

Synaptic organizations and dynamical properties of weakly connected neural oscillators

I. Analysis of a canonical model

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Abstract. We study weakly connected networks of neural oscillators near multiple Andronov-Hopf bifurcation points. We analyze relationships between synaptic organizations (anatomy) of the networks and their dynamical properties (function). Our principal assumptions are: (1) Each neural oscillator comprises two populations of neurons: excitatory and inhibitory ones; (2) activity of each population of neurons is described by a scalar (one-dimensional) variable; (3) each neural oscillator is near a nondegenerate supercritical Andronov-Hopf bifurcation point; (4) the synaptic connections between the neural oscillators are weak.

All neural networks satisfying these hypotheses are governed by the same dynamical system, which we call the canonical model. Studying the canonical model shows that: (1) A neural oscillator can communicate only with those oscillators which have roughly the same natural frequency. That is, synaptic connections between a pair of oscillators having different natural frequencies are functionally insignificant. (2) Two neural oscillators having the same natural frequencies might not communicate if the connections between them are from among a class of pathological synaptic configurations. In both cases the anatomical presence of synaptic connections between neural oscillators does not necessarily guarantee that the connections are functionally significant. (3) There can be substantial phase differences (time delays) between the neural oscillators, which result from the synaptic organization of the network, not from the transmission delays. Using the canonical model we can illustrate self-ignition and autonomous quiescence (oscillator death) phenomena. That is, a network of passive elements can exhibit active properties and vice versa. We also study how Dale's principle affects dynamics of the networks, in particular, the phase differences that the network can reproduce. We present a complete classification of all possible synaptic organizations from this point of view. The theory developed here casts some light on relations between synaptic organization and functional properties of oscillatory networks. The major advantage of our approach is that we obtain results about *all* networks of neural oscillators, including the real brain. The major drawback is that our findings are valid only when

the brain operates near a critical regime, viz. for a multiple Andronov-Hopf bifurcation.

1 Introduction

Neurophysiological studies of various brain structures (Rakic 1976; Shepherd 1976) show that there is a pattern of local synaptic circuitry in many parts of the brain: local populations of excitatory and inhibitory neurons have extensive and strong synaptic connections between each other so that action potentials generated by the former excite the latter which, in turn, reciprocally inhibit the former (Fig. 1). They can be motoneurons and Renshaw interneurons in the spinal cord, mitral and granule cells in the olfactory bulb, pyramidal cells and thalamic interneurons in the corticothalamic system, etc. Such pairs of interacting excitatory and inhibitory populations of neurons can also be found in the cerebellum, hippocampus, olfactory cortex and neocortex (Shepherd 1976). This is one of the basic mechanisms for the generation of periodic activity in the brain. Such a pair is called a *neural oscillator*.

The neural oscillators within one brain structure can be connected into a network because the excitatory (and sometimes inhibitory) neurons can have synaptic contacts with other, distant, neurons. For example, in the olfactory bulb the mitral cells have contacts with other mitral cells (Fig. 2), whereas the granule cells apparently do not make any distant contacts – they do not even have axons. Their only purpose is to provide a reciprocal dendro-dendritic inhibition for the mitral cells. Sometimes inhibitory neurons can also have long axons; for example, the periglomerular cells in the olfactory bulb.

Though on the local level all neural oscillators appear to be similar, the types of connections between them may differ. In this case we say that the networks of such oscillators have different *synaptic organization*. For instance, in the Fig. 2 the contacts between mitral cells and distant granule cells (dashed line) might or might not exist. These cases correspond to various synaptic organizations and, hence, to various dynamical properties of the network. The notion

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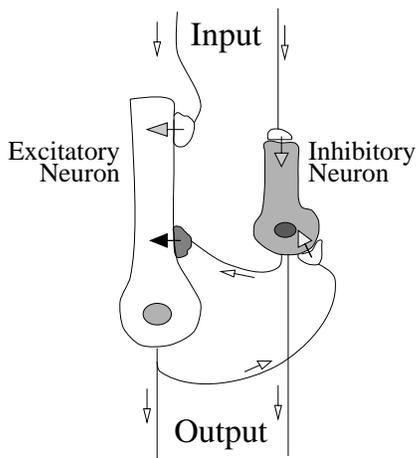
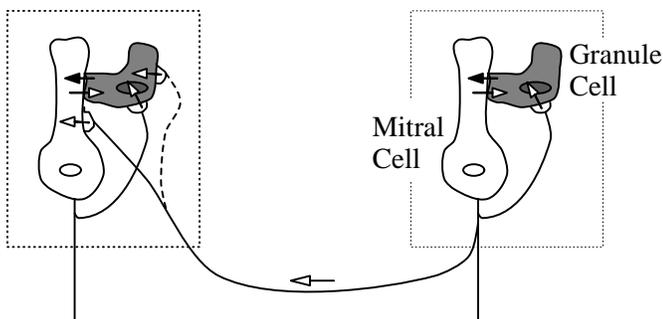


Fig. 1. Schematic representation of the neural oscillator. It consists of excitatory (white) and inhibitory (shaded) populations of neurons. For simplicity only one neuron from each population is pictured. White arrows denote excitatory synaptic connections, black arrows denote inhibitory synaptic connections



Olfactory Bulb

Fig. 2. The neural oscillators (dotted boxes) are connected into a network. The mitral cell makes contacts with other mitral cells and may have contacts with other granule cells

of synaptic organization is closely related to the notion of anatomy of the brain. In this sense, we study relationships between anatomy and functions of the real brain.

In this article we study the relationship between synaptic architectures and the dynamical properties of weakly connected networks of the neural oscillators. In our next article (Hoppensteadt and Izhikevich 1996) we study learning processes in the networks. For example, we show that some synaptic organizations allow the network to memorize time delays, or phase information, whereas the others do not allow such a possibility.

For the sake of clarity we always depict only two neural oscillators and the synaptic connections only in one direction, as in Fig. 2. It is implicitly assumed that the network consists of many neural oscillators and that synaptic connections of the same type exist between any two oscillators and in all directions.

Throughout this article we use Dale's principle (Dale 1935; Shepherd 1983), by which we mean the following: *The excitatory neurons may have only excitatory synaptic connections with other neurons and inhibitory neurons may have only inhibitory synaptic connections.* This principle im-

poses some restrictions on possible synaptic organization of the networks and we study how it affects the dynamical properties of the networks.

There are neurophysiological data about the importance of oscillations and chaos in the brain (Skarda and Freeman 1987; Eckhorn et al. 1988; Gray et al. 1989; Gray 1994), and there have been many studies of the role of oscillations in the processing of information by the brain. Most of them are devoted to study of the synchronization phenomenon (Hoppensteadt 1989; Schuster and Wagner 1990; Aronson et al. 1990; von der Malsburg and Buhmann 1992; Kazanovich and Borisyuk 1994). Pattern memorization and recognition by oscillatory neural networks have been studied, for example, by Baird (1986), Erdi et al. (1993) and Li and Hopfield (1989). To the best of our knowledge, there have been no attempts to connect dynamical properties, such as the possibility of learning a pattern, with the synaptic organization of a network. We think that such attempts could reveal the relationship between function and structure of the real brain.

In this and the following article (Hoppensteadt and Izhikevich 1996) we study synaptic organizations and learning processes in a general network of neural oscillators, governed by the dynamical system

$$\begin{cases} \dot{x}_i = f_i(x_i, y_i, \lambda) + \varepsilon p_i(x_1, y_1, \dots, x_n, y_n, \varepsilon) \\ \dot{y}_i = g_i(x_i, y_i, \lambda) + \varepsilon q_i(x_1, y_1, \dots, x_n, y_n, \varepsilon) \end{cases} \quad (1)$$

where $i = 1, \dots, n$ and $\dot{} = d/dt$. The variables x_i and y_i are excitatory and inhibitory activities of the i th population of neurons, respectively. $\lambda \in \Lambda$ is a bifurcation parameter. The parameter ε is small, reflecting our restriction to weakly connected neural networks (Neu 1979; Zak 1989; Aronson et al. 1990; Hoppensteadt and Izhikevich 1995; Izhikevich 1996).

While (1) is quite general and most oscillatory neural networks can be written in that form, near multiple Andronov-Hopf bifurcation points (1) can be reduced to a much simpler system (see the appendix in Aronson et al. 1990) of the form

$$z_i' = b_i z_i + d_i z_i |z_i|^2 + \sum_{j=1}^n c_{ij} z_j, \quad (2)$$

where z, b, d, c are complex numbers. We call (2) the canonical model for (1). To be near on Andronov-Hopf bifurcation is a severe restriction. Nevertheless, it arises naturally when one considers a weakly connected neural network near an equilibrium, i.e., when each neural oscillator is silent. Then, it follows from the Fundamental Theorem of Weakly Connected Neural Network Theory (Izhikevich 1996) that each neural oscillator must be near a bifurcation in order to make a nontrivial contribution to the entire network dynamics. While an Andronov-Hopf bifurcation is one of many possible bifurcations to be considered for the dynamics of each neural oscillator, it corresponds to a transition from equilibrium to periodic activity and thus has biological relevance.

We derive the canonical model (2) in Sect. 3, where we show that the whole network can be divided into pools of oscillators having equal (or nearly equal) natural frequencies. Interactions between pools are negligible even when there are nonzero synaptic connections between them.

In Sect. 5, where we study stability of the equilibrium $z_1 = \dots = z_n = 0$, we show that (2) can exhibit self-ignition and oscillator death, i.e., a network of intrinsically passive elements can have active properties and vice versa.

In the canonical model (2) the complex-valued coefficients c_{ij} denote the values of synaptic connections between neural oscillators. They depend upon p_i and q_i from (1). The absolute value $|c_{ij}|$ encodes the strength of connection from the j th to the i th oscillators, whereas the argument of c_{ij} encodes phase information. We call $\text{Arg } c_{ij}$ a natural phase difference because it coincides with the phase difference between a pair of neural oscillators connected in one direction. The phase difference has a meaning of time delay and is a result of synaptic organization of the network, not a propagation or transmission delay which might occur in real neurons.

When we perform the reduction of (1) to (2), we derive an expression for c_{ij} in terms of p_i and q_i . In Sect. 7 we reverse the process, i.e. we solve the inverse problem: knowing c_{ij} we find some possible choices for p_i and q_i . This allows us to relate any mathematical results about the canonical model back to the original network (1) and to interpret them in plausible neurophysiological terms, such as synaptic organization, interactions between excitatory and inhibitory populations of neurons, and Dale's principle. For example, we find that the existence of synaptic connections between neural oscillators does not necessarily mean that these oscillators interact, so nontrivial synaptic functions p_i and q_i in (1) can correspond to zero synaptic coefficients c_{ij} in (2).

Mathematical proofs are given in the Appendix.

2 Weakly connected networks of neural oscillators

We use the following definition throughout the article. By a *local population of neurons* we mean a set of (strongly) coupled neurons that are close to each other, and have similar patterns of synaptic connections and dynamic behavior. By the *activity* of a local population of neurons we mean any reasonable neurophysiological activity observable. For example, it can be the number of spikes per unit time, or the amount of neurotransmitter released in synaptic clefts. Throughout this article we assume that the activities x and y are one-dimensional variables. This is a technical assumption made to simplify our computations and to allow us to use Dale's principle. We sometimes abuse language and refer to a local population of neurons simply as being a neuron and the activity of the population as being the activity of the neuron.

A *neural oscillator* is described by a dynamical system of the form

$$\begin{cases} \dot{x} = f(x, y, \lambda) \\ \dot{y} = g(x, y, \lambda) \end{cases}$$

where $x, y \in \mathbb{R}$ are the activity of excitatory and inhibitory neurons, respectively. The parameter $\lambda \in \Lambda$ is an internal (bifurcation) parameter and Λ is some multidimensional Banach space. We assume that the functions $f, g : \mathbb{R}^2 \times \Lambda \rightarrow \mathbb{R}$ are as smooth as is necessary for our computations. A typical example of the neural oscillator is Wilson and Cowan's model (1972, 1973).

We call the oscillator *neural* to emphasize its connections with neuroscience. Thus, using Dale's principle we can gain some information about f and g , viz.

$$\frac{\partial g}{\partial x} \geq 0 \text{ and } \frac{\partial f}{\partial y} \leq 0$$

for all x, y and λ . The first inequality means that x excites y . The second inequality means that y inhibits x .

Let $(x_i, y_i) \in \mathbb{R}^2$ denote the activity of the i th neural oscillator for $i = 1, \dots, n$.

Definition 1. A **weakly connected network of neural oscillators** is a dynamical system of the form

$$\begin{cases} \dot{x}_i = f_i(x_i, y_i, \lambda) + \varepsilon p_i(x_1, y_1, \dots, x_n, y_n, \varepsilon) \\ \dot{y}_i = g_i(x_i, y_i, \lambda) + \varepsilon q_i(x_1, y_1, \dots, x_n, y_n, \varepsilon) \end{cases} \quad (1)$$

satisfying for all x, y, λ and $i \neq j$ Dale's principle

$$\frac{\partial p_i}{\partial x_j} \geq 0, \quad \frac{\partial q_i}{\partial x_j} \geq 0, \quad \frac{\partial p_i}{\partial y_j} \leq 0 \text{ and } \frac{\partial q_i}{\partial y_j} \leq 0 \quad (3)$$

where $p_i, q_i : \mathbb{R}^{2n+1} \rightarrow \mathbb{R}$ are functions that represent synaptic connections from the whole network onto the i th neural oscillator.

We do not impose any conditions on p_i and q_i except smoothness and (3). One can think of (1) with (3) as being a generalization of Wilson's and Cowan's model of an oscillatory neural network (Wilson and Cowan 1972, 1973).

The parameter $\varepsilon \geq 0$ represents the strength of synaptic connections between different neural oscillators. The assumption that ε is small has some neurophysiological justifications. More about the hypothesis of weakness of synaptic connections can be found in Hoppensteadt and Izhikevich (1995) (see also the appendix in Kopell 1986).

We will study (1) under the additional assumption that each equation in the uncoupled ($\varepsilon = 0$) system

$$\begin{cases} \dot{x}_i = f_i(x_i, y_i, \lambda) \\ \dot{y}_i = g_i(x_i, y_i, \lambda) \end{cases} \quad i = 1, \dots, n \quad (4)$$

has a stable equilibrium point (x_i^*, y_i^*) for some λ^* . So

$$\begin{aligned} f_i(x_i^*, y_i^*, \lambda^*) &= 0 \\ g_i(x_i^*, y_i^*, \lambda^*) &= 0 \end{aligned}$$

Throughout this article we denote the Jacobian matrix for the i th neural oscillator by

$$L_i = \begin{pmatrix} a_1 & a_2 \\ a_3 & a_4 \end{pmatrix}_i = \frac{\partial(f_i, g_i)}{\partial(x_i, y_i)} = \begin{pmatrix} \frac{\partial f_i}{\partial x_i} & \frac{\partial f_i}{\partial y_i} \\ \frac{\partial g_i}{\partial x_i} & \frac{\partial g_i}{\partial y_i} \end{pmatrix},$$

where all derivatives are evaluated at the equilibrium point (x_i^*, y_i^*) . The matrices L_1, \dots, L_n could differ because we do not assume that the neural oscillators are identical. Sometimes we denote entries of the Jacobian matrices by $a_{i1}, a_{i2}, a_{i3}, a_{i4}$ to stress that they belong to L_i .

The matrices

$$S_{ij} = \begin{pmatrix} s_1 & s_2 \\ s_3 & s_4 \end{pmatrix}_{ij} = \frac{\partial(p_i, q_i)}{\partial(x_j, y_j)} = \begin{pmatrix} \frac{\partial p_i}{\partial x_j} & \frac{\partial p_i}{\partial y_j} \\ \frac{\partial q_i}{\partial x_j} & \frac{\partial q_i}{\partial y_j} \end{pmatrix} \quad (5)$$

denote rescaled synaptic connections from the j th to i th neural oscillator (Fig. 3) because the actual synaptic connections have order ε and look like εS_{ij} . Note that according to Dale's principle (3) the synaptic matrices have signature

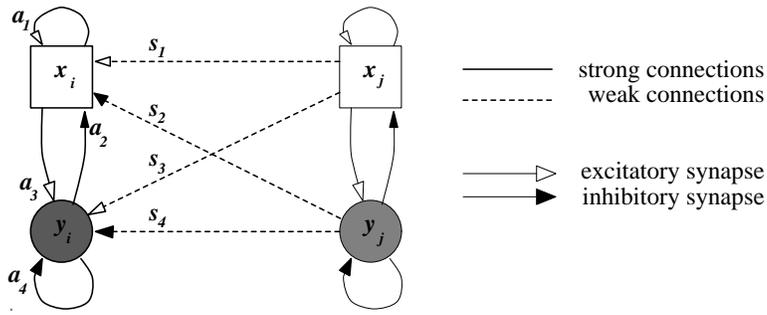
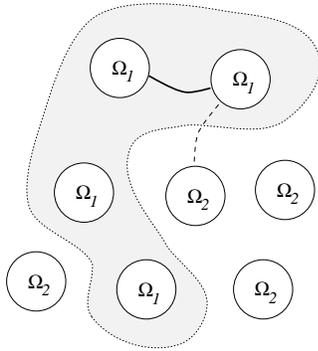


Fig. 3. A network of two neural oscillators. *Open boxes* are local populations of excitatory neurons, *shaded circles* are local populations of inhibitory neurons. The real numbers a_1, a_2, a_3, a_4 are entries of the Jacobian matrix of the i th neural oscillator. The real numbers s_1, s_2, s_3, s_4 denote the strength of synaptic connections



----- functionally insignificant connections

———— functionally significant connections

Fig. 4. Synaptic connections between neural oscillators having different natural frequencies are functionally insignificant. Therefore, the network can be divided into subnetworks (pools) of oscillators having equal or ε -close natural frequencies

$$\begin{pmatrix} + & - \\ + & - \end{pmatrix}$$

The weakly coupled system (1) can be considered as being an ε -perturbation of (4). Using the Implicit Function and Hartman-Grobman theorems it is possible to show that (1) and (4) have topologically equivalent local flow structures if each oscillator is near a hyperbolic equilibrium. In this case the dynamics of (1) are locally linear and uncoupled and, hence, (1) cannot sustain complex dynamics (e.g., multiple attractors, oscillations or chaos). Thus, in order to exhibit interesting nonlinear properties at least one of the neural oscillators must be near a non-hyperbolic equilibrium, which corresponds to a bifurcation point.

We consider the case when each oscillator is near a non-degenerate supercritical Andronov-Hopf bifurcation point. Hence the whole network (4) is near a multiple Andronov-Hopf bifurcation. The case of multiple fold (saddle-node) and pitch-fork bifurcations as well as multiple cusp singularity is considered by Hoppensteadt and Izhikevich (1995) and by Izhikevich (1996).

The equilibrium point (x_i^*, y_i^*) corresponds to the Andronov-Hopf bifurcation if

$$\text{tr } L_i = a_1 + a_4 = 0 \text{ and } \det L_i = a_1 a_4 - a_2 a_3 > 0.$$

In this case we can associate with each neural oscillator its natural frequency

$$\Omega_i = \sqrt{a_{i1} a_{i4} - a_{i2} a_{i3}}.$$

Throughout this article we assume that

$$\lambda = \lambda(\varepsilon) = \lambda^* + \varepsilon \tilde{\lambda} + \mathcal{O}(\varepsilon^2) \quad (6)$$

for some $\tilde{\lambda} \in \Lambda$. Thus, all neural oscillators are ε -close to the Andronov-Hopf bifurcation and their natural frequencies are

$$\Omega_i + \varepsilon \omega_i$$

for some $\omega_i \in \mathbb{R}$, which are ε -perturbations of Ω_i . Therefore, every time we say that two neural oscillators have equal natural frequencies, we actually mean that their natural frequencies are ε -close.

3 Canonical model for multiple Andronov-Hopf bifurcations

The main result of this section is the following

Theorem 1. *Suppose each neural oscillator in (4) is at an Andronov-Hopf bifurcation point. Then there is an invertible change of variables*

$$\begin{aligned} x_i(t) &= \sqrt{\varepsilon} \left(e^{i \frac{\Omega_i}{\varepsilon} \tau} z_i(\tau) + e^{-i \frac{\Omega_i}{\varepsilon} \tau} \bar{z}_i(\tau) \right) + \mathcal{O}(\varepsilon) \\ y_i(t) &= \sqrt{\varepsilon} \left(\frac{a_{i4} + i \Omega_i}{a_{i2}} e^{i \frac{\Omega_i}{\varepsilon} \tau} z_i(\tau) \right. \\ &\quad \left. + \frac{a_{i4} - i \Omega_i}{a_{i2}} e^{-i \frac{\Omega_i}{\varepsilon} \tau} \bar{z}_i(\tau) \right) + \mathcal{O}(\varepsilon) \end{aligned} \quad (7)$$

which transforms (4) to

$$z_i' = b_i z_i + d_i z_i |z_i|^2 + \sum_{\substack{j \neq i \\ \Omega_j = \Omega_i}}^n c_{ij} z_j + \mathcal{O}(\sqrt{\varepsilon}) \quad (8)$$

where $' = d/d\tau$; $\tau = \varepsilon t$ is 'slow' time and $b_i, c_{ij}, d_i, z_i \in \mathbb{C}$. If for some indices i and j $\Omega_i = \Omega_j = \Omega$, then

$$c_{ij} = \frac{1}{2} \left(1 + \frac{ia_4}{\Omega}, -\frac{ia_2}{\Omega} \right)_i \begin{pmatrix} s_1 & s_2 \\ s_3 & s_4 \end{pmatrix}_{ij} \begin{pmatrix} 1 \\ \frac{a_4 + i\Omega}{a_2} \end{pmatrix}_j \quad (9)$$

where $i = \sqrt{-1}$. We refer to (8) as being the canonical model for weakly connected neural networks near a multiple Andronov-Hopf bifurcation.

This result is proved in the Appendix.

Each variable $z_i \in \mathcal{C}$ in (8) describes the activity of the i th neural oscillator. Each complex coefficient c_{ij} denotes the synaptic connection from the j th to i th neural oscillator. We will reveal its meaning in the next section.

There is a remarkable resemblance of (8) with the canonical model for a weakly connected neural network at multiple pitch-fork bifurcation point. The latter has the same form as (8) except that all variables are real.

Expression (9) is important for neurobiological interpretations of our theory developed below. It allows us to interpret all results obtained by studying (8) in terms of the original weakly connected neural network (1), i.e., in terms of excitatory and inhibitory populations of neurons and interactions between them.

One direct consequence of Theorem 1 is the following:

Corollary 1. *All neural oscillators can be divided into groups, or pools, according to their natural frequencies Ω_i . Oscillators from different pools have different natural frequencies and interactions between them are negligible (Fig. 4).*

Proof. The i th neural oscillator governed by (8) depends on the j th neural oscillator only if $\Omega_i = \Omega_j$. \square

Thus, oscillators from different pools work independently from each other even when they have nonzero synaptic contacts c_{ij} , i.e., one neural oscillator can ‘feel’ another one only when they have equal (or ε -close) natural frequencies. It is reasonable to speculate that the brain has a mechanism for regulating the natural frequencies Ω_i of its neural oscillators so that some oscillators can be entrained into different pools at different times simply by adjusting Ω_i . This might be related to such phenomena as attention and dominance (Hoppensteadt 1991; Kryukov 1991; Kazanovich and Borisjuk 1994).

Since interactions between neural oscillators from different pools are negligible, we study interactions between neural oscillators from the same pool. Such oscillators have ε -close natural frequencies. Thus, without loss of generality in the rest of this article, we study a network of neural oscillators having $\Omega_1 = \dots = \Omega_n = \Omega$.

4 Natural phase difference

It is sometimes convenient to rewrite (8) in polar coordinates. If $z_i = r_i e^{i\phi_i}$, $b_i = \rho_i + i\omega_i$, $d_i = \alpha_i + i\beta_i$ and $c_{ij} = |c_{ij}| e^{i\psi_{ij}}$, then (8) is

$$\begin{cases} r_i' = \rho_i r_i + \alpha_i r_i^3 + \sum_{j \neq i}^n |c_{ij}| r_j \cos(\phi_j + \psi_{ij} - \phi_i) + \mathcal{O}(\sqrt{\varepsilon}) \\ \phi_i' = \omega_i + \beta_i r_i^2 + \frac{1}{r_i} \sum_{j \neq i}^n |c_{ij}| r_j \sin(\phi_j + \psi_{ij} - \phi_i) + \mathcal{O}(\sqrt{\varepsilon}) \end{cases} \quad (10)$$

We see that $|c_{ij}|$ represents the strength of synaptic connections between j th and i th neural oscillators while $\psi_{ij} = \text{Arg } c_{ij}$ encodes phase information of the synaptic connections, which we call *the natural phase difference*.

Indeed, consider a network consisting of two identical neural oscillators having synaptic connections only in one direction, for example, from z_2 to z_1 . Suppose also that

$\text{Im } d_i = \beta_i = 0$, i.e., the frequency does not depend on the amplitude. Such a network is governed by the dynamical system of the form

$$\begin{cases} r_1' = \rho r_1 + \alpha r_1^3 + |c_{12}| r_2 \cos(\phi_2 + \psi_{12} - \phi_1) + \mathcal{O}(\sqrt{\varepsilon}) \\ \phi_1' = \omega + \frac{1}{r_1} |c_{12}| r_2 \sin(\phi_2 + \psi_{12} - \phi_1) + \mathcal{O}(\sqrt{\varepsilon}) \\ r_2' = \rho r_2 + \alpha r_2^3 + \mathcal{O}(\sqrt{\varepsilon}) \\ \phi_2' = \omega + \mathcal{O}(\sqrt{\varepsilon}) \end{cases}$$

The unique stable solution of this system satisfies

$$\phi_2(\tau) + \psi_{12} - \phi_1(\tau) = 0 \pmod{2\pi} + \mathcal{O}(\sqrt{\varepsilon})$$

i.e., the oscillators have constant phase difference ψ_{12} . This motivates our definition of the natural phase difference since it occurs ‘naturally’ in a pair of neural oscillators connected in one direction.

Notice that when $\psi_{12} < 0$, an observer sees that one of the oscillators (viz. z_1) oscillates with some time delay. Obviously, it would be wrong to ascribe this to spike propagation or synaptic transmission delays. As we will see in Sect. 8, the coefficient ψ_{12} may assume many values depending on the synaptic organization of the network, not the speed of transmission of spikes through axons, dendrites or synapses.

If the neural oscillators are connected in both direction (i.e., $c_{12} \neq 0$ and $c_{21} \neq 0$), then the phase difference between them generically differs from $\text{Arg } c_{12}$ or $\text{Arg } c_{21}$. Nevertheless, even for a network of n interconnected neural oscillators we can prove the following result

Lemma 1. *If $c_{ij} \neq 0$, then there are values of the parameters ρ_1, \dots, ρ_n such that after a short transition period*

$$\phi_i(\tau) - \phi_j(\tau) \pmod{2\pi} = \psi_{ij} + \mathcal{O}(\sqrt{\varepsilon}), \quad (11)$$

i.e., the i th and j th oscillators have constant phase difference ψ_{ij} .

Proof. Fix j and let $\rho_j = 1$, $\rho_i = -\frac{1}{\sqrt{\varepsilon}}$ for $i \neq j$. After rescaling ($z_i \rightarrow \sqrt{\varepsilon} z_i$ for $i \neq j$) the system (8) transforms to

$$\begin{cases} z_j' = (1 + i\omega_j) z_j + d_j z_j |z_j|^2 + \mathcal{O}(\sqrt{\varepsilon}) \\ z_i' = \frac{1}{\sqrt{\varepsilon}} (c_{ij} z_j - z_i) + \mathcal{O}(1) \quad i \neq j \end{cases}$$

Applying singular perturbation methods (Hoppensteadt 1993) to the second equation we see that

$$z_i(\tau) = c_{ij} z_j(\tau) + \mathcal{O}(\sqrt{\varepsilon}, e^{-\frac{\tau}{\sqrt{\varepsilon}}}).$$

After a short initial transition period (e.g., $\tau > \mathcal{O}(|\sqrt{\varepsilon} \log \varepsilon|)$), this equation gives (11). \square

It follows from this proof that the choice of parameters corresponds to the case when the amplitude of the j th neural oscillator is much bigger than that of the other neural oscillators. One can consider the j th oscillator as the leading one that synchronizes the whole network. A similar phenomenon was studied by Kazanovich and Borisjuk (1994).

Now consider the canonical model (8) with arbitrary choice of parameters. The representation (10) of the canonical model is interesting since one can obtain valuable information about the behavior of coupled oscillators simply by looking at (10), without any further mathematical analysis.

Indeed, it is easy to see that an impact of one oscillator on the amplitude of another one is maximal when their phases are synchronized so that (11) holds, because

$$\cos(\phi_j + \psi_{ij} - \phi_i) = \cos(\psi_{ij} - \psi_{ij} + \mathcal{O}(\sqrt{\varepsilon})) = 1 + \mathcal{O}(\varepsilon)$$

reaches its maximal value then. If the two oscillators are out of phase, i.e., if

$$\phi_i(\tau) - \phi_j(\tau) \bmod 2\pi = \psi_{ij} \pm \frac{\pi}{2}$$

then $\cos(\phi_j + \psi_{ij} - \phi_i) = 0$ and the influence of the j th neural oscillator on the amplitude r_i of the i th neural oscillator is negligible even when $|c_{ij}|$ is very large.

It is also easy to see that the larger is an oscillator amplitude r_j , the larger its impact on the other oscillators. Conversely, if the i th neural oscillator has very small amplitude r_i , then it is susceptible to the influences of the other oscillators because of the term

$$\frac{1}{r_i} \sum_{j \neq i}^n |c_{ij}| r_j \sin(\phi_j + \psi_{ij} - \phi_i)$$

which can grow as $r_i \rightarrow 0$.

We next study some local properties of (8), in particular, the stability of the origin $z_1 = \dots = z_n = 0$.

5 Oscillator death and self-ignition

We can take the limit $\varepsilon \rightarrow 0$ in (8). From now on we consider (8) with $\varepsilon = 0$.

Note that the canonical model (8) always has an equilibrium point $z_1 = \dots = z_n = 0$ for any choice of parameters. If all ρ_i are negative numbers with sufficiently large absolute values, then the equilibrium point is stable.

In this section we study how the equilibrium can lose its stability. Using the canonical model we also illustrate two well-known phenomena: oscillator death (or quenching, or Bar-Eli effect) and coupling-induced spontaneous activity (or self-ignition). We consider (8) for the most interesting case when $\text{Re } d_i < 0$ for all i . This corresponds to a supercritical Andronov-Hopf bifurcation, i.e., to the birth of a stable limit cycle.

We start from the observation that in the canonical model each oscillator is governed by a dynamical system of the form

$$z' = (\rho + i\omega)z + dz|z|^2 \quad (12)$$

Obviously, if $\rho < 0$, then the equilibrium $z = 0$ is stable. As ρ increases through $\rho = 0$ (12) undergoes Andronov-Hopf bifurcation. As a result, the equilibrium loses its stability and (12) has stable limit cycle of radius $\mathcal{O}(\sqrt{\rho})$ for $\rho > 0$.

We can characterize the qualitative differences in dynamic behavior of (12) for $\rho \leq 0$ and $\rho > 0$ as follows:

- When $\rho \leq 0$, dynamical system (12) describes an *intrinsically passive* nonlinear element incapable of sustaining periodic activity.
- When $\rho > 0$, dynamical system (12) describes an *intrinsically active* oscillator, or pacemaker.

In the uncoupled network ($C = 0$)

$$z_i' = (\rho + i\omega)z_i + d_i z_i |z_i|^2, \quad i = 1, \dots, n \quad (13)$$

of such oscillators the equilibrium point $z_1 = \dots = z_n = 0$ is stable for $\rho \leq 0$ and unstable for $\rho > 0$.

We ask what happens when we consider the canonical model (8) with nonzero matrix $C = (c_{ij})$. A partial answer is given in the following theorem.

Lemma 2. *Let α denote the largest real part of all eigenvalues of connection matrix $C = (c_{ij})$. Consider the network of identical oscillators governed by*

$$z_i' = (\rho + i\omega)z_i + d_i z_i |z_i|^2 + \sum_{j=1}^n c_{ij} z_j, \quad i = 1, \dots, n \quad (14)$$

The equilibrium point $z_1 = \dots = z_n = 0$ is stable if

$$\rho < -\alpha.$$

It is unstable if

$$\rho > -\alpha.$$

Proof of this lemma is given in Appendix.

Remark 1. If C has only one eigenvalue with maximal real part, then it is possible to show that (14) undergoes Andronov-Hopf bifurcation with birth of a stable limit cycle, as ρ increases through $\rho = -\alpha$.

Note that in this case the coordinates of the limit cycle depend upon the matrix C ; more precisely, upon the eigenvector that corresponds to the ‘leading’ eigenvalue of C . Thus, to understand the dynamics of the canonical model (14), one should understand what structures of the connection matrix $C = (c_{ij})$ are possible and how they depend upon the synaptic matrices S_{ij} . We study the relationship between c_{ij} and S_{ij} in the later sections.

In the rest of this section we use Lemma 2 to illustrate two interesting effects:

- If $\alpha < 0$, then the network (14) is stable even when
- $$0 < \rho < -\alpha.$$

That is, even though each oscillator is a pacemaker, the coupled system may approach $z = 0$. This effect, which can be called *oscillator death*, was studied numerically by Bar-Eli (1985) and analytically for general systems by Aronson et al. (1990).

- If $\alpha > 0$, then the network (14) can exhibit spontaneous activity even when

$$-\alpha < \rho < 0$$

i.e., when each oscillator is intrinsically passive, coupling can induce synchronous activity in the network. This effect, which can be called *self-ignition* (Rapaport 1952), is discussed in detail by Kowalski et al. (1992).

Recall that the canonical model describes any weakly connected neural network near a multiple Andronov-Hopf bifurcation point. Hence both phenomena discussed above are generic. The question of whether each neuron in the brain is intrinsically active or passive should be approached with a caution, since generically a network of passive elements

can exhibit active properties and vice versa. This depends crucially upon the connection matrix C , which in turn depends upon the synaptic matrices S_{ij} [as follows from (9)], and, hence upon the synaptic organization of the network.

6 Type A and B neural oscillators

Recall that according to Dale's principle $a_2 < 0$ and $a_3 > 0$. Hence, each Jacobian matrix L generically has a signature either

$$\begin{pmatrix} + & - \\ + & - \end{pmatrix} \quad \text{or} \quad \begin{pmatrix} - & - \\ + & + \end{pmatrix}$$

In the first case we say that the neural oscillator is of *type A*, in the second case *type B*.

Consider the differences between these types. Suppose the neural oscillator is at the equilibrium point (x^*, y^*) and we apply a short impulse to its excitatory neuron so that its new activity becomes $x^* + \delta x$, where δx is small. Since the equilibrium (x^*, y^*) is stable and the Hopf bifurcation is nondegenerate, the activity vector $(x(t), y(t))$ approaches (x^*, y^*) .

If the neural oscillator is of type A, the relaxation to (x^*, y^*) has the following form: The excitatory neuron increases its activity x , further increasing the inhibitory neuron activity y . After a while, y reciprocally inhibits x and both neuron activities decrease (Fig. 5a).

If the neural oscillator is of type B, then there is no such initial amplified response of excitatory neuron activity, but there is an increase in inhibitory neuron activity (Fig. 5b). We see that in type A neural oscillators it is possible for excitatory and inhibitory neurons to be active simultaneously, whereas for type B neural oscillators it is not.

The differences between type A and B neural oscillators were not essential for our analysis so far. Nevertheless, they are crucial in sections below and in our next paper (Hoppensteadt and Izhikevich 1996) where we show that type A neural oscillators have some interesting properties: in some sense they are 'smarter'.

7 Dale's principle and the effectiveness of synaptic connections

There are some neurophysiological implications of formula (9). We first observe that if the weakly connected neural network (1) is uncoupled then so is the canonical model (8). Indeed, if $p_i = q_i = 0$ for all i , then

$$S_{ij} = \begin{pmatrix} \frac{\partial p_i}{\partial x_j} & \frac{\partial p_i}{\partial y_j} \\ \frac{\partial q_i}{\partial x_j} & \frac{\partial q_i}{\partial y_j} \end{pmatrix} = \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}$$

and, hence, from (9) $c_{ij} = 0$ for all i and j .

It turns out that the converse is not true. There could be nonzero connection functions p_i and q_i such that the synaptic coefficient $c_{ij} = 0$. This means that although two neural oscillators can be physically connected ($S_{ij} \neq 0$), the synaptic connections between them are not effective because the canonical model is uncoupled ($c_{ij} = 0$). The existence of such a phenomenon follows from the next theorem.

Theorem 2. *If the i th and the j th neural oscillators are of type A, then there are nonzero synaptic configurations S_{ij} between them satisfying Dale's principle such that $c_{ij} = 0$. On the other hand, if the neural oscillators are of type B, then such synaptic configurations always violate Dale's principle.*

Proof. Consider formula (9) for c_{ij} . After rearrangement we see that it is equivalent to

$$c_{ij} = v_1 s_1 + v_2 s_2 + v_3 s_3 + v_4 s_4, \quad (15)$$

where

$$v_1 = \frac{1}{2} + i \frac{a_{i4}}{2\Omega}$$

$$v_2 = \frac{a_{j4} - a_{i4}}{2a_{j2}} + i \frac{a_{j4}a_{i4} + \Omega^2}{2a_{j2}\Omega}$$

$$v_3 = -i \frac{a_{i2}}{2\Omega}$$

$$v_4 = \frac{a_{i2}}{2a_{j2}} - i \frac{a_{j4}a_{i2}}{2a_{j2}\Omega}$$

are four complex numbers. Consider v_1, v_2, v_3 and v_4 as vectors in \mathbb{R}^2 . Obviously, they are linearly dependent. Hence the equation

$$0 = v_1 s_1 + v_2 s_2 + v_3 s_3 + v_4 s_4, \quad (16)$$

has nontrivial solutions.

In order to satisfy Dale's principle s_1 and s_3 must be non-negative and s_2 and s_4 non-positive. Thus we must find solutions for

$$0 = v_1 s_1 + (-v_2)|s_2| + v_3 s_3 + (-v_4)|s_4| \quad (17)$$

with non-negative coefficients $s_1, |s_2|, s_3$ and $|s_4|$.

If the neural oscillators are of type B, then all the complex numbers $v_1, -v_2, v_3$ and $-v_4$ have positive imaginary parts (Fig. 6b). All their nontrivial linear combinations with non-negative coefficients also have positive imaginary parts. Thus (16) and Dale's principle cannot be satisfied simultaneously.

If the neural oscillators are of type A, then $v_1, -v_2, v_3, -v_4$ have imaginary parts with different signs (Fig. 6a), and it is easy to see that (17) can be satisfied. Indeed, one can take a linear combination of v_1 and $-v_4$ so that the real part (projection on horizontal axis) of $v_1 s_1 + (-v_4)|s_4|$ is zero and add v_3 or $-v_2$ or both to kill the imaginary part (projection on vertical axis). Thus, (16) and Dale's principle can be satisfied simultaneously. \square

Theorem 2 could be a revelation for neuroscientists. Indeed, it is probably difficult to accept that the existence of synaptic connections between neurons from two different neural oscillators does not necessarily imply that the oscillators interact. We have already seen this for oscillators that have different natural frequencies Ω (see Corollary 1). In Theorem 2 the neural oscillators could be identical; they can even act as though they were synchronized, but the synaptic connections between them are not responsible for that. If we somehow suppress one of them, the other one will not 'feel' it. Its amplitude and phase will be unchanged. It should be noted that the effect described above is a synergetic phenomenon, and can be observed at the level of interacting

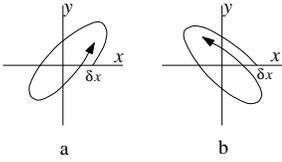


Fig. 5a,b. Differences in dynamic behavior of type A and B neural oscillators. See text for details

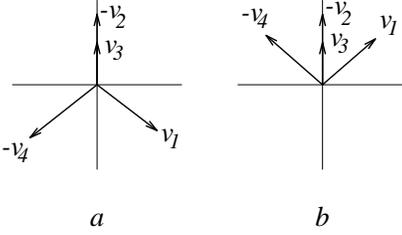


Fig. 6a,b. Complex numbers $v_1, -v_2, v_3, -v_4$ as vectors on the complex plane. For simplicity we depict $-v_2$ with zero real part. **a** Type A neural oscillator. **b** Type B neural oscillator

neural oscillators, but possibly not at the level of interacting neurons.

A direct consequence of the preceding proof is the following

Corollary 2. *The phenomenon described in Theorem 2 can be observed only in networks with the synaptic configurations depicted in Fig. 7.*

Proof. From Fig. 6 it follows that (17) has nontrivial solutions with non-negative coefficients only if $s_1 \neq 0$, $s_4 \neq 0$ and either $s_2 \neq 0$ or $s_3 \neq 0$. The result follows from Fig. 3. \square

It is not the case that for any of the synaptic configurations depicted in Fig. 7 the synaptic coefficients $c_{ij} = 0$. In order to exhibit this phenomenon there must be some linear relation between entries of S_{ij} , viz. (16).

In all the synaptic configurations the inhibitory neurons should be long-axon neurons capable of forming long-distance synaptic contacts (i.e., contacts from one neural oscillator to another one), which is rare in the brain.

8 Classification of synaptic organizations

According to Lemma 1 the values $\psi_{ij} = \text{Arg } c_{ij}$ decode phase information. Let us determine possible values of the natural phase differences ψ_{ij} for various synaptic configurations S_{ij} satisfying Dale's principle. It is easy to do this using (15) and the vectors from Fig. 6. Indeed, if for example, S_{ij} has the form

$$S_{ij} = \begin{pmatrix} s_1 & 0 \\ s_3 & 0 \end{pmatrix}$$

where s_1 and s_3 are some positive numbers, then

$$c_{ij} = v_1 s_1 + v_3 s_3,$$

and, hence, possible values of c_{ij} are linear combinations of v_1 and v_3 with positive coefficients. Values of c_{ij} may be anywhere between lines spanned through v_1 and v_3 in

Fig. 6a or b. Thus, ψ_{ij} is an angle between $\text{Arg } v_1$ and $\pi/2$ as shown in Fig. 8.

Complete classification of c_{ij} for all S_{ij} is given in Fig. 8. We see that type A neural oscillators are able to reproduce the entire range of natural phase differences if they are suitably connected, while type B oscillators cannot. Indeed, all possible values $\psi_{ij} = \text{Arg } c_{ij}$ for type B oscillators are between $\text{Arg } v_1$ and $\text{Arg } (-v_4)$. Type B neural oscillators cannot even have natural phase difference $\psi_{ij} = 0$, whereas type A oscillators can.

Using the classification in Fig. 8 we can solve a number of problems. Knowing the phase shift between two neural oscillators we can find possible synaptic configurations that can produce the shift; knowing changes in synapses we can find changes in phase shifts and vice versa, etc.

We will use this classification in our next article (Hoppensteadt and Izhikevich 1996), where we analyze possible synaptic organizations from the point of view of memorization of phase information.

9 Conclusion

Below is a summary of our basic assumptions in this article.

- Each neural oscillator is modeled by an ordinary differential equation. Activity is described by a continuous variable which has a meaning of firing rate. Thus, we model *nonspiking* neurons.
- We model *no transmission delays*. The phase differences (delays) in activity of neural oscillators occur here as a result of the synaptic organization of the network.
- Neural oscillators are *weakly* connected. This assumption is justified by the fact that the amplitude of passive excitatory postsynaptic potential is less than 1% the amplitude of an action potential.
- We consider *local* dynamics of each neural oscillator near an *equilibrium*. Thus we study the case when each oscillator is silent, or resting. It follows from the Fundamental Theorem of Weakly Connected Neural Network Theory (Izhikevich 1996) that each neural oscillator must be near a bifurcation (phase transition, threshold) or else the network is essentially uncoupled.
- Each neural oscillator is near an *Andronov-Hopf* bifurcation, which corresponds to the appearance (or disappearance) of periodic activity. Some other bifurcations (saddle-node, pitch-fork, cusp, etc.) are studied elsewhere (Izhikevich 1996).

We consider a general network of neural oscillators written in the form (1). Then, we use the well-known fact that (1) near a multiple Andronov-Hopf bifurcation is governed by the dynamical system (2). To our surprise, there have not been any attempts to reveal the relationship between the synaptic functions p_i and q_i in (1) and the synaptic coefficients c_{ij} in (2) (Bard Ermentrout, personal communication). Since functions p_i and q_i are responsible for the synaptic organization (anatomy) of (1) and the complex-valued synaptic coefficient c_{ij} affects the dynamical properties of (2), the expression (9) reveals the relationship between the anatomy and its function.

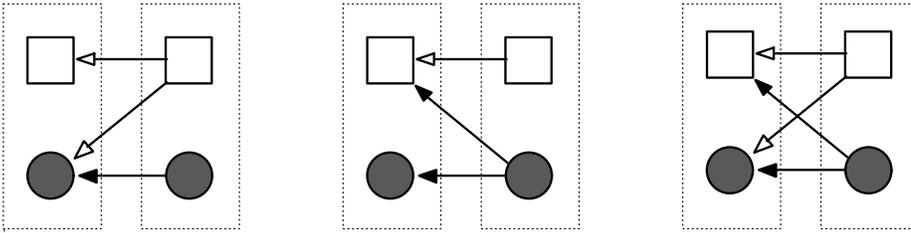


Fig. 7. Synaptic configurations that can exhibit the phenomenon described in Theorem 2 provided the values of synaptic coefficients are chosen appropriately. *Open boxes* depict excitatory neurons and *shaded circles* depict inhibitory neurons. A *vertical pair* of excitatory and inhibitory neurons is one neural oscillator. Connections within each neural oscillator (continuous lines in Fig. 3) are not shown for simplicity. They are not assumed to be zero

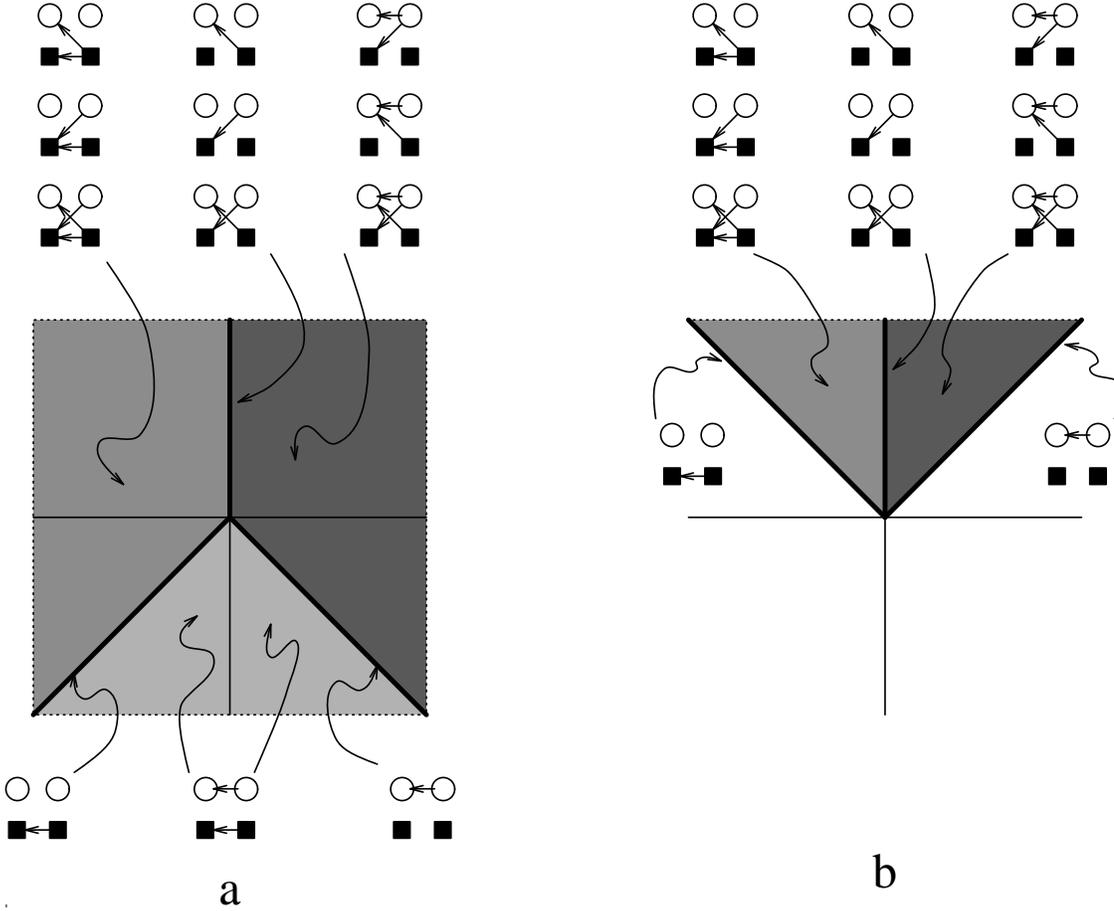


Fig. 8a,b. Possible values of synaptic connections c_{ij} for different synaptic configurations S_{ij} satisfying Dale's principle. For synaptic configurations that are not explicitly depicted the possible values of c_{ij} may occupy all *shaded areas*. **a** Type A neural oscillator. **b** Type B neural oscillator

It should be stressed that our results are generic but local. They are valid for any system of the form (1) but in a restricted area of parameters. One of the major restriction is that the network is near a multiple bifurcation. We choose to study an Andronov-Hopf bifurcation since it captures the transition from resting to periodic activity state. We are inspired by the fact that in the Hodgkin-Huxley model (and some other models) the equilibrium loses stability via an Andronov-Hopf bifurcation. Thus, this bifurcation is relevant to neuroscience.

Our article is not intended to take into account multiple time scales. Although they are important, we focus on phase deviations that occur through synaptic organization. This is important as well since phase deviations observed in

experiments might be the result of the synaptic organizations rather than transmission times.

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Appendix. Proofs of theorems

Theorem 1. *If each neural oscillator in (4) is at a non-degenerate Andronov-Hopf bifurcation point, then the weakly connected network*

$$\begin{cases} \dot{x}_i = f_i(x_i, y_i, \lambda) + \varepsilon p_i(x_1, y_1, \dots, x_n, y_n, \varepsilon) \\ \dot{y}_i = g_i(x_i, y_i, \lambda) + \varepsilon q_i(x_1, y_1, \dots, x_n, y_n, \varepsilon) \end{cases} \quad (1)$$

of such oscillators can be transformed into the dynamical system

$$z_i' = b_i z_i + d_i z_i |z_i|^2 + \sum_{\substack{j \neq i \\ \Omega_j = \Omega_i}}^n c_{ij} z_j + \mathcal{O}(\sqrt{\varepsilon}), \quad i = 1, \dots, n \quad (\text{A1})$$

where $\tau = \varepsilon t$ is 'slow' time and $b_i, c_{ij}, d_i, z_i \in \mathbb{C}$. If $\Omega_i = \Omega_j = \Omega$ then

$$c_{ij} = \frac{1}{2} \left(1 + \frac{ia_4}{\Omega}, -\frac{ia_2}{\Omega} \right)_i S_{ij} \begin{pmatrix} 1 \\ \frac{a_4 + i\Omega}{a_2} \end{pmatrix}_j \quad (\text{A2})$$

where S_{ij} was defined in (5). One can think of (A1) as the canonical model for weakly connected neural networks near multiple Andronov-Hopf bifurcation.

Proof. Formal derivation of formula (A1) can be found, for example, in Aronson et al. (1990). Here we present a rigorous derivation using an approach that in addition enables us to derive formula (A2) for the synaptic coefficients c_{ij} .

Since each

$$L_i = \begin{pmatrix} a_1 & a_2 \\ a_3 & a_4 \end{pmatrix}_i = \begin{pmatrix} \frac{\partial f_i}{\partial x_i} & \frac{\partial f_i}{\partial y_i} \\ \frac{\partial g_i}{\partial x_i} & \frac{\partial g_i}{\partial y_i} \end{pmatrix}$$

is nonsingular, the Jacobian matrix

$$L = \begin{pmatrix} L_1 & 0 & \cdots & 0 \\ 0 & L_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & L_n \end{pmatrix}$$

of the whole system (4) is nonsingular at the equilibrium point $(x_1^*, y_1^*, \dots, x_n^*, y_n^*)$. Hence, by the Implicit Function Theorem there exists a family of equilibrium points $(x_1^*(\varepsilon), y_1^*(\varepsilon), \dots, x_n^*(\varepsilon), y_n^*(\varepsilon))$ for the weakly connected neural network (1) if ε is sufficiently small and (6) holds.

Let (x_i, y_i) be the local coordinates at $(x_i^*(\varepsilon), y_i^*(\varepsilon))$. Consider the Taylor series of (1)

$$\frac{d}{dt} \begin{pmatrix} x \\ y \end{pmatrix}_i = L_i \begin{pmatrix} x \\ y \end{pmatrix}_i + \varepsilon \sum_{j=1}^n S_{ij} \begin{pmatrix} x \\ y \end{pmatrix}_j + \mathbf{N}_i(x_i, y_i) + \text{h.o.t.} \quad (\text{A3})$$

where

$$S_{ij} = \begin{pmatrix} s_1 & s_2 \\ s_3 & s_4 \end{pmatrix}_{ij} = \begin{pmatrix} \frac{\partial p_i}{\partial x_j} & \frac{\partial p_i}{\partial y_j} \\ \frac{\partial q_i}{\partial x_j} & \frac{\partial q_i}{\partial y_j} \end{pmatrix}, \quad i \neq j$$

and all nonlinear terms in f_i and g_i are accounted for in the vector function $\mathbf{N}_i : \mathbb{R}^2 \rightarrow \mathbb{R}^2$, and 'h.o.t.' denotes higher-order terms in $x_1, y_1, \dots, x_n, y_n$ and ε .

It is easy to see that corresponding to eigenvalues $\pm i\Omega_i$ of L_i are eigenvectors

$$v_i = w_i \begin{pmatrix} 1 \\ \frac{a_4 + i\Omega}{a_2} \end{pmatrix}_i \quad \text{and} \quad \bar{v}_i = \bar{w}_i \begin{pmatrix} 1 \\ \frac{a_4 - i\Omega}{a_2} \end{pmatrix}_i,$$

where $w_i \in \mathbb{C}$ takes into account the ambiguity of choosing the eigenvectors.

Let V_i be a 2×2 -matrix whose columns are v_i and \bar{v}_i , respectively, i.e.,

$$V_i = \begin{pmatrix} w & \bar{w} \\ w \frac{a_4 + i\Omega}{a_2} & \bar{w} \frac{a_4 - i\Omega}{a_2} \end{pmatrix}_i \quad (\text{A4})$$

then we define $z_i \in \mathbb{C}$ by

$$\begin{pmatrix} z \\ \bar{z} \end{pmatrix}_i = V_i^{-1} \begin{pmatrix} x \\ y \end{pmatrix}_i.$$

Each complex-valued variable z_i describes the activity of the i th neural oscillator. Thus, we have

$$\begin{pmatrix} x \\ y \end{pmatrix}_i = V_i \begin{pmatrix} z \\ \bar{z} \end{pmatrix}_i. \quad (\text{A5})$$

There is a canonical way to associate a phase with each z_i , viz., the phase of z_i is $\text{Arg } z_i$. Since we have freedom of choosing the phase for $(x_i, y_i) \in \mathbb{R}$, we assume that its phase is zero when x_i reaches its maximum value. In this case the phases of z_i and (x_i, y_i) coincide. In order to do this, the ambiguity variable w_i in (A4) should be real. Without loss of generality we take $w_i = 1$. Other choices of w_i produce the same result but the notation becomes cumbersome.

Substitution of (A5) into (A3) gives

$$V_i \frac{d}{dt} \begin{pmatrix} z \\ \bar{z} \end{pmatrix}_i = i\Omega V_i \begin{pmatrix} z \\ -\bar{z} \end{pmatrix}_i + \varepsilon \sum_{j=1}^n S_{ij} V_j \begin{pmatrix} z \\ \bar{z} \end{pmatrix}_j + \tilde{\mathbf{N}}_i(z_i, \bar{z}_i) + \text{h.o.t.}$$

After multiplying by V_i^{-1} we get

$$\frac{d}{dt} \begin{pmatrix} z \\ \bar{z} \end{pmatrix}_i = \begin{pmatrix} i\Omega z \\ -i\Omega \bar{z} \end{pmatrix}_i + \varepsilon \sum_{j=1}^n V_i^{-1} S_{ij} V_j \begin{pmatrix} z \\ \bar{z} \end{pmatrix}_j + \hat{\mathbf{N}}_i(z_i, \bar{z}_i) + \text{h.o.t.}$$

Direct computation shows that

$$V_i^{-1} S_{ij} V_j = \begin{pmatrix} c_{ij} & e_{ij} \\ \bar{c}_{ij} & \bar{e}_{ij} \end{pmatrix} \quad (\text{A6})$$

where c_{ij} and e_{ij} are some complex numbers. Since the second equation is the complex-conjugate of the first, it suffices to consider only the equations for z_i :

$$\frac{dz_i}{dt} = (i\Omega_i + \varepsilon c_{ii}) z_i + \varepsilon \sum_{j \neq i}^n (c_{ij} z_j + e_{ij} \bar{z}_j) + N(z_i, \bar{z}_i) + \text{h.o.t.}$$

Let $\tau = \varepsilon t$ be the 'slow' time. After the change of variables

$$z_i(t) \rightarrow \sqrt{\varepsilon} e^{i\frac{\Omega_i}{\varepsilon} \tau} z_i(\tau) \quad (\text{A7})$$

we obtain

$$z_i' = c_{ii} z_i + \sum_{j \neq i}^n \left(c_{ij} e^{i\frac{\Omega_j - \Omega_i}{\varepsilon} \tau} z_j + e_{ij} e^{i\frac{-\Omega_j - \Omega_i}{\varepsilon} \tau} \bar{z}_j \right) + e^{-i\frac{\Omega_i}{\varepsilon} \tau} N_i(\sqrt{\varepsilon} e^{i\frac{\Omega_i}{\varepsilon} \tau} z_i, \sqrt{\varepsilon} e^{-i\frac{\Omega_i}{\varepsilon} \tau} \bar{z}_i) + \mathcal{O}(\sqrt{\varepsilon}).$$

If we rewrite $N_i(z_i, \bar{z}_i)$ as

$$N_i(z_i, \bar{z}_i) = b_{i1} z_i^2 + b_{i2} |z_i|^2 + b_{i3} \bar{z}_i^2 + d_{i1} z_i^3 + d_{i2} |z_i|^2 + d_{i3} \bar{z}_i |z_i|^2 + d_{i4} \bar{z}_i^3 + \mathcal{O}(|z_i|^4)$$

then

$$z_i' = c_{ii} z_i + \sum_{j \neq i}^n \left(c_{ij} e^{i\frac{\Omega_j - \Omega_i}{\varepsilon} \tau} z_j + e_{ij} e^{i\frac{-\Omega_j - \Omega_i}{\varepsilon} \tau} \bar{z}_j \right) + \frac{1}{\sqrt{\varepsilon}} e^{i\frac{\Omega_i}{\varepsilon} \tau} b_{i1} z_i^2 + \frac{1}{\sqrt{\varepsilon}} e^{-i\frac{\Omega_i}{\varepsilon} \tau} b_{i2} |z_i|^2 + \frac{1}{\sqrt{\varepsilon}} e^{-i\frac{3\Omega_i}{\varepsilon} \tau} b_{i3} \bar{z}_i^2 + e^{i\frac{2\Omega_i}{\varepsilon} \tau} d_{i1} z_i^3 + d_{i2} |z_i|^2 + e^{i\frac{-2\Omega_i}{\varepsilon} \tau} d_{i3} \bar{z}_i |z_i|^2 + e^{i\frac{-4\Omega_i}{\varepsilon} \tau} d_{i4} \bar{z}_i^3 + \mathcal{O}(\sqrt{\varepsilon}).$$

After averaging (see Hoppensteadt 1993) all terms that have the factor $e^{i\frac{\Delta}{\varepsilon} \tau}$ with $\Delta \neq 0$ vanish, and we obtain (A1).

Finally, we compute the synaptic coefficients c_{ij} when $\Omega_i = \Omega_j = \Omega$. First, from (A4) we have that

$$V_i^{-1} = \frac{1}{2} \begin{pmatrix} 1 + i\frac{a_4}{\Omega} & -i\frac{a_2}{\Omega} \\ 1 - i\frac{a_4}{\Omega} & i\frac{a_2}{\Omega} \end{pmatrix}_i.$$

Substituting this formula and (A4) into (A6) we obtain the expression (A2) for c_{ij} . It suffices to take the first row from V_i^{-1} and the first column from V_j to evaluate c_{ij} .

The invertible change of variables (7) is a superposition of (A4) and (A7). \square

Lemma 2. Let α denote the largest real part of all eigenvalues of the connection matrix $C = (c_{ij})$. Consider the network of identical oscillators governed by

$$z_i' = (\rho + i\omega) z_i + d_i z_i |z_i|^2 + \sum_{j=1}^n c_{ij} z_j, \quad i = 1, \dots, n$$

The equilibrium point $z_1 = \dots = z_n = 0$ is stable if

$$\rho < -\alpha$$

It is unstable if

$$\rho > -\alpha$$

Proof. The full system has the form

$$\begin{cases} z_i' = (\rho + i\omega)z_i + dz_i|z_i|^2 + \sum_{j=1}^n c_{ij}z_j, \\ \bar{z}_i' = (\rho - i\omega)\bar{z}_i + d\bar{z}_i|z_i|^2 + \sum_{j=1}^n \bar{c}_{ij}\bar{z}_j, \end{cases} \quad i = 1, \dots, n \quad (\text{A8})$$

It is easy to see that the origin $z_1 = \bar{z}_1 = \dots = z_n = \bar{z}_n = 0$ is always an equilibrium point of (A8). The $(2n) \times (2n)$ Jacobian matrix J at the origin has the form

$$J = \begin{pmatrix} (\rho + i\omega)E + C & 0 \\ 0 & (\rho - i\omega)E + \bar{C} \end{pmatrix}$$

where 0 and E are the $n \times n$ zero and identity matrices, respectively.

Suppose $\lambda_1, \dots, \lambda_n$ are the eigenvalues of C counted with their multiplicity and suppose that v_1, \dots, v_n are corresponding (generalized) eigenvectors. Direct computation shows that J has $2n$ eigenvalues

$$\rho + i\omega + \lambda_1, \quad \rho - i\omega + \bar{\lambda}_1, \quad \dots, \quad \rho + i\omega + \lambda_n, \quad \rho - i\omega + \bar{\lambda}_n$$

and $2n$ corresponding eigenvectors

$$\begin{pmatrix} v_1 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \bar{v}_1 \end{pmatrix}, \dots, \begin{pmatrix} v_n \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ \bar{v}_n \end{pmatrix}$$

where 0 denotes a vector of zeros. Stability of (A8) is determined by the eigenvalues of J with maximal real part. These eigenvalues are of the form

$$\rho + i\omega + \lambda, \quad \rho - i\omega + \bar{\lambda}$$

where λ are eigenvalues of C . Let $\alpha = \text{Re } \lambda$, then the origin is stable if

$$\rho + \alpha < 0$$

and unstable if

$$\rho + \alpha > 0.$$

□

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