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Semi-passivity and synchronization of neuronal oscillators

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Abstract: We discuss synchronization in networks of neuronal oscillators which are linearly coupled via gap junctions. We show that the neuronal models of Hodgkin-Huxley, Morris-Lecar, FitzHugh-Nagumo and Hindmarsh-Rose all satisfy a semi-passivity property, i.e. that the state trajectories of such a model remain oscillatory but bounded provided that the supplied (electrical) energy is bounded. As a result, for a wide range of coupling configurations, networks of these oscillators will possess ultimately bounded solutions. Moreover, when the coupling is strong enough the oscillators become synchronized. We demonstrate the synchronization of Hindmarsh-Rose oscillators by means of a computer simulation.

Keywords: Neural dynamics, networks, synchronization

1. INTRODUCTION

Synchronous behavior is witnessed in a variety of biological systems. Examples include the simultaneous flashing of fireflies and crickets that are chirping in unison (Strogatz and Stewart, 1993), the synchronous activity of pacemaker cells in the heart (Peskin, 1975) and synchronized bursts of individual pancreatic β-cells (Sherman et al., 1998). For more examples see Pikovsky et al. (2003) and Strogatz (2003) and the references therein. It is well known that individual neurons in parts of the brain discharge their action potentials in synchrony. In fact, synchronous oscillations of neurons have been reported in the olfactory bulb, the visual cortex, the hippocampus and in the motor cortex (Gray, 1994; Singer, 1999). Presence or absence of synchrony in the brain is often linked to specific brain functions (e.g. epilepsy). Hence, understanding conditions that will lead to such behavior, exploring the possibilities to manipulate these conditions, and describe them rigorously is vital for further progress in neuroscience and related branches of physics.

We present results on synchronization of ensembles of neuronal oscillators which are being interconnected via gap junctions, i.e. a linear electrical coupling of the form $g(V_1(t) - V_2(t))$ where the constant $g$ represents the synaptic conductance and $V_1(t) - V_2(t)$ denotes the difference in membrane potential of the neurons at the pre-synaptic and the post-synaptic side at time $t$, respectively. Recently it has been pointed out that gap-junctions play an important role in synchronization of individual neurons (Bennet and Zukin, 2004). Note that in literature this type of coupling is commonly referred to as diffusive coupling (Pogromsky and Nijmeijer, 2001). Hence, in the remainder of this paper we mean by diffusive coupling an interconnection via gap-junctions.

From the zoo of models of neuronal activity (see Izhikevich (2004) for a review) we have selected four of the most popular oscillators, namely the biophysically meaningful models of Hodgkin-Huxley (Hodgkin and Huxley, 1952) and Morris-Lecar (Morris and Lecar, 1981), and the more abstract models derived by FitzHugh-Nagumo (FitzHugh, 1961; Nagumo et al., 1962) and Hindmarsh-Rose (Hindmarsh and Rose, 1984). First we demonstrate that, despite the difference in the range of behavior that these models are capable to produce, these models have an important collective property. This property is that each model is semi-passive\(^1\). Second, using the concept of semi-passivity, introduced in Pogromsky (1998), we will show that a set of these diffusively coupled neuronal oscillators will always possess bounded solutions. Next, under condition that the coupling between the neurons is large enough, i.e. there is a high-conductive pathway between the neurons, we show that the oscillators will become synchronized.

This paper is organized as follows. In Section 2 we introduce the notion of semi-passivity. In addition, a theorem adopted from Pogromsky and Nijmeijer (2001) is presented which provides sufficient conditions under which the oscillators show synchronous behavior. Next, in Section 3 we show that four models mentioned above are all semi-passive. Finally, by means of computer simulations we demonstrate in Section 4 that ensembles of these oscillators can be synchronized and Section 5 concludes of the paper.

Throughout this paper we use the following notations. The symbol $\mathbb{R}$ stands, as usual, for the real numbers, $\mathbb{R}_+$

\(^1\) we will formally introduce semi-passivity in Section 2.
denotes the following subset of $\mathbb{R}$: $\mathbb{R}_+ = \{ x \in \mathbb{R} | x \geq 0 \}$. The Euclidian norm in $\mathbb{R}^n$ is denoted by $\| \cdot \|$, $\| x \|^2 = x^\top x$ where the symbol $\top$ stands for transposition. The symbol $I_n$ defines the $n \times n$ identity matrix and the notation $\text{col}(x_1, \ldots, x_n)$ stands for the column vector containing the elements $x_1, \ldots, x_n$. A function $V: \mathbb{R}^n \to \mathbb{R}_+$ is called positive definite if $V(x) > 0$ for all $x \in \mathbb{R}^n \setminus \{0\}$. It is radially unbounded if $V(x) \to \infty$ if $\| x \| \to \infty$. If the quadratic form $x^\top P x$ with a symmetric matrix $P = P^\top$ is positive definite, then the matrix $P$ is positive definite, denoted as $P > 0$. The symbol $C^r$ denotes the space of functions that are at least $r$ times differentiable. Consider $k$ interconnected systems and let $x_j$ denote the state of a single system, then the systems are called synchronized if $\lim_{t \to \infty} \| x_i(t) - x_j(t) \| = 0$, $i,j \in \{1,2, \ldots , k\}$.

2. SEMI-PASSIVITY AND SYNCHRONIZATION

We represent a neuronal oscillator as the general system

$$\begin{align*}
\dot{x} &= f(x) + Bu, \\
y &= Cx,
\end{align*}$$

(1)

where state $x \in \mathbb{R}^n$, input $u \in \mathbb{R}$ is a depolarizing or hyperpolarizing current and output $y \in \mathbb{R}$ denotes the membrane potential of a single neuron. Furthermore, $f: \mathbb{R}^n \to \mathbb{R}^n$ is a $C^1$-smooth vector field and the vectors $B$ and $C$ are of appropriate dimensions. Note that many neuronal models are in this form or can be put in this form via a well-defined change of coordinates.

Definition 1. (Passivity and semi-passivity). See Willems (1972) and Pogromsky and Nijmeijer (2001). The system (1) is called

i) passive in $\mathcal{D}$ if there exists a nonnegative function $V: \mathcal{D} \subset \mathbb{R}^n \to \mathbb{R}_+$, $\mathcal{D}$ is open, connected and invariant under (1), $V(0) = 0$, such that the following dissipation inequality

$$\dot{V}(x) = \frac{\partial V(x)}{\partial x} (f(x) + Bu) \leq y^\top u$$

(2)

holds; if $\mathcal{D} = \mathbb{R}^n$ the system is called passive;

ii) semi-passive in $\mathcal{D}$ if there exists a nonnegative function $V: \mathcal{D} \subset \mathbb{R}^n \to \mathbb{R}_+$, $\mathcal{D}$ is open, connected and invariant under (1), $V(0) = 0$, such that

$$\dot{V}(x) = \frac{\partial V(x)}{\partial x} (f(x) + Bu) \leq y^\top u - H(x),$$

(3)

where the function $H: \mathcal{D} \subset \mathbb{R}^n \to \mathbb{R}$ is nonnegative outside the ball $B$ with radius $\rho$

$$\exists \rho > 0, \| x \| \geq \rho \Rightarrow H(x) \geq g(\| x \|),$$

with some nonnegative continuous function $g(\cdot)$ defined for all $\| x \| \geq \rho$; if $\mathcal{D} = \mathbb{R}^n$ the system is called semi-passive;

iii) strictly semi-passive (in $\mathcal{D}$) if the function $H(\cdot)$ is positive outside some ball $B \subset \mathcal{D}$.

A semi-passive system behaves similar to a passive system for large enough $\| x \|$. Hence a semi-passive system that is interconnected by a feedback $u = \varphi(y)$ satisfying $y^\top \varphi(y) \leq 0$ has ultimately bounded solutions (Willems, 1972; Pogromsky and Nijmeijer, 2001), i.e. regardless how the initial conditions are chosen, every solution of the closed-loop system enters a compact set in a finite time and stays there, see Figure 1. Moreover, this compact set does not depend on the choice of initial conditions.

Consider $k$ identical neuronal oscillators of the form

$$\begin{align*}
\dot{x}_j &= f(x_j) + Bu_j, \\
y_j &= Cx_j,
\end{align*}$$

(4)

where $j = 1, \ldots, k$ denotes the number of each system in the network, $x_j \in \mathbb{R}^n$ the state, $u_j \in \mathbb{R}$ the input and $y_j \in \mathbb{R}$ the output of the $j$th system, i.e. the membrane potential, smooth vector field $f: \mathbb{R}^n \to \mathbb{R}^n$ and vectors $B = [1 \ 0 \ \ldots \ 0]^\top$ and $C = [1 \ 0 \ \ldots \ 0]$ are of appropriate dimensions. Note that many neuronal models are in this form or can be put in this form via a well-defined change of coordinates.

The $k$ dynamical systems (4) are coupled via diffusive coupling, i.e. a mutual interconnection through linear output coupling of the form

$$u_j = -\gamma_{j1} (y_j - y_1) - \gamma_{j2} (y_j - y_2) - \cdots - \gamma_{jk} (y_j - y_k)$$

(5)

where $\gamma_{ji} = \gamma_{ij} \geq 0$. Clearly this type of coupling corresponds to the case where the synapses of two neurons make direct contact and thus the influence of the neurons on each other is driven by the difference in membrane potential multiplied by the conductance of the interconnection.

Defining the $k \times k$ coupling matrix as

$$\Gamma = \begin{bmatrix}
\gamma_{1j} & -\gamma_{12} & \cdots & -\gamma_{1k} \\
-\gamma_{21} & \sum_{j=1,j\neq 2}^{k} \gamma_{2j} & \cdots & -\gamma_{2k} \\
\vdots & \vdots & \ddots & \vdots \\
-\gamma_{kj} & -\gamma_{k2} & \cdots & \sum_{j=1}^{k-1} \gamma_{kj}
\end{bmatrix}$$

(6)

the diffusive coupling functions (5) can be written as

$$u = -\Gamma y$$

(7)

where $u = \text{col}(u_1, \ldots, u_k)$ and $y = \text{col}(y_1, \ldots, y_k)$. Since $\Gamma = \Gamma^\top$ all its eigenvalues are real and $\Gamma$ is singular because the row sums equal zero. Moreover, applying Gerschgorin’s theorem (cf. Stewart and Sun (1990)) about the localization of the eigenvalues, it is easy to verify that $\Gamma$ is positive semi-definite. We assume that the network cannot be divided into two or more disconnected networks. Hence the matrix $\Gamma$ has a simple zero eigenvalue.

We wish to emphasize that the mutual interaction of diffusively coupled systems might lead the trajectories of the systems to become unbounded, even when the uncoupled systems show bounded solutions! (see v.d. Steen and Nijmeijer (2006) for an example with diffusively coupled Chua systems.) However, semi-passivity of the systems in the diffusively coupled network guarantees bounded solutions.
Consider a network of \( k \) diffusively coupled systems (4), (5). Assume that each system in the network is semi-passive, then the solutions of all connected systems in the network are ultimately bounded.

**Proof.** The proof is adopted from Pogromsky and Nijmeijer (2001). Let the \( j^{th} \) system in the network be semi-passive with the storage function \( V(x_j) \), where \( x_j \) is the state of the \( j^{th} \) system. Denote \( W(x) = \sum_{j=1}^{k} V(x_j) \) where \( x = \text{col}(x_1, \ldots, x_k) \), then

\[
W(x) = \sum_{j=1}^{k} \dot{V}(x_j) \leq \sum_{j=1}^{k} \gamma_j u_j - H(x_j) \\
= -y^\top \Gamma y - \sum_{j=1}^{k} H(x_j).
\]

(8)

Remark 2.1. It follows from (8) that even if the systems are not identical, but each individual system is semi-passive, then the network will still have bounded solutions.

Since the matrix \( CB \) is nonsingular, the systems (4) can be transformed into the following form

\[
\begin{align*}
\dot{y}_j &= a(y_j, z_j) + CBu_j = a(y_j, z_j) + u_j, \\
\dot{z}_j &= q(z_j, y_j),
\end{align*}
\]

where \( y_j \in \mathbb{R}, u_j \in \mathbb{R}, z_j \in \mathbb{R}^m, m = n - 1, \) and smooth functions \( a : \mathbb{R} \times \mathbb{R}^m \to \mathbb{R}, q : \mathbb{R}^n \times \mathbb{R} \to \mathbb{R}^m \).

**Theorem 3.** Pogromsky and Nijmeijer (2001) Consider the \( k \) systems (9) and assume that:

1. each system
   \[
   \dot{y}_j = a(y_j, z_j) + u_j, \quad \dot{z}_j = q(z_j, y_j),
   \]
   is strictly semi-passive;
2. there exists a \( C^2 \)-smooth positive definite function \( V_0 : \mathbb{R}^m \to \mathbb{R}_+ \) and a positive number \( \alpha \in \mathbb{R} \) such that the following inequality is satisfied
   \[
   \big(\nabla V_0(z' - z'')\big)^\top (q(z', y') - q(z'', y')) \leq -\alpha \|z' - z''\|^2
   \]
   (11)
   for all \( z', z'' \in \mathbb{R}^m \) and \( y' \in \mathbb{R} \).

Then, for all positive semi-definite matrices \( \Gamma \) all solutions of the closed-loop system (9), (7) are ultimately bounded. Let the eigenvalues of \( \Gamma \) be ordered as \( 0 = \gamma_1 < \gamma_2 \leq \ldots \leq \gamma_k \). Then there exists a positive number \( \bar{\gamma} \) such that if \( \gamma_2 \geq \bar{\gamma} \) there exists a globally asymptotically stable subset of the diagonal set

\[ A = \{ y_j \in \mathbb{R}, z_j \in \mathbb{R}^m : y_i = y_j, z_i = z_j, i, j = 1, \ldots, k \}. \]

**Remark 2.2.** One can easily verify that Theorem 3 remains true in case that each system (9) is semi-passive in \( D \), for \( D \) as defined in Definition 1.

**Theorem 3** shows that the problem of examining the asymptotic stability of the synchronized state of all oscillators in the network is reduced to

1. verification of the assumptions for an individual oscillator, and
2. computation of the eigenvalues of the coupling matrix \( \Gamma \).

Moreover, once the conditions stated in Theorem 3 have been verified the analysis of the stability of the synchronous state in networks with different topologies and/or weights on the interconnections will be reduced to computing the eigenvalues of \( \Gamma \), see also Wu and Chua (1996).

### 2.1 Convergent systems

There exists a sufficient condition to check whether inequality (11) of Theorem 3 is satisfied or not. Therefore, let us introduce the notion of convergent systems.

**Definition 4.** (Convergent systems). See Demidovich (1967); Pavlov et al. (2006). Consider the system

\[
\dot{z} = q(z, w(t)), \quad \text{(12)}
\]

where the external signal \( w(t) \) is taking values from a compact set \( \mathcal{W} \subset \mathbb{R} \). The system (12) is called convergent if

1. all solutions \( z(t) \) are well-defined for all \( t \in (-\infty, +\infty) \)
2. there exists an unique globally asymptotically stable solution \( z_w(t) \) on the interval \( t \in (-\infty, +\infty) \) from which it follows
   \[
   \lim_{t \to \infty} \|z(t) - z_w(t)\| = 0
   \]
   for all initial conditions.

The long term motion of systems of this type is solely determined by the driving input \( w(t) \) and not by initial conditions \( z(0) \). A sufficient condition for a system to be convergent is given in the next lemma.

**Lemma 5.** From (Demidovich, 1967; Pavlov et al., 2006). If there exists a positive definite symmetric \( m \times m \) matrix \( P \) such that all eigenvalues \( \lambda_i(Q) \) of the symmetric matrix

\[
Q(z, w) = \frac{1}{2} \left[ P \left( \frac{\partial q}{\partial z}(z, w) \right) + \left( \frac{\partial q}{\partial z}(z, w) \right)^\top \right] P
\]

(13)

are negative and separated from zero, i.e. there is a \( \delta > 0 \) such that

\[
\lambda_i(Q(z, w)) \leq -\delta < 0,
\]

(14)

with \( i = 1, \ldots, m \) for all \( z \in \mathbb{R}^m, w \in \mathcal{W} \), then the system (12) is convergent.

It follows that if there exists such a matrix \( P \) such that each system \( \dot{z}_j = q(z_j, y_j) \) satisfies (13), (14), i.e. each system \( \dot{z}_j = q(z_j, y_j) \) is convergent, then inequality (11) of Theorem 3 is satisfied.

### 3. Semi-passivity of Neuronal Oscillators

The machinery presented in the previous section provides a powerful tool for analyzing synchronous behavior in diffusively coupled neuronal networks. In this section we prove that the neuronal models of Hodgkin-Huxley, Morris-Lecar, FitzHugh-Nagumo and Hindmarsh-Rose all satisfy the semi-passive property. Thus the solutions of networks of these oscillators with a diffusive coupling exist and are bounded.
3.1 The Hodgkin-Huxley model

The most important model in computational neuroscience is probably the Hodgkin-Huxley model (Hodgkin and Huxley, 1952). Consider the Hodgkin-Huxley equations

\[
\begin{aligned}
C \dot{x}_1 &= g_{Na}x_2^2x_3 (E_{Na} - x_1) + g_K x_4^2 (E_K - x_1) + g_M (E_M - x_1) + I + u, \\
\dot{x}_j &= \alpha_j(x_1) (1 - x_j) - \beta_j(x_1)x_j, \quad j = 2, 3, 4,
\end{aligned}
\]  

(15)

where \( y = x_1 \) is the membrane potential, state \( x \in \mathcal{X} \subset \mathbb{R}^4 \), input \( u \in \mathbb{R} \), positive constants \( g_{Na}, g_K, g_M, C \in \mathbb{R} \) and constants \( I, E_{Na}, E_K, E_M \in \mathbb{R} \). The functions \( \alpha_j(\cdot) \) and \( \beta_j(\cdot) \) are defined as

\[
\begin{align*}
\alpha_2(s) &= \frac{25 - s}{10 (e^{(2.5 - s/10)} - 1)}, \\
\alpha_3(s) &= 0.07 e^{-s/20}, \\
\alpha_4(s) &= 0.01, \\
\beta_2(s) &= 4 e^{-s/18}, \\
\beta_3(s) &= \frac{1}{e^{(3 - s/18)} + 1}, \\
\beta_4(s) &= 0.125 e^{-s/80}.
\end{align*}
\]

The states \( x_j \) represent so-called activation particles which satisfy \( x_j(t) \in [0, 1] \) for all \( t \geq 0 \) whenever \( x_j(t_0) \in [0, 1] \).

Proposition 6. The Hodgkin-Huxley model is semi-passive in \( \mathcal{X} \) where

\( \mathcal{X} = \{ x \in \mathbb{R}^4 : 0 \leq x_j \leq 1, \ j = 2, 3, 4 \} \).

Proof. First, we will prove that for all \( t_0 \leq t_1, t_0, t_1 \in \mathbb{R} \):

C1) \( x_1(t) \) exists on the interval \( t \in [t_0, t_1) \) and remains bounded if the input \( u \) is bounded;

C2) \( x_i(t) \in (0, 1) \) on the interval \( t \in [t_0, t_1) \) provided \( x_i(t_0) \in (0, 1) \).

We do so by invoking a contradiction argument. Suppose that C1) does not hold. Let us denote

\[
u^* = \sup_{t \in [t_0, t_1]} \| u(t) \|.
\]

(16)

According to assumptions of the proposition such \( u^* \) must exist. The right-hand side of (15) is locally Lipschitz, hence its solutions are defined over a finite time interval. Let \( [t_0, T] \) be the maximal intervals of their existence. Let us pick some arbitrarily large constant \( M \in \mathbb{R}_+ \). Then there should exist a time instant \( t'_1 \) such that

\[
\| x(t) \| \geq M, \quad \forall \ t \geq t'_1.
\]

(17)

Consider the internal dynamics

\[
\dot{x}_i = \alpha_i(x_1) (1 - x_i) - \beta_i(x_1)x_i, \quad i = 2, 3, 4.
\]

(18)

One can easily verify that \( \alpha_i(x_1) > 0, \beta_i(x_1) > 0 \) for all \( i = 2, 3, 4 \). Hence on the boundary \( x_1 = 0 \) we have \( \dot{x}_i > 0 \) and at the boundary \( x_1 = 1 \) we have \( \dot{x}_i < 0 \), i.e. \( x_i \) can not cross the boundaries. Hence the set \( (0, 1) \) is forward invariant under the dynamics, i.e. for all \( x_1(t_0) \in (0, 1) \),

\[
0 < x_i(t) < 1, \quad \forall \ t \in [t_0, T).
\]

(19)

Then, according to (19), (15) the following holds

\[
\| x(t) \| \leq e^{-\lambda(t-t_0)} |x_1(t_0)| + \rho + \frac{1}{\lambda} u^*, \quad \forall \ t \in [t_0, T)
\]

(20)

where \( \rho, \lambda \) are positive constants of which the value do not depend on \( M \). Combining (17) and (20) we obtain

\[
M \leq \| x(t) \| \leq e^{-\lambda(t-t_0)} |x_1(t_0)| + \rho + \frac{1}{\lambda} u^*, \quad \forall \ t \in [t_1', T]
\]

(21)

where \( M \) is arbitrarily large and \( \rho, x_1(t_0), \) and \( 1/\lambda u^* \) are fixed and bounded. Hence we have reached contradiction, and C1) hold. This automatically implies that C2) holds too.

To finalize the proof of semi-passivity of (15), consider the storage function \( V : \mathcal{X} \to \mathbb{R}_+ \), \( V = \frac{1}{2} e_t^2 + \frac{1}{4} \sum_{i=2}^4 x_i^2 \). Then

\[
\dot{V} = x_1 u - (g_{Na} x_2^2 x_3 + g_K x_4^2 + g_L) x_1^2
+ (g_{Na}^2 x_2^3 E_{Na} + g_K x_4^2 E_K + g_L E_L + I) x_1
- \sum_{i=2}^4 \left( \alpha_i(x_1) \left( (x_i - \frac{1}{2})^2 - \frac{1}{4} \right) + \beta_i(x_1)x_i^2 \right).
\]

(22)

Note that \(- \left( \alpha_1(x_1) \left( (x_1 - \frac{1}{2})^2 - \frac{1}{4} \right) + \beta_1(x_1)x_1^2 \right) \leq 0 \) for each \( x_i \) outside \((0, 1)\). Because C2) holds we obtain

\[
\dot{V} \leq x_1 u - g_L x_2^2 + c_1 x_1
- \sum_{i=2}^4 \left( \alpha_i(x_1) \left( (x_i - \frac{1}{2})^2 - \frac{1}{4} \right) + \beta_i(x_1)x_i^2 \right).
\]

(23)

where constant

\[
c_1 = \max_{x_1 \in [a, b] \subset [0, 1]} |d_1 g_{Na} E_{Na} + d_2 g_K E_K + g_L E_L + I| \times
\]

\[
\times \ \text{sign}(d_1 g_{Na} E_{Na} + d_2 g_K E_K + g_L E_L + I).
\]

(24)

Given that (23) holds for all \( t \), the Hodgkin-Huxley model is semi-passive in \( \mathcal{X} \).

\[\Box\]

3.2 The Morris-Lecar model

The Morris-Lecar equations (Morris and Lecar, 1981) show similarities to the Hodgkin-Huxley equations. In fact, it can be considered as an simplification of the Hodgkin-Huxley model. Because the model is (only) two-dimensional is has become one of the most popular models in the field of computational neuroscience. The Morris-Lecar model is given by the following equations

\[
\begin{aligned}
C \dot{x}_1 &= g_L (E_L - x_1) + g_C a_{\infty}(x_1)(E_{Ca} - x_1) + g_K x_2 (E_K - x_1) + I + u, \\
\dot{x}_2 &= \eta (x_1) (\beta_{\infty}(x_1) - x_2),
\end{aligned}
\]

(25)

with \( y = x_1 \) denoting the membrane potential, state \( x \in \mathcal{X} \subset \mathbb{R}^2 \), input \( u \in \mathbb{R} \), constant parameters \( E_L, E_{Ca}, E_K \in \mathbb{R} \), positive constants \( g_L, g_C, g_K \in \mathbb{R} \) and functions

\[
\begin{align*}
\alpha_{\infty}(s) &= \frac{1}{2} \left( 1 + \tanh \left( \frac{s - E_1}{E_2} \right) \right), \\
\beta_{\infty}(s) &= \frac{1}{2} \left( 1 + \tanh \left( \frac{s - E_3}{E_4} \right) \right), \\
\eta(s) &= \tilde{\eta} \cosh \left( \frac{s - E_4}{2E_4} \right),
\end{align*}
\]

with \( \tilde{\eta} > 0, E_1, E_2, E_3, E_4, \tilde{\eta} \in \mathbb{R} \). Like in the Hodgkin-Huxley equations, the states \( x_2 \) represent an activation particle which satisfies \( x_2(t) \in [0, 1] \) for all \( t \geq t_0 \) provided \( x_2(t_0) \in [0, 1] \).
Proposition 7. The Morris-Lecar model is semi-passive in $\mathcal{X}$ where 
$$\mathcal{X} = \{x \in \mathbb{R}^2 : 0 \leq x_2 \leq 1\}.$$ 

Proof. Notice again the forward invariance of the set $[0, 1]$ under the $x_2$ dynamics. Then the proof is similar to the proof for the Hodgkin-Huxley equations. \hfill $\square$

3.3 The FitzHugh-Nagumo model

The FitzHugh-Nagumo model (FitzHugh, 1961; Nagumo et al., 1962) is one of the simplest models of the spiking dynamics of a neuron. The model is given by the following set of differential equations

$$\begin{align*}
\dot{x}_1 &= x_1 - \frac{x_1^3}{3} - x_2 + I + u, \\
\dot{x}_2 &= \phi(x_1 + a - bx_2),
\end{align*}$$

where $y = x_1$ represents the membrane potential, state $x = (x_1, x_2)$ $\in \mathbb{R}^2$, input $u \in \mathbb{R}$ and positive constants $a, b, \phi \in \mathbb{R}$. The constant parameter $I \in \mathbb{R}$ determines the output-mode of the model (either spiking or quiet).

Proposition 8. The FitzHugh-Nagumo equations satisfy the semi-passivity property (3).

Proof. Consider the storage function $V : \mathbb{R}^2 \to \mathbb{R}_+$

$$V = \frac{1}{2} \left(x_1^2 + x_2^2\right).$$

Then

$$\dot{V} = x_1 u - \frac{x_1^4}{3} + x_1^2 + I x_1 - b x_2^2 + a x_2.$$ (28)

Therefore $V(x_1, x_2) \leq x_1 u - H(x_1, x_2)$ with $H(x_1, x_2) = \frac{x_1^4}{3} - x_1^2 - I x_1 + b x_2^2 - a x_2$, i.e. the FitzHugh-Nagumo neuron is semi-passive. \hfill $\square$

3.4 The Hindmarsh-Rose model

Consider the Hindmarsh-Rose (Hindmarsh and Rose, 1984) equations

$$\begin{align*}
\dot{x}_1 &= -ax_1^3 + bx_1^2 + x_2 - x_3 + I + u, \\
\dot{x}_2 &= c - dx_2^2 - x_2 \\
\dot{x}_3 &= r(x_1 + u) - x_3,
\end{align*}$$

where $y = x_1$ represents the membrane potential, state $x = (x_1, x_2, x_3)$ $\in \mathbb{R}^3$, input $u \in \mathbb{R}$ and constant positive parameters $a, b, c, d, r, s, w \in \mathbb{R}$. The constant parameter $I \in \mathbb{R}$ determines again the output-mode of the model, which in this case, depending on the choice of parameters, can be resting, bursting or spiking. Moreover, for some sets of parameters the model will have chaotic solutions.

Proposition 9. The Hindmarsh-Rose model is semi-passive.

Proof. The proof is adopted from Ou and Tsykin (2004). Consider the storage function $V : \mathbb{R}^3 \to \mathbb{R}_+$

$$V = \frac{1}{2} \left(x_1^2 + x_2^2 + \frac{1}{s} x_3^2\right)$$

with constant $\mu > 0$. Hence

$$\begin{align*}
\dot{V} &= x_1 u - ax_1^3 + bx_1^2 + x_2 - x_3 + I + u c - dx_2^2 - x_2 - \mu x_2^2 + w x_3 - \frac{1}{s} x_3^2,
\end{align*}$$

(31)

Let

$$\begin{align*}
-ax_1^4 - \mu x_2^2 x_2 &= -a \lambda_1 x_1^4 - a(1 - \lambda_1) x_1^2 \\
&\times \left(x_1^2 + \frac{\mu}{2a(1-\lambda_1)} x_2^2\right)^2 + \frac{\mu^2}{4a(1-\lambda_1)} x_2^2.
\end{align*}$$

(32)

4. AN EXAMPLE

In the previous section we have shown that all four models satisfy the semi-passivity condition. In addition, one can easily verify that the internal dynamics of these models are equivalent to a convergent system (use $P = I$ in (13) and the result follows). Therefore, according to Theorem 3 a network consisting of the presented oscillators shows bounded solutions and, in case the coupling is strong enough, all oscillators will end up in perfect synchrony.

Let us demonstrate this result with a network of eight diffusively coupled Hindmarsh-Rose neurons

$$\begin{align*}
\dot{x}_{j,1} &= -ax_{j,1}^3 + bx_{j,1}^2 + x_{j,2} - x_{j,3} + I + u_j \\
\dot{x}_{j,2} &= c - dx_{j,2}^2 - x_{j,2} \\
\dot{x}_{j,3} &= r(s(x_{j,1} + u) - x_{j,3})
\end{align*}$$

(35)

where $j = 1, \ldots, 8$ denotes the number of the oscillator in the network. We use the following set of parameters: $a = 1$, $b = 3$, $c = 1$, $d = 5$, $r = 0.005$, $s = 4$, $w = 1.6180$, $I = 3.25$. With these parameters each Hindmarsh-Rose neuron has chaotic solutions, cf. (Hindmarsh and Rose, 1984). Let the eight oscillators be connected as shown in Figure 4 with corresponding coupling matrix.
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network of eight Hindmarsh-Rose oscillators. This is demonstrated by a computer simulation of a large enough, the oscillators will asymptotically synchronize. Moreover, when the strength of the coupling is high enough, the network consisting of these oscillators will possess bounded solutions. Hence, when being interconnected via gap junctions, any Hindmarsh-Rose all satisfy a semi-passivity property, and hence, when being interconnected via gap junctions, any network consisting of these oscillators will possess bounded solutions. Moreover, when the strength of the coupling is large enough, the oscillators will asymptotically synchronize. This is demonstrated by a computer simulation of a network of eight Hindmarsh-Rose oscillators.

\begin{equation}
\Gamma = \begin{bmatrix}
4k & -k & -k & 0 & 0 & 0 & -k & -k \\
-k & 4k & -k & -k & 0 & 0 & 0 & -k \\
-k & -k & 4k & -k & -k & 0 & 0 & 0 \\
0 & -k & -k & 4k & -k & -k & 0 & 0 \\
0 & 0 & -k & -k & 4k & -k & -k & 0 \\
0 & 0 & 0 & -k & -k & 4k & -k & -k \\
-k & 0 & 0 & 0 & -k & -k & 4k & -k \\
-k & -k & 0 & 0 & 0 & -k & -k & 4k
\end{bmatrix}
\end{equation}

The smallest nonzero eigenvalue of \( \Gamma \) is \( \lambda_2 \approx 2.58k \). Our simulations show that the synchronization threshold yields \( \lambda_1 = 1.00 \) which agrees with the numerical results obtained in, for instance, Belykh et al. (2005). Figure 3 shows the simulation results of the network of Hindmarsh-Rose oscillators with coupling \( k = 0.39 \) such that \( \lambda_2 \approx 1.01 \). The top panel shows the \( x_1 \) states of the eight oscillators, the middle panel shows the \( x_2 \) states and the \( x_3 \) states are depicted in the bottom panel. The first 500 [s] the systems are uncoupled and one sees the systems are not synchronized. After 500 [s] the coupling becomes active, indicated by the arrows in Figure 3, and all systems rapidly synchronize.

5. CONCLUSION

We have presented sufficient conditions for synchronization in networks of diffusively coupled neuronal oscillators. In particular we showed that the neuronal models of Hodgkin-Huxley, Morris-Lecar, FitzHugh-Nagumo and Hindmarsh-Rose all satisfy a semi-passivity property, and hence, when being interconnected via gap junctions, any network consisting of these oscillators will possess bounded solutions. Moreover, when the strength of the coupling is large enough, the oscillators will asymptotically synchronize. This is demonstrated by a computer simulation of a network of eight Hindmarsh-Rose oscillators.

REFERENCES


