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Effect of delay on phase locking in a pulse coupled neural network

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Abstract. Using a slightly simplified version of the integrate and fire model of a neural network with delay, I study the stability of the phase-locked state dependent on the coupling between the neurons and especially on a delay time. The coupling between neurons may be arbitrary. It is shown that the phase-locked state becomes less stable with increasing delay and that relaxation oscillations occur.

PACS. 05.45.Xt Synchronization; coupled oscillators – 87.18.Sn Neural networks

1 Introduction

The study of phase locking in neural nets has been the subject of numerous papers because of the intrinsic interest in such effects and their experimental discovery in animal brains [1,2]. While phase locking between two oscillators has been studied since long in the context of radio-engineering [3] and laser physics [4], the locking between many oscillators has come to the focus of interest more recently. In his fundamental work Kuramoto [5] studied the locking using a sinusoidal coupling between the individual phases in the context of chemical waves, and he applied his work more recently to neural networks also [6]. Another line of approaches is based on integrate and fire models to which a considerable body of papers has been devoted [7–9]. (For further references *cf.* [8,9].) To the best of my knowledge, there is, however, only one paper that studies the impact of delay on phase locking. Ernst *et al.* [9] studied phase locking between two neurons analytically and used numerical simulations in the case of many coupled neurons. In this case they assumed a mean field approach, *i.e.* each neuron was coupled to any other with the same strength. It is well-known that delay differential equations have intrinsic difficulties that require specific efforts to be overcome [10,11]. Our recent analytical study [12] on the lighthouse model [13] of a pulse coupled neural net reveals that time delays may have a considerable impact on the stability and relaxation towards equilibrium of a phase-locked state. Since the lighthouse model and the integrate and fire model present the response of the dendrites of neurons differently, the question arises whether in the case of the integrate and fire model similar phenomena can be found. This will be the topic of the present paper.

To simplify our present approach, we study the integrate and fire model in the approximation of small damping of the action potential. We allow for arbitrary couplings between the neurons, however.

2 The basic equations including delay and noise

In order to formulate the following equations, we remind the reader of a few basic experimental facts (*cf.* Fig. 1).

A neuron, labelled by k, sends out signals in the form of short pulses (~ 1 ms) through its axon. This axon is connected to the dendrites, labelled by m, of other neurons *via* synapses. Hereby electric currents are generated in the dendrites. In this way, also the neuron k under consideration receives inputs from the other neurons *via* dendritic currents. In addition, the neurons may directly receive (external) sensory inputs, *e.g.* from the eyes. The basic equations that describe the coupling between dendritic currents ψ and axonal pulses P read as follows. The current ψ_m of dendrite m obeys the equation

$$\left(\frac{\mathrm{d}}{\mathrm{d}t}+\gamma\right)^2 \psi_m(t)=\sum_k a_{mk}P_k\left(t-\tau_{km}\right)+F_{\psi,m}(t), \quad (1)$$

where γ is the damping constant, a_{mk} are coupling coefficients, $P_k(t-\tau_{km})$ is the pulse of axon k with delay time τ_{km}, $F_{\psi,m}(t)$ is a random force. The pulses are assumed in the form

$$P(t)=f(\phi(t)), \quad (2)$$

where

$$f(\phi(t))=\dot{\phi}\sum_n \delta(\phi-2\pi n). \quad (3)$$

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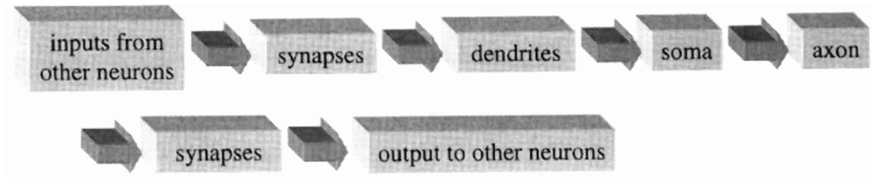

Fig. 1. Diagram of neural net. The neuron k (consisting of "soma" and "axon") receives inputs from *several* dendrites and sends outputs to *several* dendrites m ("output to other neurons").

The function $\phi(t)$ is interpreted as a phase angle, that in case of axon k obeys the equation

$$\dot{\phi}_k(t)=S\left(\sum_m c_{km}\psi_m\left(t-\tau'_{mk}\right)+P_{\mathrm{ext},k}-\Theta_k\right)+F_{\phi,k}(t). \tag{4}$$

In many typical neurons, $S(X)$ is a sigmoidal function of its argument X (*cf. e.g.* [14]). Since in our paper we wish to treat not too high external inputs (which would lead to saturation), it will be sufficient to approximate $S(X)$ by a linear function, or by a suitable scaling of variables, by its argument X. On the other hand, since S must be nonnegative, X must also be nonnegative, which is for instance guaranteed by positive external signals. Thus our approach works in a specific, though realistic window of external inputs. In the following we shall use $S(X)=X$. The quantities in (4) are defined as follows: c_{km} coupling coefficients, τ'_{mk} delay times, $P_{\mathrm{ext},k}$ external signal, Θ_k threshold, $F_{\phi,k}$ fluctuating force.

The dendritic currents can be eliminated from (1) and (4) in two ways. Here we describe one way, another can be found in Section 3. We treat the linear region of (4) and apply the operator

$$\left(\frac{\mathrm{d}}{\mathrm{d}t}+\gamma\right)^2 \tag{5}$$

to both sides of (4), which yields

$$\left(\frac{\mathrm{d}}{\mathrm{d}t}+\gamma\right)^2\dot{\phi}_k(t)=\sum_{k'm}c_{km}a_{mk'}P_{k'}\left(t-\tau_{k'mk}\right)+C_k(t)+\hat{F}_k(t), \tag{6}$$

where we have used the abbreviations

$$\tau_{k'mk}=\tau_{k'm}+\tau'_{mk}, \tag{7}$$

$$C_k(t)=\left(\frac{\mathrm{d}}{\mathrm{d}t}+\gamma\right)^2\left(P_{\mathrm{ext},k}-\Theta_k\right), \tag{8}$$

$$\hat{F}_k(t)=\sum_m c_{km}F_{\psi,m}\left(t-\tau'_{mk}\right)+\left(\frac{\mathrm{d}}{\mathrm{d}t}+\gamma\right)^2F_{\phi,k}(t). \tag{9}$$

Because c carrying on the indices k', m, k of τ as well as the product $c_{km}a_{mk'}$ in (6) would make the following treatment clumsy, we relabel the corresponding quantities. As a simple analysis shows, we may relabel $\tau_{k'mk}$ by τ_ℓ and replace $c_{km}a_{mk'}$ by $A_{jk,\ell}$. (We first arrange all $\tau_{k'mk}$ according to their size which allows us to introduce the label ℓ.) In a more concise form (6) can be written as

$$\left(\frac{\mathrm{d}}{\mathrm{d}t}+\gamma\right)^2\dot{\phi}_j(t)=\sum_{k,\ell}A_{jk,\ell}f\left(\phi_k\left(t-\tau_\ell\right)\right)+C_j(t)+\hat{F}_j(t). \tag{10}$$

In the present paper I assume

$$\hat{F}_j=0,\quad C_j(t)=C. \tag{11}$$

The case with nonvanishing fluctuating forces will be treated elsewhere.

Before we go on to study the phase-locked state, we establish a connection of our approach with the integrate and fire model.

3 Connection with integrate and fire model

Usually, in integrate and fire models, the dendritic currents ψ_m do not occur explicitly (*cf. e.g.* [8]). In our formulation of equations (1) and (4) they can be easily eliminated. To this end we write (1) in the form

$$\left(\frac{\mathrm{d}}{\mathrm{d}t}+\gamma\right)^2\psi_m(t)=g_m(t). \tag{12}$$

Under the initial conditions

$$\psi_m(0)=0,\quad \dot{\psi}_m(0)=0 \tag{13}$$

the formal solution of (12) reads

$$\psi_m(t)=\int_0^t(t-\sigma)\mathrm{e}^{-\gamma(t-\sigma)}g_m(\sigma)\mathrm{d}\sigma, \tag{14}$$

which can be inserted into (4). To make further contact, we note that the phase ϕ can be connected with the action potential U by means of $\phi=2\pi U$ and constraining ϕ to $0\le\phi<2\pi$. We write (4) (after elimination of the dendritic currents) in the form

$$\dot{\phi}=I, \tag{15}$$

where – in the same notation – the basic equation of the integrate and fire model reads

$$\dot{\phi}=-\gamma'\phi+I, \tag{16}$$

where usually time and I are scaled such that $\gamma' = 1$. To bring out the essence of the difference between (15) and (16), we assume I time-independent. Then the time interval Δ during which $\phi(U)$ increases from 0 to 2π, (0 to 1) is given in case (15) by

$$\Delta = \frac{2\pi}{I}, \tag{17}$$

whereas in case (16) by

$$\Delta = -\frac{1}{\gamma'} \ln\left(1 - \frac{2\pi\gamma'}{I}\right). \tag{18}$$

In a limit

$$2\pi\gamma'/I \ll 1 \tag{19}$$

that we may call medium to strong coupling or weak damping, (18) reduces in the leading approximation to (17) so that both models coincide.

4 The phase locked state

This state is defined by

$$\phi_j(t) = \phi(t) \quad \text{for all} \quad j. \tag{20}$$

When we insert (20) into (10), we obtain an equation for the phase-locked state. Thereby we note that trivially the left-hand side becomes independent of the index j. Thus, also the r.h.s. must be independent of j. A sufficient condition for this to happen is (11) and

$$\sum_k A_{jk,\ell} = A_\ell \quad \text{independent of} \quad j. \tag{21}$$

From (10, 11, 21) we derive

$$\left(\frac{\mathrm{d}}{\mathrm{d}t} + \gamma\right)^2 \dot{\phi} = \sum_\ell A_\ell f\left(\phi\left(t - \tau_\ell\right)\right) + C. \tag{22}$$

We expect that ϕ increases monotonously and that its time derivatives are periodic

$$\ddot{\phi}\left(t_{n+1}\right) = \ddot{\phi}(t_n), \quad \dot{\phi}\left(t_{n+1}\right) = \dot{\phi}(t_n), \tag{23}$$

but that after a time interval

$$\Delta = t_{n+1} - t_n \tag{24}$$

the phase ϕ has increased

$$\phi\left(t_{n+1}\right) - \phi(t_n) = 2\pi. \tag{25}$$

We integrate (22) on both sides over the time interval (24). Note that f (3) contains exactly one peak in this interval. We obtain

$$\int_{t_n}^{t_{n+1}} \left(\dddot{\phi} + 2\gamma\ddot{\phi} + \gamma^2\dot{\phi}\right) \mathrm{d}t = \sum_\ell A_\ell + \Delta C. \tag{26}$$

Because of (23), (25) and (24), the relation

$$\Delta = \frac{1}{C}\left(2\pi\gamma^2 - \sum_\ell A_\ell\right) \tag{27}$$

can be derived, *i.e.* we determined the period Δ.

5 Stability equations of the phase locked state

We integrate (10) with (11) over time, which yields

$$\left(\frac{\mathrm{d}}{\mathrm{d}t} + \gamma\right)^2 \phi_j(t) = \sum_{k,\ell} A_{jk,\ell} H\left(\phi_k(t - \tau_\ell)\right) + Ct, \tag{28}$$

where

$$H(\phi) = (2\pi)^{-1}(\phi - \phi \bmod 2\pi). \tag{29}$$

To study the stability of the phase-locked state ϕ, we make the hypothesis

$$\phi_j = \phi + \xi_j. \tag{30}$$

Inserting (30) into (28) and subtracting the corresponding equation for ϕ, we obtain

$$\left(\frac{\mathrm{d}}{\mathrm{d}t} + \gamma\right)^2 \xi_j(t) = \sum_{k,\ell} A_{jk,\ell}(2\pi)^{-1}\left\{\phi + \xi_k - (\phi + \xi_k) \bmod 2\pi - (\phi - \phi \bmod 2\pi)\right\}_{t-\tau_\ell}. \tag{31}$$

To bring out the essential steps that allow us to evaluate the r.h.s. of (31), we first treat this equation without delay, $\tau_\ell = 0$ and put $A_{jk,\ell} = A_{kj}$. Below we shall show how our results can be generalized to the case $\tau_\ell \neq 0$. Since $\mid \xi_j \mid$ may be a small quantity, we may certainly assume

$$0 \le \xi_k < 2\pi. \tag{32}$$

By means of the curly bracket in (31), we define

$$[...] = (2\pi)^{-1}\{...\}. \tag{33}$$

$$\text{At time } t_{nk}^-, \text{ where } \phi + \xi_k = 2\pi n, \ [...] \text{ suffers a jump } +1, \tag{34}$$

and

$$\text{at time} \quad t_n^+, \phi = 2\pi n, \quad \text{a jump back to} \quad 0. \tag{35}$$

Equation (31) can be formally solved by means of a Green's function K (*cf.* Sect. 3)

$$\xi_j(t) = \sum_k A_{jk} \int_{-\infty}^{t} K(t, \sigma)[...]_\sigma \mathrm{d}\sigma. \tag{36}$$

Because of (34) and (35), the r.h.s. of (36) can be written more explicitly

$$\xi_j(t) = \sum_k A_{jk} \sum\nolimits_n' \int_{t_{nk}^-}^{t_n^+} K(t,\sigma)\mathrm{d}\sigma, \tag{37}$$

where

$$\sum\nolimits_n' = \sum_n^{t_n^+ \le t}. \tag{38}$$

We assume that $K(t,\sigma)$ changes in the interval $[t_{nk}^-, t_n^+]$ but little. This allows us to perform the integral in (37)

$$\xi_j(t) = \sum_k A_{jk} \sum\nolimits_n' K\left(t, t_n^+\right)\left(t_n^+ - t_{n,k}^-\right). \tag{39}$$

To conclude our derivation of the equations for ξ_k, we must determine $\left(t_n^+ - t_{nk}^-\right)$. To this end, we recall from (34) and (35)

$$\phi\left(t_{nk}^-\right) + \xi_k\left(t_{nk}^-\right) = 2\pi n, \tag{40}$$

$$\phi\left(t_n^+\right) = 2\pi n, \tag{41}$$

and by subtracting (41) from (40)

$$\xi_k\left(t_{nk}^-\right) = \phi\left(t_n^+\right) - \phi\left(t_{nk}^-\right). \tag{42}$$

Because of

$$t_n^+ - t_{nk}^- \quad \text{small}, \tag{43}$$

we may assume that up to higher order

$$\xi_k\left(t_{nk}^-\right) \approx \xi_k\left(t_n^+\right). \tag{44}$$

Using the approximation

$$\phi\left(t_n^+\right) - \phi\left(t_{nk}^-\right) \approx \dot\phi\left(t_n^+\right)\left(t_n^+ - t_{nk}^-\right), \tag{45}$$

we eventually find

$$t_n^+ - t_{nk}^- \approx \dot\phi\left(t_n^+\right)^{-1} \xi_k\left(t_n^+\right). \tag{46}$$

If the derivative of ϕ has a jump at t_n^+, we define

$$\dot\phi\left(t_n^+\right) = \frac{1}{2}\left(\dot\phi(t^+ + \epsilon) + \dot\phi(t^+ - \epsilon)\right). \tag{47}$$

We can replace $t_n^+ - t_{n,k}^-$ in (39) by means of (46)

$$\xi_j(t) = \sum_k A_{jk} \sum\nolimits_n' K\left(t, t_n^+\right)\dot\phi\left(t_n^+\right)^{-1} \xi_k\left(t_n^+\right). \tag{48}$$

In order to convert (48) into a differential equation, in a first step we cast it into the form

$$\xi_j(t) = \sum_k A_{jk} \int_{-\infty}^{t} K(t,\sigma) \sum_n \delta\left(t - t_n^+\right)\dot\phi\left(t_n^+\right)^{-1} \xi_k(\sigma)\mathrm{d}\sigma. \tag{49}$$

The same analysis can be performed with negative ξ_k leading to the same formal result (49). Finally, it is possible to take into account delays, $\tau_\ell \neq 0$ by means of a simple trick. On the r.h.s. of the equations (31, 36, 37, 39, 48, 49) and in all the other formulas (40–46) we replace in each individual sum term

$$\phi(t) \quad \text{by} \quad \tilde\phi(t) = \phi\left(t - \tau_\ell\right), \tag{50}$$

$$\xi_k(t) \quad \text{by} \quad \tilde\xi_k(t) = \xi_k\left(t - \tau_\ell\right). \tag{51}$$

Accordingly, (49) can be rigorously generalized to

$$\xi_j(t) = \sum_k A_{jk,\ell} \int_{-\infty}^{t} K(t,\sigma) \sum_n \delta(t - t_n^+)\dot\phi\left(t_n^+ - \tau_\ell\right)^{-1} \times \xi_k\left(\sigma - \tau_\ell\right)\mathrm{d}\sigma. \tag{52}$$

Because of the periodicity of $\dot\phi$, we may use

$$\dot\phi\left(t_n^+ - \tau_\ell\right) = \dot\phi\left(t_0 - \tau_\ell\right) \quad \text{independent of} \quad n. \tag{53}$$

Returning to our original problem (31), we convert the integral equation (49) into the corresponding differential equation

$$\left(\frac{\mathrm{d}}{\mathrm{d}t} + \gamma\right)^2 \xi_k(t) = \sum_{k,\ell} a_{jk,\ell} \sum_n \delta\left(t - t_n^+\right)\xi_k(t - \tau_\ell), \tag{54}$$

where we introduced the abbreviation

$$a_{jk,\ell} = \dot\phi\left(t_0 - \tau_\ell\right)^{-1} A_{jk,\ell}. \tag{55}$$

We note that the whole procedure is valid for more general differential operators

$$\left(\frac{\mathrm{d}}{\mathrm{d}t} + \gamma\right)^2 \to L\left(\frac{\mathrm{d}}{\mathrm{d}t}, t\right), \tag{56}$$

if the kernel K is replaced by a Green's function belonging to L.

6 Solution of stability equations

In order to show how equations (54) can be solved, we cast them into vector form

$$\left(\frac{\mathrm{d}}{\mathrm{d}t} + \gamma\right)^2 \boldsymbol{\xi}(t) = \sum_\ell \hat A_\ell \sum_n \delta\left(t - t_n^+\right)\boldsymbol{\xi}(t - \tau_\ell) \tag{57}$$

and treat a single delay time so that

$$\tau_\ell = \tau, \quad \hat A_\ell = \hat A. \tag{58}$$

We first seek the eigenvectors and eigenvalues of

$$\hat A \mathbf{v}_\mu = \lambda_\mu \mathbf{v}_\mu. \tag{59}$$

We assume a non-degenerate case and represent $\boldsymbol{\xi}(t)$ as

$$\boldsymbol{\xi}(t) = \sum_{\mu} \xi'_{\mu}(t)\mathbf{v}_{\mu}. \tag{60}$$

To proceed further, we project both sides of (57) on the vectors $\mathbf{v}_\mu$. In order to facilitate the writing, we drop the index μ of $\xi_\mu(t)$ and put

$$\lambda_\mu = a. \tag{61}$$

Thus we have to deal with equations of the form

$$\left(\frac{\mathrm{d}}{\mathrm{d}t} + \gamma\right)^2 \xi'(t) = a \sum_n \delta\left(t - t_n^+\right) \xi'(t-\tau). \tag{62}$$

We note that

$$t_n^+ = n\Delta \tag{63}$$

and assume that the delay time τ is an integer multiple of Δ

$$\tau = M\Delta. \tag{64}$$

As we are showing elsewhere by a related model [12], the general behavior is similar if M is not integer. Equation (62) with the δ-functions on its r.h.s. can be treated in the usual way. We assume continuity of ξ', *i.e.* in particular

$$\xi'(t_{n+1} + \epsilon) = \xi'(t_{n+1} - \epsilon). \tag{65}$$

Here and in the following we write t_n instead of t_n^+. To take care of the δ-functions, we perform the integral

$$\int_{t_{n+1}-\epsilon}^{t_{n+1}+\epsilon} ...\mathrm{d}t \tag{66}$$

on both sides of (62), which jointly with (65) yields the jump condition

$$\dot{\xi}'(t_{n+1} + \epsilon) = \dot{\xi}'(t_{n+1} - \epsilon) + a\xi'(t_{n+1-M}). \tag{67}$$

From equations (65, 67) we can derive recursive equations. To this end, we solve (62) in the region

$$t_n < t < t_{n+1}, \tag{68}$$

where the r.h.s. of (62) vanishes. The solution reads

$$\xi'(t) = g_n \mathrm{e}^{-\gamma(t-t_n)} + h_n(t-t_n)\mathrm{e}^{-\gamma(t-t_n)}. \tag{69}$$

From the continuity condition (65) and the jump condition (67), we obtain

$$g_{n+1} = g_n \mathrm{e}^{-\gamma\Delta} + h_n \Delta \mathrm{e}^{-\gamma\Delta}, \tag{70}$$

$$h_{n+1} = h_n \mathrm{e}^{-\gamma\Delta} + a g_{n+1-M}, \tag{71}$$

respectively. To solve these equations, we make the hypothesis

$$g_n = g_0 \beta^n, \tag{72}$$

$$h_n = h_0 \beta^n, \tag{73}$$

which yields the equations

$$g_0\beta = g_0 \mathrm{e}^{-\gamma\Delta} + h_0 \Delta \mathrm{e}^{-\gamma\Delta}, \tag{74}$$

$$h_0 \beta^M = h_0 \mathrm{e}^{-\gamma\Delta}\beta^{M-1} + a g_0. \tag{75}$$

The requirement of a vanishing determinant yields

$$\left(\beta - \mathrm{e}^{-\gamma\Delta}\right)^2 \beta^{M-1} = a\Delta \mathrm{e}^{-\gamma\Delta}. \tag{76}$$

For its solution we make the hypothesis

$$\beta = \mathrm{e}^{-\gamma\Delta} + \delta, \tag{77}$$

which yields in lowest order of δ

$$\delta = \pm\sqrt{a\Delta}\mathrm{e}^{\gamma\Delta M/2}\mathrm{e}^{-\gamma\Delta}. \tag{78}$$

If $a < 0$, δ is imaginary. To obtain the further solutions, we assume

$$\beta \neq \mathrm{e}^{-\gamma\Delta} + \delta, \quad M \geq 2, \tag{79}$$

or more precisely

$$\mid \beta \mid \ll \mathrm{e}^{-\gamma\Delta}. \tag{80}$$

This yields the $M-1$ roots

$$\beta = \left(a\Delta \mathrm{e}^{\gamma\Delta}\right)^{1/(M-1)} \mathrm{e}^{2\pi \mathrm{i} j/(M-1)}, \quad j = 0, 1, ..., M-2. \tag{81}$$

Since there are $M+1$ eigenvalues $\beta_k, k = 1, ..., M+1$ of (76), there are $M+1$ solutions (g_{0k}, h_{0k}) to (70, 71). The general solution of (70, 71) has the form

$$\begin{pmatrix} g_n \\ h_n \end{pmatrix} = \sum_{k=1}^{M+1} c_k \begin{pmatrix} g_{0k} \\ h_{ok} \end{pmatrix} \beta_k^n, \tag{82}$$

where the coefficients must be determined from the initial conditions (*cf.* [12]). Because the eigenvalues (81) and, if $a < 0$, (78), are complex, (82) represents oscillatory behavior. Both (78) and (81) show that damping decreases with increasing M, *i.e.* increasing time delay τ (64). Finally we note that due to the different eigenvalues λ_μ, the most general solution to (57, 58) has the form (*cf.* (60))

$$\boldsymbol{\xi}(t) = \sum_{\mu=1}^{N} \mathbf{v}_\mu \sum_k c_{k\mu} \Big(g_{0k\mu} \mathrm{e}^{-\gamma(t-t_n)} + h_{0k\mu}(t-t_n)\mathrm{e}^{-\gamma(t-t_n)} \Big) \beta_{k\mu}^n \tag{83}$$

for $t_n \leq t < t_{n+1}$.

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