TWO COUPLED NEURONS

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Abstract. We review the dynamical behaviour of a system of two coupled neurons. We consider symmetric and asymmetric linear coupling.

The internal dynamics of each neuron is modeled by the space-clamped Hodgkin-Huxley equations. We start with the symmetric case. Results in the literature show that for strong enough coupling the two neurons show the same behaviour at all times. They may be periodically spiking or at rest. We define these states as perfect synchrony. When decreasing the coupling strength to small positive values almost perfect synchronization is retained. As we move towards negative values of the coupling the two neurons still synchronize but in a different way, they spike periodically with half-period phase shitf from each other. As we go towards lower negative values, the system becomes totally unstable. Periodic states where the two neurons synchronize are also defined as 1 : 1 phase locked modes. The asymmetric coupled system is studied as a perturbation from the symmetric case.

1. Introduction

Many authors have been interested in modeling the electrical behaviour of nerve cells. In 1952, Hodgkin and Huxley [4] introduced a 4×4 system of nonlinear ordinary differential equations to model the electrical activity in the giant axon of a squid under certain controlled parameters (Nobel Prize in Physiology and Medicine in 1963).

Numerical experiments show that when two equations similar to the Hodgkin-Huxley model are coupled, their solutions seem to synchronize. These results are prompted by experimental findings of sychronization in excitable tissue. Nevertheless, mathematical models for these systems are typically very complicated.

In this paper, we study two identical nerve impulse equations, coupled only through the electrical potential of each cell. We consider linear symmetric and asymmetric coupling. We are concerned in identifying regions in parameter space where the two neurons lose synchrony. The symmetry simplifies the analysis and the asymmetric coupled system may then be studied as a perturbation from this case.

It is proved in [7] that large enough coupling strengths force the cells to have exactly the same behaviour regardless of the initial condition. As we move towards smaller values of the coupling the perfect synchrony states (spiking or at rest) are lost, though the two neurons still show the same asymptotic behaviour, periodic spiking with half-period phase shift from each other. The periodic solutions are also defined as 1 : 1 phase-locked modes. For smaller negative values of the coupling the system is totally unstable.

More information in the symmetric case can be found in [6].

1.1. **Equations modeling neurons.** The space-clamped Hodgkin-Huxley (HH) equations are given by:

$$\begin{aligned} \frac{dv}{dt} &= f(v, y) - I \\ \frac{dy_i}{dt} &= \Phi\left(\alpha_i(v)(1 - y_i) - \beta_i(v)y_i\right) \end{aligned}$$

where v is the difference of electrical potential across each cell membrane, I is the intensity of an external current stimulus, and $\Phi = 3^{\frac{T-6.3}{10}}$, is the temperature compensating factor. The function f is defined as

$$f(v, y) = -g_0(v - V_0) - \sum_{i=1}^{2} g_i\varphi_i(y)(v - V_i)$$

Each term $g_i\varphi_i(y)(v - V_i)$ models an ionic channel that regulates the voltage along the membrane of the axon. The variable $y = (y_1 y_2, y_3)$, and the functions φ, with $\varphi_1 = y_1^3 y_3$, $\varphi_2 = y_2^4$, are considered probabilities and must be in the interval $[0, 1]$. The functions $\alpha_i(v)$ and $\beta_i(v)$, $i = 1, 2, 3$, are defined by Hodgkin and Huxley in [4]. The equations have an equilibrium point $(v, y) = (v_\star, y(v_\star))$ for $I = f(v_\star, y(v_\star))$ (see [6]). We use the value $v_\star = \lambda$ as a bifurcation parameter.

In numerical simulations, we use the parameter values of [4], namely $V_L = -10.599$, $V_{Na} = -115.0$, $V_K = 12.0$, $g_L = 0.3$, $g_{Na} = 120.0$, $g_K = 36.0$. We refer to these as the Hodgkin-Huxley values of the parameters.

2. Coupled equations

The coupled system of two neurons, with internal dynamics modeled by the Hodgkin-Huxley equations, has the form:

$$\begin{aligned} \frac{dv_i}{dt} &= f(v_i, y^i) - I - \frac{k_i}{2}(v_i - v_l) \\ \frac{dy_j^i}{dt} &= \Phi\left(\alpha_j(v_i)(1 - y_j^i) - \beta_j(v_i)y_j^i\right) \end{aligned}$$

where $y^i = (y_1^i, y_2^i, y_3^i)$, $i, l = 1, 2$, $i \neq l$, $j = 1, 2, 3$, the k_i are the coupling constants and all functions and variables are defined as in section 1.1.

When $k_1 = k_2$ the coupled system is symmetric, with symmetry group $\mathbf{Z}_2 = \{Id, flip\}$ where

$$Id = \begin{pmatrix} I & 0 \\ 0 & I \end{pmatrix} \qquad flip = \begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix}$$

and I is the identity 4×4 matrix. Periodic solutions of the symmetric system have *spatio-temporal symmetries*, the two neurons may be shifted by zero or by half-period, see [1, 2]. These states are also defined as $1:1$ phase-locked modes.

The subspace of symmetric solutions (X, X) with $X = (v, y)$ is invariant in both the symmetric and the asymmetric case. In particular, for each value of $\lambda = v_\star$ there is a symmetric equilibrium $(X, X) = (\lambda, y(\lambda), \lambda, y(\lambda))$.

In this paper we study the way perfect synchronization of the two neurons is lost when we vary the coupling strength $k = k_1 + k_2$ and the parameter $\lambda = F^{-1}(I)$, where I is the value of the intensity stimulus for which there is a symmetric equilibrium of the coupled system.

In order to study this system, we start by computing the matrix L of the linearization at a symmetric equilibrium. Taking coordinates of the form (X, X) and $(k_1X, -k_2X)$, $X \in \mathbf{R}^4$, $k_1 \neq 0$, $k_2 \neq 0$, $X = (v, y) \in \mathbf{R}^4$, puts the matrix in block-diagonal form:

$$L = \begin{pmatrix} H & 0 \\ 0 & H - \dfrac{(k_1 + k_2)}{2} J \end{pmatrix}$$

where H is the matrix of the linearized decoupled system, and J is a 4×4 matrix with the first entry equal to 1 and zero otherwise. Notice that the subspace of vectors of the form $(k_1X, -k_2X)$ is not invariant for the nonlinear equations of the coupled system.

We use the linearization to compute steady-state and Hopf bifurcations. Steady-state bifurcations take place when the linearization at an equilibrium has a zero eigenvalue. In the Hopf bifurcation we are interested in computing eigenvalues with zero real part. For more information see [6].

3. Bifurcation diagrams

In this section we describe the structures arising in the symmetric system through bifurcation from the symmetric equilibrium. Eigenvalues of a general matrix $H-kJ$, for $k = (k_1 + k_2)/2$ are computed (see Figure 1). Thus, if we perturb slightly the value of k in the symmetric system so that we have an asymmetric system with $k_1 \sim k_2$ then we expect this system to behave similarly to the symmetric one. For more information see [6, 9].

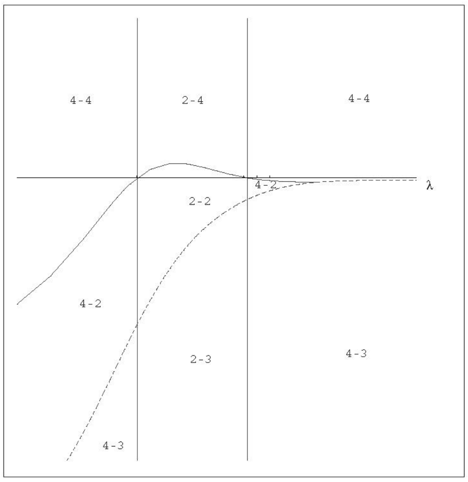

Figure 1. Stability of symmetric equilibrium for the symmetric coupled system in the $\lambda \times k$ plane for temperature $T = 6.3$, Hodgkin-Huxley values of the parameters. Full line, Hopf bifurcation, dashed line, pitchfork. The numbers m–n indicate eigenvalues with negative real part, m for H and n for $H - kJ$.

Figure 1 shows, for $T = 6.3$, the points in the $\lambda \times k$ plane where there is a local bifurcation of the coupled system at a symmetric equilibrium. Vertical lines correspond to k-independent bifurcations arising from the submatrix H, curves correspond to bifurcations arising from $H - kJ$. These lines (except for the λ axis) divide the plane into regions corresponding to different hyperbolic behaviour for the symmetric equilibrium.

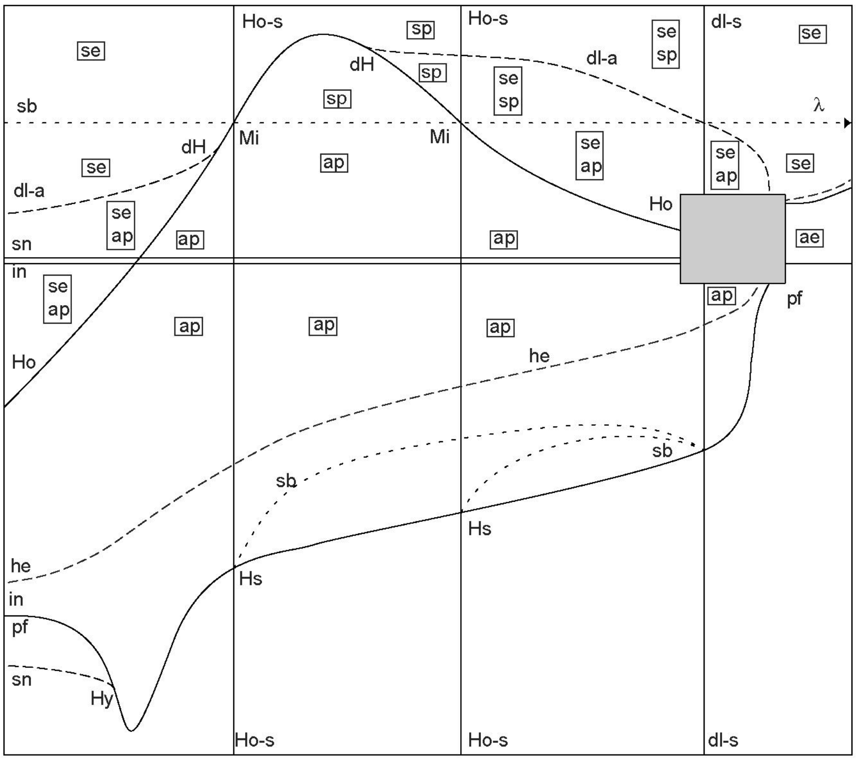

FIGURE 2. Qualitative bifurcation diagram for the symmetric coupled system in the $\lambda \times k$ plane for $T = 6.3$. Full lines were found numerically: Ho = Hopf bifurcation; pf = pitchfork points; dashed lines added to complete the diagram. Detail for gray rectangle in [6]. Stable structures indicated inside rectangles: se=symmetric equilibrium, sp=symmetric periodic orbit, ap= asymmetric periodic orbit, ae=asymmetric equilibrium. Other structures: pf= pitchfork, sn= saddle-node, in= a pair of saddle-nodes goes to ∞, dl-a= asymmetric double loop, dl-s= symmetric double loop, he= heteroclinic connection, sb= secondary bifurcation.

Local bifurcations take place in two transverse directions, that may be analyzed independently, except for intersection points. The k-independent bifurcations give rise to symmetric solutions of the form $(X(t), X(t))$. The two neurons are in a state of perfect synchrony. These solutions are exact copies of solutions of the single HH equations, see [8, 5].

Asymmetric solutions appear at the curves computed from the eigenvalues of $H - kJ$, corresponding to solutions that bifurcate in the $(X, -X)$ direction. This subspace is invariant under the linearization, but not under the full equations.

Structures arising through static bifurcation from the unique symmetric equilibrium (labelled **se**) are one or two pairs of asymmetric equilibria (**ae**) of the form (X, Y) and (Y, X). Hopf bifurcation from the symmetric equilibrium gives rise to $1 : 1$ phase locked modes. In the symmetric direction it gives rise to one or two symmetric periodic solutions (**sp**) of the form $(X(t), X(t))$, $X(t) \in \mathbf{R}^4$. In the asymmetric direction it yields an asymmetric periodic solution $(X(t), Y(t))$, labelled **ap**. In this case the set $\{(X(t), Y(t)) \quad t \in \mathbf{R}\}$ is symmetric ($\mathbf{Z}_2$-invariant) although the solution is not.

More complicated solutions arise at secondary bifurcations [6].

4. Conclusion

In this section, we summarize our results on synchronization and $1 : 1$ phase locking modes in the symmetric case.

For positive k, the two neurons are fully synchronized either in a equilibrium or in a periodic solution ($1 : 1$ phase locked mode), depending on parameter values. For large values of $k > 0$ the space of symmetric solutions is a global attractor [7]. Smaller positive values of k lead to some unstable asymmetric solutions that bifurcate from the unstable equilibrium, but the perfectly synchronized states still attract almost all solutions.

Asymmetric periodic solutions are the ubiquitous stable objects for $k < 0$. They are $1 : 1$ phase locking modes with $1/2$ period phase shift. In some regions of the parameter plane they coexist with a stable symmetric equilibrium.

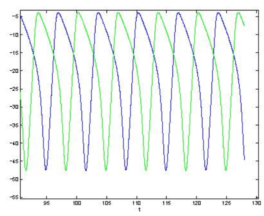

FIGURE 3. Plot of $v(t)$ and $u(t)$ for the symmetric coupled system, showing spatio-temporal symmetry, for $k = -0.08$, $I = 100$, $T = 6.3$, Hodgkin-Huxley values of remaining parameters. Initial condition $[1.0, 0.5, 0.2, 0.8, -1.0, 0.9, 0.5, 0.1]$.

Asymmetric periodic solutions of the coupled system arising through Hopf bifurcations still have spatio-temporal symmetry. The bifurcation of this type of solutions is studied in [1], [10] in the context of coupled networks of nerve cells governing animal gaits.

For negative k further away from zero all bifurcating solutions lose stability — in figure 2 there are no stable solutions below the curve of heteroclinic connections. In simulations with **dstool** [3] we observed that in this region solutions become unbounded, regardless of the initial condition.

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