{\text{per}}$, while F is now a nonlinear operator on $L^2_{\text{per}} \times L^2_{\text{per}}$ defined by

$$F(x, y) := \begin{pmatrix} -\alpha x + \beta(1 + \gamma g(y)) \\ -\eta y + \delta f(x) + (\varepsilon + \theta h(y))((f \circ x) * \Lambda) \end{pmatrix} .$$

We are still assuming that (14.7) holds. Accordingly, we again deduce that the vector $(0, 0)$ is an equilibrium point only in the case of $\beta = 0$, i.e. only in the case of zero input. In the case of nonzero input one can extend the trivial nullcline $(0, 0)$ following the same idea of Section 14.3.2. The somewhat technical proof of the following theorem is similar to that of Theorem 14.4 and it is based on the Banach space version of the implicit function theorem.

Theorem 14.3 *Let $\gamma, \delta, \varepsilon$ be fixed real numbers and f, g, h be given Fréchet differentiable operators on L^2_{per}. Let them satisfy* (14.7)*, where* 0 *now denotes the costant zero function. Then for all numbers α_0, η_0 such that $\alpha_0\eta_0 \neq 0$ there exists a neighborhood U of $(\alpha_0, 0, \eta_0)$ and a Fréchet differentiable function $\kappa = (\kappa_1, \kappa_2)$ such that $(x, y) = (\kappa_1(\alpha, \beta, \eta), \kappa_2(\alpha, \beta, \eta))$ is a stationary state for all $(\alpha, \beta, \eta) \in U$.*

We compute the Fréchet derivative of F at any vector $(r, s) \in L^2_{\text{per}} \times L^2_{\text{per}}$ and obtain

$$DF(r, s) = \begin{pmatrix} -\alpha & \beta\gamma g'(s) \\ \delta f'(r) + (\varepsilon + \theta h(s)) f'(r)((f \circ r) * \Lambda) & -\eta + \theta h'(s)((f \circ r) * \Lambda) \end{pmatrix} .$$

Letting $\beta = 0$, by (14.7), we thus obtain

$$DF(0, 0) = \begin{pmatrix} -\alpha & 0 \\ \delta f'(0) & -\eta \end{pmatrix} .$$

Thus, one can linearize around the origin and investigate asymptotics of the system in the same way as in Section 14.3. Performing bifurcation analysis in infinite-dimensional Banach spaces is technically more involved, and goes beyond the scope of this chapter. We refer, e.g., to [3] for details. We will address the complete mathematical analysis of the present case of a ring structure in a later paper (in preparation).

14.6 Discussion and Conclusions

In the present paper we have investigated stability issues for the neural network model presented by Neumann and coworkers in [1, 13, 17]. The basic unit of the model represents essentially two neurons coupled via feedforward and feedback connections. The model consists of three computational stages: (1) an input filtering stage; (2) a modulatory feedback stage; and (3) a final competititve center surround mechanism at the output stage. These stages can be modeled by a coupled system of three differential equations. In this chapter we addressed the case of input signals that were assumed temporally constant (i.e. they do not vary over time after onset). Furthermore, we have assumed a spatially homogeneous surround input to the center-surround competition stage. This fact reduces the general system to a two-dimensional system that can be represented as a single Cauchy problem. We have discussed the problem of existence of solutions and investigated their stability properties. In the trivial case of zero input, the only stationary state is the inactive state. The existence of solutions has also been proved for the case of nonzero input, where the conditions on the different parameters characterizing the equations have been derived. Two parameters play a crucial role for the stability of the system, namely α and η of (14.6). If these two parameters are positive, then the solution of the system (14.6) is uniformly stable. Let us recall that the ODE system (14.6) describes the neural activities x and y of the computational model given by (14.2 and 14.3). Within this framework, α and η represent the time constant of the decay terms and therefore the conditions $\alpha, \eta > 0$ are satisfied when a concrete neural model is being considered.

We stress that the mathematical analysis of the stability conditions here presented is valid in the case of nontrivial input but inside a certain neighborhood of zero input. This means that if the input increases beyond this neighborhood, the conclusions stated here may no longer be valid.

Numerical simulations for the neural activities and the trajectory of the system have been presented for two different sets of parameters (for nonzero input). For these particular choices, the neural activities converge to stationary solutions and the corresponding trajectories evolve to a stable node or stable focus, respectively.

Finally, the case where the basic units are recurrently coupled to form a ring structure has been briefly analyzed. This corresponds to the more realistic case where the neurons interact via lateral connections. The extension of the stability analysis to the ring structure has been sketched.

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